Embryology of Flowering Plants

Terminology and Concepts

Volume 3: Reproductive Systems

Edited by
T.B. Batygina

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DEPARTMENT OF EMBRYOLOGY
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Inserenememory
ofElena Gerassimova-Navashina, Vera Poddubnaya-Arnoldi, Veronika Vasilevskaya, Katherine Esau and Barbara Haccius- women-scientists, who made a great input to the developmentofcomplicatedproblemsofplantmorphogenesisandreproduction

Preface

The third volume of *Embryology of Flowering Plants* is a concluding volume of the edition. This encyclopaedic dictionary has no analogies in the world. It is an original attempt to combine the principles of constructing a terminological dictionary with monographic description of structures and processes.

The publication consists of three volumes. Volume 1 (2002), *Generative Organs of Flower,* is divided into three parts: **Flower, Anther, Ovule.** Volume 2 (2005), *Seed,* comprises the following: **Double Fertilization, Endosperm, Perisperm, Embryo, Seed, Seed Dormancy and Germination.** The third volume, *Reproductive Systems,* includes seven principal parts: **Plant Reproduction, Pollination and Breeding, Seed Propagation, Vegetative Propagation, Molecular-Genetic Aspects of Reproduction, Population and Ecological Aspects of Reproduction** and **Embryological Bases of Reproductive Strategies.**

Specialists in different disciplines of botany, such as embryology, morphology, genetics, geobotany and ecology, give their interpretation of such many-sided notions as "systems of reproduction" or "living strategies". In this connection some key notions are considered, including reproduction, renewal, propagation, amphimixis, apomixis, reproductive effort, reproductive success, potential seed productivity and real seed productivity. For the first time, all these aspects are covered in this, the third volume of *Embryology of Flowering Plants.*

When preparing the book we used such well-known monographs, as F. Netolitzky, *Anatomie der Angiospermen-Samen* (1926); K. Schnarf, *Embryologie der Angiospermen. Archegoniaten* (1929) and *Vergleichende Embryologie der Angiospermen* (1931); R. Souèges, *Les Lois du Devéloppement* (1937) and *Embryogeńie et Classification* (1939); P. Maheshwari, *"An Introduction to the Embryology of Angiosperms* (1950); D. A. Johansen, *Plant Embryology* (1950); P. A. Baranov, *The History of Plant Embryology* (1955); A. L. Takhtajan, *Foundations of Evolutionary Morphology of Angiosperms* (1964), *Outline of the Classification of Flowering Plants* (1980) and *System Magnoliophyta* (1987); V. A. Poddubnaya-Arnoldi, *General Embryology of Angiosperms* (1964b) and *Cytoembryology of the Angiosperms: Principles and Perspectives* (1976); G. Davis, *Systematic Embryology of Angiosperms* (1966); T. B. Batygina, *Wheat Embryology* (1974), *The Grain of Cereals* (Atlas) (1987); E. S. Teryokhin, *Parasytic flowering plants. The Evolution of Ontogenesis and the Mode of Life* (1977); E. Corner, *The Seeds of Dicotyledons* (1976); K. Esau, *Anatomy of Seed Plants* (1977); B. M. Johri (ed.), *Embryology of Angiosperms* (1984); T. B. Batygina and M. S. Yakovlev (eds.), *Comparative Embryology of Flowering Plants* (1981, 1983, 1985, 1987, 1990); V. Raghavan, *Experimental Embryogenesis in Vascular Plants (1976), Embryogenesis in Angiosperms: A Developmental and Experimental Study* (1986), *Developmental biology of fern gametophytes* (1989) and *Molecular embryology of flowering plants* (1997); M. F. Willson, *Plant Reproductive Ecology* (1983); B. M. Johri, K. Ambegaokar, P. S. Srivastava, *Comparative Embryology of*

Angiosperms (1992); B. Rodkiewicz, *Embryology of flowering plants* (1973) and *Embryology of gymnosperms* (1984); Hu-Han and Yang Honjyuan, *Haploids of higher plants in vitro* (1986); M. Cresti, P. Gori and E. Pacini, *Sexual Reproduction in Higher Plants* (1988); P. R. Bell, *Green plants. Their origin and diversity* (1992); K. G. Mukerji, *Seed Biology* (1992); E. Ottaviano, D. L. Mulcahy, M. Sari-Gorla and G. B. Mulcahy, *Angiosperm pollen and ovules* (1992); R. B. Primack, *Essentials of Conservation Biology* (1993) and others.

For more precise definition of terms the following dictionaries were used: M. C. Cooke, *A Manual of Botanic Terms* [1873?]; B. D. Jackson, *A Glossary of Botanic Terms* (1916); N. N. Zabinkova and M. E. Kirpichnikov, *Latin-Russian Dictionary for Botanists* (1957); M. E. Kirpichnikov and N. N. Zabinkova, *Latin-Russian Dictionary for Botanists* (1977), *Biological Encyclopedical Dictionary* (1986, 1989); *The Oxford English Dictionary* (1989) and others.

While preparing the publication of the 3-volume edition on Russian, English and Farsi some new data has become available on the various aspects of the developmental biology. The editorial board has made a principal decision not to include the data into the new issued volumes, because it will take a tremendous effort and will cause delay in issuing of these unique books. However, we considered it possible to mention at least some publications of recent years, in which some problems, considered in the 3-volume edition, were solved: E. S. Teryokhin, *Seed and seed reproduction* (1996); E. S. Teryokhin, *Weed broomrapes systematics, ontogenesis, biology, evolution* (1997); T. B. Batygina and V. E. Vasilyeva, *Plant propagation (Textbook)* (2002); N. N. Kruglova, T. B. Batygina, V. Yu Gorbunova, G. E. Titova and O. A. Seldimirova, *Embryological bases of wheat androcliny: Atlas* (2005); T. B. Batygina, E. A. Bragina, A. V. Ereskovsky and A. N. Ostrovsky, *Viviparity in plants and animals: invertebrates and lower chordates* (2006); T. I. Serebryakova, N. S. Voronin, A. G. Elenevskiy, T. B. Batygina, N. I. Shorina and N. P. Savinych, *Botany with basics of phytocoenology: Anatomy and morphology of plants (Textbook for higher school)* (2006); T. B. Batygina, G. Yu. Vinogradova, *Phenomenon of Polyembryony. Genetic Heterogeneity of Seeds* (2007); 1.1. Shamrov, *Ovule of flowering plants: structure, functions, origin* (2008).

In this encyclopedic edition the principles of constructing the dictionary with monographic description of embryonic structures and processes are combined. However, **unlike traditional dictionary structure, the terminological articles in every part of the book are placed not in alphabetical order, but according to the theme to create the integrated picture of each main seed structure. A subject index is given at the end of the book.**

Terminological articles comprise the main part of the text and include: the definition and semantics of the terms, their history, and major data about the origin, development, functions and classification of the structure described. In a number of cases, questions concerning evolutionary transformations and the character of distribution of embryological features among flowering plants are discussed.

The second group of articles combines conceptional, and hence the most complex articles presenting the discussion of questions of modern angiosperm embryology. Some cases of difference between the author's terms and terms accepted in this edition are footnoted.

Most of terminological and conceptional articles are complemented with illustrations such as drawings, microfotographs, schemes and diagrams.

Complete bibliographical data are given in the References at the end of the volume.

T.B. BATYGINA

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T.B. BATYGINA

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Introduction

T. B. Batygina

Plant embryology, dealing with the regularities of initiation and the first stages of development of organism, is now flourishing because of overall progress being made in natural sciences. Such discoveries of the 20th century as production of plants from a single somatic cell, experimental haploidy, and parasexual hybridisation were of general biological significance. They promoted studies in the field of morphogenesis of reproductive structures. In its turn the further development of biology is unthinkable without knowledge of the first stages of ontogenesis. Embryological information becomes increasingly essential for theoretical and experimental studies of reproduction. For this reason, embryology has been the focus of attention of geneticists, biochemists, geobotanists, physiologists, cytologists, biophysicists and plant breeders (Figs. 1 and 2). The combined efforts of embryologists, geneticists and molecular biologists yielded the discovery of specific genes that control meiosis, egg cell development and early stages of embryogenesis. The tendency to synthesize data of embryology and genetics has become increasingly noticeable. It is connected with the fact that the majority of problems connected with morphogenesis, such as differentiation, specialization, the evaluation of features and the definition of the notions "gene and feature" and "genotype and phenotype", concern embryology and genetics (embryogenetics) in one way or another.

At the junction of embryology, anthecology, carpology, genetics, physiology and plant breeding, a new and rapidly evolving discipline, **reproductive biology,** has emerged. **Elaboration of theoretical foundations of sexual and asexual reproduction** is one of the objectives of reproductive biology. Reproductive biology involves studies of various interrelated stages of ontogenesis: flower organogenesis, anthesis, pollination, fertilization, embryogenesis seed maturation, dispersal and germination, and propagation by seeds. All of these are in one way or another connected with embryology in the broad sense.

The primary objective is to tackle the problems of amphimixis and apomixis, to elucidate the mechanisms of embryogenesis, incompatibility and self-incompatibility, as well as the patterns of variation in potential and actual seed productivity and, consequently, in crop yield.

The development of reproductive biology is especially important for the introduction and repatriation of rare and vanishing plants, as well as plants of great agricultural importance. Cytoembryological studies concerned with the effect of pollutants on reproductive structures (anthecology) constitute part of the environmental protection programme. Investigations of this kind have become increasingly important in recent years (the age of ecological stresses), because it is reproductive structures that suffer most from adverse environmental factors.

Of special interest are apomixis phenomena requiring full-scale studies. Parthenogenesis, apospory, diplospory and polyembryony call for further intensive investigations to meet practical needs. Such types of agamospermy as vivipary and adventive embryony, i.e. possible intermediate forms between vegetative reproduction and propagation by seeds, merit special attention of plant embryologists.

Elucidation of evolutionary patterns of ontogenesis in conjunction with the problems of phylogeny and systematics remains a major line of inquiry in modern embryology. Relatively conservative, embryological features can be employed to supplement and refine our present notion of the systematic position of some orders, families, genera and even species. One urgent task is to investigate poorly studied taxa. This is essential for refining the criteria of evolutionary and taxonomic significance of embryological features.

New data accumulated by descriptive and experimental biology, morphology, reproductive and developmental biology should stimulate studies in evolutionary embryology. An important contribution is also forthcoming from some recently published monographs, particularly those concerned with various aspects of **descriptive** and **comparative embryology.** The new evidence promoted working out of new classification with better approximation to actual evolutionary processes and deeper involvement of embryologists in research on systematics and phylogeny of flowering plants. During the last years plant embryology has become a ramification of developmental biology.

In evolutionary embryology, a new approach to the study of evolutionary adaptation of plant organisms, developed by E. S. Teryokhin - **an ecomorphological approach** - has emerged. Studies with parasitic plants have revealed that underlying the evolutionary transformations of their reproductive structures are such general biological phenomena as metamorphosis, neoteny, and reduction.

Ecological embryology is the most important line of investigation of early ontogenesis directed towards identifying critical periods in it. Plasticity and tolerance of reproduction systems are also the subject matter of ecological embryology. In this connection it is important to study embryonal structures (ovules, embryos, etc.) with a view to assessing the potentialities and sustainability of biological systems.

This line of inquiry merges with **population embryology** concerned with morphogenetic and phenotypic variability within a population (life cycle variation and reproduction system diversity).

The immunological direction in embryology is expected to play an important role in overcoming the barriers of cross-incompatibility.

Recent trends incorporate **synthesis of embryological and genetic evidence, i.e., genetic embryology.** Already N. K. Koltsov (1935) had already pointed out that "it is only the integration of the two disciplines [experimental embryology and genetics - T.B.] with one another, as well as with cytology and biochemistry, that will create a single science capable of solving problems of general biology". All the problems related to morphogenesis - differentiation, specialization, evaluation of characters, definition of such concepts as "gene and character", "genotype and phenotype" - are to a greater or lesser extent the concern of embryology and genetics.

As far back as 1950, the outstanding plant embryologist P. Maheshwari predicted that the future of embryology would undoubtedly lie with experimental embryology. The needs of practical breeding (e.g. uncovering the causes of sterility and partially

filled ear, with subsequent correction; use of adventive embryos; etc) have spurred the development of experimental plant embryology. An **experimental embryology,** unlike descriptive one, provides answers not only to the question of how complex morphological processes of embryonal development evolve, but also why specific processes show this or that particular trend.

Plants regenerated from cultured cells, tissues, organs and embryos (embryoculture) have become, especially in recent years, a model for studying mechanisms of differentiation and molecular genetic laws of morphogenesis of embryonal structures. Some interesting results have been obtained on the effects of various abiotic factors on plant morphogenesis and possible ways of formation of embryoids and other structures suggested. Of vital importance is **the elaboration of a theoretical basis for the *in vitro* cultivation** of vegetative and generative structures (ovary, anther, ovule, embryo, endosperm, embryo sac, sperm, etc.). Success of an embryoculture depends on the correct choice of the developmental stage of the generative structure to be used in the *in vitro* culture as well as on the state of donor plants. The experimental approach, combined with thorough knowledge of the genesis of reproductive structures, allows one to predict the morphogenetic pathways of regenerants, to determine the optimal developmental stage of the embryo to be used for embryoculture, etc., as T.B. Batygina (1974-2008) absolutely correctly supposes. This direction merges with cell engineering and biotechnology.

Embryological evidence becomes increasingly important in designing genetic and breeding programmes and developing effective biotechnology methods, since it provides an insight into the processes leading to normal seed formation and uncovers the causes of abnormalities arising during embryogenesis.

A systems approach to generative structures used in the *in vitro* culture elaborated by embryologists of the Komarov Botanical Institute has enabled some theoretical assumptions to be made, in particular concerning the autonomy of the embryo, critical periods in the development of generative structures, and so on. These principles are applied in breeding work and have resulted in the production of new plant forms.

It has become increasingly apparent that **applied embryology** holds much promise. Among the problems to be addressed, the following should be mentioned.

Ecological problems: development of special approaches and methods for producing normal seeds of rare and economic plants; conservation of plant genetic resources, i.e. establishing a genebank (seeds, embryos, gametes); estimating the degree of plasticity and tolerance of reproductive systems, and the proportions of different modes of reproduction within various taxa of plants exposed to adverse factors.

Biotechnology problems: the development of effective methods for mass production (propagation) of new forms and varieties as well as of rare and vanishing plant species. This can be done on the basis of embryoidogenesis (somatic embryogenesis) and gemmorhizogenesis (organogenesis); increasing actual producing capacity; development of news forms and varieties via distant and parasexual hybridization; overcoming the barriers of cross-incompatibility; etc.

The researchers of the Department of Embryology and Reproductive Biology for many years have been working on the priority problems of developmental biology, which are extremely significant for considering the reproductive strategies and expand the fields of embryology mentioned above. These problems include:

- **Reproduction, multiplication and renewal of plants** - see Vol. 3, *Reproduction, Propagation and Renewal* (T. B. Batygina);
- **Elaboration and unification of notions for revealing the mechanisms of rise of organism's cells "sternness" at various stages of development; stem cells and their role in the regeneration of tissues, organs and formation of new organism;**

The evolutionary process in plants is characterized by a great diversity of modes and ways of propagation. The plasticity of plant development and reproduction is primarily related to the multifaceted activity of plant somatic cells with characteristics of stem cells.

In botanical, zoological, and medicinal literature, the term stem cell is a functional notion because any universal genetic or epigenetic markers of these cells are not known.

Each plant cell could be found in different morphological and physiological states; one state corresponds to the characteristics of stem cells, whereas others correspond to actively dividing meristematic cells. Transitions between these states are of a probability character; in most cases, histogenesis and organogenesis are related to the loss of stem cell traits but other transitions are also possible.

The stem cells characteristics are:

(1) toti- or pluripotency, i.e., a capability of forming not only various types of tissues and organs but also novel individuals through various morphogenetic pathways (embryogenesis, embryoidogenesis, and gemmorhizogenesis);

(2) self-maintenance, i.e., the production of the pool of cells mainly by symmetric divisions and the system of intercellular interactions;

(3) a capability of proliferation and forming the cell precursors of various tissue types (niches) due to asymmetric divisions occurring under the influence of definite signals;

(4) rhythmic and multistage character of formation in the tissue or organ and a capability of switching over developmental programs through various molecular-biological mechanisms.

So, along with similar spatial position, stem cells are characterized by similar processes occurring in the domain. Relatively symmetric divisions are related to the maintenance of the stem cell pool; asymmetric divisions are related to the entering of daughter cells into a definite path of differentiation. Derivatives of stem cells, initials of cell lines of various tissues, create niches for stem cells. A specific feature of the surrounding of domains of differentiating cells is the presence of sister cells.

A diversity of morphogenetic processes consists of the two components: potentially endless functioning of the meristems determined by the functioning of quiescent center cells, which are in the intermediate differentiated state, and the loss of stem cell state, senescence, and apoptosis.

Our investigation has revealed, that:

(1) Plant stem cells are formed in various organs (flower, stem, leaf, and root) and at various stages of the life cycle (sporophyte and gametophyte); stem cells' functioning depends on their location and destination.

(2) Zygote is a stem cell of the first order; it is a progenitor of stem cells of all other orders.

(3) Plant stem cells are capable of forming not only various types of tissues and organs but also new individuals (sexual and somatic embryos of various origin).

(4) Total properties of stem cells (toti or pluripotency, rhythmic and multistage character of their formation, and especially a capability of switching over developmental programs) provide for the system of plant reliability at various developmental stages.

T.B. Batygina, G.E. Titova, I.I. Shamrov, E.A. Bragina, V.E. Vasilyeva, I.V. Rudskiy, *Problem of stem cells in plants (from the position of embryology),* in Construction Units of Plant Morphology, Kirov, 2004, P. 20-30;

I.V. Rudskiy, T.B. Batygina, *Role of Stem Cells in Plant Morphogenesis,* Qntogenez, 2005, V. 36, N 5, P. 390-392;

T.B. Batygina, I.V. Rudskiy, *Role of Stem Cells in Plant Morphogenesis,* Doklady Biological Sciences, 2006, V. 410, P. 400-402;

P.W. Barlow, *Stem cells and founder zones in plants, particularly their root,* Stem cells, Ed. C.S. Poten, London, 1997, P. 29-57.

- **The phenomenon of polyembryony. Genetic heterogeneity of seeds;**

Different types, ways, and forms of plant reproduction appeared in the course of evolution as a consequence of the attached mode of life and autotrophy. There are **two ways of formation of a new individual:** sexual process => gamospermy involving meiosis and gamete fusion and asexual process => agamospermy without meiosis and gamete fusion and **two types of reproduction:** seed and vegetative. Both processes may take place simultaneously in one seed, as a result of which many embryos of different origins are formed: uniparental and biparental inheritance. Traditionally, this phenomenon is called polyembryony. It comprises **embryoidogeny** (a new category of vegetative reproduction): formation of somatic embryos (= embryoids) in the flower, seed, and on vegetative organs. **Genetic heterogeneity** is one of the most important characteristics of seeds, which is based on different phenomena, such as **embryogeny, embryoidogeny,** and **gametophytic** and **sporophytic apomixis.** When describing two types of polyembryony, sporophytic (nucellar, integumental, cleavage) and gametophytic (synergidal, antipodal), a great attention is paid to characterization of initial cells of the sexual and adventive embryos. A new concept of apogamety is developed **from new positions** (totipotency and "stemmness"), which is based on different genesis of cells of the egg and antipodal systems. Five possible pathways of formation of the adventive embryos have been proposed from cells of the egg apparatus. **Specific features** of the formation of **adventive embryos** in the case of gametophytic apomixis, such as **androgenesis** and **semigamy,** are discussed. **Morphogenesis of the sexual** and **adventive embryos** proceeds in the mother organism and **is determined by the origin and formation of their initials, types of ovule and embryo sac,** and **specific features of developmental biology.** This determines parallelism in their development. The main difference lies in the way of reproduction: heterophasic and homophasic. The phenomenon of polyembryony and genetic heterogeneity of seeds is essential for development of the theory of reproduction and applied research related to seed productivity of plants.

T.B. Batygina, G.Yu. Vinogradova, Phenomenon of polyembryony. Genetic heterogeneity of seeds, Russian Journal of Developmental Biology, 2007, Vol. 38, N. 3, P. 126-151.

- **Vivipary in plants and animals;**

  The first generalization and analysis of vivipary in flowering plants, invertebrates and lower chordates is presented. On the base of original and published data the morphogenesis of reproductive structures in viviparous plant and animal species has been described. Much attention has been paid to functional morphology and genetics of vivipary in different groups of plants and animals. The original classifications of this phenomenon have been suggested. The courses of vivipary arising in the plant and animal world are being discussed. The role of vivipary in reproduction system of certain species has been determined with population and ecological aspects being examined. The lists of plant and animal species, for which vivipary is typical, are given with indication of its form. A special attention is paid to explanation of notions and terms related to reproduction systems and viviparous organisms. Original figures and photos were used as illustrative materials.

  T.B. Batygina, E.A. Bragina, A.V. Ereskovsky, A.N. Ostrovsky, *Viviparity in plants and animals: invertebrates and lower chordates,* Publishing House of St.-Petersburg State University, St.-Petersburg, 2006.

- **Critical stages and periods in plant ontogenesis and development of various reproductive structures.**

  The theory of critical periods in plant ontogenesis has been elaborated from studies of integral morphogenetic processes on different levels. The periodization of the development of various reproductive structures (anther, microspore, pollen grain, ovule, megagametophyte, egg cell, zygote and embryo) has been worked out from data on morphogenesis using systemic and complex morphophysiological approaches. Critical phases, stages and periods have been revealed, for example the stage of autonomy in different flowering plants, by means of culture *in vitro.* The concepts of "critical period" and "critical mass" in relation to embryonal structure periodization are discussed here. Also there addressed the question of allometry and the significance of morphogenetic fields and rhythms of cell division for revealing critical periods and the management of ontogenesis. Examination of the genesis and structure of anthers and ovules in various flowering plant species has permitted us to discover general regularities in their development and the occurrence of three common critical periods: premeiotic, meiotic and postmeiotic. Embryo development in angiosperms is characterized by two common phases (proembryonal/blastomerization and embryonal/organogenesis) and five critical periods (zygote and proembryo, globular, heart-shaped, torpedo-shaped, and mature embryo). The combination of common and specific critical periods and stages determines the taxon-specific morphogenesis of reproductive structures and contributes to the plasticity and tolerance of the reproductive systems of different species of flowering plants, and of ontogenesis as a whole.

  T.B. Batygina, V.E. Vasilyeva, *Periodization in the development of flowering plant reproductive structures: critical periods,* Acta Biologica Cracoviensia, Ser. Bot., 2003. Vol. 45, N1, P. 27-36.

Authors' findings on the problems of propagation were used previously for solving a complex of practical tasks in the plant cultivation, seed growing, genetics, breeding and biotechnology. The dihaploid androclinous (i.e. inheriting the paternal genotype) lines of soft spring wheat have been obtained. The homozygous material and breeds of barley (resistant to phytopathogenes) have been produced during

extremely short period. The research on the application of the results of fundamental investigations into agricultural practice are undertaken not only with cereals, but with other plants as well: technical (the breed "Dulcinea" of stevia plant with high content of steviaside, the sweetener, used in food industry, has been produced in collaboration with the All-russian Institute of Plant Breeding), medical (officinal raw material from the plant regenerants of Rauwolfia vomitoria), rare and endangered species for the sake of their conservation and repatriation (boreal orchids). The overall result of the many-years fundamental and applied researches was the awarding of the authors by the Government Premium of Russian Federation in the field of science and techniques in 2002.

Progress in embryology is largely dependent on application of modern methods of electron microscopy, autoradiography, tracer labelling, modelling, microsurgery, *etc.* These methods open up new vistas for research at different levels of organization: molecular, cellular, tissue, organ, organismal, and population.

Unique data on fine structure and functions of generative organs and tissues have been obtained with the aid of such methods as fluorescence (including immunofluorescence), phase-contrast, electron (TEM, SEM), Nomarski-interference microscopy, as well as application of methods of modern cell biology: immunocytochemistry, time-lapse photography, video-image processing, *etc.* Some other findings are also worthy of mention: sperm dimorphism, feasibility of enzymatic isolation of such structures as generative cell and sperms, embryo sac, as well as of individual cells of the female gametophyte. Utilization of endoenzyme markers has enabled elucidation of specific features of meiosis.

Quantitative mRNA studies in pollen grains and sperms have provided new evidence on their fine structure, mRNA as well as specific genes controlling microsporogenesis were identified in mature anthers.

All the above prompted preparation of the present 3-volume publication, *Embryology of Flowering Plants: Terminology and Concepts.* Participating in the preparation of the edition have been plant embryologists and morphologists of the Komarov Botanical Institute (Russian Academy of Sciences), their colleagues from CIS (the Ukraine and Georgia) and from other countries of the world: the USA, the Netherlands, Poland, Slovakia, India, and Sweden. In this publication, the results of studies, the hypotheses and conceptions advanced by Russian embryologists are presented more comprehensively than in any of the latest monographs of plant embryology (Johri [ed.], 1984; Johri et a1, 1992).

It is hardly possible for a large team of authors to maintain uniformity of style. It was the Editor's task, therefore, to impose uniformity and to avoid unnecessary repetition of material in different sections. Individual articles, along with an objective presentation of factual evidence, unavoidably reflect the author's own view of the structures and processes described. This makes some of the articles open to discussion. But disputes are essential for the progress of science. In this respect, the present publication will be useful to research workers, experts in plant embryology, anatomy, taxonomy, genetics, physiology, cytology and ecology; to specialists in molecular biology, biotechnology, plant growing and to plant breeders; as well as to college and university students and lecturers of biology and to all those interested in biology. This 3-volume work on plant embryology should hopefully demonstrate the great role played by modern embryology in solving problems of general biology in this age of ecological stresses. It ought also to further theoretical and experimental studies in plant embryology. Any criticisms and useful suggestions are welcome and will be taken into account in future work.

PART ONE–PLANT REPRODUCTION

OVERVIEW

Reproductive Biology

Reproductive processes have exceptional significance not only in regular renewal of plant cover, but also in restoration of the foundation of our existence — the diverse world of plants, which has been disturbed in consequence of the continuous rise in anthropogenic pressures. Hence, repeated attempts to draw the attention of scientists to the problems of reproduction, and especially seed propagation, are well justified.

Levina (1981) undertook one such attempt in her book *Reproductive Biology of Seed Plants. Problem Review* (Fig. 1). While highly appreciating this work and realizing its importance for the development of our knowledge on reproductive processes in plants and approaches to their investigation, we find that certain aspects of concepts that entered our scientific practice in the context of reproductive biology should now be critically evaluated. This needs to be done because the reproductive biology in Levina's work is represented as a new synthetic approach to the study of reproductive cycles. The question that could and should be raised nowadays is whether the notion "reproductive biology" reflects a new scientific problem and consequently a new scientific approach, or whether it is only a more modern designation of a particular area of research in botany.

According to Levina, plant reproductive biology developed gradually from the direction of plant reproduction and propagation studies, which was earlier referred to as "biology of propagation". She emphasized that reproductive biology is first of all distinguished by a larger volume of investigations, connected with various levels of study of propagation processes. The biology of propagation has been studied just at the organism level and has taken into consideration hereditary morphophysiological peculiarities of an organism, whereas reproductive biology is studied at the species level and reflects the dependence of propagation on the ecological situation.

Some remarks should be made here on the implication of the terms discussed probably need to be made here. Ponomarev (1969), examining the same subject, came to the conclusion that the traditional terms "biology of flowering" and "biology of flowering and pollination" should be abandoned as they did not clearly reflect the essence of the phenomenon. To his mind, the term "antecology" was more acceptable; it was more exact in meaning, more convenient to use, and more comprehensive, because it included both the ecology of the flower and the ecology of pollination. Here the ecology of the flower represents, as a matter of fact, its ecological morphology, elucidating different structures, mechanisms and peculiarities of flower development from the point of view of their significance in fulfilling functions inherent to a flower. Ponomarev uncovered a wide spectrum of approaches to the investigation of the flower and its functions within antecology. Biology has to be understood correctly as a science of living organisms as a whole, comprehending all their divisions, as was suggested by Heksli in his time.

Thus, from the position mentioned above, the expression "reproductive biology" seems to be preferable as the term for this particular research area, rather than the name of a new scientific approach, problem or direction. The perspective of the intact

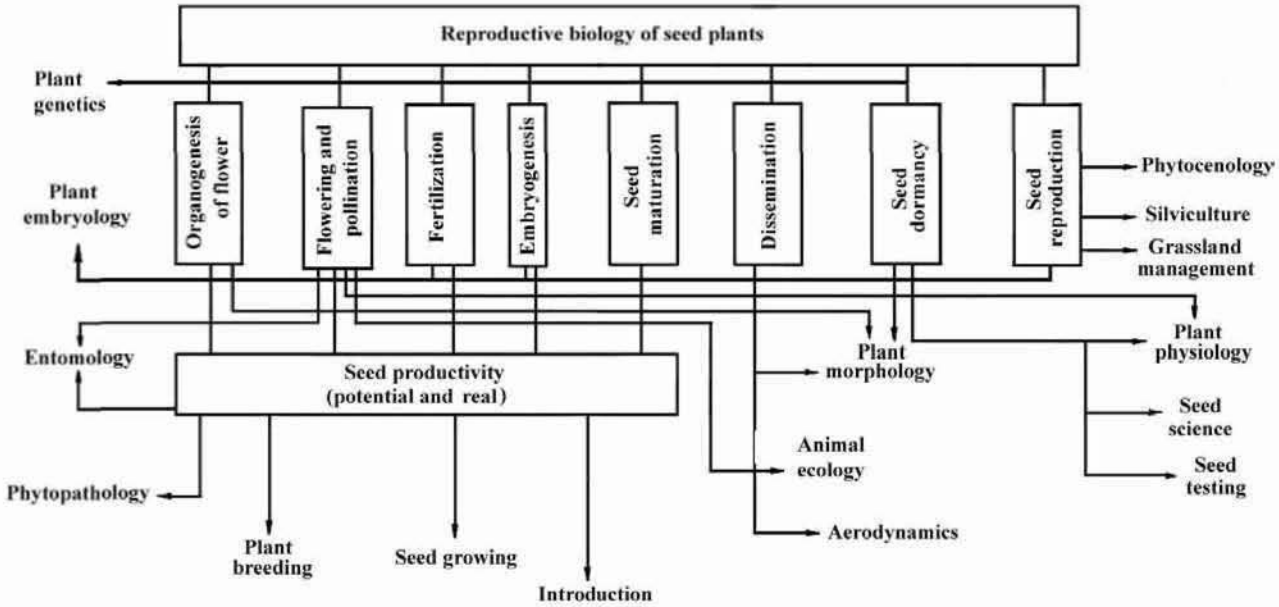

Fig. 1: Interrelations of plant reproductive biology and the different branches of fundamental and applied sciences (modified from Levina, 1981).

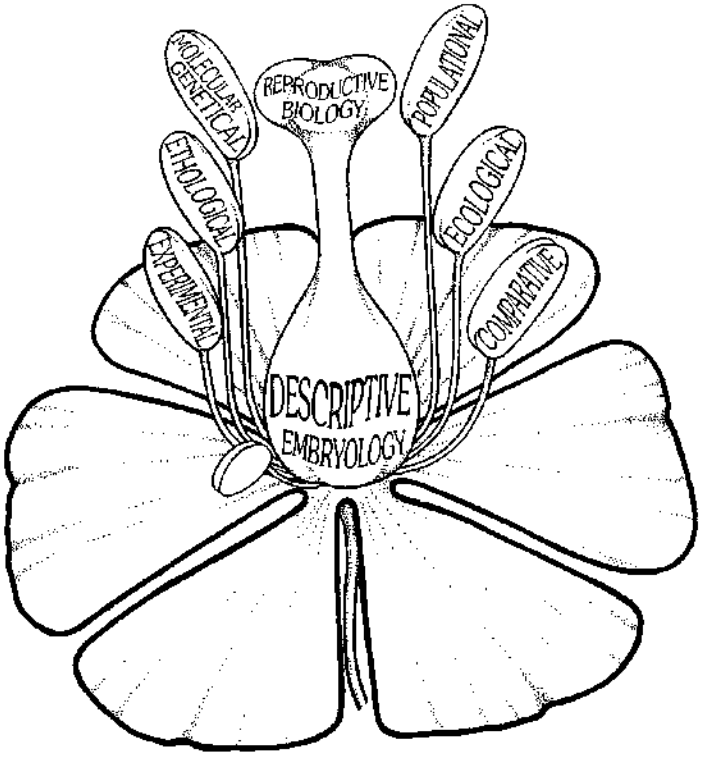

Fig. 2: Principal directions of modern plant embryology.

(here meaning complex) approach to the study of reproductive processes is undoubtedly attractive, since it gives essential addition of new knowledge. Nevertheless, this "addition of knowledge" implies, as could be understood, their widening and generalization rather than a new step to a deeper cognition of reproduction regularities.

Starshova (1989) appreciated the overall contribution of Levina to the elaboration of reproductive biology as a problem that lies, in her opinion, in the creation of a synthetic approach to the study of reproductive cycles. The general ideas of such an approach are as follows. The reproductive biology of species ought to be studied at the organism, population, species and biocoenocytic levels. What Levina and Starshova refer to as "levels" are from our point of view more probably "areas" of investigation or their methodical aspects. These "levels" of organization of living beings in themselves have no direct relation to the problem discussed. For example, antecology could be investigated only in coenocytic and population "areas" (correctly, in these aspects — E. Teryokhin), irrespective of whether such investigations are examined within reproductive biology or alongside it. On the other hand, embryology and carpology, depending on the tasks set, can be perfectly emcompassed by research at the organism level. So, from our point of view, this thesis does not testify a principally new approach to the study of reproduction.

The next idea is that "biology of seed propagation" and "reproductive biology" are different in terms of their controlling systems. The first applies to the organism level, for which the structural controlling system is characteristic. The second is a process occurring in systems above the organism level, by stochastic type of control. To our mind, stochasticity is associated with individual and population level, as well as with the "structural" controlling system. The question arises only in their ratio in any "area".

Reproductive biology (correctly, the reproductive processes—E.T.) plays a vital role in the struggle for species preservation. It is characterized by large quantitative reserves and ecological plasticity of certain stages. One cannot but agree with this thesis. However, it contains nothing that confirms the need to divide reproductive biology (but not the study of reproductive processes —E.T.) into specific scientific problems.

In this connection, the statement that reproductive biology, believed to be a specific intact and complex problem, requires collective elaboration according to single methods is also vulnerable to criticism.

In our opinion, the investigation of concrete peculiarities of reproductive processes in various taxa and ecologically differentiated groups of plants in all levels of their organization indeed proves to be the scientific problem (Salisbury, 1942; Teryokhin, 1988, 1997). The integrity of scientific notions about any reproductive cycle is gradually being proved, as a consequence of the analysis of concrete results of investigation. With such an approach, the "collective elaboration according to single methods" is not required. This requirement is probably more suitable to experimental research in biotechnology than to the investigation of the specifics of reproduction in natural conditions.

In the above context, the importance of ecologization of investigation in the field of plant reproduction cannot escape attention.

I venture to claim that notions on ecology by Levina (1981), consonant enough to the time in which her book was being written, currently seem to be rather one-sided. As can be seen from the context of the book, she adopts the notion of ecology, including the ecology of reproduction, as the diverse influences of biotic and abiotic factors on the reproductive process.

In this regard, a comparison of Levina's work with Willson's *Plant Reproductive Ecology* (1983) is quite pertinent. There are considerable distinctions between the contents of the two works, especially the approaches to the same structures and processes and the analysis of interacting phenomena and factors.

Thus, there exist two different approaches to the investigation of reproductive cycles. All this does not mean that Willson's views on reproductive processes are preferable to Levina's. They are simply different. To our mind, Willson's ecological interpretations are distinguished by a superfluously "economized" approach to the analysis of reproduction phenomena. It is quite competent but probably not adequate. Deeper reflection on the role and significance of plant behaviour in the reproductive cycle is necessary.

In this connection, one cannot but cite the statement of Faegri and van der Pijl (1966) from their book *The Principles of Pollination Ecology* in reference to the investigation of a flower. In their view, the flower structure should be contemplated from the perspective of pollination ecology, i.e., as a functional unit. Otherwise, the

flower morphology loses all meaning and the development of the flower itself and its elements becomes unclear and can be interpreted only from the position of orthogenesis or similar theoretical concepts. On the problem of adaptative significance of reproductive processes, some authors remark that it would be extremely imprudent to assume that most exact and complicated relations between animals and plants observed during pollination have arisen accidentally, as a result of indirect variability. The adaptive capacity of an organ cannot be denied just because we do not know its functions.

In this way, the scientific community has already answered the question whether the reproductive biology of plants is the division of botany involving detailed investigation of reproductive processes or a specific scientific problem. It answered this question in the form of such new concrete research directions as antecology (Faegri and van der Pijl, 1966; Ponomarev, 1969), ecological carpology (van der Pijl, 1969) and ecological embryology (Teryokhin, 1977,1988,1997). In the last few years, in connection with the rapid development of new ideas and methods in the sphere of developmental genetics and biotechnology, such new directions of reproductive biology as investigation of fine mechanisms of pollination (the problem of self-incompatibility), genetic control of flower formation, genetic engineering of gametes and embryos, genetic control of apomixis and genetic control of the development of hybrid seeds have emerged and are rapidly progressing.

These directions, presented in the third volume, reflect current problems and new approaches in the sphere of reproductive biology of plants.

New discoveries in the area of reproductive biology of plants and their practical value are hard to foresee, but even those that have been achieved strike the imagination.

Ecological Embryology

Ecological embryology is the division of embryology comprising investigation of causative interactions between environmental factors, plant behaviour and adaptive peculiarities of organization of generative and embryonal structures. By definition, this sphere of research appears to be part of evolutionary botany. Ecological causal approach to embryological investigations is essentially close to the causal-functional analysis in carpology (Pijl van der, 1969), anthecology (Faegri and van der Pijl, 1980), but it has other trends in the study of ecological functions, as well as in the spectrum of structures investigated.

Ecological embryology is just beginning to develop, and that sets certain limits in the choice of subjects for study. Such subjects must be ecologically distinct, amenable to accurate and detailed ecological analysis, and perfectly studied morphologically.

The following groups of angiosperms correspond to these criteria: plant-xenoparasites with different modes of nutrition (Scrophulariaceae - subfamilies Orobanchoideae and Rhinanthoideae, Balanophoraceae, Cuscutaceae, Hydnoraceae, Loranthaceae, Rafflesiaceae, Viscaceae), mycoparasitic plants (Ericaceae — subfamilies Monotropoideae and Pyroloideae, Burmanniaceae, Orchidaceae, some genera of the Gentianaceae) and also predatory plants, including water plants (Droseraceae and Lentibulariaceae). Some taxa of submersed plants (Potamogetonaceae, Ruppiaceae, Zosteraceae) also meet those criteria (Fig. 3).

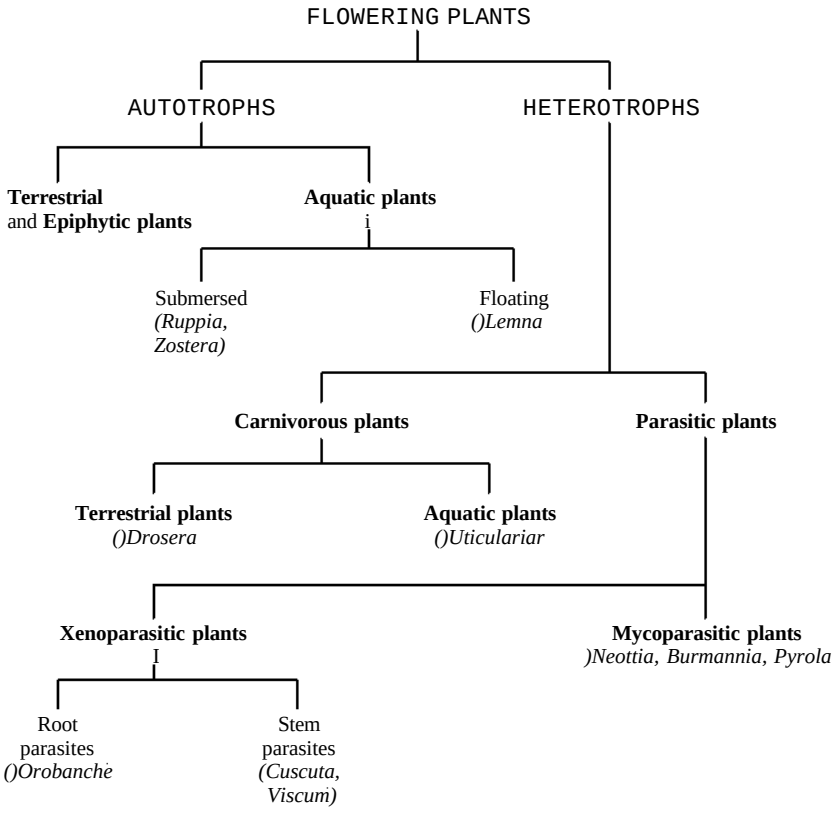

Fig. 3: General modes of flowering plant nutrition (after Teryokhin, 1977).

The theoretical basis of ecological embryology consists of the following concepts. The first is the adaptive character of evolutionary modifications of ontogenesis. We extend the concept of adaptive modifications directly to the processes of macroevolution as well, referring to the mechanisms of such modifications in relation to the concept of "new synthesis" (Gilbert *et ah,* 1996). The second is the acceptance of evolutionary priority and guiding role of ecological functions with regard to evolutionary structural modifications. Herewith we understand the ecology in the same way as Lemee (1967) did. According to his notions, the investigation of connections between environmental factors and organisms has two aspects: (1) **the study of the character of the environment in which organisms are living, mesological ecology** or **mesology,** and **(2) the research of behaviour and reaction of organisms in this environment, etological ecology** or **etology.** We consider the reactions of organisms to mesological influences to form the definite complexes that are referred to as behaviour (e.g., nutritive or reproductive behaviour), depending on aims of directional activity. Behaviour is inherent to all types of organisms, including plants (Teryokhin, 1972,1977).

Behaviour plays, in our opinion, a specific role in the evolution of ontogenesis, as far as it is behavioural changes that direct evolutionary modifications of structures

(Teryokhin, 1991). Stress being a trigger factor is a very productive concept when discussing behavioural changes and appropriate structural modifications. It could be proposed that stresses, particularly "ecological" stresses (i.e., stresses caused by mesological factors) are effective trigger mechanisms of evolution, especially in the processes of ecological niche shifting, e.g., during the transition from autotrophic to parasitic (heterotrophic) mode of nutrition (Teryokhin, 1996).

Interaction of ecological (mesological and etological) factors can be followed on the example of adaptive evolution of certain ecologically distinct groups of flowering plants.

The ecological niche of members of the subfamily Rhinanthoideae (Scrophulariaceae) is "root" parasitism, i.e., parasitism on the roots of suitable host plants, usually monocots (Fig. 4). This subfamily is especially interesting due to the fact that it includes species and genera with different degrees of specialization in root parasitism: from facultative parasites *(Euphrasia minima, Melampyrum lineare)* up to highly specialized achlorophyllous parasites *(Harveya coccinea, Hyobanche sanguined, Striga gesnerioides).* The degree of specialization of these plants in root parasitism is reflected mostly visually in the reduction of their embryo size (Table 1).

Transition of a number of flowering plants to root parasitism was induced essentially by insufficient humidity of soil (Kostychev, 1937). This limited factor appeared to evoke the state of stress in autotrophic plants that were in similar conditions. Discomfort triggers the search for a way to avoid the stress condition. At the frequent spontaneous coalescence of roots of autotrophic plants in soil the pumping of water from the cells of one of the coalescent roots to the cells of another could be the way out of stress. This process occurs under the condition of different osmotic pressure in the cells of coalescent roots. Osmotic pressure in the cells of plant-parasites is higher than in the cells of host plants. For example, the osmotic pressure in parenchyma stem cells in root parasite *Orobanche crenata* was 14 atm and in its haustorium cells it was 12.7 atm, but in parenchyma cells of the affected host roots it was 8 atm (Geumann, 1954).

It could be proposed that in these conditions natural selection promoted the fixation of such frequently repeated spontaneous contacts, advantageous for parasites, transferring them to regular phenomena. It is apparent here that parasitism at the initial stages of its evolution had to develop on a facultative base. Actually, in some of the least specialized genera of parasitic Scrophulariaceae, species with facultative parasitism *(Euphrasia minima, Melampyrum lineare, Odontites verna, Rhinanthus minor,* some *Castilleya* species) were observed (Heinricher, 1917; Hambler, 1958; Curtis and Cantlon, 1965). Facultative parasites are able to complete their development even in the absence of host plants. Their parasitism is based on the occasional contacts with the roots of suitable host plants. Facultative parasites are just able to form haustoria but have no specialized (e.g., chemical) mechanisms for the search of suitable host plants. Except in the capacity to form haustoria during accidental contacts, facultative parasites are similar in their function and development to related autotrophic plants. The initiation (expression) of haustorium structures itself does not seem to be an inevitable property of their genome.

It is obvious that in suitable conditions, about which little is known at present, the facultative forms of parasitism are modified in obligate forms. Stress is likely to have stimulated this transition.

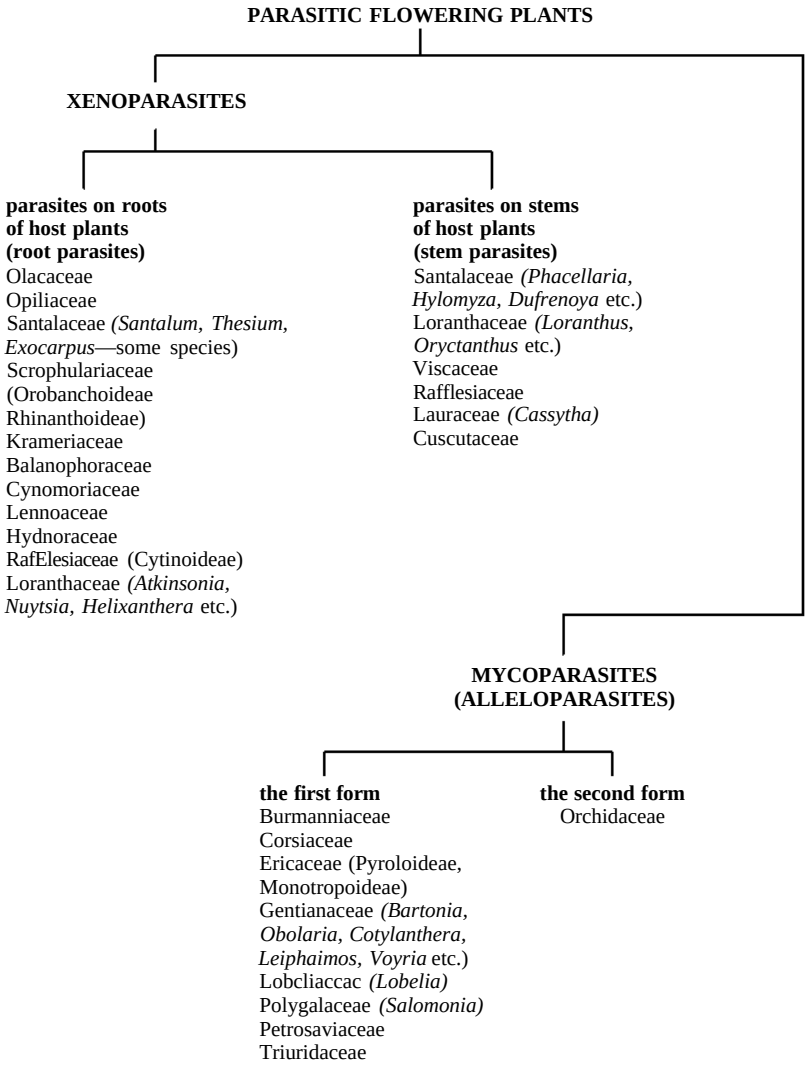

Fig. 4: Main groups of parasitic flowering plants (after Teryokhin, 1977).

After the transition of parasitic plants into obligatory forms, stress pressure takes another direction. It is connected with the dependence of further progress towards intensification of plant-parasite adaptive specialization on the influence of such mesological factors as the discrete distribution of nutrition source (host plants) in the area of one or another species of parasitic plants (Salisbury, 1942; Teryokhin, 1977). This strong factor, affecting parasites by means of natural selection, causes the changes, primarily in ecological functions, connected with a search for a suitable host plant. In fact, the ecological specificity of obligatory parasitism lies in the need (cyclically repeated in each new generation) to search for an available companion in

Table 1. Evolutionary reduction of embryos in subfamily Rhinanthoideae (Scrophulariaceae) as a result of adaptation to "root" parasitism (after Teryokhin, 1977).

Degree of adaptation to parasitism \ Plant species	up — *minima* *Melampyrum lineare*	u *stilkya pallida* *Rhinchocorus orientalis*	*Tozzia alpina*	*Lathraea squamaria*	*Striga hermonthica*	*Striga gesnerioides*	*Ha — coccinea*
FACULTATIVE PARASITIC PLANTS							
O LIGATORY PARASITIC PLANTS							
Plants-parasites with green leaves							
Achlorophyllous plants with photosynthesizing reproductive shoots							
Achlorophyllous plants with bipolar development of seedling (without "nodule" stage)							
Achlorophyllous plants with photosynthesizing shoots, bipolar development of seedling and "nodule" stage							
Achlorophyllous plants with bipolar development of seedling and "nodule" stage						**$D**	
Achlorophyllous plants with unipolar development of seedling, "nodule" stage and metamorphosis							

parasitic symbiosis and establishment of metabolic contact with it. This contact is established every time by haustorium penetration of parasitic seedling in root tissues of the host plant. At the same time, the problem of the search for a suitable host remains on a stochastic base. It is clear in this situation that the more seeds the plant-parasite produces, the higher the possibility that its seedling will meet a suitable nutrition source.

Here the problem seems to lie in the limited energy resources of the parasitic plant. Plant-parasites get out of this situation by means of two adaptations: the establishment of donor-dependent germination and increase in the number of reduced seeds (Teryokhin, 1977, 1988, 1997). Donor-dependent germination is realized in the fact that the parasite seed germinates only after being exposed to root secretions of the host plant. The parasitic seedling then changes geotropic functions of radicle apex to chemotropic, obtaining a new vector of germination-promoting survival.

The quantity of seed produced by the parasitic plant increases by two means: by enhancing the surface of placental structures owing to their growth and rumination and by reducing ovules. The transition to the total obligate nutrition on account of metabolic connections with host plant results in the replacement of bipolar development of the parasitic seedling to unipolar development (in the case of root parasitism, due to the preservation of morphogenetic potential at the basal, root pole of the embryo). The reduction of one of the morphogenetic potentials ensures the possibility of considerable reduction of embryo organs and tissues.

Thus, rather complicated interactions of mesological and etological factors lead parasitic plants to their fundamental adaptive structural changes. The general structural modifications in this direction are the reduction of ovules and embryos concurrent with considerable increase in seed quantity. The extreme forms of these changes can be observed in the most specialized taxa. With far-reaching specialization in root parasitism, the seedlings of *Harveya coccinea*, *H. obtusifolia*, *Hyobanche sanguined* (subfamily Rhinanthoideae) and all members of subfamily Orobanchoideae transfer to development with metamorphosis (see Metamorphosis). Root parasites from Hydnoraceae and Rafflesiaceae families travel a similar pathway of evolutionary modifications, which also leads to extreme reduction of seeds and embryos in these plants (Figs. 5 and 6).

Owing to the extreme reduction of seeds ("dust-like" seeds), there is a transition to anemophilous seed dispersion instead of, for example, myrmecochory in genera *Melampyrum* or *Pedicularis.* Anemophilous distribution of seeds without address is a strong etological factor facilitating the reduction of seeds and embryos in conditions of discrete distribution of nutritional substrate (host plants).

A somewhat different situation is seen in such "ancient" families of root parasites as Balanophoraceae and Cynomoriaceae. In *Cynomorium coccineum,* against considerable reduction of embryos, the developed structures of seed coat and endosperm remain in seed. One-seeded fruit seems to be the unit of dispersion and insects (beetles, ants) are the agents of distribution. The embryo is reduced to a globular structure. These peculiarities of reduction are conditioned by the character of distribution agents. In our opinion, myrmecochory, preserved here, explains the special organization of the fruit-seminal complex. The larger diaspore number is manifested in this species in the increase of fruit number on inflorescence. Together with this the massive inflorescences of *Cynomorium* are always disposed in a soil surface that undoubtedly facilitates myrmecochory.

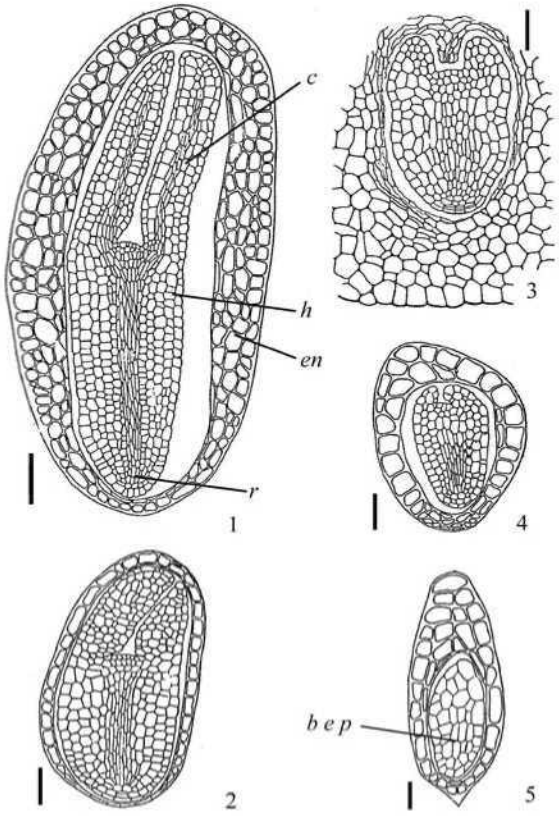

Fig. 5: Embryos in seeds of Rhinanthoideae (Scrophulariaceae) members with different degrees of adaptation to parasitism (after Teryokhin, 1977)

1 — Castilleya pallida, 2 — Striga baumanii, 3 — Lathraea squamaria, 4 — Striga hermonthica, 5 — Harvey a obtusifolia; b e p —basal embryo pole, c —cotyledon, *en* — endosperm, *h* — hypocotyl, *r*—radicle. Scale: 0.05 mm.

In a similar direction, evolutionary modifications of generative structures occurred in the Balanophoraceae. In transitional forms of this family the gradual reduction (with further elimination) of ovule structures and then also of placenta can be observed (Teryokhin, 1985). So, in the most highly specialized taxa *(Balanophora, Langsdorffia)* the fruits, containing endosperm and extremely reduced embryo, absolutely lack seeds and present minute, dust-like diaspores. It is a rare case that the fruit completely replaces the seed both in the ecological-functional and in the morphological sense.

Different factors and results of adaptive structural evolution can be observed in the families of stem parasites. Among these plants, three pathways of adaptation to stem parasitism are clearly distinguished. The first pathway is connected with direct address transfer of generative diaspores (fruits) from the stem of the parasite to the stem of the host plant *(Viscum album).* Fruits in *Viscum album* are rather coarse, having

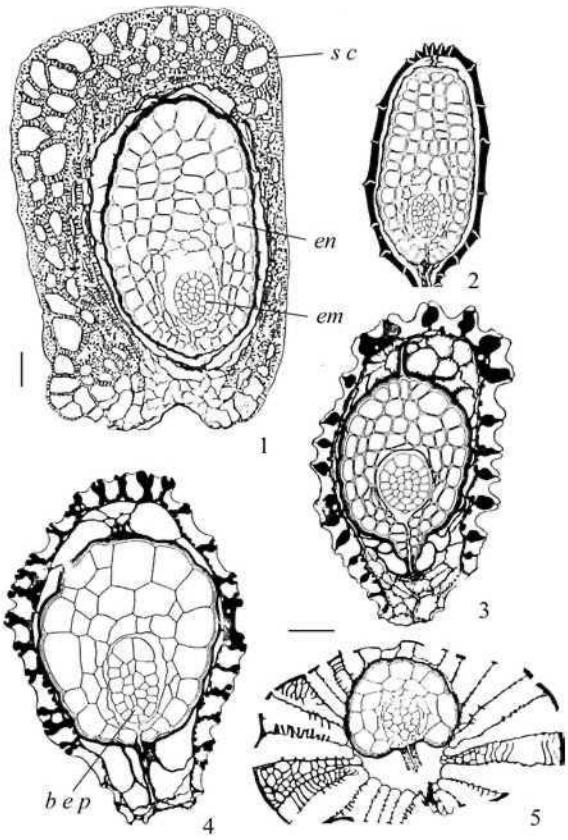

Fig. 6: Reduced embryos in mature seeds of parasitic members of Orobanchoideae (Scrophulariaceae) (after Teryokhin and Nikiticheva, 1981).

1 — Conopholis americanum, 2 — Epifagus americanum, 3—*Mannagettaea hummelii,* 4 — *Phacellanthus tubiflorus, 5 — Xylanche himalaica; b e p*—basal embryo pole, *em — embryo, en* — endosperm, s c — seed coat. Scale: 0.05 mm.

no seeds but containing in their cavity an embryo well differentiated into organs and endosperm. However, the radicle in such embryos is modified into a massive haustorium structure. Mesocarp of fruits contains a sticky substance (viscin) encouraging adhesion of fruits on the branches of host plants after they are discarded by birds together with excrement. Seedling geotropism is replaced in these plants by negative phototropism. *Viscum album* in Europe comprises at least three biotopes (physiological races) connected with different taxonomic groups of host plants (Tubeuf, 1923). The dispersion of diaspores in *Viscum album* precludes the necessity for each plant to produce a great number of them. Besides that, the necessity of reaching the host conductive system through the massive bark of its branches preserves a massive haustorial structure in the parasite embryo.

The second pathway of stem parasitism evolution is connected with the dispersal of generative diaspores from parasite to soil to stem of host plant (Lauraceae — genus

Cassytha, Cuscutaceae). The peculiarity of this group of plants is that the seedlings, being fixed in soil, begin the active search for a suitable host plant. It is exactly that with which the properties of evolutionary adaptive embryo modifications of these plants (selective reduction of cotyledons and radicle), original modification of endosperm tissues in mature four million seeds, and peculiarities of seedling growth and organization are connected (Teryokhin, 1977).

The scope of the present volume does not permit us to discuss in great detail the peculiarities of the adaptive evolution in mycoparasites, free-swimming predatory plants and some groups of submersed plants (Teryokhin, 1977,1985). We shall note only certain general aspects of these processes.

It is rather obvious that the adaptive evolution in the various ecological groups mentioned above is subordinated as a whole to the same regularities that exist in the groups of xenoparasitic plants, taking into account the mesological and etological factors influencing their morphological evolution. Meso-etological complexes of such factors initiate the definite directions of adaptive evolutionary modifications in ontogenesis and determine their results. For example, in the group of "monotropoidous" mycoparasitic plants (Scheme 2) from the Ericaceae (Monotropoideae, Pyroloideae), Burmanniaceae and some others, we observe a sharp intensification of seed propagation with substantial reduction of embryo and endosperm. In this group of plants, extreme embryo reduction in mature seeds can be observed, when the embryo consists of just two or three cells *(Allotropa virgata, Hypopitys monotropa).* Here, as in *Orobanche*, morphogenetic potential of seedling development also remains at the basal (root) pole of the embryo. On the contrary, in Orobanchaceae family the morphogenetic potential in embryos with the other form of reduction is concentrated in the apical (stem) pole (Teryokhin, 1977). Anemochorous seed dispersion in all mycoparasitic plants with some discretion in host distribution (mycorrhizal fungi of definite taxa) is attended by the formation of a large number of dust-like seeds in the fruit; in some orchid species more than four million seeds are produced in each fruit.

It is the predatory water plants that are characterized by the selective reduction of embryos together with obligatory modification of embryo basal part into parenchymal reserve structure similar to that of orchids (Teryokhin, 1977,1985).

The theoretical significance of the direction developed here — evolutionary ecological embryology — is that the ecological-morphological approach permits us objectively to determine the trends of evolutionary modifications in ontogenesis, revealing the complexes of mesological and etological factors that stipulated such modifications.

Reproduction, Propagation and Renewal

Reproduction and propagation is proved to be the basic property of living beings. All processes resulting in the increase of biological units are referred to as propagation in the broad sense of the word; in addition, succession is expected to occur between old and new structures. Propagation can take place on different levels — molecular, cellular, tissue, organ, organism and populational. Cell division is the basis of propagation.

In spite of a large number of investigations devoted to different aspects of propagation phenomena, the biological entity of definite types, modes and forms of reproduction and their interactions are considered insufficiently clear.

The classification of propagation types (sexual, asexual and vegetative) is likely to be revised, although it is widely accepted and recorded in textbooks and specialized works (Battaglia, 1963; Vassilyev *et al*, 1978; Pisyaukova, 1980; Serebryakova, 1980; John, 1984).

Such terms as **"vegetative propagation"** and **"renewal"** are not entirely clear. The content of the term **"reproduction"** also has to be verified, as various interpretations are found in literature. Such notions as "sexual process" and "sexual reproduction" need to be verified.

The term **"sexual process"** is an example of how confused the terminology of propagation is. The sexual process in plants in its typical form is usually treated as the **fusion of two sexual cells (gametes)** and the formation of a **zygote.** Mogie (1986) examined the biological and genetic meaning of the term "sexual process" in relation to the phenomenon of automixis. He suggested that the notion "sexual process" comprehends all the reproductive **processes** involving the fusion of nuclei, independent of their **origin** (from **different meioses** or **single meiosis).** Fincham (1983) excludes from sexual process **the fusion of sperm with meiotic unreduced egg cell.** Meanwhile, Harlan and De Wet (1975) regarded this phenomenon, sporadically observed in most organisms because of meiosis disturbance, to be of **great significance for plant phylogeny.** Most authors consider this the usual pathway of polyploidization in plants (see Frank, 1988).

Thus, in the interpretation of the notion "sexual process" in flowering plants, **one of its key periods or phases, meiosis, is ignored.**

From our point of view, the sexual process includes **meiosis and fusion of gametes** (from different meioses) as a result of which a zygote, i.e., a new individual, arises (Batygina, 2005).

The term "sexual process" is often replaced in literature by **"sexual propagation".** But these terms are not synonyms. During sexual process there is no increase in individual number, since **a single new organism** forms, as a rule, from the zygote, developing as a result of the fusion of male and female gametes. That's why, when **sexual process alone** takes place, it should be referred to as **reproduction, not propagation. Increase in sexual progeny** is provided by all the ovules, pollen grains, gametes and zygotes and so by **"the set of sexual processes".** Therefore it is not appropriate to use the term "sexual propagation" with reference to flowering plants.

The definitions "sexual" and "asexual" should be used for the mode of new individual formation only (with or without contribution of meiosis and gametes).

Various types of sexual processes are observed in plants: e.g., isogamous, heterogamous, oogamous. Oogamy alone is inherent in the flowering plants (see Vassilyev *et al.*, 1978).

In literature the notions "propagation", "reproduction" and "renewal" are often mixed, and occasionally the latter is understood even as "the sexual process". In this matter first Darlington (1958) and later John and Lewis (1975) and other authors designated "sexual reproduction" (but not sexual process—T.B.) as a process comprising meiosis and fertilization. Dick (1987) also used the term "sexual reproduction" to explain sexual process (fusion of nuclei, produced by different

meiosis (allo- and autogamy)). Unlike Mogie (1986), he referred to the fusion of nuclei of single meiosis as "pseudosexual reproduction". In this case the author practically also mixes different notions. It is likely correct to speak about pseudosexual process. Sladkov (1986) replaces the notion "reproduction" with the term "generative propagation" and connects it with the change of nuclear phases. In addition he includes in it sexual propagation and asexual propagation (by spores). All this testifies how difficult and debatable this problem is and how much it complicates the understanding of all phenomena observed in plant propagation. It is from the context that we can understand in what sense the authors use the term "reproduction", to mean either reproduction itself or propagation.

One of the greatest Italian scientists, Battaglia (1963), somewhat cleared up this most complicated biological question. It is known that organisms are able to arise in the same phase (in the ontogenetic sense, i.e., sporophyte from sporophyte) or in the antithetic phase (i.e., sporophyte from gametophyte). From this perspective, reproduction can be accordingly divided into **homophasic** and **heterophasic.** Battaglia suggests we use two different terms: **"reproduction"** (for heterophasic increase in number) and **"multiplication"** (for homophasic increase).

We presume the term "reproduction" to be used for a new individual formation irrespective of the mode (by sexual or asexual processes) and the term "propagation" for the increase of sexual and asexual progeny in number (Batygina, 1992,1993a). In order to clarify what type of progeny we have to deal with, the definition "sexual" (heterophasic reproduction) or "asexual" (homophasic reproduction) can be added to the term "reproduction", but not to "multiplication".

The processes connected with different forms of propagation are heterogeneous and before analysing their biological significance we need to agree upon their differentiation. At first sight, all questions connected with multiplication may seem purely rhetorical, since plant multiplication, its forms and its types are supposedly well known. Unfortunately, as we have seen, the interpretation of most notions does not reflect the essence of the phenomenon either from a genetic or from a generally biological point of view.

Let us examine the terms "asexual" and "vegetative" propagation. One speaks of asexual propagation "in the narrow sense" and "in the broad sense". The first implies multiplication by spores and the second implies vegetative propagation realized by vegetative parts, organs, and certain plant cells. Vegetative propagation encourages the preservation of heterosis, polyploid forms and various somatic mutations (Petrov, 1964; Pisyaukova, 1980; Solntseva, 1991). Pisyaukova suggested using "vegetative multiplication" only, considering the term "asexual multiplication" to be a tautology. We share this opinion. Let us try to explain this. It is accepted that spores of flowering plants have lost their main functions connected with multiplication and dispersal. From this point of view, the flowering plants lack asexual propagation.[1]

If the maternal plant produces numerous daughter specimens without contribution of sexual process, i.e., asexually, this process is usually accepted as vegetative multiplication.

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[1]In fact, in the course of evolution in flowering plants, the process of formation of new individuals from mega- and microspores practically lost its significance. Nevertheless, it should be mentioned that these potentials (reserves) have been preserved, which is confirmed by experimental data on the obtaining of haploid and diploid individuals from micro- and megaspores in culture *in vitro* (Batygina, 1987a).

It should be mentioned that in the process of evolution the morphogenesis pathways, while producing new individuals asexually, probably underwent changes. The evidence is that in some flowering plants vegetative propagation is realized not only by buds and roots (gemmorhizogenesis), but also by specialized bipolar vegetative diaspores or propagules, represented either by embryoids (homophasic viviparity) (Batygina *et al.*, 1996) or by brood buds (Batygina, 1989a,b,c, 1990; see also Diaspore).

Hence, the vegetative propagation of flowering plants is believed to be one of the types of multiplication in which new individuals (specimens) are produced by two modes, gemmorhizogenous and embryoidogenous.

The notion "plant propagation" includes seed propagation in addition to vegetative propagation (see Seed and Seed Propagation). The **correlation** of these processes in different taxa continues to be uncertain. Perhaps that could be explained by the methodological difficulties of the investigations of these prolonged processes. In discussing different types, forms and modes of reproduction and multiplication, the following questions also arise: how do **"seed propagation"** and **"seed renewal",** as well as **"vegetative propagation"** and **"vegetative renewal",** correlate with each other (Shalyt, 1960; Rabotnov, 1969a,b, 1974; Serebryakov, 1952; Levina, 1981)?

The terms **"propagation"** and **"renewal"** are usually discussed together. However, they should be distinguished, as **the first applies to the individual** and **the second to the population. It** should also be mentioned that, although the renewal of species in total (or population) is based on the propagation of individuals, the term **"propagation" is not applied to systems above organism level** (see Levina, 1981).

The term "vegetative renewal" is thus understood as the **renewal of population by vegetative propagation.** The process of restoring lost epigeal parts is referred to as **"regrowth";** four types of regrowth were distinguished (Rabotnov, 1974).

Levina identifies the **maintenance of optimal population density owing to the seed propagation of individuals as "seed renewal",** which serves as an index of biological effectiveness of reproductive process.

Seed propagation, as well as vegetative renewal, depends on numerous environmental factors and therefore is a stochastic process. Meteorological, edaphic, allelopathic, and parasitic factors and competition are probably the main factors.

All the processes and phenomena mentioned above—**sexual and asexual processes, heterophasic and homophasic reproduction, seed and vegetative propagation and renewal**—occur in connection with one another; in addition, certain correlations are revealed between them that maintain the homeostasis of species and population.

Use of the term "alternation of generations" has also proved to be debatable. The term was borrowed by Hofmeister (1851) from zoological literature. Subsequently, the classical investigations of Hofmeister, Strasburger, Gorozhankin, Belyaev, Arnoldi, Nawaschin and Meyer demonstrated that all plants (mosses, club-mosses, ferns, gymnosperms and angiosperms) undergo in their development **two phases that alternate with each other: an asexual** spore-formed generation (sporophyte phase), and a **sexual** gamete-formed generation (gametophyte phase). Thanks to Hofmeister, most investigators refer to these phases as "generation alternation", but that does not reflect the essence of the phenomena taking place in the life cycle of flowering plants.

As Poddubnaya-Arnoldi quite justly noted (1976), in earlier research, especially on flowering plants, gametophyte and sporophyte were often considered in isolation and were attributed too independent a significance. This is, probably, one of the reasons these different developmental phases in the life cycle are referred to as "generations". Poddubnaya-Arnoldi therefore assumed that it is accurate to speak of **phases,** because they are so closely connected with each other that they should not be examined in isolation, in so far as the plant is a total organism. The author emphasized that the general difference of these phases lies not in their chromosome number but in their biology. These phases ("generations") do not always alternate with the change of nuclear phases, because at some forms of apomixis in certain plants during individual development the change of nuclear phases is known to be absent.

Besides that, the term "alternation of generations" is appropriated by geneticists, who use it in its full sense as reproduction of new individuals derived from the maternal organism (in addition every new generation that arises during propagation process usually has the main morphological and biological peculiarities of the species).

Perhaps one could agree with Levina (1961) that in the light of current data the term "alternation of generations" is better not used for flowering plants, since it does not correspond to the essence of the phenomenon. Nevertheless, it should be mentioned that the concept has played a positive role in science in that it revealed the unity of origin in different plant groups.

Viviparity (Latin *vivus* - living, *pario* - to bear) is the mode of reproduction and propagation by which a generative diaspore containing an embryo or a vegetative diaspore without dormancy period forms seedlings (propagules) on the maternal organism itself **(Plate I).**

The phenomenon of viviparity in animals has been recorded even in the times of Aristotle (4th century B.C.). He used viviparity as a character of animal classification (viviparous and ovoviviparous). Viviparity in plants *(Festuca ovina)* was first described by Linnaeus (1737).

At present viviparity is known in 265 species of flowering plants[2] belonging to families situated both at the base of the phylogenetic system (Nymphaeaceae, Ranunculaceae) and in its upper part (Orchidaceae, Poaceae). The process of seedling formation with definite generative and vegetative organs is taxon-specific (Batygina, 1996b).

The first review of viviparous plants was undertaken by Braun (1859), who understood the phenomenon of viviparity broadly. Most scientists (Sernarder, 1927; Stebbins, 1951; Heslop-Harrison, 1953; Genkel, 1979; Batygina, 1989a,b,c; Batygina *et ah,* 1996) supported this opinion. Braun divided viviparity into six groups according to the following features:

1. Mature seeds germinate on the mother plant in the dehisced fruits *(Juncus, Epilobium, Agrostemma)* or inside the indehisced fruits *(Cucurbita melopepo, Carica papaya, Persea gratissima, Araucaria brasiliensis, Bulbine asiatica,* members of *Rhizophora, Ceriops, Kandelia, Bruguiera* genera). Such germination proves to be **regular or sporadic.**

[2] Besides flowering plants, 197 species of viviparous ferns belonging to eight families are known (McVeigh, 1937).

2. Vegetative buds are produced in fruits instead of seeds (Amaryllidaceae). However, the author himself had doubts about the possibility of this type of viviparity, indicating the need for additional investigations.
3. Viviparous structures arise as the result of pistil modification *(Nymphaea alba, N. lotus).*
4. Bulblets form in the place of flowers or close to them *(Polygonum viviparum, Allium oleraceum, Gagea bulbifera, Lilium tigrinum, Dioscorea batatas, Locheria pedunculata, Alisma natans).*
5. Inflorescence or just its upper part is transformed into a vegetative shoot *(Ananas, Plantago lanceolata, Eryngium viviparum, Poa alpina* var. *vivipara, P. bulbosa* var. *vivipara).*
6. Bulblets arise on leaves *(Cardamine, Nymphaea, Kalanchoë = Bryophyllum, Hammarbya paludosa).* Depending on their location on the leaf, the author divides these plants into various groups (see more detailed Brood Bud; Bulblet and Bulbil).

The meaning of the concept of "viviparity" continues to be debated even today owing to poor study of its structural bases.

Since two types of diaspores exist (generative and vegetative) (see Diaspore), Sernarder (1927) suggested that viviparity be divided into **generative** (production of seedlings from seeds in mangroves) and **vegetative** (production of seedlings in inflorescence of *Poa bulbosa, Festuca ovina* var. *vivipara).* Depending on the role that this phenomenon plays in the life of plants, he distinguished **obligatory** and **facultative** viviparity.

However, some investigators regard only germination of embryo on the maternal plant in a number of mangroves as viviparity, so-called **true viviparity** (Goebel, 1933; van der Pijl, 1982; Robyns, 1971). The transformation of some flowers or their parts or all flowers in an inflorescence into vegetative shoots that often serve as organs of vegetative propagation is referred to as **"false viviparity"** or **"pseudoviviparity"** (Goebel, 1933; van der Pijl, 1982). According to Shultz (1939), "pseudoviviparity is one of the cases of prolification".

Some authors consider certain cases of viviparity such as formation of bulblets in the place of flowers or inflorescence (Winkler, 1908; Stebbins, 1951; Heslop-Harrison, 1953) in addition to flowers (Gustafsson, 1946) as vegetative apomixis.

When only upper flowers in an inflorescence are modified into bulblets, and lower ones possess a normal structure, it is referred to by some authors as **semiviviparity** (Turesson, 1926,1930,1931; Wycherley, 1953).

Occasionally, abnormal flower modification (Gandilyan, 1961) is referred to as viviparity; the term "teratological viviparity" is also used (Juncosa, 1982).

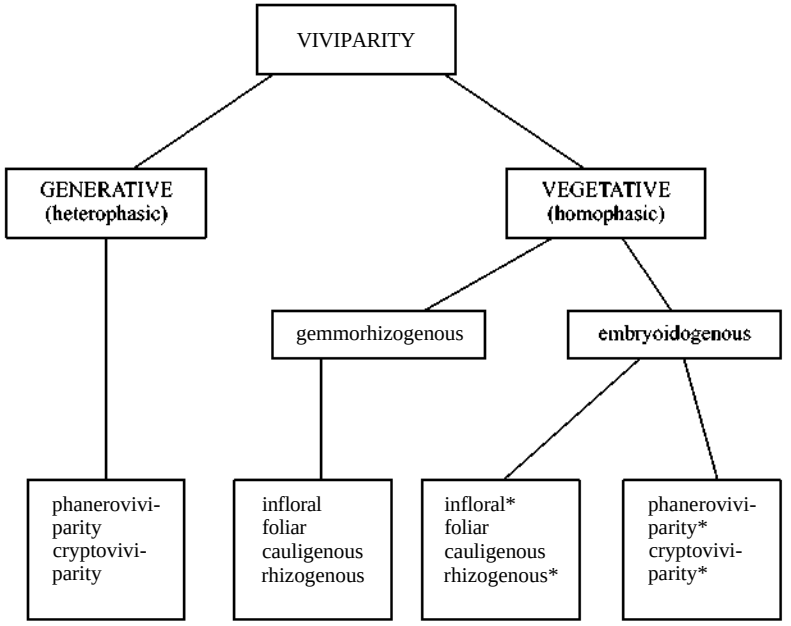
The attempt to describe all cases of viviparity was undertaken by Genkel (1979), who suggested a distinction between euviviparity and pseudoviviparity. The first type includes (1) reproductive viviparity (a single seed germinates on maternal plant), (2) cryptoviviparity (embryo germinates inside the fruit on maternal plant) and (3) reproductive-vegetative viviparity (bulblets are produced on inflorescence instead of seeds). The second type comprises (1) vegetative pseudoviviparity (the formation of buds on stems, leaves and leaf axiles) and (2) reproductive pseudoviviparity (germination of seeds in sheaves in damp weather).

From our point of view, the principle used by Genkel when dividing viviparity into eu- and pseudoviviparity is not adequate, as the author describes cases of viviparity having a common structural basis as different exhibitions of viviparity. For example, although brood buds forming in flower or inflorescence or on leaf and stem all originate from somatic ("body") cells of the sporophyte, the author classifies them in different categories of viviparity. The germination of seeds in sheaves in damp weather is more logically referred to as euviviparity, as if it happens without a period of dormancy, as also during the development of mangrove sexual embryo.

The division of viviparity into true (euviviparity) and false (pseudoviviparity), in our opinion, is not justified, because in both cases a new viable plant is formed. The classification suggested by Genkel is hard to use, as it not only fails to make clear the complicated phenomenon of viviparity, but also confuses most of its aspects. Nevertheless, the distinguishing of seed germination in the fruit as a special type of viviparity (cryptoviviparity) is undoubtedly useful.

When classifying various cases of viviparity, we proceeded first of all from the fact that plant reproduction seems to be heterophasic (meiosis and gamete fusion) and homophasic (without meiosis and gamete fusion) (Battaglia, 1963; see Reproduction, Propagation and Renewal). While elaborating the classification, we used the division of viviparity into generative and vegetative, suggested by Sernarder (1927). Besides this, we accounted for the origin of a new plant, i.e., its genotype, the mode of its formation and the pathway of morphogenesis (Fig. 7).

Both generative and vegetative viviparity can possess obligate and facultative forms. Unlike the classification of Sernarder (1927), we hold that cases of seedlings



*The viviparity forms are theoretically possible.

Fig. 7: Classification of viviparity phenomena.

forming on leaves or as the result of pistil metamorphosis also should be referred to as vegetative viviparity.

Formation of viable vegetative diaspores germinating on maternal plant has to be distinguished from metamorphosis of flower in consequence of proliferation.

The formation and germination of vegetative diaspores in inflorescence, if there are normal flowers in them, as well as the formation by the plant of two types of inflorescence (only with vegetative diaspores and only with flowers) we understand as **semiviviparity.**

Generative Viviparity

Generative viviparity is realized on the base of a generative diaspore containing a sexual embryo that is able to germinate on maternal plant. Here the seedling formed is either released from fruit coats (phaneroviviparity, Greek *phaner(o)* — obvious + *vivus* + *pario),* or remains in them (cryptoviviparity, Greek *kriptos*—hidden + *vivus* + *pario).*

In most mangroves located in different parts of the tropics, obligate viviparity is observed. This is the common coastal vegetation of sea inlets, straits, lagoons and mouths of large rivers. The mangrove plants grow in temporary or permanent flooding by salt water (Genkel and Fan I-sun, 1958). Most of them (particularly *Rhizophora, Bruguiera, Ceriops)* are characterized by unusual seed germination: embryo develops without the period of dormancy, leaves seed coat and runs through the fruit wall, which remains together with the seedling on the maternal plant (Ray, 17th century, cited by Davis, 1940; Braun, 1859; Warming, 1883; Karsten, 1891; Haberlandt, 1895; Kipp-Goller, 1940; Morshchikhina, 1981; Plisko, 1996).

In the *Rhizophora* ovary, four ovules are formed, but after fertilization in most cases only one develops (Cook, 1907; Kipp-Goller, 1940). Embryogenesis conforms to Onagrad type. The mode of initiation and early stages of cotyledon development in Rhizophoraceae members are unusual for angiosperms. **Cotyledons** resulting from **congenial fusion grow as a united "cotyledonary body" for a long time.** In later embryogenesis and post-seminal development in *Rhizophora, Bruguiera* and *Ceriops,* **three phases of embryo growth and germination are distinguished: embryo growth in seed, "germination" and preparation for seedling separation** (Cook, 1907; Juncosa, 1982).

During the **first phase** the most intensive growth takes place in the apical part of the cotyledonary body. The cotyledonary body coalesces with the inner integument, forming a placental organ through which embryo nutrition is realized. It is not until the cotyledonary body fills the seed cavity that the hypocotyl is formed as a result of intensive growth of the basal part of the embryo. The endosperm also grows actively; it projects from the opened micropyle and penetrates deep into the aerenchymal portion of the fruit and also spreads between seed coat and fruit wall, functioning as a haustorium; in addition, its outer layers are observed to have meristematic activity (Chapman, 1962; Plisko, 1996). In the outermost endosperm layer the signs of specialization typical of transfer cells appear (Gunning and Pate, 1969). The largest portion of endosperm inside the seed is consumed by the embryo to the end of the first phase.

At "germination" stage the hypocotyl grows and its tissues are differentiated (Nikiticheva and Yakovlev, 1985; Plisko, 1996). From a tiny structure of 1 mm length the seedling grows up to 1 m (Haberlandt, 1895; Kipp-Goller, 1940). Concurrently the tissues of hypocotyl and root tip are compressed (tannins accumulate, druses of calcium oxalate form, and trichoblasts and petrosal cells differentiate). Since the tip of the main root escapes the fruit even when a few centimetres long, adventive and lateral roots (5-10 roots) form. The main root dies commonly before seedling separation, but in *Bruguiera* it persists (Kipp-Goller, 1940). Lenticulate formations *(Rhizophora, Ceriops)* or stomata *(Bruguiera),* implementing gas exchange, differentiate on the hypocotyl surface (Kipp-Goller, 1940; Juncosa, 1982; Plisko, 1996). Cotyledon body outside micropyle acquires the form of "frigous cap" and serves as a support to the hard seedling. In the process of seedling development the conductive system is differentiated (Haberlandt, 1895; Cook, 1907; Carey, 1934; Kipp-Goller, 1940; Juncosa, 1982). As a result of the activity of shoot apical meristem in *Rhizophora mangle* and *Ceriops candolleana* three pairs of epicotylar stipulate leaves arise (the first of which in *Rh. mangle* dies) (Juncosa, 1982).

In **the phase of preparation for seedling separation,** the differentiation of the conductive system and further development of lateral roots continue. The intensive growth of the basal part of the cotyledonary body and the formation of cotyledonary tube, covering the plumule, begin. Basal growth occurs until the plumule, being encircled by the cotyledonary tube, appears outside the fruit. The separating layer is formed at the level of plumule in the cotyledonary node in *Rhizophora* and between cotyledons and hypocotyl in *Bruguiera* (Kerner, 1896; Cook, 1907; Juncosa, 1982). The seedlings remain on the tree for 30-39 weeks and sometimes a year (Morshchichina, 1981).

The seedlings eventually fall (in *B. eriopetala* together with the fruit) and drive into the silt almost vertically (Karsten, 1891; Haberlandt, 1895; Schimper, 1898; Kipp-Goller, 1940). Shaded seedlings lying on firmer ground take root in that position, gradually becoming vertical. Mangrove seedlings are able to survive being in the salt water up to a year and long drying periods, up to 68 days (Morshchichina, 1981). During rising tide seedlings have been reported to travel considerable distances, the range of which mostly depends on seedling weight (Schimper, 1898; Genkel and Fan I-sun, 1958).

Generative viviparity was also observed in *Avicennia* (Avicenniaceae) and in the sea herb of the genus *Amphilobis* (Cymodoceaceae) (Chapman, 1962; Tzvelev, 1981; Juncosa, 1982). It was marked in a number of mutants of *Zea* (Robertson, 1955) and *Arabidopsis* (Koornneef *et al.*, 1984; Koornneef, 1986; Giraudat *et al.*, 1992).

Precocious germination of embryos in cereal caryopses and in the fruits of some plants (apple, strawberry, and some pumpkins) should be referred to as **facultative generative viviparity.** Stress (change of humidity and temperature) can cause facultative viviparity (Chapman, 1962).

Vegetative Viviparity

Vegetative viviparity is realized on the base of vegetative diaspore, occurring without contribution of sexual process. Vegetative diaspore can develop by two morphogenesis pathways—gemmorhizogeny or embryoidogeny (Batygina, 1987a, c,

1989a,b,c, 1991a,b, 1993a; see also Embryoidogeny is a New Type of Vegetative Propagation). According to this we divide vegetative viviparity into **gemmorhizogenous** and **embryoidogenous.** While systematizing the phenomenon of viviparity, we took into consideration the location of vegetative diaspores on the plant (inflorescence—**infloral viviparity,** leaf—**foliar,** caulis (stem) —**cauligenous,** root—**rhizogenous).**

Gemmorhizogenous Viviparity

Infloral viviparity was first described by Linnaeus (1737) in *Festuca ovina.* At present the viviparous forms are mentioned in numerous cereal species. In one species they occur exclusively, in others they are observed rather frequently. Viviparous forms of cereals are grown in mountainous countries of Europe, from the Atlantic up to the Arctic Ocean as well as to the territories of the Russian north (Shultz, 1939). Out of 130 cereal species growing in Scotland, 4 species prove to be viviparous *{Festuca vivipara, Poa alpina, P. xjemtlandica* and *Deschampsia alpina)* and 28 are able to proliferate (Harmer, 1984). Plants growing from vegetative diaspores formed on the inflorescence possess a greater tendency to viviparity than plants obtained from seeds. The viviparous forms of cereals appear to be ecotypes, closely connected with the forms producing normal seeds (Salvesen, 1986). The viviparous forms have likely replaced the seeded ones in their previous habitation (Harmer, 1984).

Viviparous fescues of high-mountain latitudes (Spitsbergen Islands and east part of Canadian Arctic Islands) propagate only vegetatively; they entirely lack generative organs (Fernald, 1933; Scholander, 1934). However, on the south border of the range semiviviparity is observed (Turesson, 1926,1930,1931; Wycherley, 1953), and there the hybridization of viviparous fescues with non-viviparous groups becomes possible, if they grow nearby (Siplivinsky, 1973).

The formation of bulblets in viviparous and semiviviparous forms of *Poa bulbosa* was investigated in detail (Popolina, 1960, 1962a,b; Rozhanovsky, 1961; see also Brood Bud). The spikelet of viviparous form at the early stage of the formation is similar in structure to the vegetative shoot and in the process of further development is modified into the bulblet. The mature bulblet in natural conditions enters dormancy, the longevity of which is determined by the concrete conditions of habitation. The question whether it germinates on maternal plants remains open (Rozhanovsky, 1961). Propagation by means of vegetative diaspores is also typical for the two closely related species P. *alpigena* and P. *sublanata* (Sarapultzev, 1998). In some cereal species (e.g., P. *alpina* var. *vivipara)* **the temporary return of viviparous form to fruit-bearing form is possible** (Hunger, 1887; Schuster, 1910; Exo, 1916).

The experimental work on viviparity introduction in *Deschampsia flexuosa* and *Agrostis vulgaris* (Shultz, 1939) merits attention. A short day (10 h) induced increased branching, a longer vegetation period, and a modified appearance of panicles with viviparous spikelets. The increase of flower number in the spikelet and the change of the structure of lower spikelets or all spikelets or total panicle was mentioned. The greening of bases of spike and flower glumes as well as the reduction of stamens and ovaries were observed. Most panicles possessed semiviviparous character: some spikelets were fertile, the others represented shortened shoots. However, spontaneous fall of these shortened shoots was not observed in experimental conditions.

Flower or spikelet metamorphosis in *Triticum* into a vegetative shoot at the base of which roots form was noted (Gandilyan, 1961). Here the flower axis was transformed into the leaf plate and the glumes were transformed into the leaf sheath.

Infloral gemmorhizogenous viviparity was also observed in *Polygonum viviparum* distributed from arctic zones to temperate zones. The habit of this plant varies considerably depending on the conditions of its habitat. There is variability in plant dimensions, the quantity of flowers and tubercles in inflorescence, perianth and nodule colour (Belyavskaya, 1949; Engell, 1973; Law *et al*, 1983). An inverse correlation was revealed between the quantity of flowers and tubercles. In spite of the presence of flowers in the inflorescence, some authors had doubts about the efficiency of sexual reproduction, because in the material studied no viable seeds were found (Callaghan, 1973; Engell, 1973). However, it was demonstrated that in favourable conditions sexual reproduction was still possible (Law *et al*, 1983).

Internal biotic factors (plant genotype, inflorescence number on one plant) and external environmental factors (density of plant cover) play a role in the control of appearance and development of flowers and tubercles (Law *et al*, 1983). The most influential external factor is humidity. Tubercles of P. *viviparum*, for example, begin to grow in conditions of increased humidity (Callaghan, 1973; Engell, 1973, 1978; Petersen, 1981).

The observation of seed-producing and viviparous representatives of *Allium* genus has shown that successive transitions appeared between them (Ustinova, 1944). According to Ustinova, the typical viviparous species must be considered as variations separated in the process of evolution. Bulblets in *Allium* arise in bract axils after the initiation of flower buds.

Facultative infloral viviparity was noted in the members of *Cymbopogon* genus (Dutt and Bradu, 1973; Naveen *et al.*, 1977). Increase in air and soil humidity (after the rainy season) has resulted in the formation of new plants on the previous year's inflorescences: either on each inflorescence node or on the axis of covers of old racemes. We observed the formation of seedlings on inflorescence in *Bryophyllum daigremontianum* at the end of blossoming.

Foliar viviparity. The formation of new plants on leaves was described in *Cardamine pratensis* and *Nymphaea guianensis* (Braun, 1859; Kerner, 1898; Ilyinsky, 1945) and in *Hammarbya paludosa* (Fuller, 1966; Taylor, 1967; Reeves and Reeves, 1984; Vakhrameeva *et al.*, 1991; Tatarenko, 1996; Batygina and Bragina, 1997). Vegetative propagules in *H. paludosa* are formed exogenously because of the cell proliferation of upper leaf epidermis. From meristematic centres the meristematic tubercles, possessing dorsoventral structure, develop. On the outer side of the tubercle periclinal divisions begin, spreading all over the circumference. This results in the appearance of a sickle-like ridge and then, during its further development, in the formation of an unbroken circle (first leaf primordium). The first propagule leaf gradually overgrows the middle part of the meristematic tubercle; at the same time, the organization of the inner part of the propagule takes place.

Cell differentiation in the inner part of the propagule ("egg-shaped structure") is later observed; three zones can be distinguished — apical, middle and basal. These zones differ in cell contents and occurrence of starch in cells. At a later developmental stage the egg-shaped structure acquires dorsoventral organization owing to the growth of one of its lateral sides. As a result, meristematic cells in the apical zone are repositioned on the lateral side of the top of the egg-shaped structure. The central

bundle of stretched cells passes from the zone of these cells through the entire propagule. The shoot apex with the primordia of three leaves is formed by the derivatives of apical meristem.

The first propagule leaf fulfils protective and trophic functions. A high degree of totipotency of its cells, on account of which secondary structures can be produced in certain conditions, is the peculiarity of the development of the first propagule leaf. The formation of the adventive root in the propagule at the end of the vegetative period (November) was not observed. Perhaps its initiation and development happen after the propagule separates from the leaf (in winter or early spring).

Embryoidogenous viviparity. Foliar viviparity is typical for *Bryophyllum* (Yarbrough, 1932,1934; Batygina, 1989a,b,c; Batygina *et al.,* 1996; see Embryoidogeny is a New Type of Vegetative Propagation). Vegetative propagules are produced regularly from the meristem in hollows at the leaf margins in B. *daigremontianum, B. tubiflorum* and B. *rosei* or sporadically in B. *pinnatum,*[3] B. *crenatum* and *B.fedtschenkoi.*

The development of vegetative propagules takes place only in the conditions of a long day (Dostál, 1944; Catarino, 1965; Khovanskaya, 1970). This is connected with the change in basipetal transport of auxin from shoot apex and with the induction of auxin synthesis in propagules proper (Warden, 1970). In this period, cytokinin endogenous content increases in leaf plate from its base up to the top. Such distribution of hormone appears to be one of the factors determining basipetal development of vegetative propagules (Slaby and Sebanek, 1984). While growing, the vegetative propagules attract not only assimilates but also kinetins from roots (Kazaryan and Gevorkyan, 1985). The increase in zeatin + zeatin riboside and indoleacetic acid ratio (Z+ZR/IAA) probably induces cell divisions in meristematic zone of leaf margin, from which the primordium of the propagule is formed. At the "heart-shaped" stage, the change of Z+ZR/IAA ratio (> 1) is attended by initiation of procambium in the larger "cotyledon" (Polevoy and Bragina, original data).

In short day conditions, the suppression of propagule growth appears to be responsible for the high content of IAA and consequently the ratio Z+ZR/IAA < 1. It is only 6-benzylaminopurin and kinetin that possess the specific capacity to induce the formation of vegetative propagules in short day conditions (Vardar and Acarer, 1957; Catarino, 1965; Chailakhyan *et al.,* 1969; Yazgan, 1970). IAA, gibberellins and triiodbenzoic acid are able to stimulate the development of vegetative propagules only in the occurrence of cytokinin (Dostal, 1970). The oc-naphthylacetic acid has the effect of promoting their growth (Chailakhyan, 1988).

Cauligenous viviparity was mentioned in *Ranunculus sceleratus* (see Embryoidogeny, Vol. 2).

Genetic Aspects of Viviparity

In normal seed development the phase of maturation includes the synthesis of reserve nutrients, the cessation of embryo growth and the establishment of drought resistance

[3]The data on the morphogenesis of vegetative propagules in some *Bryophyllum* species suggest that the propagule of B. *pinnatum* is a somatic embryo (embryoid) and that of B. *daigremontianum* is a transitional form between somatic embryo and bud (Batygina *et al.,* 1996).

(McCarty, 1995). Abscisic acid (ABA), which brings about responses to various extreme conditions, is known to be the key regulator of gene expression in late embryogenesis (Skriver and Mundy, 1990). The changes in the synthesis of and sensitivity to ABA appear to be one of the causes of viviparity.

According to the content and the degree of sensitivity to ABA, the viviparous mutants of maize were divided into two classes (Neill *et al,* 1986,1987). In mutants of the first class *(vpl, vpb, psl(vp7), vp8, vp9),* the lower level of ABA (Neill *et al,* 1986) and the change of carotenoid synthesis (Robertson, 1955) are observed.

In the mutant *vpl,* belonging to the second class, the level of endogenous ABA in the embryo is not changed (Neill *et al,* 1987), but the mutant is not sensitive to exogenous hormone (Robichaud *et al.,* 1980; Robichaud and Sussex, 1986). It was established that the product of *Viviparous-1 (VP-1)* gene belongs to regulatory proteins that stimulate caryopsis maturation and dormancy (McCarty and Carson, 1991; McCarty *et al,* 1991). The gene product *VP-1* is the factor of transcription (McCarty *et al,* 1989a,b; Hattori *et al,* 1992; McCarty, 1992; Hoecker *et al,* 1995) and is required for the expression of genes *Cl, Globium* and *Em* (McCarty *et al,* 1989b; Hattori *et al,* 1992; Thomann *et al,* 1992; Paiva and Kriz, 1994; Vasil *et al,* 1995; Hill *et al,* 1996). Furthermore, the protein VP1 proves to be the repressor for genes of oc-amylase, functioning during germination in the cells of aleurone layer (Hoecker *et al,* 1995).

In the seeds of maize viviparous mutants, the genes contributing to the synthesis and recognition of ABA were detected (Tan *et al,* 1997). The embryos of one of the mutants (upl4) possess normal sensitivity to ABA. However, the content of ABA in the mutant embryos was 70% lower than in the embryos of wild type, which indicates the disturbance in ABA synthesis.

Most viviparous mutants of *Arabidopsis* have phenotypes similar to that of maize viviparous mutants (e.g. mutant *abiS).* The mutation *abi3* affects seed dormancy, accumulation of reserve proteins and lipids, chlorophyll disintegration, ability to respond to ABA and drought resistance (Koornneef *et al,* 1984,1989; Koornneef, 1986; Finkelstein and Somerville, 1990; Nambara *et al,* 1992; Giraudat *et al,* 1992). Characteristics of mutant *abi3* alleles confirmed the hypothesis that ABB protein participates in the cascade of reactions of ABA perception and transduction (Giraudat *et al,* 1992). The normal perception of ABA by ABB gene is necessary but not enough for most critical stages of embryogenesis in *Arabidopsis* (Meinke *et al,* 1994). The similar sequences and analogous phenotypes VP1 and ABB suggest that they are functionally homologous genes (Giraudat *et al,* 1992).

In *leafy cotyledon (led)* and *fus3 Arabidopsis* mutants prematurely germinated seeds are rarely observed (Miiller and Heidecker, 1968; Meinke, 1992; Meinke *et al,* 1994). The comparison of these mutants suggests that the genes LEC1 and FUS3 are able to fulfil connected but not identical functions in embryogenesis (Meinke *et al,* 1994). They code the regulatory factors, which activate the wide spectrum of embryogenetic programmes, beginning with the heart-shaped stage. LEC1 and FUS3 positively regulate the increased content of protein ABB in the seed (Parcy *et al,* 1997).

The mechanisms of viviparity regulation in mangroves appear to be compatible with that of *Zea* and *Arabidopsis* mutants.

Many investigators made attempts to discover the causes of vegetative viviparity appearing in flowering plants. In particular, some authors consider viviparous forms

of cereals to be spontaneously arisen, hereditary and more or less stable mutations (Schroter, 1908; Jenkin, 1922; Turesson, 1926,1930,1931). However, Ernst (1918), on the basis of resemblance in the character of sexual apparatus degeneration in cereal viviparous forms and numerous hybrids, propounded the hypothesis of the hybridous origin of viviparous plants. Some investigators tried to connect viviparity with polyploidy (Turesson, 1930,1931).

The phenomenon of viviparity is observed in plants growing in various ecological conditions. For instance, **obligate generative viviparity** is typical of mangrove vegetation. This peculiarity together with the other features proved to be the adaptation to periodical flooding and high degree of salinization. Seed germination on mother plant in mangroves encourages the formation of salt-resistant seedling able to root quickly (Joshi, 1933; Genkel and Fan I-sun, 1958; Morshchikhina, 1981). Salt content in the seedling increases with age (Walter and Steiner, 1936). Adaptation to salinization proceeds as salts gradually pass from mother plant to seedling. The seedling is more plastic than the adult plant, which has already adapted to the particular degree of soil salinization. The more salt-resistant the mother plant, the quicker and easier the adaptation of the juvenile plant to salinization (Genkel, 1962). The interesting suggestion was made that viviparity in mangroves arose as a result of inhibiting effect of chlorine-ion on fruit shedding and this effect combines with the lack of dormancy period in seed formation (Stroganov *et ah,* 1956; Solovyev, 1960; Genkel, 1962).

The capacity of plants for **facultative generative viviparity** is one of the reserves of the reproductive system. When environmental conditions change, some seeds become able to produce viable seedlings.

The viviparous plants for which **vegetative viviparity** is characteristic grow mainly in polar, alpine and desert regions. These plants have at their disposal a very short period with favourable conditions in which to leave descendants. In certain cases, seed formation in them is difficult or impossible owing to the lack of pollinators or disturbances in the development of male and female gametophyte (e.g., some *Allium* species). The capacity for vegetative viviparity then becomes almost the only possible means by which to maintain and enlarge the population.

In the reproductive system of certain plants, normal seed development and viviparity are combined, and that provides the accumulation of different genotypes in a population of descendants (species of *Poa* genus and *Polygonum viviparum).* The capacity for viviparity in arctic cereal species permitted them to settle rapidly the lands released from glaciers (Salvesen, 1986).

Depending on the particular conditions prevailing, the plant is able to produce enough descendants, by either seed propagation or vegetative viviparous diaspores. Semiviviparous individuals or populations can enlarge their number in two ways. As mentioned above, heterogeneity of populations by the degree of viviparity expression allows for hybridization with sexual forms (F. *vivipara).*

The formation of new plants on the vegetative organs allows the seed and vegetative propagation to disperse in space and in some cases in time *(Cardamine, Hammarbya, Bryophyllum).*

The capacity for viviparity seems to be universal for flowering plants (see Autonomy of the Embryo, Vol. 2). Viviparity, which probably arose independently in different groups of plants (Joshi, 1933), plays a substantial role in plant reproduction

(Batygina, 1994). The different degree of viviparity expression in any population ensures the plasticity of the reproductive system. The preservation of biological diversity mostly depends on the successful combination of different modes of propagation (including the formation of viviparous diaspores) in the total system of reproduction.

Metamorphosis (Greek *metamorphosis*—transformation) is the total and profound modification of individual structure during developmental process. The substitution of one form of individual organization for another also takes place.[4] Metamorphosis is conditioned by the change of environment and accordingly the mode of life in the course of individual development.

Metamorphosis is widespread in the animal kingdom: it is peculiar to most taxa of invertebrates as well as some groups of vertebrates (amphibian, seven-eyes, langfishes). As Gilyarov (1957) emphasized, the cause of metamorphosis is extensive adaptation to different functions of the animal at larva and imago stages. In amphibians, metamorphosis is connected with the transition from life in water to life on land, and in most insects it is connected with the transition from life in water (or hidden in substrate) to life in open air. It is obvious that with metamorphosis the general living functions also rapidly change. For example, the nutrition function at the larva stage in insects is replaced by functions of propagation and distribution at the imago stage. This is called **holometaboly** (complete transformation).

Metamorphosis is frequently observed also among angiosperms. **Three main types of metamorphosis** should be distinguished in plants. The **first type, metamorphosis of organs** (the term was introduced for the first time by Goebel, 1898-1901), consists of evolutionary modifications of meristematic organs, conditioned by the change of their functions. The modifications of leaves *(Berberis,* members of Cactaceae family) or stems *(Crataegus, Prunus spinosa)* into spines, fulfilling the function of plant protection from herbivorous animals, could be examples. The formation of pneumatophores (epigeal respiratory roots) in mangroves (e.g., *Jussiena repens, Sonneratia alba)* or rhizomes (hypogeal shoots), fulfilling the functions of vegetative propagation or reserve functions and occasionally functions of dispersal *(Elytrigia, Convallaria, Vaccinium,* etc.), pertains to the same type of metamorphoses. In this type the mode of development of organ initials changes and their changed structure is preserved in subsequent generations.

In the **second type of metamorphosis (temporary or seasonal metamorphosis),** during ontogenesis in plants the organization is temporarily transformed and then there is a return to the initial structure. This metamorphosis type is connected with adaptations to unfavourable seasonal conditions in perennial herbaceous plants. The clearest example is the production of bulbs in the species of Liliaceae family.

The **third type of metamorphosis,** which this article is devoted to, is connected with **the total** and **irreversible transformation (holometaboly) of sporophyte organization** during individual development, conditioned by the transition of the plant to parasitic nutrition. With these types of adaptive modifications, accompanied by profound reduction processes, seed and vegetative propagation are realized because of the formation of adventive organs from new meristematic centres (similar

[4]In theoretical morphology the term "metamorphosis" is also used for indicating evolutionary modifications of certain plant organs.

to "imaginal discs" in animal larvae) as a result of redifferentiation of some parts of a new specialized organ, the tubercle. Such a mode of development with metamorphosis is peculiar to the representatives of some highly specialized taxa of flowering plants, adapted to root parasitism (e.g., Balanophoraceae, Lennoaceae, Orobanchaceae, Rafflesiaceae, Scrophulariaceae) (Fig. 8).

Metamorphosis with total sporophyte reorganization in the course of ontogenesis, which is accompanied by necrosis of structures that have fulfilled their function and by the production of adventive structures from newly forming meristematic centres, appears to be the closest according to the character and the depth of modifications to holometabolitic metamorphosis in the animal kingdom (Gilyarov, 1957; Teryokhin, 1968,1977,1988).

Unlike land autotrophic plants, which develop bipolarly (shoot-root) in two environments, air and soil, the embryos and seedlings of specialized parasitic plants

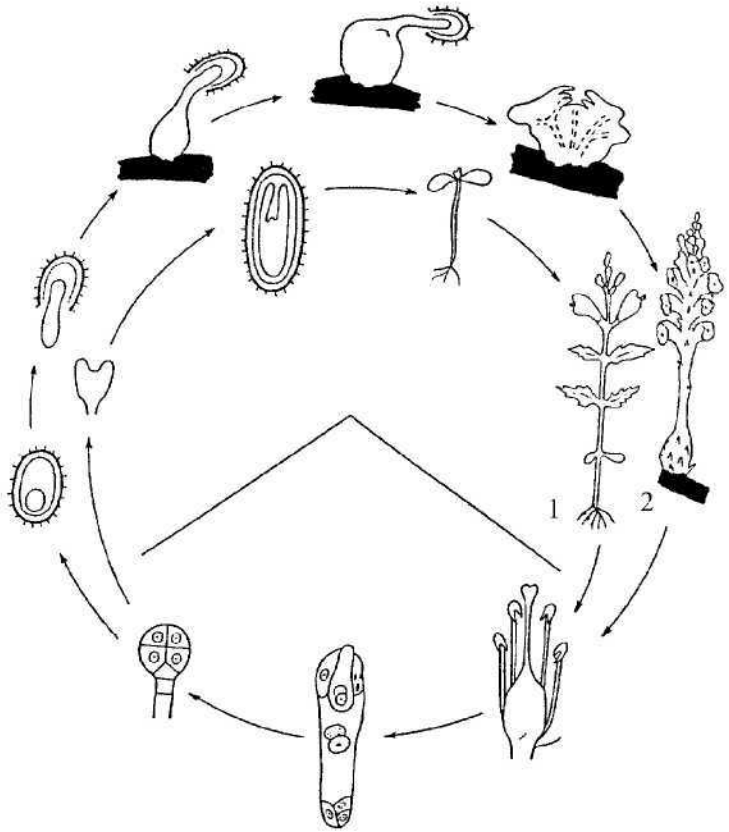


Fig. 8: Ontogenesis without metamorphosis (1) and with metamorphosis (2) in the Scrophulariaceae (after Teryokhin, 1977).

1—Euphrasia (Rhinanthoideae), *2—Orobanche* (Orobanchoideae); similar stages of life cycle are indicated by sector.

are prepared functionally and morphologically for the fulfillment of the main function, the search for a host plant and penetration into the tissues of its root in order to establish metabolic connections with the host conductive system. The root of suitable species of host plant seems to be the single nutrition source for parasitic plant. Since, as even Salisbury (1942) noted, host plants are located more or less discretely in the environment, the parasitic plant has to produce many seeds. In this situation, with limited energy resources of parasitic plant, natural selection leads to progressive reduction of seeds and embryos (Teryokhin, 1977). For example, in dust-like seeds of a highly specialized parasitic plant, for instance, *Orobanche crenata*, one can see reduced embryos having lost all main organs (cotyledons, epicotyl, radicle, hypocotyl) and being represented by an oval cluster of cells ("globular proembryo") not obviously differentiated into two tissue zones. The morphogenetic potential in such embryos remains only in the basal (root) pole. Therefore, the development of "thread-like" seedlings from these embryos is monopolar. The cells of the apical (stem) pole of reduced embryo also serve a haustorial function in the endosperm, and then this zone dies together with the part of the seedling adjoined to the seed coat (Fig. 9).

It should be mentioned that such a mode of seedling development is attended by a number of circumstances. Specialized parasitic plants are characterized by so-called donor-dependent germination. This means that the germination of their embryos is conditioned not by the occurrence of humidity and suitable temperature, but by the specific chemical secretion from roots of host plants. That is why the seeds germinate only near the growing root of the host (usually within 0.5 cm), and the direction of growth of thread-like seedlings is determined not by geotropism, but by the gradient of concentration of substances secreted by the host root. After reaching the root surface of the available host plant, the seedling attaches to it by means of a mucus that is secreted (Teryokhin, 1988). Apical cells of the thread-like parasite seedling are modified into haustorial and penetrate into the root through intercellular spaces.

After establishment of connections with the conductive system of host plant root, the parasite seedling produces the tubercle in the place of penetration; this structure has no homologies in the plant kingdom and is used initially for accumulation of nutrients. With the beginning of tubercle development the transformation of all seedling organization commences. In the tubercle, because of the necessity of reproductive shoot formation and as a result of redifferentiation of certain parts of parenchymal tissue, the meristematic centres arise, as was already noted. From such endogenous centre the shoot apex and its two primary bracts are produced. The third and subsequent bracts arise even on the stem apex of reproductive shoot. From lateral meristematic centres the secondary haustorial roots appear, the organs of secondary haustorium formation and occasionally the organs of vegetative propagation *(Orobanche cernua* ssp. *rajahmundrica).*

The successive stages of evolutionary establishment of metamorphosis with total transformation can be observed on the parasitic representatives of Scrophulariaceae family. In certain species of the genus *Striga*, which have not lost green leaves yet, the gradual reduction of embryos is already seen, highly essential in achlorophyllous species *Striga gesnerioides.* The seedlings of these plants preserve bipolar development; moreover, in *S. hermonthica* and *S. gesnerioides*, seedling development is already accompanied by the production of tubercles that have not yet obtained functions leading to metamorphosis. Seedling development with total reorganization

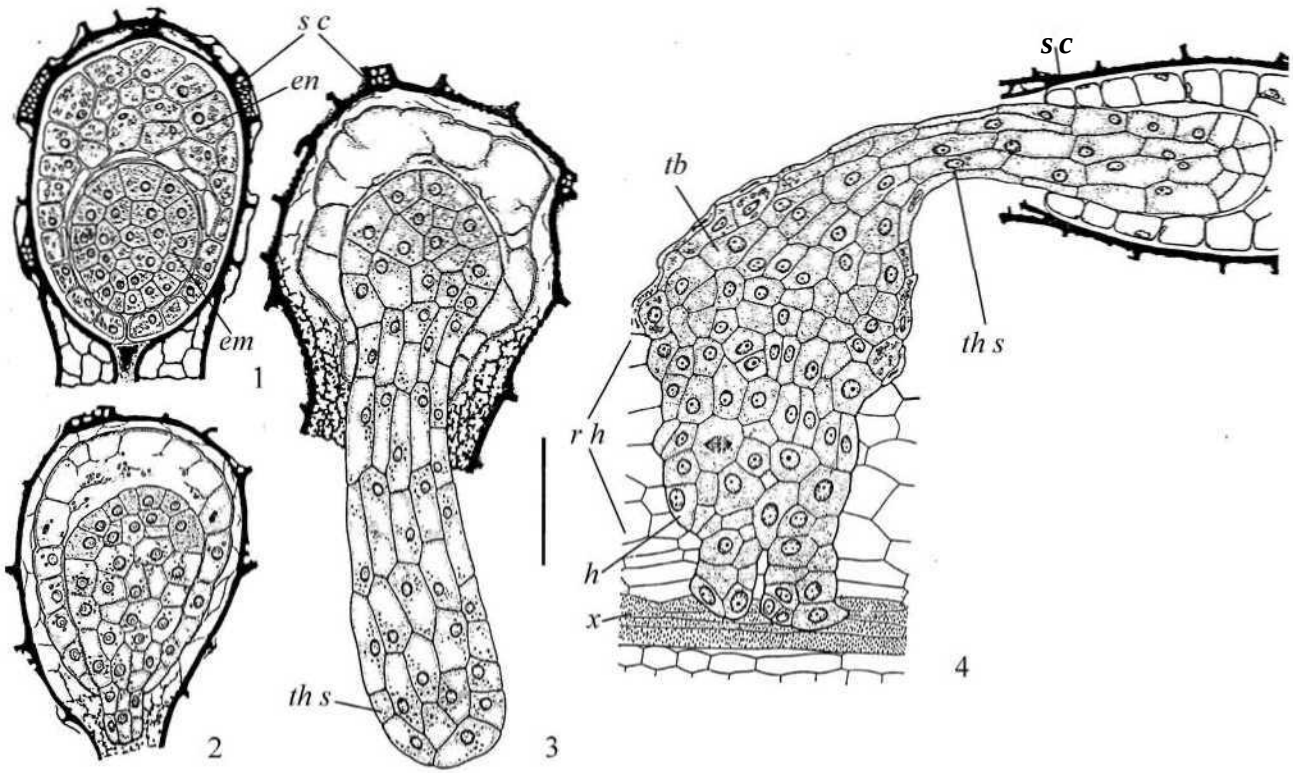


Fig. 9: Metamorphosis in development of seedling in *Orobanche crenata* (after Teryokhin, 1977).
1 — mature seed, 2 — the beginning of germination, 3 — thread-like seedling, 4 — the beginning of tubercle formation above the place penetration of seedling haustorium into host plant root;

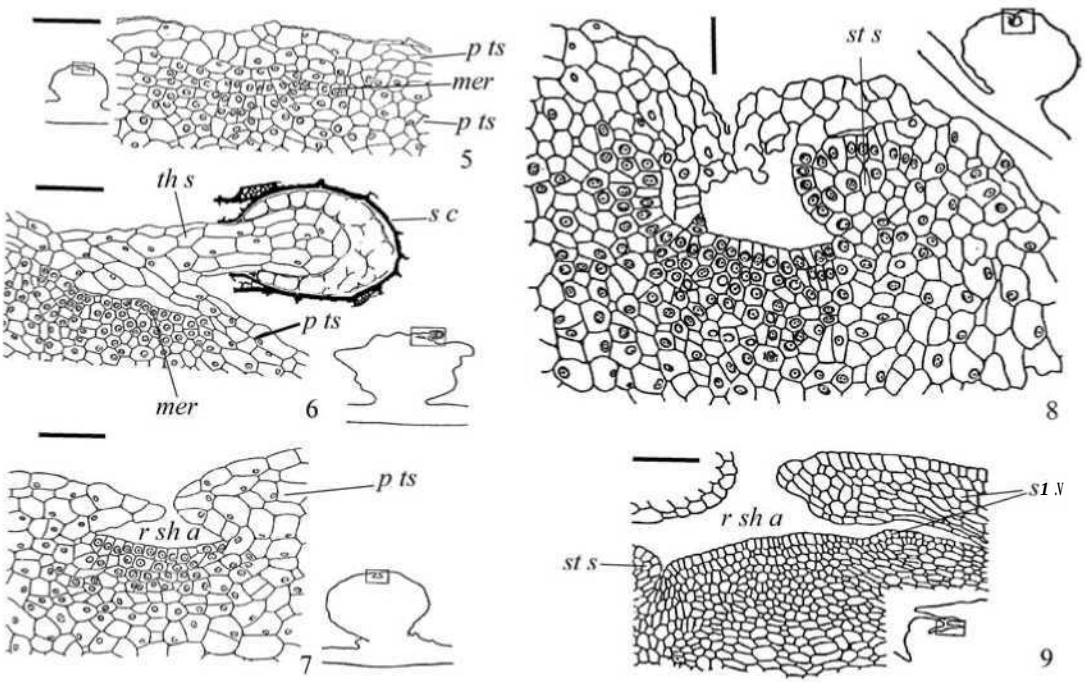


Fig. 9 (Confi.)

5—formation of meristem in tubercle parenchymal tissue, 6—formation of extracellular space between the shoot apex meristem and t
dying tissues of thread-like seedling, 7—further differentiation of reproductive shoot apex, 8, 9 — differentiation of the first stem scales
reproductive shoot apex; em —embryo, *en* — endosperm, *h*—haustorium, *mer*—meristem, *p ts*— parenchymal tissue dying, *r h*—root of h
plant, *r sha*—reproductive shoot apex, s c—seed coat, sfs —stem scale, *tb* — tubercle, *th s* — thread-like seedling, x — xylem of host root. Sca
1-7, 9-0.1 mm, 8-0.05 mm.

is typical for species of *Harveya* and *Hyobanche*. Embryo reduction in mature seeds in these plants is comparable with that in *Orobanche crenata* (Teryokhin, 1977). In highly specialized taxa of xenoparasitic plants with root parasitism, the adaptations connected with realization of metamorphosis result in fundamental changes of the whole developmental process of the parasitic sporophyte. In Fig. 8, the inner cycle indicates the development of slightly specialized "green" parasitic plant *Euphrasia* (Scrophulariaceae), and the outer one indicates the development of highly specialized, achlorophyllous plant *Orobanche* (Orobanchaceae).

Heretofore we have written about so-called xenoparasitic plants, when the parasite uses other flowering plants for its own nutrition. Another ecological group includes mycoparasitic (alleloparasitic) plants, companions in parasitic symbiosis of some groups of fungi forming mycorhiza (Raven *et ah,* 1986). Mycoparasitic plants exchange different metabolic substances with fungi. A number of taxa of monocots (Burmanniaceae, Corsiaceae, some genera of achlorophyllous Orchidaceae, e.g., *Epipogon* and *Corallorrhiza)* as well as of dicots (Ericaceae — subfamilies Monotropoideae and Pyroloideae) belong to highly specialized mycoparasitic plants. Of course, these plants have their own peculiarities of development, but the principal features of sporophyte metamorphosis are also inherent to them.

In members of some other, less specialized taxa or taxa with other modes of adaptation to parasitism (e.g., Cuscutaceae, Loranthaceae, Viscaceae), metamorphosis is not so profound as in the plants described above. It occupies a somewhat transitional position between metamorphosis of certain organs in autotrophic angiosperms and total metamorphosis in highly specialized parasitic flowering plants.

Seed propagation in most xenoparasitic and mycoparasitic plants is characterized by the great increase in r-strategy. Sometimes they produce an enormous quantity of very small seeds with reduced embryos. For example, in root xenoparasite *Aeginetia indica* (Orobanchaceae) up to 70,000 seeds are formed in each fruit (Kuijt, 1969). Pronounced r-strategy is typical also for mycoparasitic plants. In some members of Orchidaceae family (e.g. *Anguloa* and *Cattleya)* that do not even lose chlorophyll, one fruit produces up to four million extremely reduced seeds (Poddubnaya-Arnoldi, 1964a,b).

Metamorphosis in parasitic flowering plants testifies to the profound overall regularity in adaptive evolutionary modifications of plant life cycles and animal ontogenesis. Such modifications in plants as well as in animals are connected with the sharp change of life functions in the course of individual development.

Life Cycles

Life cycles of plants vary, above all, in the time and place of meiosis and in the degree of development and duration of diplophase and haplophase. Most green algae in their vegetative state are haploid, and it is only their zygote that is diploid (Volvocales, Chlorococcales, Conjugatophyceae). Meiosis occurs during the germination of zygote **(zygotic reduction** or **zygotic meiosis),** resulting in four haploid cells, which produce, through mitotic division, new haploid cells or a multicellular thallus, which eventually produces gametes.

In Diatomeae and in *Fucus,* thalluses are diploid and in their cells gametes are formed after the meiosis **(gametic reduction** or **gametic meiosis)** and then are joined to form a diploid zygote. The zygote germinates without meiotic division into a new diploid thallus.

These two types of life cycles exist only in lower plants (Algae) and have a lengthy haplophase, where meiosis is zygotic, and a lengthy diplophase where meiosis is gametic.

The third type of life cycle—with **sporic meiosis** or **sporic reduction—**is typical of plants with digenesis, whereby two generations (bionts) alternate: sporophyte (diplobiont) and gametophyte (haplobiont), which differ genetically and in the mode of reproduction. Sporophyte is a diploid asexual generation on which zoospores are formed in the cells of thallus (some Algae) or in zoosporangia, specialized organs of asexual reproduction (many Phaeophyta), or spores are formed in sporangia, as in all higher plants. Meiosis takes place before the spore formation in sporangium (sporic reduction), spores develop into gametophytes, multicellular haploid organisms. Gametophyte is a sexual generation in the life cycle; it produces gametes either in ordinary vegetative cells of the thallus (some Algae) or in specialized organs of sexual reproduction: gametangia, oogonia and anteridia (lower plants), archegonia and anteridia (higher plants, except Angiospermae). After the fusion of the gametes, a zygote is formed, which without meiosis germinates into a diploid sporophyte. Organs of sexual and asexual reproduction in lower plants are normally unicellular, except for Charophyta and many Phaeophyta, and in higher plants they are multicellular. Algae have various types of sexual process, and gametes are joined in water (isogamy, anisogamy, heterogamy), as in many green algae, or in oogonium (oogamy), as in Charophyta and many Phaeophyta. In higher plants the female gamete, the egg-cell, is always fixed, and the sexual generation, gametophyte, ensures the fertilization process.

In life cycles with digenesis, sporophyte and gametophyte may be identical both morphologically and in life duration. Such digenesis is called **isomorphous.** Where the sporophyte and gametophyte differ in form, structure and lifetime, digenesis is called **heteromorphous.**

In lower plants, digenesis may be both isomorphous and heteromorphous. In case of isomorphous digenesis in Algae, each of the generations is represented by an independently existing individual *(Ulva, Ectocarpus, Dictyota);* that is why two (if the gametophyte is bisexual) or three (if the gametophyte is diclinous) independent and identical plants are present in the life cycle.

Where digenesis is heteromorphous, the generations develop independently of each other (Laminariales, equisporous Lycopodiophyta, Equisetophyta, Pteridophyta), or one of the generations, unable to develop independently, exists at the expense of the other (Bryophyta and all ovulated plants), but only one of the generations, either sporophyte or gametophyte, is always dominant in the life cycle.

For example, in Laminariales life cycle, a large differentiated sporophyte with a lifetime of many years, which dominates, alternates with a microscopical filiform gametophyte (prothallium) having a lifetime of 1-4 months (Petrov, 1977).

In higher plants, digenesis is always heteromorphous. The gametophytic evolutionary line where gametophyte prevails in the life cycle is shown only in Bryophyta, in which the sporophyte (sporogonium) develops as a capsule with spores on the green moss plant, which is a gametophyte. In the gametophyte,

antheridia and archegonia are formed. Zygote is formed in the abdominal part of archegonium and germinates into a sporogonium consisting of a spore capsule and a stalk through which the sporogonium penetrates the body of gametophyte and receives nutrients from it. Spores develop inside the capsule, in the sporangium, as a result of sporic meiosis and germinate in soil into a protonemata, which further forms an adult moss plant (gametophyte). Thus, in Bryophyta, gametophytes are always independent as regards nutrition, whereas sporophytes are permanently attached to gametophytes and depend on these.

All other higher plants (Lycopodiophyta, Equisetophyta, Pteridophyta, and all seed plants) belong to the sporophyte line of evolution, an asexual generation, sporophyte being dominated in their life cycle. The sporophyte is a cormophyte, on which sporangia develop and spores are formed, whereas the gametophyte (prothallium) is less developed and short-lived. Thus, in equisporous Pteridophyta, Lycopodiophyta and Equisetophyta, gametophytes look like thalline plants (prothallia) not differentiated into organs, green or colourless (Lycopodiophyta) ranging in size from a few mm to 3 cm, with a lifetime of a few weeks (rarely years, as in Lycopodiophyta or Marattiopsida). In equisporous Pteridophyta, prothallia are bisexual. In heterosporous higher plants, including Gymnospermae and Angiospermae, gametophytes are heterosexual and develop out of micro- and megaspores.

Heterospory entails drastic reduction of prothallia. The gradual reduction of gametophyte is the main trend of the higher plant evolution and reveals itself in the succession Pteridophyta—Gymnospermatophyta—Angiospermatophyta (Komarnitsky *et al*, 1975).

Thus, in heterosporous Pteridophyta, Lycopodiophyta, and Equisetophyta, gametophytes develop without separating from micro- and megaspores, and often consist of 1-2 vegetative cells (e.g., male prothallia in *Selaginella, Salvinia)* or more (female prothallia of these).

In Gymnospermae and Angiospermae, both male and female gametophytes are still more reduced. The germination of the megaspore and formation of female prothallium, fertilization and development of a new sporophyte (embryo) always occur inside the megasporangium (nucellus) while the sporophyte is still on the mother plant. This shows that the female sexual generation of ovulated plants has become completely incapable of independent existence, and all its development occurs in the sporophyte inside the megasporangium.

In Gymnospermae, the female gametophyte is a multicellular haploid endosperm with two (in *Pinus)* or more (in other Gymnospermae) archegonia, also greatly simplified. The female gametophyte **(embryo sac)** in most angiospermous plants is normally reduced to seven cells and has no archegonia.

The male gametophyte in Gymnospermae and Angiospermae develops from the microspore and represents pollen grain, which subsequently germinates into a pollen tube. The pollen tube channels male gametes or sperm cells (which have lost mobility in most species of Gymnospermae and all species of Angiospermae) to female gametes (egg cells), which are contained in the female prothallium inside the megasporangium. The male sexual generation of seed plants has undergone a still greater reduction than the female. All the development of male gametophyte, for example in *Pinus,* including the formation of sperms, is confined to five mitotic

divisions, three of which occur inside the microsporangium (anther loculus) and the last two in the pollen tube.

In Angiospermae, the male gametophyte is extremely simplified (Takhtajan, 1980a,b), its development consisting of two mitotic divisions only. The first division occurs under the microspore envelope and the second either in the pollen grain (mature tricellular pollen, mainly in more advanced orders, including Asterales and Poales) or in the pollen tube (mature bicellular pollen, typical of many relatively primitive groups, including Magnoliales and Laurales).

PART TWO–POLLINATION AND BREEDING

POLLINATION SYSTEMS

Anthecology (Greek *anthos*—flower, *oikos*—house, dwelling, *logos*—doctrine) encompasses the study of flower and pollination ecology. The term was introduced by Robertson (1904). In educational and scientific literature, "biology of a flower" and "biology of a pollination" are widely used as synonyms. In our opinion (Ponomarev, 1970), they are ambiguous and should be replaced with the term "anthecology", which is brief and comprehensive, including ecology of a flower and ecology of pollination. In the literature these last two usually are considered identical (Kugler, 1955,1970; Faegri and van der Pijl, 1980).

The **ecology of a flower** (or traditionally biology of a flower) is understood to comprise various adaptations in a flower (morphological and physiological characters), promoting cross-pollination or self-pollination. The ecology of a flower in such a sense is limited to its morphology, considered to be part of the adaptive value of various structures to cross-pollination by different agents (e.g., insects, birds, wind) or to self-pollination. The ecology of a flower can be studied from positions of evolutionary morphology and phylogenetic systematics. It is impossible to judge modes of pollination from the appearance of flowers: the ecology of a flower cannot correspond to modern conditions of species dwelling and may even be in drastic contradiction with them. For example, despite entomophilous habit many plants of Faroes (Hagerup, 1951), polar tundras (Shamurin, 1958b), and taiga (Ponomarev and Vereshchagina, 1973) took up self-pollination because of lack of insect-pollinators. Numerous examples of discrepancy of morphology of flowers and their modes of pollination were described by Pervuchina (1970,1979).

The **ecology of pollination** is characterized by other approaches to a problem. It investigates dependence of pollination processes not only on the direct agents that carry them out, but also on many other indirectly working ecological factors. The latter can promote or, on the contrary, prevent pollination success. In anemophilous plants, for example, pollination depends on climatic and biotic conditions determining range of pollen dispersion (e.g., wind, temperature and relative humidity of air, rains, mass character of growth). In entomophilous plants, pollination depends not only on the presence and abundance of insect-pollinators, but also on landscape and biocenotic conditions as a whole (e.g., weather conditions, nesting stations, presence and abundance of competing plants). The pollination ecology should be studied in ecological-geographical and biocenotic aspects, in different biotic areas of the corresponding biogeocenosis. Similar observations have been carried out in different botanic-geographical areas in tundra zone (Shamurin, 1958b; Kajgorodova, 1976), taiga (Ponomarev and Vereshchagina, 1973), deciduous woods (Antonova, 1976), steppes (Ponomarev, 1954, 1960; Shamurin, 1958a; Ponomarev and Demyanova, 1978; Demyanova, 1981a,b), deserts of South-East Kazakhstan (Demyanova, 1970), and high mountains of Pamir (Novozhilova, 1982).

Now the term "anthecology" is used in a wider sense, including different aspects of reproductive systems, evolution and speciation, and ecosystem functioning (Baker, 1979).

Sexual Polymorphism (Greek *poly*—much, many, and *morpha—iorm)* refers to the differences in flowering plants connected with the sexual type of the flowers in one specimen or one population.

During the evolutionary process, certain morpho-physiological features have developed that are connected with the sexuality of the specimens. They contribute to the success of cross-pollination and expansion of the species areas.

Linnaeus (1735) distinguished four principal sexual forms: hermaphroditic, monoecious, dioecious and polygamous plants. Kerner von Marilaun (1898) picked out 15 sexual types of flowering plants. However, his classification did not receive further support, though it clearly demonstrated the diverse expression of sex in flowering plants. More detailed classifications of sexual types in angiosperms exist (Yampolsky and Yampolsky, 1922; Correns, 1928; Rosanova, 1935; Kozhin, 1941; Kordyum and Glushchenko, 1976).

Five principal sexual types of flowering plants are distinguished, and they are subdivided into several sexual forms (according to Demyanova's classification, 1990, with some alterations).

Type I. **Hermaphroditic plants** — the overwhelming majority of flowering plants with bisexual flowers; the mechanisms preventing autogamy are dichogamy or di- and tristyly.

Type II. **Monoecious plants** — Different sexual types of flowers are found in one specimen. The following sexual forms are distinguished:

1. Monoecious (in the full sense) — the staminal (male) and the pistillate (female) flowers develop on one specimen (Alismataceae, Araceae, Cyperaceae, Juglandaceae, Typhaceae);
2. Andromonoecious plants—bisexual and staminal flowers are situated on one specimen (Apiaceae, Poaceae, Ranunculaceae, Rosaceae);
3. Gynomonoecious plants—bisexual and pistillate flowers are situated on one specimen (Asteraceae, Caryophyllaceae, Chenopodiaceae);
4. Trimonoecious plants—bisexual, staminal and pistillate flowers develop on one specimen (Amaranthaceae, Cucurbitaceae, Polygonaceae).

Type III. **Dioecious plants—**bisexual and staminal flowers or bisexual and pistillate flowers, or staminal and pistillate flowers develop on different specimens. The following sexual forms are distinguished:

1. Dioecious (in the full sense) — some specimens form only pistillate flowers, others form only staminal flowers (Elaeagnaceae, Moraceae, Urticaceae);
2. Androdioecious—some specimens form bisexual flowers, while others form only staminal ones (Lardizabalaceae, Liliaceae, Ranunculaceae, Rosaceae);
3. Gynodioecious — some specimens form bisexual flowers and others form only pistillate flowers (Asteraceae, Campanulaceae, Dipsacaceae, Lamiaceae);
4. Polygamous-dioecious — some specimens form staminal and pistillate flowers, while others form bisexual flowers *(Rumex,* Polygonaceae).

Type IV. **Trioecious plants** — the different sexual types of flowers (bisexual, pistillate, staminal) and their combinations are expressed with three or more specimens*(Calligonum,*Polygonaceae).

Type V. **Polygamous-polyoecious plants—**bisexual flowers, unisexual flowers develop on different specimens (andromono- and androdioecious,

gynomono- and gynodioecious, trioecious) (Asteraceae, Cucurbitaceae, Dipsacaceae).

Sexuality in the flowering plants is distinctly enough correlated with the morphological features of the vegetative and reproductive spheres. The sexual forms of plants differ in their physiological and diurnal times and the continuity of blooming in the population. Thus, they can be regarded as different ecological races with the species. The unequal demands of the sexual forms of flowering plants to the conditions of the habitat decrease intraspecific competition and increase the viability of the species as a whole.

Monoecy (Greek *monos*—one, *oikos*—house) is the presence of unisexual flowers, female and male, on the same plant. The term was introduced by Linnaeus (1735).

Examples of monoecious plants can be representatives of Begoniaceae, Betulaceae, Casuarinaceae, Fagaceae, Juglandaceae, Lemnaceae, Palmae, Pandanaceae, Platanaceae, Sapindaceae, Sparganiaceae, Typhaceae and many others. Basically monoecious forms (with rare exception) are found in Achariaceae and Cucurbitaceae (Yampolsky and Yampolsky, 1922; Kordyum and Glushchenko, 1976).

According to the summary of Yampolsky and Yampolsky (1922), monoecious plants make up about 7% of world flora. In some investigated botanical-geographical areas the proportion of monoecious plants may be different. British flora, for example, contains 5.4-8.7% monoecious species (Lewis, 1942; McComb, 1966; Kay and Stevens, 1986), Southern Australian flora contains 3.1% (Parsons, 1958). About the same proportion of monoecious plants is found in flora of Western Australia (McComb, 1966). In tropical flora of Puerto Rico and the Virgin Islands (Flores and Schemske, 1984) and tropical deciduous woods of Mexico (Bullock, 1985), the share of monoecious species is much higher (10.5 and 12% respectively). Such a position is connected, probably, with wide wood spreading in tropical flora among which monoecy is widely distributed.

The presence of monoecy in different families that frequently are unrelated suggests independent origin of monoecy in different phyletic lines of angiosperms. Some authors hold that monoecy and dioecy are related. On the basis of the analysis of British flora, for example, Lewis (1942) concluded that dioecy could frequently, but not always, arise from monoecy.

Monoecy is more often peculiar to monocotyledonous than dicotyledonous plants (Yampolsky and Yampolsky, 1922; Daumann and Synek, 1968; Kugler, 1970; Daumann, 1972b). Apparently, isolation of sexes among monocotyledons comes to an end at the stage of monoecism, and among dicotyledons it goes further up to full dioecism (Monyushko, 1937; Williams, 1964).

Monoecy, as a rule, is connected with anemophily, for example, in monoecious species of families Cyperaceae, Chenopodiaceae, and also species of genera *Alnus*, *Betula*, *Carpinus*, *Fagus* **and** *Quercus* (Kerner, 1896,1898; Sporne, 1949; Meeuse, 1965; Daumann and Synek, 1968; Kugler, 1970; Faegri and van der Pijl, 1980). However, according to McComb (1966), 38% of non-hermaphrodite species (including monoecious and dioecious) are entomophilous.

According to modern representations, the display of attributes of a sex in plants is managed not only with genotype, but also with factors of an environment (Chailakhyan, 1947; Heslop-Harrison, 1957a,b, 1972; Williams, 1964; Chailakhyan and Khryanin, 1980,1982).

Ratio of flowers of different sexuality can vary in the course of ontogenesis in perennial monoecious plants. For example, on young plants of *Eucommia ulmoides*, *Diospyros kaki* and *Aleurites* sp., mainly male flowers are formed, and in mature plants more female flowers are formed (Minina, 1952). Proportions of male and female flowers can change during one season. In *Musa* spp. there is a transition from female flowers to male, and in *Ritinus communis*, as well as in *Cucumis sativus*, the opposite phenomenon is observed (Frankel and Galun, 1977). These authors came to the conclusion that ratio of flowers of different sexuality is not occasional and gradually changes in the course of ontogeny.

All of the above pertains to monoecious plants in the narrow sense of the word. Monoecious plants in a broader sense include all sexual forms that contain flowers of different sexuality (hermaphroditic and diclinous) within the limits of one plant (Correns, 1928; Rozanova, 1935; Monyushko, 1937; Kozhin, 1941; Kordyum and Glushchenko, 1976). According to such classification, besides monoecious forms, gynomonoecious, andromonoecious and trimonoecious species can be classified as monoecious plants.

An overwhelming majority of gynomonoecious species are found in Asteraceae, tribe Anthemideae (Poljakov, 1967). Here gynomonoecy is quite a steady systematic attribute. Quantitative ratios between hermaphroditic and pistillate flowers are stable within the limits of an inflorescence, genetically fixed and poorly subject to the influence of environment (Lloyd, 1972a, b). As a rule, pistillate flowers are on the periphery of the inflorescence, the centre of which is occupied with hermaphroditic flowers *(Achillea, Artemisia* (subgenus *Artemisia), Erigeron, Filago, Inula).* Parallel evolution of dioecy and monoecy from hermaphroditism appeared to take place in Asteraceae (Lewis, 1942; Poljakov, 1967). Monoecy occurred independently in different species of Asteraceae. Probably, gynomonoecy was also developed independently.

Andromonoecy is described in Chenopodiaceae, Fabaceae, Ranunculaceae and other families, but it is most widely distributed among Apiaceae and Poaceae (Knuth, 1898; Yampolsky and Yampolsky, 1922; Fryxell, 1957; Kordyum and Glushchenko, 1976). Male flowers are an additional source of pollen during cross-pollination. In the overwhelming majority of the andromonoecious species of grasses *Andropogon, Arrhenatherum, Hierochloe, Holcus, Panicum, Phragmites, Setaria* and *Sorghum,* proper sequence in flowering of hermaphroditic and male flowers was found (Ponomarev, 1964). As a rule, male flowers opened later than hermaphroditic flowers. The difference in time could reach 2-4 days. Dicliny and time break in flower opening of different sexuality promotes cross-pollination.

In Apiaceae, andromonoecy has long been known and is rather well investigated (Kerner, 1896, 1898; Knuth, 1898; Broak and Kho, 1958; Ponomarev, 1960, 1961; Kordyum, 1967; Tyurina, 1971, 1974; Singh and Ramanujam, 1973; Kordyum and Glushchenko, 1976). Localization of male flowers within the limits of a plant is subordinated to the law that the quantity of male flowers increases with rising of umbel order. Less often they are in umbels of all orders together with hermaphroditic flowers (e.g., in *Coriandrum sativum).* Male flowers preponderate over hermaphroditic in a quantitative ratio (Doust, 1980). The increase in quantity of male flowers, especially in umbels of higher orders, increases general pollen saturation in a population. Localization of male flowers is different in limits of umbellules in different plants: they can be marginal, median, or median and marginal or have other

position. The tendency to form male flowers is defined genetically, but it can be influenced by surrounding conditions (Broak and Kho, 1958; Singh and Ramanujam, 1973).

In umbelliferous plants, andromonoecy is accompanied by dichogamy in the protandry form, which is peculiar to some flowers and umbels, and it is frequent also in a plant as a whole (Beketov, 1889; Kerner, 1896,1898; Knuth, 1898; Ponomarev, 1960,1961). The flowering, passage and change of anther and stigma phases in all umbels of any order occur successively and repeatedly in each individual. Protandry covering all individuals ensures strict cross-pollination and completely excludes geitonogamy.

Trimonoecy was marked in Anacardiaceae, Apiaceae, Araliaceae, Chenopodiaceae, Fabaceae, Orchidaceae, Palmae and other families (Yampolsky and Yampolsky, 1922; Simonova, 1980). Sexuality is accompanied by a sharply expressed protandry in hermaphroditic flowers that even more actively promotes cross-pollination.

Not only dicliny but also other attributes of cross-pollination dichogamy (usually in the protogeny form, seldom as protandry) and self-incompatibility are peculiar to monoecy (in the broader sense of this term) (Fryxell, 1957; Nettancourt, 1977). At the same time, there are many apomictic forms among monoecious plants (Asteraceae and Poaceae-Khokhlov, 1967; Khokhlov *et ah*, 1978). The totality of different life strategies promotes the occurrence of monoecy among angiosperms.

Gynodioecy (Greek *gyne*—woman, *di*—double, twice, *oikos*—house) is the phenomenon in which the population of one species consists of individuals with hermaphroditic flowers and those with functionally pistillate (androsterilious) flowers (Fig. 10). The term was offered by Darwin (1877), who wrote the morphological description on the example of the Asteraceae, Boraginaceae, Dipsacaceae, Lamiaceae and Plantaginaceae representatives.

Features of androsterilious flowers, according to Darwin, are a reduction of androecium, full sterility of pollen, and reduction of the perianth sizes (especially a corolla) in comparison with hermaphroditic flowers. Darwin connected the development of gynodioecy as sexual form with the increased seed productivity of female forms. He discovered individuals with flowers of transitive type alongside hermaphroditic and female plants among gynodioecious species, which indicates the origin of female individuals from hermaphroditic by means of reduction of androecium. Together with the different level of androecium degeneration, anthers of such flowers contain a small amount of fertile pollen. Grosset (1974) categorized half-sterile individuals of gynodioecious species as intersex.

Darwin (1877) considered the smaller perianth to be an important phenotypic attribute of female dioecy. However, morphological distinctions of sexual forms are not expressed quite clearly in all families. For example, some representatives of the Campanulaceae *(Campanula bononiensis, C. wolgensis)* and Scrophulariaceae *(Pedicularis kaufmannii, P. dasystachys)* have considerably varying sizes of perianth and it is difficult to judge an accessory of a flower as indicating a certain sexual form by appearances (Demyanova and Titova, 1981). Only by viewing a large amount of material and processing it manually can we reliably judge the large sizes of hermaphroditic flowers in comparison with female flowers. Half-sterile flowers occupy the intermediate position between hermaphroditic and pistillate flowers.

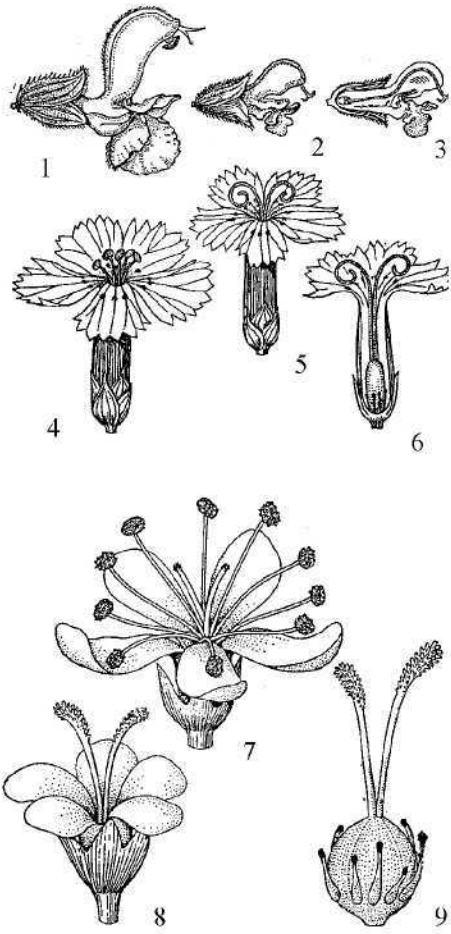


Fig. 10: Gynodioecy (after Ponomarev and Demyanova, 1980).
1-6—*Salvia stepposa* (1-3) and *Dianthus versicolor* (4-6): 1, 4—bisexual flower, 2, 5—female flower, 3, 6—the same flower in longitudinal section, reduced stamens are seen, 7-9—*Gypsophilla altissima: 7*—bisexual functionally male flower, 8—functionally female flower, 9—the same flower without perianth, reduced stamens are seen.

According to the hypotheses of Baker (1957) and Plack (1957), the hormones allocated by stamens influence the perianth sizes of female forms. The reduction of anthers and the pollen, which takes place at the early stages, has a more pernicious effect than their degeneration during a later period. In androsterilious flowers, the reduction of male sphere is not connected in any way with reduction of the female sphere, which Darwin (1877) specified. The better-expressed receptive surface of stigmata of the pistillate flowers, marked among gynodioecious species (Eleuterius and McDaniel, 1974; Demyanova and Pokataeva, 1977), should be considered the adaptation of female forms to cross-pollination, unique and inevitable.

After Darwin's work (1877), the list of gynodioecious species has considerably lengthened (Mailer, 1881; Knuth, 1898; Yampolsky and Yampolsky, 1922; Khokhlov, 1968; Ponomarev and Demyanova, 1975; Demyanova, 1985). The last list is the longest: it includes 613 species from 185 genera, which pertain to 52 families of flowering plants from different floristic areas of the world. The results of analysis suggest that gynodioecy probably had an independent origin in the evolution of angiosperms: it is found in different orders and families, and frequently they are not connected with each other in a phylogenetic way. The greatest number of species is noted in subclasses Caryophyllidae, Caryophyllaceae and Lamiidae, Lamiaceae. Gynodioecy is frequent among Apiaceae, Boraginaceae, Dipsacaceae, Geraniaceae and Plantaginaceae. The overwhelming majority of them occupy the upper position in the phylogenetic system (Takhtajan, 1980a,b) and are characterized by three-cell mature pollen. In families in which two- and three-cell mature pollen are found, gynodioecy as a rule is associated with species having three-cell pollen and is absent or extremely rare in the species with bicellular pollen. An especially precise interrelation is traced in Lamiaceae (Demyanova, 1981b), where gynodioecy was found in species with three-cell pollen (in *Glechoma, Origanum, Salvia, Thymus* and other genera) and it is not found in species with bicellular pollen *(Ajuga, Galeopsis, Leonurus, Phlomis* and other genera). Such correlation between gynodioecy and mature three-cell pollen is probably connected with the necessity and inevitability of cross-pollination in female forms. In this respect, three-cell pollen has certain advantages over two-cell pollen (Hoekstra, 1973; Hoekstra and Bruinsma, 1978).

Gynodioecy is mainly common among perennial forms and it is rare among annuals and biennials. Only family Caryophyllaceae represents an exception, because female dioecy is often marked in annuals too *(Dianthus, Silene).* However, in this case also, in natural populations of such plants the share of female individuals is rather insignificant. Gynodioecy is seen much more often among entomophilous plants than in anemophilous plants.

Female dioecy can be found in combination with other sexual forms: andromonoecy (a combination of hermaphroditic and male flowers in a single individual) among umbellates (Knuth, 1898; Ponomarev, 1961; Webb, 1979; Tyurina, 1987) or gynomonoecy (a combination of hermaphroditic and pistillate flowers in a single individual) among Asteraceae, Lamiaceae, Polemoniaceae, Valerianaceae, etc. In some gynodioecious species, gynomonoecious individuals are seen even more often than female *(Dracocephalum thymiflorum, Polemonium caeruleum, Silene noctiflora, Stellaria nemorum, Valeriana rossica, V. tuberosa).*

The proportion of female individuals in a population of gynodioecious plants changes in different species over a very wide range (from tenths of one per cent up to 60% and more), but in each species it is certain and usually steady on a significant extent of taxon areas (Ponomarev and Demyanova, 1975; Demyanova and Ponomarev, 1979; Demyanova, 1981a,b, 1988,1997).

Interpretation of sex ratio among gynodioecious species is extremely complicated without full data on genetics, including data concerning inheritance of a sex. Only for a few investigated species have both cytoplasmatic conditionality of female dioecy (Correns, 1928; Simmonds, 1971) and nuclear character of sex inheritance (Lewis and Crowe, 1956) been proved. In gynodioecious grass *Cortaderia richardii,* male sterility is inherited as ordinary recessive (Connor, 1965). Thus, the character of male sterility inheritance in gynodioecious species is various and can be

unequal within a family and even within a genus, for example, *Salvia* (Linnert, 1955, 1958). Krupnov (1973) considers gynodioecy to be a special case of male sterility.

There is no doubt that pistillate flowers do originate from hermaphroditic flowers in evolution. Cytoembryological researches have shown that pistillate flowers start out as hermaphroditic. Furthermore, the whole scale of deviations from normal current of embryological processes at different stages of androecium formation is observed within the limits of a single plant. Attributes of degeneration can be found at stages of archesporial cells, microsporocytes, microspores and pollen grains. At the prophase I meiosis, cytomixis is noted quite often in potentially pistillate flowers (Vereshchagina and Malanina, 1974; Demyanova and Pokataeva, 1977; Demyanova, 1978). Numerous examples of various anomalies in a microsporogenesis in female forms of gynodioecious species are reported by Kordyum and Glushchenko (1976).

Gynodioecy is frequently considered to be the intermediate stage between hermaphroditism and true dioecy (Monyushko, 1937; McComb, 1966; Ross, 1970). This idea was first stated by Darwin (1877). Cases in which dioecy developed through gynodioecy were noted in *Pimelea* (Thymelaeaceae) (Burrows, 1960; Carlquist, 1966), *Braussaisia arguta* (Saxifragaceae) and *Gouldia* sp. (Rubiaceae). Other authors, on the contrary, consider that gynodioecy, being a steady sexual form with a well-balanced system of crossing, does not tend toward true dioecy (Lewis, 1942; McComb, 1966).

The wide distribution of gynodioecy among flowering plants is probably connected with the opportunity for successful combination of cross-pollination (in hermaphroditic and female individuals) and self-pollination (in hermaphroditic individuals). In female plants, cross-pollination serves as the only mode of pollination, which considerably strengthens hybridization processes, frequently "washing away" barriers between related species. Female dioecy *(Thymus, Mentha)* has an essential influence on intra- and interpopulational variability of species.

Heterostyly (Greek *heteros*—different and *stylos*—style) is the condition of having styles of different lengths relative to the stamens in different individual plants (Fig. 11). The term was introduced by Persoon (1794, cit. after Schneider, 1905).

There are two types of heterostyly: **dimorphic** (heterodistyly) and **trimorphic** (heterotristyly).

Dimorphic heterostyly is the existence of two types of flowers, long-styled and short-styled, in the same species (e.g., in *Fagopyrum, Linum, Primula).* Stamens in long-styled flowers of *Primula* are located in the depth of the corolla, whereas in short-styled flowers they are at the top. Classical dimorphic heterostyly was described for Boraginaceae, Caesalpiniaceae, Capparidaceae, Commelinaceae, Gentianaceae, Iridaceae, Oleaceae, Oxalidaceae, Plumbaginaceae, Polygonaceae, Primulaceae, Rubiaceae, Turneraceae and Verbenaceae (Vogel, 1955; Vuilleumier, 1967). Heterostylous plant forms show additional differences. Short-styled flowers in comparison with long-styled ones have a larger pollen and smaller stigmatic papillae. The more general term "heteromorphy" would therefore be more appropriate. Self-pollination and cross-pollination between individuals of the same morphological type result in the tiny quantity of seeds (self-incompatibility), whereas pollen transfer between plants with different style length is very effective.

Trimorphic heterostyly is the existence of three flower types in the same species: long-, medium- and short-styled.This form of heterostyly was found in species from

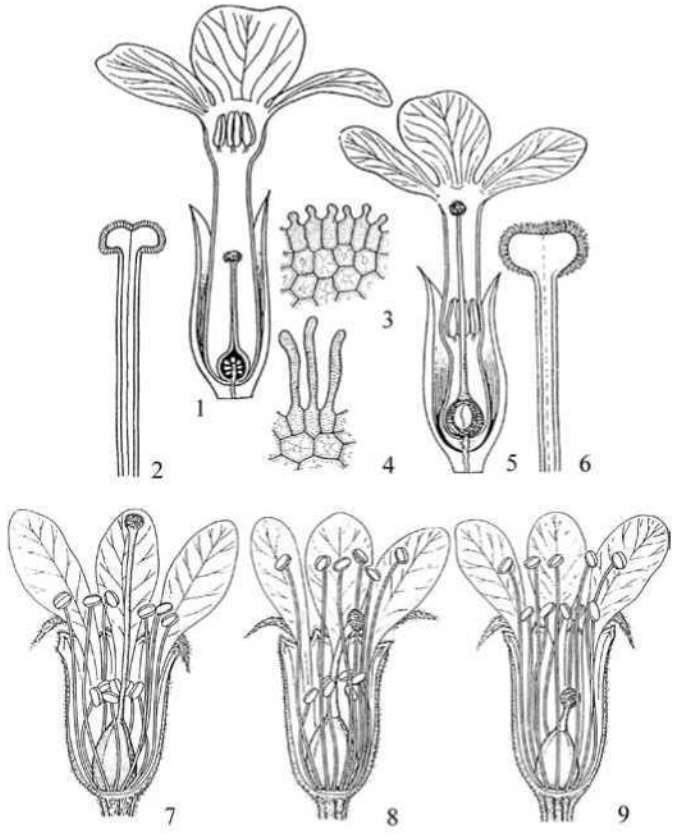


Fig. 11: Heterostyly (after Ponomarev and Demyanova, 1980).
1-6—heterodistyly in *Primula* sp. (1-3—short-styled and 4-6—long-styled types): 1, 5—flower, longitudinal section, 2, 6—style with papilliform surface of stigma, 3, 4—stigma surface (increased); 7-9—heterotristyly in *Lythrum salicaria:* long-styled (7), middle-styled (8) and short-styled (9) types of flowers.

Linaceae, Lythraceae (e.g., *Lythrum salicaria),* Oxalidaceae and Pontederiaceae (Baker, 1962). Fertilization turns out to be very effective when the stigma of each flower type is pollinated by pollen originating from stamens of corresponding length from two other flower types.

Heterostyly may be considered a structural-functional mechanism, which interdicts autogamy and promotes xenogamy. Pollination occurs in case the stigma and anthers are in the same position, e.g., short style and low anthers (from a long-styled flower). Such pollination is legitimate and it is always cross-pollination (Levin, 1968; Mulcahy and Caporello, 1970). Heterostyly is followed by self-incompatibility (Ornduff, 1970; see Self-incompatibility: Structural-functional Aspects, Vol. 2).

Heterostyly appears to contribute to speciation. Levin and Berube (1973) have described two species of *Phlox,* which were characterized by different types of heterostyly. According to Baker (1960), heterostyly is one source of emergence of

unisexual plant in *Mussaenda* species. This proposal, made first by Darwin, explains how dioecy could arise in groups and inbreeding prevented by various mechanisms, e.g., in *Nymphoides* (Ornduff, 1966). Baker (1960) suggested the following sequence of heterostyly emergence for Plumbaginaceae: incompatibility leading to pollen dimorphism, then to stigma dimorphism and heterostyly.

Dichogamy (Greek *diche*—separate and gamos — marriage) is the condition in which anthers and stigmata in the individual flower mature at different times (Figs. 12 and 13). The term was introduced by Sprengel (1793, cit. after Schneider, 1905).

Dichogamy includes two forms: **protandry** and **protogyny** (Hildebrand, 1867). Protandry occurs where anthers dehisce and shed their pollen at a time when the stigma is not receptive. The cases when anthers shed before the stigma becomes receptive were observed in *Saxifraga* and *Impatiens.* If stigma ripens before pollen is liberated, this is protogyny.

The flowers occur in male and female phases in turn. This is regarded as an adaptation to cross-pollination. Dichogamy, however, does not exclude self-pollination. Sometimes autogamy may occur at the end of anthesis when the anthers and stigmata ripen simultaneously. Self-pollination in dichogamous plants is also possible if the numerous flowers on the same plant are at different developmental stages. A combination of cross-pollination and self-pollination played a positive role in evolution.

Protandry happens more often than protogyny and more closely corresponds to the normal sequence of development of the flower appendages. This type of dichogamy was found in many representatives of Asteraceae, Campanulaceae, Caryophyllaceae, Fabaceae, Lamiaceae, Malvaceae and Ranunculaceae.

For example, in Campanulaceae, anthers dehisce when in the bud. Pollen is shed on the upper part of the style and on the outer surface of firmly closed lobes of the stigma, holding on to it by short unicellular hairs.

After that the corolla opens and all the stamens and the bases of staminal filaments become dry and twisted, forming a highly coloured nectary accessible to insects. For some time the style only serves as pollen supply to the pollinators, which inevitably touch the style hairs covered with pollen and direct them to the nectarous disc. The flower passes into the female phase after the pollen is collected by insects. The stigma lobes (three to seven usually) begin to open and twist their own inner surface to the style. Now that the stigma is receptive, the pollinator visiting the flowers in one way or another touches the papillae of the stigma and then pollination occurs. Many investigators suppose that self-pollination is possible if pollen remains on the style. Self-pollination may occur also in species with pendant blossoms, if pollen remaining on the style hits the turned-back lobes of the stigma (Zhinkina, 1995).

Flowers of *Silene multiflora* and *S. chlorantha* open in the evening and are in the male phase. The next morning flowers are closed, and stamen wither. The third day only stigma move forward. Thus, autogamy is excluded.

In species from Apiaceae, protandry is typical and embraces not the only the individual compound umbels, but the whole plant. It is due to the strict order of priority in blossoming of different umbels and its full synchronization in umbels of the same order. In consequence of which flowers of the individual plant are now in male, now in female phase (e.g. in *Libanotis intermedia).*

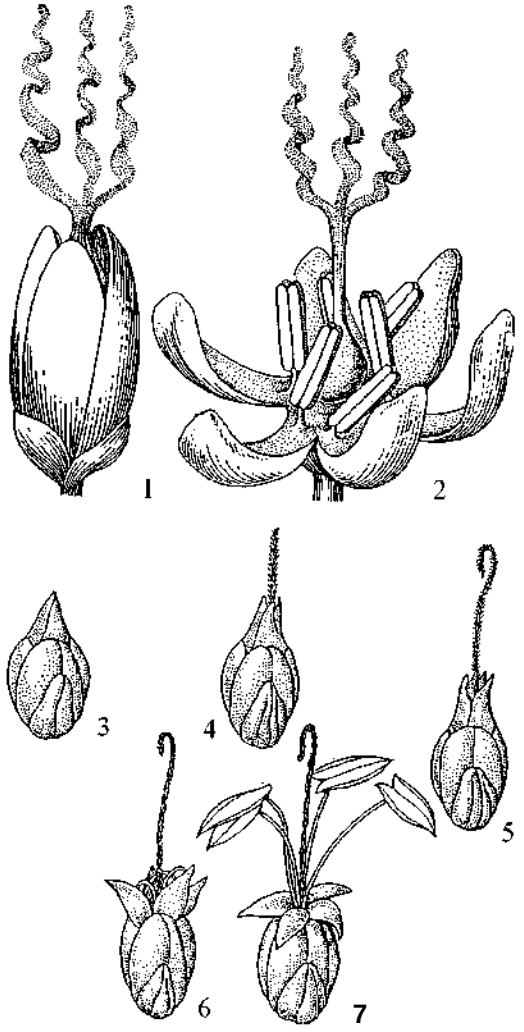


Fig. 12: Protogyny (after Ponomarev and Demyanova, 1980).
1,2—*Juncus gerardii:* 1 — flower at the female phase, in the evening, 2 — open flower at the moment of pollination; *3-7—Plantago cornutii:* 3—flower bud, 4—stigma emergence, 5—stigma wilting, 6 —flower opening and stamen moving forward, 7—flower in the male phase.

Such protandry with repeated alternation of male and female phases is called Libanotis type. Another type of protandry, Peucedanum type, occurs very seldom. It is characterized by a single change of phases, occurring simultaneously in all flowering umbels of the individual plant regardless of the order to which they belong. This type of protandry was only described in *Peucedanum lubimenkoanum* (Ponomarev and Demyanova, 1980). Clear protandry in the same inflorescence, and synchronous

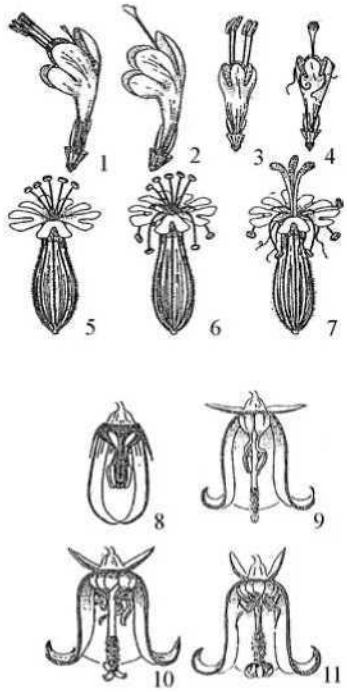


Fig. 13: Protandry.
1-4—*Scabiosa ochroleuca:* 1—marginal flower in the male phase, 2—the same flower in the female phase, 3—middle flower in the male phase, 4—the same flower in the female phase; 5-7—*Silene dichotoma: 5*—flower in the male phase, the first day of anthesis, 6—the same flower in the male phase, the second day of anthesis, 7—the same flower in the female phase, the third day of anthesis (all stamens wilted); 8-11—*Campanula* species: 8—flower bud, anthers forming the tube around the style dehisce and shed pollen on the style, 9—early anthesis, the style elongates and stamen filaments curve and touch the surface of style by the anthers, the lobes of stigma are still closed, 10—middle anthesis, anthers shed pollen, become dry and curve remaining in the depth of flower, the lobes of stigmata open and stigmata become receptive, 11—late anthesis, the lobes of stigma continue to grow, then curve and contact the pollen left in the upper part of the indumentum of the style.
1-7—after Ponomarev and Demyanova, 1980; 8-11—after Faegri and van der Pijl, 1980.

or non-synchronous change of flowering phases in inflorescences of different orders, are characteristic of *Knautia arvensis* and *Scabiosa ochroleuca*, Dipsacaceae (Kamelina, 1981).

The phenomenon of protogyny is characteristic of the Berberidaceae, Brassicaceae, Caprifoliaceae, Caricaceae, Poaceae, Juncaceae, Rosaceae and Thymelaeaceae. In species of Parietaria (Urticaceae) and in the Annonaceae, the styles are found to shed before anther dehiscence. In trap flowers (e.g., in Calycanthaceae), protogyny is one of the main signs of the pollination syndrome (Faegri and van der Pijl, 1980). Protogyny is more expressed in wind-pollinated plants both bisexual and

monoecious, and dioecious (Cariaceae, Poaceae, Chenopodiaceae—*Artemisia*, Plantaginaceae—*Plantago).* The role of protogyny in these cases is that the stigma exposure beforehand is favourable to fast wind pollination during the short diurnal periods of pollen shedding.

Sometimes dichogamy is partial, i.e., the stigma matures before the anthers cease to function.

Dichogamy has an adaptive character. Protogyny is a more effective mechanism for preventing autogamy than protandry. For effective protandry all the self-pollen should be swept out of the flower before the stigma is receptive. Only then is the possibility of contamination with self-pollen eliminated.

Functions of presentation and reception of pollen in the individual blossom may be separated not only in time, but also in space (herkogamy). For example, in *Plantago major* the style projects from a closed corolla; the corolla opens only later and then the stamens develop (Faegri and van der Pijl, 1980).

The pollinators first visit flowers in female phase with receptive stigma and will only later be covered by pollen from younger, higher flowers in male phase with open anthers. In the tropics the fact that some plants are always in the male stage and others in the female stage *(Persea*—Stout, 1926; *Nephelium*—Khan, 1929) may produce a second-order dioecy.

Population Aspects of Sex Determination

Examination of the most important problems of sex determination at population and species levels reflects the aspiration of investigators to comprehend different aspects of the reproductive cycle and to estimate the efficiency of various models of sexuality from the position of reproductive strategy. The terminology connected with these problems is always being revised. Initial notions such as sex differentiation or sexualization, sex determination and sexual polymorphism were created at the organism level of research and then adapted to the population level. A number of new terms are connected with different investigation aspects, certain concepts and methods, and elaboration of relative exponents of sex estimation.

Sex determination is the combination of genetic, cytoembryological, physiological-biochemical and other mechanisms promoting the formation of primary and secondary sexual features. We suggest referring to populational mechanisms taken as a whole and responsible for sexual state of population as **sex determination of population.**

Sexual differentiation or sexualization is the total combination of sexual distinctions at different levels of biological system organization as a consequence of sex determination mechanisms. Levina (1979,1981) gave the clearest indication of this notion.

Sexual polymorphism is traditionally defined as simultaneous occurrence of two or more sexual types of individuals in the population, differing by a combination of morphological features (dimorphism is a particular case of polymorphism). In flowering plants, it is usually realized in the reproductive sphere only: structure of flowers, linear dimensions of flowers and inflorescences. Sexual polymorphism in vegetative sphere is feebly marked and scantily studied. In population investigations it is revealed only statistically at the level of reliability of differences in feature

average index. Meagher (1984) includes in the indication of sexual dimorphism not only morphological but also ecological and behavioural features, life cycle, and distribution of resources between sexes. The author suggests the occurrence of genetic and ecological mechanisms in populations limiting further increase in sexual dimorphism that provides sufficient ecological communication of sexes and efficient seed propagation. Various mechanisms of evolutionary establishment of sexual dimorphism are under discussion: advantages of cross-pollination, sexual selection, divergence on the basis of disrupted selection, independent influence of selection on male and female individuals (Bawa, 1980,1984; Willson, 1982; Baker, 1984; Meagher, 1984; Sun and Genders, 1986; Sakai *et al,* 1997).

For the characteristics of sexual polymorphism at population level, Sidorsky (1991) suggested the terms **"sexual type of population"** and **"sexual organization of population".** He distinguishes sexual types of populations by the presence and combinations of flower sexual forms and he understands sexual organization as the division of populations into subsystems depending on the number of individual sexual groups. From the 1970s to the 1990s, the elaboration of the system approach to the study of seed propagation gave rise to the use of the term **"system of reproduction"** (e.g., hermaphroditic, dioecious, monoecious) (Lloyd, 1972a,b; Willson, 1982; Anderson and Stebbins, 1985; Sutherland, 1986a).

Sexual structure is one of the basic characteristics of dioecious populations. Initially this notion was identified as numerical ratio of different sexual types of individuals within the population (Demyanova and Ponomarev, 1979) and later it was extended up to the limits of species (Demyanova, 1987). Attempts are being made to discover the relation between sexual structure and main characteristics of a population (size, density, age spectrum, vitality) (Dommee *et al,* 1978; Antonova, 1988; Escarré *et al,* 1987; Lebedev, 1989; Zimmermann, 1989; Ackerly and Jasienski, 1990; Delph, 1990; Korpelainen, 1992; Klinkhamer *et al,* 1993). The lability of sexual state and its adaptive significance and the influence of ecological factors on the process of sex determination by the degree of tolerance of individual sexual types in conditions of ecological stress are also widely discussed (Volkovich, 1972; Freeman *et al,* 1980,1984a,b; Vereshchagina, 1980; Conn and Blum, 1981a,b; Doust and Cavers, 1982; Demyanova, 1981a,b, 1985,1987,1996; Freeman and McArthur, 1984; Lebedev, 1989; Zimmermann, 1989; Delph, 1990; Sakai and Weller, 1991; Schlessman, 1991; Starshova, 1993; Starshova and Barannikova, 1998).

A great number of monoecious, dioecious and subdioecious species are characterized by the alteration of sexual status as a response to environmental changes as well as in accordance with dimensions and age of individuals (Freeman *et al,* 1980; Day and Aarssen, 1997). The authors explain this by the capacity of plants to redistribute resources between male and female functions and mention the tendency toward increase in the former in conditions of ecological stress.

There are several hypotheses concerning determination of population sexual structure and estimation of adaptive significance of sexual polymorphism. According to the hypothesis of **"ecological niches",** worked out by Sheremetyev (1983) to prove the adaptive significance of sexual differentiation in flowering plants, the advantage of sexual polymorphism is connected not only with outbreeding, but also with the reduction of intraspecific competition owing to accommodation of sexes in various ecological niches, which enhances overall species adaptivity. This hypothesis is based on the analysis of different response of sexes to ecological factors. It corresponds to

the common notion of "ecological niche" adopted in geobotany. Baker (1984) and Meagher (1984) take similar positions. Some authors consider this hypothesis to be insufficiently grounded, giving more significance to the space distribution of sexes because of peculiarities of their reproductive biology (Bierzychudek and Eckhart, 1988).

The hypothesis of **"mosaic"** in distribution of sexual types in a population (Brockmann and Bosquet, 1978; Demyanova and Ponomarev, 1979) was suggested for gynoecious species. It is closely allied to the hypothesis of "ecological niches".

The hypothesis of regulation of population sexual structure by a **negative feedback mechanism** is well known (Geodakyan and Kosobutsky, 1967; Geodakyan, 1977,1978). The principal conclusion of the hypothesis concerns the great phenotypic dispersion of the male sex and conservatism of the female sex. The female sex transfers "old" (hereditary) information from one generation to another more effectively, the male sex transfers "new" (ecological) information. Secondary correlation of sexes (the number of viable seedlings) is variable and depends on the tertiary correlation (correlation of different types of individuals in generative state). When there is a deviation from optimum in the tertiary sex correlation the feedback is realized through the number of pollen grains reaching the stigma and bearing information on abundance of male plants. With a large quantity of pollen grains pollen with female potency is realized; with a small quantity, pollen with male potency is realized. But this hypothesis is acceptable only with a number of limitations: true dioecy with strict genetic control for sex exhibition, definite age (annual plant) and lack of vegetative propagation.

Kozhin (1941) propounded a concept based on the **notion that sex in plants is a quantitative phenomenon.** His main point is that, within the population of dioecious and monoecious species, different manifestation of male and female functions takes place; the populations are characterized by many quantitative modifications of phenotypic sex display. He considers the expression of sex in flowering plants to be a result of realization of the genetic mechanism and the influence of general metabolism and environment. For the last two decades this concept has been successfully elaborated (Lloyd, 1972a,b, 1980a,c; Cruden, 1976a,b, 1977; Horovitz, 1978; Bertin, 1982; Doust and Doust, 1983; Bawa, 1984; Freeman *et al*, 1984; Lloyd and Bawa, 1984; McKone and Tonkyn, 1986; Preston, 1986; Robbins and Travis, 1986; Sun and Ganders, 1986; Sutherland, 1986a,b; Campbell, 1989).

The **ratio of pollen production and ovules** was suggested as an ideal estimation of male and female functions (see Pollen-ovule ratios in different breeding systems). This index is widely used for the analysis of intrapopulation and interpopulation variability and to compare different systems of seed reproduction (Cruden, 1976a,b, 1977).

Willson (1979,1982,1991) substantiated the hypothesis of **sexual selection** for hermaphroditic populations, according to which competition between individuals for "the right" to carry out pollen and for "the right" to obtain it is thought to create the correlation between male and female functions.

The **sexual specialization of teleianthous flower** is an advantage for its function as donor or acceptor of pollen. There are individual groups in a hermaphroditic population corresponding to this specialization (Willson, 1982; Ellstrand and Marshall, 1986; Robbins and Travis, 1986; Brunet and Charlesworth, 1995). The statement that male function dominates in teleianthous flower is closely connected

with the hypothesis of sexual selection (Sutherland and Delph, 1984). Experiments confirm that evolution of attractants depends on carrying out of pollination, i.e., on male reproductive success (Stanton *et ah,* 1986; Stanton and Preston, 1988; Mitchell, 1993). Female reproductive success (production of ovules and seeds) increases chiefly because of biomass accumulation. In spite of individual variability in pubescent population the male and female functions are in general manifested identically. Because of variation of male function in teleianthous flower the phenomenon of particular androsterility realized structurally and functionally is of interest (e.g., in Caryophyllaceae—Starshova, 1966; Demyanova, 1982).

Floral ratio of sexes is one more index for estimation of male and female functions of populations. It is calculated as the ratio of flowers that are pollen donors to those that are acceptors, taking into account sexual flower forms as well as male and female reproductive spheres of teleianthous flower (Sutherland, 1986a,b). On the example of the analysis of four reproductive systems (hermaphroditic compatible, andromonoecious, androecious and dioecious) the floral ratio of sexes is considered to have shifted towards greater efficiency of male function. The **floral ratio** should be understood as proportions of flowers of different sexual forms (Starshova, 1993); the participation of all potential pollen donors and acceptors in the pollination process is better referred to as **pollination potential.**

With the transition to the concept of quantitative sex exhibition, the notion of **"gender"** was established, which could be interpreted as the degree of **sex expression** (Lloyd, 1972a,b, 1980a-c; Lloyd and Bawa, 1984; McKone and Tonkyn, 1986; Robbins and Travis, 1986). This term comprehends besides gamete production the actual reproductive success, i.e., genetic contribution to fertilization, seed production, their dispersal and viability of progeny up to sexual maturation. This is the principal notion in the concept. The quantitative method to determine the degree of sex expression was elaborated and two more basic notions, **"phenotypical gender"** and **"functional gender",** were suggested (Lloyd, 1972a,b, 1980a-c; Lloyd and Bawa, 1984).

Phenotypical gender is the enclosure of parental resources in the production of pollen grains and ovules at the moment of pollination, or energy consumption on sexual strategy. Phenotypical gender is measured from the ratio of male and female flowers, pollen grains and ovules or proportions by weight of reproductive resources that were enclosed by paternal and maternal functions to pollen and seed production. Phenotypical gender individuals in population can vary. In monoecious species *Ambrosia artemisifolia,* it varies from purely female to almost male individuals (McKone and Tonkyn, 1986). Lloyd and some other authors refer to the scope of variation of individual phenotypical gender compared with the average for the population as **"sex expression in populations".** In six species *oiAtriplex,* the leading role of sex variability in determination of sex ratio in natural populations was shown (Freeman and Me Arthur, 1984).

Functional gender is the real genetic contribution of parents to progeny through the male and female functions from pollination up to mature progeny (the result of sexual strategy). It reflects genetic contribution of parents to tertiary correlation of sexes. Particular individuals are not similar as pollen donors, producers of seeds and of viable progeny.

The average expression of phenotypic and functional gender in a population is 0.5, irrespective of population sexual type, cross system and absolute quantity of

resources put into male and female functions. Phenotypical and functional genders are closely connected but not identical. The second index is more mobile, as the environment is varying: there are different chances for pollen grains and ovules during pollination and fertilization processes, drift of pollen and seeds from other sources, viability of seeds and competitive capacity of seedlings. Owing to this, Lloyd and Bawa, while analysing modifications of gender, base their observations on phenotypical sex.

Quantitative approach is productive for the research of process of sex determination with different cross systems in evolutionary, taxonomic and ecological aspects as well as for revealing the importance of sexualization in reproductive biology of species.

Modes of Pollen Transfer and Pollinating Agents

The main pollination type in flowering plants is cross-pollination. The pollination effectiveness is connected with the mode of pollen transfer from flower to flower in many respects (Faegri and van der Pijl, 1980).

Abiotic pollination. Transport of pollen by wind (anemophily) and water (hydrophily) is wasteful because an overwhelming quantity of pollen is lost without reaching the pistil of a flower of the same species. **Anemophily** is the prevailing type of abiotic pollination (Betulaceae, Cyperaceae, Fagaceae, Juncaceae, Poaceae). High concentration of pollen near its source and massive pollen deposition for each taxon area are necessary for successful anemophily. On average this value varies from a few tens to several hundreds of metres, and in exceptional circumstances up to a kilometre.

Anemophilous plants are characterized by simplified flower structure: the perianth is unobtrusive, strongly reduced or absent; anther and stigma protrude above the rest of the flower and inflorescence parts; the stigma has a large receptive surface, easily catching pollen from the air; pollen is abundant and, as a rule, it is rather small, dry, loose and light, and its surface is smooth. In many anemophiles (amentiferous plants), unisexual flowers can be observed that open before the leaves appear. In grasses, pollination is highly effective because of its diurnal rhythmicity , which is regulated by the explosive liberation of pollen from the anthers and by the dynamics of exposure of the stigma.

Hydrophily can occur either on the water surface **(ephydrophily),** or in the water **(hyphydrophily).** It is characteristic for an insignificant number of aquatic plants (Ceratophyllaceae, Cymodoceaceae, Najadaceae, Posidoniaceae, Potamogetonaceae). Their flowers open in the water and they do not project above the water surface. The peculiar structure of pollen grains, with well-developed intine and strongly reduced exine and practically no sporopollenin, increases their floating ability and enhances pollination success. The peculiarity of family Cymodoceaceae is the existence of filamentous pollen grains reaching 5000 |im in length (Yamashita, 1976). Unlike hyphydrophily, ephydrophily occurs in a two-dimensional medium. The pollen liberated from the anthers in the water and rising to the surface is quickly distributed by the water surface film and reaches the stigmas, also exposed on the water surface *(Callitriche, Neotunia, Ruppia, Vallisneria).* Such pollination ensures great pollen economy, which is why the ephydrophilous species of aquatic plants, as a rule, form a comparatively small number of the pollen grains in the anthers.

Biotic pollination is realized with the help of various animals. The progressive character of biotic pollination in comparison with abiotic consists in its stimulating the transformation of both components: in the process of co-evolution the structure of the flower and the inflorescence is improved, and the behaviour and structure of the pollinator itself are changed (Grinfeld, 1978).

The relationships between the plant and the pollinator are established by the presence of the various attractants in the flowers, which are responsible for the approach and visit of the pollinator. **The primary attractants** are responsible for the pollinator's visit to the flower or the inflorescence, and the **secondary attractants** help attract the visitors. Pollen, nectar food bodies, oils and others are refered to as primary attractants. The most important secondary attractants are odour, shape and colour of the flowers and inflorescences. Pollination by means of various biotic agents in the early stages of the evolution of flowering plants is what stimulated the great morphological diversity of flowers (see Flower, Vol. 1).

The most broadly distributed agents of biotic pollination are insects. Several forms of **entomophily** exist.

Cantharophily is pollination by beetles. Beetles constitute one of the most ancient groups of insects and they often damage flower parts. The flowers of cantharophilous plants are usually large, saucer-shaped, with flat perianth parts; the primary attractants, namely pollen, food bodies and oils, are easy to reach.

Melittophily is pollination by bees, bumblebees, and wasps. Bees, bumblebees, and wasps represent the most important and effective group of pollinators. The adult specimens use mainly nectar, but for larval nutrition they gather not only nectar, but also pollen, oils and other primary attractants. Most important, during a particular period of time they visit the flowers of just one species, and this ensures successful cross-pollination.

Psychophily is pollination by butterflies, and **phalaenophily** is pollination by moths. Butterflies as well as bees are "intelligent" visitors, because they do not disturb the flower structure and do not "steal" the nectar. Flowers that are pollinated by moths are usually white or straw-coloured, have a strong odour and open late in the evening. Some flowers have a place for landing, but most phalaenophilous plants are pollinated by hawk moths sailing near the flower.

Myophily is pollination by flies, mosquitoes, flower flies, bee flies and similar insects. This group of dipteran insects is not very well adapted for cross-pollination. They are not "intelligent" insects and their behaviour in the flowers is usually chaotic. The special indicators of the nectar formed on the perianth in many respects restrict the useless and harmful actions of these dipters in the flowers. The majority of the dipters readily visit the campaniform, tubular, and funnel-form flowers. These flowers often serve as a shelter for them during the frosts at night, especially in extreme habitats (e.g., tundra, taiga, alpine zone).

Myrmecophily is pollination by ants. Ants also are not very successful pollinators; their smooth bodies are not adapted to pollen transfer. However, in deserts, semideserts, and other extreme environments with a restricted number of pollinators, ants contribute to pollen transfer. Usually trifine is greatly expressed at the pollen surface, so the pollen sticks to the ant's body. Because of their rather small size these insects have free access into flowers of any type. Ants do not always carry out pollination; more often they act as pilferers of nectar.

Other invertebrates also participate in the pollination process. Earwigs, grasshoppers, snails, and thrips have been observed on flowers and inflorescences. However, their role in cross-pollination is obscure and they should be considered chance visitors.

Vertebrates (e.g., birds, bats, lizards, non-flying mammals) have great importance as pollinators. Extremely interesting relationships between them are noted in the Americas, Africa and Australia. In Europe their role is insignificant.

Ornithophily is pollination by birds, which are the leaders among vertebrate pollinators. They have good vision and their bodies are covered with feathers, to which pollen sticks well. Birds are extremely effective pollinators because of the high speed and precision of their flight and their adaptation to visit particular species of plants flowering at certain times. Many of them can visit hundreds and even thousands of flowers in a day. Bird-pollinators belong to various systematic groups. In America they include hummingbirds and honeycreepers, in the countries of the Old World they include sun-birds, honey eaters and white-eyes, and in Australia they include parakeets and lorikeets.

Chiropterophily is pollination by bats. Bats are good pollinators because their body surface, covered with fur, holds pollen safely and, like birds, they fly quickly and travel great distances; also, they are nocturnal. Though plants pollinated by bats belong to different systematic groups, their flowers and inflorescences have a number of common features, resulting in stabilizing selection. These plants open late in the evening or at night, their flowers are white, cream-coloured or yellowish and have a strong and usually pleasant odour, and their perianth is solid; usually there is a lot of pollen and nectar. Bats normally sail near the flowers and inflorescences and more seldom they land on inflorescences.

Pollination by non-flying vertebrates is carried out by larger marsupials, rodents, lizards and even monkeys. All of them visit the flowers and the inflorescences for the sake of nectar, pollen, the various food bodies and other primary attractants. The plants pollinated by these agents belong to various families of monocotyledons and dicotyledons. They have a solid perianth and produce a large amount of pollen and nectar.

By these various means, in the process of evolution plants have begun to use biotic and abiotic agents in order to carry out cross-pollination and give rise to viable progeny.

Chasmogamy (Greek *hasma*—opening, *gamos*—marriage) is pollination in an open flower. The term was introduced by Axell (1869).

In chasmogamous flowering, pollen transfer occurs by means of various agents (e.g., wind, insects, birds). According to Darwin (1877), flowers open for pollination are called accomplished. It is well known that the perianth serves to attract pollinators and protect generative organs. As a result of coevolution the most complicated mechanisms were developed in flowers directed toward realization of cross-pollination (Church, 1908; Kozo-Polyansky, 1946; Grant, 1949; Armstrong, 1979). However, the mode of pollination cannot be judged on the basis of external morphology. Plasticity of pollination mechanisms is characteristic of many plants (Pervuchina, 1970,1979). Depending on particular conditions of existence in various regions of the distribution area, the same species can be pollinated in different ways.

Cleistogamy (Greek *kleistos*—closed, *gamos*—marriage) is one form of self-pollination taking place in a closed flower. The term was introduced by Kuhn (1867).

Cleistogamy is widely distributed among wild and cultivated plants (Darwin, 1877; Uphof, 1938). It was found in 287 monocotyledonous and dicotyledonous plants from 59 families (including Balsaminaceae, Commelinaceae, Fabaceae, Malpighiaceae, Orchidaceae, Oxalidaceae, Poaceae and Violaceae) (Lord, 1981). The analysis of the data testifies that cleistogamy is observed in annuals more often than in perennials. *Viola (V. mirabilis, V. collina, V. hirta* and others) and *Oxalis acetosella* are the best-known examples of cleistogamic plants.

Cleistogamy has an ecological character and is caused by unfavourable environmental conditions such as the lack or surplus of water, high or low relative humidity of air, shade, low or high temperature, poverty of soil, soil drought, discrepancy of photoperiod length or lack of pollinators (Uphof, 1938). The action of many factors is difficult to explain because of the appearance of chasmogamic flowers after cleistogamic flowers on the same plant and vice versa. Nevertheless, in a number of works the influence of ecological factors on cleistogamic flower occurrence has found experimental justification (Uphof, 1938; Mayers and Lord, 1983a,b).

Cleistogamy is an extremely non-uniform phenomenon. No standard classification on cleistogamy exists (Darwin, 1877; Goebel, 1904; Hackel, 1906; Uphof, 1938; Lord, 1981; Frankel and Galun, 1977). The most comprehensible classification represents cleistogamy as obligate and facultative (Ponomarev and Demyanova, 1980).

Obligate cleistogamy includes cases in which cleistogamic flowers are formed constantly in a species. As a rule, obligate cleistogenes form chasmogamous and cleistogamous flowers on the same individual, the cleistogamous flowers being fertile. Chasmogamic flowers are fruitless when cross-pollination fails.

The two forms of flowers of a species develop in different vegetative periods; more seldom they develop simultaneously. Only cleistogamic flowers are extremely seldom observed in plants (e.g., in grasses *Leersia oryzoides, Sporolobus subinclusus, Tetrapogon spathaceus;* Hackel, 1906; Uphof, 1938). These examples demand reivestigation, as clearly cleistogamous populations are not revealed. Cases in which flowers of both forms are found on different individuals, for example, in some Cistaceae (Uphof, 1938), are exceptional. Alongside chasmogamic flowers, sometimes two types of cleistogamous flowers and, accordingly, two types of fruits are formed on the same individual. Subterranean and above-ground cleistogamic flowers of annual bean plant *Amphicarpa bracteata* are developed on the cotyledonary node and on the first three epicotylar nodes accordingly and chasmogamic flowers on the uppermost nodes (Juncosa and Webster, 1989). Chasmogamic flowers in cleistogamous species can be cross-pollinated by various agents and self-pollinated (autogamous).

The ratio of cleistogamous to chasmogamic flowers in obligate cleistogenes is determined by ecological factors and may vary during different vegetative seasons. Balance between cleistogamy and chasmogamy is a dynamic adaptive attribute (Wilken, 1982). Cleistogamic flowers of such plants are smaller than chasmogamic ones; they never open and remain buds. As a rule, they do not produce nectar or emit an aroma. All parts of the flower are reduced to a greater or lesser extent. The calyx is modified less than other parts of the flower, but nevertheless it is smaller. The corolla usually loses characteristic colour; petals are rudimentary or absent. The nectaries are reduced. Full or partial reduction of lodicules and spikelet scales are observed in grasses (Hackel, 1906; Ponomarev, 1964). In cleistogamous flowers the number of

stamens is reduced; anthers are smaller than in chasmogamic flowers and do not contain enough pollen. Pollen grains are small and some of them can be sterile. According to Madge (1929), pollen grains in chasmogamous and cleistogamous flowers can have different forms. Endothecium is poorly advanced. Usually pollen grains do not shed on stigma and they germinate in anthers through the anther wall or through a break in it (Gorczynski, 1929; Madge, 1929; Solntseva 1965a,b; Vereshchagina, 1965,1980; Poddubnaya-Arnoldi, 1976; Anderson, 1980; Mayers and Lord, 1983a,b). Solntseva (1965a,b) observed the dehiscence of anthers in cleistogamous flowers of spear-grasses. The mechanism of pollen tube growth to stigma is poorly investigated.

The number of carpels is quite often reduced. Styles are short, and poorly advanced surface is quite often marked only on top of carpel. Anthers settle in immediate proximity of stigmata, which facilitates self-pollination. All researchers specify synchronism of pollen and embryo sac formation in cleistogamous flowers. The meiosis in embryo sac proceeds without deviations. Sometimes fertilization is not revealed in cleistogamous flowers, as against chasmogamous flowers, which suggests the apomictic nature of an embryo (Lorenzo, 1981).

According to Uphof (1938), it is necessary to consider cleistogamic flowers as being late in their development and early-functioning forms of chasmogamic flowers. The gradual transition from chasmogamic flowers to cleistogamic, accompanied by an increasing reduction of perianth, is noted in many cleistogamous plants (e.g., *Viola* species, *Oxalis acetosella).* Cleistogamic flowers are similar to buds of chasmogamic flowers and are narrowly specialized to constant self-pollination, which is their only means of pollination.

Facultative cleistogamy can occur without an appreciable reduction in flowers. It seems to represent an initial stage of development of this phenomenon. It is found at later stages when the flower is ready to bloom only under certain combinations of environmental conditions that are unfavourable for open flowering. Depending on ecological conditions, pollination occurs in open or closed flowers; thus, both types of flowers can replace the other. In case of facultative cleistogamy, its origin from chasmogamy is even more obvious.

Facultative cleistogamy is found often enough in wild grasses and has been investigated in detail in *Stipa* (Hackel, 1906; Ponomarev, 1961, 1964; Solntseva, 1965a,b). Cleistogamous flowering is caused in *Stipa* by soil drought or low temperature during flowering (Ponomarev, 1964).

For desert species of the Chenopodiaceae *(Climacoptera brachiata, Girgensohnia oppositiflora, Halimocnemis villosa, Petrosimonia triandra),* cleistogamy is caused by lack of soil moisture and high temperatures during flowering (Ponomarev and Lykova, 1960; Lykova, 1964). In this family cleistogamy occurs at the early stage of formation and does not affect the morphological structures of a flower. The perianth of cleistogamous flowers is closed, anthers do not appear outside, and they surround the stigma from different directions like a muff. The flowers have bracts and never open wide.

This creates favourable conditions for cleistogamy or, more correctly, near cleistogamy, as a barely noticeable separation of leaflets of perianth is observed.

The genetic aspects of cleistogamy are poorly investigated. There is little data on the inherited character of obligate cleistogamy (Uphof, 1938). With facultative display

cleistogamic variations are not inherited in posterity: they are triggered by surrounding conditions (e.g., temperature, light, water). The presence of cleistogamous and chasmogamic flowers in the same species makes its system of reproduction steady, combining benefits of cross-pollination and self-pollination.

Cleistogamy acquires a special value (as do other forms of self-pollination) during migration of plants to new habitats. According to the observation of Campbell (1982), cleistogamic species of the cosmopolitan genus *Andropogon* most successfully colonize degraded habitats. Higher survival rate of sprouts germinated from seed in cleistogamous flowers in comparison with "chasmogamous" sprouts is found in grass *Danthonia spicata* (Clay, 1983). According to Schemske (1978), energy power for chasmogamy is two to three times as energy-intensive as for cleistogamy.

The connection between cleistogamy and autogamy is clear. This correlation is especially evident in Orchidaceae (Catling, 1983), where both modes of self-pollination are widely observed. Cleistogamy represents the further development of autogamy, or its extreme form.

Specific Features of Cleistogamy in Annual Species of Genus *Medicago* L. (Fabaceae) (Plate II)

Flowers of annual species have a structure typical for genus *Medicago.* Unlike perennials, however, they have a flag much longer than wings and carina. Wings can be longer or shorter carina, and this ratio has a taxonomic value. The pistil surrounded with staminal tube, or stamen-pistil column, has an ovary with various number of ovules in different species, the short style and fungaceous stigma.

The majority of flowers of annual species, as well as of perennial species, are opened by autotripping when the stamen-pistil column jumps out, like a spring, from the carina, hitting a flag. In perennial species tripping is carried out by insect-pollinators. In all annual species investigated by us, flowers are rarely and accidentally visited by pollinators. Tripping of the majority of flowers of annual species does not depend on pollinator visit. After explosive pollination, within one to three hours the flower slowly closes until the flag will not enclose a pistil and the petals turn pale. Annual species have a daytime rhythm of opening and tripping of flowers. In annual species, there are flowers in which autotripping does not occur. The number of non-tripping flowers varied from 6% to 12% in M. *arabica*, *M. intertexta*, *M. orbicularis*, *M. scutellaria* and *M. turbinata* and from 1% to 35% in M. *lupulina* in different conditions of growth, in *M. radiata* such flowers are single.

Research by methods of light and luminescent microscopy of buds and of flowers in annual species on constant and time preparations has revealed flowers in which pollination occurred in a bud. Even in green buds at the earliest stages of development bicellular pollen and pollen grains with the first attributes of germination (swelling of cytoplasm in the field of the aperture) are marked. In buds at later stages of their development, pollen tubes in which length already exceeds the diameter of a pollen grain are observed. Anthers in a bud densely adjoin the stigma, and pollen tubes through the anther wall will penetrate the ovules and embryo sacs.

Early and almost synchronous development of male and female gametophytes, germination of pollen grains in anther of buds, and cases of double fertilization in flowers up to tripping are the conditions of bud cleistogamy in annual species of

Medicago. The term "bud cleistogamy" was used by Kalin Arroyo (1981) in the characterization of reproductive systems in Fabaceae *(Hippocrepis, Lotononis, Ornithopus, Scorpiurus).* Bud cleistogamy was found in seven annual species of *Medicago,* which on occurrence of cleistogamous flowers can be arranged as follows: *M. orbicularis* (the greatest number), *M. scutellata, M. lupulina, M. turbinata, M. arabica, M. intertexta, M. radiata* (single) (Novosyelova, 1997, 1998; Vereshchagina and Novosyelova, 1997).

It is necessary to note that cleistogamic flowers, like chasmogamic flowers, open and without special research it is difficult to distinguish the two (see Chasmogamy; Cleistogamy). Apparently, some cleistogamic flowers have already lost the mechanism of autotripping as there are non-tripping flowers. Chasmogamic and cleistogamic flowers can be found on one plant and even in a single inflorescence. Bud cleistogamy combines attributes of obligatory form (a small amount of the pollen grains germinating through the anther wall) and facultative form (inconstancy of the phenomenon and absence of reduction of corolla).

The Evolution of Wind Pollination[1]

Before we can address questions concerning the evolution of wind pollination in the angiosperms, we need to establish that it did, indeed, evolve in the angiosperms. If wind pollination is merely the persistence of an ancestral trait, then its presence in the angiosperms requires no further explanation. Wind pollination is virtually the only mode of pollen dispersal used by modern plants without flowers (Ginkgoales, Coniferales, Cycadales and Gnetales). However, Stevenson (in prep.) argues for extensive biotic pollination in the cycads, and Meeuse *el al.* (1990) present convincing evidence for entomophily in *Ephedra aphylla.* In addition, the spore-plants (ferns, lycopsids, sphenopsids, bryophytes) are all wind dispersed. Crepet (1983) suggests that the insect-pollen interactions may date from the Carboniferous, but there is little evidence that anything but wind pollination was the most common mode of pollen dispersal. From this it is obvious that wind pollination is the ancestral mode of spore or pollen dispersal in land plants, but that the ancestral angiosperms were probably biotically pollinated (Whitehead, 1969; Faegri and Van der Pijl, 1980). Wind pollination in the angiosperms is a derived feature that evolved numerous times from the ancestral biotic pollination system. Consequently, we can ask questions about the evolution of wind pollination in the angiosperms, as we are not simply dealing with the persistence of an earlier pollination syndrome.

There are three central questions in the evolution of wind pollination.

1. Under what ecological conditions can we expect wind pollination to evolve? These are factors extrinsic to the plants that select for wind pollination or against biotic pollination.
2. What morphological features may predispose a lineage to the evolution of wind pollination? This addresses the conditions internal to the plants that may facilitate the transition to wind pollination.

[1]This research was conducted with financial assistance from the Foundation of Research Development, South Africa, and the University of Cape Town.

3. What macro-evolutionary patterns may be associated with wind pollination, and what could these tell us about the consequences of the evolution of wind pollination?

Wind pollination has been a rather neglected area; it lacks the glamour of animal-plant interactions, which has recently stimulated a spate of research. Therefore, many aspects of wind pollination are still poorly understood. This review consequently raises more questions than answers and will hopefully stimulate further research into the problems associated with the evolution of wind pollination.

Ecological questions. Wind pollination is thought to be advantageous in cold and windy environments in which the vegetation is low and open. There are several large-scale eco-geographical patterns that illustrate this. One of the earliest was documented by Knuth (1906), who showed that anemophily increased in frequency on the more exposed, bleaker North Sea islands. He suggested that the increased dominance of anemophily might be due to the fact that insects are blown away by the persistent winds on the more exposed islands. This highlights the two central variables linking the environment and wind pollination: environmental factors that increase the efficiency of wind pollination and those that inhibit biotic pollination. This could be expressed as the cost of wind pollination (in greater pollen wastage, or pollination limitation of seed-set, or whatever factor might increase the cost) versus the cost of biotic pollination. In theory, a shift from biotic to wind pollination may occur when the cost of wind pollination is less than the cost of biotic pollination, and so it is necessary to examine both these variables in order to understand why in any environment a shift to wind pollination may occur.

Wind pollination is said to be more frequent at higher latitudes and with increasing altitude (Faegri and van der Pijl, 1980; Regal, 1982; Whitehead, 1983), but there has been no global survey of wind pollination to test this pattern. At one extreme, lowland equatorial rainforests have very few wind-pollinated plants, while temperate woodlands are dominated by anemophilous trees (Daubenmire, 1972). Regal (1982) demonstrated both these patterns at a finer scale for trees in North America, but it is not evident how the patterns would change if herbaceous plants, especially grasses and sedges, were included in the study, as it is possible that the tropics could be very rich in these species. A further variable that should be taken into account is the cover or abundance of the different species and pollination types in the communities that are being compared, rather than the number of species.

The reasons for these geographical patterns are not clear. Whitehead (1983) listed their possible environmental causes.

1. Decreased species diversity, leading to denser populations of anemophilous species. The assumption is that wind pollination is effective only in dense populations, when individuals of the same species are close together. Regal (1982) suggested that, even in very species-rich rainforests, individuals still often occur in clumps, and Midgley (1989) showed that even isolated individuals of *Podocarpus falcatus* in the South African temperate forests were being successfully pollinated.
2. Longer dry seasons during which the pollen would not be washed out of the air.
3. A more open vegetation that would not interfere with pollen movement between the plants. This is supported by the dominance of deciduous trees in the largely anemophilous north-temperate woodlands (Sprengel, 1793). However, the

southern temperate forests are evergreen, and there is some indication that there is successful air movement even in dense forests (Bawa and Crisp, 1980).

4. More distinct seasonality leading to more precise flowering cues.
5. Selection for longer-distance outcrossing, and hence for biotic pollination, in unpredictable environments, as suggested by Regal (1982).

However, it is clear that there are exceptions to each of these patterns, and it is not obvious that the community ecology approach can find "reasons" for these ecogeographical trends. It is difficult to disentangle unrelated factors and causes, such as the north-temperate correlation of high-latitude vegetation, deciduous trees and anemophily. A more productive research programme might be to look for the environmental conditions associated with the transitions from biotic to wind pollination.

There have been very few studies that correct for the phylogenetic pattern: most research has been based on the numbers of wind-pollinated species in each ecosystem, and their dominance in the system. Such species counts could lead to incorrect answers on the ecological parameters that might select for wind pollination. One approach is to carry out comparative infraspecific or infrageneric studies of sister-taxa of wind- and insect-pollinated groups. Gómez and Zamora (1996) showed that high-altitude populations of *Hormathophylla spinosa* (Cruciferae) are wind pollinated, while low-altitude populations are insect pollinated. They interpreted this as a dual response to a shortage of pollinators, as well as an abundance of wind, operating in a situation where the population density of the plants is high, and the surrounding vegetation low. A similar situation was documented for *Urginea maritima,* which flowers in autumn in the Levant, when pollinators are rare. Wind dispersal gradually removes the dry pollen from the anthers and is moderately efficient in effecting pollination (Dafni and Dukas, 1986). In a careful study, Berry and Calvo (1989) demonstrated that two high-altitude species of *Espeletia* (Asteraceae) were wind pollinated, while the remaining 11 species, at both high and lower altitudes, were pollinated by insects or hummingbirds. Increase in altitude was correlated to decreasing temperatures and rainfall and, possibly more significantly, to decreasing insect numbers. Species with wide altitudinal ranges showed decreased seed-set at higher altitude, probably due to pollinator limitation. This suggests that the shift to wind pollination at higher altitudes is at least to some extent due to the decreased efficacy of insect pollination. This study could neither demonstrate nor falsify the hypothesis that wind pollination was more efficient at higher altitude than at lower altitude, but overall from the few studies available it appears as if pollinator limitation might be important in driving plants towards wind pollination.

There is clearly a need for more comparative studies such as the Berry and Calvo work. It may be possible to avoid the need for phylogenies by working on ambophilous species. A number have been documented over the years: *Plantago lanceolata* (Clifford, 1962; Stelleman, 1978), *Dichromena ciliata* (Leppik, 1955), *Acrocomia aculeata* (Scariot and Lleras, 1991), *Calluna vulgaris* (Faegri and van der Pijl, 1980) and several species of *Salix* (Argus, 1974; Vroege and Stelleman, 1990). It might be possible in these complexes to show which environmental attributes are regularly associated with the transition to wind pollination. A more penetrating analysis would be to use species pairs or genera, as in the Berry and Calvo study, but ideally this sort of work should be based on a phylogenetic hypothesis. It would also be of great value if the costs of the various approaches could be quantified.

Morphological conditions. The morphological attributes of wind pollination are well documented, in greatest detail by Faegri and van der Pijl (1980), but also by others, such as Sprengel (1793), Knuth (1906), Whitehead (1969,1983) and Proctor *et al.* (1996).

— Flowers clustered in dense inflorescences.
— Flowers small.
— Perianth reduced or absent; when present often dully coloured.
— No nectar production with nectaries often totally absent.
— Anthers with abundant pollen and explosive dehiscence mechanisms although the number of anthers is not usually increased. The anthers are often borne on long filaments outside the flowers.
— Stigma surface expanded, often variously elaborated as brushes or feathers, sometimes enlarged and sticky and usually projecting beyond the perianth.
— Sexes separated, either monoecious or dioecious; bisexual flowers dichogamous.
— Pollen grains small, smooth, surface dry (Sprengel, 1793; Wodehouse, 1935; Hesse, 1978,1979a-c).
— Frequently a reduction in the number of ovules, often to a single ovule per ovary (Pohl, 1929a).

These features are often used to infer the pollination mode of the plants, but there are so many exceptions that they can be quite misleading. A further problem is that there is a danger of circularity when morphological features are used to establish wind pollination, and these so-called wind-pollinated plants are then used to support the "wind pollination syndrome".

Some features, however, are universal in all wind-pollinated plants. Dry pollen, which is freely distributed by the wind, is always found in anemophilous species. Reduction in pollenkitt has long been postulated to be associated with wind pollination (Sprengel, 1793; Pohl, 1929b), and the details of the reduction were meticulously documented by Hesse (1978,1979a-c), who showed that this reduction was achieved by a variety of different methods, from storing the kitt out of reach in intratectal cavities to "wasting" it on the anther wall, or producing substantially less kitt. Hesse showed that in species-pairs comparisons of European wind- and biotic-pollinated species, dry pollen was always found in the wind-pollinated species. The functional importance of dry pollen is obvious, as sticky pollen forms large clumps that do not stay in the air, are difficult to remove from the anther, and will stick to any surface they come into contact with. Dry pollen does not preclude biotic pollination, and such plants may either be ambophilous (such as many *Erica* species and *Calluna vulgaris),* or primarily insect pollinated. Sprengel (1793) made the interesting observation that sticky pollen could be an adaptation to insect pollination, as it would stop the wind from blowing the pollen away before the insects could get to it. Dry pollen could therefore be an exaptation (Gould and Vrba, 1982) for wind pollination.

Linder (1998) argued for small, actinomorphic flowers as a condition for the evolution of wind pollination. There are very few known instances of the origination of wind pollination in lineages with zygomorphic flowers, and it is very rare in lineages with large, showy flowers. For example, there are numerous originations of wind pollination in the asterids, which are frequently zygomorphic, but the originations are all in actinomorphic groups, such as Asteraceae, Oleaceae and Rubiaceae. The only exception is *Plantago,* which is embedded within the complex-

flowered, zygomorphic Scrophulariaceae. But even in this group, the sister-group to *Plantago* is *Veronica*, which is insect pollinated and has simple, actinomorphic flowers (Reeves and Olmstead, 1998). Wind pollination evolved most commonly in the rosids, with their simple, actinomorphic flowers. The Chenopodiaceae—Amaranthaceae complex and the Palmae, in which probably numerous shifts between biotic and wind pollination occurred, have small, simple, actinomorphic flowers. By contrast, in groups characterized by large, showy flowers, wind pollination did not evolve at all. Pollen stickiness, unlike perianth type, appears to be more labile and appears to switch readily from sticky to dry. This change might be able to occur readily, and its absence probably would not constrain the evolution of wind pollination.

Most of the morphological features of the wind pollination syndrome appear to evolve after wind pollination and could be interpreted as adaptations that make wind pollination more efficient but are not essential for the functioning of the pollination system. For example, multiple ovules in the ovaries are found in Juncaceae; bisexual flowers are found in the wind-pollinated species of *Erica;* nectaries are still present in *Cannabis* and the wind-pollinated species of *Espeletia* (Berry and Calvo, 1989); simple stigmas are found in *Olea* and *Fraxinus.*

Linder postulated a model in which the "general" angiosperm condition would be a small, simple, actinomorphic flower, like the open flowers typical of many of the rosids. These simple flowers could be either wind or insect pollinated. Once a lineage becomes either wind or insect pollinated, then a series of adaptations to these new pollination systems become established. In the case of biotic pollination, it usually involves the elaboration of the perianth in various ways, in addition to the various specializations typical of the different pollinators. In the case of wind pollination, it tends to result in a reduction of the perianth, its further simplification, and ultimately the loss of the means to attract insects and other pollinators. Once these specializations are established, it becomes difficult for the process to be reversed. The few cases of reversals from wind to biotic pollination illustrate the morphological changes that have to occur to adjust to a different pollination mode, and to re-invent the means of attracting pollinators.

The evolution of the wind-pollinated syndrome can be illustrated using the Poales — Cyperales clade, which is the largest clade of wind-pollinated plants. The phylogenetic relationships among the families in the clade are reasonably well understood (Linder and Kellogg, 1995) (Fig. 14), and those portions of the phylogeny about which there is some doubt would not affect the interpretations below.

Wind pollination in the Poales — Cyperales evolved once. The evolution of the "typical" wind pollination characters can be traced by optimizing the characters of the extant families to the internal nodes of the phylogeny. For this, we can establish the following:

Perianth: at the ancestral node, the perianth lobes were all colourless and bract-like. It would appear that, since Bromeliaceae are closely related to this lineage, the reduction to at least a bract-like outer perianth-whorl occurred before wind pollination. Further reduction in the perianth occurred after the evolution of wind pollination: a reduction to bristles in Cyperaceae, in some cases complete loss of the perianth in Centrolepidaceae and some species of Restionaceae, and the reduction of the perianth lobes to lodicules in Poaceae. The most extreme form of reduction in the clade is found in Centrolepidaceae, where flowers appear to be reduced to the gynoecia, and these are then fused to form a "capitulum" type of inflorescence, which

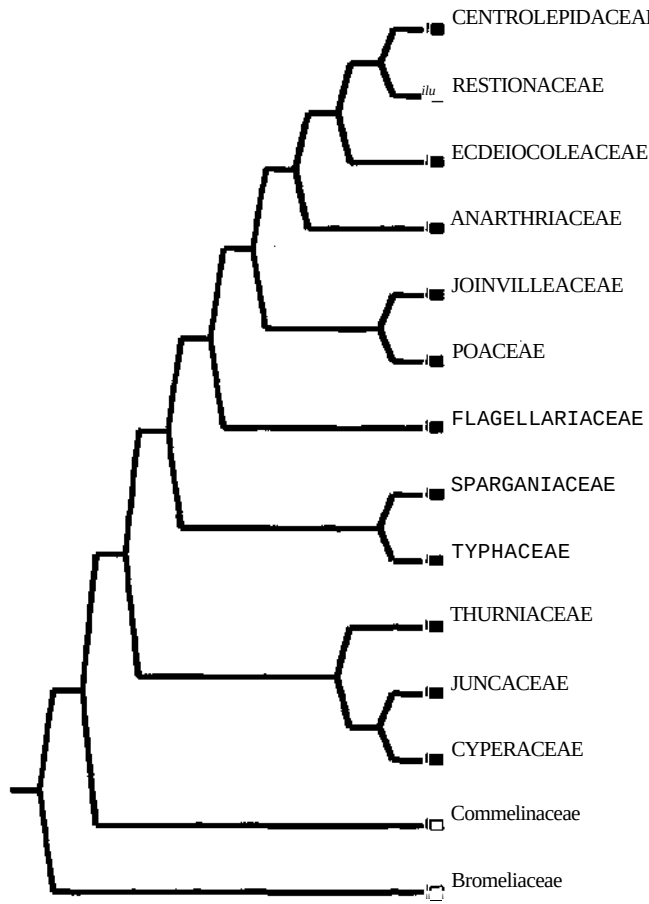


Fig. 14: Phylogeny of the Poalean clade of monocots.

looks like a bunch of grapes, consisting of partly fused ovaries and numerous free styles (Hamann, 1962,1975).

Nectaries: these appear to have been lost at the origination of wind pollination. If they were lost afterwards, then they were lost in all wind-pollinated species of the group, as none of them currently have nectaries. Nectaries generally disappear quickly after the transition to wind pollination, and there are few records of functional nectaries in wind-pollinated plants (e.g., in *Espeletia;* Berry and Calvo, 1989).

Reductions in the gynoecium: at the ancestral node the gynoecium consists of three locules, each with numerous ovules. This situation is currently found in most species of Juncaceae, as well as in Prionaceae (see Munro and Linder, 1997,1998). In most descendent families each carpel is fertile with a single ovule (Flagellariaceae, Anarthriaceae, many genera of Restionaceae), and this is followed by the loss of two carpels, thus leaving each flower with a pseudomonomerous gynoecium containing a

single ovule (Cyperaceae, Poaceae, many Restionaceae). Thus the reduction is taken as far as possible, where each female flower produces a single ovule.

The **stigmas** are all feathery in the clade; this condition probably arose at the ancestral node. The degree of branching is somewhat varied, from feathery to densely plumose, but this pattern has not been explored here.

The **pollen grains** are all porate with a smooth exine. The transition to a smooth exine occurs at the same time as the shift to wind pollination, and a smooth exine has been shown to be associated with wind pollination in the Asteraceae (Berry and Calvo, 1989; Bolick, 1990). We argue that porate pollen is linked functionally to wind pollination, but it is not clear how. The outgroups of the wind-pollinated monocots all have colpate pollen, thus it is probable that the ancestor of the wind-pollinated monocots had a porate grain. There are interesting modifications in the structure of the pore margins in the group (see Linder and Ferguson, 1985), as well as the development of pollen tetrads in Cyperales, and the reduction of these to pseudomonads in Cyperaceae (Zavada, 1983).

Inflorescence structure: the ancestral lineages of this clade have large, paniculate inflorescences (e.g., Juncaceae, Flagellariaceae, Anarthriaceae, Joinvilleaceae), but this is followed by various forms of aggregation of the flowers, in great elongated spike-like inflorescences (e.g., *Typha),* globules (Sparganium), or spikelets (e.g., Poaceae, Cyperaceae, Ecdeiocoleaceae, many Restionaceae). It is not clear what the functional advantage of these spikelets are, but it is interesting that in this clade spikelet-like structures evolved at least six times.

The **breeding system** of the flowers shifts from bisexual flowers at the base of the tree *(Prionium, Flagellaria, Joinvillea)* to unisexual flowers, and in a few cases to dioecy. This reduction happened numerous times, but in few cases does it characterize large clades. For example, almost all of Restionaceae are dioecious, suggesting that this evolved once at the base of the Restionaceae. By contrast, in Poaceae there are many cases of unisexual flowers, often characterizing large groups. However, this must have evolved several times. Similarly, the reduction to dioecy occurs occasionally in the grasses and must have evolved numerous times.

There have been no comparable analyses in Dicotyledonae. The evolution of the pollen characteristics in response to wind pollination has received most attention. Bolick (1990) documented the pollen transitions in the Asteraceae, and Hesse (1978; 1979a-c) did the same for a number of dicotyledonous genera, but there has been no analysis of the sequential character change in a large clade. The pollen aperture evolution was surveyed for the angiosperms by Linder (1998), in a broad-scale comparative analysis, but this has not been done for all possibly involved characters on a clade-by-clade basis. There are some very interesting clades to analyse, and the prime candidate would be Urticales. What makes Urticales particularly interesting is the apparent reversal to wasp pollination in *Ficus,* and in particular the morphological shifts that attract pollinators to unisexual flowers (which consequently cannot offer pollen as a reward) that have lost their nectaries. However, the problem with such an analysis at the moment is the lack of a phylogeny for the Urticales (Berg, 1989). In addition, the pollination biology of many of the tropical members of the clade is still unknown.

Phylogenetic Patterns. Wind pollination is much more common in the monocots (about 40% of the species) than in the angiosperms as a whole (10.8%), with the ranunculids, magnoliids, asterids and rosids under-represented, while the

Table 2. Distribution of anemophily in the different groups of angiosperms (the groups are largely based on the molecular phylogeny of the angiosperms, based on the analysis by Chase *et ah,* 1993).

Subclass	Origin-ations	Genera			Species		
		Anemo-philes	Total	Percentage	Anemo-philes	Total	Percentage
Angiosperms	**65**	1322	13,573	**9.8%**	26,000	241,000	10.8%
Magnoliids	**7**	10	303	**3%**	50	8,010	0.6%
Ranunculids	**2**	5	180	**3%**	20	3,654	0.5%
Rosids	**28**	180	3,964	**5%**	2,800	74,872	3.7%
Caryophyllids	**8**	185	601	**31%**	2,800	9,462	29.6%
Asterids	**16**	24	4,596	**0.5%**	8,004	7,710	1%
Dicots	**61**	408	10,865	**3.8%**	5,125	189,000	2.8%
Monocots	**4**	914	2,708	33.8%	21,000	52,000	40.4%

caryophillids and monocots are over-represented (Table 2). When the proportion of genera in each of these angiosperm groups is compared, a similar pattern to that shown for species is observed, but the pattern for families is rather different. This could be due to the method of counting: with the exception of the relatively small number of ambophilous species, all species are either totally wind or biotically pollinated, and this also applies largely to genera. The families, however, are very different, and more than half the families in which wind pollination occurs have significant numbers of biotically pollinated families. The second confusing factor is that families cannot all be regarded as being equal. In this survey I have followed the family delimitations of Cronquist (1981), which are very different from the delimitations of Takhtajan (1997). It appears as if in the Cronquist system several wind-pollinated groups were separated at family level from their biotically pollinated "ancestors", thus creating paraphyletic families. Clearly, the counts of the numbers of wind-pollinated families therefore become confusing.

The number of times of origination was established by starting at the smallest unit for which the information was available — either a genus or a family. I then searched for the sister-taxon (either genus or family, respectively); if it is biotically pollinated, then this counts as an origination. If not, the search continues for the next sister-taxon, until the transition to biotic pollination is located. This method requires the minimum phylogenetic information to establish the number of times wind pollination has evolved, but in many cases even this information is not available. The major source of error might be with families such as Arecaceae and Chenopodiaceae, which possibly contain a large number of wind-pollinated species, but also many biotically pollinated species, and the pollination mode of the species has not been adequately documented; these are like ambophilous families. I have not included the Arecaceae in this count, and I included Chenopodiaceae as a single origination. The second source of error is that I counted each genus with more than one species of wind-pollinated plants as a single origination, and this may constitute a severe underestimate. In the mega-genus *Erica,* for example, wind pollination originated

independently in a number of lineages (Oliver, pers. com.). This underestimate would be extended to family level in cases where there is no generic-level phylogeny available (most of the cases!). The last source of error is that I have almost certainly missed a very large number of originations of wind pollination, which are reported in local natural history publications but may be difficult to access.

Despite these caveats, it is clear that there is no relationship between the frequency of wind pollination in any large angiosperm group, and the number of originations. Of the 26,000 wind-pollinated species, 21,000 are found in the monocots, almost all originating from a single origination, which led to the Poales—Cyperales—Typhales radiation. Most of the originations of wind-pollinated species result in groups of less than 10 species, only a few have more than 100 species (e.g., the "higher hamamelids", which include Betulaceae, Nothofagaceae, Fagaceae, Casuarinaceae, Juglandaceae and Rhoipteleaceae—296 species; Chenopodiaceae—2000 species; *Artemisia* (Asteraceae)—390 species; and Urticales—1500 species).

Is it possible to make deductions about the phylogenetic consequences of a shift to wind pollination? One of the frequent questions is whether it leads to an increase in the number of species in the lineage, or whether it constitutes a "dead end" for the evolution in that lineage.

There is enormous variation in the results of the originations of wind pollination: in some instances it has resulted in a single species, scarcely distinct from its sister-group, and in extreme cases the differentiation has not yet led to species; this might be the case in some of the ambophilous species. In other cases the resulting species are so different from their relatives that their taxonomic affinities are obscure (e.g., *Theligonium,* see Rutishauser *et ah,* 1998). Some of these anemophilous segregates have even been separated at family level; this could apply to Julianaceae (separated from Anacardiaceae) and Achatocarphaceae (separated from Phytolaccaceae) due to strong morphological differences that might be more reflective of the pollination system than the phylogeny. At the other extreme are rather speciose groups of clades of wind-pollinated plants; these tend to be herbaceous (Poales, Chenopodiaceae, many Urticales, *Artemisia),* and here the large numbers of species might be the result of a herbaceous habit rather than wind pollination.

Clearly questions as to the phylogenetic effects of a shift to wind pollination can only be evaluated by comparing sister-lineages to ensure that both groups, one biotically pollinated and the other wind pollinated, are of the same age. It would further be useful if the two groups were as similar to each other as possible, to prevent other factors (e.g., herbaceous and woody characteristics) from confusing the analysis. Such analyses are not yet available.

I raise three evolutionary questions concerning wind pollination: under what extrinsic conditions (ecological conditions) is it most likely to evolve, what intrinsic (morphological) factors favour the evolution of wind pollination, and what are the likely phylogenetic consequences of the evolution of wind pollination?

The ecological conditions favouring wind pollination are those that increase the cost (or decrease the likelihood) of biotic pollination, while also increasing the efficiency of wind pollination. However, there have been no studies that have explicitly investigated these, as most have either summarized the community conditions (which is not informative on the circumstances in which the transition to wind pollination occurs) or emphasized either the climatic conditions or the shortages or otherwise of pollinators.

The intrinsic, morphological conditions have received more attention, and it appears as if dry pollen and small, simple flowers are prerequisites for the evolution of wind pollination, while all the other characters (e.g., further reduction in the perianth, loss of nectaries) are adaptations that might enhance the efficiency of wind pollination but are not absolute requirements for its functioning.

The phylogenetic effects of a transition to wind pollination are hardly known, except that they are highly variable—from enormous success, as in the Poales lineage, to hardly any differentiation.

BREEDING SYSTEMS

Autogamy (Greek *autos* — itself, *gamos* — marriage) is the phenomenon in which pollen from a flower hits the pistil stigma of the same flower. It is a form of self-pollination (along with geitonogamy and cleistogamy). The term was introduced by Delpino (1871).

Autogamy is peculiar to chasmogamous hermaphroditic flowers. It arises on the basis of cross-pollination as a result of disturbance of its major mechanisms: herkogamy, dichogamy or self-incompatibility. Dichogamy becomes as though erased because of asynchrony of initial phases (stigmatic or staminal) in flower development. Owing to suppression of genes in a locus of self-incompatibility (Lewis, 1954), there is a shift towards more or less full self-compatibility.

Autogamy occurs in flowers during the different periods of flowering: right at the beginning of it, sometimes even in flower buds (flower bud pollination), during the entire period of flowering, or right at the end of it.

Flower bud pollination is seldom encountered. Examples of this form of self-pollination are known in the Faroes (Hagerup, 1951) and are noted in plants of different families: e.g., *Galium saxatile* (Rubiaceae), *Potentilla erecta* (Rosaceae), *Euphrasia borealis, Veronica beccabunga* (Scrophulariaceae), *Cerastium caespitosum, Stellaria media* (Caryophyllaceae), and *Lotus corniculatus* (Fabaceae). Flower bud pollination is known also in cultivated plants, especially for leguminous plants (e.g., *Arachis hypogaea, Phaseolus vulgaris, P. aureus, Pisum sativum, Vicia sativa)* and grasses, wild *(Agropyron trachycaulon, Lolium temulentum)* and cultivated (in genera *Triticum, Hordeum, Avena, Oryza)* (Frankel and Galun, 1977). Anthers are usually dehiscent in a bud. In *Striga asiatica* (Scrophulariaceae), a harmful parasite on grain cereals in North Carolina state (USA), the pollen is shed on the stigma in the flower bud phase. Pollen grains germinate immediately and fertilization occurs by the time a flower opens. In studies of natural populations of the same species in Nigeria, autogamy was not revealed (Nickrent and Musselman, 1979). Bud pollination by its functional value is rather close to cleistogamy.

Autogamy is more usual at the end of flowering, when cross-pollination with the help of wind or insects has not taken place for some reason (e.g., rainy and cold weather, absence of pollinators). In this case, autogamy has a clear function of ensuring pollination.

In flowers of angiosperms there are various adaptations to autogamy, not less surprising than adaptations that developed in them for maintenance of cross-pollination.

Autogamy is realized by different modes: direct contact of stigma and anthers (contact autogamy), pouring out of pollen from anther and its settling on a stigma under its own weight (gravitational autogamy), wind (wind autogamy), or the smallest insects living in a flower (thrips autogamy).

Contact autogamy (the term was first used by Hagerup, 1954) is the most usual. In the beginning of flowering, when opportunities for cross-pollination are not yet lost, anthers and stigmata ripen usually at various times or they are situated so that

direct contact between them is impossible. Later, there are changes in the relative positioning of anthers and stigma. They are connected with growth movements and there is lengthening or bending of stamens or styles, which is the reason open anthers and susceptible stigma end up at one level and in immediate proximity (Kerner, 1896, 1898; Knuth, 1898; Kugler, 1970). Contact autogamy can be observed in characteristic plants of a taiga - *Circaea alpina, Maianthemum bifolium, Trientalis europaea* (Knuth, 1898; Ponomarev and Vereshchagina, 1973). Similar mechanisms of autogamy are marked in some cultivated Fabaceae such as *Arachis hypogaea, Glycine max, Pisum sativum,* and *Vicia angustifolia* (Frankel and Galun, 1977).

Contact autogamy can occur in other ways. In the Faroes, for example, the withering nimbus, being compressed, covers and brings together stigma and stamens in *Hypericum pulchrum, Lychnis flos-cuculi,* and *Armeria vulgaris,* causing self-pollination (Hagerup, 1951). According to observations of Hagerup (1951, 1954), confirmed by Shamurin (1958a,b), in some Ericaceae *(Andromeda polifolia, Arctostaphylos uva-ursi, Cassiope tetragona)* pollen is drawn on to the falling corolla slipping near the stigma. Closing of a perianth for the night or before rain also can result in autogamy (Kerner von Marilaun, 1898; Knuth, 1898; Kugler, 1970). For the listed plants autogamy has more or less casual character. There are no structural adaptations to autogamy in a flower and the reductions connected to it. When insects visit a flower, cross-pollination is quite probable. Obligatory contact autogamy was marked in *Asarum europaeum* (Daumann, 1972a,b; Ponomarev and Vereshchagina, 1973): even with functioning stigma (protogyny) anthers of six long stamens in an internal circle move between lobes of stigma and, being opened, always leave pollen on them. Germination of pollen and growth of pollen tubes is observed by the time anthers dehisce. Obligatory autogamy in *A. europaeum* is very close to cleistogamy. Sometimes in this plant there are closed flowers in which self-pollination occurs. Obligatory contact autogamy was also revealed in *Hypopitis monotropa* (Monotropaceae) (Hagerup, 1954; Ponomarev and Vereshchagina, 1973).

Gravitational autogamy is rather frequent for representatives of Ericaceae, Pyrolaceae, and Vacciniaceae: pollen appears on stigma shed from drooping flowers. Thus, the style in their flowers is directed not upward, but downward, which facilitates the hit of pollen on stigma. The wind can favour gravitational autogamy and geitonogamy, promoting more active spill of pollen from anthers (Knuth, 1898; Kerner von Marilaun, 1898).

Thrips, the smallest insects living in a flower, can promote autogamy (thrips autogamy). This form of autogamy is found among representatives of different families (usually with small flowers in dense inflorescences), more often in Asteraceae and Ericaceae (Knuth, 1898; Kerner von Marilaun, 1898; Hagerup, 1950; Hagerup and Hagerup, 1953; Shamurin, 1956).

Self-pollination (in any form) is considered a secondary phenomenon caused by extreme conditions of environment that are adverse for cross-pollination. In such cases it acts as insurance. Autogamy can play a positive role in settling in new territories when creation of a homogeneous population can be favourable, in the absence of necessary pollinators, for early flowering until pollinators appear, and in other situations.

Autogamy is more peculiar to annuals than to perennials (Fryxell, 1957; Williams, 1964; Frankel and Galun, 1977). According to Stebbins (1957), it is

connected with the following circumstances. Population size of annual plants is subject to significant fluctuations in different years. Autogamy allows such a population to be restored more easily and quickly, when it is reduced to a small number of individuals or even a single one. Besides, annual plants are usually connected with narrowly limited and particular habitats. Because of autogamy, their adaptation to habitats is quite steady and that gives them advantages in the competitive struggle (Levin, 1972a,b; Solbrig and Rollins, 1977). Nevertheless, in group autogamous annuals the opportunity for cross-pollination is not lost and that can raise heterozygosity of populations and create the conditions for their movement into and development of new habitats. Even the insignificant percentage of crosses can support sufficient heterozygosity providing gradual adaptation of populations to fluctuations of a climate and other factors of an environment. A certain level of genetic variability is supported in self-pollinated populations, too (Allard *et ah,* 1968).

Allogamy (Greek *allos*—another, *gamos*—marriage) is pollen transfer from one flower to the stigma of another one.

The term was introduced by Kerner von Marilaun (1891; see Kerner von Marilaun, 1896). The author subdivided allogamy into **geitonogamy** (neighbouring pollination in which pollen from one flower gets on another flower on the same individual) and **xenogamy** (a similar process between different individuals of the same species). Now geitonogamy is considered one form of self-pollination in terms of genetic relation.

In classical pollination ecology (Knuth, 1898), the terms "self-pollination" and "cross-pollination" were used only in relation to a flower. From then on there was confusion in the use of the terms "allogamy" and "xenogamy", which were quite often regarded as identical.

Geitonogamy (Greek *geiton*—neighbour, *gamos*—marriage) is the phenomenon in which pollination occurs within a single plant with transfer of pollen from oneflower to another in various ways. The term was introduced by Kerner von Marilaun (1891; see Kerner von Marilaun, 1896).

Geitonogamy is possible not only in hermaphrodite plants, but also in monoecious ones. Under the influence of its own weight, pollen from the upper flowers of inflorescences can get on stigmata of lower flowers. In this way there is pollination in lopsided brushes of many Ericaceae and Vacciniaceae in which all wilting flowers direct their fauceses to one side, obliquely downwards. When entomophily fails (Reader, 1975), pollen from upper flowers easily gets on lower ones. At the end of flowering the stigma always extends far beyond the perianth and can easily catch pollen from neighbouring flowers.

Such factors as the wind or visiting animals, more often insects or birds (in the tropics), can influence geitonogamy. Moving in search of nectar and pollen, animals, birds and insects promote geitonogamy. There may also be direct contact of susceptible stigmata of some flowers with opening anthers of neighbouring flowers. In such cases the lengthening of styles or staminal strings that facilitate contact of generative organs is frequently observed. Similar contact is quite often noted in dense inflorescences consisting of small flowers (e.g., in some species of Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Juncaceae). Numerous examples of geitonogamy are specified in the reports of Kerner von Marilaun (1891; see Kerner von Marilaun, 1896), Knuth (1898), Hagerup (1951), and Kugler (1970). It is notable

that geitonogamy occurs usually only at the end of flowering, when chances of cross-pollination are lost.

In the genetic perspective, geitonogamy is equivalent to autogamy as pollination occurs inside one genotype (idiogamy). Self-compatibility promotes geitonogamy. However, neighbouring pollination is also possible in dichogamous and self-incompatible plants as a reserve mode of pollination when cross-pollination fails. In such cases there is suppression of genes of self-incompatibility (S-genes) and a shift to more or less full self-compatibility (Williams, 1964). Dichogamy becomes as though erased owing to lengthening of initial phases (staminal or stigmatic) in development of a flower due to which these phases are combined and promote geitonogamy.

Geitonogamy as one form of self-pollination is found more often in annual plants than in perennials (Baker, 1955, Fryxell, 1957; Stebbins, 1957; Faegri and van der Pijl, 1980; Frankel and Galun, 1977). It has great value in weed plants, where according to the "law" of Baker (1955, 1967a,b) self-pollination is the condition for successful migrations.

Geitonogamy as well as autogamy is frequent in conditions complicating cross-pollination: in tundras (Shamurin, 1969; Kusnetsova, 1970; Tihmenev and Levcovsky, 1973), a dark-needle taiga (Ponomarev and Vereshchagina, 1973), high mountains (Amosova, 1980), and deserts (Hagerup, 1932; Demyanova, 1975).

Xenogamy (Greek *xenos*—alien, *gamos*—marriage) is cross-pollination. The term was introduced by Kerner von Marilaun (1891; see Kerner von Marilaun, 1896). The author understood it as transfer of pollen from a flower of one plant to the stigma of another plant. In modern studies of cross-pollination another term is frequently used: allogamy (Faegri and van der Pijl, 1980).

Cross-pollination occurs with the help of abiotic factors (water and wind) and biotic factors (animals). In the evolution of entomophily, ornithophily and chiropterophily, plants and animals had a set of mutual adaptations promoting cross-pollination. In many cases, changes in their attributes occurred together by co-evolution (Grant, 1949; Berg, 1956,1958; Baker, 1961,1963; Grinfeld, 1962; Proctor and Yeo, 1973; Susman and Raven, 1978; Armstrong, 1979; Ford *et al.*, 1979; Faegri and van der Pijl, 1980).

Anemophily in flowering plants is secondary, it has originated from entomophily. Anemophily is characterized by high specialization and represents the special form of adaptation of plants to the conditions limiting opportunities for biotic pollination, particularly entomophily. In middle and especially high latitudes the wind sometimes is a more reliable agent of cross-pollination than insects (Daumann and Synek, 1968,1972a,b; Kugler, 1970; Ponomarev and Demyanova, 1980; Faegri and van der Pijl, 1980).

Cross-pollination has been considered the basic type of pollination in angiosperms since the times of Sprengel (1793) and Darwin (1876). Morphological and physiological adaptations preventing or even limiting self-pollination are usual in angiosperm flowers. The main adaptations are sexuality, dichogamy, heterostyly and self-incompatibility.

Sexuality is usually considered to be the major adaptation for xenogamy, and dioecy is the most effective means of achieving this purpose. However, among botanists there is no consensus on an evolutionary estimation of dioecy as a final stage of sexuality. According to some, dioecy most effectively provides heterozygosity, and

consequently variability and viability (Zhukovsky, 1967). Other researchers do not incline to reassessment of the role of dioecy in the evolution of flowering plants. Williams (1964), for example, believes that dioecy represents only a short-term reaction on outbreeding: in competition with hermaphroditic species in which the system of self-incompatibility reduces inbreeding, dioecious species should disappear or come back to hermaphroditism.

Cross-pollination is promoted along with other sexual forms (e.g., monoecy, gyno- and andromonoecy, gyno- and androdioecy, trimono- and trioecy). This classification was developed by Kerner von Marilaun (1896,1898), Yampolsky and Yampolsky (1922), Rosanova (1935), Monyushko (1937), and Kordyum and Glushenko (1976). It is known that, within the limits of a species, many plants are found in various combinations of sexual forms. For example, in *Plantago media*, besides hermaphroditism, four more sexual forms are noted: gynomonoecy, gynodioecy, andromonoecy and androdioecy (Knuth, 1898). The variety of sexual forms is great in cultivated plants, too. In many monoecious Cucurbitaceae, with regard to one species but different varieties, not only quantitative ratios of staminate and pistillate flowers vary frequently, but also their distribution on plants. According to Kozhin (1941), in each real condition the direction of selection created forms with a structure and character that satisfied problems of cross-pollination in the best way.

The variety of sexual forms is increased with male and female sterility (Jain, 1959; Krupnov, 1973). In similar cases hermaphroditic flowers depending on a degree of gyno- or andro-sterility act as unisexual or functionally unisexual, and such plants are called physiologically male or physiologically female (Rosanova, 1935).

The above-mentioned adaptations to cross-pollination (dicliny, dichogamy, heterostyly) are connected to structural features of flowers. The most effective physiological barrier against self-pollination is considered to be self-incompatibility. It is widely distributed among flowering plants (Bateman, 1952; Lewis, 1949, 1954, 1979; Fryxell, 1957; Nettancourt, 1977; Charlesworth and Charlesworth, 1979).

A combination in the same species of the various systems promoting cross-pollination is of special interest. For example, in *Zea mays* monoecy is combined with dichogamy, and in monoecious species *Betula pendula* and *B. pubescens* self-incompatibility is found. In heterostylous plants, besides morphological barriers against self-pollination and self-fertilization, self-incompatibility is widely reported. The combination of heterostyly and self-incompatibility has a regular character; in this connection the heterostylous system of cross-breeding can be considered one form of self-incompatibility (heteromorphic incompatibility) (Lewis, 1949,1954,1979; Baker, 1953a,b; Crowe, 1964; Vuilleumier, 1967; Surikov, 1972; Nettancourt, 1977; Ganders, 1979; Vishnyakova, 1997).

Nevertheless, despite numerous adaptations to cross-pollination, in case of its failure the majority of plants can begin self-pollination. More often self-pollination occurs at the end of flowering and is accompanied by a disturbance of mechanisms of dichogamy and self-incompatibility. Moreover, depending on the conditions favouring xenogamy or interfering (e.g., non-flying weather for insects, absence of necessary insects, moving into new habitats) the same species can show a propensity to cross-pollination or self-pollination. High mobility and lability of pollination modes (Pervuchina, 1970) are peculiar to flowering plants.

Pollen-Ovule Ratios in Different Breeding Systems

Plant reproduction and propagation in different breeding systems are associated with certain energy expenditures for pollination. Energy expenditure for the pollination of one flower is usually called "pollen-ovule ratio" or P/O (Cruden, 1976a,b, 1977).

The breeding or recombination systems provide the equilibrium between the processes that create variability and the processes providing genotype reproduction. Three modal states of these systems are distinguished: open, limited and closed recombination systems. Characteristic of these systems are, respectively, broad outcrossing, preferable autogamy and agamospermy (Solbrig, 1976; Grant, 1981). There is an opinion that open recombination systems demand great energy expenditure. This is connected, first of all, with the flower adaptations—the changing of morphology, size and colour and the formation of pollen surplus for the attraction of pollinators and for cross-pollination (Ornduff, 1969; Solbrig, 1976; Cruden, 1977; Grant, 1981; Teryokhin, 1996). Cross-pollinated plants produce more pollen than self-pollinated plants (Baker, 1967a; Gibbs *et al.*, 1975), and the number of pollen grains per ovule is much higher in the former (Cruden, 1977).

The analysis of 86 species of flowering plants (Cruden, 1977) has shown that P/O increases in the following direction: cleistogams (4.7), obligate autogams (27.7), facultative autogams (165.5), facultative allogams (796.6) and obligate allogams (5859.2). There is an exception: representatives of the families Asclepiadaceae, Mimosaceae, Onagraceae, and Orchidaceae have very low P/O in comparison with other outcrossing plants. However, the efficiency of pollination is relatively high, because the pollen in these plants is gathered in massulae and pollinia (Cruden, 1977; Nazarov, 1995).

Energy expenditure (in calories) is consistent with the regularity found. For example, in *Impatiens capensis* the expenditure for the seeds formed as a result of cross-pollination in chasmogamous flowers is much higher (135 cal), than the expenditure for the seeds formed by self-pollination in cleistogamous flowers (65 cal) (Waller, 1979).

The discovery of P/O is becoming the necessary element of investigations in reproductive biology. For example, for tropical lianas *Combretum farinosum* and C. *fruticosum* characterized by low seed set, a high P/O value was found (4569.9). This fact testifies that the species studied are cross-pollinated plants and self-incompatibility is characteristic for them. Regardless of the pollinator activity, the degree of outcrossing in them is rather low (Schemske, 1980; Bernardello *et al.*, 1994).

A relationship between flower types (submarine and surface) and type of recombination system was found in *Potamogeton* species. Plants with submarine flowers are autogamous forms and have low P/O, while forms with surface flowers are characterized by allogamy and high P/O, the pollen being larger (Philbrick and Anderson, 1987).

It is known that establishment of different breeding systems in flowering plants has adaptive significance. When settling new territories (as with annual plants of the deserts), the pollination and breeding systems develop from obligate autogamy to obligate allogamy via intermediate systems with facultative auto- and allogamy (Lloyd, 1972a,b; Arroyo, 1973; Baker, 1974; Grant, 1981). The change of the breeding systems is accompanied by increasing P/O (Cruden, 1977).

Stigmatic and Ovular Receptivity—Facts and Hypotheses

In angiosperms, unlike in gymnosperms, the stigma-style forms a barrier between the pollen and the ovules. This barrier makes male gametophytic competition possible and hence natural selection (Ottaviano and Mulcahy, 1989); it also enables recognition between the male gametophyte and the female counterpart, which, according to the type of incompatibility, may occur at different points in the pistil (Heslop-Harrison, 1983; Williams *et al,* 1994).

Although many studies and reviews exist on pollen viability and how to prolong it, little work has been done on female receptivity. The length of female receptivity is important because the response of the male gametophyte may vary in relation to when pollination occurs (van der Walt and Littlejohn, 1996). In *Trifolium repens,* 60% fewer seeds are produced when pollination takes place on the fifth day that the flower is open than on the first day (Jacobsen and Martens, 1994). The aim of the present study was to define female receptivity and to make some hypotheses on what it depends on and how to prolong it.

With reference to a reproductive structure, the term "receptivity" indicates a disposition to accept or encounter the opposite sex. Many terms have been used to indicate different aspects of male and female receptivity; these aspects differ in concept and in the way they can be detected.

Pollen becomes available to dispersing agents when the anthers open. The fact is often overlooked but it is crucial because male receptivity, which decreases in time at a rate that varies from species to species (Pacini *et al,* 1997), begins from this moment. Pollen is regarded as viable when it has the capacity to germinate and to produce a pollen tube capable of reaching the ovules. The various ways of determining whether pollen has this capacity are reviewed by Stone *et al.* (1995).

Female receptivity can be regarded as the capacity of the gynoecium to allow pollen germination, pollen tube growth and fertilization of the ovules. When the stigma and style are distinct in the pistil, there is not only ovular receptivity but also stylar and stigmatic receptivity. The latter allows pollen germination, whereas stylar receptivity allows the pollen tubes to grow. Ovular receptivity enables the ovules to be penetrated by the tubes and fertilization to occur. For fertilization to take place, in most cases these three types of receptivity must coincide for at least a few hours. Stigmatic receptivity, on the other hand, may last longer than ovular receptivity (Nepi and Pacini, 1993).

Receptivity of the sexes in time. The anthers may open before the flower and female receptivity may begin before the flower opens (Pacini, 1992). In *Cucurbita pepo,* female receptivity begins the day before the flower opens (Nepi and Pacini, 1993); in *Mercurialis annua,* it begins a few days afterwards (Lisci *et al,* 1994).

The pollen can come from the flower that carries the pistil in the case of hermaphrodite flowers, from unisexual flowers on the same plant in monoecious plants, or from unisexual flowers on different plants in dioecious plants. Male and female receptivity must therefore work together to bring about fertilization and often to avoid self-fertilization.

In hermaphrodite plants, both sexes are not always receptive at the same time (Bertin and Newman, 1993). Because of the arrangement of the flower involucres, the male part, which is more external, is usually receptive first (Heslop-Harrison, 1972).

In *Macadamia integrifolia,* the anthers open two days before the flower and the stigma becomes receptive two days after anthesis (Sedgley *et al,* 1985). The receptivity of the two sexes is limited in time in plants in which anthesis occurs between opening and closing of the flower. However, female receptivity varies considerably from species to species and may be short or long. Examples of short duration range from a few hours in the Poaceae to a day in most Compositae (Heslop-Harrison, 1983). Examples of long duration range from three weeks or more in *Helleborus foetidus* and *H. bocconei* (Vesprini, unpublished data) to more than a month in some Orchidaceae. However, there is a fundamental difference between the orchids and the genus *Helleborus:* in the former the female gametophyte is not mature and completes its development after pollination (Fredrikson *et al,* 1988), whereas in *Helleborus* it is mature.

In cleistogamic plants, since the pollen does not travel in the atmosphere and the flowers do not open, the two types of receptivity have to be perfectly synchronized.

Receptivity may be phased in the flower or in the inflorescence, whether the latter consists of hermaphrodite flowers as in the sunflower or flowers of one sex such as the male and female flowers in *Ricinus.* This mechanism may be designed to avoid self-pollination, especially in hermaphrodite flowers. On the other hand, if the inflorescence has many flowers that are receptive at the same time, geitonogamy may occur.

Dry and wet stigmata. Stigmata have been classified by Heslop-Harrison and Shivanna (1977) as dry and wet according to whether or not there is stigmatic exudate. Stigmatic exudate is coupled with characteristics such as type of self-incompatibility or number of cells. The stigma of Fabaceae such as *Cassia* sp. may have a crater or orifice that is a continuation of the style canal (see below) and the ovary cavity (Dulberger *et ah,* 1994; Owens *et al,* 1995): only pollen falling on the orifice germinates. The stigmatic surface may be smooth as in *Fuchsia* or papillate as in many Solanaceae; the papillae may be unicellular as in *Actinidia deliciosa* (Gonzalez *et al.,* 1995) or pluricellular as in watermelon and other Cucurbitaceae (Sedgley, 1981; Nepi and Pacini, 1993). Stigma morphology is also related to the type of pollination and hence to the type of pollen-dispersing unit (Pacini and Franchi, 1997). For example, the feathery stigmata of the Gramineae and Urticaceae are well exposed so that they can trap pollen on the wind.

The surface of dry stigmata has a protein layer that often has esterase activity, determinant for pollen-stigma recognition (Mattsson *et al.,* 1974; Shivanna and Sastri, 1981). The rapid loss of receptivity of the stigma (silk) in maize seems due to loss of water and withering, which cause the cuticular rods to come together, preventing pollen hydration and pollen tube emission (Heslop-Harrison, 1979; Schoper *et al.,* 1987).

Stigmatic exudate is produced by stigmatic cells under the papillae and by the papillae themselves before anthesis; it builds up under the cuticle, which detaches from the wall (Kreitner and Sorenzen, 1985). In species such as *Acacia retinodes,* stigmatic receptivity begins as soon as there is exudate (Knox *et al.,* 1989); in others, such as *Petunia* and *Nicotiana,* receptivity does not depend on the presence of exudate (Shivanna and Sastri, 1981).

The type of stigma is a constant characteristic of the families; one of the few exceptions to this rule is found in the Liliaceae (Heslop-Harrison and Shivanna, 1977). Just as the stigma may be dry or wet, the pollen may or may not have a viscous coating of materials such as pollenkitt or tryphine. Various combinations of the

properties of these two reproductive surfaces exist (Pacini and Franchi, 1997). The duration of receptivity is not related to stigma type. In dry stigmata such as those of grasses, the duration is usually short, e.g., 6 hours in barley (Pande *et al.*, 1972).

Solid and hollow styles. Styles can be defined as solid or hollow. They are hollow, as in many monocots, when they have a roughly prismatic cavity and the pollen tubes grow on the wall surface of this cavity. They are solid, as in the Solanaceae and Compositae, when this cavity is absent and the pollen tubes grow in the intercellular spaces as in kiwi (Hopping and Jerram, 1979) or inside the cells as in spinach (Wilms, 1981).

Many species such as the lily, which has a wet stigma, have a hollow style containing exudate of a different chemical composition to that of the stigma (Miki-Hirosige *et al*, 1987).

Number and position of ovules. The placenta surface has an outer layer of transmitting tissue on which the pollen tubes grow before penetrating the ovules. In *Lilium regale* this tissue consists of cells with wall ingrowth of the transfer cell type (Singh and Walks, 1995).

The number of ovules per ovary may vary from one to many thousand as in the orchids. The fewer the ovules, the higher the male gametophyte competition; the more numerous the ovules, the higher the female gametophyte competition. In some cases, as in the Cucurbitaceae and some Liliaceae, the ovules, which are normally arranged in one or more rows in the ovary, are not all receptive at the same time, but some closer to the stigma or the opposite pole mature and are fertilized first (Stephenson *et al.*, 1988). This mechanism may enable pollen that is not the first to land on the stigma or that grows more slowly to fertilize. Hence these ovules or seeds are spatially separate from the first ones fertilized.

Functional limitations of receptivity. The duration of female receptivity depends on the receptivity of the various components of the pistil and also on functional limitations such as the opening and closing of flowers. In *Cucurbita pepo* the pistil is already receptive the day before anthesis but is inaccessible to insects (Nepi and Pacini, 1993). Female receptivity also begins before the flower opens in the Cruciferae, and bud pollination can be performed to overcome self-incompatibility (Shivanna *et al.*, 1978). The same is true in *Linaria vulgaris, Myrtus communis, Silene dioica* and *Solanum aviculare* (Pacini and Franchi, unpublished data).

Opening of the flower indicates that one or both sexes are receptive; closure or wilting of the flower, however, may indicate different things. It may be reversible in species with long periods of receptivity such as *Dalechampsia stipulacea* (Euphorbiaceae) and *Vicia faba*, the flowers of which open for a few hours a day, closing at night (see Nepi and Pacini, 1993). In *Nymphaea elegans* they open for three consecutive days (Schneider, 1982), the first day at 9 a.m. and the second and third at 8.30 a.m., and are already closed by 2 p.m. The flowers presumably close at certain times of day to limit access to pollinators and/or keep pollen viability and stigmatic receptivity high by protecting them from water loss during the heat of the day (Nepi and Pacini, 1993).

The flower may close or wilt as soon as pollination occurs; in many orchids this takes only 5-15 minutes and occurs after a given period, whether or not fertilization has taken place (Endress, 1994a,b).

Pollen tube growth is initially autotrophic (Mascarenhas, 1993), using only the water supplied by the female counterpart to rehydrate the pollen (Pacini, 1990), but as

soon as the tubes reach the style it becomes heterotrophic. This means two things, namely, that stigmatic receptivity is influenced by the water status of the plant, temperature and relative humidity (RH), especially in the case of dry stigmata (Schoper *et al.*, 1987; Jacobsen and Martens, 1994), and that stylar receptivity depends on substances that become available for pollen tube growth (Mascarenhas, 1993).

Pollen tube growth does not occur without obstacles or gaps that in turn affect the duration of female receptivity. Obstacles include thinning of the transmitting tissue, as occurs in the Gramineae (Heslop-Harrison *et al.*, 1985) and *Cucurbita pepo* (Nepi and Pacini, submitted). This may increase competition. Gaps include the ovary cavity between the end of the style and the placenta, as in *Lycopersicum peruvianum* (Webb and Williams, 1988), and between the base of the style and the obturator of the peach ovary, where the tubes stop for five days until the starch of the obturator hydrolyses to form a polysaccharidic layer (Arbeloa and Herrero, 1987). A similar phenomenon but with a slightly different physical mechanism occurs in *Pistada vera* (Martinez-Palle and Herrero, 1995).

Methods of determining receptivity duration. Stigmatic receptivity can be evaluated from a cytological point of view by observing the turgidity of the stigmatic papillae as described by González *et al.* (1995) for the kiwi. Other empirical methods include changes in colour and the presence of exudate, which may be reabsorbed when receptivity ceases, as in *Arum italicum* (Pacini and Franchi, 1981, and more recent unpublished data). Another empirical method is histochemical evaluation of enzymatic activities (e.g., esterase, peroxidase) (Dafni, 1992).

The only objective method consists in pollinating the stigmata at a known stage of development and checking whether the pollen germinates. The percentage of germination varies with stigma age (Nepi and Pacini, submitted), eventually falling to zero. In *Ricinus communis*, for example, the pollen fails to adhere to the papillae in the last days of stigmatic receptivity and percentage of germination drops sharply. Stigmatic receptivity is long in this species, and the stigma withers a few hours after pollination.

There are no empirical methods for evaluating stylar receptivity. The only way is to check for pollen tubes in style sections or crushed material if the style is short. A measure of stylar receptivity is obtained by comparing the number of pollen tubes at the apex and base of the style. No data are available on any differences in the duration of receptivity of hollow and solid styles.

Ovular receptivity can only be determined by direct methods, namely: by observing whether pollen tubes penetrate the ovule; by observing the growth of the ovary and its transformation into fruit; and by observing the number of seeds produced and their position in relation to the ovary axis in polyspermic fruits. The last method, however, is affected by competition for nutrients between developing seeds.

Growth of the ovary and development of seeds also occurs in apomictic plants. To ascertain that the plant is not apomictic, the stamens must be removed and the flowers bagged before the anthers open. If they develop seeds then they are apomictic.

In angiosperms, the pollen germinates on the stigma; experimentally, however, it can also germinate on stumps of style devoid of stigma or on ovaries without style or stigma (Bowman, 1984). This type of research has only been done for a basic

understanding of pollen germination, particularly to overcome self-incompatibility, but it has never been used to determine the duration of ovular receptivity.

The duration of female receptivity can be determined by the presence or release, by part of the pistil, normally the ovules, of chemiotrophic substances that attract the pollen tubes (Hepler and Boulter, 1987).

The duration of stigmatic and ovular receptivity is correlated with the duration of pollen viability, as in *Cucurbita pepo* (Nepi and Pacini, 1993). On the contrary, many orchids have long pollen viability and stigmatic receptivity (more than a month) but the ovules do not have a mature gametophyte and resume development only after pollination has occurred. Short and long stigmatic and ovular receptivity are found both in zoophilous and anemophilous species (Table 3).

Chronology of receptivity. In *Cucurbita pepo* (Cucurbitaceae) anthesis lasts from just after dawn to about midday of the same day, after which the flower closes. It has been shown experimentally that stigmatic receptivity lasts 4 days, from the day before to 2 days after anthesis. Stylar receptivity lasts 3 days, from the day before to the day after anthesis. Ovular receptivity lasts only 2 days, the day before and the day of anthesis. The ovary is not fertilized when pollination occurs one day after anthesis, but the pollen tube reaches the ovary. Two days after anthesis, the stigma is still receptive but the tubes fail to go beyond it (Nepi and Pacini, 1993).

Linaria vulgaris (Scrophulariaceae). Stigmatic receptivity lasts 15 or 16 days, starting 2 days before anthesis. The plant has a corolla with a spur in which nectar accumulates; the corolla withers and falls 3-7 days after anthesis, depending on the temperature regime. The stigma remains receptive for approximately another week.

Myrtus communis (Myrtaceae). Stigmatic receptivity is very long (11 days). Ovular receptivity lasts 5 days. The flower has more than 100 stamens that present pollen simultaneously for a mean period of 3 days, which corresponds to the period of anthesis of the flower. The stigma and ovules are receptive from a day before anthesis until after the petals and stamens have fallen. The same occurs in other members of the family, e.g., *Feijoa sellowiana.* In these species, as in *Linaria*, the attractants for insects are lost when the corolla and stamens fall, and the type of pollination changes.

Helleborus foetidus and *H. bocconei* (Ranunculaceae). The gynoecium of *H. foetidus* consists of two carpels and that of *H. bocconei* consists of three to five. The carpels are fused at their base. The stigma is dry with unicellular papillae; the styles are long and the ovary contains an average of 10 ovules in both species. Female receptivity was studied in these species without distinguishing the two components. The stigmata are

Table 3. Examples of long and short stigmatic and ovular receptivity in relation to type of pollination.

Mode of pollination	Stigmatic and ovular receptivity	
	long	short
Anemophily	*Mercurialis annua:* OR 6 d, SR 12 d	grasses: SR a few h
Zoophily	*Convallaria majalis:* OR 17 d, SR 20 d	*Cucurbita pepo:* SR 4 d, OR 2 d

SR, stigmatic receptivity; OR, ovular receptivity; d, days; h, hours.

receptive from when the flowers open until a week after pollination, irrespective of the period of receptivity in which this occurs. The stigma then withers. Flowers bagged to prevent insects from visiting them are receptive a month after the flower opens. The flower withers after 35 days, by which time it has lost its stamens and nectar. In both species, the sepals and petals, transformed into nectaries, are photosynthetic; this may explain the long life of the flower and its receptivity. The flower is self-sufficient and does not consume other reserves of the plant (Vesprini, unpublished data).

Arum italicum (Araceae). This species has a spadix-type inflorescence with the female flowers below and the male flowers above. On the first day of anthesis, only the former are receptive and insects bring foreign pollen. If pollination does not occur the first day, the female flowers remain receptive for an extra day and are self-pollinated by the pollen that falls from the overhanging anthers (Franchi and Pacini, 1996). Male and female receptivity are out of phase so that cross-pollination can occur. Failing this, female receptivity is prolonged for self-pollination.

Thus, the duration of stigmatic receptivity is closely correlated with the type of pollination, the number of ovules per ovary, and the type of environment. Many pollen grains at a time can reach the stigma by entomophilous pollination. In the case of *Cucurbita pepo,* bees take an average of 224 ± 181 pollen grains each time they visit a male flower, and most of them can be deposited on the stigma (Nepi and Pacini, 1993). With anemophilous pollination, the pollen grains mostly travel singly, as occurs, for example, in conifers and grasses, since grains are not coated with pollenkitt. They reach the stigma in clouds that become more and more rarefied with increasing distance from the pollen source (Lisci *et ah,* 1996). When the number of ovules per ovary is very high, stigmatic receptivity should be longer to enable many pollen grains to fall on the stigma and germinate. However, if an appropriate number of pollen grains reaches the stigma at an early stage, stigmatic receptivity ceases almost at once. This happens in anemophilous plants (Gramineae, *Mercurialis annua,* etc.) and entomophilous plants *(Helleborus,* Orchidaceae, etc.). The environmental parameters that most affect stigmatic receptivity are temperature, RH and soil moisture (Jacobsen and Martens, 1994; Fan *et al.,* 1995).

As far as ovular receptivity is concerned, we have two modes of maturation of the female gametophyte: (1) the female gametophyte may be mature before the pollen reaches the stigma; (2) the female gametophyte is not ready but completes its development once the pollen reaches the stigma. The advantages of the various types of receptivity being out of phase are discussed by Bertin and Newman (1993). Protracted receptivity, however, is uneconomical because energy is required to keep the female gametophyte viable. This may be why, in many orchids, stigmatic receptivity lasts more than a month and the ovules only develop the gametophyte once the pollen tubes have begun to grow in the style.

The high cost of maintaining male and female receptivity over a long period is often correlated with the maintenance of floral accessories such as nectaries and corollas. In the Gramineae and Cactaceae, male and female receptivity are brief. There are plants in which both male and female receptivity are long but intermittent, so as to protect exposed pollen and the stigma during the night or the heat of the day. Finally, there are plants in which male and female receptivity occur at different times; for example, in the hazelnut, the plant first invests only in the stigma and style, the other parts of the flower developing once pollination has occurred. This takes place in the

hazelnut from January to April, depending on the latitude; the ovary and ovules develop 16-20 weeks after pollination. In the meantime, the pollen tubes wait in the style. In the gymnosperms, fertilization occurs in a similar manner and can be regarded as a way of reducing the initial investment in female structures; the second part of the investment is made when the pollen tubes are growing in the style, that is, when fertilization is certain.

Pollination Failure in Natural Populations: Implications for the Conservation of Rare Plants

The familiar adaptations of angiosperm flowers to pollination by wind, animals and water are widely known (Proctor *et at,* 1996). They have been accumulated from the achievements of outstanding field biologists applying painstaking precision and single-mindedness to their studies, particularly during the end of the 19th century and the beginning of the 20th (Mailer, 1883; Knuth, 1906-1909; Church, 1908). More recently, pollination biological research has perceptibly shifted from an observational phase to an experimental one (Wilcock, 1980). Several sources are now available that highlight the applicability of new developments (Little and Jones, 1983; Real, 1983) and also the practical techniques employed in them (Dafni, 1992; Kearns and Inouye, 1993). It is now possible, for example, to document changes in pollen viability with time and climate, study germination and stylar growth using the fluorochromatic reaction (FCR) test (Thomson and Thomson, 1992), track pollen flow by paternity analysis using polymorphic marker loci (Meagher, 1986), identify supporting nectar sources on pollinated stigmata by identification of foreign pollen (Neiland and Wilcock, 1994), detect pollen carryover by radioactive labelling (Schlising and Turpin, 1971), and determine the presence of non-random mating after pollination from anatomical studies (Hill and Lord, 1986).

Pollination is the primary step in seed formation and pollen spread is a critical dispersal phase that permits the mating of genetically different individuals during sexual reproduction. The central role played by pollination mechanisms in the breeding system of angiosperms is widely recognized (Richards, 1986) and the outcomes of interbreeding have a major influence on evolution and population structure. The integrated roles of pollination and breeding system are best understood as part of the reproductive process as a whole, including the processes of seed formation and development, dispersal and seedling establishment, and it is only from studies in all these areas that reproductive success can be fully established. Volumes such as *Plant Reproductive Biology, Patterns and Strategies* (Lovett Doust and Lovett Doust, 1988) and *Ecology and Evolution of Plant Reproduction* (Wyatt, 1992) have served to highlight the diversity of achieving successful plant reproduction rather than to uncover guiding principles but, nevertheless, these complexities provide fascinating insights into our present knowledge of reproductive processes. At the same time, a considerable broadening of our understanding of the physiological processes of sexual reproduction has been achieved by plant biochemists using as laboratory organisms agriculturally important crop plants such as maize (Heslop-Harrison, 1987), but the full impact of these studies for wild plants in a natural environment has not yet been fully appreciated.

Many different mechanisms of pollen transfer can exist within a single ecosystem, including both biotic and abiotic modes, and most communities exhibit a wide diversity, often within a small area (the Mediterranean; Aronne and Wilcock, 1994).

Three broad types of pollination syndrome have been identified by Proctor (1978), which he supposed evolved at an early stage in angiosperm evolution and between which plants have been continuously changing. These types are wind pollination, specialized zoophily and generalist zoophily (Table 4). Both Proctor (1978) and Moldenke (1975, for data from California) show that a wide spectrum of pollination mechanisms is present in most communities and that the more stable communities have slightly higher proportions of specialized zoophily.

However, neither Moldenke nor Proctor point to the likely responses to environmental stress inherent in the different types, although Proctor notes that in some important families adaptations have apparently reached a dead end. This clearly applies to the special resource-independent pseudo-copulation mechanisms present in such orchids as *Ophrys* spp., where adaptations inevitably lead to a closer and closer simulation between mimic and model. Indeed, from the most recent data the mimics bear not only the olfactory and optical characteristics of the model, but also tactile ones (Agren *et al.*, 1984). In such circumstances these specialized mechanisms are clearly at great risk from the loss of the special pollinator, even if environmental conditions change only enough to remove the bee out of the area of distribution of the orchid to a more favourable environment.

The two large families Asteraceae and Apiaceae are classic examples of generalist pollination mechanisms with easily accessible food rewards and dense, flat-topped inflorescences. These are usually visited by a wide range of promiscuous pollinators with most inflorescence adaptations characteristically diverted towards improvement of display. In both Apiaceae and Asteraceae, peripheral flowers in the inflorescences exhibit enlargement of one or more petals of the corolla (e.g., *Heracleum sphondylium* and *Chrysanthemum leucanthemum).* Further, the presence of a dark red central sterile flower in *Daucus carota* has been shown to increase pollinator visitation by stimulating the interest and aggregative behaviour of Muscidae and thereby increasing pollination activity (Eisikowitch, 1980). Such species, which are effectively pollinated by a wide taxonomic diversity of pollinators, are clearly more

Table 4. Pollination syndromes, pollen economy and their sensitivity to the effects of environmental change.

Pollination syndrome	Pollen economy	Pollinator sensitivity to environmental change	Examples of plant families
Specialist zoophily	Highly efficient	Environmentally sensitive	Orchidaceae
Non-specialist zoophily	Intermediate	Environmentally buffered	Asteraceae Apiaceae
Anemophily	Highly wasteful	Independent of animals	Poaceae Cyperaceae

environmentally buffered than their special counterparts. Small-scale environmental fluctuations are unlikely to cause any long-term reproductive failure in these plants. Only those in an area subjected to an environmental catastrophe, caused, for example, by pesticide use or reduction of insect population due to extensive agriculture, will be likely to experience a significant depression in seed set.

The pollination of anemophilous species is independent of animals and, at first sight, appears to be of greatest adaptational benefit for long-term pollination success, but this potential benefit must be balanced by the greater need to produce more pollen to achieve successful reproduction and therefore imposes an additional resource cost (Aronne and Wilcock, 1994).

While the special zoophilous mechanisms should be closely examined for any effects of pollinator loss, pollen itself may be at risk from loss of viability in a changing environment. The effects of growing conditions on pollen viability have been recognized only recently. Pollen viability decreases more rapidly on exposure to higher humidities and temperatures, and Pacini and Franchi (1984) have shown that the male gametophyte is more sensitive to drought than the female.

Pollination, resource allocation and reproductive failure

Resource allocation to male and female function at the time of reproduction places an additional demand on the nutrient balance of an individual plant (Aronne and Wilcock, 1994), and the critical resource may be energy, a mineral nutrient, or even water (Willson, 1983). Energy-efficient means of pollen transfer have evolved (Richards, 1986) and it is increasingly clear that the resources allocated to pollination are subject to selection for economy. Aronne and Wilcock (1994), for example, have shown that while both anemophily and zoophily occur in the Mediterranean ecosystem, the primary selective factor operating on the diversity of pollination and breeding system is resource limitation caused by nutrient and water stress. The anemophilous species produce pollen of lower caloric value than the entomophilous taxa (Petanidou and Vokou, 1990) but this must be balanced against the need to produce greater quantities of pollen because of a less efficient mechanism of pollen transfer. The formation of nectar as a reward poses a cost to reproduction. Pyke (1991) has shown that increasing nectar production experimentally from flowers by its removal (as in pollination) decreases seed number as a direct result of the additional costs of extra nectar production. Within the Mediterranean the entomophilous species follow two diverging trends. A group of dioecious taxa, in which nectar production is lower or absent in the females, is pollinated by small nectar-seeking insects that visit females by mistake, e.g., *Osyris alba* (Aronne *et ah,* 1993). The second group is hermaphroditic taxa that do not maintain the advantage of hermaphroditism (over dioecy) without substantial reductions in pollination costs, which we have termed "pollination on the cheap" (Aronne and Wilcock, 1994). Such examples range from the offer of pollen-only rewards, as in the Asteraceae and Fabaceae, through the interfloral mimics within a population (where the mimic is nectarless, as in *Cerinthe major;* Gilbert *et ah,* 1991), to the numerous Mediterranean orchid taxa, which provide no reward at all for insect pollinators (Dafni, 1987) and are pollinated by deceit.

Evidence that deceptive pollination mechanisms may be affected by pollinator discrimination has been shown by Le Corff *et ah* (1998), where rewarding male flowers of *Begonia tonduzii* are visited 15.4 times more frequently by bees than the non-

rewarding, mistakenly pollinated females. This indicates that a high level of pollinator discrimination may operate in communities of flowers with varying degrees of floral rewards such that rewardless plants may be threatened by a reproductive bottleneck caused by pollinator behaviour. The inability to produce a nectar reward may pose a substantial threat to the reproductive potential of rewardless plants. Reproductive success in orchids worldwide is affected in this way with nectariferous species being, on average, twice as successful as nectarless ones in fruit set and, in addition, the absence of this reward is linked to rarity in British orchids (Neiland and Wilcock, original data).

So, clearly, pollination mechanisms must now be viewed as subject to the same rule of evolutionary efficiency in resource allocation as every other facet of the life of the angiosperm. Soil nitrogen levels have recently been shown to affect pollen performance and spatial heterogeneity in soil nitrogen can influence the paternity of seeds in plant population (Lau and Stephenson, 1993). Work with *Zea mays* has shown that water stress alone (rather than lack of assimilate supply) during flowering can decrease reproductive success (Zinselmeier *et ah,* 1995; Zhou *et ah,* 1997). Taken together the presence of resource-limited reproduction suggests that the reproductive success of plants may be significantly reduced when they grow in soils of low nutrient status and in environments subject to increasing temperatures and/or drought.

Recent studies of the pollination biology of *Dactylorhiza lapponica* have shown that successful pollination of this non-rewarding species is dependent on floral mimicry with *Pedicularis sylvatica* (Neiland and Wilcock, original data). Evidence of effective floral mimicry was shown by the presence of holes punctured in the functionless spur, probably by short-tongued bees. This attempt at nectar robbing is typical of some bee behaviour at P. *sylvatica* (Koeman-Kwak, 1973). There is no evidence of self-pollination in *D. lapponica* and the capsule set is very low (< 18%). With such low frequencies of successful pollination, the maintenance of a threshold level of pollinator density in the community is clearly critical. The recognition of the association between D. *lapponica* and P. *sylvatica* is an important step in obtaining a fuller understanding of the reproductive biology of this rare marsh orchid. Clearly, successful long-term management must also include in the protocol the maintenance of the nectar-rewarding P. *sylvatica,* so that pollination levels may be sufficient to maintain the pollinator population.

There is a high proportion of non-rewarding orchids in the Scottish flora and these generally exhibit lower levels of reproductive success than their rewarding confamilials. Community-dependent pollination in generalist orchids (which are conservation-sensitive) requires the recognition and conservation of the critical co-flowerers in the local habitat (Neiland and Wilcock, 1994). *Dactylorhiza lapponica* is just one of several orchids that probably belong to this category.

Pollen limitation and reproductive failure

Discrepancies in an ovary between the number of ovules produced and the number of seeds formed is sometimes due to the quantity and quality of pollen transferred (pollen limitation). Variations in abundance of pollinators can have a considerable overall impact on reproductive success. Fluctuations in pollinator abundance can occur naturally by environmental change or by human disturbance such as pesticide use and transformation of natural habitats into agricultural land.

Pollen limitation caused by loss of specific pollinators. Special mechanisms of pollen transfer are clearly at risk from the loss of the specific pollinator. Plants with this sort of pollination usually exhibit adaptations to the specific requirements of the pollinator, with much structural modifications of the flower, accurate pollen and stigma presentation, and high pollen economy (for example, the interaction between the *Yucca* moth and *Yucca* flower, James *et ah,* 1993, and the specific bee and wasp interactions with *Ophrys* spp., Kullenberg, 1973). In these cases the disappearance of the pollinator leads to total reproductive failure, from which there may be no evolutionary return (because of the extreme floral adaptation) except self-pollination or apomixis.

Ixianthes retzioides is a very rare shrub of the southwest Cape in South Africa and its floral morphology suggests pollination by a large oil-collecting bee. However, no such bee has been observed at the sites, in spite of several years of observation, and fruit and seed set is very low (Steiner, 1993; see Table 5). Crossing data show that the species is self-compatible and that a limited amount of fruits (10.6%) and seeds (2.6%) forms by self-pollination. Over and above this level are the small amounts of additional fruit and seed set caused by pollinating visits from pollen-collecting insects. Steiner concludes that *Ixianthes* has lost its specific pollinating bee and suggests that environmental fluctuations in the past may have eliminated or critically reduced the specialized pollinator population. Persistence of *Ixianthes* is the result of self-compatibility resulting in some self-pollination and the occasional pollinating activities of pollen collectors. The long-term future of the species will depend on floral flexibility and the gradual adoption of new pollinators.

A similar situation may have occurred in some European *Ophrys* spp., a few of which have extended ranges well beyond the Mediterranean region where there is the greatest species concentration. *Ophrys apifera* and *O. sphegodes* are both frequently self-pollinated by the falling of the pollinia from the rostellum on to the stigmatic surface below. Visitation and effective pollination of these two species is rare and most fruit set is probably attributable to selfing events. The special pollinators of these taxa are rare or absent and, again, the plant-pollinator interaction appears to have become uncoupled. The frequency of self-pollination appears to maintain populations and has permitted dispersal well beyond the probable range of the special pollinator (Godfrey, 1921).

Pollen limitation caused by fragmentation of the habitat and reduction of pollinator abundance. Fragmentation of the habitat and subsequent distribution restrictions of a plant species range have been shown to reduce reproductive success. Jennersten (1988) has shown that habitat fragmentation of the butterfly-pollinated *Dianthus deltoides* in southwest Sweden reduced pollination success by 75% in the

Table 5. Fruit and seed set in *Ixianthes retzioides*, a rare shrub of the Scrophulariaceae from the southwest Cape (modified from Steiner, 1993).

Treatment	**n**	**Fruit set** (%)	Seed **set** (%)
Open pollination	251	19.1	6.5
Bagged, unmanipulated	211	3.3	12.3
Selfed	48	100.0	37.3
Outerossed	97	96.9	43.8

Table 6. Effect of habitat fragmentation on seed set in mainland and island sites of open-pollinated *Dianthus deltoides* in southwestern Sweden (from Jennersten, 1988).

Year	Site	Mean seed number	Mean ovule number
1986	Mainland	65.34	120.06
	Island	27.11	113.09
1987	Mainland	52.22	97.06
	Island	23.65	99.97

fragmented area because of lower diversity and abundance of flower-visiting insects compared within the larger area of distribution (see Table 6). Island populations generally may have lower seed set than mainland populations because lower pollinator availability results in pollen limitation (Spears, 1987) and the presence of a higher proportion of generalist pollination mechanisms in islands has been interpreted as a result of island-induced reductions in pollinator diversity (Linhart and Feinsinger, 1980).

The loss of seed set observed in Victorian coastal populations of the rewardlesss Australian orchid, *Thelymitra epipactoides,* has been attributed to the reduction of the flowering plants in these heathland communities by constant fires, and the consequent lack of ability of the floral community to remain attractive to potential pollinators (Cropper and Calder, 1990). Elsewhere, the orchid is pollinated deceptively by polylectic bees of the genus *Nomia,* which forage for pollen in the more flora-rich communities.

The impact of fragmentation on population size may cause widespread reproductive failure for a variety of reasons (see also Implications of reproductive failure for conservation - p. 93). The annual herb *Clarkia concinna* fails to produce seed in small, isolated populations because it receives insufficient pollinator services (Groom, 1998). Small, isolated patches attract few pollinators, have chronically low reproductive success, and have correspondingly higher extinction rates than large patches, regardless of their degree of isolation.

Pollination limitation caused by competition for pollinators. Competition for pollinators may induce pollen limitation in poor competitors and frequently occurs among co-flowering species sharing the same set of pollinators (Rathcke, 1988). Karron (1987) has shown that the rare *Astragalus linifolius* receives significantly lower levels of pollinator visitation than its more widespread congener, *A. osterhouti,* when growing together in the same habitat (see Table 7). It is possible that this low success in competition for pollinators may have contributed to, and probably helps to maintain, the rarity of *A. linifolius.*

Nectarless species should lose to nectariferous species in competing for pollinators when sharing the same habitat. These species may reward their pollinators by pollen presentation or be completely non-rewarding. The presence of floral mimicry, e.g., *Orchis israelitica* with *Bellevalia flexuosa* (Dafni, 1987) and *Cephalanthera rubra* with *Campanula* spp. (Nilsson, 1983), among the non-rewarders has been reported for several other orchids (Weins, 1978; Dafni, 1984) but is probably more widespread than generally realized. Pollen-only rewarders appear to achieve high levels of pollination success in many habitats, without the need to support their pollinators with nectar. The pollinators are generalists, often being physiologically

Table 7. Visitation rate to two co-occuring *Astragalus* spp. from Colorado (from Karron, 1987).

	Visits/hour			
	per plant		per 100 flowers	
	1984	1986	1984	1986
Astragalus linifolius (restricted)	**4**	**4**	**8**	7
A. linchicarpus (widespread)	**16**	**10**	**28**	32

Note: $p < 0.05$.

maintained entirely by other co-flowering species in the community. The strategy of deceptive pollination, although energy saving, appears to be less reproductively successful than that of closely related rewarding counterparts (Melampy and Hayworth, 1980) and is at great risk from learned avoidance behaviour by intelligent pollinators.

From studies of the corbicular contents of bees visiting *Cimicifuga rubifolia* and C. *data*, two restricted North American endemics, Pellmyr (1986) has shown that the two species exhibit different solutions to the problem of insufficient pollinator attraction. Although possessing the same general floral morphology, C. *data* is geitonogamous, while *C. rubifolia* is obligately xenogamous and dependent on associated nectar-producing plants for attraction of its pollinators. Consequently there was pollen of only one other floral species among the corbicular pollen of bees collecting in the habitat of C. *data*, whereas the loads were much more diverse on bees collecting from C. *rubifolia*. The possibility of between-flower self-pollination in C. *data* ensures that virtually every bee visit results in pollination when visit frequencies are low. Self-incompatible individuals will be at a strong selective disadvantage by having high reproductive failure with low pollinator frequency, and mutations inducing self-compatibility will be of selective advantage (Baker, 1955). In C. *data* there is a much higher pollen:ovule ratio than in C. *rubifolia* and pollinators are rewarded with pollen. However, C. *data* has insufficient pollen (as well as being nectarless) to ensure pollinator constancy and is dependent for pollination on the pollinator density maintained by other rewarding species in the habitat. Nectar-seeking bees apparently encounter this species accidently while foraging in the community. This conclusion was supported by (1) negative correlation between fruit set and nearest nectar source (Fig. 15), (2) extended flowering period and (3) fruit set independent of *Cimicifuga* floral display and density.

Incompatibe pollination and reproductive failure

Plants have a wide range of mechanisms to prevent self-pollination, but genetically determined self-incompatibility poses potential difficulties in seed formation to rare plants living in isolated patches composed of one or a few genotypes, especially where pollen movement is limited in dispersal distance.

Linnaea borealis is a clonal, highly self-incompatible, dwarf shrub that forms widespread patches in boreal forests. Fruit formation is reported to be rare (Jackson, 1939; Polunin, 1959; Clapham *et al.*, 1962; Barrett and Helenurm, 1987; Ross and La

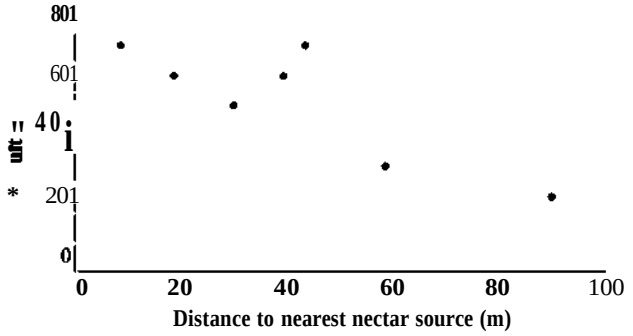


Fig. 15: Relationship between fruit set and nearest nectar source in *Cimicifuga* spp. (from Pellmyr, 1986).

Table 8. Percentage seed set in experimentally manipulated and open-pollinated flowers of *Linnaea borealis* at Deeside, Aberdeenshire (from Wilcock and Jennings, 1999).

Treatment	No. of inflorescences	No. of flowers	Seed set (%)
Xenogamous pollination	10	21	28.6
Autogamous pollination	9	16	0.0
Bagged, unmanipulated	64	126	1.6
Open pollination	93	173	16.2
De-sexed	6	12	0.0

Note: $p < 0.005$.

Roi, 1990; Eriksson, 1992). Open and experimental pollination at two sites in East Aberdeenshire (Table 8) has shown fruit set is not pollen limited but the result of lack of xenogamous pollination within large patches of a single genet (Wilcock and Jennings, in press). Seed set is increased among different genets in mixed patches of smaller size and hand cross-pollination increases seed set (Table 9). Limitation of seed set by the lack of xenogamous pollen transfer in large, self-incompatible clonal plants has been referred to as partner limitation (Eriksson, 1989). It has been reported to occur in *Rubus arcticus* (Tammisola, 1982), *Podophyllum peltatum* (Swanson and Sohmer, 1976) and the gynodioecious *Glechoma hederacea* (Widen, 1992). Widen and Widen (1990) have shown that the reproductive success of female clones was inversely related to the distance from the nearest hermaphrodite clone, and Laverty

Table 9. A comparison of seed set in *Linnaea borealis* at two different sites in North-Eastern Scotland (from Wilcock and Jennings, 1999).

Site	No. of genets	No. of inflorescences	Seed set (%)
Deeside	>4	281	25.1
Huntly	/	66	1.5

Note: $p < 0.05$.

and Plowright (1988) have shown a negative correlation between patch size and seed set in mixed populations of the self-incompatible P. *peltatum*. Partner limitation is probably a relatively common occurrence in clonal plants and may be especially common in rare or restricted populations.

In distant populations of highly self-incompatible species such as *Linnaea borealis*, composed of single genets or a few, it is improbable that pollen could move between them by natural pollination. Partner limitation reduces their capacity to produce seed so that population survival will depend on vegetative maintenance by the stolons alone. Recovery of such populations to new sites, without constant artificial intervention of new plants, depends on their capacity to produce seed. Evidence from this study, which effectively restored sexual reproduction to an isolated clone by artificial importation of pollen (Table 10), suggests that it is the absence of potential mating partners that is the main cause of reproductive failure in *Linnaea borealis* in Scotland. Thus, by transplanting small pieces of *Linnaea* of a suitable compatible mating type into sterile populations composed of single or only a few genets, it should be possible to greatly increase seed set through natural xenogamous pollen transfer. It will be important to establish the genetic structure of small widely scattered populations. If they mostly turn out to be composed of one or a few genets, the results of this study suggest a possible technique that may be employed in their long-term conservation without constant human intervention.

A similar impact of low population densities in self-incompatible plants on reproductive success has been reported in *Diplotaxis erucoiides*, where widely spaced plants had lower fruit set and fewer seeds per silique than did plants growing close to conspecific neighbours (Kunin, 1992). More recently (Daehler, 1998), evidence that founding populations of self-incompatible plants may experience reproductive failure has been found in *Spartina alterniflora*, where most plants in small populations flowered prolifically but set little or no seed. A few clones appeared to have consistently (from year to year) higher selfing capacities and produced most of the viable seeds in the population. Clearly, in recovering populations of rare, self-incompatible plants a great deal of dependence will need to be placed on those genotypes, if any, with some degree of selfing capability.

Implications of reproductive failure for conservation

It is increasingly evident that knowledge of the breeding system and reproductive biology of rare species is an important consideration in the development of protocols

Table 10. Restoration of sexual reproduction in an isolated population of *Linnaea borealis*, where the recorded level of natural fruit set is extremely low, by using imported pollen from another location (from Wilcock and Jennings, 1999).

Mode of pollination	No. studied	No. aborted	No. of fruits set	No. with embryo and endosperm	Seed set (%)
Flowers hand-pollinated with pollen from a distant population	40	26	14	14	35
Flowers tagged and open-pollinated at site	26	26	0	-	0

for their long-term conservation. Fieldwork, experimental pollination and laboratory studies are necessary to obtain a full appreciation of the critical steps of the reproductive cycle and to highlight the place where significant failure occurs. Examination of pollination failure is just one aspect of this process. From the evidence presented, studies of pollination biology in rare species are most likely to be of greatest relevance in the following situations:

1) species pollinated by special pollinators;
2) rewardless species/female flowers that depend on other co-occurring rewarding plants/male flowers for the maintenance of their pollinators;
3) species on the margins of agricultural land, or otherwise with a fragmented distribution;
4) populations of clonal, self-incompatible species with reduced genetic diversity;
5) species exposed to environmental change (by performing experimental pollinations);
6) species living in soils with low nutrient status or water stress.

Ex situ conservation of a large number of rare plants is unlikely to be undertaken because of the high maintenance costs to conserving institutes (Wilcock, 1990), and *in situ* programmes are likely to prove most cost effective. Detailed management schemes usually emphasize the need for reduction in large-scale herbivory and long-term monitoring of population changes. The pollination ecology of species with restricted ranges, or composed of only a few individuals, has received very little attention (Karron, 1987), but the value of biological studies of the plants concerned and particularly of their breeding systems is beginning to be recognized (Karron, 1991). Some reports are accumulating to show that the reproductive success of wild plants is extremely variable and susceptible to environmental changes (Travis, 1992) and that, when carefully examined, many plant populations exhibit very low levels of seed set in nature (Neiland and Wilcock, 1994). Pollination limitation is, of course, only one aspect of the reproductive process that may cause loss of seed set in plants, but recent data gathered in my laboratory have indicated that failure of pollination might be a major concern for conservation of rare plant species or populations.

The lack of pollination or successful fertilization in rare plants may lead directly to their extinction if they have no means of vegetative propagation. As pointed out by Bond (1994), some rare species at high risk from reproductive failure survive *in situ* through regular vegetative propagation. Because of their lack of reproductive success, however, the capacity of these species to respond to changing environments through evolution is severely compromised. Moreover, and perhaps more critically in the short term for their conservation, their capacity to **recover** and **spread** by seed recruitment is also compromised. As a result, such species are completely dependent on the identification (and removal) of any threats to their local habitats, since if these habitats are destroyed the only possible conservation action is immediate removal of the rare plants and their *ex situ* conservation.

We might expect rare species with reproductive difficulties but vegetative maintenance to accumulate in a community subject to increasing fragmentation and only slowly be subject to extinction, whereas those species with reproductive failure but no capacity to maintain themselves by vegetative propagation would more rapidly face extinction. It may be that the identification of whether a rare species has the capacity for maintenance by vegetative propagation might be the first, most

telling, step in the development of any conservation action plan aimed at its recovery. These two groups have been identified within the rarest Scottish plants and reproductive failure appears to be associated with species more restricted in Scotland than their distribution elsewhere would suggest (Wilcock and Neiland, 1998). Identification of the causes of reproductive failure should indicate whether there is any possibility of restoring natural reproduction within a population by conservation management (e.g., introduction of compatible mating partners as with *Linnaea borealis)* and the potential for longer-term survival without constant intervention. Recognition of a species with reproductive failure but without the possibility of its restoration by intervention should warrant conservation action to place a high priority on *in situ* habitat protection. Rare annuals, biennials and those species without vegetative propagation need regular monitoring to check that the population is not diminishing in numbers.

Significance of Hybridization in the Higher Plant Evolution

Hybridization in the higher plants was well known even to Linnaeus (1735), who produced artificial hybrids and assumed some species to be of hybrid origin. However, for a long time hybridization was not thought to have an essential role in evolution, as hybrids were considered either to be sterile or to split subsequently, forming the parent species again.

By the beginning of the 20th century, a great deal of new data on hybridization was accumulated, which permitted Lotsy (1916) to propound the hypothesis of hybridization as the main factor of plant world evolution. Popov (1927,1954,1956) and Anderson (1934,1949) supported this hypothesis that all angiosperms arose as a result of ancient hybridization between primary Cycadopsida and Gnetopsida. Stebbins (1956,1959,1969,1985) also stressed the role of hybridization in evolution, assuming in particular that the evolution of angiosperms has been "reticular" to a marked degree and that it was not the frequency of successful hybridization so much as the perspectives of its results for future evolution that had primary significance.

Heiser (1949) and some other authors were more sceptical about the role of hybridization in evolution. Such a position is usually suggested by presently occurring total or particular genetic isolation (with the formation of non-viable or sterile hybrids) existing between species of the same genus in any particular region. If species growing together hybridize successfully, they could be expected to evolve very soon into a single new species. That is why one cannot but agree with Popov (1927) that mass production of new hybridogenous species (including ancestors of higher-rank taxa) happens in critical situations, during substantial changes of the earth surface or climate, during which contact becomes possible between species and even whole floras that were earlier isolated from each other (e.g., after the drying up of the eastern part of the ancient Tetis Sea). In general, genetic isolation does not always occur between geographically isolated species.

During the Pleistocene glaciation, contacts between species coming down to the plains from mountains grew and when the glacier moved on Eurasia contacts of species of Siberian origin with European ones resulted in the creation of new species. The combination of human cultivation of species with different origins gave rise to many hybridogenous species, first spontaneous and then artificially obtained, such as

garden *Gladiolus* and *Dendranthema,* derived from the crossing of a series of wild species of these genera.

The opponents of the great evolutionary significance of hybridization processes often refer to the impossibility of creating something new by recombining genes already existing in parent species. The hybrids indeed possess intermediate features, often deviating to one or another of the parent species. However, even Lotsy (1916) mentioned in *Antirrhinum* as an example that absolutely new features also could appear as a result of hybridization. But the most important fact is that recombination creates absolutely new possibilities of evolution that can lead to the formation of new taxa of the highest ranks.

The result of the progressive evolution of hybridogenous taxa is determined partly by their despecialization, occurring during hybridization, in comparison with parent taxa. This happens partly because of the presence of two different hereditary bases in hybrids that creates their great adaptivity to new environmental conditions. Parent taxa, usually primary diploids, as a rule, possess imperceptible activity and diminish their areas, while hybridogenous taxa, usually amphipolyploids, become very active and rapidly extend their areas. For example, tetraploid (2n=28) *Aegilops triuncialis* is common for almost all the ancient Mediterranean area, but its diploid (2n=14) ancestors, *A. caudata* and *A. umbellulata,* have limited areas in South-West Asia and on the Balkan peninsula. The absolute age of A. *triuncialis* is said to be 8000-10,000 years. Another example is *Poa annua* (2n=28), which has turned out to be almost cosmopolitan and formed in the Pleistocene as a result of hybridization of the diploid (2n=14) species Mediterranean P. *infirma* and mainly Siberian P. *supina. Poa annua* not only adapted to a considerably larger range of ecological conditions (from the Arctic to the tropics), but also obtained an absolutely new peculiarity, the capacity to blossom during all seasons, from early spring till autumn frosts, whereas its ancestors had definite and short periods of flowering.

Another equally essential property of most hybridogenous taxa is their despecialization in reference to morphological (and probably other) features, which is likely the consequence of domination of more ancient and therefore more primitive features of their parents (Tzvelev, 1972, 1975, 1992). That is why the species of hybridogenous genus *Elymus* (2n=28,42) from Poaceae family appear less specialized in the totality of features in contrast with their diploid (2n=14) ancestors from the genera *Elytrigia s. I.* and *Hordeum s. I.* Hence, it is clear that while comparing only morphological features of close genera or species one could easily mistake more ancient ancestor taxa for younger versus their despecialized progenitors. There are similar examples and the fact that hybridization permits ancient highly specialized taxa to despecialize, in any case, already is of great evolutionary importance. Some despecialization of hybridogenous taxa induces considerable difficulties in reconstruction of phylogeny by means of the method of cladistic analysis. The possibilities of overcoming these difficulties are discussed in the work of Funk (1985), who also accepted the fundamental role of hybridization in higher plant evolution.

The role of hybridization in evolution is closely connected with the general biological significance of sexual processes, the appearance of which in the groups of primary organisms was a strong stimulator of their evolution. In sexual processes the fusion of two gametes with not quite the same genotypes also enables some despecialization of progenitors in comparison with their parents and hence, as Darlington (1937a,b) affirmed, the individuals of all species having sexual processes are hybrids in a manner.

Hybridization is considered to be one of the basic factors of increase of biological diversity in nature (Popov, 1927; Anderson, 1949; Gates, 1958; Bobrov, 1980; Tzvelev, 1991,1992). High organization in vertebrates and arthropods is the main hindrance to their hybridization. It is not accidentally that many zoologists accept genetic isolation as the fundamental criterion distinguishing species from subspecies. In the higher plants, which are at a much lower level of organization, this criterion is not valid.

However, in angiosperms, the higher specialization of flowers to entomophily results in considerable decrease of hybridization possibilities. In Fabaceae and Lamiaceae families, for example, many members of which have flowers pollinated by definite insect species, cases of hybridization are extremely infrequent, while in Rosaceae family with flowers opened for insect visits or in the anemophilous family Poaceae, even spontaneous interspecific hybrids are known: e.g,. *Sorbocotoneaster*, *Elyhordeum*(Knobloch,1972).

Let us also mention that the possibilities of stabilization of hybrids in annuals, as a rule, are much lower than of hybrids in perennials. This is probably due to the fact that the first blossoming of hybrids the flowers are often sterile, and during the next blossoming their fertility is partly restored. In annuals the first blossoming is the only one, and the occurrence of primary diploid chromosome number is frequently observed, while allied perennial species are polyploids. In this case, a mistake can easily be made if proceeding from chromosome number, holding annual diploid chromosome number derived from polyploid.

Of course, before hybrids become independent taxa, they have to stabilize and occupy a definite place in nature. Stebbins (1959) mentions two main modes of hybrid stabilization in the higher plants. First, it is very often achieved by means of amphipolyploidy, which frequently occurs even during hybridization and then results in quite stable and fertile hybrids: amphiploids. For example, the hybridization of the primary diploid (2n=14) wheat unigrain *(Triticum monococcum)* with diploid (2n=14) species of *Sitopsis* section of *Aegilops* genus resulted in the arising of tetraploid (2n=28) wheat species, which in turn, when hybridizing with diploid (2n=14) *Aegilops tauschii,* gave the most productive and widely cultivated soft wheat *(Triticumaestivum)*with2n=42.

The second mode of hybrid stabilization is realized in the course of introgressive hybridization, rather widespread in nature (Anderson, 1949; Zimmerman, 1966; Bobrov, 1980), when at repeated hybrid crossings with one of the ancestor species its fertility is gradually restored. In this case, because of the additional penetration of the genes of this ancestor into the hybrid genotype, it is able to stabilize without change of chromosome number. Introgressive hybridization often takes place during direct climatic changes, when one of the species, more adaptive to new conditions, attacks the position of less adaptive species, which infrequently become totally "absorbed" by attacking species as new hybridogenous taxa arise.

The widespread mode of hybrid stabilization in the higher plants also proves to be the transition to apomixis (the complexes of apomictic species are usually the result of hybridization of several initial species), viviparity or vegetative propagation. The fact that in extreme habitat conditions the possibilities of hybridization are extended also merits attention. The species of the genus *Poa* from the sections *Poa* and *Stenopoa* could exemplify this; they do not hybridize with each other in the temperate warm zone, but in the Arctic and high mountains hybridization becomes possible and results in the occurrence of intermediate hybrids by features intersection.

The data on genome analysis of genera from tribe Triticeae of Poaceae family (Dewey, 1982, 1984), demonstrating undoubtedly the great significance of hybridization in the evolution of this tribe, are very interesting. According to these data, the largest tribes, *Elymus* and *Leymus* (2n=28, 42), are derived as a result of the hybridization of diploid (2n=14) species of *Hordeum* and *Elytrigia* genera (from relation of *E. strigosa)* in the case of *Elymus*, and *Psathyrostachys* and *Elytrigia* (from relation of *E. juncea)* in the case of *Leymus*. The genotype of American species *Elytrigia smithii* was founded from four different genomes as a consequence of hybridization between the species *Elymus* and *Leymus* (Dewey, 1975). Love (1982,1984), based on genome analysis, offered the new system of Triticeae tribe, the genus number of which almost doubled; the genera with primary genomes in this tribe number 24, including nearly 200 species, and secondary, hybridogenous genera with compound genomes number 15, involving nearly 300 species. Some of the genera that Love distinguished are slightly isolated morphologically; however, the surplus information occurring in their genotypes appears to reflect on their future evolution.

It is obvious that the tribe Triticeae is not unique among angiosperms; it is only thoroughly studied genetically because it includes the most important crop plants, such as wheat, rye, barley and many valued fodder plants. There are some data on the other angiosperm groups also. Stebbins's (1959) proposal about the conceivable origin of the subfamily Pomoideae of Rosaceae family in the result of hybridization between the ancestors of Spiraeoideae and Prunoideae subfamilies is confirmed by cytological and biochemical investigations.

Thus, hybridization proves to be if not basic then one of the chief factors of higher plant evolution. Hybridization can give rise to successful phyla, which in due time become the taxa of the highest ranks. It permits many highly specialized taxa to despecialize and continue to evolve, promotes increase of biological diversity on Earth, supplying abundant material for natural selection, and plays a significant role in the selection of cultivated plants.

PART THREE-SEED PROPAGATION

AMPHIMIXIS AND APOMIXIS

Amphimixis (Greek *amphi*—both, dual, and *mixis*—mixing) is the process of female and male gamete unification leading to the formation of a new individual. Synonyms: fertilization, sexual process.

The term was first suggested by Weismann (1892). The modes of sporophyte formation in amphimixis are diverse; for example, in the lower plants holo-, iso-, hetero- and oogamy are distinguished. Amphimixis in animals refers to the short phase of fusion of male and female pronuclei (haploid nuclei of gametes) and formation of zygotic diploid nucleus or synkaryon. This phase follows the activation phase and is absent at gynogenesis (Reimers, 1991).

In the flowering plants amphimixis is represented by syngamy in the narrow sense, that is, "true fertilization", and in the broad sense by double fertilization, syngamy and triple fusion (see Syngamy; Triple fusion, Vol. 2).

Usually the term amphimixis is used in opposition to the term apomixis (gametophytic in a narrow sense). In addition, amphimixis is considered in various aspects: as a sexual process or fertilization, as a reproductive phenomenon (together with **apomixis** and **pseudomixis)** and as a **system of reproduction** (see *The Oxford English Dictionary,* 1989).

As a sexual process, amphimixis comprises **karyomixis** (Greek *karyon*— nucleus + *mixis)* or the formation of the zygotic synkaryon and of the synkaryon of embryo sac central cell, and **plasmomixis** (Greek *plasmat*—plasma + *mixis)* the fusion of male and female gamete cytoplasm.

However, proceeding from the original definition of amphimixis proposed by Weismann (1892), "mixing of the hereditary substance of two individuals", one can see that this term underlines genetic character and sexual mode of a new individual formation first of all, that is, it more exactly reflects the biological essence of the phenomenon than simply "fertilization" or sexual process.

In many textbooks and dictionaries, amphimixis is defined as "the mode of sexual propagation of plants and animals". In this connection it is necessary to recall that the terms "amphimixis" and "apomixis" cannot be used as synonyms of the terms "sexual" and "asexual propagation" respectively (see Reproduction, propagation and renewal).

The biological importance of amphimixis should be connected with the biological essence of the certain aspects of the fertilization process. Darwin, who revealed "the great law of nature", spoke about the progressive importance of sexual origination in the history of the organic world and considered cross-pollination the source of hereditary enrichment. Because of biparental inheritance (maternal from the egg cell and paternal from the sperm cell), amphimixis results in more viable organisms that possess a wider spectrum of variation than apomictic plants.

Apomixis (Greek *apo*—without, *mixis*—mixing) is formation of the embryo without gamete fusion. The term "apomixis" was first introduced by Haacke (1893) for animals, and later it was used by Maire (1900, 1901) in a somewhat different interpretation.

The various aspects of apomixis have been written about for more than 100 years. Considering apomixis in different plant groups, Winkler (1908) defined it as "the formation of sporophyte from the gametophyte cells without gamete fusion". In one of his last works (1934) he broadened this term to include viviparity (vegetative propagation—T.B.). Such interpretation of the term "apomixis" (all modes of reproduction and propagation that are not connected with the sexual process) was accepted by most authors (Fagerlind, 1940; Stebbins, 1941; Gustafsson, 1946,1947a,b; Maheshwari, 1950; Levina, 1961,1981; Poddubnaya-Arnoldi, 1976; Petrov, 1979,1988; Grant, 1981; Crane, 1989; Czapik, 1996a,b). A broad understanding of apomixis containing these heterogeneous phenomena demanded a more detailed definition of some statements. Cases of seed formation without fertilization unlike the seeds where embryo is formed as a result of syngamy are called "agamospermy" (Tackholm, 1922). In this connection, Fagerlind (1940) and Stebbins (1941) divided apomixis into "agamospermy" and "vegetative apomixis". Gustafsson (1947a,b) also accepted the term "apomixis" in its broad sense and demarcated two groups of processes: **propagation with the help of vegetative organs** (vegetative propagation, including viviparity) and **propagation by seeds,** where embryo is formed without fertilization, that is, **agamospermy.** In agamospermy he included **diplospory-parthenogenesis, apospory-parthenogenesis** and **adventive embryony.**

The views of Gustafsson were accepted by Grant (1981), who developed them in the closer definition of some peculiarities of sexual reproduction (specifically, the distinct division of the concepts of vicinism and autogamy).

Grant considers adventive embryony (nucellar and integumental) the type of agamospermy that most closely approaches viviparity as a form of vegetative propagation (or false viviparity, according to van der Pijl, 1972).

Some authors divide apomixis in the broad sense into four types (see Maheshwari, 1950).

1. In **irregular apomixis,** a haploid embryo sac is formed as a result of normal meiosis and the embryo develops from the egg cell **(haploid parthenogenesis)** or from the other cells of the gametophyte **(haploid apogamy).** The plants appearing in this way contain one set of chromosomes (n) and usually are sterile; apomixis does not recur in the subsequent generations.
2. In **regular apomixis,** a diploid embryo sac can arise from the archesporial cell **(generative apospory)** or from nucellar cells **(somatic apospory);** the embryo can appear from the egg cell **(diploid parthenogenesis)** or from another cell of gametophyte **(diploid apogamy).**
3. **In adventive embryony** or sporophytic budding, the embryo forms from the sporophyte (somatic cells of nucellus and integument), regardless of the mode of appearance and ploidy of gametophyte. Winkler considers this a peculiar case of vegetative propagation.
4. In the last **type of apomixis, flowers** are replaced by **bulblets** or other organs of vegetative propagation, which often germinate in the plant (viviparity).

However, the broad interpretation of the term "apomixis" does not reveal the discrepancies between the reproduction forms at the basis of generation alternation (heterophasic reproduction) and without generation alternation (homophasic reproduction). Battaglia (1963) was perhaps the first to consider the term "apomixis" in its more exact and narrow sense, as the process of heterophasic reproduction

without amphimixis participation. He categorizes the phenomena of sporophytic (adventive) embryony as homophasic reproduction, with vegetative propagation excluded from the term "apomixis". Khokhlov (1967) also excluded vegetative propagation from apomixis. Petrov (1988) considers apomixis to be like asexual propagation, connected with seed formation. Asker (1980) and Nogler (1984a) have marked out the term "gametophytic apomixis": the female gametophyte as the morphological formation exists, but usually meiosis and fertilization are absent.

Two modes of female gametophyte formation are possible in gametophytic apomixis: **apospory** and **diplospory** (see Apospory, Diplospory). In the literature, the development of diploid gametophyte and diploid embryos, which form from the cells of female gametophyte, is considered more often. Diplospory and apospory permit the preservation of alternation of generations even without nuclear phase alternation.

In apospory, the embryo sac is formed by means of mitosis from somatic cells of nucellus or chalaza of the ovule. In diplospory, the female gametophyte arises immediately from the archesporium or maternal cell of the embryo sac; usually meiosis does not take place. Aposporous and diplosporous embryo sacs develop relatively normally and the cells of the female gametophyte are able to give rise to parthenogenetic embryos.

Thus, two developmental directions arise: **diplospory-parthenogenesis** and **apospory-parthenogenesis.** Each of these sequences is found in a distinctly expressed form. They can be present in flowering plants simultaneously when both diplosporic and aposporic embryo sacs develop.

Diplospory and apospory do not exclude meiosis and fertilization completely. In exceptional cases, the reduced embryo sac matures, and both reduced and unreduced egg cells can be fertilized (Nogler, 1984b).

The **synergids** and **antipodals** can form **diploid parthenogenetic embryos** also, and more seldom **haploid** ones. Embryo development by apogamy was described for a number of flowering plants: from the synergids *Taraxacum, Hieracium, Alchemilla, Alnus, Lilium* and *Poa,* and from antipodals *Hieracium, Elatostema* and *Allium* (Maheshwari, 1950; Nogler, 1984a,b).

Thus, an **agamospermous plant produces seeds in which embryos or embryoids are formed exclusively asexually,** but sometimes **it can produce progeny as a result of sexual process.** The first case is obligatory apomixis, and the second is facultative apomixis. For example, *Hieracium aurantiacum* in the Carpathians (Poland) form fertile ovules of two types in one inflorescence. Some ovules contain reduced embryo sacs that were formed as a result of normal meiosis, while others contain unreduced embryo sacs that arose as a result of apospory. In the latter, embryo and endosperm develop autonomously, while in the former they need fertilization as a prerequisite to further development. Owing to this, in one inflorescence the embryos develop by both sexual and asexual modes. The ratio of seeds with embryos of the two types varies in different plants (Brow and Wilson, 1956).

Formation of normal matroclinous progeny (usually obligatory apomixis) and sometimes aberrant progeny (facultative apomixis) is observed in gametophytic apomixis. Various modes of development of aberrants exist (Asker, 1977; Nogler, 1984a).

As Nogler (1984a) notes quite fairly, **different forms of gametophytic apomixis and sexuality (sexual process) are not alternative** (in the formal sense) and represent

independent modes of formation of the new sporophyte, modes that can coexist in one species simultaneously. **The gametophytic apomixis does not suppress amphimixis and does not lead to complete loss of sexuality** as was supposed earlier. For all apomicts studied, **partial heterozygoty** was noted.

Moreover, it should be mentioned that plants with normal sexual process have the potential to form unreduced embryo sac, and this potential can be realized under certain conditions. The crossing of apomicts is possible, because almost all of them form a certain quantity of viable pollen. Nogler is probably right in that for the majority of plants **the sexual process and the female gametophyte formation** represent a **unified** (inseparable) process, while **for apomicts this connection** is probably **disrupted,** and this is the explanation of the "complexities" and peculiarities of **parthenogenetic (gametophytic) embryo** formation.

In recognition of the widespread notion of **agamospermy** as a "unified" process (realized with the help of seeds, but without gamete fusion), Nogler used the compromise term **"seed apomixis"** (= apomixis), which combines the processes of gametophytic apomixis and adventive (nucellar) embryony. In our opinion, the somatic embryos (embryoids) formed in adventive embryony cannot be unified with gametophytic embryos and cannot be included in the term "apomixis" (seed apomixis) owing to their different mechanism of development (homophasic and heterophasic reproduction respectively), though they develop in the seed.

Fagerlind, Stebbins, Battaglia, Grant and many others were probably right when, considering apomixis phenomena, they singled out gametophytic apomixis, and separate forms of sporophyte apomixis (including nucellar embryony) as peculiar type of vegetative propagation.

Besides, according to the logic of Nogler's reasoning, the phenomenon of monozygotic cleavage embryony (formation of twins, triplets and so on), as well as of integumental embryony should be included in apomixis. However, for intelligible reasons, the author ignores this phenomenon, though it also occurs in the seed and is often found in different flowering species (see Webber, 1940; Maheshwari, 1950; Lakshmanan and Ambegaokar, 1984).

Thus, there is no consensus about the content of the term "apomixis". At present the majority of authors use it in the narrow sense (gametophytic apomixis) or in a slightly broader sense (gametophytic apomixis + nucellar embryony).

In our opinion, many of the contradictions mentioned above that are connected with this problem, specifically concerning the role of different forms of embryoidogeny (nucellar, integumental and monozygotic cleavage) in reproductive systems, can be solved by considering embryoidogeny a new category of vegetative propagation (see Embryoidogeny is a new type of vegetative propagation). The cloning of the maternal organism (from cells of the same ovule) and the formation of matroclinous progeny occur in gametophytic apomixis and adventive embryony. In the first case the cloning is realized by means of parthenogenetic embryos from the egg cell, synergids, antipodals, and central cell (usually without the fertilization process). In the second case, it is a result of the nucellar and integumental embryoid formation. In monozygotic cleavage embryony, the cloning of the new daughter organism and formation of matroclinous progeny also occur, but usually with another genotype.

Apospory (Greek *apo-* without, *spord-* seed) is the process of embryo sac formation not from the megaspore but from somatic cells of the nucellus as a result of mitosis **(Plate III).** Synonyms: somatic apospory, somatic euapospory, euapospory, apomeiotic spory. The term was suggested by Bower (1885) for ferns.

Apospory has been observed in systematically different groups of flowering plants (Khokhlov *et al.*, 1978; Zhou-Zhi Qin and Yu Nong Li, 1995; Carman, 1997). This phenomenon is widespread among species of such families as Asteraceae, Poaceae and Rosaceae. In other families (Adoxaceae, Boraginaceae, Brassicaceae, Chenopodiaceae, Cyrillaceae, Cucurbitaceae, Globulariaceae, Myrtaceae, Orchidaceae, Polygonaceae, Ranunculaceae, Rutaceae, Taccaceae, Urticaceae), apospory was found sporadically in a few species.

Apospory can be observed cytoembryologically at early stages of ovule development from meiosis to the megaspore tetrad formation. In nucellus, two different processes often take place at the same time: differentiation of megasporocytes followed by meiosis and differentiation of the initial cells of aposporous embryo sacs. Aposporous embryo sacs are often more competitive than sexual ones. Nevertheless, the sexual (haploid) embryo sac and aposporous (diploid) embryo sacs might occur in the same ovule.

One or two initial cells of the aposporous embryo sac differentiate in the nucellus close to the megaspore or megaspore tetrad. Later, the number of these cells might increase. Not all initials are able to fulfil their potential to become the aposporous embryo sac; the most successful is the one that appears earliest. The position of aposporous initials in the nucellus is not strictly determined, but it cannot be subepidermal (Chen and Kozono, 1994; Naumova and Willemse, 1995). The positional effect of initials plays a great role and the aposporous embryo sacs placed closer to the micropyle are more competitive (Chen and Kozono, 1994). During differentiation of aposporous initial cells certain structural and functional reorganization occurs inside them (see Ultrastructural aspects of apomixis).

Two types of aposporous embryo sac development are known: Panicum-type and Hieracium-type (Rutishauser, 1969). There are some intermediate variations. The number of mitotic divisions that occur and the number of nuclei and cells of mature aposporous embryo sac are the main criteria by which the type is estimated.

Hieracium-type of aposporous embryo sac development is characterized by three mitotic nuclear divisions of the initial cell. Hieracium-type embryo sac is bipolar, consists of seven cells (three cells of egg apparatus, three antipodals and central cell with two polar nuclei) and morphologically is very similar to the meiotic embryo sac of Polygonum-type. Hieracium-type embryo sac was first described in *Hieracium* species.

Panicum-type of aposporous embryo sac is characterized by two mitotic nuclei divisions of the initial cell. The mature embryo sac is monopolar and consists of the egg cell and two synergids or egg cell and one synergid and central cell with one or two polar nuclei respectively. Antipodals are absent. This type of embryo sac was first described in *Panicum maximum.*

The nuclei in the aposporous embryo sacs of Hieracium- and Panicum-type are diploid and genetically identical to each other. In particular, the DNA content of the nuclei of aposporous embryo sac of Panicum-type in *Pennisetum dliare* was 2C according to Feulgen-reaction of cytometric analysis (Sherwood, 1995).

The fine structure of diploid egg cell of aposporous embryo sac is similar to that of haploid egg cell (see Ultrastructural aspects of apomixis). This finding explains the possibilities of fertilization and origin of triploid plants in nature and in experiments (Hanna and Burton, 1986). It was shown in grasses (Miroshnichenko, 1964, 1978; Matzk, 1991; Naumova *et al*, 1993) that the diploid egg cell has the ability to develop the embryo without fertilization. Often the formation of these parthenogenetic embryos starts before flowering, while the role of pollination in the initiation of diploid parthenogenesis is not yet clear.

The processes of endosperm development in aposporous embryo sacs as well as the viable seed formation are not well known. Theoretically the endosperm nuclei might be triploid (2n+n), tetraploid (2n+2n) or pentaploid. The formation of pentaploid endosperm nuclei (2n+2n+n) was shown in experiments by use of flow cytometry technique (Naumova *et al.*, 1993). These nuclei can be the result of the fertilization of two diploid polar nuclei with the haploid sperm cell.

New approaches to screen for apospory are in the process of development: molecular genetic (searching for molecular markers), flow cytometry (estimation of the nucleus ploidy level of generative cells), and histochemical (callose test) along with classical embryological methods using light microscopy and transmission electron microscopy (Lubbers *et al.*, 1994; Lutts *et al.*, 1994; Ozias-Akins *et al.*, 1994a,b; Naumova, 1997). The phase-contrast microscopy of cleared ovules with the embryo sac of Panicum-type can be recommended for the quantitative analysis of apospory in progeny at population level (Naumova and Wagenvoort, 1999).

Diplospory (Greek *diplos* - double and *spord)* is the process of embryo sac formation from unreduced megasporocyte or diploid megaspore due to abnormal meiosis or complete substitution of meiosis by mitosis **(Plate IV).** Synonym: generative apospory.

Diplospory was first described by Gustafsson (1939) and later it was included in classification of apomixis by Fagerlind (1940). Certain types of abnormal meiotic divisions were described: semi-heterotypic, pseudohomeotypic, apohomeotypic and mitotic division of the megasporocyte (Fagerlind, 1940; Battaglia, 1963; Solntseva, 1969,1989; Longly, 1984).

Semi-heterotypic division of the megasporocyte (in some representatives of Asteraceae) is different from normal meiosis (Fig. 16) and is characterized by abnormalities that occur in meiotic prophase I. There is no chromosome pair formation (asyndesis), univalents do not move to the cell poles but remain in cell centre, and the metaphase cell plate is not formed. All chromosomes sit together and as the result the nucleus becomes restitutional and diploid, the nucleus shape changes from double-bell to spherical. The second meiotic division is normal and it results in the formation of cell plate and two diploid "megaspores". One of the "megaspores" produces the embryo sac of Taraxacum-type (Fig. 16).

Pseudohomeotypic division of the megasporocyte was described by Gustafsson (1946). It was observed together with semi-heterotypic division in members of the Asteraceae family. The first meiotic division is modified and characterized by the presence of only unpaired chromosomes (univalents) rather than pairing configurations. The chromatids of each univalent are distributed on opposite spindle poles at anaphase I and dyad of cells with diploid nuclei are formed. The second meiotic division is omitted. A similar type of division was described by Jongedijk (1985, 1991) in aberrant diploid line of *Solarium tuberosum.* Some scientists

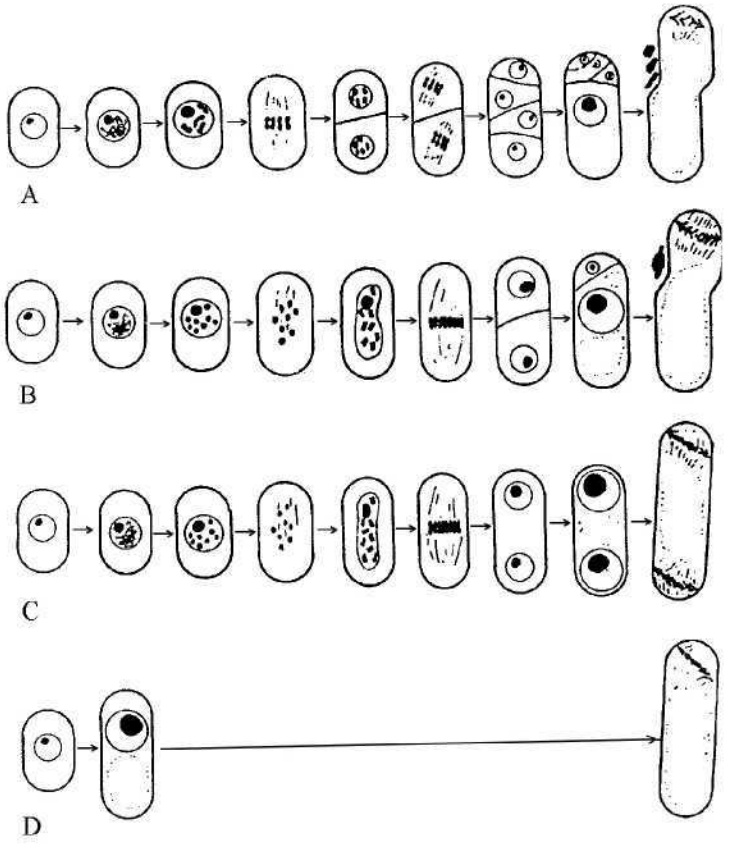


Fig. 16: Meiosis and megasporogenesis at diplospory (after Nogler, 1984, modified from Fagerlind, 1944).

A—typical meiosis and megasporogenesis; B — semi-heterotypic division and formation of two cells with diploid restitutional nuclei, chalazal cell develops into the embryo sac of Taraxacum-type; C — apohomeotypic division and formation of cell with two diploid restitutional nuclei, developing into embryo sac of Ixeris-type; D — switching over meiosis to mitosis with subsequent development of Antennaria-type embryo sac.

(Rutishauser, 1967) raised the question of the existence of pseudohomeotypic division.

Apohomeotypic division occurs when megasporocyte is followed by meiotic prophase I characterized by abnormalities, that is, there is asyndesis and later on the restitutional nucleus is formed, which follows mitotic division without cell formation. These two diploid nuclei produce the embryo sac of Ixeris-type (Fig. 16, C) as the result of two mitotic divisions.

Mitotic division of the megasporocyte (mitotic diplospory) is similar to normal mitosis by way of nucleus division. As a result of the first and second and third nuclear divisions the embryo sac of Antennaria-type is formed (Fig. 16, D).

Besides the types of abnormal meiosis mentioned above, there are numerous other varieties. Among scientists the idea exists that the differences between the abnormal meiotic types are not important enough and these subdivisions can be interpreted as formal. Nogler (1984a) showed that transition from one abnormal meiotic type to another and their close similarity can be observed in many representatives of Compositae *(Antennaria, Eupatorium, Taraxacum). A* similar conclusion was drawn by Izmailow (1986) and Czapik (1996a,b) as the result of investigations of the members of Rosaceae family, which possess multicellular archesporium. In these cases, the differences between the types of abnormal meiosis as well as between the types of apomeiotic (apomictic) embryo sac development become obscure (see Apospory).

The lack of callose deposition around the megasporocyte is one characteristic feature of diplospory (see Ultrastructural aspects of apomixis). At the same time, the callosic wall forms in megasporocytes that follow abnormal meiosis. It was observed in some species of genera *Elymus* and *Tripsacum,* where diploids were sexual but tetraploids and hexaploids showed diplospory (Crane and Carman, 1987; Carman *et al.,* 1991; Leblanc *et al.,* 1995b). Callose deposition test can be used to screen for diplospory in flowering plants.

Some types of diplosporous embryo sac development are described: Taraxacum-, Antennaria-, and Ixeris-types (Gustafsson, 1946; Battaglia, 1963; Solntseva, 1969; Nogler, 1984a,b). These embryo sacs differ from each other in the number of mitotic divisions, ploidy levels and distribution of nuclei inside the embryo sac. Diplosporous embryo sacs are often diploid, but aneuploid and tetraploid embryo sacs are also possible (Solntseva, 1989).

Embryo sac of **Taraxacum-type** is bipolar and consists of eight nuclei and seven cells; it originates from micropylar cell of the dyad, which was produced by semi-heterotypic division of the megasporocyte. The nucleus of this cell follows three mitotic divisions. The developed embryo sac consists of three cells of egg apparatus, central cell with two polar nuclei and three antipodals. All the nuclei of the embryo sac are diploid. The embryo sac of Taraxacum-type was described in the families Asteraceae *(Antennaria),* Brassicaceae *(Arabis),* and Poaceae *(Agropyron, Paspalum)* (Asker and Jerling, 1992).

The embryo sac of **Antennaria-type** is bipolar; it consists of eight nuclei and seven cells. It originates from the megasporocyte, the nucleus of which follows three mitotic divisions to produce embryo sac *(Poa palustris* and P. *nemoralis* - Zhirov, 1967, 1969; Osadtchiy and Naumova, 1996).

The embryo sac of **Ixeris-type** is bipolar; it consists of eight nuclei and seven cells. It develops from two-nucleate megaspore that originated as a result of apohomeotypic nuclear division of the megasporocyte; diploid nuclei follow two mitotic divisions to produce the embryo sac with three cells of the egg apparatus, central cell with two polar nuclei and three antipodal cells. The embryo sac of Ixeris-type is characteristic for genus *Ixeris* (Asteraceae) and *Statice oleaefolia* (Plumbaginaceae). There is the opinion that the differences between the embryo sacs of Ixeris-type and Taraxacum-type are not important enough and the Ixeris-type can be included in Taraxacum-type (Nogler, 1984a).

All three embryo sacs, Antennaria-, Taraxacum- and Ixeris-types, are similar to each other morphologically at the stage of maturity.

Some other types of embryo sac development that are a result of diplospory were described: e.g., Rudbeckia, Oxyria, Potentilla (Crane, 1989; Solntseva, 1989).

Diplospory is widespread among flowering plants *(Allium, Antennaria, Artemisia, Cucumis, Elymus, Hieradum, Ixeris, Paeonia, Poa, Potentilla, Rubus, Rudbeckia, Sorbus, Sorghum, Taraxacum, Tripsacum, Zephyranthes)* (Khokhlov *et al,* 1978; Carman, 1997; Shamrov, 1997a). Some of these genera show diplospory and apospory at the same time. Diplospory occurs in some economically important species: *Manihot esculenta*, *Sorghum bicolor* (Wu-Shu Biao *et al,* 1994; Ogburia and Adachi, 1996).

The parentage and controlling factors of diplospory are not known. There are some hypotheses based on data of genetics and cytoembryology. The genetic model of the regulation of diplospory on the example of *Taraxacum* was provided by Mogie (1988,1992). He proposed that only one locus of the chromosome controls the meiosis, where allele of wild type directs the meiotic reduction, while the additional copies of mutant apomictic gene regulate the apomeiotic processes directed to the formation of the egg cells with unreduced chromosome number. Dominant relations between the alleles are determined by their ratio and environmental factors.

Genetic regulation of diplospory was also investigated in genera *Amelancier, Beta, Potentilla* and in some hybrids (Asker, 1979; Jassem, 1990; Rieger *et al,* 1993; Peel *et al,* 1997). Only the nuclear genes were taken under consideration as the possible genetic regulators of apomixis. At the same time, it is significant that, in case of diplospory, the inheritance does not obey Mendelian laws. It was supposed that polyfunctional character of mitochondria and plastids that have DNA and the presence of canonical genes might be important in regulation of inheritance (Birky, 1991,1994). The role of cytoplasm in the processes of inheritance was discussed in a few publications. The hypothesis of controlling factors was forwarded on the basis of experiments with genera *Zea* and *Poa* (Maccklintock, 1956; Jacob and Wollman, 1961; Zhirov, 1967,1969; Zhirov and Shevtsova, 1970). A similar conclusion about the importance of cytoplasmic factors in inheritance was drawn by other authors who observed the apomixis loss in apomictic plants growing in tissue culture (Lehnhardt and Nitzsche, 1988). Cytological and genetic aspects of diplospory are intensively discussed (Hanna *et al,* 1991; Burson, 1994; Carman, 1997).

Information about the frequency of diplospory, parthenogenetic embryo development, and viable seed formation within the species, variety or sort is not abundant. Practically, the quantitative ratio between diplospory, parthenogenesis and apomictic seed formation (98%, 94% and 98% respectively) was calculated in *Allium tuberosum* only (Kojima and Nagato, 1997). These results as well as the data about hybrids that originated after crosses of sexual and apomictic plants are very important for the understanding of genetic mechanisms that regulate diplospory and apomixis.

Parthenogenesis (Greek *parthenos* — virgin, *genus* — origin) is embryo development without fertilization. The term was suggested by Owen (1849). Such formulation in essence is accepted by all embryologists, although there are some marked specific peculiarities of parthenogenesis in animals (Riger and Mihaelis, 1967; Tokyn, 1987) and plants (Maheshwari, 1950; Poddubnaya-Arnoldi, 1976; Bannikova and Khvedinich, 1982; Nogler, 1984a). This is connected with chromosomal sex determination in animals and double fertilization in plants. As for plants, their parthenogenesis is divided into reduced and unreduced. In the first case the embryo is haploid, in the second it is diploid or polyploid (as a result of apomeiosis). Below we give synonyms, which have been used from the early 20th century.

Unreduced parthenogenesis is parthenogamy, ovoapogamy, somatic parthenogenesis, zygophatic parthenogenesis, diploid parthenogenesis, gonial apospory, zygoid parthenogenesis, diploparthenogenesis, diplospory with following parthenogenesis, generative apospory, aposporic and apoarchesporic apozygoty, aneuspory.

Reduced parthenogenesis is generative parthenogenesis, homophatic parthenogenesis, true parthenogenesis, haploid apozygotic parthenogenesis, haploparthenogenesis, euspory, sporic apozygoty.

Unreduced parthenogenesis in angiosperms was first described by Juel (1898) and reduced parthenogenesis by Goldshmidt (1912) and Kusano (1915). Both forms of parthenogenesis have subsequently been found in some hundreds of species from different families.

Many embryological and genetic reasons for reduced and unreduced parthenogenesis have been discovered. (Poddubnaya-Arnoldi, 1976; Tyrnov, 1976a,b, 1992; Nogler, 1984a; Petrov, 1988).

At first sight, the phenomenon of parthenogenesis seems rather simple. However, many questions arise in connection with (1) non-synonymy of interpretations of some concepts, (2) new factual data, (3) discovery of common regularities in heterogeneous phenomena, and (4) absence of clear understanding of evolutionary and genetic-selective consequences of parthenogenesis. Genetic and biotechnological approaches to experimental production of parthenogenesis depend on the resolution of these questions. These factors are not fully reflected in existing classifications and terminology.

First of all it is necessary to answer the question, what is the principle of determination of parthenogenesis: "development without fertilization" or "development without egg fertilization"? The term "parthenogenesis" was originally used in relation to animals. Since they have no other female initials besides eggs, the main semantic load of the term "parthenogenesis" is "development without fertilization". The use of this term to describe plants raises certain terminological problems. In plants, the embryo sac contains, besides the egg cell, other cells (synergids, antipodals) that can give embryos without fertilization. The possibility of embryo formation even from endosperm cells cannot be ruled out (Johri and Ambegaokar, 1984).

Proceeding from this, parthenogenesis has to be understood as embryo development without fertilization not only from eggs, but from any cells of the embryo sac. Possibly, it is understood exactly so by some scientists. For example, they refer to "parthenogenetic development of polar nuclei" (Nogler, 1984a) or "parthenogenetic development of synergids" (Lakshmanan and Ambegaokar, 1984). However, the term **"apogamety"** is used more often for cases of embryo development not from eggs, but from other cells of the embryo sac (Poddubnaya-Arnoldi, 1976; Czapik, 1997,1998).

Introduction of an additional term, emphasizing one side of the problem, demands answers to two essential questions, at least: (1) How exactly does the term "apogamety" reflect an essence of the phenomenon? (2) Is apogamety one of the forms of parthenogenesis or are parthenogenesis and apogamety independent phenomena? The answer to the second question is given at the end of this article. The answer to the first cannot be positive if the following factors are taken into account:

1) Synergids and antipodals that do not realize their functions and behave like eggs cannot be considered synergids and antipodals, at least functionally.
2) A great number of facts are known concerning weak differentiation of egg apparatus cells and occurrence of so-called egg-like synergids as well as embryo sacs with morphologically almost identical cells of egg apparatus and antipodals (Gerassimova-Navashina and Batygina, 1958; Enaleeva, 1979).

For these reasons, the term "apogamety" is not widely accepted. Other authors confirm this opinion (see Apomixis classification). Some of them think that the term is entirely unnecessary (Nogler, 1984a). Probably, that last point of view is not correct for the present. Epigenetic variability of specialized cells is well known. They can lose a part of their genetic material that has become surplus in connection with narrowing of functions. So dedifferentiation (or another direction of differentiation) can have definite genetic consequences. Therefore, the potentially atypical course of gametogenesis must be reflected in the terminology. In addition, it must be verified whether dedifferentiation of typical synergids and antipodals is factually impossible (e.g., by some experimental influences and *in vitro* culture). We suppose that in cases where some cells of the embryo sac behave functionally like eggs but resemble other cells in some characters (e.g., topography, morphology), the term "gametoids", applied to animals, is more suitable to describe them (gametoids are structures that behave like gametes) (Riger and Michaelis, 1967). Consequently, the term **gametoid parthenogenesis** is used. If transition to embryogenesis is done by cells partly like synergids or antipodals or found in their typical place, this can be reflected as an additional characteristic (e.g., gametoid synergid parthenogenesis). In this case there is no direct embryo formation from synergid, which would be apogamety, but the cell that would become synergid behaves like a gamete.

The second range of questions is connected with so-called "virgin" development. The phenomena, which can be characterized as a result of "incomplete" or "atypical" sexual process, sometimes are related to a category of parthenogenesis. They can be connected with gynogenesis, androgenesis *in vivo* (male parthenogenesis), and hemigamy (semigamy).

Gynogenesis is embryo development in which the male gamete penetrates the egg cell, activates it to morphogenesis, but does not participate in subsequent development or participates to an insignificant extent (Riger and Michaelis, 1967). Sometimes, parthenogenesis and gynogenesis are practically considered the same and gynogenesis is thought of as "female parthenogenesis" (Poddubnaya-Arnoldi, 1976; Bannikova and Khvedynich, 1982).

At the same time, the effects observed in gynogenesis may essentially differ from those arising from truly virgin reproduction, when embryo development proceeds without the participation of male gametes. This is connected with the fact that extrachromosomal chromatin, cytoplasmic autoduplicated particles, and organelles can be introduced in the egg cell by penetration of sperm (Riger and Michaelis, 1967). The male gamete can be a source of unorganized nuclear chromatin and, consequently, DNA and RNA.

It is well known that exogenous nucleic acids provoke mutagenic, transformative and other genetic effects, and cytoplasmic inheritance of some most important characters is connected with organelles. Hence, gynogenesis can have significant genetic, evolutionary and selective consequences.

The phenomenon of plant development in culture *in vitro* from unfertilized ovaries and ovules is sometimes named "gynogenesis". In our opinion, this is absolutely inadmissible, even if only the essential definition of the term "gynogenesis" is taken into account. Probably, "parthenogenesis *in vitro"* would be a more acceptable term. But in some cases gynogenesis *in vitro* can actually take place. For example, experiments on haploid production are known in which pollination is carried out by dozens of irradiated pollen and then isolated ovaries are cultured (Raquin, 1985). This confirms the inadmissibility of confusion of the concepts.

In androgenesis (male parthenogenesis), the sperm nucleus replaces the egg nucleus. The latter does not function and is somehow eliminated completely (Tyrnov, 1986a).

Consequently, this phenomenon is parthenogenesis only in that the embryo develops from the egg cell, and full (true) fertilization does not happen. However, "virginity" can not even be mentioned here. The extent of participation of gametes in fertilization is here much higher than in gynogenesis. Male parthenogenesis gives rise to individuals, called nuclear-cytoplasmic hybrids or alloplasmatic forms, which have a nucleus of male parent and maternal cytoplasm. This was proved by use of lines with different types of cytoplasmic male sterility (Tyrnov, 1986a-c). It is also known that cytoplasm can influence many important characters: e.g., immunity, length of vegetation period, productivity, resistance to different biotic and abiotic factors. Therefore, male parthenogenesis essentially differs from female parthenogenesis in its genetic, evolutionary and selective consequences. There can be a situation in which both male and female parthenogenetic individuals are identical, for example in their development after self-pollination of homozygous (pure) lines. At the same time the disturbance of virginity is determined not only by the fact of fertilization and influence of maternal cytoplasm. It was stated that androgenic plants and their progeny can possess some nuclear characters of maternal form. It is suggested that that could be a result of disintegrated egg DNA influence. Such a phenomenon was discovered in maize (Tyrnov, 1986a).

In hemigamy (see Hemigamy, Vol. 2), the following variants are noted: (1) the sperm nucleus penetrates the egg cell, but it does not divide; (2) both egg nucleus and sperm nucleus divide simultaneously with or without formation of cell walls.

The consequences of sperm penetration in egg cell have been considered above. In hemigamy, additional phenomena are observed: chimerical embryos can arise, whose tissues have cells of maternal, paternal and hybrid types. The origin of the last is connected with fusion of maternal and paternal nuclei in the early stages of embryogenesis. In cotton (Turcotte and Feaster, 1973, 1974) and maize (Tyrnov, 1986a), lines were found that more frequently produced androgenic plants and plants that had chimerical tissues of maternal and paternal types. Their origin, in all probability, is also connected with hemigamy.

In maize we observed androgenic-matroclinic twins, and also androgenic and matroclinic seedlings in combination with hybrids. The phenomenon is characteristic of parthenogenetic lines (Tyrnov, 1986c). Matroclinic-androgenic twins were also discovered by crossing maize with apomictic *Tripsacum* ^{x} *Zea* hybrids (Belousova and Fokina, 1984). In connection with this, we think that hemigamy may not be connected with stimulation of egg cell by sperm, but that in apomicts the sperm comes into the cytoplasm of the egg cell, which is already activated to morphogenesis. It prevents karyogamy and simultaneously leads to division of nuclei and cells derived from

sperm. Thus, hemigamy can be a consequence of parthenogenesis, but the reverse is not true. Simultaneous manifestation of female and male parthenogenesis can be termed **biparental parthenogenesis.**

The problem of both maternal and paternal plant development as a result of chromosome elimination deserves special consideration. It has been shown that in some remote crossings zygote can form, but later, beginning with the first divisions of proembryo cells, chromosomes of one parent gradually, but rather quickly, are eliminated (Davies, 1974; Bennet *et al*, 1976; Jensen, 1977; Laurie *et al*, 1990; Pershina, 1995). Thus, in the beginning, the embryo develops like one arising from sexual process, but in the end it looks like the result of a "virgin" reproduction. The results of genome interactions in those cases have not been examined in full. Introduction of male parent organelles in egg, somatic crossing-over and inclusion of individual chromosomes is possible. Nevertheless, a variant can be assumed in which exclusively maternal characters are preserved (outwardly it more often looks so). In this case, the final results will not differ from those by true parthenogenesis. An appropriate term for this phenomenon does not exist. Since there is fertilization, the zygote is formed, but as a result of chromosome elimination, the return (reversion) to initial genome of one parent takes place and that can be termed **"reverse parthenogenesis".**

There is one principal difference of parthenogenesis in plant and animals. Double fertilization is characteristic of angiosperms, and most apomictic species are characterized by pseudogamy, i.e., a phenomenon in which the egg cell develops without fertilization, but the endosperm develops as a result of fertilization.

Formally such cases can be related to pure "virgin" development, since the male gamete cannot even come near the egg cell. However, it is known that by use of different pollen parents, pseudogamous apomicts can differ from one another by some characters (Nogler, 1984a; see Embryo-endosperm interrelations in apomixis). Endosperm influence on progeny is suggested. Therefore, only those cases are related to parthenogenesis in which embryo development combines with autonomous endosperm development. In a case of sexual origin of endosperm, it is possible to use the term **pseudogamous parthenogenesis.**

Thus, there are a number of phenomena having many common characters: parthenogenesis, gynogenesis, androgenesis, hemigamy, apogamety (gametoid parthenogenesis), reverse parthenogenesis. To create a classification and uniform interpretation of phenomena and concepts, it is necessary to reach an agreement about the following questions:

1. Is every one of the numerated phenomena an independent one or are some of them only details of others? For example, gynogenesis can be considered both an independent phenomenon and one form of parthenogenesis. Do the concepts reflect some final results or only the modes and causes of parthenogenesis?
2. Can parthenogenesis be considered a peak in the hierarchy of concepts or is it one of the forms of another phenomenon of higher order?

In our opinion, in relation to angiosperms, neither the arising of embryo from the egg cell alone nor "absolute virginity" can constitute the basis of determination and classification of parthenogenesis.

Therefore, the concept of parthenogenesis must be related to the phenomenon of gametophytic apomixis and it must be considered the mode of apomictic embryo

formation. The other concepts only underline some additional heterogeneous characteristics of parthenogenesis (structural, functional, topographic) or reflect cause-effect connections of attendant processes and phenomena. For example, gynogenesis and reverse parthenogenesis can be considered modes or causes of the origin of parthenogenesis and male parthenogenesis and apogamety (gametoid parthenogenesis) structural characteristics. Besides, male parthenogenesis can be a consequence of hemigamy and chromosomal elimination in maternal form. Therefore, the other phenomena can be considered forms of parthenogenesis differing in some specific peculiarities.

Take all this into account, a scheme of interrelations of parthenogenesis with different phenomena is proposed (Fig. 17). It is based on the following:

1) embryo development **from any cells of female gametophyte** that are able to play the part of gametes without fertilization, including the omission of typical joining of parental genomes in the case of penetration of male gametes in cell of female gametophyte;
2) division in forms, connected with fertilization;
3) phenomena that precede or accompany parthenogenesis;
4) the modes and reasons of parthenogenesis and structural peculiarities.

A short interpretation of additional terms and commentary on the basic scheme is given below.

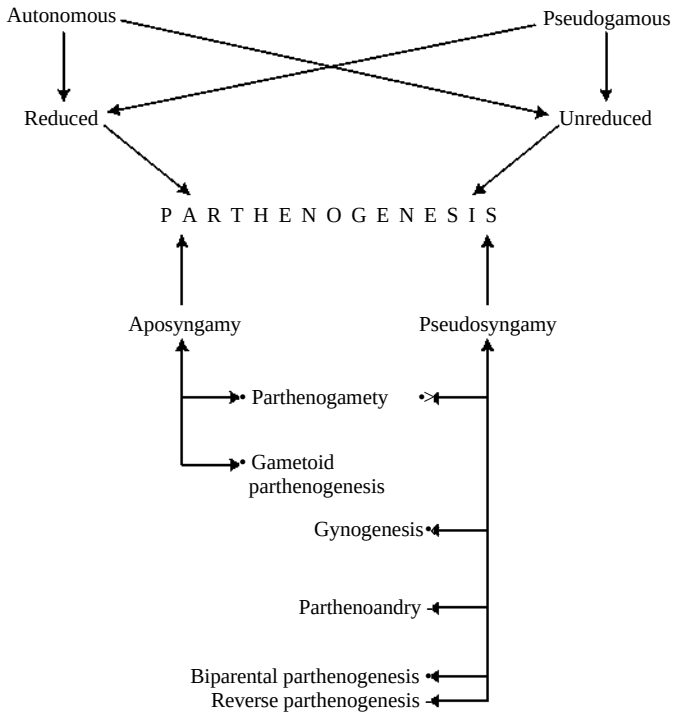


Fig. 17: Parthenogenesis in higher plants.

Aposyngamy is embryo development without participation of male gametes.

Pseudosyngamy is embryo development after fusion of male and female gametes without typical karyogamy, due to the fact that the progeny have karyotype and characters peculiar entirely or chiefly to one of the parents.

Parthenogamety is embryo development from the egg cell without participation of male gametes.

Parthenoandry is embryo development from the egg cell, the nucleus of which is replaced by sperm nucleus. This term is proposed instead of "androgenesis", which is a broader concept.

Gametoid parthenogenesis is embryo development from cells that in some characters can be related to other cells of the embryo sac, excluding the egg cell.

Biparental parthenogenesis is simultaneous male and female parthenogenesis in the same embryo sac; formation of hybrid and chimerical embryos is possible.

Reverse parthenogenesis is embryo development by elimination of one parent's chromosomes after karyogamy.

The use of other definitions included in the scheme depends on the problems connected with them, and on resolving some questions. The concepts of **pseudogamous** and **autonomous** are introduced because the presence of pollen by pseudogamy can be considered the condition of seed formation, the source of mistakes by diagnosis of parthenogenesis, a condition for return to sexual reproduction and segregation of new parthenogenetic forms after hybridization; autonomy (independence from pollination) is an extremely important evolutionary and selective character.

The concepts of **unreduced** and **reduced** serve as important genomic characteristics, since haploids and unreduced apomicts differ in selective and evolutionary possibilities. Including the concepts of **aposyngamy** and **pseudosyngamy** in the scheme is expedient because, in spite of the absence of typical fertilization, the mere penetration of male gametes in the female gametophyte can have serious genetic, evolutionary and selection consequences. In many cases, we do not know what has happened after pollination: e.g., gynogenesis, elimination of chromosomes. So, the term "pseudogamy" can be used as a partly integrative concept.

In some cases, additional characteristics can be included. For unreduced parthenogenesis, the following terms can be used to specify the mode of reduction elimination: automixis, apomeiosis, apo- and diplospory. The most important cytogenetic processes, conditioning crossing-over, recombinogenesis, and maintenance of homo- and heterozygosity, are connected with them.

Introduction of additional characteristics—**induced and heritable parthenogenesis**—is possible and can be provoked by environmental factors (temperature, hormones, anomalies of pollen) or genetic factors. Since induction of parthenogenesis is not inherited in the subsequent generations, it is difficult to study selection of parthenogenetic forms. Indications on the induced or genetically conditioned nature of parthenogenesis can be useful in many cases, especially for plant breeders.

The addition of such definitions as **obligate, facultative, cyclical,** and **abortive** to **parthenogenesis** in appropriate cases can not be ruled out. The last two definitions are used most frequently in relation to zoological objects (Riger and Mihaelis, 1967).

Abortive parthenogenesis can be an extended term for plants, since cases in which parthenogenetic development is not realized to the end and stops at any stage are frequent.

Such phenomena can be caused also in culture of isolated ovaries, ovules and embryo sacs. In those cases, the term "in vitro" is added (e.g., androgenesis *in vitro,* gynogenesis *in vitro).*

Apogamety (Greek *apo*—without, *gametes—spouse)* is development of additional embryos from unfertilized cells of the embryo sac, such as synergids (synergid apogamety) or antipodals (antipodal apogamety) **(Plate V).** Synonyms: apogamy, euapogamy.

This phenomenon was first described for ferns as apogamy (de Bary, 1878), or euapogamy (Farmer and Digby, 1907). The term "apogamy" was used in the first classifications of apomixis in flowering plants (Winkler, 1908, 1920), but later on it was replaced by the more exact "apogamety" (Renner, 1916), which is used in the modern classifications also.

Apogamety was found in the haploid embryo sacs of amphimicts and in diploid ones of apomicts. In the first case, it is called by various names, including meiotic (Farmer and Digby, 1907), generative (Winkler, 1908,1920), haploid (Hartmann, 1909; Renner, 1916; Fagerlind, 1940; Poddubnaya-Arnoldi, 1940), sporic (Khokhlov, 1958) or reduced apogamety (Poddubnaya-Arnoldi, 1964a, 1976). In the second case, it is called somatic (Winkler, 1908,1920; Hartmann, 1909; Ernst, 1918), diploid (Renner, 1916; Fagerlind, 1940; Poddubnaya-Arnoldi, 1940; Gustafsson, 1946, 1947a,b), zygophatic (Winkler, 1934), aposporic and apoarchesporic (Khokhlov, 1958) or unreduced apogamety (Poddubnaya-Arnoldi, 1964b, 1976), among other names. The prerequisites of haploid embryo formation from synergids are the differentiation of the synergids by the egg cell type (e.g., Iridaceae, Combretaceae), the weak differentiation of all cells of the egg apparatus, when all three cells are approximately equal in size and contain small vacuoles (Liliaceae, Brassicaceae), and long existence of the intact synergid. Obviously, the presence of the filiform apparatus in the synergid does not play a role because the synergid division can be observed in both cases: when it is not expressed (Liliaceae, Tetradiclidaceae) and when it is well represented (Alliaceae, Trilliaceae). The nuclear division in the synergid occurs after the egg cell fertilization, sometimes earlier than in the zygote; it is accompanied by cytokinesis. Cases of coenocytic embryo formation were noted in Amaryllidaceae (Vorsobina and Solntseva, 1990). In the majority of cases, synergid embryo develops only up to several cells and then degenerates. Apogametic embryos are smaller than zygotic ones, as a rule (Papaveraceae—Sachar, 1955; Trilliaceae—Naumova and Yakovlev, 1975).

Prerequisite for embryo formation from antipodals is the differentiation of the antipodal apparatus by the egg cell type (some species of the Asteraceae, Liliaceae, Ulmaceae-Plyushch, 1992; Pajak, 1998).

The synergid and, particularly, antipodal apogamety in the flowering plants are seldom found. The synergid apogamety is noted for 28 families, 17 orders of dicotyledonous plants and for 10 families, 5 orders of monocotyledonous plants. Antipodal apogamy is noted only for a number of families and, moreover, the most reliable data are for the family Asteraceae (the species of the genus Rudbeckia—Battaglia, 1955; Solntseva, 1973) and, obviously, Alliaceae (Modilewsky, 1925,1931).

The adduced values for frequency of apogamety in flowering plants seem to be somewhat too high at present (Solntseva, 1998).

It was suggested that **realized** (real) **apogamety,** when the synergid or antipodal embryos develop to maturity, be distinguished from **unrealized** (potential) apogamety, when such an embryo develops two or several cells and then dies (Kamelina, 1994a, 1995). Realized apogamety is one of the reasons for polyembryony. Such seeds contain, together with zygotic embryo, synergid or antipodal embryos (Alliaceae, Asteraceae, Liliaceae, Orchidaceae). In the majority of cases, unrealized apogamety is still observed.

Apogamety can be combined with other forms of apomixis: hemigamy, parthenogenesis, nucellar and integumentary embryony. It is very difficult to identify apogametic embryos in the last case. Parthenogenesis in combination with synergid apogamety is the most widely distributed phenomenon and can be observed even in aberrant ovules (e.g., in species of the Paeoniaceae family—Shamrov, 1997a).

Some authors of the apomixis classifications do not consider apogamety the original type of apomixis (Nogler, 1984a; see Classification of apomixis), or exclude the possibility of polyembryony with antipodal apogamety in flowering plants (Lakshmanan and Ambegaokar, 1984). However, the formed dicotyledonous antipodal embryo in the maturing seed found in *Rudbeckia laciniata* testifies to the presence of realized antipodal apogamety in this species (Solntseva, 1973).

To counter opponents, Czapik (1998) makes convincing arguments for the independence of this type of apomixis and notes that the main difference of apogamety from parthenogenesis consists in the origin of the proembryo initial cell. In parthenogenesis the initial cell is the egg cell; in apogamety the initial cell is the synergid or antipodal cell, but not the egg cell. What is more, attention is paid to the sexual form of apogamety, which was not considered earlier because it was not within the strict framework of apomixis. Cases in which the proembryo is formed from the haploid cell after its fertilization are referred to as the sexual form of apogamety. *Tamarix ericoides* (Tamaricaceae) can be the example of this: from one and even from two fertilized synergids, additional embryos develop and sometimes reach maturity (Sharma, 1939; Johri and Kak, 1954), that is, the realized synergid apogamety is observed.

There are a number of problems in studying apogamety, which are important for embryology and apomixis (Czapik, 1997,1998). These include not only terminology, but also early identification of cells in the embryo sac, their differentiation, specialization and the possibility of dedifferentiation, and also of the factors that influence the cell totipotency in the embryo sac, which are still unknown.

Classification of Apomixis

The first classification of apomixis was proposed by Winkler (1908, 1920). He included in apomixis, side by side with parthenogenesis and apogamy, adventive embryony, viviparity and vegetative propagation by buds, bulbs, rhizomes and other parts. According to his conception, apomicts are secondary asexual forms that for one or another reason have lost sexual reproduction, in contrast to **amicts,** primary asexual primitive forms of organisms, in which sexual differentiation and fertilization are absent. Other classifications of apomixis have been proposed.

Among researchers there is no unanimity even on the definition of "apomixis". Some consider it as broadly as Winkler (Fagerlind, 1940; Gustaffson, 1946-1947a,b; Modilewsky, 1948; Petrov, 1964,1979), others limit its content to seed propagation forms (Ernst, 1918; Poddubnaya-Arnoldi, 1964b; Khokhlov, 1967; Asker, 1981) or attribute to apomixis only its gametophytic forms, excluding adventive embryony (Battaglia, 1963; Batygina, 1990; Shishkinskaya, 1991; Teryokhin, 1996). Some authors (Asker, 1980,1981; Grant, 1981; Nogler, 1984a; Batygina, 1989a-c, 1993a, 1994a, 1998) prefer to use simultaneously with the term "apomixis" its synonym **"agamospermy" and, as a rule, divide it into gametophytic apomixis and adventive embryony.**

Even in a scheme by Ernst (1918), vegetative propagation was excluded from apomixis and two types of apomixis were distinguished: induced and autonomous.

Gustafsson's classification (1946-1947a,b) was widely used (Fig. 18). Its main merit is simplicity. After Winkler, Gustafsson considered all forms of apomixis

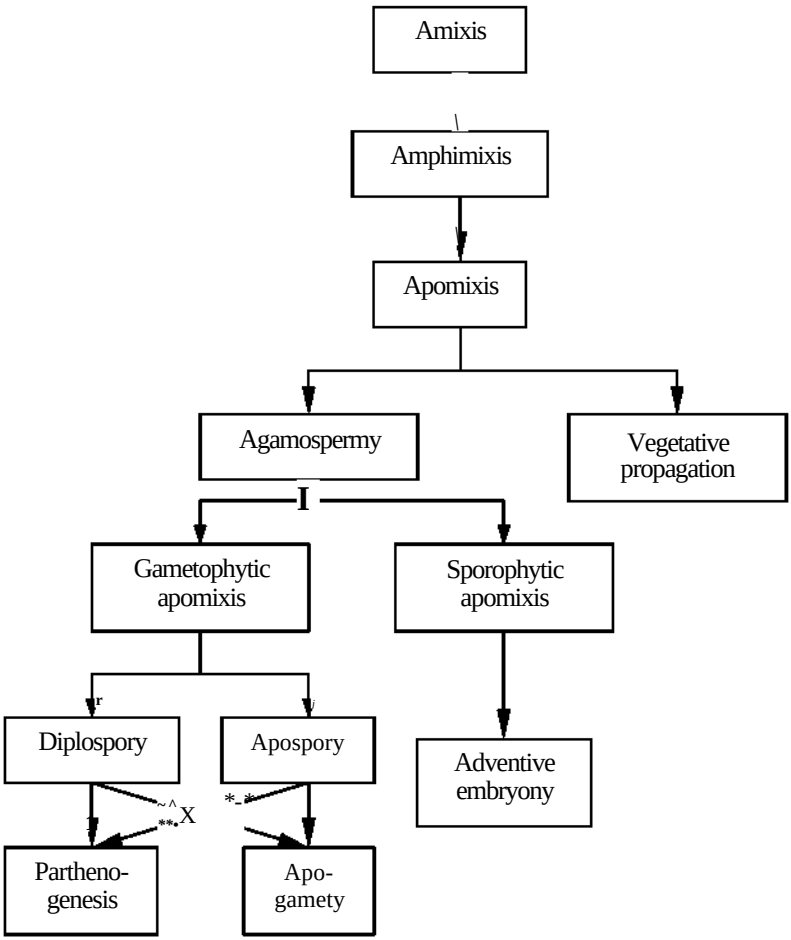


Fig. 18: Gustafsson's classification of apomixis types (1946-1947).

secondary ones in relation to sexual reproduction. The different types of generative (i.e., gametophytic) apomixis, in accordance with his scheme, arise as a result of combination of the different modes of female gametophyte formation **(diplospory** or **apospory)** with different modes of embryo formation **(parthenogenesis** or **apogamety).**

Gustafsson's classification was a starting point for creation of many subsequent systems of classification. An example is the scheme of Petrov (1964,1979) (Fig. 19), wherein there are "some moments of apomixis classification systems by Maheshwari and Fagerlind". Irregular (haploid) and regular (diploid) apomixis were distinguished in it, and for the first time the mode of embryo formation was included: **pseudogamy** and **autonomous apomixis,** that is, a number of important additions were made to Gustafsson's scheme. However, one essential shortcoming is notable: phenomena of different order, for example, mode of embryo sac formation (diplospory and apospory) and mode of embryo formation (adventive embryony) were put in the same row in this classification.

The classification of Poddubnaya-Arnoldi (1964b, 1976) was obviously most popular among Russian researchers, especially embryologists, who preferred to use

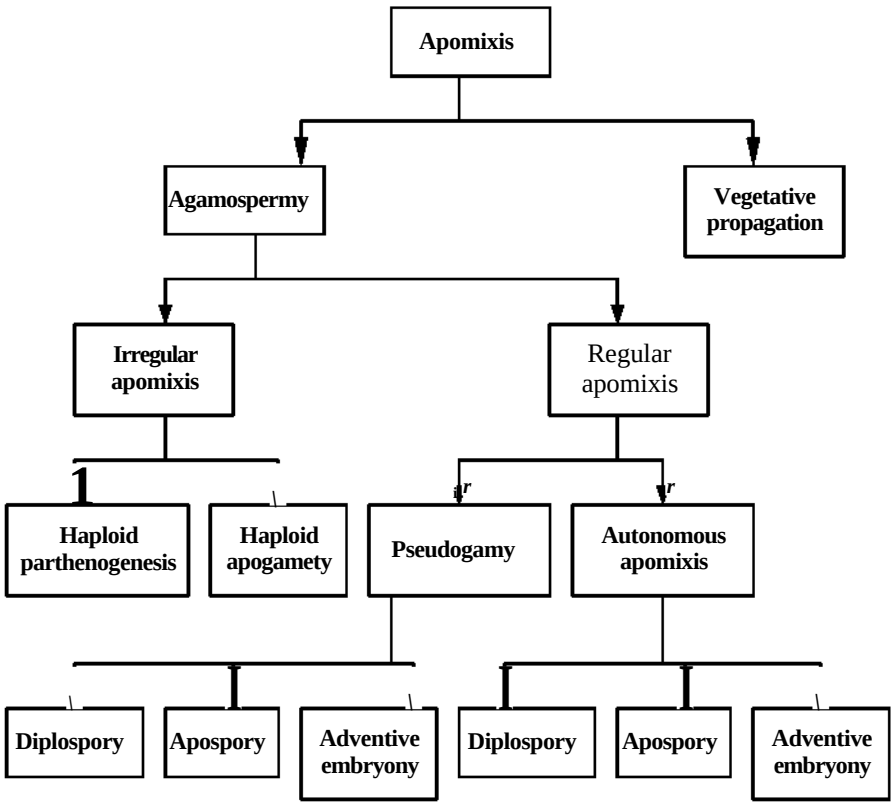


Fig. 19: Petrov's classification of apomixis types (1964).

just its terminology. The author distinguishes the following types of apomixis: parthenogenesis, apogamety, apospory, nucellar and integumental embryony, dividing the first two types into reduced and unreduced forms. Apospory in turn is divided into somatic apospory (euapospory) and generative apospory (synonym of diplospory). In justice to the simplicity and accessibility of Poddubnaya-Arnoldi's classification and terminology, it has to be noted, however, that in one case a mode of gametophyte formation (apospory) was considered an independent type of apomixis, but in all other cases it was considered a mode of embryo formation, while regular apomixis is a result of their combination.

The most original classification of apomixis, and one kept in a common key, to our mind, was worked out by Khokhlov (1967) (Fig. 20). The author considered apomixis as a result of changes proceeding at different stages of sexual reproduction. He distinguished four elements of gametophytic apomixis:

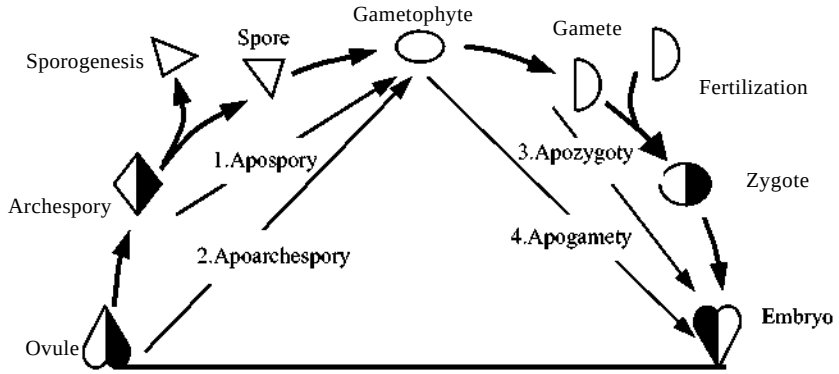
1) **apospory,** development of unreduced embryo sac from archesporic cell or from cells derived from it;
2) **apoarchespory,** development of unreduced embryo sac from somatic nucellar cell;
3) **apozygoty,** embryo development from unfertilized egg cell; and
4) **apogamety,** embryo development without fertilization from synergid or antipodal cell.

Their combination with one another or with elements of sexual reproduction—spory (development of embryo sac from reduced megaspore) and zygoty (development of embryo from fertilized egg cell)—leads to manifestation of balanced (diploid) or unbalanced (haploid) forms of gametophytic apomixis. Adventive embryony was first named an "apogametophytic" form of apomixis, since in that case embryos develop not from elements of the embryo sac, but from ovule somatic cells. Interrelations of apomixis elements in the plant seed reproduction system were represented by the author as grating, wherein there is a place practically for all forms of apomixis that are well known in nature.

Khokhlov (1970) made an attempt to unify terminology by adding the prefix "apo-" to the names of elements. However, double names of apomixis forms made the proposed terminology rather complicated. The author also introduced a number of new terms (apozygoty instead of parthenogenesis, apoarchespory instead of somatic apospory), and used the term "apospory" in an unusual sense as a synonym for generative apospory or diplospory. These terminological complications prevented widespread recognition of this original classification.

The classification proposed by Battaglia (1963) is most consonant with modern ideas about apomixis. He excluded from apomixis system not only vegetative propagation, but adventive embryony as well, and that led to the use of the term "apomixis" only in relation to its gametophytic forms.

The sequence of elements in Battaglia's system exactly corresponds to the natural course of events in generative organs: at first there is a mode of female gametophyte formation, then a mode of embryo formation (Fig. 21). Such phenomena as **androgenesis** and **semigamy** (hemigamy) are included in the classification. However, the expediency of including semigamy is doubtful because of its indefinite status: many people consider this phenomenon a deviation from normal sexual process.



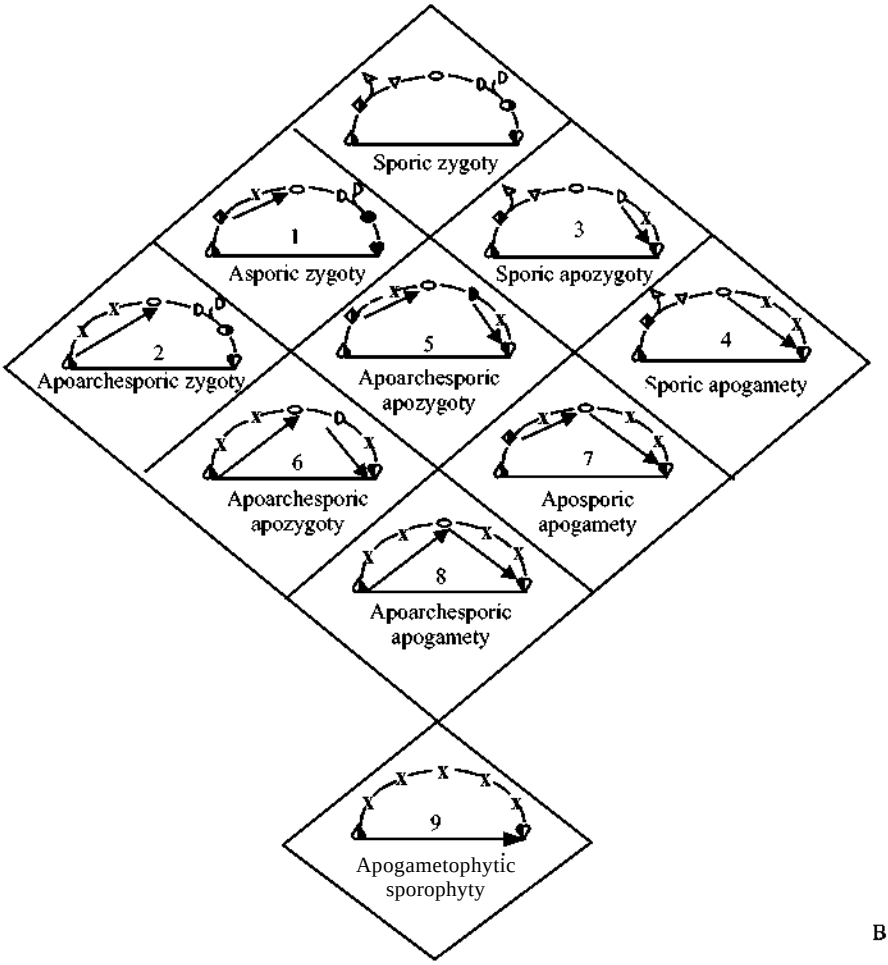


Fig. 20: Khokhlov's classification of apomixis types (1967).

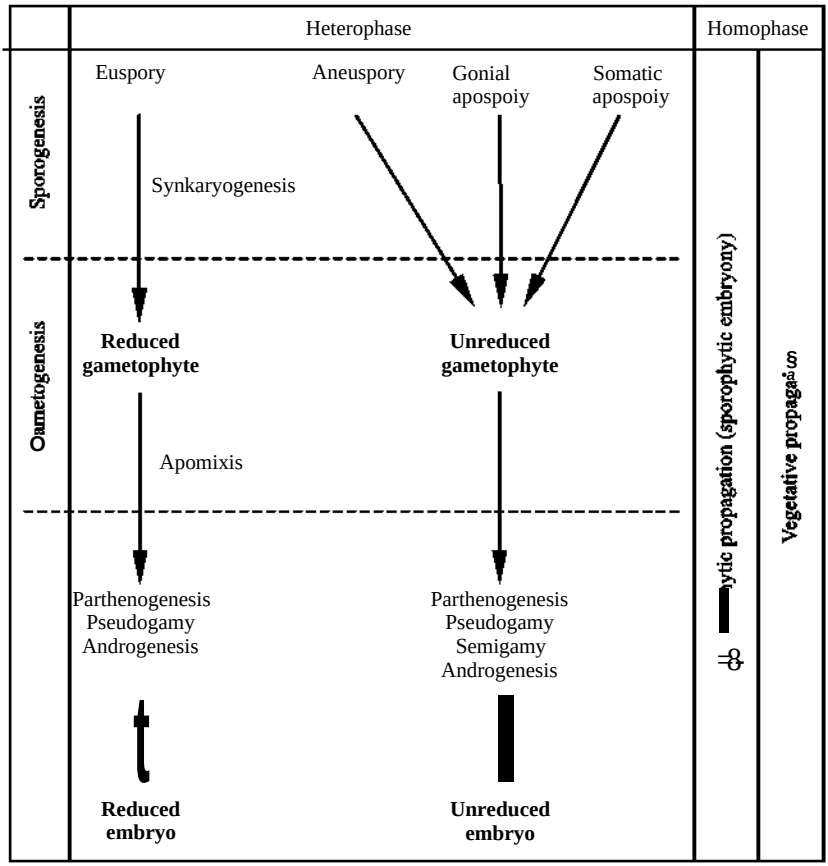


Fig. 21: Battaglia's classification of apomixis types (1963).

As regards exclusion of adventive embryony from apomixis system, Winkler (1920) attributed it to vegetative propagation. The problem of interrelation of adventive embryony and apomixis has attracted the attention of researchers working on culture *in vitro* (Maheshwari and Rangaswamy, 1958; Batygina *et ah*, 1978; Rangaswamy, 1980; Batygina, 1984,1990,1999a,b; Wilms *et ah*, 1983; Batygina and Zakharova, 1997). The authors believe that embryogenesis, observed in culture *in vitro*, with morphophysiological positions is analogous to the process of formation of adventive embryos. In connection with this some authors relate adventive embryony (nucellar, integumental and cleavage) to embryoidogenic type of vegetative propagation (Batygina, 1990; see also Embryoidogeny is a new type of vegetative propagation).

Battaglia's classification was enlarged and detailed by Solntseva (1970, 1990, 1997). However, as was noted above, needless details may make it difficult to use a system of apomixis classification.

A new point of view on the problem of classification was given by Bara and Ghiorghita (1974), who used a non-traditional system approach. In the author's opinion, the principal difference between sexual and apomictic reproduction is at the level of system organization of appropriate plant forms and it is determined by their informative content. Sexual reproduction sums up information from two individual systems that lead to manifestation of new qualities in progeny. In the case of apomixis, information goes from ancestors to offspring without input from another system, and therefore the initial (parental) information content is preserved.

Use of system-information approach led to inclusion in the same group of all asexual, in their opinion, forms of reproduction—both secondary (apomicts) and primary (amicts) — and isolated apomixis absolutely from another component of seed propagation system, amphimixis.

Such a view contradicted the idea, developed gradually, of close interrelation of apomixis and amphimixis within a common seed propagation system. Although the nature of genetic control of apomixis has not been determined in full till now, most researchers, beginning with Thomas (1940), consider its manifestation a result of mutations affecting the processes of sporo- and gametogenesis in sexual forms (Powers, 1945; Gustafsson, 1946,1947a,b; Nygren, 1954; Petrov, 1964,1979; Khokhlov, 1967; Asker, 1980, 1994; Savidan, 1982a,b, 1992; Nogler, 1984a,b; Mogie, 1988; Kindiger *et ah,* 1994; Teryokhin, 1994). The opinion is expressed that processes leading to apomixis must be connected or directly interrelate with a system of genetic control acting by sexual reproduction for the purpose of preservation of the sequence of events that connect gametophyte formation with the beginning of embryogenesis (Murrey, 1992). Studies on transgression of apomixis genes from *Tripsacum* to *Zea* are in full swing (Savidan and Berthaud, 1994; Savidan *et ah,* 1994). They associate localization of these genes with a certain segment of *Tripsacum* chromosome 16 (Kindiger *et ah,* 1994). In case of successful completion we can expect an essential hitch in the sphere of genetic control of apomixis.

One more aspect of modern ideas on apomixis has to be noted. Apomixis traditionally has been opposed to amphimixis as asexual to sexual reproduction. But now, chiefly owing to the work of geneticists, there is a trend towards unity of the two modes of reproduction within a common reproductive system (Nogler, 1984a). Supposing a community of genetic controlling mechanisms of apomixis and amphimixis, realization of both processes on the same ground (sexual organs, gametophytes, gametes) makes it possible to consider them not as alternative, but as mutually complementary modes of reproduction, in a condition of balance (Nogler, 1984a). Taking into account that sexual process in plants cannot be reduced to the act of egg fertilization only, and that all other events (which embryologists call "plural fertilization") take place as in sexual and apomictic forms, there are grounds to consider apomixis the same competent component of sexual reproduction system as amphimixis (Kupriyanov, 1989; Shishkinskaya, 1991). It is attributed, in the first place, to pseudogamous apomicts, wherein fertilization of the central cell is necessary for endosperm development. In autonomous apomicts only one sex takes part in formation of progeny, but they can form some quantity of fertile pollen, which fertilizes egg cells of their sexual relatives (Petrov, 1964). The full reduction of male generative sphere must be in a very limited group of obligate apomicts (it is doubtful if they are at all). But in that case it is more correct to speak of unisexuality or uniparental reproduction (Teryokhin, 1994).

About the term "asexual seed propagation", proposed by Khokhlov as synonym for the term "apomixis", Poddubnaya-Arnoldi points out that although formation of embryo, endosperm and seeds here is not connected with fertilization, sex in apomictically reproducing plants is expressed well enough (Poddubnaya-Arnoldi, 1976: p. 358).

The view of apomixis as asexual reproduction was considered by Kupriyanov (1989) as a consequence of identification of amphimixis with sexual process. But the fact is that conception of "sexual process", as the author points out, is considerably broader than amphimixis, and an act of amphimixis is not the self-expressing essence of sexual reproduction but only one of many elements, parallel with others, including apomixis. The author gives the definition of sexual reproduction, the main parameters of which he considers amphimixis and apomixis: "In multicellular organisms the systems of reproduction are sexual, when individuals in many generations pass the phase of the single cell" (p. 14).

Sharing that opinion of the sexual essence of apomixis, we use as arguments the aforesaid genetic and structural criteria, i.e., community of both genetic control system and structural-functional base (Shishkinskaya, 1991). According to our idea of the place of apomixis in seed propagation system, the main element of apomixis is parthenogenesis, as its presence is obligatory for manifestation of apomixis (Fig. 22). One of three different types of embryo sac formation usually is combined with it: **diplospory** or development of gametophyte from unreduced megaspore, **apospory** from megaspore mother cell, and **apoarchespory** from somatic cell of ovule.[1] Sometimes, for manifestation of diploid apomixis, parthenogenesis is sufficient, as in the case of spontaneous duplication of chromosomes in haploid egg cell, for example, in wheat (Kandelaki, 1970). In the scheme apogamety is absent, since we consider it a particular case of parthenogenesis. Synergid or antipodal cell take an **uncharacteristic path of differentiation** before they give rise to embryo development and become "egg-like" cells (Narayanaswamy, 1940; Gerassimova-Navashina and Batygina, 1958; Weimarck, 1967; Sinder *et al.*, 1980; Thirumaran and Lakshmanan, 1982; Batygina, 1987a; Shishkinskaya, 1992, 1995). They are found with certain but very low frequency in many species inclined to apomixis. Apogamety is not an independent mode of reproduction; it accompanies parthenogenesis, as a rule, and it is one of the reasons for polyembryony.

In conclusion, it may be said that in trying to create universal system of apomixis classification, we in fact reinvent the wheel, as the analogous situation has taken place in case of amphimixis. Here the main element, fertilization, combines with three other elements of sexual reproduction, **monospory, bispory** and **tetraspory,** which personify three different types of female gametophyte development in sexual species. Nevertheless, classification of embryo sac development types is quite sufficient for characterization of all variants of sexual process realization. Why cannot such an approach be used in the description of apomixis? Some authors have already made attempts to classify the types of embryo sac development in apomictic species (Battaglia, 1963,1983; Khokhlov, 1967; Solntseva, 1990,1997; Asker and Jerling, 1992; Koltunov, 1993; Crane, 1995; Teryokhin, 1996). With the exception of a recently proposed integrative classification by Crane (1995), in which the author refuses the

[2]The use and interpretation of these terms do not agree with generally accepted views (see Apomixis; Apospory; Diplospory).

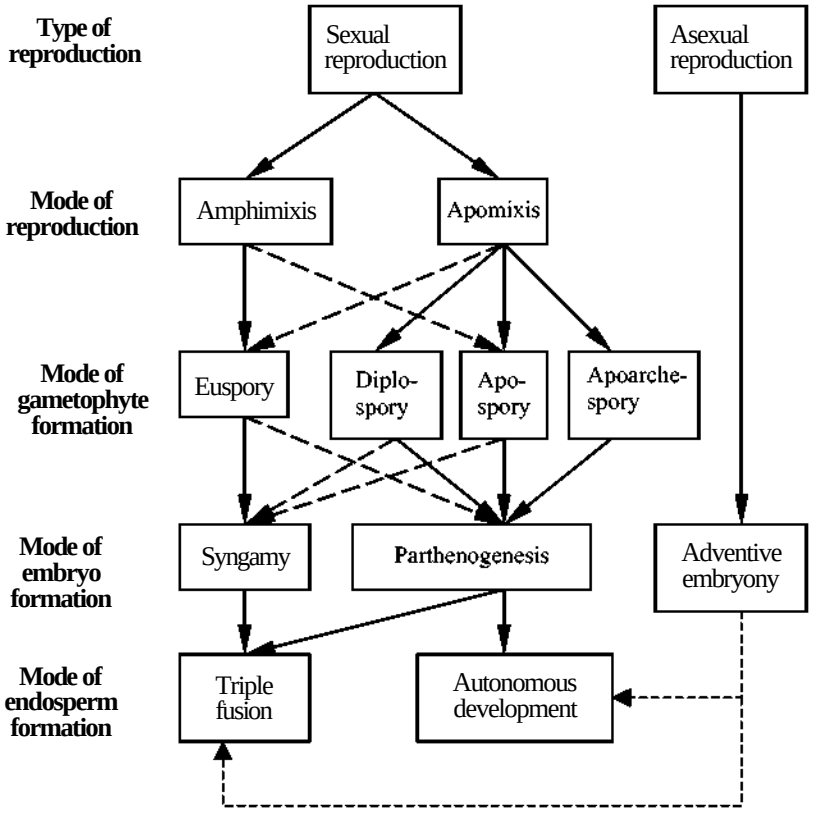


Fig. 22: The system of seed propagation in angiosperms (after Shishkinskaya, 1991).

traditional division of apomixis into two principal types (diplospory and apospory), all others differ from one another only in the quantity of isolated types and degree of detail. Taking Khokhlov's table (1970) and slightly enlarging it, we formed a classification that characterized all the diversity of apomixis manifestation in plants (Table 11). It reflects the conception, which was developed in embryology, that Polygonum-type of embryo sac development exemplifies the initial sequence of events by embryo sac formation, which could be the base for the origin of both reduced and unreduced megagametophytes in evolution. The preservation of meiosis for production of reduced gametes (only a final stage of division can be changed — cytokinesis) is common to all types of embryo sac development in sexual species. In the formation of diplosporic and aposporic embryo sacs a major role is played by meiotic mutations, resulting in omission of meiosis or replacement of it by other division types and, as a consequence, formation of unreduced gametes. As for apoarchespory, it is possibly a result of the change of expression level of the genes, starting the development of reduced embryo sac in the ovule. It can be supposed that their raised expression stimulates the megaspore mother cell and then adjacent somatic cells to formation of gametophyte.

Table 11. Classification of embryo sac development types.

		MMC	I division of meosis	II division of meosis	1st mitosis	2nd mitosis	3rd mitosis	Embryo sac	Developmental type
Amphimixis	Eusporу	Ⓒ			0				Polygonum-type
		+	+		→	+	+		Allium-type
		+	0		→		+		Adoxa-type
Aposporу	Diplosporу	endomitosis	+		→	+	+		Allium-nutans-type
		+			+	+	+		Taraxacum-type
		+		0	→	+	+		Ixeris-type
	Aposporу	+			+	+	+		Antennaria-type
		+			+	+	→		Erogrostis-type
	Apoarchesporу	Ⓒ Ⓒ	+	+	+ +	+ +	+ +		Poa-type
		Ⓒ Ⓒ			+	+	+		Bouteloa-type
		Ⓒ Ⓒ			+	+	→		Chloris-type
		Ⓒ Ⓒ	+		+	+	→		Panicum-type
		Ⓒ Ⓒ			+	+	→		Andropogon-type
		Ⓒ			+	+	+		Heteropogon-type
		Ⓒ			+	+	+		Paspalum-type

→ MMC, megaspore mother cell; +, repetition of proper stage of Polygonum-type embryo sac development; omission of development stage.
● degeneration of generative elements on the different stages of embryo sac development, beginning with MMC.
⊙ apoarchesporic elements.
■ degeneration of archesporic cell.
Only three principal types of reduced embryo sac development have been given: monosporic (Polygonum-type), bisporic (Allium-type) and tetrasporic (Adoxa-type).

It can be noted that in apomictic species even within one developmental type the final result (i.e., gametophyte structure) may be different because of anomalies appearing at the final stage of embryo sac formation and involving, in particular, the processes of differentiation and polarization of its elements. Instability of mature embryo sac structure in apomicts is a feature differentiating them from sexual species on the population level.

We hope that such an approach saves researchers from abortive attempts to work out a universally acceptable classification of apomixis against a background of disagreement on the essential description of this phenomenon and its place in the seed propagation system. Such a classification can be achieved only after a consensus, as the mechanism of genetic control of the different forms of apomixis is exactly ascertained.

Embryo-Endosperm Interrelations in Apomixis

Endosperm development by different forms of apomixis has specific features.

Reduced apomixis (haploidy). Occurrence of matroclinic haploids (reduced apomicts) in crossings depends heavily on both paternal and maternal forms. In the first case it is connected with anomalies of sperm cell structure, leading to single fertilization and, accordingly, to induction of parthenogenesis; in the second case it is conditioned by nuclear and/or cytoplasmic factors of maternal forms (Tyrnov, 1976a,b). On the basis of these and other facts the conception of inherited and induced forms of haploidy in different species was developed (Tyrnov, 1992,1994). Each form is characterized by specificity of embryo and endosperm development (Tyrnov and Enaleeva, 1983; Enaleeva and Tyrnov, 1997).

The induction of reduced apomixis is accompanied by precocious development of endosperm. The number of endosperm nuclei may be small (close to eight). It testifies that the haploinduction is not connected with trophic function of endosperm and most likely results from the influence of physical or chemical factors. In favour of a hypothesis of "chemical stimulus" influence is the fact that the endosperm, beginning with early developmental stage, produces hormones and other substances that influence growth and morphogenesis of the embryo. Early embryogenesis may also be connected with osmotic gradient arising from fast growth of endosperm (Khudyak, 1963; John and Rao, 1984; Vijayaraghavan and Prabhakar, 1984).

Reduced apomixis, at least in some crops, is connected exclusively with pseudogamy. In investigated matroclinic maize haploids (more than 20,000), the endosperm was shown to be of hybrid origin (Tyrnov and Zavalishina, 1984; Tyrnov, 1998a,b). A probability of hybrid endosperm was proved in a study of haploids in potato (Montelongo-Escobedo and Rowe, 1969; Laptev, 1984). Hybrid endosperm also accompanied haploid and diploid androgenesis (Tyrnov, 1986a).

A slightly different picture is observed in the inherited form of reduced apomixis. In unpollinated maize ovaries, the development of embryo up to globular stage can proceed without endosperm formation (Tyrnov and Enaleeva, 1983; Enaleeva and Tyrnov, 1997). In many embryo sacs (over 82%), autonomous endosperm development was revealed. It might be combined with autonomous embryogenesis. The first two endosperm divisions usually passed normally, but subsequent development was anomalous. In the absence of pollination, there was no

normal endosperm development. At the same time, the opportunity for autonomous endospermogenesis is of great significance. The probability is rather high that this autonomy may be a result of pleiotropic action of the same factors that cause parthenogenesis, as both traits are transferred together to progeny (Tyrnov, 1997, 1998a). This may considerably simplify further work on production of forms with autonomous apomixis, not demanding pollination at all. The conclusion of the autonomous nature of apomixis is often based only on cytoembryological analysis of the first stages of embryo and endosperm development. Therefore, taking into account the phenomenon described above of autonomous parthenogenesis by reduced apomixis, it is necessary to reconsider similar conclusions concerning unreduced apomicts. A close connection appears to exist between reduced and unreduced apomixis. For example, reduced pseudogamy was observed in wild strawberry, for which unreduced apomixis is characteristic (Koloteva and Zhukov, 1994). In dihaploids of sugar beet, high frequency (upwards of 85%) of unreduced parthenogenesis was noted (Shirajeva *et al.,* 1989).

Unreduced apomixis. The same peculiarities of morphogenesis are observed in unreduced apomixis. So, in many pseudogamous apomicts (species of genera *Hierochloe, Hypericum, Panicum, Pennisetum, Ranunculus, Rubus),* endosperm formation usually precedes development of embryo (Nogler, 1984a). In pseudogamous biotype of *Atraphaxis frutescens,* parthenogenetic development of egg cell starts at the stage of eight-nuclear endosperm (Sitnikov, 1986).

In other pseudogamous apomicts (species of genera *Botriochloa, Parthenium, Poa, Potentilla, Tripsacum),* embryogenesis begins before endospermogenesis, and it may occur even before pollen tubes penetrate the embryo sacs (Nogler, 1984a; Shishkinskaya *et al.,* 1994). Such a phenomenon is defined as "premature embryony". Parthenogenetic embryos may consist of 100-200 cells (e.g., in apomictic biotypes of *Potentilla).* However, they later degenerate, if endosperm does not form.

In some species (genera *Paspalum, Potentilla),* both premature and normal embryony were observed by pseudogamy. However, such variability may be a result of influence of environmental factors. So, in our experiences with maize the delay of pollination for 1-2 days to 7-10 days increased the frequency of reduced apomixis from 3.8% to 71.6%. It is possible that the age of unpollinated ovaries will influence "normality" or "prematurity" of embryogenesis in unreduced apomicts too.

In autonomous as well as in pseudogamous apomicts, premature embryony can take place *(Hieracium, Taraxacum),* or egg cell division begins after the start of endosperm development *(Cortaderia, Crepis)* (see Poddubnaya-Arnoldi, 1976; Nogler, 1984a; Czapik, 1991). In *Taraxacum officinale* and some species of *Pilosella* (Bludneva *et al.,* 1994; Kashin and Chernisheva, 1997), all variants of autonomous development were observed: parthenogenesis, endospermogenesis and, finally, parthenogenesis + endospermogenesis. The rates of endosperm development also might be various. In sugar beet, by isolation of inflorescences, embryo with endosperm and also endosperm without embryo were observed (Maletzki and Maletzkaya, 1996).

Either autonomous or pseudogamous apomixis is usually peculiar to species of the same genus, but, at the same time, both types were noted in *Poa* and *Malus* (Nogler, 1994) and *Kalidium caspicum* (Gusejnova and Kurbanov, 1994). In apomictic populations of *Poa* and *Festuca* at least at early stages of development, variants of embryo- and endospermogenesis are possible: sexual embryo, apomictic endosperm; apomictic embryo, sexual endosperm; or apomictic embryo, apomictic endosperm

(Shishkinskaya, 1995). Different modes of reproduction were revealed even within one clone of triploid raspberry: pseudogamy was observed in spring flowering, autonomous endosperm development in autumn (Dorogova, 1994). In wild strawberry, autonomous endospermogenesis was not usually observed without pollination. However, when using partly inactivated pollen, cases of penetration of two sperms into an egg cell were noted, and thus nuclei of endosperm were observed. Such a phenomenon is determined to be stimulate-autonomous endosperm development (Suchareva and Baturin, 1994).

Endosperm ploidy. In amphimixis, endosperm ploidy, at least on its first divisions, is equal to 3n in diploids; in even polyploids it is a multiple of 3. Some endospermal cells can have other ploidy owing to endopolyploidy (Yoffe, 1971; Vijayaraghavan and Prabhakar, 1984; D'Amato, 1984).

In a case of apomixis, such phenomena as omission of meiosis, autonomy, pseudogamy, fusion or non-fusion of polar nuclei can essentially change endosperm ploidy. In amphimixis, the change leads to significant anomalies or to a complete halt in endosperm development (which naturally entails destruction of the embryo). This feature is explained by different reasons: disturbance of the genomic ratio of 2:3:2 between embryo, endosperm and maternal tissues; discrepancy between volume of cytoplasm and the number of genomes; different "genetic value" of maternal and paternal endospermal genomes; disturbance of gene balance in endosperm; or genomic imprinting in endosperm (Nishiyama and Yabuno, 1978; Ehlenfeldt and Hanneman, 1988; Haig and Westoby, 1991). The last is considered to have a direct relation to apomixis.

Genomic imprinting is the phenomenon of various expression of a gene depending on whether it is received from the mother or from the father. It follows that seed development depends on the ratio of maternal and paternal genomes in the endosperm. The ratio 2:1 is normal. In the necessity of paternal genome for endosperm development, the authors see a reason for wide distribution of pseudogamy, but at the same time they are at a loss to explain from these positions autonomous apomixis, wherein endosperm arises without participation of paternal genome (Haig and Westoby, 1991). There is a point of view (on the basis of the endosperm ploidy analysis in apomictic species of genus *Tripsacum)* that evolution of aposporic apomixis is limited to species with small requirements for imprinting or without such requirements (Grimanelli *et al,* 1997).

In spite of the opportunity, autonomous endosperm development in case of haploidy in maize never comes to completion. The reason may be connected with non-optimum level of endosperm ploidy, n or 2n (Tyrnov, 1998b). There are data to suggest that in case of pseudogamous reduced apomixis in maize, endosperm is most likely triploid (Chase, 1969). In tetraploid potato with reduced apomixis, hexaploid endosperm (i.e., having ploidy multiple of 3) corresponds to dihaploid embryo (Peloquin *et al.,* 1995). It cannot be excluded that on the basis of reduced apomixis it will be possible to produce autonomous unreduced apomicts by changing endosperm ploidy, for example, in experimental creation of triploids or hexaploids. In favour of this hypothesis is that unreduced apomicts of some species are triploids.

In case of unreduced apomixis, the following variants of endosperm ploidy are theoretically possible with its autonomous development from polar nuclei or secondary nucleus of the central cell: 2x (4x), 3x (6x), 4x (8x), etc. Conformity to theoretically expected level of ploidy was observed in some cases, at least, on early

stages of endosperm development; later the ploidy of some cells, as well as by amphimixis, might be increased owing to endopolyploidy. In pseudogamy the endosperm ploidy can change depending on the number and ploidy of the male gametes taking part in fertilization. Change of endosperm ploidy also cannot be excluded in autonomous apomicts, as sometimes their polar nuclei can be fertilized too (Nogler, 1984a). From crossing of plants with different ploidy, odd polyploids can arise (3x, 5x, 7x, etc.), and diversity of endosperm ploidy grows with their transition to apomictic reproduction. Crossings of amphimicts 2x x 4x and 4x x 2x, giving endosperm with ploidy 4n and 5n, respectively, and as though modelling the situation with unreduced apomixis, when fusion of polar nuclei results in formation of the central nucleus with ploidy 4x, and its fertilization by reduced pollen in case of pseudogamy (5x) are of interest. Tetraploid endosperm, as a rule, does not develop, and pentaploid endosperm has different degree of completeness (Tyrnov, 1987). Defectiveness of endosperm probably does not depend on level of ploidy alone. In case of pollination of maize tetraploids by different diploids, especially by hybrids, we observed a different degree of endosperm development, from thin pellicles to half the size of typical kernels.

There are also other mechanisms of endosperm ploidy regulation. It is established that both polar nuclei and a nucleus of central cell are capable of division. Hence, a fusion of nuclei is a non-essential condition of mitotic endosperm activity (Nogler, 1984a). In *Poa* species growing in Kamchatka, endosperm development was observed after fertilization of one polar nucleus (Shishkinskaya *et ah,* 1994). Endospermal cells with ploidy 3n, 5n and 3n+2n were found in apomictic pseudogamous rice line. These cells appeared to have arisen because one polar nucleus was fertilized and the second divided without fertilization (Cai *et al.,* 1995). Besides, in case of pseudogamy, only one polar nucleus can be fertilized and another, unfertilized, degenerates. This can be considered one mechanism of ploidy reduction (Nogler, 1984a; Dorogova, 1994) up to an optimum level or maintenance of a typical genomic ratio in endosperm; two maternal and one paternal genome (Haig and Westoby, 1991).

Endospermal embryony. It is possible that in apomixis the different cells of the embryo sac possess the capacity for embryogenesis. In pseudogamous apomict *Brachiaria setigera,* cases were noted that were treated as embryo formation from egg cell, synergid and endosperm cells (Muniyamma, 1977). Peripheral cells of mature endosperm behaved like meristematic ones and formed globular or spindle-like cellular masses. They were joined with endosperm by the structure similar suspensor. In this species, triploid seedlings were discovered. Triploidy may indirectly testify to their origin from endosperm. However, they could arise from the fertilization of unreduced female gametes by haploid sperm cell; consequently, additional experiments are necessary to prove embryo origin from endosperm (Johri and Ambegaokar, 1984).

Unusual cases of "endospermal" embryony were marked in sugar beet (Shirajeva, 1986; Yarmoluk *et al.,* 1994). First, in advanced endosperm, large rounded initial cells—somacytes—were formed. After several divisions, they were transformed into rounded or wrongly formed embryos without suspensor, which settled in the centre of the embryo sac or nearly so in the chalazal region. It was noted that own endosperm was formed around such embryos. The further fate of such embryos is not established for the present.

Development *in vitro.* In parthenogenetic maize lines, embryo development up to formation of plant-regenerant can proceed even on mediums without hormones. Endosperm can also develop, but it usually is a factor interfering with the development of embryo (Alatortseva and Tyrnov, 1994, 1997). This fact should be taken into account by development of the methods of regenerant production in culture of ovaries and ovules, not only apomictic but also the usual sexual forms, as *in vitro* both embryo and endosperm can develop irrespective of the mode of reproduction.

Evolutionary aspects. It is considered that absence of fertilization may lead to various negative evolutionary consequences (see The problem of evolutionary significance of apomixis). Therefore, one would think that the process of apomict appearing first should affect not the embryo, but the endosperm, which carries out a short-term function and does not influence the further evolutionary fate of descendants. However, the phenomenon in which the embryo is sexual and the endosperm is autonomous is not distributed in nature, though separate cases are observed by distant hybridization (Khudyak, 1963) and in some apomicts (Shishkinskaya, 1995). What is the reason for such apparent "illogicality" of evolution? There is a point of view that triple fusion and endosperm development serve as a barrier to casual hybridization and a mechanism of biological isolation (Nishiyama and Yabuno, 1978).

We believe that one of the possible functions of endosperm concerns the preservation of sexual reproduction stability (Tyrnov, 1987,1998). The frequency of spontaneous embryo development without fertilization, probably, varies within the limits of 0.1-0.001%. Taking into account the great number of seeds produced in nature, even with such relatively small frequencies, the total number of resulting apomictic plants can reach a significant value. Embryo development without fertilization is a phenomenon constantly accompanying sexual plant reproduction and creating a real danger of its replacement by apomixis. Hence, there should be mechanisms of stabilization of sexual propagation system; one of them may be based on interaction of embryo and endosperm. Apomictic endosperm, as a rule, has genomic structure that does not allow it to develop normally. Incomplete development of endosperm results in destruction of embryo and, hence, elimination of forms with the tendency to apomixis.

On the other hand, it is considered that a combination of apomictic and amphimictic modes of reproduction can give significant evolutionary and adaptive advantages. Loss of pollen would lead to existence of autonomous apomicts only. Availability of pollen in case of pseudogamy leaves an open channel for return to sexual reproduction and origin of new apomicts by segregation.

This may be one of the reasons for the prevalence of pseudogamy and, accordingly, preservation of the sexual nature of endosperm.

Pseudogamy may have another role. A phenomenon has been observed that can be defined as "pseudogamous heterosis" (Haskel, 1960; Schmidt, 1964); dependence of seed dormancy and speed of their germination from male parent was noted in apomicts (Nogler, 1984a). Therefore, it can be assumed that endosperm influences the very important characters of the formed embryo and individual.

Thus, all available facts unequivocally show that, irrespective of the mode of reproduction, interrelations of embryo and endosperm are major elements of the plant reproductive system.

Ultrastructural Aspects of Apomixis (Plate VI)

Ultrastruchiral aspects of apospory. The initial cells of aposporous embryo sacs in *Panicum maximum* (Naumova and Willemse, 1995) are rather similar to the megasporocyte at the early stages of their differentiation, but later on their functional activity increases drastically. In the nucleolus, the granular component dominates, which indicates the active synthesis of the RNA. Numerous electron-dense inclusions present in the nucleoplasm can be interpreted as congestions of rRNA molecules that are transported from nucleolus to cytoplasm. Cytoplasm of the initial cells is rich in ribosomes, polysomes and rough endoplasmic reticulum (RER, which often contacts with nuclear envelope), which are responsible for the protein synthesis. There are a large number of vesicles transporting the cell substances. Vacuoles of middle size are located evenly inside the cell. Mitochondria with developed crista system are abundant and are responsible for the high energy level of the cell. Plastids have no starch accumulation; obviously the starch is in intensive use. The cell wall of the initial cell is gradually thickened (a similar process was observed in *Poa pratensis*— Abeln *et al.,* 1984) and the number of plasmodesmata decreases. The plasmodesmata loss results in the reduction of the signals and variability of metabolites that penetrate the cell by finer sorting. As a result, the initial cell becomes more isolated in comparison with other nucellar cells. Reduction of the number or loss of the plasmodesmata is the characteristic feature of megasporocytes and other generative cells that are not of apomictic origin.

The size and functional activity of the initial cell of the aposporous embryo sac gradually increase. The uninucleate aposporous embryo sac has two large vacuoles at the poles and a nucleus in the centre. The thickness of the cell wall increases approximately seven times from the initial thickness, and plasmodesmata disappear completely. The cells of the nucellus, which are adjacent to the embryo sac, degenerate. Uninucleate aposporous embryo sac, as well as uninucleate meiotic embryo sac, is therefore isolated from other viable cells of the nucellus.

Aposporous embryo sac of *Panicum maximum* develops according to the Panicum-type. Abnormalities during megagametogenesis were not observed. The egg apparatus usually has three cells (egg cell and two synergids) and rarely two cells (egg cell and synergid). The differences in the number of egg apparatus cells obviously are conditioned by the position of the nuclei in the coenocyte before cell wall formation. The central cell has one or two polar nuclei; antipodals are not present. Differences in fine structure of the egg apparatus in Panicum-type and Polygonum-type embryo sacs were not found (Naumova and Willemse, 1995). Similar data were obtained for *Brachiaria brizantha* (Claudia *et al.,* 1998). The outgrowths of the cell wall in the chalazal part of the Panicum-type embryo sac occur in hybrids of *Pennisetum;* they were not present in the embryo sac of one of the parents with the embryo sac of Polygonum-type (Chapman and Busri, 1994). The formation of the cell wall around the egg cell in *Pennisetum dliare,* which possesses the parthenogenetic embryo formation, occurs some days before pollen tube penetration. This fact was used to explain the presence of the cell wall as an obstacle in egg cell fertilization (Vielle *et al.,* 1995).

Ultrastructural aspects of diplospory. The processes dealing with diplosporous embryo sac formation can be subdivided into some stages: archesporial cell, mother cell of diplosporous embryo sac, uninucleate embryo sac and developed embryo sac. Each of the stages has certain morphological and functional characteristics.

The archesporial cell is isodiametric, with low developed vacuolar system *(Poa nemoralis, P. palustris* - Osadtchiy and Naumova, 1996; Naumova *et al.*, 1999). The nucleus of the cell is large and spherical; the chromatization is poor. The nuclear envelope has few pores, and the contacts with endoplasmic reticulum (ER) are not found. The nucleolus is large, with numerous "vacuoles". The cell is poor in ribosomes and polysomes. Plastids and mitochondria have slightly developed inner membrane systems. The ER is poorly developed, the dictyosomes are scarce and functionally inactive. Vacuoles are small. In cytoplasm there are the lysing areas enclosed by two- or multimembrane structures. The cell wall is rather thin with numerous plasmodesmata, which are more abundant in the chalazal part than in the micropylar. The ultrastructural features of the archesporial cell in diplosporous species of *Poa* thus show that this cell possesses low functional activity. The identical ultrastructure is characteristic of archesporial cells that undergo meiosis in sexually reproduced plants.

Mother cell of diplosporous embryo sac increases the vacuolization and because of that the cell length is greater than the width. The nucleus is large and becomes irregular in shape. The nuclear envelope shows numerous protuberances and invaginations and the number of nuclear pores increases. Chromatization of the nucleus is weak. Nucleolus increases in size. Sometimes congestions of heterochromatin (like fasten discs at the chromosome ends at prophase I meiosis) are present. The number of ribosomes and polysomes increases. The ER becomes more developed and placed near the nucleus; contacts of ER with nuclear envelope are rarely observed. The number of dictyosomes and their functional activity increase. The morphological conditions of the plastids and mitochondria remain unchanged in comparison with those in the archesporial cell. Lysis in cytoplasm is not observed. The cell wall is thickened, the plasmodesmata present at the chalazal part of the cell only, but it is not clear whether they are functional. In total, the complex of ultrastructural characteristics of the mother cell of diplosporous embryo sac (increase of the nucleolus size and of the number of ribosomes, polysomes, ER, dictyosomes and vacuoles) shows that there are intensive exchange processes between nucleus and cytoplasm, which deal with synthesis and transport of the ribosome precursors and proteins. So, in spite of the absence of meiosis, the structural and functional reorganizations that occur in nucleus and cytoplasm of the mother cell of diplosporous embryo sac are analogous to those that are characteristic for the nucleus and cytoplasm of megasporocytes which will follow the normal meiosis (see van Went and Willemse, 1984). The absence of callose deposition around mother cell of diplosporous embryo sac is one of the differences between apomeiotic and meiotic megasporocytes. It was shown by light microscope investigations of genera *Elymus* and *Tripsacum* (Crane and Carman, 1987; Carman *et al.*, 1991; Leblanc *et al.*, 1995a,b).

The transition from the mother cell of diplosporous embryo sac to the uninucleate embryo sac is characterized by the elongation of the cell and intensive vacuolization. The nucleus remains irregular in shape. The nuclear envelope has numerous pores and protuberances. Ribosomes and polysomes are abundant. The ER is well developed, the cisterns are branching and placed all over the cell. The contacts of ER with nuclear membrane are usual. Dictyosomes are numerous and functionally active. Some parts of ER participate in lysis of the cytoplasm. The number of plastids and mitochondria increase and their internal membrane systems become well developed. The cell wall thickens, plasmodesmata are not observed. These

ultrastructural data indicate increase in synthetic activity and protein transport inside the cell. The energy level of the cell increases because of the activity of plastids and mitochondria. The loss of plasmodesmata leads to more pronounced isolation of the uninucleate diplosporous embryo sac from surrounding nucellar cells. The ultrastructural characteristics of both diplosporous and meiotic uninucleate embryo sacs show similarity. The developed diplosporous embryo sac was not investigated at ultrastructural level.

Ultrastructural aspects of parthenogenesis. Ultrastructural investigations of diploid and haploid parthenogenesis are very limited and deal with few genera of grasses *(Hordeum* - Mogensen, 1982; *Pennisetum* and *Panicum* - Chapman and Busri, 1994; Naumova and Willemse, 1995; Vielle *et al.,* 1995). In natural conditions, the egg cell of alloplasmatic parthenogenetic line of T. *aestivum* shows high level of functional activity even three days before pollination, when the flower is closed (Naumova and Matzk, 1997). In terms of level of activity, this cell is comparable with the zygote. The morphological criteria of egg cell activation are: increase in size of the egg cell, its nucleus and nucleolus; change in their shape to irregular; and changes of fine structure of the cell organelles in cytoplasm. The egg cell, being pear-shaped, increases in size 2-2.5 times by extension and vacuolization (large chalazal and numerous small vacuoles all over the cell appear). The size of nucleus and nucleolus also increases 2-2.5 times, the appearance of additional nucleoli is possible. The granular component, which actively produces ribosomal RNA, prevails in nucleoli; the ribosomal subunits are concentrated close to the nuclear envelope. In cytoplasm at that time the number of ribosomes and polysomes increases intensively. The number of ribosomes functioning on the ER cisterns and on the nuclear envelope increases also. Numerous pores appear in the nuclear envelope. The cisterns of rough ER show numerous contacts with outer nuclear membrane. These facts indicate the presence of intensive exchange processes between nucleus and cytoplasm. Rough ER consists of numerous cisterns that differ in their length and thickness, the contacts with Golgi apparatus are regular. The vesicles move from Golgi apparatus to the vacuoles and endoplasmic membranes. Mitochondria with well-developed internal membrane system are distributed all over the egg cell. Plastids with starch (amyloplasts) are numerous. The lipid bodies as a reserve material are present.

The cell wall of the parthenogenetic egg cell is incomplete during the flowering period: the plasma membrane is present only on the chalazal region of the cell. The presence of a complete cell wall around the diploid egg cell was found some hours before the sperm cell penetrated the embryo sac of *Pennisetum dliare* (Vielle *et al.,* 1995). It is necessary to underline that the zygote of many angiosperms (Plyushch, 1992) shows very similar ultrastructural characteristic to those inherent for parthenogenetic egg cell.

Space and Time Organization of the Megasporo- and Megagametophytogenesis in Amphimictic and Apomictic Plants

The arising of apomixis appeared to be caused by spatial and temporal peculiarities in the process of micro- and megagametophytogenesis in apomicts.

The comparative morphometric and cytochemical analysis of megagametophytogenesis was performed in two sexual species *(Crepis capillaris,*

Haplopappus gracilis) and two apomictic species *(Rudbeckia laciniata, Taraxacum offidnale)* of angiosperms with different embryological and caryological characteristics to check our hypothesis (Gussakovskaya, Emakov, 1988).

Megasporo- and megagametophytogenesis could be conventionally treated as the process of development of a **single reproductive cell** passing successively through a number of morphologically distinguishable stages: (1) nucellar cell; (2) archesporial cell; (3) megasporocyte before meiosis (its isolation from neighbouring nucellar cells, the initiation of primary layer of integumentary tapetum); (4) meiocyte (the megasporocyte, entering in the prophase of the first meiotic division); (5) cells of the dyad; (6) cells of the tetrad; (7) functional megaspore. The cell size and nucleus size of the amphimictic and apomictic reproductive cells change in a similar way. They are maximal at the meiocyte stage and minimal at the dyad stage. At the megaspore stage, they reach a maximum again (Figs. 23 and 24).

At the same time, differences can be found between the apomicts and the amphimicts in the nature of growth of the reproductive cell and its nucleus, especially in the transition from archesporial cell to megasporocyte. In amphimicts, the cell and nucleus sizes increase during this transition about 1.5 times, whereas in apomicts the sizes barely change.

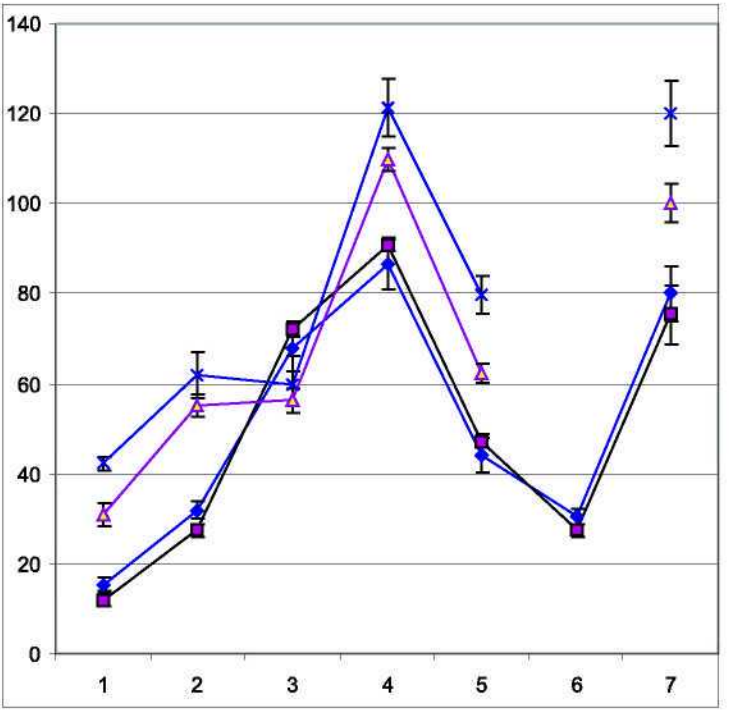


Fig. 23: Changing of the reproductive cell size.
x-axis: 1 - nucellar, 2 - archesporial, 3 - megasporocyte, 4 - meiocyte, 5 - dyad cell, 6 - tetrad cell, 7 - megaspore; y-axis: cell size (C) in conventional units. • - C. *capillaris,* • - *H. gracilis, A - T.officinale, x-R. laciniata*

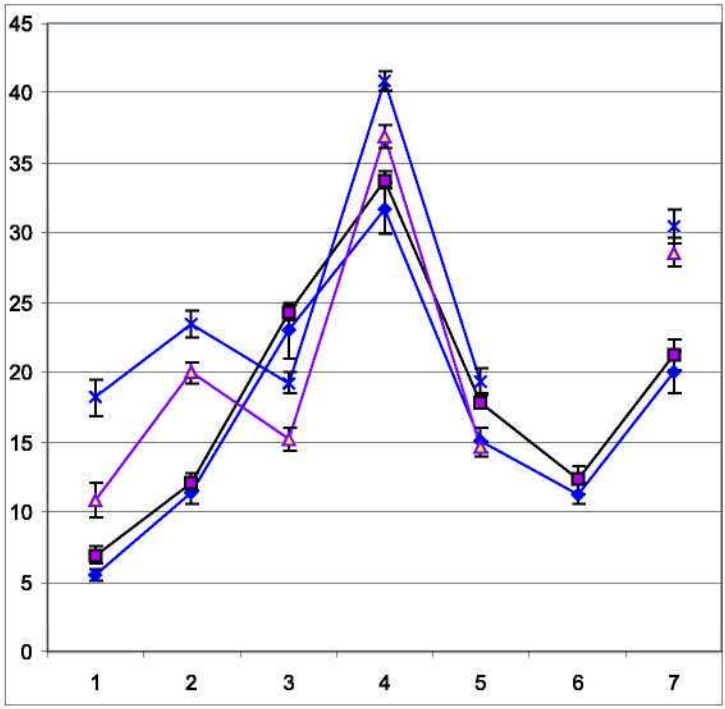


Fig. 24: Changing of the reproductive cell's nucleus size.
x-axis: 1 - nucellar, 2 - archesporial, 3 - megasporocyte, 4 - meiocyte, 5 - dyad cell, 6 - tetrad cell, 7 - megaspore; y-axis: nucleus size (N) in conventional units. • - C. *capillaris*, • - *H. gradlis, A - T.officinale, x-R. laciniata*

This fact is worthy of note. As many investigators note, the polarity of the embryo sac is already defined at the stage of archesporial cell. It is possible that this characteristic is not a single one that is determined at this stage. The possibility exists that a number of features of the embryo sac and its ontogenetical precursors become defined at this stage.

To explain the differences observed between amphimicts and apomicts, two simple suppositions seem to be obvious. One possibility is that the apomictic reproductive cell has a relatively short period of transition from archesporial cell to megasporocyte and failed to grow in time up to the same proportion as the amphimictic cell. Another possibility is that the growth of the apomictic reproductive cell during the transition from archesporial cell to megasporocyte is delayed or slowed down for some reason. Whatever the reason for this delay, it probably causes the apomictic reproductive cell and its nucleus to enlarge just two times during the transition from archesporial cell through megasporocyte to meiocyte, whereas the amphimictic reproductive cell and its nucleus enlarge three times. These differences appear to imply that the pool of substances sufficient to provide two meiotic divisions is absent in the former cell at the beginning of meiosis. The pool available is enough only for one division.

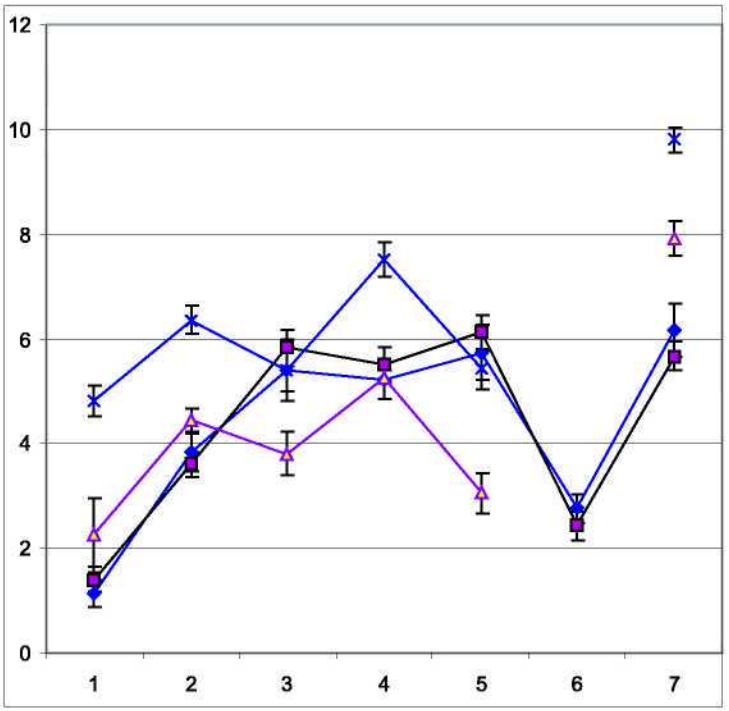


Fig. 25: Changing of the reproductive cell's nucleolus size.
x-axis: 1 - nucellar, 2 - archesporial, 3 - megasporocyte, 4 - meiocyte, 5 - dyad cell, 6 - tetrad cell, 7 - megaspore; y-axis: nucleolus size (NL) in conventional units. • - C. *capillaris*, • - *H. gradlis*, *A - T.officinale*, *x-R. laciniata*

This supposition is confirmed indirectly by the results of the nucleolus size measurements in the nucleus of the reproductive cell (Fig. 25). In course of transition from nucellar to archesporial cell, the nucleolus increases in apomicts 1.5-2.0 times, whereas in amphimicts it increases 2.5-3.0 times. During the next transition from archesporial cell to megasporocyte, the nucleolus in amphimicts continues to enlarge, whereas in apomicts it does not change or even decreases. Such opposite changes of nucleolus size take place also in two further transitions, megasporocyte to meiocyte to dyad, though not so pronounced.

The different nature of changes of nucleolus size probably suggests the different intensity of protein synthesis in premeiotic interphase of reproductive cell in amphimicts and apomicts. The whole pattern of changes is still actually the same. The impression could arise that the apomictic reproductive cell often is delayed or anticipates the amphimictic one in demonstration of protein-synthetic system activity. However, it is unclear what are the reasons for opposite changes in nucleolus size in the transitions mentioned and for the great similarity of the amphimicts and apomicts studied, reflected in Figs. 23 and 24 as compared with Fig. 25.

The similarity between the graphs of changing sizes of the reproductive cell itself and its nucleus suggests the presence of a correlation between these two

characteristics. In this connection, the question arises of the morphometric model of the meiosis. There are no such models available, so we used cell cycle models, presenting the meiosis as two consecutive, rapidly alternating cycles.

According to one of the popular cell cycle models, the cells in permanently growing cultures have the cycle duration (T) related with the average cell size in interphase (C) by the equation $C \cdot T = const$, where *const* depends on the cell type. This is apparently the simplest model of the relation between the morphometric and chronometric characteristics of the cell and the cell cycle. It is unlikely that the CT model can help to reveal similar relations between the characteristics of the reproductive cell and the chronometrical characteristics of the meiosis this cell undergoes. More preferable in this sense is, from our point of view, the model of Hertwig (1908), according to which initially in the course of the cell cycle the cell growth anticipates the nucleus growth, and this causes the N/C ratio to decrease. Then the nucleus growth anticipates the cell growth, and the N/C ratio increases. When N/C reaches the initial value typical for cells of this type, the cell will divide. The Hertwig model supposes indirectly that at the beginning of division the cell size and its nucleus size are twice as large as the initial sizes. So, in the beginning and at the end of the cycle the equation of N/C relations looks like $N/C = 2N/2C$. However, the cell could reach the initial N/C value at the end of the cycle also with other values N and C. If this takes place, then, possibly, the cell undergoes differentiation during the cycle. Hence, according to the Hertwig model, the changing of cell morphometric characteristics during the cell cycle can be treated as the probable sign of its differentiation.

As mentioned above, the reproductive cell and its nucleus in amphimicts enlarges about three times during the transition from archesporial cell through megasporocyte to meiocyte, whereas in apomicts it enlarges just two times. The equation of N/C ratio in the beginning and at the end of the premeiotic interphase in the former looks like $N/C = 3N/3C$, and in the latter it is $N/C = 2N/2C$.

As shown by a number of authors (e.g., Craigie and Cavalier-Smith, 1982), the number of plant cell divisions, which relatively quickly follow one another, depends on the cell size. The modelling of two meiotic divisions by such mitotic divisions returns us to the already mentioned supposition that the insufficient growth of apomictic reproductive cell in premeiotic interphase does not allow accumulation of the pool of substances necessary for two subsequent divisions. Possibly, this cell has to reach a certain size to continue its development. The blocking of its second division is realized by the system of control of the morphometric relations, which acts at the cell level.

As Craigie and Cavalier-Smith (1982) suppose, the only way to explain the patterns of mitotic divisions they observed is to assume that after each division the daughter cells correct their volume and divide in the next cycle only if the volume exceeds some minimum that is characteristic for cells of this type. The existence of critical cell size, reaching of which turns on the key processes defining the further course of cell cycle, was proposed earlier by Fantes (1980).

One possible reason for limitation of the reproductive cell's ability to correct morphometric characteristics during meiosis is the limit of time. In amphimicts the main events of megagametophytogenesis obviously have to be quite strictly correlated in time with the main events of microgametophytogenesis. In apomicts these correlations are broken up to a certain extent; for example, in *Taraxacum officinale*

the parthenogenetically developing embryo often can be observed in the ovary by the moment of pollination. It is unlikely that this means the reproductive system of the species has freedom in choice of the optimal moment of parthenogenesis induction, and, particularly, the moment of induction of the apomictic megagametophytogenesis. It is possible that the reproductive process, more than any other ontogenetic process, is affected by "missing the boat".

To develop the above-mentioned idea of Gustafsson (1947a) one could suppose that apomixis is related with dichogamy,[2] i.e., the separation in time of two moments: the moment of pollination, predicted by the plant organism (and, consequently, the predicted moment of microgametophyte readiness for fertilization), and the moment of megagametophyte readiness for fertilization. Dichogamy is probably one of the most archaic and primitive mechanisms providing allogamy. It is worth recalling that dichogamy occurs more often in the form of protandry and rarely in the form of protogyny, and the protogynic time shift as a rule is much shorter than the protandric one. So, the phenomenon of dichogamy has a sharply obvious asymmetry toward the micro- and megagametophytogenesis, and this probably is not accidental. The phenomenon itself and its asymmetry occur not only among the angiosperms, but also among other higher and lower plants known to possess anisogamy or anisospory.

The foregoing suggests a need to analyse the N/C ratio in the reproductive cell as a characteristic that cannot be simplified to average values of N and C. The data about the dynamics of the N/C ratio (Fig. 26) suggest the coincidence of N/C values at corresponding stages of development of the reproductive cell in the amphimictic and apomictic species studied. The changing of N/C ratio during the transitions from archesporial cell through megasporocyte to meiocyte, i.e., in premeiotic interphase, is in conformity with the model of Hertwig. If average values are taken for Hertwig's N/C variations within the single cell cycle, then the following pattern will appear for amphimicts.

All average N/C values (except the value at the megaspore stage) fit within the strict range 0.36-0.39. The cited evaluations of average value errors suggest the narrow range of the average values maintained by the system of regulation of embryo sac ontogenesis, which in turn suggests the significance of these values.

The coincidences of average values of the N/C ratio and the strict control of them are not specific to amphimictic megagametophytogenesis in the species studied. The apomictic species show a similar picture in this aspect, though the average values themselves appear to be a bit different.

Another question is how common is the tendency mentioned above. Possibly, it takes place only in some Asteraceae, including the species investigated by us. What about the strict control of the morphometric ratios in the reproductive cell during megagametophytogenesis? We suppose it to be universal and caused by the regulatory mechanisms of the embryo sac ontogenesis, which are common for amphimicts and apomicts.

The morphometric characteristics of the reproductive cell, at least at some stages of its development, probably could be used as an addition to traditional embryological signs, which are used in systematical and phylogenetic considerations.

•^ee Dichogamy for more details.

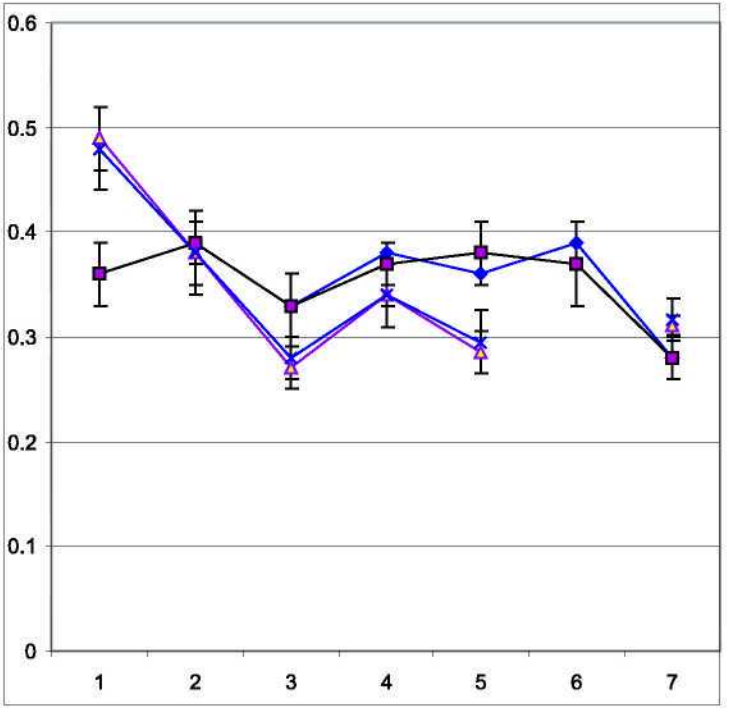


Fig. 26: Changing of the nucleus/cell ratio in the reproductive cell.
x-axis: 1 - nucellar, 2 - archesporial, 3 - megasporocyte, 4 - meiocyte, 5 - dyad cell, 6 - tetrad cell, 7 - megaspore; y-axis: nucleus square to cell square ratio (N/C). • - C. *capillaris*, • - *H. gradlis*, *A - T.officinale*, *x-R. laciniata*

The investigators had come to such a conclusion quite long ago. Referring to the investigations of Smith (1973, 1975) concerning the detection of morphometric characteristics of embryo sacs in *Cornus* genus, Herr (1984:686) wrote: "Among the various kinds of investigation, those directed to the female gametophyte perhaps have the greatest potential value in taxonomic considerations." The morphological and chronological characteristics of the ontogenetic precursors of the embryo sac, and the correlations between these characteristics, could help to solve or at least significantly clarify a number of problems in systematics and phylogeny.

It is time to return to dichogamy in the context of apomixis: the thing that corresponds to temporal separation of the micro- and megagametophytogenesis is their spatial separation, which can manifest itself in different forms in different plants. Animals have such separation expressed in extreme form because of their ability to move. Plants do not have that ability. Plants and animals have a different kind of relation between the temporal and the spatial aspect of gametogenesis. That is why, for example, analogies between parthenogenesis in animals and in plants could have limited applicability for analysis of the apomixis problem.

The reproductive process in flowering plants is almost unstudied because of the obstacles mentioned in the earlier cited papers by Smith (1973, 1975). The

corresponding data about the morphometric characteristics of embryo sacs were obtained with very poor statistics (3-5 measurements). Similar analysis of the ontogenetical precursors of the embryo sac will entail even more difficulties. The relatively small number of papers using precise quantitative methods of reproductive process analysis in angiosperms suggests difficulties of another kind.

Turning back to our data, note the similarity of the average N/C values at the megaspore stage in all four species studied: 0.28 ± 0.04 (C. *capillaris)*, 0.28 ± 0.02 *(H. gracilis)*, 0.31 ± 0.01 (T. *officinale)*, 0.32 ± 0.02 *(R. laciniata)*. This similarity possibly suggests that **reaching certain values of morphometric characteristics is necessary for the reproductive cell to continue development.** The archesporial cell takes a special place among the ontogenetic precursors of the embryo sac. This statement is doubtless true for the functional megaspore as well.

Our data about the N/C ratio in the reproductive cell were calculated using the squares, but not the volumes. To evaluate the volume ratio, we need to raise the obtained ratios to the power 3/2. Performing this procedure leads us to estimated value N/C = 1/2 for the megaspore. So, in all four species studied, the volume of the megaspore nucleus is twice as small as the volume of the megaspore itself.

The nucellar cell in *C. capillaris* and *H. gracilis* has N/C = 0.36; in T. *officinale* and *R. laciniata* it has N/C = 0.49. On the other hand, at the stage of archesporial cell, the N/C values are quite similar in all four species. In the archesporial cell, as well as in the megaspore, the nucleus volume appears to be about half the volume of the cell itself. If it is supposed that such N/C ratio is obligatory for the reproductive cell to continue development, then the decrease of N/C in apomicts from 0.49 to 0.33 during the differentiation of the nucellar cell into the archesporial cell appears to be forced. After such decrease of N/C, the system of control of the morphometric ratios in apomictic reproductive cell will keep N/C almost in the same limits as those inherent for amphimictic reproductive cell. What follows is just the result of the events happening during the transition from nucellar cell to archesporial cell. The subsequent development of reproductive cell into amphimictic or apomictic embryo sac probably proceeds using considerably the same programme and mechanisms.

If the apomictic genes manifest themselves as the peculiarities of spatial and temporal organization of the premeiotic interphase, then it becomes obvious how difficult it is to find their expression at the levels in which this expression used to be sought.

As we suppose, the morphologically distinguishable stages of development of the reproductive cell in the plants studied correspond to the generally accepted stages of premeiotic interphase as follows:

$$G_x \text{-} > S \text{-} > G_2$$

nucellar cell —> archesporial cell —> megasporocyte —> meiocyte

The results of determination of nucleic acid content in the reproductive cell do not directly support such a superposition (Fig. 27). However, it is necessary to note that the method used reveals mainly the ribosomal RNA, which may make as much as 90% of total nucleic acids in the cell. The presented data suggest that the specific features of apomictic megagametophytogenesis are defined sufficiently at the moment of transition from nucellar cell to archesporial cell, or perhaps even earlier. The increased nucleic acids accumulation in the reproductive cell of amphimicts, beginning from the stage of archesporial cell, is quite noticeable. The apomictic

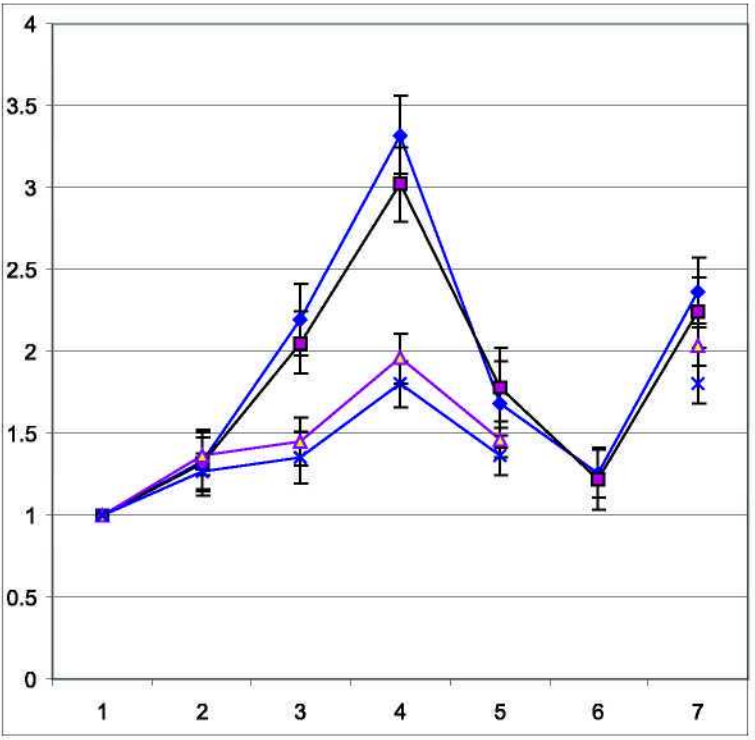


Fig. 27: Changing of the nucleic acid content in the reproductive cell (scaled to content in the nucellar cell).

x-axis: 1 - nucellar, 2 - archesporial, 3 - megasporocyte, 4 - meiocyte, 5 - dyad cell, 6 - tetrad cell, 7 - megaspore; y-axis: nucleic acid content in conventional units. • - C. *capillaris,* • - *H. gradlis, A - T.officinale, x-R. laciniata*

reproductive cell continues to accumulate nucleic acids with the same intensity. This suggests a relative delay of growth of the apomictic reproductive cell. According to Darzynkiewicz *et al.* (1981), the rate of passing cell cycle and its particular phases correlates with the ribosome number.

Strictly speaking, it is necessary to distinguish the cell cycle and the cycle of cell division. The latter necessarily implies the presence of mitosis; that is why it is called the mitotic cycle, or cycle of division. At the same time, as we know, the cell in the course of differentiation could pass through all the stages of the cell cycle without division, i.e., without undergoing mitosis. Such a sequence of events could be called "differentiation cycle" and included in the more common term "the cell cycle". The two cycles are connected by two transitional "points", R_x and R_2 (the points of resting phase, see Epifanova *et al.,* 1983), situated in the second half of phases G_1 and G_2 respectively. In R_x and R_2, cell advancement through the cycle is delayed. One cannot exclude the possibility that the control of the morphometric characteristics, their possible correction and decisions about the further pathway of cell development occur in these local phases of delay in the premeiotic interphase of the reproductive cell.

Experimental Induction of Apomixis *in vivo* and *in vitro*

Experimental induction of apomixis is a poorly developed problem. It especially concerns the induction of diplo- and aposporу. In *Nicotiana tabacum*, in *in vitro* culture of immature ovaries under high temperature (37°C), unreduced megaspores and embryo sacs develop, which has not been observed under normal and low temperatures (Lobanova, 1992). The high temperature increases the probability of archesporial cell development by the pathway of unreduced megaspore formation also in natural conditions. Colchicine treatment of the immature ovaries of *Cucumis sativus in vivo* resulted in formation of the aposporous and diplosporous embryo sacs (Dzevaltovsky, 1971,1973). Structures similar to the initial aposporous cells and the aposporous embryo sacs from the nucellar cells were observed by the treatment of mature *Zea mays* inflorescences *in vivo* with solutions of IAA and its synthetic analogues, and also with gramicidine C and D, coumarin, glutathione, dimethylsulfoxide (DMSO), and some salts of calcium (Kashin, 1992, 1993). Successful induction of parthenogenesis was obtained by use of irradiated and foreign pollen (Dore and Marie, 1993).

Experiments on the chemical induction of parthenogenesis *in vivo* are, apparently, the most informative about mechanisms of switching on the apomictic pathway of reproduction, though forms with a genetic inclination to apomixis are mainly used. In such forms, increase of apomictic seed output in several times, in comparison with the control, was observed on treatment with solutions of some substances. For the treatment, various auxins, kinetin, gibberellic acid, sodium salt of ATP, casein hydrolysate, arginine, and proline were used (Arendt, 1960; Britikov, 1975; Arendt and Kazas, 1978; Romanova *et al.*, 1983).

Parthenogenetic seed formation was induced in forms that were not inclined to apomixis by the following treatment: DMSO and double combinations of colchicine and hydrolysate of maleic acid in *Zea mays* (Zhao and Gu, 1984), colchicine in combination with DMSO in *Gossypium hirsutum* (Zhou Shi-Qi *et al.*, 1991), DMSO in *Ribes nigrum, Lycopersicon esculentum* (Vermel and Solovova, 1973), and *Cucumis sativus* (Popov, 1978), brassinolide in *Arabidopsis thaliana, Brassica juncea* and *Tradescantia paludosa* (Kitany, 1994). At the level of megagamete activation, kinetin, 6-BAP, rutin, gramicidine C and D, cholecalciferol, riboflavine, papain, coumarin, glutathione, NADP, DMSO, ethanol, and some calcium salts were effective when the *Zea mays* inflorescences were treated. Auxins (IAA, NAA, 2,4-D) and gibberellic acid did not demonstrate any activity (Kashin, 1993).

The parthenogenetic embryos that were able to develop in plants were obtained from *in vitro* culture of unfertilized ovaries and ovules *(Hordeum vulgare*-San Noeum, 1976). The method of obtaining them was worked out also for *Oryza sativa* (Asselin de Beauville, 1980), *Gerbera jamesonii* (Sitbon, 1981), *Nicotiana tabacum* (Zhu and Wu, 1981), *Triticum aestivum* (Zhu *et al.*, 1981), *Beta vulgaris* (Hosemans and Bossoutrot, 1983), *Zea mays* (Truong-Andre and Demarly, 1984), *Allium cepa* (Campion and Alloni, 1990) and other plants.

However, special experiments on the physiology of megagamete activation and the early development of the parthenogenetic embryos in the culture of unfertilized ovaries are rare. Nevertheless, some laws are already clear. It has been demonstrated that, for megagamete activation in culture of *Panicum miliaceum* unfertilized ovaries, the cytokinin level must exceed the auxin level 2-5 times; for further proliferation, it

must be 5-10 times the auxin level (Kashin *et al.*, 2000). Probably for this reason, the treatment of inflorescences with aqueous solutions of auxins at the stage of opened flower, resulting in the development of shriveled caryopsis with the developed embryo but without endosperm (Matzk, 1991), is effective for revealing pseudogamous forms in cereals. For all this, auxins have an effect not on the egg cells, but on non-differentiated embryos, determining their differentiation, which occurs only after development of endosperm in pseudogamous forms. This points to participation of auxins in differentiating action of endosperm on early embryogenesis.

In culture of unfertilized ovaries of *Triticum aestivum*, parthenogenesis and apogamy were induced only with rather high kinetin concentrations. At the same time, nucellar and integumental embryony were induced under an equal ratio of summary concentration of auxins and kinetin in the medium, irrespective of which auxins were used and in which combination (Zhu *et al.*, 1981; Muchambedjanov *et al.*, 1991a,b). In those cases in which such auxins as IAA and NAA were tested, the successful induction of gynogenesis *in vitro* took place either in the absence of auxins in the medium (Svirchevskaya and Bormotov, 1994; Bohanes *et al.*, 1995) or when the concentration of cytokinins exceeded that of auxins (Yang and Zhou, 1982; Pavlova, 1987; Bugara and Rusina, 1988), or at an approximately equal content of auxins and cytokinins (Doctrinal, 1990; Campion *et al.*, 1992). In a course of *Zea mays* unfertilized ear cultivation *in vitro*, the seeds with parthenogenetic embryos also were formed at a high level of kinetin in the medium (2 mg/1) (Huang and Gu, 1995). Sharp increase (by three times) of cytokinin (zeatin-riboside) level in the ovaries of *Triticum aestivum* in the period between pollination and fertilization has also been demonstrated *in vivo* by immunoenzymic analysis (Ermakov *et al.*, 1997).

Thus, it could be suggested that cytokinins are a limiting factor of megagamete activation in flowering plants, and the more profound mechanism of this process, apparently, is connected with a sharp change in calcium homeostasis in a megagamete, as well as by the animal egg cell activation (Kashin, 1992,1993).

Applied Aspects of Gametophytic Apomixis

The practical uses of apomixis have been discussed repeatedly and this was reflected in a series of reviews (Khokhlov, 1971; Petrov, 1979; Nogler, 1984a; Jefferson, 1994; Calzada *et al*, 1996).

Such peculiarities of apomixis as omission of meiosis, absence of fertilization, non-segregation of heterozygotes, and formation of haploid sporophytes have important selective, biotechnological and economical consequences.

Unreduced and reduced forms of apomixis have principally different applied significance.

Unreduced parthenogenesis. One practical use of unreduced parthenogenesis is the fixation of heterosis in hybrids owing to the absence of segregation in apomicts in the following generations.

The mass production of hybrid seeds in some cultivated plants is difficult because of peculiarities of their flower structure. Besides, the open state of flowers necessary for production of hybrids can lead to fungal infection and other diseases. So, hybrids of many crops (particularly very important crops such as wheat, barley,

millet, alfalfa, or soyabean) are seldom or never used and, consequently, 20-100% of potential yield is not gathered.

The problem of heterosis fixing is real also for other unique characteristics of hybrids such as resistance to different factors, length of vegetation season, or photoperiodism. It is known that meiosis proceeds irregularly in remote hybrids. Usually it leads to sterility. At the same time, the principal hindrance to many hybrid combinations is probably absent, as suggested by the restoration of fertility by allopolyploidy. It is possible, therefore, that as a result of omission of meiosis, hitherto unknown, unique, fertile interspecific hybrids and hybrids between taxa of higher rank can be produced. So the involvement of apomictic forms in studies on somatic hybridization on the basis of protoplast fusion is highly desirable.

Many factors (heat, drought, rains) are known to be unfavourable to pollen and the course of pollination. For some plants (e.g., legumes, buckwheat), the yield losses can be caused by deficit of insect-pollinators or their extermination by chemical treatments. In such cases, because of the absence of fertilization, apomixis can increase their seed productivity.

It is advisable to use apomixis also in growing some edible tubers, a significant part of whose production is used as sowing material. For example, the use of seeds instead of tubers in potato would give significant economic gain. The use of seeds of common potato is impossible, because it is a complex polyploid, and sexual reproduction would lead right away to segregation with loss of sort qualities. Apomictic seeds preserve the same genetic structure as tubers.

Simultaneously, another problem can be solved by seed propagation. "Aging of clones", virus infection and various diseases are known to accompany repeated vegetative propagation in wood and shrub cultures as well as in potato. To solve this problem, complex and expensive technologies of microclonal propagation based on tissue culture are used. These technologies could be replaced by seed propagation, which automatically ensures "sanitation".

In some species the non-balanced polyploids are the most productive. In particular, the highest production of sugar beet with high sugar content is observed in triploid forms. Triploid seed production (based on crossing of diploid and tetraploid forms) is labour-intensive and expensive. Therefore, fixation of triploid level on the basis of apomixis is worthy of special research, especially because apomixis has been recorded repeatedly in this crop.

In production of hybrid sorghum on the CMS (Cytoplasmic male sterility) base, undesirable hybrids appear from pollination by pollen of a wild relative. Apomixis can prevent the exchange of genes between cultured and wild species.

A new problem arises in connection with transgenic plant production. Apprehensions are expressed that extremely undesirable consequences of "genetic obstruction" of ecosystems cannot be excluded. On one hand, weeds can acquire the introduced genes (e.g., for resistance to herbicides). On the other hand, some species acquiring the new qualities (e.g., resistance to deleterious insects) can supplant other species in the coenosis. It is desirable, therefore, that transgenic plants should be autonomous apomicts and have no pollen (as carrier of genes to other species).

It is also necessary to remember in this connection that long-term data on varieties, lines or hybrids at the apomictic level are not presently available. Intensification of mutagenic variability, accumulation of lethals, excess

heterozygosity, aneuploidy, transition to uniploid condition and other problems cannot be ruled out. These problems must be studied.

Reduced parthenogenesis. Practical uses for haploid plants produced as a result of reduced parthenogenesis are various (Krupnov, 1976; Tyrnov, 1986b, 1998b; Sydorov, 1990). Here we discuss the main ones, with a short statement of the principles or methods in which they are grounded.

1. Production of constant forms (homozygous lines). Usually this task is solved by means of self-pollination in 5-10 and more generations. By experimental reduplication of chromosome number in haploids, this task is solved in the first generation.
2. Production of aneuploids and translocations. The methods are based on meiosis specificity in haploids. Their chromosomes disperse in disorder to poles. This leads to formation of gametes with chromosome deficit and monosomics during subsequent pollination by normal pollen. The frequent conjugation of non-homologous chromosomes due to the presence of homologous sections in the different chromosomes can result in translocations.
3. Increase in the efficiency of studies on selection and cell and genetic engineering; the production of mutants and test-objects. The methods are based on the fact that in haploids (especially in monoploids) the effects of all mutations, both dominant and recessive, are manifested.
4. The overcoming of incompatibility. A number of polyploid crops have diploid wild relatives, which usually carry many valuable characters. The use of dihaploids facilitates crossing with these diploid species owing to equalization of chromosome numbers and similarity of physiological-biochemical characteristics, depending on ploidy level. In the presence of incompatibility alleles the probability of crossing increases because of decrease of their number in haploids.
5. Selection and genetic analysis of the complex of characters. Probability of combination of the different linkage groups in haploids, diploids and tetraploids is determined by the formula (1/2), (1/4) and (1/36) to the nth power, where n = chromosome (genes) number. The use of haploids greatly decreases the number of plants necessary for selection on complex of unlinked genes. For example, by use of haploids one homozygote for five genes can be produced among 32 plants: (1/2) to the fifth power. By use of tetraploids in an analogous case more than 60 million plants will be needed: (1/36) to the fifth power.
6. The rapid production of alloplasmatic lines. The traditional method of back-crosses takes a long time (several generations) and does not always produce absolutely like analogues. In some cases, female gametes of hybrids can be formed normally and function only by presence of certain chromosomes of maternal form. So, even by long back-crosses, it is difficult or even impossible to replace them by chromosomes of paternal form. The maternal characters can be preserved also owing to crossing-over. The use of androgenesis (male parthenogenesis) overcomes these shortcomings and produces the desired lines, including lines with CMS, in the first generation.
7. Production of unreduced apomicts. Reduced parthenogenesis can be hereditary (conditioned by genotype of maternal parent) and non-hereditary (induced). The hereditary forms are of interest for subsequent synthesis of unreduced apomicts

on the basis of combination of signs of parthenogenesis, non-reduction and normal endosperm development (Tyrnov and Enaleeva, 1983; Tyrnov, 1994, 1997).

The foregoing list chiefly concerns the problems of practical breeding. However, haploids can also be used for solution of theoretical problems such as genomic analysis and genome evolution, genetics and morphology of meiosis, genetics of quantitative signs and dose of genes, detection of functional diploidization of polyploids, control of homo- and heterozygosity, genetic burden and its elimination, heterosis.

Alchemilla L. (Rosaceae) is a Classic Object for Studying Facultative Apomixis (Plate VII)

Most of the *Alchemilla* species are facultative apomicts and only some of them are amphimicts. These species, especially facultative apomicts, are characterized by the multiplicity of modes of megasporogenesis and megagametophytogenesis.

In ovules of *Alchemilla*, as in other Rosaceae *(Fragaria, Potentilla)*, the multicellular archesporium is formed, which, after a series of mitotic divisions, gives rise to the sporogenous complex (Solntseva, 1965b; Rutishauser, 1967). The structure and topography of such complex in *Alchemilla* was described (Glazunova, 1977, 1983, 1987) according to the terminology proposed by Rutishauser (1967).

Cells of the sporogenous complex are arranged in longitudinal rows: central, two lateral (one on each side) and two parietal. In each row, the primary, secondary and subsequent megasporocytes are distinguished from the bottom upwards. In the central primary megasporocyte, meiosis commonly occurs; however, aneumeiosis (disturbed meiosis) may be observed as well. The lateral and parietal primary megasporocytes undergo aneumeiosis. As a result of a normal meiosis (eumeiosis), a tetrad of reduced megaspores appears, while the aneumeiosis results in the formation of a dyad of non-reduced megaspores. In the same inflorescence, the entire set of the above-listed modes of megasporogenesis occasionally occurs. Viable megaspores become the mother cells of reduced or non-reduced embryo sacs. In the case of degeneration of the megasporocytes from the central longitudinal row (or their derivatives), a derivative of the division of megasporocytes from the lateral rows may become a mother cell of the embryo sac. The aneumeiosis of megasporocytes results in diplospory. The mitosis of somatic cells of the nucellus usually leads to the formation of non-reduced apospores, i.e., apospory. A reduced embryo sac develops from a megaspore according to the Polygonum-type. Unreduced embryo sacs develop according to the Taraxacum-type; however, the polar nuclei are not fused. From apospores, unreduced embryo sacs develop according to the Hieracium-type (Glazunova, 1984). On the basis of available data, species of the genus *Alchemilla* can be divided into three groups, including the eusporic (amphimictic), diplosporic and aposporic (facultatively apomictic) forms.

In some species, the anther and the male gametophyte develop normally. After the simultaneous formation of the tetrahedral tetrads of microspores, pollen grains with fertility of 90-95% are formed. Pollen grains are bicellular; their contour is smooth, the texture pattern is reticulate, and the exine is two-layered (Demtschenko, 1974; Glazunova and Permjakov, 1980).

The majority of species display certain disturbances in microsporogenesis and tapetum functioning; this results in the sterility of pollen (occasionally, up to 100%), abnormal pollen grains, underdeveloped anthers, etc.; the degree of pollen sterility varies from year to year (Glazunova, 1983). As was marked by Strasburger (1904), the anthers dehisce only if normal pollen grains prevail.

The pollen is found on the stigma of open flowers. The agents of pollination are insects and water. In flower buds immediately before opening, the pollen is not observed on the stigma. However, their embryo sacs contain either unfertilized egg cells or bicellular proembryos (parthenogenesis) with intact synergids and non-fused polar nuclei.

In amphimictic species, double fertilization followed by normal development of seeds has been described. In facultatively apomictic species, cases of double fertilization are scarce. More frequently they display the parthenogenetic formation of embryos combined with pseudogamy: Embryo of two to seven cells formed in a flower bud develops if the polar nuclei are fertilized in the open flower. In some species, the embryo and endosperm have been shown to develop autonomously.

In addition to sexual and parthenogenetic development of embryos, certain species are characterized by apogamety (A. *acutiloba)* or false polyembryony (A. *baltica).* If the sporogenous complex degenerates, adventive embryos are occasionally observed in the chalazal part of the nucellus and at the base of the integument (nucellar and integumentary embryony). Embryos of different ploidy (of sexual and somatic origin) are formed in the same inflorescence.

Let us consider particular features of different *Alchemilla* species, from true amphimicts to diplosporic and aposporic facultative apomicts. An example of an amphimictic species is A. *pentaphyllea* from the central and southern Alps. The central megasporocyte of the multicellular sporogenous complex passes a normal meiosis to form four haploid megaspores. A single embryo sac develops according to the Polygonum-type. The embryo and endosperm appear as a result of double fertilization. In four other alpine species (A. *ftssimima, A. trullata, A. sabauda* and A. *pentaphylloides),* a sexual embryo normally is formed. However, embryo sacs, as in apogamety, and degenerative ovules are also recorded (Strasburger, 1904).

In East European species combined under the name *Alchemilla vulgaris* L. sensu lato, diplospory and apospory are usually observed, although euspory sometimes occurs. All of these modes of megasporogenesis have been recorded in A. *sarmatica* and examined in detail in A. *filicaulis* and A. *glaucescens* (Plisko, 1970; Glazunova, 1984,1987). In the latter two species, a large number of pollen grains of both normal and abnormal structure are often found on the stigma in flowers. These species are characterized by differences in the development of male generative structures. In A. *glaucescens,* 100% of pollen was sterile because of degeneration of microspores over all the years of observations (Glazunova, 1981). In A. *filicaulis,* the meiosis in microsporocytes usually proceeded normally; disturbances were rarely recorded (Glazunova, 1983). The fertility of pollen in this species in different years ranged from 86 to 48%. In dehisced anthers, pollen grains of normal structure prevail. These facts disagree with the opinion of the monographer of the genus who believed that underdeveloped anthers and pollen grains occur in all East European lady's-mantles (Yuzepchuk, 1941).

Rare cases of double fertilization were found in the pollinated flowers of A. *baltica, A. glaucescens* and A. *heptagona.* Embryo and endosperm develop normally.

However, the above-mentioned species and *A. acutiloba* and *A. filicaulis* are more commonly characterized by pseudogamy and the parthenogenetic formation of embryo. Autonomous parthenogenesis in the absence of pseudogamy was marked in *A. sarmatica* (Plisko, 1970). Thus, the species of the group *A. vulgaris* sensu lato show a significant variability of embryological processes, diplospory with unreduced parthenogenesis being commonly observed. These species should not be regarded as obligatory apomicts, since they produce a large amount of fertile pollen and have (although rarely) euspory and sexual process.

For the purpose of comparison, let us consider the data obtained by a number of researchers concerning the development of female characteristics in the species distributed outside Eastern Europe. In the African species *A. johnstonii* and *A. argyrophylla*, degeneration of the central megasporocyte after a disturbed meiosis was described (Hjelmquist, 1956). The embryo sacs develop from the derivatives of the lateral and parietal megasporocytes. In the European species *A. spedosa* and *A. alpina*, disturbed meiosis with the formation of dyads was observed in the central and lateral megasporocytes (Strasburger, 1904). The second species can develop the aposporic embryo sacs from the chalazal cells of the nucellus. The same processes of embryo sac formation occur in *A. monticola* and *A. subcrenata* (Mandrik, 1976, 1980). Thus, diplospory combined with apospory is characteristic for a number of *Alchemilla* species.

The ratios of different types of embryo sac development are given for separate species. The data on the middle European species of the sections Calicinae and Coriaceae (Izmailow, 1984,1986) are of special interest in this regard. Diplospory and apospory were also discovered in them. In particular, in *A. indsa*, aposporic embryo sacs develop in 90% of ovules, both types of embryo sacs develop in 8% of ovules, and diplosporic embryo sacs develop in 2% of ovules. In the species examined from these two sections, no signs of pollination and fertilization are observed. The embryo (unreduced parthenogenesis) and endosperm are formed without sperm cell participation. The anthers contain degenerative pollen. The embryogenesis conforms to the Geum-type (Souèges, 1923). In 35% of ovules, the embryo and endosperm are simultaneously formed. In 39% of cases, the embryo begins to develop first, and in 26% of ovules, the endosperm develops earlier.

A comparative analysis of modes of seed formation in *Alchemilla* shows a transition from the species with regular renewal of genetic information (meiosis, sexual process, gamospermy) to species with the prevalence of seeds with matroclinous inheritance (diplospory and apospory unreduced parthenogenesis and adventive embryony, agamospermy). In some cases of diplospory, genetic information may change (Rutishauser, 1967). The presence of different modes of seed formation in the same species likely provides for an increase in the stability of seed production.

The Problem of Evolutionary Significance of Apomixis

From Mendel's works, sexual process was regarded as the evolutionary peak of the plant reproductive system, the significance of which is conditioned by the presence of mechanisms providing genetic recombination, i.e., meiosis and fertilization. These create the reserve of hereditary variability that is necessary for evolution. The

recombination effect is stronger when more genetically heterogeneous components are involved in hybridization. Apomicts, lost meiosis and genetic recombination were declared forms incapable of competition in comparison with sexuals and having no perspectives in evolution (Komarov, 1940; Stebbins, 1941; Gustafsson, 1946-1947a,b; Kozo-Polyansky, 1947). Stebbins categorically named apomictic species as "evolutionary deadlock" and "closed systems", inevitably condemned to extinction. Other famous scientists expressed a similar point of view. In particular, in Dubinin's opinion, individuals of apomictic population are like numerous copies of the same genotype; they lack evolutionary plasticity and inevitably make way for sexual species when environmental conditions change.

An absolutely contrary estimate of the evolutionary significance of apomixis was stated by Khokhlov (1946). He considered apomixis a regular step in the evolution of angiosperm reproductive system and a reflection of the tendency to gametophyte reduction, characteristic of it. In confirmation of the positive evolutionary role of apomixis (Khokhlov, 1967; Khokhlov and Malisheva, 1970), a list of the signs of biological progress of apomictic species was given, including wide distribution of apomixis in angiosperms, attribution of it to young and progressive systematical groups, wide geographical areas and high quantity of individuals of apomictic species in nature, extreme taxonomic differentiation and colossal intraspecific polymorphism, and high seed productivity. In some of these indicators apomicts significantly exceed the proper sexual forms. On the basis of molecular genetics, Khokhlov (1970) pointed to a number of potential genetic mechanisms able to compensate for the absence of meiotic recombination in apomicts. He advanced a bold assumption that at a certain evolutionary stage the apomictic species will supplant sexual ones, and the era of apomixis will begin.

From the 1950s, the evolutionary significance of apomixis was connected with preservation of its contacts with sexual process (Clausen, 1954; de Wet and Harlan, 1963,1970a,b; de Wet, 1965,1968,1971a,b; de Wet and Stalker, 1974; Nogler, 1984a). The greatest effectiveness is attributed to reproductive systems based on a close interrelation of apomixis and amphimixis. In confirmation of this point of view, the authors used the data obtained by examination of agamic complexes, i.e., native associations, including different biotypes of one or some relative species (Babcock and Stebbins, 1938). An agamic complex consists of groups of individuals having different levels of ploidy and different modes of reproduction (sexual, asexual, facultative or obligatory apomictic). Between these groups there is a constant exchange of genetic information. In such complexes apomixis is assigned the role of a mechanism preserving forms with non-stable genetic constitution (haploids, polyploids, aneuploids, hybrids). The main load, in the author's opinion, falls on facultative apomicts, which realize contacts with sexual species necessary for preservation of heterozygosity and polymorphism of populations. Facultative apomicts can simultaneously use both alternative modes of seed propagation: apomictic and sexual. This makes reproductive system of apomicts themselves and the population as a whole dynamic and flexible, providing prosperity of agamic complexes.

Many agamic complexes were described (see Grant, 1981). Analysis of their genetic structure shows that the complexes possess evolutionary potential, if they are not panapomictic. In general, apomixis is extremely rarely the only mode of reproduction for any systematic group; obligatory autonomous apomicts, if they

indeed exist (some researchers have doubts of it), are exceptions. Most apomictic populations are characterized by facultative apomixis, more often by its pseudogamous type.

It has to be noted that de Wet and Stalker (1974) give apomixis the more modest role in comparison to sexual reproduction, confirming that highly adapted agamic complexes prosper because they are facultative sexual ones, but not because they reproduce apomictically. In their opinion, neither apomixis nor polyploidy give the population advantages that would not be provided by the sexual reproductive system. The main role of apomixis, from their point of view, is that it helps to prevent sterility of genetically non-balanced genotypes arising by recombination. The mode of reproduction itself is not important, the authors think; what is important is the achievement of necessary balance between mechanisms providing a minute advantage (adaptation) and mechanisms creating variability. Too high a variability is as deleterious for the population as too low a variability. A balance can be attained by simultaneous use of different modes of reproduction.

A higher estimate of the contribution of apomixis to the evolutionary process was given by Read and Bashaw (1969). These authors believe that even a short contact between sexual and apomictic forms with fertile pollen can produce many new hybrids. When isolated in nature, the developing apomictic forms, differing morphologically from their parents, can become, in due course, the new species.

This problem was fundamentally addressed in Petrov's works (1957,1964,1979, 1988). This author suggested that apomixis in cooperation with sexual reproduction was able to provide long existence of the species when environmental conditions changed and was the basis for progressive evolution. Proceeding from the hypothesis of existence of some recessive genes, controlling different elements of apomixis, he asserted that accumulation of such genes in the composition of genetic burden in populations of cross-pollinating plants, its change in homozygous condition, and then their combination by hybridization lead to manifestation of the different forms of apomictic reproduction. Wide and far-ranging "migration" of these genes into adjacent species and genera leads to formation of the constant heterosis of species and varieties, easily penetrating formerly inaccessible ecological niches and fixing in them (Petrov, 1988). Other authors also pointed to apomixis as an important factor of speciation (Doll, 1974; Urbanska-Worytkiewicz, 1974 (1975); Glazunova, 1976; Dujardin and Hanna, 1987).

Even obligatory apomixis is not always an evolutionary deadlock (Petrov, 1988). Preservation, to some extent, of pollen fertility by obligatory apomicts promotes their hybridization, which subsequently results in either a return of hybrids to sexual reproduction or a stabilization of apomixis. Aneuploidy can also be the reason for return of obligatory apomicts to sexual mode of reproduction, as in the case of disomy (3n+2) in triploid *Taraxacum* (Sorensen, 1958) or transition on lower ploidy level (Khokhlov *et ah*, 1976). As well as apomicts, "segregation" of the sexual forms may be of interest from the evolutionary point of view. According to Gustafsson (1942), such "derivative sexuality is very important for origin of new biotypes". In *Potentilla* species, it was shown that a great number of new biotypes, becoming stable in subsequent generations, were produced by return from apomictic to sexual mode of reproduction (Muntzing and Muntzing, 1943).

In writing of the evolutionary role of apomixis, one must mention its reduced forms (haploidy). Khokhlov and co-authors (1976) considered haploidy a mechanism

of depolyploidization of polyploids, realization of closed genetic information, or return of initial species from "genetic captivity". For example, in apomictic species of *Poa*, *Avena*, and *Dactylis*, polyhaploids were isolated that resemble other species or subspecies of the same genera. Besides, in angiosperms there is an ascertained connection of reproductive mode with ploidy level (sexual species are diploids, apomicts are polyploids), and the return of polyploids to diploid level ensures an agamic complex by necessary advantages of sexual reproduction (hybridization, recombination, deliverance from lethals, selection of adaptive and heterosis combinations). On the other hand, functioning of unreduced gametes leads to increase in ploidy level and restoration of apomictic reproduction mode.

The process of depolyploidization can promote the overcoming of non-crossing barriers, appearing by combination of the forms with different ploidy levels owing to equalizing of these levels or decrease in a number of incompatibility genes.

There are other opportunities for participation of haploids in the evolutionary process. As a result of anomalous course of meiosis in haploids, gametes with non-balanced chromosome numbers can be formed. Their fertilization leads to formation of aneuploid progeny, whose fertility can contribute to apomictic reproduction. Besides, conjugation of non-homologous chromosomes is not infrequently observed in haploids; that can be the reason for translocations and, as a consequence, karyotypic and genomic reorganization (Tyrnov, 1986c).

One more form of reduced apomixis is androgenesis (male parthenogenesis). As a result of sperm penetration in the egg cell and death of its nucleus, the original "nuclear-cytoplasmic hybrids" appear. It is well known that cytoplasm can influence many important characters, such as heterosis, resistance to unfavourable factors, non-crossing, sterility, or mutability level. So the change of plasmon can be a factor of variability and increase in adaptive potential (Tyrnov, 1986a).

On the basis of data accumulated over the past few decades, it can be stated that the evolutionary role of apomixis is diverse and is not limited to preservation and reproduction of valuable genotypes. Facultative apomixis widens the limits of genomic recombination by involving unreduced gametes in the sexual process (Vielle, 1992; Martinez *et al.*, 1994). In a case of simultaneous use of two modes of embryo formation in seeds, apomixis and amphimixis, the plant produces progeny possessing different genetic constitution and different reproductive systems (Berthaud *et ah*, 1995; Noirot, 1993). It is more able to compete and, consequently, will have more chances to be preserved and influence the gene pool of the population. If combination of apomixis with amphimixis is realized in many individuals of a population, it leads to increase in information flows (Cambell, 1995), growth of population genetic polymorphism, and intensification of the role of synthezogenetic and saultation factors of evolution (Kashin, 1998), i.e., such a reproductive system drives the evolutionary process. Non-balanced genetic forms (haploids, aneuploids, odd polyploids, hybridogeneous derivatives), once having arisen, can be a basis for construction of new stable genotypes. These new forms, preserving a long reproductive isolation by stable apomictic reproduction, can be in time transformed into new species. The changes accumulated in them over the period of isolation can provide the preservation of their species status, even if the mode of reproduction changes.

Thus, according to a modern estimate, apomixis makes a significant contribution to plant evolution, quite comparable with that made by amphimixis. Interrelation of

apomixis and amphimixis within the same seed propagation system creates the most favourable conditions for progressive evolution of species.

The Evolution of Gametophytic Apomixis

Two divergent hypotheses have been advanced in recent years to explain the evolution and genetic regulation of apomixis. The first, and most popular of recent years, claims apomixis arose by one or more apomixis-specific mutations (Mogie, 1992; Savidan and Carman, 1999). As evidence, those endorsing this hypothesis point to genetic analyses suggestive of simple inheritance. The second is the duplicate-gene asynchrony hypothesis, which claims apomixis results from rare secondary contact hybridizations in which specific combinations of rare ecotype-specific alleles induce asynchronous (apomictic) development (Carman, 1997; Savidan and Carman, 1999). According to this hypothesis, apomixis may arise in diploid hybrids, interracial autopolyploids, and allopolyploids.

Hypotheses for the origin of apomixis

The simple inheritance mutation hypothesis. This hypothesis is widely accepted (Nogler, 1984a, 1994; Mogie, 1992; Savidan and Carman, 1999). Recent versions include naturally occurring preconditions that are considered critical for apomixis to evolve. Mogie (1992) suggested that a pre-existing tendency for haploid parthenogenesis could allow a single dominant meiotic mutation at one of many loci to cause apomixis. Two or more mutations would be required in the absence of the conditions for parthenogenesis.

Another condition is absence of an endosperm balance number requirement. In plants, a single reduced sperm nucleus (paternal, P) fuses with two fused but reduced embryo sac nuclei (maternal, M) to initiate endosperm formation, and this 1P:2M genome ratio is often essential for successful endosperm formation. Many apomicts comply with this requirement in that a single reduced sperm nucleus fuses with a single unreduced maternal nucleus (Haig and Westoby, 1991). Hence, the "unreduced state" of both eggs and centrally located nuclei in embryo sacs of apomicts may in some cases fulfil genomic requirements for zygotes and central cells, respectively. However, two unreduced embryo sac nuclei unite to form the central cell in apomictic *Tripsacum dactyloides*, which results in a 1P:4M genomic ratio. Apparently, this species does not have an endosperm balance number requirement. According to the mutation hypothesis, the probability of apomixis becoming stabilized should be higher in plants without a 1P:2M requirement when the appropriate meiotic mutations occur. Furthermore, the presence or absence of such preconditions may explain why apomixis is generally restricted to certain families (Nogler, 1984a,b; Norrmann *et al.*, 1994; Savidan and Carman, 1999).

A shortcoming of the mutation hypothesis is that it does not readily explain facultative expression wherein normal and fully functional sexual development occurs at varying frequencies. To explain this, Mogie (1992) suggested that the mutant allele permits facultative sexuality because it is heterozygous and only mostly dominant. Heterozygosity is maintained because the wild-type allele is required in somatic cells. Mogie further speculated that the apomixis allele is dominant in

generative cells and the wild-type allele is dominant in vegetative cells because of a different "cellular" environment. This and similarly complex explanations are required to account for inconsistent genetic analyses (ratios of sexual to apomictic progeny) when apomicts are crossed with other apomicts or with different sexual species (Carman, 1997).

The duplicate-gene asynchrony hypothesis. *Tenets of the new hypothesis.* According to the duplicate-gene asynchrony hypothesis, apomixis is caused by hybridization through which rare combinations of divergent genetic backgrounds (auto- or alloploid) are produced. The divergent genetic backgrounds contain specific combinations of divergent alleles, possibly involving many loci, and these are responsible for apomixis (Carman, 1997). Specific tenets of this hypothesis include the following

— Secondary contact hybridization among ecotypes differing in environmentally regulated schedules of floral development causes apomixis, and this may accompany major climatic changes; apomixis may arise in diploids, interracial autopolyploids, allopolyploids and palaeopolyploids.

— Apomixis requires cooperation between two asynchronously expressed sets of floral genes (Fig. 28); each set usually belongs to a separate ecotypically divergent genome.

— The asynchronous expression that causes apomixis is controlled by rare ecotype-specific alleles that regulate start times and durations of various phases of floral development (Fig. 28).

— Polyploidy is prevalent in apomicts because it enhances parthenogenesis, male fertility in allopolyploid and possibly interracial autopolyploid apomicts, and the physical and functional partitioning of genomes in nuclei.

— Loss-of-function mutations that improve fitness by eliminating maladaptive aspects of asynchrony may accumulate in natural populations of apomicts.

— Mutations, deletions, chromosomal aberrations, and between-genome recombinations may cause reversion to sexuality (monospory, bispory, tetraspory, or other anomalous forms) by preventing, to varying degrees, the genomes from competing in development.

Levels of genetic control. Figure 28 reveals several potential levels of regulation for controlling the type of apomixis expressed (Fig. 29) and the frequency with which sexual development occurs (facultativeness). For apomixis to occur, two schedules of female development must be expressed asynchronously (Fig. 28). Thus, the first level of control involves the timing in which floral development occurs during each schedule. The respective "start times" are regulated by alleles that respond differentially to both environmental and phenological maturity stimuli. This level of control (allelic variation for flower initiation) is responsible for environmentally induced variations in the degree of facultativeness observed in some apomicts (discussed below).

The second level of control involves the rates at which the divergent developmental programmes advance through their various stages. For apomixis to occur, the developing megaspore mother cell (MMC) must be immature and unable to respond during the time in which the meiosis-inducing BI genes are precociously expressed. Variations in this and the first level of control influence the type of diplospory expressed, whether it be Antennaria-type (no signs of an initial meiosis),

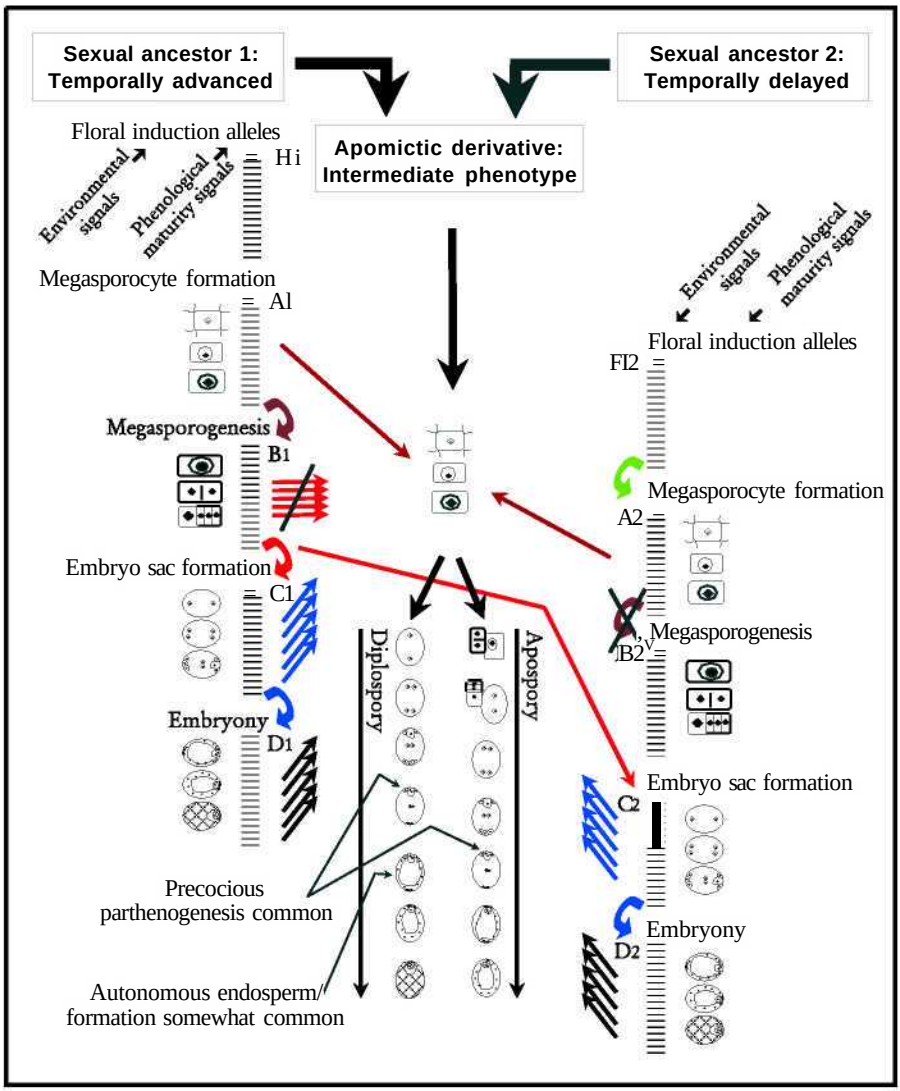


Fig. 28: The duplicate-gene asynchrony hypothesis.

Taraxacum-type (a disturbed meiotic prophase through a restitutional first division), or some other type (Fig. 29; Carman, 1997). This level of control also influences autonomous endosperm formation, which is associated with Antennaria-type diplospory (Asker and Jerling, 1992; Fig. 29).

The third level of control involves variable expressivity of the two or more asynchronously expressed female developmental programmes. Cross-genome gene silencing is common in hybrids and polyploids (Soltis and Soltis, 1993), and if one ovule development programme is sufficiently suppressed, sexual development,

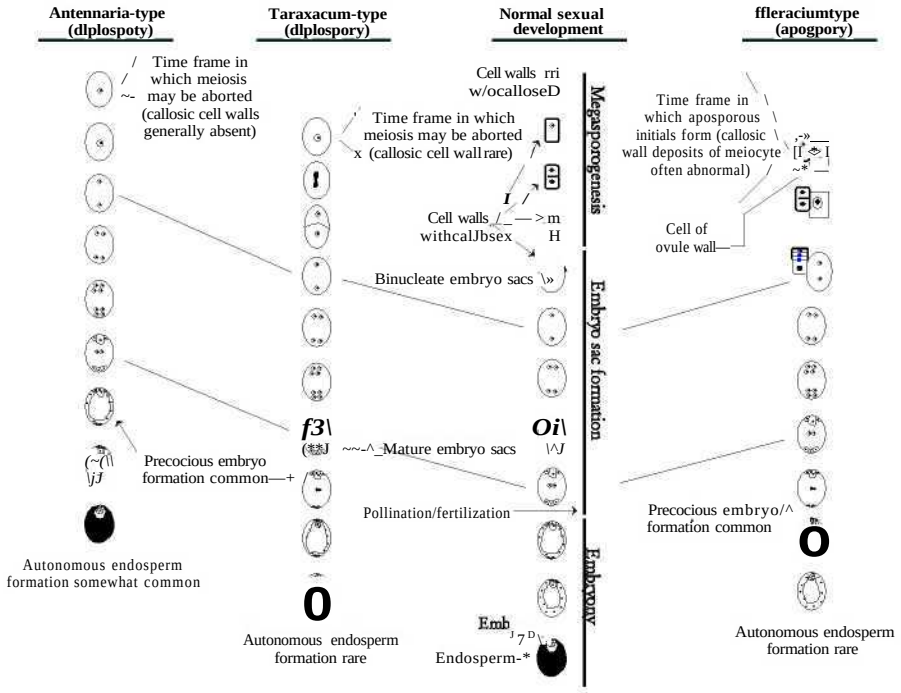


Fig. 29: Diplospory and apospory in comparison with normal sexual development.

encoded by the second ovule development programme, will ensue without interruption. This level of control (genetic and epigenetic variation in expressivity) influences within-population facultativeness and is influenced by such things as ploidy level and the nutritional status of the plant (see Asker and Jerling, 1992, for a review of within-population variation in facultativeness).

A fourth level of control appears to be responsible for bispory, tetraspory, polyembryony, several unusual forms of apomixis, and several other anomalies of female development (Carman, 1997). These more bizarre anomalies generally occur in palaeopolyploid diploids, i.e. diploidized polyploids containing physically or epigenetically fragmented (silenced) genomes, or polyploids containing palaeopolyploid genomes (Carman, 1997). They combine aspects of two asynchronously expressed pathways and/or switch between asynchronously expressed programmes such that certain developmental phases are repeated (one or more times) or deleted (Fig. 30). These complex but consistent forms of development are probably caused by specific deletions or mutations, chromosomal aberrations, and/or epigenetic forms of genome silencing (Carman, 1997). In contrast, development, though asynchronous, is more normal in common forms of apomixis (Fig. 28), which tend to occur in neopolyploids (polyploids containing complete genomes).

Other levels of control involve pre-existing conditions of the progenitor species that increase viability of the apomict once asynchrony is established. The presence of

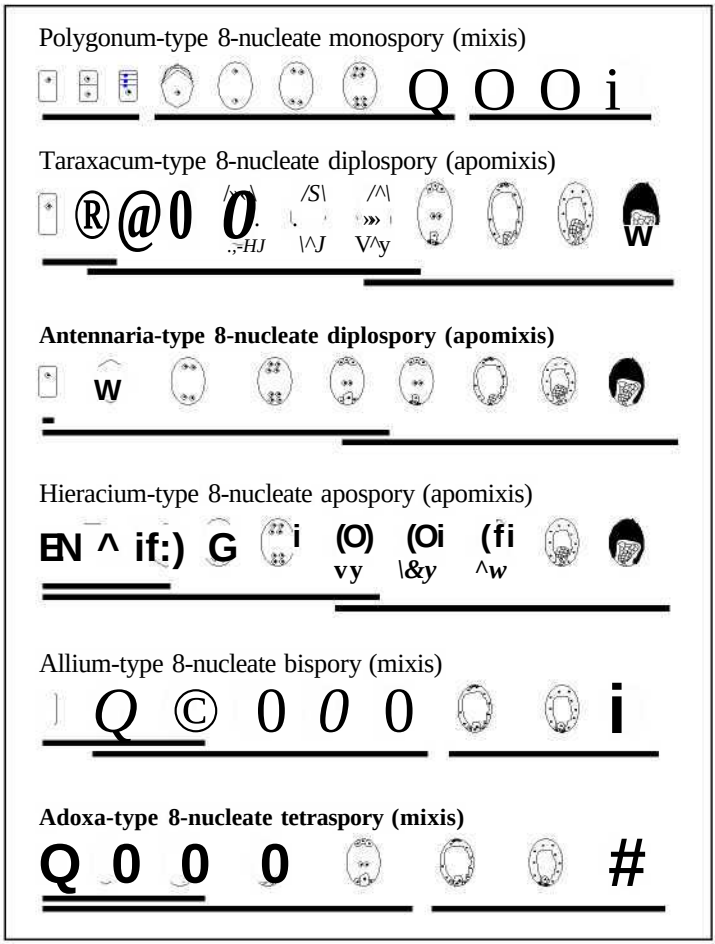


Fig. 30: Ovule and seed development with normal and apo- and diplosporous types of embryo sac formation. The left, middle and right lines represent meiosis, embryo sac and embryo and endosperm formation, respectively. Where lines overlap, portions of two developmental processes occur simultaneously. Where a line is truncated, the respective process is replaced by another.

multiple archegonia, which means the MMC may originate from one of several "archegonial" cells, is one of these. In most species, a single cell develops a high level of developmental competency for MMC formation. However, in species with multiple archegonia, each archegonial cell is capable of forming an MMC, and most aposporous apomicts occur in such taxa (Asker and Jerling, 1992).

Floral tissues in general express multiple developmental competencies. Ovary, ovule, embryo sac, and embryo formation are readily induced from floral cells and tissues *in vitro* but not from adjacent non-floral tissues (Carman, 1990). Consequently, species exhibiting high levels of competency in nucellar cells (such as those with

multiple archegonia) are more likely to express apospory when the required asynchrony, as diagrammed in Fig. 1, is present. According to the duplicate-gene asynchrony hypothesis, pre-existing tendencies for parthenogenesis, which often occur in polyploids (Randolph and Fischer, 1939; Bierzychudek, 1985), and a pre-existing absence of an endosperm balance number requirement increase the likelihood of apomixis becoming stabilized in hybrids where the progenitors express appropriately divergent schedules of female development.

Mutant or wild-type alleles? The following sections discuss the origins of apomixis with regard to palaeoclimatology, phytogeography, genome evolution, Mendelian analyses, physiological genetics, and polyploid evolution. Emphasis is placed on how well observations in these disciplines are explained by the mutation hypothesis versus the duplicate-gene asynchrony hypothesis.

Phytogeography, palaeoclimatology, and the origins of apomixis

Phytogeography and the apomixis birth rate. Nearly all apomicts are polyploids with restricted distributions and centres of diversity within the middle latitudes (Asker and Jerling, 1992). Stebbins (1971a,b) believed these observations are evidence that most apomicts are of recent origin (Pleistocenic). Such conclusions are also based on taxonomic complexity, fossil records (or the lack thereof), ploidy relationships where higher ploidy levels generally indicate more recent origin (Stebbins, 1971a,b; Asker and Jerling, 1992), and rates of molecular divergence (Crawford, 1989). Youthful apomicts with distributions contained within a broader range of sexual progenitor species, such as occurs in *Bouteloua* (Grant, 1971), *Hieracium*, and others (Asker and Jerling, 1992), probably arose during or shortly after the end of the last glacial retreat, which occurred between 20 ky and 8 ky before present (BP). In contrast, apomicts with broader distributions (within larger regions of continents) that tend to fill and transgress those of their putative sexual progenitors, e.g. apomicts in *Crepis, Dicanthium, Eupatorium, Parthenium, Rubus, Tawnsendia* (Asker and Jerling, 1992), and *Antennaria* (Bayer, 1996), may have evolved during earlier glacial periods.

Geological evidence suggests that as many as 26 major glacial periods occurred during the past 3 ky (see Frakes *et al.*, 1992). During these periods, the east-west and north-south distributions of recently evolved plants (including apomicts), which are capable of overwintering glacial cycles in lower elevation or lower latitude refuges, are often expanded. Such expansions accompany the cyclical shifting of climates associated with the advance and retreat of continental ice. For example, during the retreat of the Wisconsin ice in North America, plant associations in the northern Great Plains of the United States shifted, within a few thousand years, from a boreal spruce forest, which was extant at the glacial maxima, to the expansive grasslands of today (Wells, 1970). During this transition, species that had recently evolved in the southern Rocky Mountain cordillera, possibly including the apomict *Antennaria foggii* (Chmielewski, 1994), migrated across the forested Great Plains and became established in the mountains of eastern North America (Miller and Thompson, 1979; Webb, 1988). Such climate-induced vegetative shifts permitted new species, which evolved primarily as a result of secondary contact hybridization during earlier glacial events (from 100,000 to 3 My BP), to migrate across continents. Hence, apomicts with a very restricted distribution are probably of very recent origin, while those of a more regional to continental distribution may have evolved during previous glacial cycles.

Youthful apomicts in this latter category include continental endemics within *Crataegus* (Dickinson *et ah,* 1996), *Amelanchier, Cotoneaster, Mains, Sorbus* (Campbell and Dickinson, 1990), *Taraxacum* (Richards, 1973), *Erigeron* (Huber and Leuchtmann, 1992), *Antennaria* (Bayer, 1996), *Calamagrostis* (Nygren, 1946), and *Poa* (Kellogg, 1990).

Also important to the phytogeographic expansion of apomicts is their capacity for occasional hybridization with related sexual and apomictic species or ecotypes. Such events produce apomictic hybrid swarms (agamic complexes) with expanded ecological plasticities (Stebbins and Major, 1965; Bierzychudek, 1985; Stebbins, 1985; Kellogg, 1990; Soltis and Soltis, 1993; Murray, 1995; Bayer, 1996; Ellerstrand *et al.,* 1996). A well-documented example of expanded phytoecological capacity is found in the *Antennaria rosea* agamic complex. The facultative apomict *A. rosea,* which occurs almost exclusively as a dioecious female, has differentially assimilated, at various locations from close to the arctic circle to the U.S.-Mexican border, many unique ecological tolerances and morphologies of at least eight sexual diploids (personal observations, Bayer *et ah,* 1991; Bayer, 1996). This has occurred through (1) classical sexual introgression (n + *ri)* and (2) B_{ln} hybridization wherein unreduced eggs of *A. rosea* (almost always female) are fertilized by reduced sperm from a related sexual species, and this results in progeny of increased ploidy *i*l*n+ri).* Both mechanisms increase the ecological capacity of the progeny, which are usually apomictic.

Some tropical apomicts in the subfamily *Panicoideae* (e.g., *Panicum, Pennisetum, Setaria)* have multi-continental distributions suggestive of a more ancient origin (Asker and Jerling, 1992). The mechanism of apomixis in many of these grasses is more derived, e.g. 4-nucleate embryo sacs form. In contrast, unreduced 8-nucleate embryo sacs are more primitive (much closer to normal sexual reproduction) and typically occur in recently evolved apomicts (Reddy, 1977).

The birth dates of the more ancient apomicts may also be correlated with climatic deteriorations. A major cool period occurred during the Eocene, about 45 to 55 My BP (Fig. 31). Angiosperms prior to this time had experienced only warm tropical to warm desert climates; cool nights and cold winters had not previously occurred during the age of angiosperms, even at the poles, which had supported, prior to this time, only tropical and subtropical species (Frakes *et al.,* 1992). With the onset of the Eocene cool period, high-latitude species, adapted to tropical climates and long days, migrated to lower latitudes, where they probably hybridized with related species or ecotypes, which were adapted to tropical climates but short days. Ancient apomicts may have evolved during these periods of secondary contact hybridization among species or ecotypes that had previously been adapted to different latitudes.

Most apomicts evolved within *2%* of the life span of angiosperms. Associations between plant migration and apomixis-birth-date are most evident for youthful apomicts (< 3 My BP), which constitute the majority (Asker and Jerling, 1992). This 3 My time period represents less than 2% of the entire duration of angiosperm evolution (140+ My) and less than 4% of the evolutionary duration of modern angiospermous families (about 65 My; see Taylor and Hickey, 1996; Stewart and Rothwell, 1993). Thus, unless apomicts are evolutionary dead ends (Darlington, 1939), conditions during the Pleistocene greatly accelerated the birth rate. The evolution of many new apomicts in 33 well-differentiated families during less than 4% of the duration of modern angiospermous families is strong evidence against mutation-based hypotheses for the evolution of apomixis.

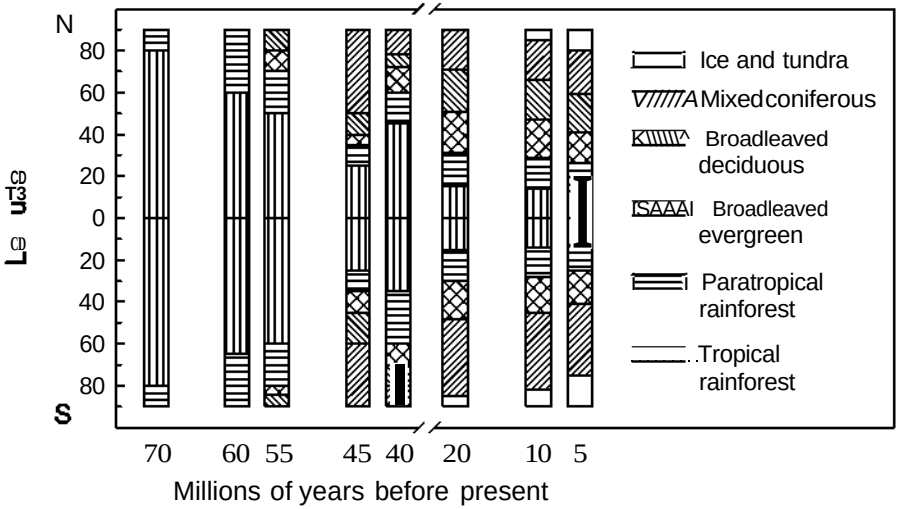


Fig. 31: Global climate deterioration and the evolution of modern angiospermous families (summarized from Webb, 1988; Frakes *et al*, 1992).

It may be argued that apomixis is, as Darlington (1939) suggested, an evolutionary dead end, that the apomixis birth rate has been constant during most of the 140+ My of angiosperm evolution (due to constant rates of mutation), and that the vast majority of apomicts went extinct during the climatic shifts of the Pleistocene. However, this is not supported by current theory. As noted above, the geographic ranges of apomicts tend to expand rapidly throughout the range of their sexual progenitor species (Bierzychudek, 1985; Murray, 1995; Bayer, 1996), which, during the Pleistocene, should have included areas in middle and lower latitudes where plants adapted to higher latitudes grew during periods of glacial maxima. Hence, if the apomixis birth rate were constant, the vast majority of apomicts should be of ancient origin with intercontinental distributions.

Multiple convergences of divergent ecotypes occurred during the Pleistocene. The quest to understand the Pleistocenic proliferation of apomicts logically starts with an analysis of the climates in which sexual and apomictic angiosperms evolved. The earliest confirmed angiospermous fossils are found in strata from 140 My BP, that is, during the Valanginian age of the early Cretaceous (Taylor and Hickey, 1996). From then until the early Palaeocene (about 65 My BP), temperate climates did not exist on earth; the vegetation from the north to south poles consisted of tropical rainforest to warm desert species (Fig. 31). Nevertheless, the fossil record from the early Cenozoic (60 My to 65 My BP) contains representatives from many extant angiospermous families, which had become well differentiated by this time (Taylor, 1990). Except for an acute Eocene cool period (45 to 55 My BP, Fig. 31), the cooling of the climate was gradual from 60 My to 20 My BP, wherein many angiospermous genera and species of modern temperate floras evolved. A more rapid deterioration of global climate occurred from 20 My to 3 My BP and culminated in the first of approximately 26 ice ages. The most severe of these occurred during the Pleistocene, which started 1.6 My BP and ended 10 ky BP (Frakes *et al*, 1992; Stewart and

Rothwell, 1993). The late Pliocenic and Pleistocenic glaciations consisted of eight major glacial/interglacial cycles, which occurred at about 100 ky intervals during the past 800 ky, and numerous minor glacial cycles that occurred from about 3 My BP until about 800 ky BP (Frakes *et al*, 1992).

The cyclical climatic deteriorations and ameliorations of the Pleistocene caused frequent large-scale plant migrations. During each cycle, many ecotypes of middle to high latitudes migrated to lower latitudes where they "overwintered" with lower-latitude ecotypes for thousands to tens of thousands of years (Fig. 32). Much secondary contact hybridization occurred during these cycles (Stebbins, 1971a,b, 1985; Bartlein, 1988; Soltis and Soltis, 1993) in both the northern and southern hemispheres (Fig. 32); for example, Chile and Argentina south of 40°C latitude and the South Island of New Zealand were glaciated during the most recent glacial cycles (see Webb, 1988). A critical variable influencing the locations in which high frequency secondary contact hybridization occurred during the ice ages was a general lack of temperature depression at the tropics during glacial maxima. If temperatures in the tropics had been depressed to the same extent as those in high latitudes, then both high- and middle-latitude species and ecotypes would have migrated to lower latitudes, many tropical species would have become extinct, and high frequency secondary contact hybridization would have been minimized. But palaeoclimatological evidence indicates that this did not occur. Mean annual temperatures near the equatorial tropics during peak glacial periods were depressed by only 3° to 4°C (Webb, 1988; Villagran, 1990). Thus, during glacial maxima, thermal gradients starting at the mid-latitude continental ice sheets (40° to 50° N and S latitude) and ending at the largely unaffected tropics (20° to 25° N and S latitude)

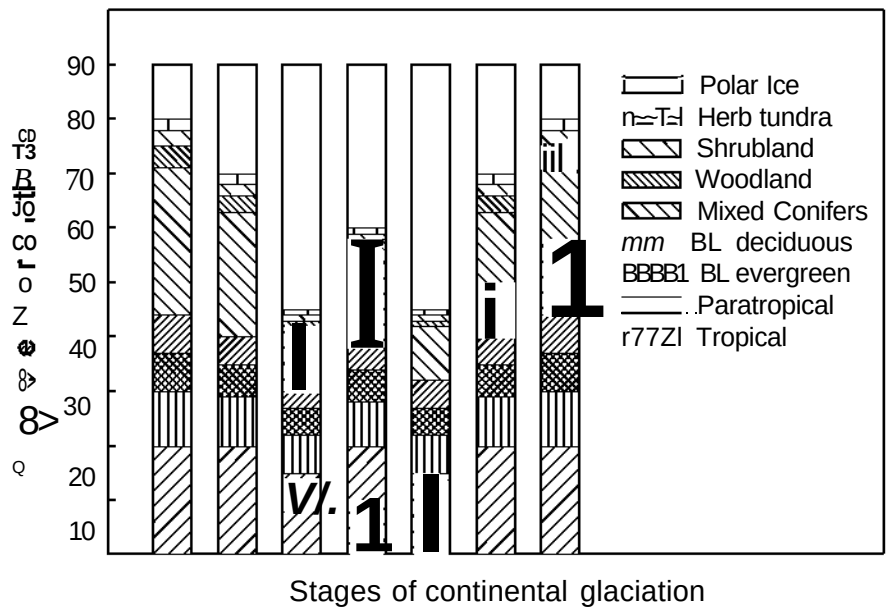


Fig. 32: General effects of continental glaciation on plant migration.

were extremely steep (Fig. 32). Within this zone (about 20° to 50° latitude), high-latitude ecotypes converged with mid-latitude ecotypes, and there was frequent secondary contact hybridization and polyploidization, involving related ecotypes and species.

During glacial maxima, mid- to higher-latitude alpine and tundra ecotypes migrated to refuge areas in the mid-latitude mountains adjacent to low elevation valleys that supported subtropical to temperate ecotypes (Fig. 32). Zones of high frequency secondary contact hybridization and polyploidization occurred in these areas along altitudinal gradients; for example, numerous neoendemics in the Sierra Nevada of California formed in this manner (Stebbins and Major, 1965). Palynological studies of lakes and bogs document a rapid northward migration of f orbs, shrubs, and trees that followed the retreat of continental ice at the end of the last ice age (Webb, 1988). The rapidity with which revegetation occurred suggests that the ecotypes involved remained adapted (genetically fixed) to high latitudes during their various overwintering periods.

Most major glacial advances were dissected many times by minor interglacial periods that lasted for only a few thousand years (Frakes *et al.*, 1992). Thus, it is possible that 80 to 100 major climate-induced large-scale migrations of plant associations (Fig. 32) occurred during the past 3 My. As described below, these geologically frequent and cyclical convergences of latitudinally divergent but related ecotypes greatly increased the frequency of polyploid formation. Furthermore, they occurred in the locations and during the times in which most apomicts evolved, and they constitute the only natural history phenomena directly linked with the explosion of new apomicts during the Pleistocene. It is unclear how such events could have caused apomixis-specific mutations.

Genomes, phytogeny and the origin of apomixis

Apomixis occurs in at least 126 angiospermous genera (Carman, 1997), which is 0.94% of those recognized by the Kew Botanical Gardens (Brummitt, 1992). Eighty-four of these (67%) belong to Asteraceae, Poaceae, or Rosaceae. Apomixis occurs quite infrequently in an additional 30 families, and it has not been reported in the remaining 430 families (Carman, 1995,1997). The Asteraceae, Rosaceae, and Poaceae are among the largest families of angiosperms and are perhaps the most cosmopolitan, i.e., their individual members tend to have broad latitudinal distributions.

Apomixis is only one of several somewhat common anomalies of female development in angiosperms. Such anomalies are frequently categorized as (1) asexual, such as gametophytic apomixis, polyembryony, and other more unusual forms of vegetative propagation, and (2) sexual, such as bispory, tetraspory, abnormal premeiotic chromosomal condensations, and the sequential formation of megasporangia (Davis, 1966; Johri *et al*, 1992; Carman, 1997). It is tempting to think of apomictic mechanisms as representing major developmental deviations from the norm and polysporic mechanisms, where sexual reduction occurs (Fig. 30), as less deviant. This is an incorrect anthropomorphism. While apomixis effectively eliminates meiosis, embryo sac development is usually much more normal in apomicts (Chapman and Busri, 1994; Naumova and Willemse, 1995) than in polysporic species (Johri *et al.*, 1992; Carman, 1997). Furthermore, apomicts tend to

contain stable genomes with low base numbers and few stabilized base numbers per genus. In contrast, polysporic species tend to contain unstable, highly derived, palaeopolyploid (diploidized) genomes with high base numbers and multiple stabilized base numbers per genus.

The statistically significant distinction in base numbers between apomicts (9.6 ± 0.4 SE) and polysporic species (15.7 ± 0.6) (Fig. 33) suggests that (1) relatively complete sets of duplicate genes encoding female development promote the expression of apomixis, and (2) incomplete sets of duplicate genes promote the expression of polyspory and related anomalies, which occur among palaeopolyploids. It is unclear how mutations could be associated with these major genomic distinctions. In contrast, an asynchronous expression of incompletely duplicated sets of developmental genes may explain all of these anomalies (18 or more different types of polyspory—Johri *et ah,* 1992; polyembryony and others—Carman, 1997).

The tendency for apomicts to contain primary genomes and polysporic species to contain palaeopolyploid genomes is only a tendency. Many apomicts clearly contain palaeopolyploid genomes, including some warm season grasses such as *Tripsacum (x* = 18), *Panicum (x* = 9,10), *Brachiaria (x* = 7,8,9), *Lamprothyrsus (x* = 12), *Paspalum (x* =

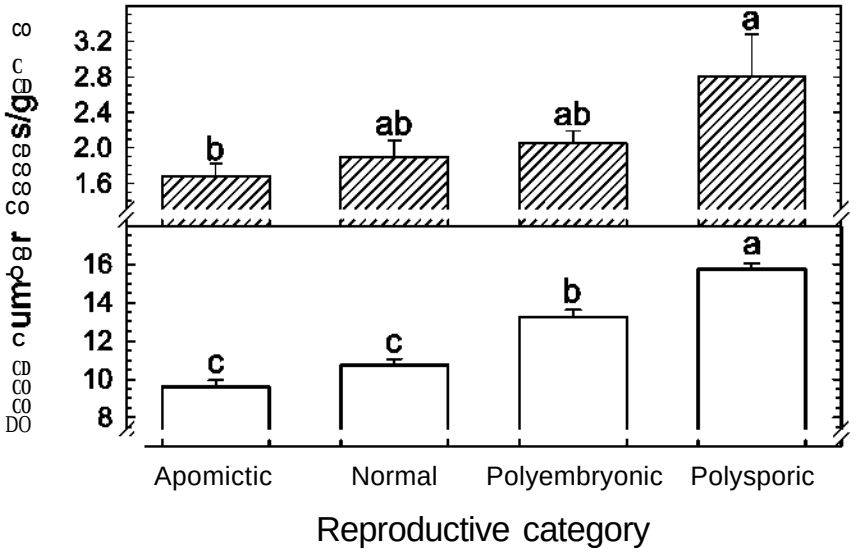


Fig. 33. Bar graph depicting (top) the mean (SE) number of different chromosome base numbers per genus (bases per genus), and (bottom) the mean (SE) chromosome base number of genera known to occur in each category (modified from Carman, 1997). A subsample of 72 sexual monosporic genera was selected at random and used for the "normal" category. "Polyembryonic" refers to bisporic and tetrasporic genera combined. Bars not represented by the same letter are significantly different according to Tukeys Multiple Comparison Test. Genera with chromosome base numbers < 10 usually contain primary genomes. Genera with base numbers >10 usually contain derived paleopolyploid genomes. Paleopolyploidy is also suspected when a genus is represented by multiple base numbers (Goldblatt, 1980).

6,10), *Pennisetum (x* = 7,8,9), most of the apomicts in the Rosaceae *(x* = 17), and many apomicts in the Asteraceae (Carman, 1997). It is also clear that gametophytic apomixis occurs in nature at the diploid level in some of these palaeopolyploid apomicts, e.g., *Sorbis eximia* (Jankun and Kovanda, 1988), *Trifolium echinatum, T. uniolea,* and T. *utriculosum* (Visser and Spies, 1994), *Arabis holboellii* (Roy, 1995), and *Allium tuberosum* (Kojima and Nagato, 1997). Furthermore, non-functional aposporous embryo sacs occur sporadically in several species of diploid *Paspalum* (Quarin, 1986; Norrmann *et ah,* 1989). Duplicate cassettes of genes for appropriate female developmental pathways may exist in these palaeopolyploid apomicts, possibly even on the same chromosome(s), and such duplications may in some cases be responsible for the stabilization of apomixis at the diploid level.

Apomixis may occasionally be a stepping stone to bispory and tetraspory. Thirty of 33 families containing apomicts also contain polysporic or polyembryonic species. The expected number, according to the independent distribution model, is 17; and this phylogenetic relationship is highly significant (Carman, 1997). Within families, apomicts occur in primitive genera with low base numbers, and their developmental mechanisms also tend to be primitive, that is, they tend to diverge little from normal sexual reproduction. In contrast, bispory, tetraspory, and polyembryony occur in related but derived genera (significantly higher base numbers), and their developmental mechanisms also tend to be derived, that is, they tend to diverge greatly from normal sexual reproduction. From an analysis of certain families, genera and species involved, Carman (1997) concluded that apomixis, instead of being an evolutionary dead end, may occasionally serve as a reproductively stable evolutionary springboard for the evolution of normal and developmentally novel (bisporic, tetrasporic, etc.) palaeopolyploid sexual species and genera.

Genetic analyses and the origin of apomixis

Most genetic analyses of apomixis (see Table 12 for representative analyses) support one or more of the following four basic conclusions:

(1) A single locus (probably a chromosomal region containing many essential genes) is associated with high frequency (near obligate) expression of apomixis.

(2) Other loci affect facultative expression of apomixis, and this genetic background requirement has confounded some genetic analyses of apomixis.

(3) Some genetic backgrounds reduce or preclude the expression of apomixis even when a known apomixis-conferring allele (or linkage group) appears to be present.

(4) Some genetic backgrounds induce the expression of apomixis even when a known apomixis-conferring allele (or linkage group) appears to be absent.

Non-recombining linkage groups are sometimes associated with apomixis. Many genetic analyses are consistent with tetrasomic inheritance wherein a single dominant allele "A" confers apomixis (Table 1—A, C, E, G, H, I, J, K). The duplicate-gene asynchrony hypothesis predicts this outcome when (1) genes from a second genome, which cause asynchrony (Fig. 28), reside on a single chromosome and (2) the apomict is an allopolyploid or an interracial autopolyploid (segmental autoalloploid, see Schultz-Schaeffer, 1980). Tetraploid apomicts meet the latter requirement by possessing three homologous genomes and one genome homeologous to the others,

Table 12. Representative studies from which four basic conclusions concerning the genetic regulation of apomixis (see text) were formulat

Cross[1]	Observed segregation		Expected segregation					Sexual ovules (%)	Notes/explanations	Conclusio supporte
	Apo	Sex	Ratio	Apo	Sex	χ^2	P			
A. *Bothriochloa/Dichanthium*[3]								Not detected	Data fit a tetrasomic random chromatid assortment model (AAaa, A; aaaa, S).	**A**
A x **S** and **S** * AA x **A**	**63**	**14**	3.7:1	61	16	0.178	.60-.70			
	75	**4**	20.8:1	75	4	0.066	.70-.80			
B. *Pennisetum dliare**						(Pooled[4])		Not reported	Epistasis: AaBb, B (a dominant mutation) causes sexuality regardless of "A" allele(s).	**A,C**
S x S	**97**	517	0.23:1	115	499	3.50	.05-10	Not reported		
Sx **A**	285	481	0.6:1	287	479	0.028	.75-.90	f or S x A progeny		
C. P. *dliare*[5]										
S (aaaa) x A (Aaaa)	298	295	1.15:1	317	276	2.320	10-.20		Tetrasomic model: rare apomicts from sexuals (0.64%) were facultative and did not have "A" allele(s).	**A,D**
S (aaaa) x A (AAaa)	140	**49**	3.67:1	149	40	2.291	10-.20			
SxS&Sselfed	**4**	623								
D. *Paspalum notatum*[6]			These data were: too variable to postulate effects of major genes, e.g., percentage apomictic jprogeny obtained when PT-2 was crossed with two different apomicts5 varied 10-fold.					Not detected	Determined by 15-plant F_2 and F_3 progeny tests. All progeny of apomictic FjS were uniform. All progeny of sexual FjS were variable.	
PT-2 (4x CDS) x WSB (4x A)	**10**	250								**A,C**
PT-2 x MHB (4x A)	**13**	**32**								**A,C**
PT-4 (4x CDS) x MHB (4x A)	**4**	**50**								**A,C**
PT-10 (4x CDS) x MHB	**17**	**64**								**A,C**

Table 12 *(Contd.)*

E. *Panicum maximum*[7]										
S (aaaa) x A (Aaaa)	71	62	1:1	66	67	0.609	.40-.50	Mostly low (range 0-	Tetrasomic random chromosome assortment	A,B,C
SFj selfed	0	126	0:1	0	127			00 A)	model (Aaaa, A; aaaa, S).	
F. *P. maximum*[9]										
S (Aaaa, carrier only) selfed	54	116	0.46:1	54	116	0.007	.90-.95	Not detected	Two (or more) loci with dosage effects cancel apomixis.	C
G. *Brachiaria*[10] (4x; aaaa, x Aaaa)									8.1 to 72.1. A polygenic system, possibly acting on	
B. ruziziensis x *decumbens*	13	14	0.87:1	13	14	0.037	.80-.90		precocity of embryo sac development, was	A,B,C
B. ruziziensis x *brizantha*	2	4	0.87:1						proposed for facultativeness, which varied greatly between	
H. *Brachiaria*[11] (4x; aaaa, x Aaaa)										
B. *ruziziensis* x *decumbens*	49	79	0.87:1	60	68	3.459	.05-10	7 to 83%	field and greenhouse plantings.	A,B,C
B. ruziziensis x *brizantha*	123	125	0.87:1	115	133	0.912	.30-.40			
I. *Pennisetum* (4x aaaa x 6x Aaaaaa)								One Fj with apomixis markers was 93% sexual	Tetrasomic random chromatid assortment model; a hemizygous apospory-specific genomic region (ASGR) was identified.	A,B,C
P. *glaucum* x *squamatum*[12]	162	235	0.87:1	185	212	5.124	.01-.02			
J. *Pennisetum* (4x aaaa x 6x Aaaaaa)										
P. *glaucum* x *squamatum*[13]	6	11?	0.87:1	8	9	0.531	.40-.50	0 to 16%	From 1 to 5% of ovules in 10 of 11 "sexual" FjS produced aposporous sacs; ASGR was probably not presenting these plants.	A, B, C, I

Table 12 *(Contd.)*

K. *Tripsacum dactyloides*[1]^ *Zea mays* (2x) x T. *dactyloides* (4x)	23	29	0.87:1	24	28	0.019	.80-.90	Not reported	Tetrasomic random chromatid assortment model; apomixis linked to Trl6 (distal Mz6L).	A
L. T. *dactyloides* x Z. mays BC lines 30 Mz+8Tr+Mz6-Trl6[15]								Not reported	Apomixis linked to long arm of Trl6.	A
M. *T. dactyloides*[16] 2x (S) x 3x (A)	43	3	Data were obtained using a subset of more fertile plants and are not applicable for genetic analysis.					0-100%	Percentage sexual embryo sacs in ovules decreased with an increase in chromosome number.	B
N. *T. dactyloides*[17] 2x (S) x 4x (A)	86 triploids from six families were scored for fertility (high = apomictic, low = sexual) and correlated with RFLP markers. High fertility was linked to five *Tripsacum* linkage groups that correspond to three linkage groups in *Zea.*									B,C
O. T. *dactyloides* x Z. mays BC lines 20Mz+18Tr[18]	The Trl6 chromosome + 17 other Tr chromosomes are present							0-3%	Gene(s) on Trl6 represent only one of several necessary linkage groups, i.e. absence of certain Tr chromosomes eliminates apomixis regardless of Trl6.	A
30Mz+9Tr (line I)[19]	Trl6 + 8 other Tr chromosomes							9-15%		B,C
30Mz+9Tr (line 2)[18]	Trl6 + a different set of 8 other Tr chromosomes							85-90%		B,C
44,47 & 51chromosome lines[20]	Mz6-Trl6 present + several other Tr chromosomes							100%		B,C
P. *Calamagrostis* (sexual x sexual)[21] C. *arundinaceae* (4x) x *epigeios* (8x)								In an ~F_1 (6x), 34% of functional embryo sacs were diplosporous; but parthenogenesis was not observed, only B_{ln} hybrids. Apomixis does not occur at any ploidy level in the parent species.		D

Table 12 *(Contd.)*

Q. *Sanguisorba minor* (sexual x sexual)[22] ssp *minor* (4x) [x] ssp *magnolii* (4x) ssp *minor* (4x) [x] ssp *muricata* (8x) ssp *muricata* (8x) [x] ssp *magnolii* (4x)				All 4x and 6x FjS were fully functional aposporous apomicts. Apospory is absent in parental and other subspecies regardless of ploidy or environmental treatments used in attempts to induce it.	D
R. *Raphanus sativus* [x] *Brassicaoleraceae*[B]	Total ovules	Aposporous ovules (%)	Aposporous embryo sacs/aposporous ovules	The listed lines are amphiploids (4x) obtained from colchicine-doubled parents from many diploid cultivars. Unreduced maternal progeny was documented from these *Raphanobrassica* lines.[24] Apospory does not occur elsewhere in the entire Brassicales order, i.e., apospory in these lines did not result from the surfacing of a genetically suppressed apomixis-specific allele.	B,D
Line 3048	117	70	2.7		
Line 3050	97	61	2.2		
Line 3051	79	57	1.8		
Line 3053	60	58	2.9		
Line 3054	66	36	1.6		
Line 3057	101	66	2.7		
S. *Sorbus aria* (2x) [x] *torminalis* (2x)[25] Diploid hybrid (S. *eximia*, 2x) Amphiploid *(S. eximia*, 4x)	Both forms of *Sorbus eximia* (2x and 4x) are geographically restricted neoendemics, and their parents are sexual diploids. At both ploidy levels, a primary group of archegonial cells form but fail to undergo meiosis. A 2nd group of archegonial cells form as the I^{s}' group degenerate. Meiosis and aposporous embryo sac formation occur simultaneously among cells of the 2nd group (compare with Fig. 30). Apospory is fully functional at both ploidy levels.				D
T. *Antennaria neglecta* [x] pZaM *taginifolia*[26] Diploid hybrid (2x)				Infrequent aposporous embryo sac formation was documented in a hybrid between these two sexual diploid species.	D

Table 12 *(Contd.)*

U. Intergenic hybrids in the Triticaceae *Hordeum vulgare* x *Triticum turgidum*[27] *H. vulgare* x T. *aestivum*[27] T. *aestivum/Leymus mcemosus/fThinopyrum elongatum*[28]	Low frequency apomixis (unreduced embryo sac and egg formation followed by parthenogenesis) occurs in various complex hybrids within the Triticeae (wheat and its wild relatives). Embryological studies are needed to determine whether parthenogenesis occurs or pollination occurs followed by chromosome elimination.	D

[·]A—apomictic, S—sexual, CDS—colchicine-doubled sexual, Mz—maize, *Tr—Tripsacum.*[2]*See* text. [3]Harlan *et al.* (1964), [4]Taliaferro a Bashaw (1966), [5]Sherwood *et al.* (1994), [6]Burton and Forbes (1961), [7]Savidan (1983), "^Savidan (1982a,b), [9]Hanna *et al.* (1973), [10]Lutts *et a* (1994), "Savidan, and Carman, 1999,[12]Ozias-Akins *et al.* (1998), ^Dujardin and Hanna (1983), [14]Leblanc *et al.* (1995a,b), [15]Kindiger *et* (1996a,b), [16]Sherman *et al.* (1991), [17]Blakey *et al.* (1997), [18]Sokolov *et al.* (1998c), [19]Sokolov *et al.* (1998a,b), [20]Victor A. Sokolov, person communication, Sept. 1998 (44, 47 and 51 chromosome segregants from the apomictic Mz6-Trl6 translocation line that contain t translocation are sexual), [21]Nygren (1946), [22]Nordborg (1967), ^Ellerstrσm and Zagorcheva (1977), [24]Ellerstrom (1983), [25]Jankun ar Kovanda (1988), [26]Stebbins (1932), [27]Mujeeb-Kazi (1981), [28]Mujeeb-Kazi (1996).

e.g. $\overline{TTT}$ T. According to the duplicate-gene asynchrony hypothesis, such genomic configurations should be common among apomicts (reviewed below).

In the configuration TTT T', recombination between the divergent T and T chromosomes is infrequent. This may explain (1) an absence of recombination in the apomixis-conferring linkage group as found in *Tripsacum* (Grimanelli *et al.*, 1998) and *Pennisetum* (Ozias-Akins *et al*, 1998) and (2) hemizygosity within the apomixis-conferring linkage group as found in *Pennisetum* (Ozias-Akins *et al*, 1998).

Homologous/homeologous chromosome sets in allotetraploids or segmental autoalloploids of the TTT T' type assort as if all four genomes were homologous. During meiosis, each of three homologous T chromosomes has an equal chance of forming a non-recombinant chromosomal association with its respective homeologous T' chromosome. Hence, if a locus common to all four chromosomes of a three homologous/one homeologous set contains alleles that are different from each other, then all six pairwise combinations of the four different alleles will occur at random in the sexual gametes. Grimanelli *et al.* (1998) observed such an assortment in a segregating maize *Tripsacum* Fl population, and they cited it as evidence for a strict autotetraploid origin of apomictic *Tripsacum.* However, lack of recombination in the apomixis-conferring linkage group (probably a T = chromosome) argues against this conclusion. In contrast, it argues in favour of an allotetraploid or a segmental autoallotetraploid ($\overline{TTT}$ T) origin, both of which readily explain the observed random assortment of chromosomes.

The duplicate-gene asynchrony hypothesis predicts that most tetraploid apomicts are allotetraploids or segmental autoallotetraploids of the type $\overline{TTT}$ T (reviewed below). This genomic configuration provides the simplest explanation for four genetic analysis observations, two of which (the second and third) are rather peculiar: (1) simple inheritance, (2) lack of recombination in the apomixis-conferring linkage group, (3) hemizygosity in the apomixis-conferring linkage group, and (4) autopolyploid-like chromosomal segregation.

Other loci affect the frequency of sexual expression (facultativeness) in apomicts. Many genetic analyses of apomixis confirm the existence of other loci that reside on other chromosomes and strongly influence the sexual to apomictic embryo sac ratio within individual plants. In genetic analyses where apomicts are crossed and backcrossed with sexuals, it is not uncommon for the percentage of sexual embryo sacs in a given plant to vary quantitatively from near 0% to above 90% (Table 12—E,G,H,I,J,N,O,R; note that in O, a difference of more than 70% facultativeness is directly related to different sets of eight *Tripsacum* chromosomes and that the elimination of some *Tripsacum* chromosomes completely eliminates apomixis even though Trl6 is present). Such studies lend themselves to analyses in which quantitative trait loci (QTL) for facultativeness could be identified using molecular markers. Physiological studies of apomixis (reviewed below) provide clues as to what these QTL control.

Genetic backgrounds reduce or preclude the expression of apomixis. There is strong evidence that a major apomixis-conferring locus is present in the plant materials referenced in Table 12—B,D,E,F,G,H,I,J,N,O but that appropriate alleles at other loci are required for a near obligate expression of apomixis. In fact, some studies (B,F,M,N,O) indicate that the major locus is inoperative in the absence of appropriate alleles at one or more different but critical loci.

Genetic backgrounds confer apomixis when "apomixis genes" are not present. Ozias-Akins and co-authors (1998, Table 12—1) demonstrated the presence of an

"apospory-specific genomic region" (ASGR) in *Pennisetum squamulatum* that co-segregated 100% with apomixis (generally high expression) in a segregating pearl millet P. *squamulatum* F_x population (162 apomicts: 235 sexuals). The authors suggested that this fits a tetrasomic inheritance model with random assortment of chromatids. However, P. *squamulatum* is an autoallohexaploid (Patil *et al.*, 1961), not a tetraploid, and recombination (crossing over between the centromere and the locus in question), which was not observed for the chromosome containing the hemizygous ASGR, is required for "random assortment of chromatids". Hence, other explanations should be considered for this unusual segregation.

As suggested above for *Tripsacum*, the apomixis-conferring region (ASGR, in the case of P. *squamulatum)* may reside on a divergent genome. Patil and co-authors (1961) demonstrated that P. *squamulatum* is an autoallohexaploid probably of the type SSSS S'S' or SSSSS S'. As for *Tripsacum* (TTT 1"), the latter configuration explains hemizygosity and an absence of recombination in the ASGR. The former configuration also explains these phenomena provided the S' genome is homozygous for the critical alleles. According to the duplicate-gene asynchrony hypothesis, this is expected; that is, alleles responsible for floral induction in the S' genome would be homozygous because of long-term selection in an environmentally divergent habitat prior to hybridization with related plants containing the S genome. They could also be homozygous because of self-pollination of an ancestral triploid (SS S) in which unreduced and gametes were involved or by chromosome doubling of the ancestral triploid.

Dujardin and Hanna (1983, Table 12—J) observed a segregation ratio of apomict to sexual F_x (6 apomicts to 11 sexuals, $\%^2$ NS) similar to that of Ozias-Akins and co-authors (1998). The percentage of aposporous ovules in the six apomicts ranged from 63% to 93%. However, more than 100 ovules of the 11 "sexual" segregants were analysed, and the percentage of aposporous ovules in 10 of these averaged 2.6% (ranged from 1% to 5%). It is improbable that all of these 10 segregants contained the ASGR ($x^2 = 16.8$, $P < 0.001$), yet aposporous embryo sacs occasionally formed in each. Thus, it appears that certain genetic backgrounds may cause apomixis in the absence of known apomixis-conferring linkage groups.

Sherwood *et al.* (1994, Table 12—C) also obtained segregation patterns consistent with tetrasomic inheritance and random assortment of chromatids. However, facultatively apomictic plants were infrequently produced when sexual lines were selfed or crossed with other sexual lines. This again suggests that appropriate recombinations of certain genetic backgrounds, which lack major apomixis-conferring linkage groups, may induce apomixis.

There are now many reports of apomixis arising through hybridization of divergent sexual germplasm. Stebbins (1932, Table 12—T) documented aposporous embryo sac formation in a hybrid between diploid sexual *Antennaria neglecta* and diploid sexual *A. plantaginifolia.* Likewise, Nordborg (1967, Table 12—Q) produced all combinations of hybrids between two sexual tetraploid and one sexual octaploid *Sanguisorba* spp. and all of the resulting tetraploid and hexaploid FjS were fertile aposporous apomicts. As stated by Nordborg, "only in hybrids has apospory been proved to give rise to embryos ... in tetraploids [2n+0], involving pseudogamy, and in hexaploids, where it is sometimes combined with sexual reproduction resulting in octaploids *[2n+n]."* Furthermore, Jankun and Kovanda (1988, Table 12—S) documented fully functional high frequency apomixis (apospory combined with

diplospory) in both diploid and tetraploid *Sorbus eximia*, which is a geographically restricted hybrid derived from *S. aria* and *S. torminalis*, both of which are sexual diploids. Nygren (1946, Table 12—P) observed apomictic embryo sacs (34% of all well-formed sacs) in a hybrid between tetraploid sexual *Calamagrostis arundinacea* and octaploid sexual *C. epigeios*, though unreduced eggs generally required fertilization for embryo development *[2n+n]*.

Low frequency apomixis has been reported in four intergeneric hybrids in the wheat grasses (Mujeeb-Kazi, 1981,1996, Table 12-U; Bothmer *et a*\., 1988; Li and Dong, 1993), and none involved *Elymus rectisetus*, the only apomict in this tribe of grasses, or even other species of *Elymus.* Similarly, high frequency unreduced male and female gametes were obtained in a hybrid between sexual *Triticum turgidum* and sexual *Aegilops longissima*, which resulted in high seed set from the F_x with double the chromosome number in the numerous F_2s that were produced (high frequency union of unreduced male and female gametes, *2n+2n).* However, parthenogenetic development from unreduced eggs was not observed (Pignone, 1993).

Finally, Ellerström and Zagorcheva (1977, Table 12-R) observed high frequency, well-formed, mature, and multiple aposporous embryo sacs in numerous lines obtained from many different hybrid combinations involving artificial amphiploids of *Raphanus sativus* and *Brassica oleracea.* Because many parental lines were involved, mutations are not a reasonable explanation for this phenomenon.

The above examples taken together provide serious evidence for Ellerström and Zagorcheva's conclusion: "In our opinion it seems therefore, more justified to conclude that the formation of aposporic embryo-sacs ... is caused by physiological disturbances, as a result of defective cooperation between the two parent genomes in the hybrid, rather than to assume the presence of specific genes governing the formation of such embryo sacs".

An impartial analysis of the many fortuitously produced apomicts of hybrid origin described above undermines the simple inheritance autonomous-gene paradigm that has reigned among plant breeders for 40 years, but not necessarily among plant biologists (see relevant opinions of Kellogg, 1990; Campbell *et al.*, 1991; Asker and Jerling, 1992; Bayer, 1996).

Physiological genetics and the origins of apomixis

Asynchronous signals modify cell cycles. Heterokaryon studies with yeast shed light on molecular mechanisms that might cause apomixis. When yeast cells in Gl are fused with yeast cells in S-phase, signals from the S-phase nuclei cause chromosomes in adjacent Gl nuclei to replicate precociously. The degree of precocity and the rates of replication increase with an increased S:G1 nuclear ratio in the heterokaryon. Likewise, when yeast cells in interphase are fused with mitotic cells, signals from the mitotic nuclei cause adjacent interphase nuclei (regardless of stage) to skip the intervening stages and abnormally assume the chromosomal activities of the mitotic nuclei (see Lewin, 1994, for a review). Apomixis may occur in an analogous manner (Fig. 28).

Sudden changes in environment can confuse cell cycles in plants in a manner similar to asynchronous nuclei in yeast heterokaryons. When certain photoperiodically sensitive plants are grown in non-conducive photoperiods, or are

moved from flowering-conducive to non-conducive photoperiods, signals are produced that cause meiosis to abort (Nielson, 1942; Madsen, 1947; Moss and Heslop-Harrison, 1968). Other floral anomalies may also occur, e.g. young floral buds may revert to vegetative growth (Krishnamoorthy and Nanda, 1968), maize tassels (Moss and Heslop-Harrison, 1968) and wheat stamens (Fisher, 1972) may become feminized, and wheat ovaries may be transformed into inflorescences (Fisher, 1972). Like apomixis, the degree to which these anomalies occur is controlled by a few major genes and many modifier genes (Thomas and Vince-Prue, 1997). These photoperiod-induced anomalies are consistent with the GPT (genotype photoperiod temperature) model of floral development (Yan and Wallace, 1998), which may also explain inconsistencies in the apomixis physiology literature. The GPT model (Yan and Wallace, 1995, 1996, 1998) assumes (1) flowering is preemptive in the absence of suppression, (2) photoperiod genes that suppress flowering are expressed during non-conducive photoperiods, and (3) genetic variation for floral suppression is substantial.

Based on the GPT model, interracial tetraploids may be envisioned in which the timing of suppression of floral development varies with genome (Fig. 28). Intermediate ovular phenotypes would then develop in which the precocious genome would produce, during belated apomeiotic prophases, end-of-meiosis check-point signals and embryo sac formation signals. Meiosis would then be skipped in a manner similar to the skipping of mitotic stages in yeast heterokaryons. Alternatively, embryo sac formation signals might, because of lengthy exposures to non-suppression, surpass threshold levels within nucelli resulting in the formation of aposporous embryo sacs (Fig. 28).

Photothermal genes may regulate apomixis. Plants are often partitioned into: (1) short-day plants (SDP), (2) long-day plants (LDP), (3) dual day-length plants (DDLP), in which characteristics of both SDP and LDP are combined (long-short-day plants, short-long-day plants, and probably intermediate day length plants and ambiphotoperiodic plants), and (4) day-neutral plants (DNP). Differences in vernalization requirements further partition these photoperiod response categories (Thomas and Vince-Prue, 1997). Essentially all plants fit into one or more of these categories.

A reasonably current list of species in which photoperiod responses have been studied was compiled by Thomas and Vince-Prue (1997). Plants targeted for such studies are generally those with distinct, easily recognized photoperiod responses. The list represents 287 angiospermous genera, of which 32 (11.2%) contain apomicts (Table 13; 16% of SDP genera, 9% of LDP genera, 20% of DDLP genera as defined above, and 11 % of DNP genera). In contrast, only 1 % of all angiospermous genera are known to contain apomicts (Carman, 1997). Hence, the percentage of genera containing apomicts in Thomas and Vince-Prue's list, which is heavily weighted with plants exhibiting strong photoperiod responses, is 11-fold higher than would be expected if apomixis were to occur independent of strong photothermal requirements. Furthermore, an analysis of variance indicated that genera containing apomicts (Table 13) were represented within the list by significantly (P d" 0.02) more photoperiod categories (SDP, LDP, DDLP, DNP) per genus (1.7 ± 0.2 SE) than genera not containing apomicts (1.3 ± 0.05 SE). These findings implicate photothermal genes in the evolution of apomixis and in its regulation.

Table 13. Photoperiodic response categories for genera listed in Thomas and Vince-Prues (1997) Appendix I (photoperiodic classification of plants), which also contain aposporic or diplosporic species; SDP, short-day plants; LDP, long-day plants; DDLP, dual day-length plants, i.e., long-short-day plants, short-long-day plants, intermediate-day plants, ambiphotoperiodic plants; DNP, day-neutral plants.

Genus	SDP	LDP	DDLP	DNP
Bouteloua	x	x	x	
Allium	x	x		x
Setaria	x		x	x
Poa		x	x	x
Paspalum	x		x	
Solidago	x		x	
Cucumis	x			x
Ranunculus		x		x
Raphanobrassica		x		x
Bidens	x			
Bothriochloa	x			
Brachiaria	x			
Helianthus	x			
Hyparrhenia	x			
Luffa	x			
Panicum	x			
Pennisetum	x			
Rubus	x			
Sorghum	x			
Beta		x		
Centaurea		x		
Chondrilla		x		
Cichorium		x		
Hieraceum		x		
Limonium		x		
Rudbeckia		x		
Aster			x	
Coreopsis			x	
Saccharum			x	
Malus				x
Ornithogalum				x
Pyrus				x

Apomixis and facultativeness are probably polygenic threshold traits. Many polygenic traits are dimorphic; they are regulated by an environmentally sensitive "switch point" that is positioned along a normally distributed polygenic variable called the "liability". Different "morphs" occur depending on whether the liability threshold is surpassed or not (Roff, 1994; Falconer and Mackay, 1996), and the liability factor (risk factor for alternative morph development) often consists of multiple and

unknown components. By combining elements of the duplicate-gene asynchrony hypothesis (Fig. 28; Carman, 1997) with elements of the GPT (Yan and Wallace, 1998) and threshold (Falconer and Mackay, 1996) models, the expression of apomixis in hybrids of sexual parents (detailed above) and the environment-induced variations in facultativeness (detailed below) are largely explained (Fig. 34).

The multiple-photoperiod-response (MPR) component of the liability variable. The MPR component of the liability variable for apomixis expression (Fig. 7) assumes that (1) the rates of degradation of floral suppressors for two genomes, A and B, are normally distributed and may be variable, and (2) the floral suppressor degradation rates for genomes A and B may respond either similarly or differently to changes in environment. Under these conditions, facultativeness should, for at least some

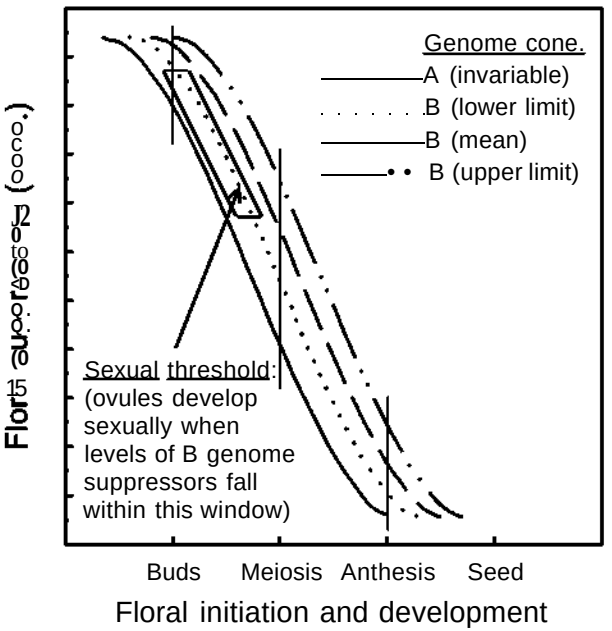


Fig. 34: The multiple-photoperiod-response (MPR) component of the liability variable. The y-axis represents the polygenic floral suppressor component of the threshold trait liability factor. The latter probably consists of many components, but the floral suppressors may be the most important (see text). Floral development ensues as suppressor levels decrease, which occurs asynchronously (between genomes) resulting in an intermediate phenotype, i.e. the bud, meiosis, and anthesis stages (vertical lines) represent compromises between the precociously expressed A genome and the delayed B genome (Fig. 1). The diagram represents the simplest case, assuming a single location (environment) for plant growth, an invariable rate of degradation of suppressors for genome A (as in DNP), and a normally distributed and variable degradation rate for genome B (as in LDP and SDP). Under these conditions, ovules develop sexually when the degradation rates for genome B approach that of genome A throughout the period from floral bud through MMC formation (sexual threshold window). In contrast, apomixis occurs when differences in degradation rates between genomes exceed the sexual threshold window (as diagrammed, the majority of ovules would develop apomictically).

apomicts, shift when plants are grown in different photoperiods or when they are moved from one photoperiod to another during growth.

In examples A through E (Table 14), sexual development is favoured when reproduction occurs during long days. This response is predicted by the MPR model (Fig. 34) provided that genomes A and B were day-neutral and long-day-selected, respectively, prior to hybridization and polyploidization. Accordingly, long days would enforce an accelerated degradation of genome-B-specific floral suppressors narrowing the gap between the B and A genome degradation curves. Consequently, more ovules would develop within the sexual threshold window (Fig. 34). In contrast, short days would broaden the gap between genomes A and B and increase the frequency of apomictic ovules. This scenario is consistent with apomixis birth dates within geologically cool periods wherein high-latitude (long-day) ecotypes migrated to lower latitudes and hybridized with lower-latitude (day-neutral) ecotypes of the same or closely related species.

Example G (Table 14) involves a unique diploid cytotype in which tendencies to form aposporous embryo sacs, which are enviable, are favoured when reproduction occurs during long days. This response is predicted by the MPR model provided the unique diploid contains both day-neutral and short-day alleles. Accordingly, long days would broaden the floral suppressor degradation gap (Fig. 34) allowing for some aposporous embryo sac development. The plant material of example F (Table 14) is a hybrid between the plant materials of E and G, and the results suggest that additional sexual threshold windows may have been established by combining day-neutral, long-day, and short-day genomes, i.e., an overall reduction in apomixis frequency was observed in this hybrid (Table 14).

The apomict *Poa pratensis* is a short-long-day plant (Thomas and Vince-Prue, 1997): short days generally enhance floral bud formation and long days enhance floral development. Hence, both short-day and long-day ecotypes were undoubtedly

Table 14. Relationships between photoperiod and apomixis frequency.

Taxa	Photoperiod (day:night)	Ovules with aposporic embryo sacs (%)	References
A. *Dicanthium aristatum*	8:16 (40 d) -16:88:16	4779	Knox and Heslop-Harrison, 1963
B. *Dicanthium aristatum*	16:813:11	5590	Knox, 1967
C. Dicanthium intermedium	14:1012:12	2263	Saran and DeWet, 1976
D. *Themeda australis*	24:08:16	1485	Evans and Knox, 1969
E. *Paspalum cromyorrhizon* (4x)	14:1012:12	7895	Quarin, 1986
F. P. *cromyorrhizon* (4x hybrid)	14:1013:1112:12	634643	Quarin, 1986
G. P. *cromyorrhizon* (2x diploid)	14:1013:1112:12	1575	Quarin, 1986

involved in its origin. Accordingly, the frequency of apomictic development should be high under both long and short photoperiods, i.e., both conditions should enforce a broad between-genome gap in schedules of floral suppressor degradation (Fig. 34). In contrast, the gap should be narrower at intermediate photoperiods allowing for infrequent sexual development. This tendency has been observed. Plants grown at five locations, which provided 15.5,15.5,15.0,14.5 h (long days), and 12.5 h (short days) of daylight, respectively, generally had higher frequencies of apomixis than plants grown at two other locations that provided intermediate day lengths (13.5 and 14 h) (Hovin *et al*, 1976). However, the differences may be inconsistent with other studies (Mazzucato *et al*, 1996), suggesting that other environmental components of the liability variable (discussed below) may also play important roles in determining facultativeness in *Poa.*

Exposure to a gradually changing photoperiod, as occurs in nature, may be necessary in some taxa to induce appropriate photoperiod responses. For example, field-grown *Hyparrhenia hirta* (N17) had significantly fewer aposporous embryo sacs than plants of the same line grown at constant 8, 12 and 16 h photoperiods (McWilliam *et al*, 1970; Table 15—A). However, no differences between field and phytotron-grown plants were observed in another line (Table 15—B) and, while phytotron photoperiods had little effect in two lines, significant effects were observed in a third line (Table 15—A,B,C). In other examples, the percentage of ovules containing apomictic embryo sacs increased when ovules of *Calamagrostis purpurea* (diplosporous; Nygren, 1946) and *Pennisetum dliare* (aposporous; Hussey *et al.*, 1991) were sampled at progressively later dates throughout the summer. In the latter study, the apomicticsexual ratios for the three collection period categories listed in Table 15-D are significantly different (χ^2 = 43.937, 2 df, P ≤ 0.001). In contrast, the apomicticsexual ovule ratios for P. *dliare* plants grown at constant 8,12, and 16 h

Table 15. Relationships between photoperiod and percentage of aposporous embryo sacs.

Taxa	Photoperiod (day:night)	Aposporous embryo sacs (%)	References
A. *Hyparrhenia hirta* (N17)	8:16 12:12 16:8 (field)	97 94 100 78	McWilliam *et al.*, 1970
B. *Hyparrhenia hirta* (N43)	8:16 12:12 16:8 (field)	87 96 88 91	McWilliam *et al.*, 1970
C. *Hyparrhenia hirta* (N64)	8:16 12:12 16:8	6.9 22.9 47.9	McWilliam *et al.*, 1970
D. *Pennisetum dliare* (Texas field)	Sampled: May 15 May 31-Aug 15 Aug 31-Sep 31	90.6 94.7 98.8	Hussey *et al*, 1991
E. *Pennisetum dliare* (phytotron)	8:16 12:12 16:8	93.6 95.0 94.4	Hussey *et al*, 1991

photoperiods did not differ (Table 15—E). Collectively, these results suggest that factors other than photoperiod are important for facultativeness (Hussey *et al.*, 1991) and/or exposure of plants to gradual changes in photoperiod is important for facultativeness.

Multiple phenotypes may be defined by multiple thresholds. It should be noted that morphs other than apomictic or sexual are often expressed. For example, a third morph, sterility, was evident for *H. hirta* (N64) (Table 15—C). Sterile embryo sac percentages were 34%, 31 %, and 16% for the 8,12 and 16 h photoperiods, respectively. It is possible that the gap between the A and B genome degradation curves (Fig. 34) was largely incompatible with either sexual or apomictic development at the 8 and 12 h photoperiods. Similar and consistent abnormality categories were reported for interspecific *Pennisetum* hybrids, in which certain F_x genetic recombinations resulted in high frequency sterile embryo sacs (Dujardin and Hanna, 1983), for *Triticum Elymus* hybrids, in which favourable growing conditions decreased the frequency of abnormal diplosporous embryo sac development (Peel et a1, 1997), and for *Taraxacum palustre*, in which 2n+0 embryos tend to form in the spring and *2n+n* embryos (B_{ln} embryos) tend to form in the autumn (Malecka, 1973). All of these anomalies appear to be regulated to a greater or lesser extent by photoperiod.

Circumscribing the threshold response liability variable. Associations of apomicts with genera known to have strong photoperiod responses (Table 13), tendencies of apomictic genera to express multiple photoperiod categories (Table 13), and tendencies for facultativeness to be influenced by photoperiod (Tables 14 and 15) suggest that photothermal genes are important components of the liability variable. However, other variables may be equally important. For example, differential genome silencing, which may eliminate asynchrony, may be under genetic control as suggested by interspecific hybrids that differentially resemble one parent more than the other. Likewise, polyploidy enhances the development of distinct genome domains within nuclei (Leitch *et al.*, 1990), and this may have a polygenic component. Finally, J. Ledyard Stebbins (personal communication, 1997) suggested that asynchrony might be greatest when plants develop rapidly, i.e., under favourable temperature, water and nutritional conditions, and these effects (environmental growth optima) may vary polygenically. The contributions of the potentially many loci important to apomixis might best be described by breeding and photothermal studies in which QTL are identified for various temporal and spatial embryological variables.

Attempts to identify QTL important to apomixis were made by Ann Blakey (1997) in *Tripsacum* and Rick Noyes (Indiana University, personal communication, 1998) in *Erigeron*. These approaches represent radical and pioneering departures from the simple inheritance paradigm, which may have impeded genetic analysis research of apomixis for much of the 20th century. However, it is clear from studies reviewed above that many QTL for apomixis are masked by non-recombinant hemizygous chromosomes. Model research systems should, if possible, avoid such genomic backgrounds.

Polyploidy and the origins of apomixis

Polyploid origins. It is now apparent that many if not most polyploid taxa have multiple origins, and this concept is supported by molecular evidence (Soltis and

Soltis, 1993). It is also apparent that many apomicts, including some within *Antennaria* (Bayer, 1987,1996), *Amelanchier* and *Crataegus* (Campbell and Dickinson, 1990), and many grass genera (Kellogg, 1990), also have multiple hybrid origins. This latter observation is incongruous with the simple inheritance mutation hypothesis; specific meiotic mutations would have had to occur repeatedly among related but genetically divergent hybrids.

Upon observing the infrequent to frequent formation of *In* gametes in many taxa, Harlan and De Wet (1975) proposed three mechanisms of polyploid origin: (1) fertilization involving one (unilateral) or two (bilateral) *In* gametes, which results in autopolyploidy (Class I polyploidy); (2) unilateral or bilateral fertilization in which the *In* gamete(s) are produced within an interracial or interspecific diploid hybrid, which results in allopolyploidy (Class II polyploidy); and (3) interracial or interspecific diploid hybrids that undergo somatic doubling (Class III polyploidy). Though difficult to prove, it is generally believed that most polyploids belong to Class I or Class II (Bretagnolle and Thompson, 1995). At the diploid level, unilateral polyploidization, resulting in triploids, is often compromised by the endosperm balance number problem (4M:1P or 2M:2P), though in the vast majority of cases this problem does not prevent the formation of at least some triploid progeny (Bretagnolle and Thompson, 1995). It is also believed that most polyploids originated during the climatic shifts of the Pleistocene (Stebbins, 1971a,b, 1985; Ehrendorfer, 1980; Bierzychudek, 1985; Bretagnolle and Thompson, 1995; Murray, 1995).

Origins of **apomixis.** The duplicate-gene asynchrony hypothesis is consistent with polyploid theory. It implies that frequencies of unreduced gametes are higher in hybrids (interracial or interspecific) whose parents encode schedules of floral development that differ in a specific manner (Fig. 34). According to this hypothesis, such hybrids are potential precursors of polyploid apomicts.

Events leading to stabilized apomixis, which are subsequent to the formation of the initial hybrid, would depend on conditions within the secondary contact hybridization zone. In such zones, the frequency of occurrence of one parent is usually much higher than that of the other. Hence, most of the viable pollen available for pollination of unreduced eggs produced by the hybrid would originate from the predominant parent. Triploids with a 2:1 genome ratio, e.g., TT T', would then be produced. Assuming some triploids also produce unreduced eggs (show tendencies for apomixis), a second round of backcrossing, in which the same predominant pollen producer again supplies the pollen, would result in the 3:1 genomic ratio TTT *T.* Such ratios are expected only when tendencies for apomixis (unreduced egg formation) are expressed at the diploid and triploid levels. This line of reasoning implies that 3:1 genomic configurations in tetraploid apomicts, which explain hemizygosity and simple inheritance segregation ratios (Table 12), may be the rule rather than the exception.

Most apomicts are outcrossing perennials, and annual apomicts are extremely rare (Asker and Jerling, 1992). Mutation-based hypotheses fail to explain this observation. In contrast, the backcrossing scenario described above depends on outcrossing and perenniality. At the diploid hybrid, BQ triploid, and BC_2 tetraploid levels, perenniality allows for numerous genetic recombinations (in pollen) to be tested. Each may provide a genetic background that confers a different degree of viability and facultativeness (Figs. 28 and 34), and only those genetic backgrounds that confer viability survive.

Outcrossing and perenniality are characteristic of families with high rates of natural hybridization, and the Asteraceae, Poaceae, and Rosaceae frequently rank near the top (Ellerstrand *et ah,* 1996). These three families contain 75% of all apomictic genera (Carman, 1997). In contrast, apomixis is seldom observed in families that rank low in hybridization rate, such as the Brassicaceae, Solanaceae, and Apiaceae (Ellerstrand *et ah,* 1996; Carman, 1997). Again, while mutation-based hypotheses fail to explain these associations, they are wholly consistent with the backcrossing origin described above. However, some families exhibit high hybridization rates that contain few or no apomicts, including the Scrophulariaceae, Salicaceae, Onagraceae and Cyperaceae (Ellerstrand *et ah,* 1996; Carman, 1997). These families may be deficient in the types of photothermal response genes required to confer apomixis, i.e., they may not be sufficiently cosmopolitan.

Polyploid genome evolution and the origin of anomalies related to apomixis. Certain genetic changes may follow polyploidy, including gene silencing, gene diversification, and genome diversification (Soltis and Soltis, 1993). With regard to the last, Song and co-authors (1995) documented the loss and/or gain of parental restriction fragments and the gain of novel fragments in F_2 to F_5 progenies derived from artificially produced intergenomic amphiploid *Brassica.* They also observed meiotic abnormalities suggestive of intergenomic (non-homologous) recombinations, which probably explain the RFLP anomalies. These genomic modifications occurred rapidly, and they suggest such changes might occur in other taxa following natural polyploidization.

As noted above, polysporic species (Fig. 30) tend to contain unstable, highly derived, palaeopolyploid genomes with high base numbers and multiple stabilized base numbers per genus. Nevertheless, these species are often closely related to apomicts, which tend to have low and stable base numbers. The findings of Song and co-authors (1995) demonstrate mechanisms of genome reorganization consistent with the hypothesized palaeopolyploidization and duplicate-gene asynchrony origin of polyspory and related anomalies (Carman, 1997). Hence, apomixis may occasionally serve as a reproductively stable evolutionary springboard from which palaeopolyploid genome reorganizations generate reproductively normal and novel species and genera (Carman, 1997).

Apomixis genes: an evolution of ideas

Data accumulated during the early 20th century suggested apomixis was a consequence of hybridization. Ernst (1918) articulated these data into a broad hybridization hypothesis, which claimed apomixis was the result of interspecific hybridization. However, it soon became clear that some apomicts were autopolyploid. Furthermore, apomixis had not been observed in man-made interspecific hybrids. These findings invalidated Ernst's hypothesis and, in the absence of a suitable alternative, the apomixis gene hypotheses developed.

The simple inheritance mutant-gene hypothesis dominated the apomixis genetics literature for most of the 20th century (see Asker and Jerling, 1992; Carman, 1997). These hypotheses developed in two directions. First, it was suggested apomixis gene(s) are recessive but require appropriate polyploid backgrounds for expression. Hence, they remain unexpressed for long periods of time and surface when

conditions are appropriate (Gustafsson, 1946, 1947a,b; Nygren, 1946). Today, apomixis genes are considered dominant, manipulatable, and the result of apomixis-specific mutations (Mogie, 1992; Kindiger and Sokolov, 1997; Grimanelli *et al.*, 1998). However, as discussed throughout this chapter, these interpretations summarily ignore results from many phytogeographic, phylogenetic, genomic, physiological, and evolutionary studies as well as some genetic studies.

Recent versions of the simple inheritance mutant-gene hypothesis include conditions, such as tendencies for parthenogenesis and a non-existent endosperm balance number requirement (Mogie, 1992; Grimanelli *et ah,* 1998). These recent versions also include appropriate genetic backgrounds with polygenic qualities (Ozias-Akins *et ah,* 1998). Hence, the gap between these versions and the duplicate-gene asynchrony hypothesis has been narrowed. The latter merely includes some additional conditions, such as (1) multiple archegonia (for apospory), (2) abundant photothermal gene variability, and (3) a high natural polyploidization rate (perenniality and outcrossing). However, two major differences remain. First, the duplicate-gene asynchrony hypothesis asserts that apomixis is regulated by a genetic background composed of duplicate female development genes that are independently regulated by divergent regulatory genes (probably photothermal genes). Second, while the regulatory genes responsible for apomixis may be few in number (provided an appropriate duplicate-gene genetic background is present), they did not evolve as apomixis-specific mutations and they will not confer apomixis in the absence of an appropriate duplicate gene genetic background. Rather, they evolved as mutations that confer a greater environmental plasticity to sexual taxa in marginal environments.

SEED PROPAGATION

Seed and Seed Propagation

The peculiar traits of the reproductive biology of flowering plants owe a great deal to the attached mode of life of adult individuals. The appearance of special formations (diaspores) intended for the propagation and dissemination of the species is one such trait. For many millions of years of plant evolution the spore (in algae and sporiparous plants) was the universal diaspore. Later this function was transferred to the seeds and this helped seed plants to take the dominant position on land.

The first seeds were found in the sediments of the Upper Devonian, approximately 370 million years ago. They were found in North America (in what is now the state of Pennsylvania) and later in the North-Western part of Ireland.

Seed is a structural unit of reproduction, propagation and dissemination containing the embryo (or embryos with different genotypes) and usually specialized reserve tissue (including endosperm and perisperm), which is enclosed in a protective envelope (seed coat).

Seeds differ in size, shape, colour, pubescence and other characteristics (heterospermy). In the seeds of some species of flowering plants **together with sexual embryo** or **its derivatives (in the case of monozygotic cleavage embryoidogeny)** the embryos are formed from the cells of gametophyte (gametophytic apomixis) and/or maternal sporophyte (nucellar or integumental embryoidogeny) (see The genetic heterogeneity of seeds. Polyembryony).

Asexual reproduction by means of somatic embryogenesis (see Embryoidogeny is a new type of vegetative propagation) or gametophytic apomixis realized in the seed substantially widens the genetic diversity of seeds, and this leads to the formation of the new generation with various hereditary basis (biparental or uniparental). That is why, when determining the population heterogeneity, the **embryogenetic features** must be considered, together with other features of the seed structure (e.g., the surface sculpture), which have important taxonomic significance.

The seed carries out the **functions of reproduction, propagation and dissemination,** and this became possible for seed plants thank to the unification of the gametophyte and sporophyte in it. The seed as a generative diaspore is an effective system, because it has special protective envelopes and a store of nutritive substances (mainly in the endosperm) and when germinating it produces the seedling at once. It should be remembered that aberrant seeds can occur among normally developed seeds.

One prerequisite of plant seed propagation is the presence of a large number of seeds and/or several embryos (probably of varying origin) in one seed. Seed propagation leads to an increase in population. Maintenance of optimal population density at the expense of seed propagation is called **"seed renewal"** (Levina, 1981). It is determined by the capacity of seed bank in the soil and the number of surviving shoots, juveniles and generative individuals. According to Levina, seed renewal is the final stage of species reproductive biology and testifies ultimately to the biological efficacy of all reproductive processes preceding it.

Among the different factors that regulate propagation and renewal, the biocenotic factors play the leading role in the emergence and survival of the shoots. Seed renewal is a multi-staged, multi-factor and self-regulated biocenotic process. One of the mechanisms of self-regulation is called "the resistance of the medium to population increase".

The way from ovule to seed is hard and full of danger, but the way from seed germination to new individual formation is no less dangerous.

Reproductive Effort

The idea of requirement of material and energy resources for plant propagation took shape in classic works of botany, but only by the end of the 20th century did it form into an integral biological concept. The nucleus of this concept is the notion of reproductive phytomass, which means the whole complex of all structural parts providing for reproduction. Reproductive phytomass is divided into: (1) phytomass of diaspores proper—seeds, spores or buds and (2) phytomass of surrounding structures, which include pericarp, perianth, and pedicel.

There are two approaches to quantitative estimation of reproductive phytomass. First, the quantity of reproductive phytomass, which varies considerably according to plant species and their growing conditions, should be estimated. Second, the share of reproductive phytomass in plant total phytomass, which appears to be an important indicator of viable active orientation to propagation and is called **reproductive effort,** can be determined. This notion was proposed by Harper (see Harper and Ogden, 1970). Both the quantity of reproductive phytomass and reproductive effort characterize metabolic value of reproduction in the same way but from different angles.

The general notion of reproductive effort was formulated quite simply: it is the share of material and energy resources directed to the reproductive process. Far more complex are the particular formulas to calculate reproductive effort and unified methods of determining it. This kind of unification is not expedient, because different methods of calculation of reproductive effort reveal different aspects of this process.

As reproduction, as a rule, is defined as a process of structure formation ensuring propagation, so it is only logical to use the data about the whole complex of such structures without singling out seeds and spores for determining reproductive effort. There is a logical sense in such an approach: diaspore production is impossible without the formation of the structures providing for their reproduction. Nevertheless, there are two main methods of calculating reproductive effort (RE) in botanical literature. According to the phytomass of the whole complex of reproductive structures (W_R):

$$RE_X = (W_R/W)100$$

or according to seed phytomass (W_{SM}):

$$RE_2 = (W_{SM}/W)\text{-}100$$

where W is the total phytomass of a plant.

Reproductive effort is estimated according to flower phytomass (W_{F1}) as well:

$$RE_3 = (W_{F1}/W)100$$

In this case, it shows the potential readiness of the plant for reproduction when it is, in fact, limited by organism resources, whereas the estimation of reproductive effort in the phase of seed and fruit production also includes success in flower pollination and fruit and seed preservation during their maturation, i.e., external conditions as far as individual plants are concerned.

In all cases, reproductive effort is calculated as a portion of total plant phytomass. To compare the data received, one should take into account the dynamics of vegetative plant phytomass during ontogenesis. It varies substantially in different species of plants. Three main variants are possible: (1) maximum of vegetative phytomass falls at the beginning of budding, whereas later it decreases sharply at the expense of organic matter flow to reproductive organs, (2) the peak of biomass is also observed at the beginning of budding and later is not substantially reduced, and (3) the growth of phytomass of vegetative organs takes place alongside reproductive process and reaches its maximum at the end of the vegetative season. With this in view, it is reasonable to use maximum value of phytomass of vegetative organs for calculating reproductive effort, but not the value taken at random at some moment of time. In modern botanical literature (Harper and Ogden, 1970; Howarth and Williams, 1972; Goldman and Willson, 1986; Krichfalushy and Mezev-Krichfalushy, 1994), the details of calculating the value of reproductive effort are often omitted and that is why data given by different researchers may not be comparable.

In some works, the reproductive effort based on energy equivalent of phytomass is estimated. Formulas for calculation remain the same, and calories or joules are used instead of grams of mass. There are even attempts to measure reproductive effort from mineral substances, carbon and highly molecular organic compounds moving to the seeds (Calow, 1979; Reekie and Bazzaz, 1987). As a rule, however, more complicated approaches and methods do not give additional biological or ecological information.

As far as leaves are the most physiologically active part of a plant, reproductive effort can be assessed as a ratio of reproductive parameters to total leaf area of the plant (A):

$$RE_4 = (W_{SM}A)\text{-}100$$

Such an approach is justified by the fact that the total phytomass of an individual for some life forms of plants is "overloaded" by dead cells and tissues, which perform supporting or protective function and add unnecessary information noise to evaluation of reproductive effort.

The number of seeds produced by a plant characterizes "reproductive pressure" of the given plant population on the habitat. That is why in certain cases reproductive effort is calculated as a ratio of the number of seeds or fruits produced (N_{SM}) to total phytomass:

$$RE_5 = (N_{SM}/W)\text{-}100$$

In monocarps there is only one reproductive cycle; polycarpous plants go through a reproductive cycle many times. That is why it is suggested that reproductive effort in perennial plants should be calculated as a ratio of phytomass of reproductive organs to annual increase of total plant phytomass (Willson, 1983) or as a sum of reproductive efforts (Markov and Pleshchinskaya, 1987).

The value of reproductive effort (when it is calculated as RE_X) varies greatly (Bierzychudek, 1982). In perennial plants it ranges from 5 to 25%, in annuals it is on the average 20-40%, and in agricultural plants it reaches 45-60% as a result of

selection. In some cases reproductive effort can amount to 61-70%. Reproductive effort in relation to organs of vegetative propagation varies in the range of 23-80% (Willson, 1983). The value of reproductive effort has a crucial significance for cultivated plants, because increased harvest in the majority of species and varieties is ensured, first of all, by the acceleration of movement of organic substances to reproductive organs (seeds and fruits) and that is why it is the main target of selection.

The concept of alternative distribution of resources in conditions of competition between particular plant organs was not universally confirmed. The negative correlation of reproductive effort to formation of organs of vegetative propagation was not observed, though it is known that tall plants always have to increase allocation in non-reproductive structures (Givnish, 1993). Further accumulation of factual material is necessary in this direction.

The link between reproductive effort and life strategy and life form of plants is not very rigid. Reproductive effort is usually higher and more stable during the years in annuals and monocarps, i.e., in r-strategists. Still, there are a number of cases in which polycarps and perennials had high values of reproductive effort (26-60%) and annuals had low ones (3-11%). In self-pollinating plants, expenditure on the formation of pistil flowers is higher than on the formation of stamen flowers, whereas the correlation is reverse in obligate cross-pollinating plants (Doust and Doust, 1983). Genetic polymorphism of species tells on the value of reproductive effort and that is why different populations can vary considerably in this parameter.

The sphere of interest of many scientists consists in determining general natural laws of reproductive effort change according to plant species and growth conditions, but factual data is not uniform. On the whole, reproductive effort is a characteristic of a species that is genetically more stable than other parameters of reproduction. Moreover, there are regular variations according to ecological and coenotic gradients. In *Amphycarpa bracteata*, for example, reproductive effort varied from 15 to 41% with change of habitat (Willson, 1983). In *Thlaspi arvense* it varied from 20.5 to 54.1% (Zlobin, 1989b). The tendency to reproductive effort reduction is observed when the plant moves from open habitats to closed communities with low supply of mineral nutrients and with lowering of absolute altitude. There are other effects as well (see Table 16).

In many cases, the change of the magnitude of reproductive effort reflects different models of plant body structure (Markov, 1990) as well as different types of specimen differentiation according to vital state and size. It is usually higher in large individuals (Barbour *et ah*, 1980; Samson and Weerk, 1986; Borisova and Malysheva, 1993), but sometimes it is vice versa. Absence of correlation between reproductive effort and the size of a plant individual was also noted. In perennials, the magnitude of reproductive effort is determined in most cases by plant size by the time of the first reproduction. The inverse correlation between the value of reproductive effort and population density follows from this. The magnitude of reproductive effort of separate ramets can decrease with age. But the general regularities of changes of reproductive effort with age are little studied so far (Kishko, 1998).

In the plant world, there are many different types of resource distribution to reproductive organs (Charlesworth and Morgan, 1991), for the description of which more than a few models have been developed. On the whole, reproductive effort is plastic, directly reflects the vital state of an individual and is important, though not the only component of reproductive success in plants.

Table 16. Changes of reproductive effort value in plants according to ecological and coenotic conditions.

Plant species	Reproductive effort value	References
Perennials		
Ambrosiatrifida	Pistil flowers only develop under stress	Bazzaz, 1984
Anemonenemorosa	Maximum in optimal coenotic conditions	Canullo, 1988
Chamaesycehirta	Decreases under ecological stress	Fenner, 1985
*Galinsoga*spp.	Decreases under water-deficit conditions	Rai and Tripathi, 1983
Polygonumcascadence	Increases in ruderal habitats	Hickman, 1975
Rumexacetosella	Decreases with an increase of successive age of habitat	Escaré and Thompson, 1991
Scrophularianodosa	Decreases with the reduction of light	Baalen *et al*, 1990
Spergulaarvensis	Decreases under water stress	Trivedi and Tripathi, 1982
Taraxacumoffidnale	Increases in ruderal habitats	Southwood, 1976
Tussilagofarfara	Increases with the growth of population density	Fenner, 1985
Annuals	Stabilizes or even grows with worsening conditions	Zlobin, 1982; Markov and Pleshchinskaya, 1987

Reproductive Success

The general notion of reproductive success in plants was discussed by Darwin (1859). But as a meaningful term it came into use only with the development of population biology of plants (Harper, 1977).

The concept of reproductive success has a different content depending on the level of biosystem organization. Reproductive success at the level of individual life is related to plant fecundity, i.e., to quantity and quality of diaspores produced by a plant (see Diaspore). The measure of reproductive success in this case is the total number of the seeds produced and the correlation between the number of fruits and flowers or the number of seeds and ovules.

Fisher (1930), while developing the concept of reproductive value of species, underlined that reproductive success should not be linked only with the number of diaspores produced. This is an important constituent of reproductive success, but not the only one. In the process of microevolution, changes in reproductive structures and processes imperceptible at first glance can be of significance. For example, in *Raphanus raphanistrum* the flowers are yellow, but in its hybrids with *R. sativus* they are white or pink. As pollinators evidently prefer yellow flowers, elimination of seed offspring occurs in such hybrids (Lee and Snow, 1998). The result of reproduction is the appearance of a new generation of plants, and in this sense, the number of seedlings and their attachment are the main and final indicators of reproductive success in plants at the population and coenotic level.

Another aspect of the problem under consideration deals with its differentiation into reproductive success as it is and preconditions making reproductive success possible. Proceeding from this, constituents of reproductive success turn out varied and include: resource allocation to reproductive organs; keeping the balance between development of vegetative and reproductive structures as an indispensable condition for maintaining plant vitality till the phase of seed dispersion; blossoming at the time favourable for pollination; seed maturing at a time suitable for their dispersion; and diaspores of a size and number that are optimal for producing a future generation. Reproductive success of a population is, in addition, connected with the age and vital condition of individuals and in unisexual plants it is connected with the ratio between stamen and pistil plants in the population.

For every stage of reproduction, there are main parameters that can be used as components of the general estimation of reproductive success (Zlobin, 1989b).

1. Phase of budding: the number of flower buds.
2. Phase of blossoming: the quantity of reproductive phytomass; the number of flowers; reproductive effort; total number of ovules.
3. Pollination and fertilization: pollen fertility; the quantity of pollen reaching stigma; the number of fertilized ovules.
4. Phase of seed production: the quantity of reproductive phytomass concentrated in diaspores; the number of seeds and fruits; germinability and viability of seeds; heterospermy.
5. Phase of seed dispersion: the number of seeds taking part in dispersion; disseminating agents and distance of seed dissemination.
6. Seed dormancy: the depth of seed dormancy; the possibility of forming seed soil bank and its capacity.
7. Phase of seed germination: the number of seeds surviving by the beginning of germination; the number of seeds that sprout.
8. Forming sprouts and seedlings: the number of sprouts and seedlings and their spatial arrangement.

After polycarpic plants have reached reproductive stage, the intensity of reproduction is not the same in different years. That is why reproductive success cannot be judged on the basis of only one count and observation.

New ideas in understanding reproductive success (Urbansca, 1989) deal with quantitative estimation of the three components of reproduction: (1) reproductive offer, which means the number of ovules and pollen grains; (2) reproduction efficiency expressed as a ratio of viable pollen grains to their total number or as a ratio of the number of matured seeds to the number of ovules; and (3) seed germinating capacity.

All these parameters can be considered as characteristics of reproductive success in plant specimens and, in this case, they are calculated per individual. But they give information about the population status and its coenotic and ecosystemic links. In this case, each of the above-mentioned parameters is calculated per unit of area of population field or biocoenosis.

There is a sophisticated link between the level of reproductive process and the development of plant vegetative organs and the total volume of its phytomass. On the one hand, reproduction sets the requirements for certain plant size, with smaller size

making reproduction impossible; on the other hand, at least in perennial plants, the growth of vegetative organs is evidently reduced in years of active reproduction (e.g., narrower year rings of wood in trees). Formulating the principle of critical threshold for plants producing reproductive organs, Yokoi (1989) underlined two main conditions of plant transition to reproductive state: reaching a certain age and reaching a certain size. Thorough investigation of this problem proved that the transition to reproductive state in annual plants is determined, first of all, by the age of an individual and in biennial plants by the size of an individual, and in perennial herbs the character of the habitat appears to be an additional factor of the transition to reproductive state. In rich habitats having highly fertile soils, the critical part in the beginning of reproduction is played by the initial size of an individual, in poor ones by the size of an individual at the beginning of blossoming. There are species of plants that blossom at any size of an individual, and there are species for which one size of an individual is critical for the beginning of blossoming and another size for fruit production. In perennial plants, the values of reproductive parameters change with age, and there is usually a positive correlation between the individual size and the quantity of seeds produced (Aarssen and Taylor, 1992), whereas in annuals the inverse correlation between growth and reproduction is characteristic. We should take into account that organogenesis of the flower and seed production are caused not only by formal parameters of individual size, but also by their life stage (Zlobin, 1981).

In the budding and blossoming phase, reproductive success is determined by the number of flowers set and their functioning. The number of flowers set reflects the state of individuals and their readiness for reproduction and depends on resource availability in the environment and the amount of reproductive allocation, i.e., metabolite movement from vegetative organs of the plant to reproductive organs. The flowers of insect-pollinated plants perform an important signal function and are expressly addressed to a certain pollinator or group of pollinators (Peisl, 1997). The photoperiod and thermoperiod should be adequate for the plant's requirements. There are always more flowers than fruits formed. The main reasons for flower death are insufficient pollination in anemophilic and entomophilic plants, resource deficit, genetic defects, ecological stress, and pest activity.

The number of pollen grains per ovule varies greatly in natural conditions, from one to three to a few millions. Larger individuals produce more pollen grains per flower. Numerous experiments with additional pollination of flowers prove that the lack of pollen is an important factor that is usually underestimated. According to the average calculations, only 55% of seeds in herbs and 11% in trees set because of the lack of pollen (Howe and Westly, 1986). The quantity of nectar produced in flowers is significant in reproductive success in entomophilous plants. It is known that flowers with large quantity of nectar attract the maximum number of insect-pollinators (Willson, 1984). Species with expressed heliotropy of flowers, increasing their temperature, which is particularly important for forest and tundra zones, also have their advantages. The loss of pollen in entomophilous plants turns out to be not less than in anemophilous plants. On the whole, cross-pollination in anemophilous and entomophilous plants occurs only in small groups of plants growing together, with alien pollen prevailing on the stigma, which inhibits the germination of its own pollen, and self-pollination often takes place (Golubev and Volokitin, 1986; Zhilyaev, 1989).

Reproductive strategy manifests itself in changes in the number of diaspores produced and their size. Production of small quantity of seeds with a large embryo and a large stock of nutrients or production of a considerable number of small seeds represent two extreme solutions. These tactics are usually connected with *K*- and *r*-strategies respectively, which plants fulfil while going through their life cycles (Pianka, 1970). According to Govindaraju (1984), who investigated 34 species of coniferous plants of North America, large seeds were characteristic for colonizer species and small ones for climax species. But this is far from being a general rule; it is rather a common delusion. The purely climax species *Sequoiadendron giganteum* produced 10^9 seeds a year per individual (Fenner, 1985). *Capsella bursa-pastoris*, a biennial plant with clear r-strategy, produced up to 200,000 seeds, whereas *Plantago major*, typical K-strategist according to Trivedi and Tripathi (1982), produced 224,000. According to Radosevich and Holt (1984), seed productivity per individual in annual weeds varies from 40 seeds *(Xanthium strumarium)* to 900,000 *(Anagalis arvensis)*. The total weight of the angiospermous seeds produced usually positively correlates with plant size.

The weight of seeds ranges widely, from 10^{-6} g (Orchidaceae) to 27 kg *(Lodoicea maldivica)*. It is determined more by the size of the mother plant than by the strategy. From a closer analysis of data, it is estimated that seeds with a mass of 328 mg on the average are characteristic of trees, those with 69 mg of shrubs, and those with 7 mg of herbs. Seed size depends on growing conditions of plants. On the whole, seed weight is more stable than other reproductive parameters and varies little even if plants grow under stress conditions. On the other hand, there is an inverse correlation between weight and the number of seeds produced: the heavier the individual seed is, the fewer seeds are formed on a plant (Kawano, 1985).

Both large and small seeds have their ecological advantages and disadvantages in terms of final reproductive success. Larger seeds have a bigger stock of nutrients and a well-developed embryo, which allow for quicker growth of photosynthesizing surface, and in the end, the seedling appears to be more competitive. However, large seeds require more water for germination and are more often damaged by phytophages. In addition, large seeds tend to concentrate near the mother plant after dispersion, which finally enhances competition between sprouts. The thorough investigation of *Lupinus texensis* made it evident that plants grown from larger seeds were distinguished by higher reproductive parameters (Schaal, 1984). On the whole, large seeds seem to be more profitable for plants (though not in all situations).

The integral estimation of reproductive success is given by the number of viable seeds produced by a plant. It is linked to reproductive effort of a plant and the size of the seeds produced by it. Available data on actual range of parameter values and on degree of correlation between them allow us to build a theoretical model from which we can form an opinion about the magnitude of reproductive pressure on habitat of plants occupying different places in the r-K-strategy continuum. It is apparent that seed output reaches its maximum in two situations: when the seeds are small (the main maximum) and when the seeds are large. The range of possible value variations of reproductive effort turns out to be similar in both situations. Minimal quantity of seeds is produced irrespective of the magnitude of reproductive effort in plants with intermediate seed size (Fig. 35).

It is natural that there are more or less substantial deviations from the theoretical model in plants pursuing different reproductive strategy. For example, in a group of

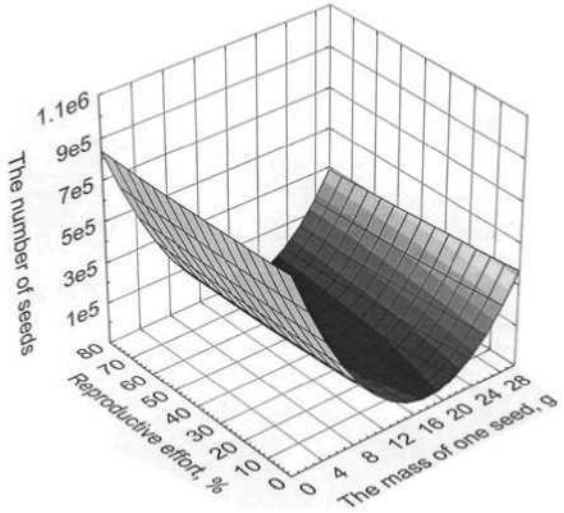


Fig. 35: Theoretical model demonstrating correlation between the seed set, reproductive effort and seed mass.

18 species of weeds and ruderal plants (data by Stevens, 1957; Salisbury, 1976 and our own observations), the maximum of seed production is reached by small seeds in combination with high values of reproductive effort or by large seeds (though this maximum was not high) in combination with low values of reproductive effort (Fig. 36).

A wide range of combinations of the three analysed parameters of reproductive success is also observed within one population, as can be demonstrated by the example *Thlaspi arvense.* Individuals with reproductive effort of 22-60% and small seeds prevailed in the above-mentioned population. Every individual produced 500-1000 seeds (Fig. 37).

Seed dispersion as a component of reproductive success is guided by a few main principles: it should ensure quick, effective settlement on the free plots of the area and avoid competition with mother plants. Seeds usually disseminate within a radius of 100 m from the mother plant, though this distance can reach 500 km in certain cases. Seed dispersion in zoochores improves with high density of maternal plants (Manasse and Howe, 1983).

Reproductive success is conditioned by structural and hormonal readiness of seeds for germination. It appears to be linked with the level of genetic, matrical, and ecological heterogeneity of seeds. The seeds of many plant species require a period of organic dormancy, which they go through in soil. Once they are dispersed, the seeds may stay on the surface of the earth and then move under the influence of runoff and wind. Seeds often move gradually deeper into the soil. In agroecosystems, large numbers of seeds are buried during ploughing or tillage.

After the seed reaches structural and metabolic readiness, water triggers mechanisms of germination (Obrucheva and Antipova, 1997). Germination takes place more quickly at optimal temperature and with a good supply of oxygen, **but**

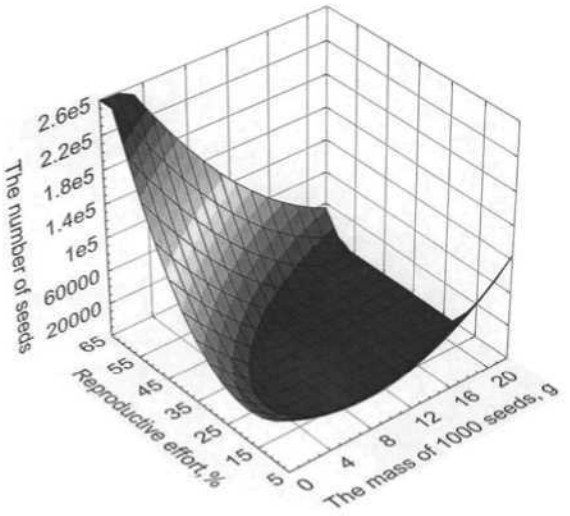


Fig. 36: Correlation between the seed number and mass, and reproductive effort in 18 species of weed plants (according to Stevens, 1957; Salisbury, 1976, and our own observations).

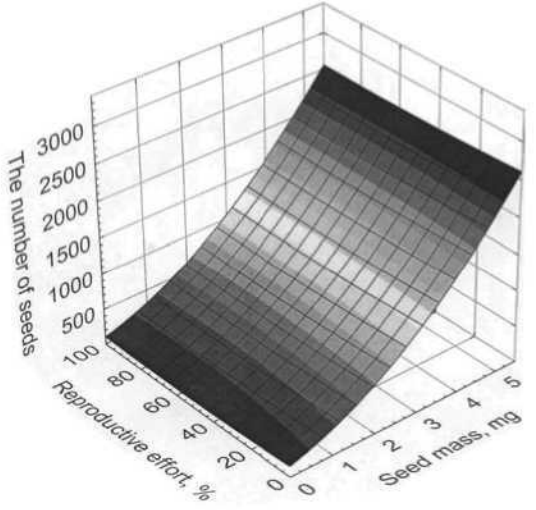


Fig. 37: Correlation between the seed number and mass, and reproductive effort in population of *Thlaspi arvense*.

these factors alone, unlike water, do not act as a trigger of germination. Seeds are known for their enhanced vulnerability related to stress factors in the germination phase. According to Angevine and Chabot (1979), there are two main tactics of germination: (1) avoiding conditions difficult for germination, by adapting the

mechanism of duration of seed dormancy period and the trigger mechanism of germination and (2) enhancing sprout resistance to unfavourable factors.

The death of sprouts and seedlings appears at its maximum compared to all other phases of the reproductive process. Even the slightest details of seed location on the soil surface are important here (Peart, 1984). Contrary to true Darwinistic view, some researchers (Cook, 1979) consider the ability of seeds to give persistently viable young plants, not plant fecundity, as the critical factor of reproductive success. Relevant here is the consideration that conclusions about ecological relations of adult individuals can be false, because plants grow where seeds are able to survive and germinate, and seedlings are able to survive, not where ecological conditions are optimal for adult plants (Sagar and Harper, 1961).

On the whole, reproductive success is the combination of a great number of factors including plant status, plant reproductive strategy, and numerous population and ecosystem relations of the organism. Final phases of reproduction appear entirely under the control of population and coenotic factors.

Potential Seed Productivity

Studies of reproduction dynamics in Angiospermae caused the necessity for subdivision of seed productivity into two categories: potential and real seed productivity. **Potential seed productivity means the highest possible quantity of seeds that a plant, population or phytocoenosis can produce in a definite period of time under the condition that all ovules inherent in flowers could form mature seeds.**

The magnitude of potential seed productivity varies in different plants. It should be mentioned that the number of carpels ranges widely from one flower to another, if there are many of them in a flower; when there are few carpels (one to five), their number, as well as the number of ovules in them, is under strict control of genotype (Khokhryakov, 1975).

Another important factor determining the level of potential seed productivity consists in strategy of plants with respect to organic matter distribution in generative organs. Such movement of organic matter to reproductive organs is closely connected with general reproductive success in plants and, in particular, with pistil success, as well as the magnitude of reproductive effort. Wide variation of the size of reproductive allocation from individual to individual within one population or from one population to another within one plant species emphasizes the importance of potential seed productivity estimates for determining reproductive pressure of plants on the habitat (Goldman and Willson, 1986).

It was shown that potential seed productivity is in non-linear relation to entire plant size (Klinkhamer *et al.*, 1992). However, there is evidence that pistil reproductive success in plants is directly related to the amount of organic matter that the plant can direct to the forming of pistils, seeds and fruits. The degree of individual participation in vegetative propagation can affect the magnitude of potential seed productivity.

In cultivated plants, as a result of long selection process, the quantity of ovules set is increased and the final size of fruits and seeds is enlarged due to acceleration of organic matter movement to them as compared to wild-growing ancestors. However,

seed viability is not purposefully selected, and that is why the nutrient store for seedling needs is not fully mobilized during seed germination of cultivated plants. Sometimes, the enzyme systems necessary for it are absent. Hence, crops do not have interrelation between the stored nutrients in the seeds and the quality of seeds as reproductive units.

The age of plants substantially influences the potential yield. In polycarpic plants that produce seeds a few times during their lives, young individuals have lower seed productivity and then it grows; in aging plants, it declines again. The highest reproductive output is maintained by middle-aged generative individuals (Ivshin, 1998). For perennial herbs, the omissions of separate years, when their potential seed productivity reaches zero level, are characteristic.

The highest potential yield is produced by plants growing in conditions of ecological and coenotic optimum (Dobretsova and Begovatova, 1974). As a consequence, the value of potential seed productivity changes with regularity along ecological and coenotic gradients (Rush, 1993; Kim, 1997). Much depends here on the species of plants, the type of the gradient and the scale of changes of main ecological factors. For example, the same number of ovules was set in *Leucojum aestivum* in forest and meadow communities of the Transcarpathian area, whereas in L. *vernum* the number of ovules decreased by 29.4% with altitude rising from 200 to 1200 m (Komendar *et al*, 1996).

On the whole, the magnitude of potential seed productivity is controlled by four groups of factors:

1) genetic factors that determine a maximum limit of possible plant fecundity;
2) physiological factors including age and vital status of specimen;
3) ecological factors including resources and conditions of plant habitat;
4) coenotic factors embracing the sphere of plant co-habitat with all living organisms of the community.

Real Seed Productivity

Real seed productivity is defined as the number of full-value seeds produced by the plant and calculated per specimen (Levina, 1981). Seed value includes, first of all, their viability, i.e., ability to germinate and to sprout. It includes also the weight of seeds (usually mass of 1000 seeds, in grams), laboratory and effective germination, and the number of healthy seeds.

Real seed productivity depends on the plant species, ranging from a few seeds to tens or hundreds of thousands per individual. Most of the seeds in the population are produced by a small number of large individuals (Hutchings, 1986). Such super-fecund specimens, the real seed productivity of which exceeds 2.4-80.0 times the average for the population, play an important part in maintaining sustainable existence of plant species (Salisbury, 1976). Real seed productivity in plants varies more than potential seed productivity. In *Narcissus angustifolius*, for example, the first of these parameters ranges within 39-69%, and the second within 12-22% (Krichfalushy and Komendar, 1990).

Determination of real seed productivity by number or weight of seeds does not give uniform results. The biological sense of these parameters does not coincide, and

there is no linear correlation between them. There are opposite situations as well. The number of seeds produced by a plant usually varies more than the weight of seeds (Primack, 1978).

To give more detailed characteristics of reproductive process in plants, the productivity coefficient (Kp_r) expressed by the percentage ratio of real and potential seed productivity was suggested (Levina, 1982). The procedure of calculating real seed productivity is specific for each plant life form. Estimation of seminification coefficient can be helpful (Vainagiy, 1990). The number of seeds formed depends on many factors, among which sufficient pollination is considered to be important. The further development of the fertilized ovules is determined by the amount of resources the maternal plant can ensure. Those resources in turn depend on the life condition of the individual, which is proved by many experiments on artificial defoliation of maternal plants at the time of seed maturation.

The question whether the number of ovules on the maternal plant is linked with seed maturation remains little studied. Separate observations prove that the size of egg-laying (this term is used in general ecology) greatly affects the final quantity of mature seeds and their quality (Pianka, 1981). Ecological stress in the phase of seed formation can also substantially reduce real seed productivity, whereas the reduction can be less than one per cent under favourable conditions. For example, in representatives of the group of nemoral herbs of broad-leaf forests, seed output decreased three to five times under the influence of recreation stresses (mainly compaction of soil) (Bashtavoy, 1998). In five species of the family Campanulaceae growing in forests under anthropogenic pressure, seed productivity coefficient falls from 14.0% to 4.4% (Boronnikov, 1998).

The continuance of seed maturation tells on the value of real seed productivity. It varies in a wide range even in plants of similar life form. In this way, according to Radosevich and Holt (1984), the period of seed maturing in annual weeds ranges from 40 days *(Setaria viridis)* to 180 days *(Chenopodium album).*

Serious damage to forming seeds is done by the activity of seed eaters or phytophages. In years of mass outbreaks of seed-eating pests or in conditions of severe ecologic stresses, all potential yield is practically lost. The relationship between the magnitude of real seed productivity and the dynamics of phytophage number is far from simple. The so-called "seed years", when the amount of seed produced rises abruptly, enable plants to reproduce successfully and to maintain their position in communities, because phytophage outbreaks do not catch up with such surges of food. Nevertheless, the highest percentage of death falls on the phase of ovules, mature seeds in general reproductive cycle (Cavers, 1983).

The ability of plants in certain years to increase sharply the real seed productivity is almost universal: seed years are known in trees as well as in perennial herbs. In wood species, seed years are more easily discerned towards the North-Eastern zone of the Eurasian continent. In closed forests, they occur less often; soil and climatic conditions influence their frequency. Seed years are especially characteristic of oak, spruce and beech and less characteristic of birch, alder and poplar.

The quality of seeds, including the ability of seeds to germinate and form viable seedlings, is considered in the estimate of real seed productivity. The concept of seed quality is wide-ranging. According to Ovcharov and Kizilova (1966), there are three main forms of seed non-uniformity at the level of an individual: (1) genetic, emerging from joining genotypes of male and female gametes; (2) matrical, connected with

differences in seed position in maternal plant; and (3) ecological, caused by the interaction of developing seeds with environmental conditions. Summing up all kinds of differences between seeds, Levina (1981) proposed to distinguish six main forms of heterogeneity of seeds (see Heterospermy).

If variation of seed parameters at the level of populations and plant species is taken into account, then the seed polymorphism spectrum turns out to be exceptionally wide (see Genetic heterogeneity of seeds; Polyembryony).

The magnitude of real seed productivity determines the success of plant reproduction in the end. Models of reproductive process of plants that demonstrate that both genetic programmes of ontogenesis and ecological and coenotic conditions of their fulfilment are extraordinarily plastic and multivarious are developed on its basis.

Seed Productivity in *Symphytum* L. (Boraginaceae)

Species of *Symphytum* (comfrey) introduced from wild flora are used as forage, honey, drug, food, and ornamental plants. High fresh yield, prolonged growth in the same place, ecological plasticity, and stress resistance may be considered the valuable properties of comfrey. However, its introduction in culture is restricted by some factors: uneven fruit maturation, shattering and low seed productivity.

Representatives of *Symphytum* genus are cross-pollinated entomophilous plants. Under the conditions of the North-West region of the Russia, flowers are visited by bumblebees and honey bees, pollination being done by *Bombus hortorum* and B. *lucorum.* Other visitors collect nectar, chewing the base of the corolla tube, and do not take part in pollination.

Comfrey flowers have entomophilous organization and mechanisms preventing autogamy: bright colour of corolla (pink, red, purple, blue) with nectar signs, funnel form, presence of floral nectaries, hercogamy, and dichogamy in protandry form. Numerous florets are collected in inflorescences, making them easily noticed by pollinators. Comfrey reproductive shoot is the united inflorescence (synflorescence), consisting of inflorescence system of different levels. The main type of inflorescence is a tirs — a complicated inflorescence—with monopodially increasing main axis and lateral inflorescences of cymoidal character, with double flower whorls. Tirses are divided into main or central and lateral ones.

Comfrey fruit is a coenobium consisting not of two (in carpel number) but four monospermous eremes. Eremes are not opened and seed not released from pericarp falls from the plant.

Research of samples of a different geographical origin has shown that the average number of flowers in a whorl, the number of whorls in central and lateral tirses and the number of reproductive shoots change with age and reach maximal value during a period of mature generative plant (4-8 years) and afterwards gradually reduce (Nayda, 1998). Variation in reproductive shoot number is especially pronounced in the old generative plants. At this time, particulation and partial falling out of the bush are seen in some plants, while others are not subjected yet to this process and their shoot number is not decreased. Species studied are characterized by high potential of fruitage and seed productivity (Table 17).

Table 17. Potential seed productivity of *Symphytum* species.

Species (specimen)	Potential fruitage*	Potential seed productivity**	
		per shoot	per plant
S. asperum (k-21)	437.3	1749.2	57198.8
S. carpaticum(h-129)	418.2	1672.8	29274.0
S. officinale (k-115)	446.9	1787.6	19663.6
S. tanaicense (k-17)	246.1	984.4	17522.3
S. x *uplandicum* (k-16)	258.1	1032.4	28391.0

* Average number of flowers per shoot (sample 30 shoots).

**Average number of ovules.

Table 18. Real seed productivity of *Symphytum* species.

Species (specimen)	Real fruitage, %	Real seed productivity		Productivity index, %
		per shoot*	per plant**	
S. asperum (k-21)	13.5	42.7	20.3	2.4
S. carpaticum (k-129)	60.8	366.3	117.5	21.9
S. officinale (k-115)	60.4	330.7	86.4	18.5
S. tanaicense (k-17)	50.1	199.8	34.7	20.3
S. x *uplandicum* (k-16)	71.4	292.2	83.6	28.3

*Average number of seeds per shoot.

**Average mass of seeds per plant (g).

Under the influence of many factors, the real seed productivity is always lower than the potential one (Table 18). One to five flower buds in a whorl do not open and some open flowers do not form fruit. The discrepancy between the bud number in a whorl and the number of fruits formed may be 45-80%. An even greater difference (in *Symphytum asperum* to 90%) is noted between the number of ovules in buds, the number of fertile ovules in the opened flowers, the number of developing seeds and mature seeds.

From four ovules forming in the gynoecium of a comfrey flower, only one to three, seldom all, are fertilized and develop into seeds. In samples *S. carpaticum, S. officinale, S.* x *uplandicum* (k-16) two to four eremes in coenobium mature as a rule; in other samples, one to two eremes mature. Therefore, the productivity index is always lower than the fruitage and ranges in species from 2.4 to 28.3%. Young and old generative plants usually have lower indices. While comparing the inflorescence productivity it should be noted that the productivity index is higher in central tirses; however, in some years the lateral ones are more productive. It appears to be connected with the meteorological conditions under which the flowering takes place.

The shoots of two generations in samples *S. officinale* and *S. carpaticum* during the growth season undergo the complete life cycle; moreover, the seed productivity level may be higher in either the first or the second generation of shoots. In 1986

productivity of shoots of the first generation in *S. officinale* was 20.9%, and of the second generation 28.6%, but in 1991 the figures were 20.4% and 15.8% respectively.

Analysis of comfrey ovules and fruits at various stages of development has suggested some causes of reduction of seed productivity (Fig. 38). Forming ovules in *Symphytum* are heterogeneous, as in many other plant species (Oryol *et ah*, 1986). They can be divided into four groups.

The first group are fertile, fertilized ovules, developing in seeds.

The second group are fertile, fertilized ovules degenerating because of disturbances in embryogenesis and endospermogenesis; moreover, development may stop at the initial and late stages.

The third group are fertile but unfertilized ovules; their number may reach 57.4-69.6%. Disturbance of pollination process and lack of fertilization may be caused by deficiency or total absence of bumblebee-pollinators due to unfavourable weather conditions. There is a linear relationship between the pollen viability and the index of seed productivity. Values of correlation coefficient (r = 0.9) and determination coefficient (d = 0.81) show that 81 % of seed productivity results from pollen viability. This group of ovules is a resource for increasing seed productivity.

The fourth group are sterile ovules, their number ranging from 8.2% to 100%. In the ovules, degeneration of archesporial cells, megaspores and embryo sacs even before pollination or the formation of embryo sacs of smaller size as well as poor nucellus development were found.

The largest percentage of fertilized ovules is observed as a rule in unpaired flowers and in the first three to four flowers of a whorl. For example, the seed productivity level (%) in unpaired flowers of *S. officinale* is 63.9; in the first flower 43.3, in the second 50, in the third 40, in the tenth 16.7, and in the fifteenth 6.7. That is, the nearer a flower in a whorl is to the top, the lower its percentage of fertilized ovules.

Ereme maturation in multi-level inflorescence of representatives of genus *Symphytum* is prolonged, its order being acropetal. Eremes in lower whorls of central tirses begin to ripen first, then this process spreads to the lateral tirses. Mature eremes should be collected before calyces are opened.

The level of potential seed productivity in *Symphytum* is species-specific. Significant variation in real seed productivity during various years is mainly due to plant age. The greatest seed productivity level is reached in the period when a generative plant is mature. Due to high potential fruitage, even at a moderate productivity index, a large number of viable seeds is produced in the end and this makes it practical to grow *Symphytum* species.

Seed Productivity in Apomicts

Seed productivity of pseudogamous apomictic forms is usually low.

Another situation takes place in autonomous apomicts, which involve the majority of members of Asteraceae family. The apomictic forms from the genera *Pilosella* and *Taraxacum* are characterized by high seed set in isolated inflorescences (58-98%). For all this, odd and even apomictic polyploids did not differ in the degree of seed set. Generally, apomictic species were not inferior to sexual ones in this parameter and more often exceeded them (Jenniskens *et ah*, 1984; Gadella, 1987,1991; Mogie and Ford, 1988; Kashin and Chernyshova, 1997; Kashin *et ah*, 1999).

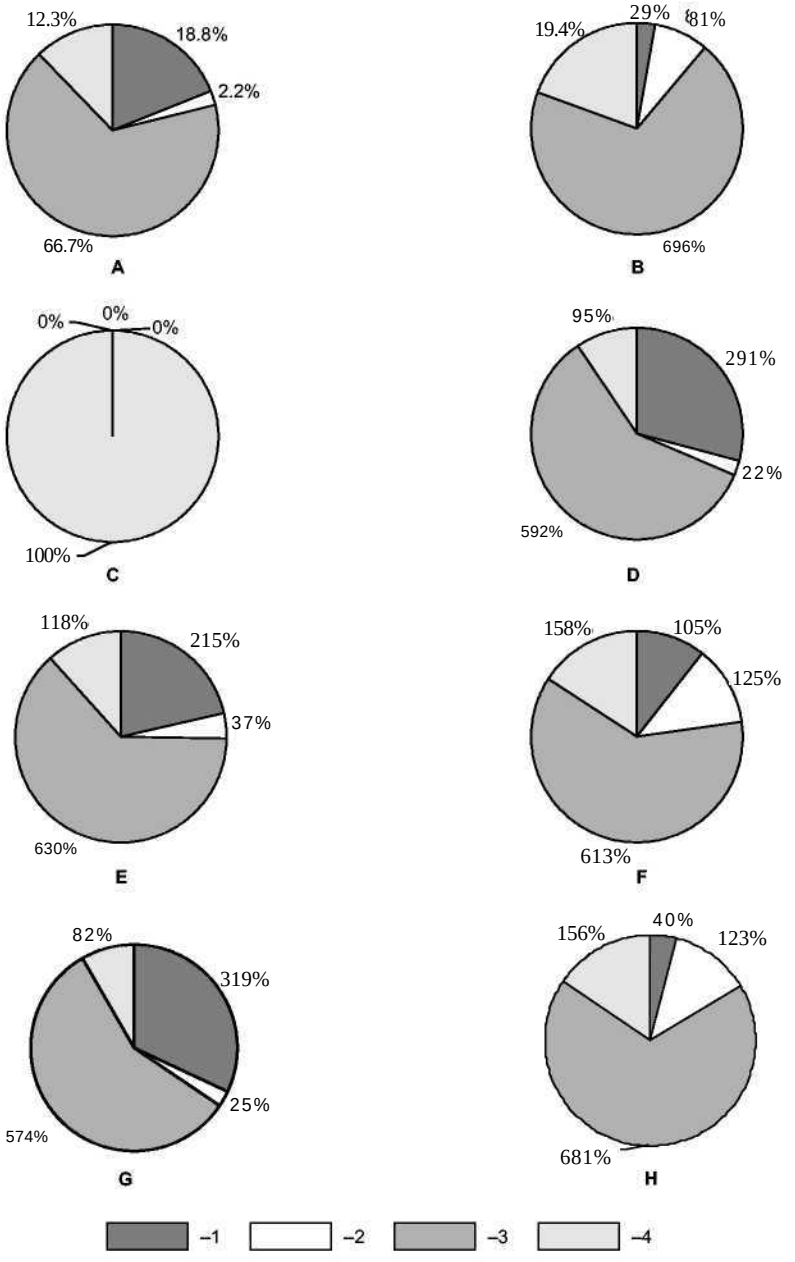


Fig. 38: Structure of seed productivity of *Symphytum* species. A-C, *S. officinale* (specimens k-115, k-28, k-193); D, *S. carpaticum;* E, *S. tanaicense;* F-G, *S.* x *uplandicum* (specimens k-51, k-16); H, *S. asperum* (specimen k-15); 1, real seed productivity; 2, ovules degenerating after fertilization; 3, fertile unfertilized ovules; 4, ovules degenerating before fertilization.

Depending on seed set in conditions of self-pollination, the species of the genus *Taraxacum* are subdivided into forms that are **facultatively agamospermous (20-80%), sexual** (close to 0%), and **obligatory agamospermous** (over 80%) (Richards, 1970; Rousi *et ah,* 1985). According to other data, the frequency of seed set under self-pollination even at the level of 85-90% suggests the forms can be regarded as facultatively agamospermous (Jenniskens *et ah,* 1984). The last point of view is nearer to the truth because there are serious reasons to consider that there are no obligatory apomictic forms in nature. Apparently, the proposed criteria of the appraisal could be applied to all the genera of the Asteraceae in which apomixis is found.

Seed productivity of the apomictic forms of Asteraceae in conditions of pollenless regime (emasculation) and self-pollination (isolation) does not differ. This testifies to their obligate allogamy (Table 19) (Kashin and Chernyshova, 1997). It was demonstrated by experiments that their sexual relatives, particularly species of the genera *Taraxacum* and *Pilosella,* are obligatory allogamous forms (Jenniskens *et ah,* 1984; Gadella, 1987). In apomictic forms of Asteraceae, seed set can increase under free flowering (Kashin and Chernyshova, 1997). This also suggests that these forms are facultatively agamospermous (Fig. 39).

In the same populations of the species from the *Pilosella* agamic complex, which were observed during five years in conditions of inflorescence isolation, a large variation of seed set by years was revealed ranging from 21 to 100% (Kashin *et ah,* 1999). This could be connected with a direct negative action of unfavourable environmental factors upon seed set and development and with the fact that the weather conditions remove the balance in the facultatively apomictic forms either to gamospermy or to primary agamospermy. The last opportunity is suggested by the

Table 19. Seed set and germination ability in populations of some species and natural hybrids of *Pilosella.*

Species and conventional population number	Seed set (%) in conditions of			Germination capacity* (%)
	self-pollination	emasculation*	free flowering	
P. *officinarum* 22a	65.7	75.4	88.0	31.8
33a	71.9	62.5		39.5
P.*praealta*	60.8	62.5		52.4
P. echioides 22f	0.0	0.0	71.0	22.0
33f	0.0	0.0		30.0
P. *vaillantii*	77.9		60.0	
*P.*x*officinarum-praealta*	89.4	82.4		46.8
P.xofficinarum-vaillantii	72.4	72.0		20.0
*P.*x*praealta-vaillantii*	75.5			54.1
*P.*x*officinarum-echioides*	47.9			6.1
*P.*x*echioides-praealta*	69.5			57.5

*Seeds were formed in P. *echioides* under free flowering and in other species under self-pollination.

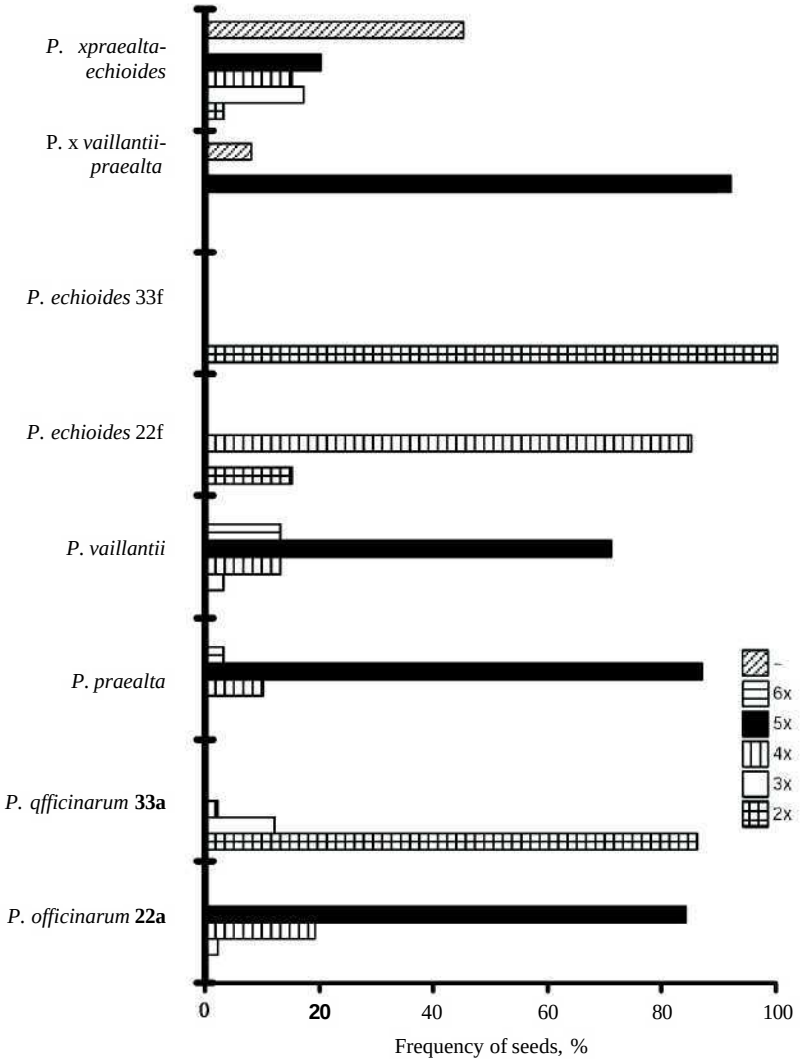


Fig. 39: Frequency of seeds with embryos of different ploidy in populations of various *Pilosella* species.

dependence of the degree of apomixis and sexuality expression in many facultatively apomictic forms on environmental conditions (Nygren, 1946; Sparvoli, 1960; Knox, 1967; de Wet and Harlan, 1970a,b; Nogler, 1984a).

When investigating germination capacity of the different *Pilosellà* species and hybrid forms, the maximal germination (52-60%) was marked in the agamospermous forms (P. *vaillantii, P. praealta)* with odd ploidy level (2n = 5x = 45). At the same time, in the two investigated populations of the sexual species P. *echioides* (22f and 33f), germinability ranged from 22 to 30%, and in the plants of apomictic form of

P. *officinarum* (even polyploid - 2n = 6x = 54) it did not exceed 40% (Table 19) (Kashin *et ah,* 1999). The average percentage of seed germination in sexual tetraploid and apomictic pentaploid biotypes of P. *officinarum* was approximately at the same level (37%) (Gadella, 1987). In interspecific natural hybrids having steady morphotype and ranked as microspecies (P. ^{x} *officinarum-vaillantii, P.* ^{x} *officinarum-praealta),* the frequency of the seed formation was high (93-100%), and germination was at the level of 39%. In addition, they behaved as facultative apomicts. Interspecific natural hybrids without steady morphotype (P. x *vaillantii-praealta)* that are vaguely represented in coenosis (seed productivity 76%, seed germination 54%) behaved in the same manner. It is significant that the two are hybrids between facultatively apomictic species. At the same time, hybrids between sexual and apomictic species P. *x officinarum-echioides,* occasionally found within the investigated coenoses, had seed set of 59%, but only a few of the seeds were able to germinate.

Hybrids between the apomictic and sexual species P. x *praealta-echioides* having steady morphotype and existing in the rank of local micropopulation had seed set of 70% and seed germination capacity of 58% (Kashin *et al.,* 2000). Seeds of hybrids between sexual (4x) and apomictic (5x) biotypes of P. *officinarum* also were characterized by lowered germinability (Gadella, 1987). It has been shown that in populations of apomictic (aposporous) and sexual forms of the *Pilosella* agamic complex, seeds with different ploidy levels (2x-6x) were formed (Figs. 40 and 41).

One of the most probable causes of formation of seeds with different ploidy in populations or even in the offspring of some individuals is the lowering of ploidy because of the parthenogenetic development of embryos in the aposporous embryo sacs. For all this, because the apomictic forms from the investigated fragment of the agamic complex were principally pentaploids, i.e., they had unbalanced genome, their transition to the lower ploidy levels occurred through chromosome number. The decrease was not two-fold but between one- and two-fold through a mechanism similar to permanent odd polyploidy recorded, for example, in *Rosa canina* (Takcholm, 1922; Darlington, 1937a; Grant, 1981).

It is interesting to note that in the sexual form of P. *echioides,* owing to the chromosome balance of genome, a return to the dihaploid level resulted more often in formation of strict dihaploids (2x = 18). This argues that genomic variability in populations is really connected, first of all, with reversion on the dihaploid level, which is a consequence of the instability of the seed reproductive system.

The levels of seed ploidy in the same apomictic populations vary from year to year, depending essentially on the environmental conditions. Their simultaneous presence in populations and in the offspring of individual plants is possible because of the dynamic equilibrium of the apo- and amphimictic systems of reproduction, euspory, apomeiosis, parthenogenesis and embryogenesis in complicated interrelation and combination.

Aberrant Ovules and Seeds: Structure and Diagnostics (Plate VIII)

Aberrant (Latin *abberans* — deviating) ovules and seeds are characterized by deviation from the norm in shape, structure or functions that results in particular degeneration or their total die off. Synonyms: aborted, abnormal, sterile ovules and seeds.

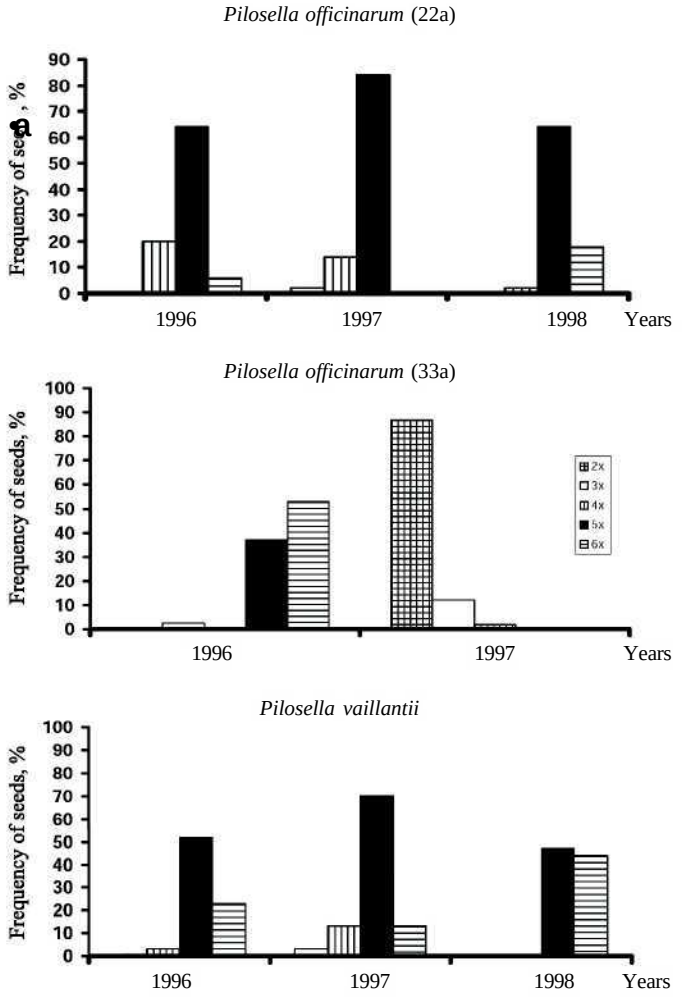


Fig. 40: Frequency of seeds with embryos having different ploidy in populations of sexual and apomictic *Pilosella* species by years.

The time of appearance of abnormalities, their character and degree of expression is believed to be taxon-specific; in various plants, different structures are destroyed. Aberrant ovules can differ from fertile ones for example by their smaller size *(Oxalis magnifica—Guih* and Weller, 1986), by increase in integument sizes and decrease in nucellus size *(Phytolacca americana—Mikesell,* 1988), or by a halt in lengthening of embryo sac *(Prunus avium—Jukey,* 1933).

Aberrant ovules could be diagnosed by the **change** in their **morphological type** (from anatropous in norm to orthotropous), **occurrence of asymmetrical integument,** which encircles nucellus incompletely, **lack** of **micropyle** or formation of an extremely wide **micropyle** *(Rhododendron nutallii*—Palser *et ah,* 1990). In the ovule of

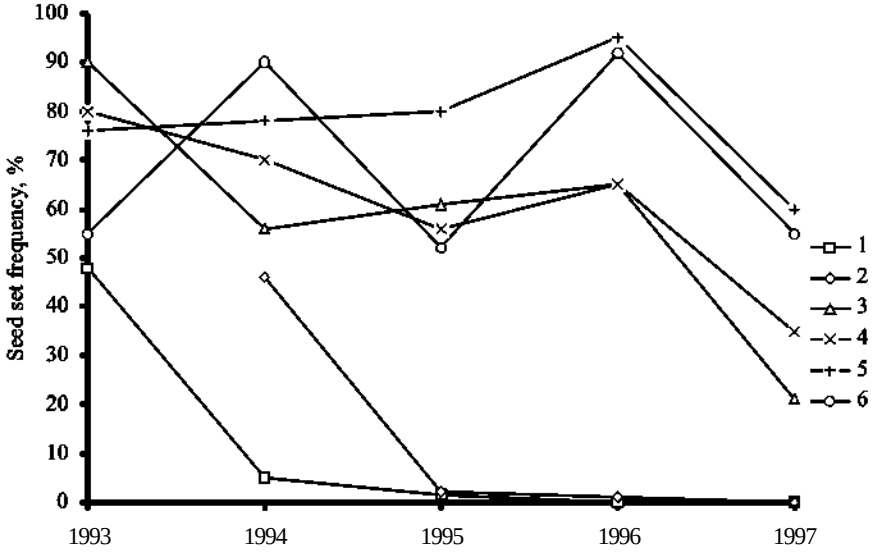


Fig. 41: Seed set frequency under self-pollination in populations of *Pilosella* species in different years of generation.

1 - *P. echioides* (33f), 2 - *P. echioides* (22f) (parthenocarpic fruits), 3 - P. *officinarum* (33a), 4 — P. *officinarum* (22a), 5 — P. *vaillantii,* 6 — P. *praealta.*

Arabidopsis thaliana mutant fee/ 1 a single structure develops instead of two integuments, which could be lobed (Robinson-Beers *et ah,* 1992). Abortion of ovules can be caused by enlargement of the nucellus and its leaving micropyle borders *(Saxegotheca conspicua — Noren,* 1908; *Rosa* sp., *Cerasus vulgaris—Savcheriko,* 1959), degeneration of the funiculus *(Pistacia vera*—Grundwag and Fahn, 1969; Bradley and Crane, 1975; Shuraki and Sedgley, 1996) or chalaza *(Persea americana—Steyn et ah,* 1993). So-called ovuloids, constituted only from the cells of outer and inner integuments *(Eucalyptus woodwardii*—Sedgley, 1989) or integument and chalaza remnants *(Vaccinium* — Bell, 1957; Eaton and Jamont, 1966; Stushnoff and Palser, 1969; Anisimova, 1997) were discovered. In aberrant ovules of *Vaccinium,* the nucellus degeneration begins at 8-nucleate stage or just after pollination, whereas in fertile ovules this process happens at 2- or 4-nucleate stage of embryo sac development. According to Hall and co-authors (1966), prolonged preservation of the nucellus and attendant processes of premature integument destruction are responsible for female sterility in certain clones of *Vaccinium angustifolium.*

Aberrant ovules of *Paeonia lactiflora* are characterized even before fertilization by the whole complex of feature-markers, such as increase of layer number and hypertrophy of cells in integumentary tapetum and apical part of the inner integument, precocious nucellus degeneration in micropylar and middle ovule parts, precocious tannin accumulation in the cells of outer epidermis of the outer integument, or the change of cell structure in placental obturator (Shamrov, 1995, 1997a). The enlargement of integumentary tapetum manifesting in increase in layer number was also noted in some other species (e.g., *Helianthus annuus*—Savchenko,

1959). In unfertilized ovules, the features of tissue and cell destruction are observed first in the inner integument and nucellus near the conductive bundle; precocious lignification of cell walls in the hypostase is noted *(Daphne arbuscula* — Erdelská, 1999). Then this process includes the outer integument.

The processes of destruction resulting in aberrant ovules and seeds often begin at the early developmental stages. Megasporocytes, megaspores and embryo sacs are able to degenerate; in addition, in the latter the disturbance of starch synthesis in the central cell is revealed (e.g., in *Medicago* and *Trifolium* — *Bingham* and Hawkins-Pfeiffer, 1984; Oryol *et al.*, 1985; Ogorodnikova, 1989; Zimnitskaya, 1992; Kazachkovskaya, 1992; Poljushkina, 1993). Lack of development of embryo sacs *(Paeonia anomala*—Yakovlev and Yoffe, 1957a,b, 1965), lack of cellularization in them *(Eucalyptus woodwardii* — Sedgley, 1989), and their degeneration during flowering *(E. cinerea* — Polunina, 1957,1963) are noted in aberrant ovules just before fertilization. After fertilization, either the embryo (mutants of *Arabidopsis thaliana* — Meinke, 1982) or embryo and/or endosperm *(Vaccinium* — Bell, 1957; Eaton and Jamont, 1966; Stushnoff and Palser, 1969; Anisimova, 1997) undergo destruction. In aberrant ovules of *Paeonia lactiflora*, the embryo sacs, as a rule, degenerate before fertilization (Shamrov, 1995,1997a). Some embryo sacs (penetration of pollen tubes in them is not revealed) exhibited the capacity for apomixis (parthenogenesis, synergid apogamety).

Not only structural abnormalities, but also the character of metabolism in certain organs present values for diagnostics of aberrant ovules and seeds. In these ovules, even before fertilization the cells of chalaza, integuments, nucellus and hypostase develop thick callose walls. As a result, the pathways of substance transport in the ovule are changed. The delay of cell lysis in the apical part of the nucellus prevents pollen tubes from penetrating into embryo sac (Brassicaceae, Fabaceae, Poaceae, Rosaceae, Solanaceae—Bingham and Hawkins-Pfeiffer, 1984; Oryol *et al.*, 1985; Briggs *et al.*, 1987; Ogorodnikova, 1989; Vishnyakova, 1991; Kazachkovskaya, 1992; Zimnitskaya, 1992; Poljushkina, 1993). Different express-tests for revealing of aberrant ovules just before fertilization were suggested: fluorescence of callose (Fabaceae, Solanaceae etc.—Vishnyakova, 1991), reaction for pectin substances, acid polysaccharides, and acid phosphatase in micropyle region *(Oenothera hookeri, O.* mut. *brevistylis, Capsella bursa-pastoris, Sisymbrium loselii*—Chudzik and Sniezko, 1997, 1999).

Abnormalities during ovule development appear to be induced by morphological, genetic, physiological, anthecological and ecological causes (see Table 20). One of the important factors is connected with the position of ovules in the ovary. In this case, fertilization of the first ovule and seed development from it in polyspermous fruits results in the redistribution of nutrient supply. As experimental investigation has shown, lack of development of seeds in the lower part of the fruit (in *Pongania pinnata* from 2-3-seeded it becomes uniseeded) is connected with inhibiting effect of plant growth hormones after fertilization of upper ovules (Arathi *et al*, 1999). In representatives of Fabaceae family, the aborted ovules can be found in different parts of the ovary: in basal part (Bawa and Webb, 1984), close to the style (Horovitz *et al.*, 1976) or in both parts (Link, 1961). The same is likely to occur in a number of other plants (e.g., in *Quercus gambelii—Mogensen*, 1975; and *Trapa natans*—Titova, 1988; Titova *et al.*, 1997).

Table 20. Possible factors of aberrant ovule formation.

Factors	References
Morphogenetic	Horovitz *et al.*, 1976; Bawa and Webb, 1984
—ovule position in the ovary	
Genetic	
—occurrence of lethal mutations in meiosis	Wiens *et al.*, 1987; Charlesworth, 1989
—apoptosis	Batygina and Voronova, 1999
Physiological	
—deficiency of resources for ovule development	Janzen, 1977; Haig and Westoby, 1988; Zimmerman and Pyke, 1988; Vaughton, 1993; Navarro, 1998
—blocking of nutrient transport in ovule	Pimienta and Polito, 1982; Ganeshaiah and Uma Shaanker, 1992
Anthecological	
—poor quality of pollen	Marshall and Elstrand, 1988
—insufficient quantity of pollen	Casper and Niesenbaum, 1993; Navarro, 1998
—concurrent development of pollen tubes	Lee, 1984; Joshi *et al*, 1993; O'Donnell and Bawa, 1993
—lack of pollinators	Menges *et al.*, 1986
—lack of the conditions for pollination	Erdelská, 1999
—low pollen-ovule ratio	Cruden, 1977
Ecological	
—inadequacy of habitat conditions (ecological stresses)	Tilton, 1980; Stephenson, 1981; Meinke, 1982; Sheridan and Neuffer, 1982; Bingham and Hawkins-Pfeiffer, 1984; Felker *et al.*, 1985; Marsden and Meinke, 1985; Hodgson, 1989
—duration of flowering periods	Stephenson, 1981; Navarro, 1998

According to Charlesworth (1989), in populations of plants, especially perennial and exclusively cross-pollinating plants, a "genetic load" (recessive lethal mutation) is accumulated that decreases the viability of the population. Seeds with "harmful" mutations die off first. Abnormalities in the development of generative organs, including ovules in some species of *Medicago* (Oryol *et al.*, 1985) as well as *Paeonia majko* (Zhgenti, 1978) and P. *lactiflora* (Shamrov, 1995, 1997a), are considered a reflection of their hybrid origin.

Experiments with *Capsicum annuum* testified to the influence of anthecological factors on the formation of aberrant ovules (Marcelis and Baan Horman-Eijer, 1997). They have shown that with insufficient quantity of pollen during flowering a considerable number of aberrant ovules and seeds was produced in the fruits. With additional pollination the number of fertilized ovules increases, but there is also abortion of the fruits developing after the first pollination. That is why for obtaining a larger number of fruits a smaller pollen quantity is recommended than needed for setting fruits from ovules available.

The occurrence of aberrant ovules in the ovary results in decrease in real seed productivity. Ovules with deviations can degenerate completely during developmental process or be preserved, transformed into seeds that are distinguished from normal ones by shape, size, colour and inner structure. The structural and often functional variations of seeds within the same fruit or the same plant are believed to be the basis of heterospermy (see Heterospermy; Real Seed Productivity).

The phenomenon of aberrant ovules and seeds is widespread in angiosperms and is connected in certain plants with adaptation to dispersal. Such ovules and seeds are observed mainly in polyspermous fruits and often in plants the fruits of which are dispersed by water, wind or animals. Here the weight of fruits decreases and in a number of cases, as in *Eucalyptus woodwardii,* aborted ovules and seeds are not completely destroyed and together with normal seeds maintain the fruit shape (Augspurger and Hogan, 1983; Sedgley, 1989; Ganeshaiah and Uma Shaanker, 1992). In *Vicia,* fruit size correlates with the total number of ovules in the ovary and the number of aborted seeds. Species with small fruits *(V. hirsuta, V. pubescens)* are characterized by small seeds and low abortion, whereas in the species with large fruits *(V. lutea, V. sativa)* the reverse dependence is seen (Ortega-Olivencia and Delesa, 1977). The appearance of aborted ovules in certain plants, connected with redistribution of nutrients from degenerating ovules to developing ones, is regarded as one of the elements of life strategy in extreme habitat conditions (Erdelská, 1999).

Investigation and diagnostics of aberrant ovules and seeds have a great importance theoretically and practically. This direction of research is especially relevant in connection with the revealing of mechanisms of unfavourable external factors influencing the reproductive structures and in connection with the preservation of biological diversity. The revealing of feature-markers and further elaboration of express-methods for appreciation of developing ovules, especially just before fertilization, remains one of the paramount tasks in the investigation of reproductive biology of rare, disappearing and economic plant species.

Heterospermy (Greek *heteros*—another, different and *sperma*—seed) is the occurrence on the same plant of seeds differing by size, weight, colour, morphology, anatomical structure, genetic characteristics, biochemical components, nature of germination and other features **(Plate IX).** Synonyms: heterogeneity, non-uniformity.

Heterospermy is widely presented in the plant world and is inherent both for wild and cultured forms. There is no precision or consensus on the concept of heterospermy or on the terminology concerning its various aspects (see Varenik, 1955; Strona, 1962,1964,1966; Ovcharov and Kizilova, 1966; Bartkov, 1972,1973; Levina, 1981; Danilova and Kirpichnikov, 1985; Makrushin, 1989).

In one of the early works devoted to the analysis of causes of heterogeneity in seeds, Tamberg (1947, 1951) distinguished its three types: vegetative (somatic) disintegration, stage heterogeneity and physiological heterogeneity. Developing these notions, Strona (1962,1964,1966), Ovcharov and Kizilova (1966) and Kizilova (1974) suggested three categories of seed heterogeneity: genetic, matrical and ecological. Gravimorphic, enantiomorphic, sexual and magnetomorphic types were also considered as independent types (Sulima, 1970; Bartkov, 1973). In Makrushin's classification (1989), the nature of factors influencing the character of variation of different seed features as well as the area of practical use were taken into account. He distinguished four categories of heterospermy: population, familiar, maternal and isolocular (conditioned by the specific character of embryonal processes in some

flowers). The population category has only ecological and trophic types. Each of the other categories is divided into three types (ecological, trophic and genotypical).

The classification of Levina and her colleagues (Voitenko *et ah*, 1980; Levina, 1981) is the result of deep analysis of factors influencing seed development and leading to non-uniformity of seeds. It is based on **quantitative, structural, biophysical, biochemical, physiological and ecological** features. The characters of non-uniformity of seeds could be expressed in different degrees, combined in different ways and manifested at various levels (fruit, individual, species, population).

In conformity with features mentioned above in Levina's classification (1981) the types, subtypes and forms of seed non-uniformity are revealed; for each form the levels at which it is manifested are indicated. The author distinguishes two types of seed non-uniformity: **hereditary** (genotypical) and **non-hereditary** (modifiable). Hereditary non-uniformity is divided into two subtypes and four forms: (1) phenotypically heterogeneous seeds, similar in genotype (heterocarpic form) and (2) phenotypically heterogeneous seeds, differing in genotype (individual, interpopulation and geographical forms). Non-hereditary heterospermy includes the forms matural,[1] topographical, age-grade, seasonal, yearly and ecological.

Batygina (1999a,b; see Genetic heterogeneity of seeds. Polyembryony) expanded the classification, adding the genetic feature. The genetic heterogeneity of seeds is regarded as the occurrence in seed of embryos of different genetic origin: sexual, gametophytic and asexual (embryoid). The other authors consider the genetic non-uniformity of seeds in a narrower sense, as the diversity of gametes participating in sexual process (Tamberg, 1951; Strona, 1962,1964,1966; Ovcharov and Kizilova, 1966; Kizilova, 1974; Levina, 1981).

Heterospermy manifests itself first in seed size: the sizes of embryo cotyledons and hypocotyl, endosperm, and seed mass can change (Apiaceae family: *Angelica, Daucus, Foeniculum, Heradeum, Peucedanum* — *Eremenko,* 1950; Lyubich, 1951; Tamberg, 1951; Makaro and Kondratyeva, 1962, 1970; Grushvitsky *et ah*, 1963; Nekrasov, 1969; Tjurina, 1971; Tkachenko, 1998; Anacardiaceae family: *Pistacia vera*— Shuraki and Sedgley, 1996).

Seed mass can vary considerably, depending on the position of seeds on the plant. For example, in *Gossypium hirsutum* and *G. barbadense* the 1000-seed weight depends on the location of the capsule within the bush, their quantity in the capsule, and consequently on the conditions of nutrition. On the lower plant layers, seed mass is always higher (these seeds possess better germination vigour and high germinating capacity). With early planting and good agrotechnics the absolute weight of seeds is higher than with very early or late planting (Bazhanova, 1960; Solovyev, 1960).

In the fruits of some representatives of Ericaceae family *(Vaccinium angustifolium* — Bell, 1957; *V. myrtillus, V. uliginosum* and *V. vitis-idaea* — Anisimova, 1997,1998; Komaletdinova and Anisimova, 1999) collected during dissemination, the seeds varied in size, morphology and anatomical structure. Large seeds had, as a rule, normally developed embryo, endosperm and seed coat; the seeds of intermediate sizes usually failed to contain the embryo, and the endosperm was either poor or missing; small seeds were presented mainly by exotesta, sometimes by the remnants

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difference in time of seed ripening on the individual.

of middle integument layers. Sometimes large and small seeds contained underdeveloped embryos.

Heterospermy also manifests in the different degree of embryo differentiation (from globular to torpedo-like stages) in mature seeds, e.g., in *Helleborus*, Ranunculaceae (Butuzova, 1997).

The complex of heterospermy features is typical for cereals. For example, in *Triticum aestivum* the sizes and weight, biochemical contents and physiological indicators of caryopses depend on their location on the spike; that is one of the causes of progeny non-uniformity (Parshakova, 1964, 1965; Batygina, 1974, 1987a). The plants produced from outside seeds in the middle spike zone were characterized by intensive growth, early beginning of all developmental phases, rapid growing of leaf mass and rich harvest. The plants obtained from inside grains of upper and lower spike parts developed more slowly and the harvest was poorer (Ryzhei and Zavgorodnya, 1959). Some authors noted the variation in protein content in seeds taken from different zones of the spike (Ryzhei and Zavgorodnya, 1959). The cereal caryopses are inherent in enantiomorphic heterospermy stipulated by left or right symmetry or asymmetry of embryo and endosperm (Sulima, 1970). In *Hierochloe stepposum* the larger seeds form on the upper layers of panicles, but depending on habitat and meteorological conditions the large seeds were produced either on the second and sixth or on the fourth and sixth layers. Beside this, within the same panicle together with seeds containing normally developed embryo, seeds with incomplete root differentiation in embryo, with several embryos and without embryo were found (Shokhina, 1971).

Heterospermy can be manifested in the peculiarities of dissemination. For example, in *Salsola ruthenica* (Chenopodiaceae) the plant produces two types of seeds: falling seeds (with helically rolled green embryo), contained in filmy pericarp with wings and non-falling seeds (with light-yellow embryo) enclosed in special structures derived from growing and firm pericarp tissues. The non-falling seeds, making up 0.4% of total seed number, are found in the lower part of the plant and germinate only after four years (Prodan, 1956). In *Atriplex nitens*, three types of seeds form within the same plant: (1) flat, large, brown, with thin coat, germinating in the year of maturation; (2) convex, black, with hard coat, germinating in the spring of the following year; and (3) convex, small, black, with very hard coat, germinating only in the third year spring or later (Lyubich, 1951). *Atriplex nitens* and *Chenopodium album* exemplified that polymorphism of seeds could be one of the causes of great morphological non-uniformity of individuals within coenopopulations (Seraya, 1979).

The causes of heterospermy are diverse and interconnected (Tamberg, 1951; Strona, 1962,1964; Ovcharov and Kizilova, 1966; Sulima, 1970; Bartkov, 1973; Levina, 1981; Makrushin, 1989). Heterospermy is conditioned first of all by differences in the structure of reproductive organs and asynchrony in their development within a flower, inflorescence and plant (Cuperman, 1950; Eremenko, 1950; Levina, 1965; Ovcharov and Kizilova, 1966; Bebin *et ah*, 1969; Eremenko and Poshechonova, 1971; Shokhina, 1971; Tjurina, 1971; Batygina, 1974; Tkachenko, 1998). Non-uniformity of seeds is conditioned not only by asynchrony of phases of budding, blossoming, and maturation on different levels of maternal plant, but also by the meteorological conditions of vegetation periods, leaf area, and the degree of photosynthetic activity of leaf surface (Bebin *et al.*, 1969).

The investigation of structural-functional bases of heterospermy is of great theoretical and practical importance, especially in seed farming. The understanding of heterospermy mechanisms will release new possibilities for improving seed qualities of economic value and enchancing plant productivity. Since ancient times the selection of large, healthy seeds is believed to be one of the agrotechnical methods for improving crop quality (Kostychev, 1877; Chernomaz, 1939; Mukhin, 1941; Musil, 1961; Strona, 1964; Ovcharov and Kizilova, 1966; Bewley and Black, 1978; Halloran and Pennell, 1982; Makrushin, 1989). The study of plant seed viability and determination of their economic suitability is indissolubly connected with the necessity of fair assessment of their physiological, cropping and technological qualities (germination vigour, laboratory and field germination, growing vigour, and the beginning and rate of germination). Seedling sizes are also suggested as an indicator of seed quality. For example, in *Lycopersicon esculentum* the seedlings from seeds of the first raceme are longer than the seedlings developed from the seeds of higher racemes; the later the seeds mature, the lower the seed germination capacity and vigour (Orlov, 1982). The significance of individuals developing from small seeds is very great. Late germination and prolonged stay in virginal period permit species to survive in unfavourable climatic conditions (Tkachenko, 1998).

Makrushin (1989), emphasizing the importance of heterospermy, suggests the establishment of a special branch of biological science: heterospermatology, which gives the theoretical bases for the modes of obtaining initial material for selection and primary seed farming, breeding of sowing material in technologically optimal conditions, and preservation and improvement of seed quality after harvest. Heterospermatology, in the author's opinion, pertains to the study of seed variability, the causes of differences of seeds in terms of features and properties, the effects of seed non-uniformity on the development and productivity of plants, and the elaboration of a test system to forecast seed crop features on the basis of these investigations in order to select biologically the most valuable sowing material, and to plan methods of its improvement during cultivation and after harvest.

Seed Bank

Seed bank includes not only the seeds proper, but also other diaspores: fruits, fruit parts and rarely multiple fruits.

The main portion of a seed bank *in situ* occurs in a soil. The reserve of seeds in a soil exists in all climate zones: from the Arctic to the tropics. Seeds are considered to be individuals in a latent state (the primary dormancy) that permits them to remain viable for a long time in unfavourable conditions. Seed distribution in soils of different types and at different depths, in various climatic zones and phytocoenoses were rather extensively investigated (Rabotnov, 1982, 1990, 1995; Petrov, 1989). Rabotnov formulated the geographical (latitudinal) regularity of distribution of viable seed number in a soil: from tundra (1000-3000 seeds per m^2) to the zone of north taiga, a rapid decrease in seed stocks is observed; towards the broad-leaved forests, meadow and proper steppes, the seed number in a soil increases (up to 10,000 seeds per m^2) and towards the desert steppes, it decreases again. The soil seed bank is formed as a result of seeding of plants presently in the coenosis and plants that were earlier in it, as well as seeds carried in from outside. The main seed mass in a soil is

produced by herbaceous plants. The capacity to accumulate the great stable reserves of viable seeds in a soil has arisen in plant species growing in unstable environmental conditions, under which the possibility of seed propagation is only sometimes realized. In unfavourable conditions, the coenopopulation may change from the active state to the dormant one and be constituted exclusively from viable seeds occurring in a soil.

There are conditions in the soil which provide the anabiotic state for seeds: anaerobic conditions, lower temperatures (especially in the Arctic), high acidity, increased CO_2 content and the products of vital activity of saprophytes.

The capacity of seeds to keep alive in soil for a long time is species-specific and has been elaborated in the process of the establishment of each species in definite conditions. The longevity of seeds varies greatly in different species: from one year (and even less) in species appearing in conditions stably favourable for seed germination and seedling development, to tens and hundreds of years in species characterized by a life cycle with alternating active and cryptic (latent) periods (Rabotnov, 1995).

Harrington (1972) analysed the world literature and collected data on the longevity of seeds in a soil for 324 species of woody, fruticose and herbaceous plants.

Preservation of seeds of wild species *ex situ* takes a wide variety of forms: the collection of seeds in museums, institutes, repositories, herbariums; the storing of seeds in seed departments of botanical gardens (often in room temperature) for exchange purposes. Modern seed banks of wild plant species have regulated conditions allowing prolonged maintenance of their viability and genetic completeness. Organization of banks of natural genetic resources is included in the international convention on preservation of biological diversity accepted by most countries.

Scientists and breeders have investigated the problem of seed longevity for more than a century. Three groups of species were distinguished according to the longevity of seeds (Ewart, 1908): **microbiotics** (seeds retain the capacity to germinate for not more than 3 years), **mezobiotics** (up to 15 years), **macrobiotics** (more than 15 years). The results of world practice on the researches of seed life duration for 116 microbiotic and 740 mezobiotic and macrobiotic species stored in laboratory conditions, herbariums and repositories were summarized by Harrington (1972).

The group of microbiotics includes some orchids, in which seeds remain able to germinate for some hours, as well as *Tussilago farfara,* species of *Salix, Populus, Aesculus, Quercus* and other genera (Barton, 1961; Li and Sakai, 1978). Seeds of microbiotics that quickly die because of drying out are referred to as recalcitrant.

The seeds of most wild species from mezobiotic group easily lose moisture after maturation (orthodox ones). Even Ewart (1908) attributed to macrobiotics 137 species from 47 genera of Fabaceae family, 15 species of Malvaceae, 14 species of Myrtaceae, and some species from the families Nymphaeaceae, Lamiaceae, Polygonaceae, Tiliaceae and Geraniaceae. The determination of viability of seeds from collections and herbariums stored in room temperature and reliably dated (Barton, 1961; Harrington, 1972; Wang *et ah,* 1993) revealed long-lived seeds (70-90 years and more) in *Canna, Astragalus, Trifolium, Daphne* and other genera.

Banks of cultivated plant seeds were first organized in the 1970s; their network now covers 65 countries all over the world, and new banks are always being created

(Tikhonova, 1995). Genetic resources of the cultivated plant species and their relatives have been collected in banks of embryo plasma; seeds of wild species that have medicinal, food, technical and other economic importance are also collected. Seed banks of wild species were first created mainly in large botanical gardens in England (Kew Gardens), Switzerland (Basel), Spain (Madrid), South Africa (Kirstenbosh) and other countries. Temperature regimes of seed storage in them are the same as in the banks of cultivated species seeds: low positive temperatures (+5°C) and freezing to -20°C (Bramwell, 1987). These regimes in comparison with room temperatures extend the life of seeds but do not lead to the rapid deceleration of metabolism. Deep freezing of seeds in liquid nitrogen (-196°C) or under vapour of it (about -160°C) is believed to be an effective regime for long-term storage, especially of seeds of microbiotics (Li and Sakai, 1978; Tikhonova, 1992a,b, 1995; Wang *et al*, 1993).

Fruit (from Latin *fructus)* is a morphological formation developing from the ovary after the fertilization of ovule.

The pistil as a whole as well as extracarpellate flower structures (receptacle, perianth elements) and sometimes the modified inflorescence portions, often participate in fruit formation. Fruits ensure the development and ripening of seeds and their distribution either by disseminating seeds or by serving as diaspores.

Morphological nature of fruits. Up to now, botanists have failed to come to a common opinion on the morphological nature (homology) of fruits. As Eames noted (1961), this is why the term "fruit" is used rather widely: both for indication of definite carpels of apocarpous gynaeceum (sometimes called "fruitlets", e.g., in *Fragaria)* and for the description of whole infructescences (e.g., in *Ananas).* In this connection, the question of probably different origin of fruits arises. Two major and, in effect, mutually exclusive points of view on morphological nature of fruits are reflected in carpological literature. According to some investigators (Eames, 1961; Levina, 1987; Spjut and Thieret, 1989; Takhtajan, 1991), the fruit originates from the flower as a result of structural and functional reorganizations of gynaeceum and often includes modified extracarpellate flower organs. That is why "the fruit should be considered as a derivative of the flower as a whole, but not of gynaeceum alone, despite the fact that its main parts are formed by carpels" (Takhtajan, 1991:199). According to other botanists, the fruit represents the ovary, modified during development (van der Pijl, 1969; Raven *et al.*, 1986; Teryokhin *et al.*, 1993), or the pistil (Tikhomirov, 1989).

As Tikhomirov emphasized (1989), the fruit is not some new or special flower organ; it always develops from other organs, being the last stage of their development. Owing to this, the standpoint of Spjut (1994), who identifies the fruit first of all as a functional "unit" or "dispersal unit", is of great interest. In his opinion, fruits represent a complex structure composed from mature ovules and attached megasporophylls of different strobilar structures. Megasporophylls can be open as in strobiles ("simple cones") of Cycadaceae, or fused into the "ovule-like" structures in "complex cones" of conifers, or closed within gynaeceum carpels of angiosperms. Spjut's ideas further extend the "homology field" of fruits, applying the notion "fruit" to the strobiles ("cone") of gymnosperms. The notion "morphological nature of fruits" becomes still more indefinite.

From our point of view, van der Pijl (1969) truly limited the evolutionary primary entity of fruit as closed structure, formed by a single carpel (fruits developing from

apocarpous gynaeceum) or several carpels (syncarpous fruits). All formations, including extracarpellate structures, especially fruits, developing from inferior ovary or with contribution of growing receptacle, are secondary in terms of evolution, derivatives from fruits formed by pericarp ("pericarp fruits").

Therefore, speaking about the ontogenetic origin of fruit, we are discussing at the same time the question of its evolutionary origin. From these positions we inevitably come to the definition of evolutionary primary fruit ("pericarp fruit") as a formation of the final stages of ovary development; Moreover, the fruit homology must be addressed at the level of ovary homology.

The ovary is a new structure, a closed cavity formed by a single or several carpels (van der Pijl, 1969). The ovary wall (pericarp) is undoubtedly homologous to megasporophyll (or fused megasporophylls), but the ovary as a whole is, in terms of evolution, a new formation ensuring angiospermy.

The evolutionary process is known to proceed by means of trial and error, as illustrated by the familiar example of formation of a "fruit-like structure" ("cone-berry") in *Juniperus.* In this plant, three upper fusing cone scales form the united fleshy "pericarp", containing one to three seeds with hard seed coat, the obvious adaptation to endozoochory. The example of *Juniperus* illustrates the possible repeated and successive evolutionary changes leading to the appearance of fruits as formations adapted to seed dispersal.

While the fruit is said to be "a mature ovary", the numerous structures in the gynaeceum, consisting of non-fused single "mature carpels" (e.g., in *Geum* and *Ranunculus),* are more logically considered peculiar unigynaeceal infructescences, as Tikhomirov proposed (1989), though using for this the already current term "anthocarpium". In such an approach one essential question inevitably appears: is it correct to contrast the flower (anthostrobil, according to Arber and Parkin, 1907; Takhtajan, 1964) with the inflorescence? Posluszny and Charlton (1993) discussed the eventuality of interpretation of flower morphological nature in Alismatidae (Helobiae) in terms of inflorescence, implying the origin of generative structures in these plants from ancestral prefloral formations similar to "inflorescence". Does "the flower" represent the simplest form of inflorescence or not? In this approach many contradictions between "evantal" and "pseudantal" theories are taking off.

Classification of fruits. Attempts to create a morphological fruit classification acceptable to the scientific community have gone on for more than two centuries (Grudzinskaya, 1968; Levina, 1987; Tikhomirov, 1989). Spjut and Thieret (1989), who investigated the history of classification of so-called "compound" and "aggregate" or "multiple" fruits, came to the conclusion that classification of fruits still remains in chaos. Van der Pijl (1969) substantially criticized the modern morphological and so-called genetic classifications of Winkler (1939, 1940), Baumann-Bodenheim (1954), Takhtajan (1959), Levina (1961) and other authors. In his opinion, these systems are based on incompatible features: the main ecologically neutral morphological peculiarities of carpels (or their complexes) on one hand and improvements due to "accidental" ecological requirements for dehiscence, consistency and other similar fruit characteristics on the other hand. In these systems, morphological fruit systems referred to as "genetic" actually are "ontogenetic". The pathways of development are described in them typologically on the basis of monophylletic concept of angiosperm phylogeny.

One of the principal reasons for lack of success in creating morphological and "genetic" fruit classifications is the replacement of the notion of "fruit as mature ovary" by the notion of "fruit as mature gynaeceum", which does not adequately reflect the real evolutionary processes. Even botanists who adhered to the notion of "fruit as mature ovary", beginning with Linnaeus (1751) and Gaertner (1788), in effect used the notion of "fruit as mature gynaeceum" (De Candolle, 1819; Lindley, 1832). This led to ambiguity of the notion "fruit", which was assigned different terms: "fruit" as the result of the development of apocarpous or syncarpous gynaeceum as a whole and "fruitlet" as the result of the development of separate unicarpellate ovary in apocarpous gynaeceum (Teryokhin *et ah,* 1993). The notion of polynomal fruit in respect of fruit aggregation, developed from apocarpous gynaeceum, was introduced by Gobi (1921). It is obvious biological and ecological nonsense, when the development and functions of such a biological system are considered from the positions of pollination, fertilization and dispersion of reproductive units constituting it.

Taking into account the above-mentioned criticisms of existing classifications of fruits (Van der Fiji, 1969,1982; Spjut and Thieret, 1989; Tikhomirov, 1989; Teryokhin *et ah,* 1993), nevertheless it should be admitted that the efforts of several generations of carpologists from Gaertner (1788) to Roth (1977) and Spjut (1994) have considerably reinforced our understanding of the main categories and types of fruits and their distribution among angiosperms. The most difficult problem today is to elucidate the real evolutionary interactions between the basic categories of fruits as well as "fruit-like" formations (such as in *Ananas* or *Fragaria).* The role of ecological (or more exactly etological) factors in the adaptive morphological evolution of fruits, according to the notions of van der Pijl (1982), must be taken into consideration. The numerous phenomena of parallel evolution, resulting in various convergences, obviously greatly hinder scientific progress in evolutionary carpology.

It is equally important to evaluate correctly the possible transitional forms between different categories of fruits and fruit-like structures, where evolutionary ecological trends are obvious, but "obvious morphological facts" are hardly considered in existing notions. A search for new approaches to the investigation of fruit evolution is necessary.

In this connection we suggested certain principles of classification proceeding from the fact that members of Magnoliophyta have not two types of formations encouraging dissemination (fruits and infructescences) but three:

Fruit is the ovary, transformed during development, a unigynaeceal structure used for dispersal and distribution of seed (dispersal unit); it is often formed with the contribution of receptacle and/or perianth and functions as separate total reproductive unit in the period after pollination and fertilization.

Infructescence is the uni- or polygynaeceal aggregation of fruits functioning as total formation in the process of attraction of dispersal agents ("compound unit") and discretely as disseminated structure.

Diasporocarpium is the formation developing from the totality of ovaries of a single or several adjacent flowers (uni- and polygynaeceal diasporocarpia), used for seed dispersal and functioning discretely (on the base of separate pistils) during flowering and as a total unit during fruitage.

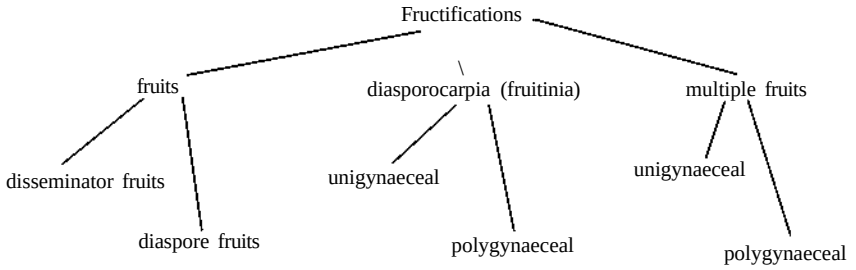


Fig. 42: Classification of angiosperm generative structures, adapted to the function of seed distribution (Teryokhin *et al.*, 1993).

In the scheme of fructifications[2] (Fig. 42) the diasporocarpia occupy "the niche" between fruits and infructescences and represent by their morphological nature uni- and polygynaeceal, highly integrated infructescences.

"Polynomal" apocarpous fruits, in our opinion, should therefore be divided into unigynaeceal infructescences and unigynaeceal diasporocarpia (Figs. 43 and 44).

Presuming that changes of ecological function are the directive factor of fruit morphological evolution, we considered it possible, as has been mentioned above, to subdivide all fruits (namely fruits and only them) into two main groups: disseminators and diaspores (Teryokhin *et al.*, 1993). These groups of fruits usually do

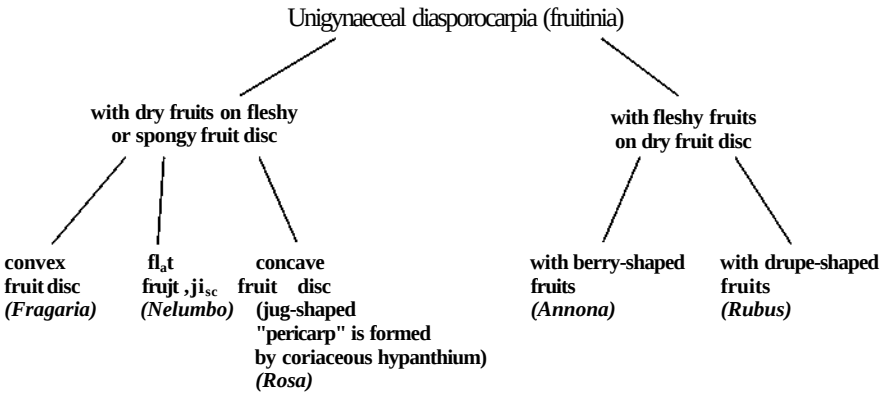


Fig. 43: Unigynaeceal diasporocarpia.

[2]**Fructifications** in modern botany (and especially in paleobotany) constitute the organs realizing seed propagation: female, male, and telianthus organs (except pollen). The term is used to describe organs both of gymnosperms and angiosperms. The flowers and inflorescences, fruits and infructescences, strobiles, simple and compound cones and other organs are referred to as fructifications (Spjut, 1994). In this connection we consider that the term "fructification" can be used as the most general name for structures (in both gymnosperms and angiosperms) producing seeds or promoting their distribution. It is especially important in cases in which such structures are difficult or impossible to reconcile with the traditional notion of fruit.

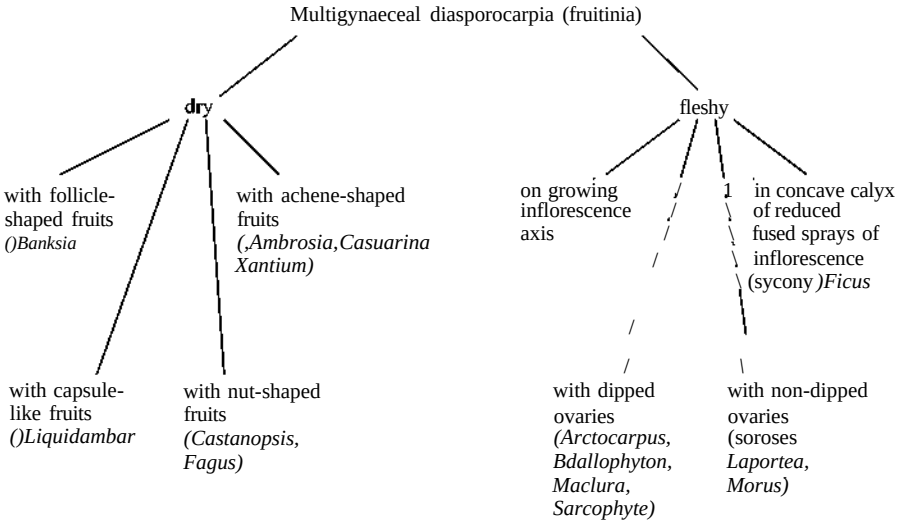


Fig. 44: Polygynaeceal diasporocarpia.

not correspond to the accepted division into "dehiscent" and "indehiscent". All fruits dehisce and the question is when and how they dehisce.

In conclusion, we must mention the remarkable statement of van der Pijl (1969) that modern morphology represents the "fossilized" ecology of former times, of course, on condition that the changes of ecological function are considered as etological, i.e., changes of behaviour (Teryokhin, 1991).

Biological significance and ecological role of fruits. Carpels, closed or fused, single or in aggregations, are the structural basis for the formation of placental tissues, the cells of which initiate ovules. After fertilization, functions of nutrient supply to seeds, their protection against exterior influences and damage, and preparation for dissemination (maturation, sometimes attended by the formation of special fruit structures) are transferred from the ovary wall to the pericarp. Modification of trophic functions due, for example, to the change of seed number in the fruit has resulted also in essential structural reorganizations of fruits during evolution. For example, in orchids the functions of pericarp and the general structure of fruit (especially development of placental formations) are connected with the development of many thousands of dust-like anemochorous seeds in a single fruit and with the fulfilment by fruit of trigger function for effective seed dispersal in air. Dry pods of orchids exemplify the large group of fruits that trigger anemochory.

It is quite obvious that the transition to unispermous endozoochorous fruits (e.g., in *Prunus),* that is, to fruits that directly contribute to the distribution, replacing some functions of seeds, requires fundamental reorganization of tissues and general structure of pericarp, its vascular system and placental structures. The examples given reveal clear dependence of the change of fruit structure and biological function on its ecological functions, i.e., on the character of fruit participation in dissemination processes.

In nature there are two main modes of fruit contribution to seed dispersal (Teryokhin *et ah,* 1993). **Disseminator fruits** initiate primary seed dispersal. Usually these fruits are dry polyspermous pods (e.g., in *Papaver, Pyrola)* that "transfer" seeds to such abiotic agents of distribution as wind or water. **Diaspore fruits** directly fulfil the process of dispersal of seeds contained in fruits, attracting biotic agents for this purpose (different modes of zoochory). In some cases *(Cocos nucifera),* unispermous fruits are distributed by water (hydrochory), but this appears to be a secondary evolutionary adaptation.

Thus, analysis of the ecological role of fruits reveals two fundamental biological processes: (1) the role of generative diaspore is taken by the seed and the fruit only promotes dissemination and (2) the function of generative diaspore is fulfilled by the fruit itself (Teryokhin *et al,* 1993).

While discussing the origin and evolution of fruits, Van der Pijl (1969) noted (after Corner, 1958) that the transfer of functions from seeds to fruits is the basic point of these processes and that it is important to trace the stages and possible variations of such replacements. The function of transfer appears to have happened in the process of evolution more than once.

The evolution of fruits. In modern carpology, there are two principally different standpoints on the problem of fruit evolution and a diversity of opinions.

The notions of Takhtajan (1991) about fruit evolution follow the strictly monophyletic concept of Hallier (1912) on the phylogenesis of angiosperms. According to him, the classification of fruits must be based on the origin of each type of fruit and categories of such types. In Takhtajan's opinion (1991), even recent evolutionary classifications of fruits (Egler, 1943; Kaden, 1947,1961; Takhtajan, 1959, 1964) do not reflect all their diversity and evolutionary relations of all types, but the main fruit types and the principal trends of their evolution are already known.

The concept of fruit evolution offered by Takhtajan (1991) includes the following basic statements.

— The primary category of angiosperm fruits is apocarpous polyfollicle with spiral arrangement of the free polyspermous fruitlets on the flower axis *{Magnolia, Caltha,Paeonia).*

— Syncarpous fruits are produced from syncarpous gynaeceum or from free carpels fusing in the course of development.

— "Dry" fruits are primary ones. In many branches of angiosperms the "dried" types of fruits give rise to endozoochorous fleshy fruits.

— Syncarpous polyachene, which dehisces during ripening in sutural regions of the upper free parts of fruitlets, is believed to be the transition form between apocarpous polyachene and typical syncarpous fruit.

— The pod is the most primitive type of dried syncarpous fruit. There are three main types of capsules: septate with axile placentation (syncarpous in narrow sense), unichambered with parietal placentation (paracarpous) and unichambered with free central placentation (lysicarpous).

— Fruits developing from the lower ovary constitute a special group. The most common type in this group is the dried septate pod.

— Many paracarpous or non-septate pods with parietal placentation are derived from septate fruits with axile placentation. However, in certain archaic taxa the

paracarpous fruits are derived directly from apocarpous ones (Annonaceae — *Monodora* and *Isolona, Wintemceae — Takhtajania,* and Canellaceae).

It should be mentioned in this connection that the statements given above are based on the definite morphological concept of angiosperm phylogenesis, as even van der Pijl (1982) emphasized, and fail to articulate carpological or ecological reasons. This pertains specifically to the notion that "dry" fruits appeared earlier than fleshy fruits in evolution. Besides, the suggested concept is closely connected with the presentation of morphological nature of the fruit as the derivative of gynaeceum as a whole, which, as shown above, is not the only acceptable notion.

Van der Pijl (1969) approached the problem of fruit evolution from the other aspect, from the positions of ecological functions of flower, seed and fruit. He considers fruit evolution to be "the last stage" in the evolution of dissemination organs (generative diaspores) in the higher plants. According to van der Pijl, the evolution of carpel (closed megasporangium) is in the improved distinction of functions between "the seed" and "the fruit" at the stages of protection of megasporangium and embryo (involving the stage of dormancy) and the attraction of distribution agents. The fundamental process of evolutionary modifications is the gradual replacement of functions and structures of "seed" by functions and structures of "fruit". The process of function transfer was gradual and variable. Van der Pijl emphasizes that certain variations of this process, e.g., early seed realized from the fruits (not from "mature" ovaries as in some Liliaceae (Monodoideae), Berberidaceae *(Caulophyllum),* and Violaceae *(Decorsella, Gymnorinorea)),* represent "angiovulate, not yet angiospermous" examples.

The main conclusions of van der Pijl (1969) seem to be absolutely opposite to that of Takhtajan (1959,1991). In the opinion of van der Pijl, the primitive fruits (carpels) were succulent and zoochorous. The "drying" and special modes of fruit dehiscence prove to be evolutionarily secondary in respect of their succulence. According to van der Pijl (1969), the origin of "carpellate" structures was polyphyletic and convergent. He has doubts about the eventuality of existence of common trends in fruit evolution, regarding their specialization in all directions with frequent "progresses" and "regresses" and "final convergence" to be presumable.

The ecological-morphological, analytical approach developed by van der Pijl was later applied to the research of the evolution of embryonal and generative structures in parasitic flowering plants (Teryokhin, 1977), as well as to the study of interactions between ecological factors and flower structure as pollination mechanisms (Faegri and van der Pijl, 1980). Following the ideas of van der Pijl, we suspect that the investigation of fruit evolution with account of the existence in angiosperms of more diverse morphological formations, as is usually accepted (not only fruits proper or "pericarp fruits", but also "diasporocarpia", "unigynaeceal multiple fruits", etc.), fulfilling the functions of seed dispersal, will encourage further progress in the elaboration of this problem.

Heterocarpy (Greek *heteros* — another, different, and *carpos* — fruit) is a genetically determined feature of the species of forming fruits with different morphological and anatomical structure on a single specimen.

Heterocarpy is peculiar mainly to annual plants or plants that survive a few years and also to species (or populations) growing in extreme environmental conditions (semideserts, deserts, Alpine regions, etc.). It is found in the representatives of many

flowering plants, but it is mostly concentrated in the families Asteraceae, Boraginaceae, Brassicaceae, Chenopodiaceae, and Fabaceae.

The following types and forms of heterocarpy are distinguished (modified from Levina, 1981).

Type I. **Heteroholocarpy:** differences between whole fruits. This type includes two forms:

a) **equivalent** form (equal number of seeds in the fruits) is noted in plants forming one-seeded fruits that do not open (Asteraceae, Dipsacaceae);

b) **unequivalent** form (different number of seeds in the fruits) is found more often in plants with many-seeded dehiscent fruits (Brassicaceae, Fabaceae).

Type II. **Heterophragmocarpy:** the morphological and anatomical differences between the constituent parts of many-seeded, separating fruits. It is subdivided into three subtypes:

a) **heteroarthrocarpy:** revealing differences between articules of the fruit (Brassicaceae, Fabaceae) and having two forms, the equivalent and unequivalent;

b) **heteromericarpy:** showing differences between the mericarps of the same fruit (Apiaceae, Hydrocotylaceae, Malvaceae);

c) **heteroeremocarpy:** showing differences between the eremes of the coenobia (Boraginaceae, Lamiaceae).

Differences of the generative diaspores are especially striking in equivalent heteroholocarpy. In this case, one-seeded indehiscent fruits may sharply differ in size, form, and anatomical structure of the pericarp, the character of the appendages that form on the surface of the fruit, and other features.

The important trait of heterocarpy is the deep differences in the seed structure. The seeds of heterocarpous fruits or their parts differ substantially in depth of dormancy, duration and character of germination. Heterocarpy thus permits plants to regulate the number and proper sequence of the germination of offspring. This has exceptional importance for annual plants.

The generative diaspores of heterocarpous plants differ in distance of distribution; this is one of the important evolutionary acquisitions.

Investigations of the heterocarpous representatives of the families Chenopodiaceae, Brassicaceae and Boraginaceae have confirmed that these plants form different kinds of diaspores:

— barochorous (falling close to the mother plant),

— epizoochorous (clinging to the fur of mammals and to bird feathers by special appendages), and

— anemochorous (distributed by air flows over a radius of several metres).

This promotes the significant and purposeful widening of the areas of the heterocarpous species. Thus, heterocarpy represents itself as one adaptation in seed propagation of flowering plants.

PART FOUR-VEGETATIVE PROPAGATION

VEGETATIVE PROPAGATION

Vegetative propagation is the increase of number of individuals of the given species or cultivar by means of separation of viable parts of the plant vegetative body (buds, shoots, roots, etc.). In many cases, vegetative propagation is accompanied by regeneration or renewal of missing organs in the detached plant parts: formation of roots on breaking twigs (e.g., in *Salix fragilis),* development of adventive buds on falling leaflets *(Cardamine pratensis),* and so on. Often, in the course of vegetative propagation, all organs of an offspring are formed prior to separation from the mother plant (for instance, rosette shoots with additional roots on stolons in *Fragaria*—Serebryakova, 1978a-c).

Offspring developed in the process of vegetative propagation are clones, genetically homogeneous individuals sharing the genotype of the mother plant. Formation of clones or **genets** (Harper, 1977) is widespread in nature among species that are propagated predominantly by vegetative mode, for example, in *Elodea, Lemna, Convallaria, Aegopodium.* Cultivars of many cultivated plants *(Solarium tuberosum, Fragaria, Rubus, Tulipa,* etc.) are clones.

Methods of clonal micropropagation of plants in *in vitro* cultures are increasingly widespread. By these means, a whole plant can be grown from a few cells or a single cell, the rates of plant propagation can be hastened a hundred- or thousand-fold, and sowing material free from viral diseases can be obtained. The method of micropropagation is economically effective in growing especially valuable cultivated, ornamental, medicinal and rare plants (Kataeva and Butenko, 1983).

The term "vegetative propagation" should not be confused with "vegetative renewal" and "vegetative spread" (Shalyt, 1960; see also Reproduction, Propagation and Renewal). Vegetative renewal is the development of new parts of plants in place of dead or damaged parts. It is well expressed in the form of seasonal rhythms of plants. Vegetative spread is an increase of individual size in plants. It is accompanied by increase of number of structural modules (the term was introduced by Harper, 1977) that compose the plant and are relatively autonomous, i.e., they can potentially live independently. Examples of such modules are rosette shoots *(Aegopodium podagrarid),* tufts *(Vaccinium myrtillus),* bunches *(Carex pilosa),* and rooting shoots *(Asarum europaeum).* Vegetative spread may easily be traced in annual, biennial and vegetatively immobile perennial plants as well in trees and shrubs. It is much more difficult to observe vegetative spread in dwarf shrubs and vegetatively mobile herbaceous perennials since a significant part of shoot systems of these life forms is situated below the ground, and it is impossible to determine boundaries and sizes of individuals without digging them up. The process of vegetative spread often leads to plant particulation, i.e., disintegration of plants into particles (see Particulation). Usually, particles are structural modules (or their systems) that have passed on to autonomous life, for instance, separated and rooted shoots *(Aegopodium podagraria, Vaccinium myrtillus)* or creeping shoots *(Lysimachia nummularid).* Such separated parts are called "ramets" (Harper, 1977).

If separated parts are viable, the particulation leads to vegetative propagation, i.e., increase of number of individuals. But if the separated parts are not viable and die

off quickly, particulation results in formation of litter. Senyaninova-Korchagina (1967) proposed the term "senile disintegration" for cases in which particulation takes place at the final stages of ontogenesis, i.e., in senile plants, and is not accompanied by rejuvenation of separated particles. Vegetative propagation differs from senile disintegration in that developing offspring is younger or at least identical with the mother plant.

In natural conditions, success of vegetative propagation is determined by age (or ontogenetic status) of plants passing to vegetative propagation, degree of rejuvenation of the vegetative offspring, distance between the offspring and maternal plant, and durability of physiological contacts between them. Using all these characters, Smirnova (1974) distinguished four types of vegetative propagation: (1) senile particulation (according to Rabotnov, 1969a,b) peculiar mainly to taprooted herbaceous perennials; (2) mature particulation without rejuvenation or with weak rejuvenation of the vegetative offspring and slow vegetative spread (tufted grasses, sedges, short-rhizomatous herbs, geoxylous shrubs); (3) mature particulation with superficial rejuvenation and active spread (long-rhizomatous herbs, dwarf shrubs); and (4) pregenerative particulation, peculiar to young plants that have not yet flowered. Pregenerative particulation is usually accompanied by deep rejuvenation of the offspring. In some biomorphs (root-sucker, stoloniferous), pregenerative particulation is related to intensive spread and expansion, in others (bulbiferous, bulbotuberous) the spread is weak, and the vegetative offspring is concentrated near maternal plants forming compact clones.

The first type of vegetative propagation is not effective because the particles die off quickly. In fact, this variant is to be attributed to vegetative disintegration. The second type is not very effective since vital status of the particles is low, though they may live for some decades. The third and fourth types of vegetative propagation are highly effective. The offspring is numerous (20-50 per plant yearly) and characterized by high growth rate. The species sharing these types of vegetative propagation (e.g., *Elytrigia repens, Aegopodium podagraria, Potamogeton* sp.) can rapidly colonize territories and water spaces. The success of vegetative propagation is determined not only by biomorphology of plants and their infraorganismic correlations but also by external conditions (Lyubarsky and Poluyanova, 1984). The maximum longevity, rates of growth and formation of vegetative offspring (ramets) vary widely in different species and seem to be determined genetically. For instance, the life span of the ramets of *Aegopodium podagraria* and *Carex pilosa* is 7-9 years, but that of ramets of *Galium odoratum* and *Stellaria nemorum* is only one year (Smirnova, 1987).

Vegetative propagation without human assistance is called **natural vegetative propagation.** It may occur by means of non-specialized and specialized organs (Serebryakov, 1952; Serebryakova, 1978a-c). Non-specialized vegetative propagation is observed in the case of decaying creeping shoots *(Trifolium repens, Lysimachia nummularia),* lodging shoots *(Veronica chamaedrys)* and epigeogenous rhizomes (i.e., those developing above ground) *(Asarum, Geum, Alchemilla).* Specialized vegetative propagation takes place through specialized and often modified shoots: long, thin, fast-decaying stolons, both above ground *(Fragaria)* and below ground *(Trientalis europaea),* hypogeogenous rhizomes *(Pyrola, Convallaria),* various storage organs: tubers *(Solanum tuberosum),* bulbotubers *(Gladiolus, Crocus),* bulbs *(Tulipa, Allium),* bulbils (e.g., in *Ficaria verna).* Tuberous, bulbiferous, and bulbotuberous plants are characterized by fast growth (regeneration) of above-ground shoots, as they utilize for growth the nutrients accumulated in storage organs.

Artificial vegetative propagation is used for growing of cultivated plants. This mode of propagation has a practical advantage over multiplication from seed, since it makes it possible to maintain the seed properties for a long time. In artificial vegetative propagation of economically valuable plants, the question of aging and longevity of clones arises because these processes determine stability and longevity of cultivars. Special investigations show that the life span of clones is limited; the vegetative offspring gradually ages and loses economically valuable traits. For instance, the offspring of gladioli propagated by a common method (by bulbotubers) demonstrate signs of aging and gradually lose cultural traits during the second or third decade of the cultivation. The aging may be significantly delayed and even practically stopped by means of regular renewal of the *in vitro* culture and selection of slowly aging individuals (Andreeva *et al.*, 1990; Matjukhin, 1994).

Artificial vegetative propagation is often based on various modes of natural propagation. Breeders only hasten the separation of vegetative offspring by cutting rhizomes *(Sansevieria, Clivia, Aspidistra),* detaching the daughter tubers, bulbs, bulbotubers *(Solatium tuberosum, Tulipa, Allium sativum, Gladiolus),* rooting layers (branches pinned to the ground, e.g., in *Grossularia)* and cuttings, i.e., parts of vegetative organs. Cuttings may include shoots (e.g., in *Ribes, Populus, Pelargonium),* roots (in *Rubus, Hippophaë rhamnoides, Cerasus),* and leaves (in *Begonia, Saintpaulia).* Cultivated plants such as apple tree or pear tree, in which root regeneration is impeded and cuttings do not root, are propagated by means of grafting.

Sarmentation (Latin *sarmentum* -runner, sobole, sarment) is formation of sarments appearing on stolons, rhizomes, and roots from apical, lateral and adventive buds and separating from the maternal plant after rooting (Fig. 45) The term "sarmentum" was used for a stem offspring that can be either above ground or below ground (Plenk, 1798).

The term "sarmentation" is used in botanical literature to mark one of the modes of natural vegetative propagation. Sarmentation contributes to intensive seizure of territory and the highest possible survival rate of daughter plants, which as a rule rejuvenate well. In the level of rejuvenation of descendants, such a mode of vegetative propagation in most cases approaches seed propagation.

Specialized organs of vegetative propagation of shoot (stolons, rhizomes) or root nature frequently form in flowering plants.

Epiterranean stolons are thin, short-lived (existing for one, more rarely two vegetation periods), mono- or sympodially growing plagiotropic shoots with elongated internodes. They serve no storage function. They regularly form early separating lateral rosette shoots and are typical for epiterranean-creeping herbaceous life forms. The stolons can bear green leaves *(Ajuga reptans, Ranunculus repens)* and along with the function of vegetative propagation take part in photosynthesis. They are quite often called **runners.** More highly specialized stolons possessing only scaled leaves (e.g., in *Fragaria vesca, Saxifraga flagellaris,* species of *Halerpestes)* are usually termed **flagella** or **sarments.**

High efficiency of vegetative propagation can also be reached by means of **subterranean stolons** specialized to different degree (with leaves of middle or lower formation) *(Trientalis europaea, Ranunculus lapponicus, R. lingua).* In stolon-tuberous *(Stachys palustris, Sagittaria sagittifolia, Circaea alpina, Ullucus tuberosus)* and stolon-bulbous forms *(Alliumangulosum, Gagea commutata, Liliumcanadense),* development of the root stolons ends with formation of terminal or lateral tubers or bulbs,

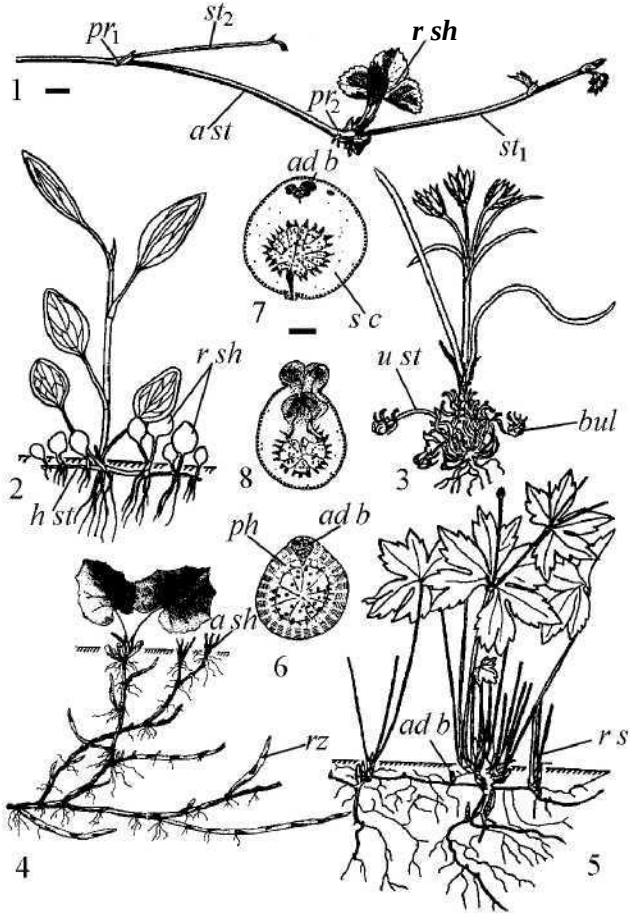


Fig. 45: Sarmentation.

1—branched sympodially growing above-ground stolon of *Fragaria vesca* with two prophylls, terminal short rosette shoot with two lateral branches; 2—adult vegetative individual of *Ranunculus lingua* with numerous axillary daughter rooting rosettes on underground stolons; 3—bulbils on short stolons in *Gagea commutata;* 4—repeatedly branching above-ground rhizomes of *Tussiligo farfara* forming above-ground shoots; 5—biennial plant of *Anemone dichotoma* with root shoots and adventive buds on roots; 6—bud initiated in phellogen of the main root of *Rubus idaeus;* 7, 8—different developmental stages of adventive buds on horizontal roots in *Rubus hirtus,* which primordia appear in the parenchyma of the wide secondary cortex; *adb*—adventive bud, *ash*—above-ground shoot, *a st*—above-ground stolon, *bul*—bulbil, *ph*—phellogen, pr_v pr_2—the first and second prophyll, *r sh*—rosette shoot, *r s*—root stock, *rz*—rhizome, s *c*—secondary cortex, s*12*, st_2—lateral stolons of the first and second order, *ust*—underground stolon. Scale: 1-5 = 10 mm, 6-8 = 1 mm.

1-after Troll, 1954; 2, 5-after Barykina, 1995; 3-after Ignatyeva and Andreeva, 1993; 4-after Korsmo, 1930; 6-8 -after Barykina, 1964.

respectively. Stolons appear in individuals of seed origin very early, in the first or second year (Golubev, 1961; Barykina and Pustovoytova, 1973); they are characterized by high speed of spread and comparatively rapid rates of development.

Long horizontal rhizomes morphologically close to stolons are mainly typical of herbaceous perennials *(Veronica longifolia, Convallaria majalis, Paris quadrifolia, Elytrigia repens, Carex pilosa)* but they are also found among geoxylous bushes *(Paeonia suffruticosa, Caragana frutex, Amygdalus nana)* and small shrubs *(Vaccinium vitis-idaea, Vaccinium myrtillus).* The ability to form clones along with degradation of the old parts of branching perennial rhizomes is also inherent in Equisetophyta and Pteridophyta). In this case, however, daughter individuals of rhizome life forms often do not experience significant rejuvenation and remain in the same age condition as the maternal plant at the time of separation.

Propagation by root suckers, i.e., above-ground, leaf-bearing, rooting shoots developing from adventive buds on the roots, is observed in many trees and bushes *(Robinia pseudo-acacia, Populus tremula, Alnus incana, Rubus idaeus, Cerasus fruticosa, Prunus spinosa).* Rootstock herbaceous perennials are quite frequent, many of them being pernicious weeds of fields, meadows, and kitchen gardens *(Convolvulus arvensis, Linaria vulgaris, Sonchus arvensis)* (Pachosky, 1915; Maltsev, 1937; Kott, 1961). Root sucker formation is particularly common among steppe and semi-desert (Kasakevich, 1922), tundra and silvitundra plants (Shitt, 1952).

Rauh (1937) distinguishes facultative, regenerative and obligatory root shoots. The first type appears only in conditions of improved nutrition and plant growth. The regenerative origin of root suckers is clear from the fact that they appear only as a result of root injury *(Trifolium montanum).* Obligatory root shoots are regularly formed during the individual development of the plant. For example, one-year plants of *Anemone dichotoma* and *Cirsium arvense* form numerous adventive buds developing into suckers first in the basal part of the main root and then on branch and adventive roots in acropetal succession. Individuals of 3-5 years form clones consisting of 30-40 rootstock particles.

Representatives of Pyrolaceae family *(Pyrola rotundifolia, Moneses uniflora, Orthilia secunda)* are of particular interest. Their reduced embryo lacks a shoot primordium; the seedling is formed as a unipolar structure because of weak spreading and branching of "radicle" (protosoma). Protosoma development ends before the inculcation of mycorrhizal fungus, after which a rhizome with reproductive shoots is formed out of it.

Study of different families (Beijerinck, 1886; Bűsgen, 1927; Ossenbeck, 1927; Krenke, 1928; Rauh, 1937; Barykina, 1954; Dore, 1955; Kondratieva-Melvil, 1957; Vasilevskaya, 1957) shows that root buds appear endogenously, often near the place where thin, suctorial, branch roots diverge from the maternal root. Various tissues still possessing meristematic activity or capable of dedifferentiation can take part in bud formation. These are pericycle *(Linaria vulgaris, Cirsium arvense, Elaeagnus argentea, Hippophäerhamnoides),* phellogen *(Rumex acetosella, Ulmus pennato-ramosa, U. campestris, Rubus idaeus),* interfascicular cambium and parenchyma of the bast part of primary and secondary pithy rays *(Heliotropium arguzioides, Slum latifolium, Rhus typhina, Prunus spinosa),* parenchyma of soft bast *(Malus silvestris),* and inner layers of secondary bark (of phelloderm origin) *(Robinia pseudo-acacia, Populus alba, Rubus hirtus).* Some preventitious buds can remain alive in the condition of dormant buds.

Adventive buds are more rarely found than preventitious buds and in a majority of cases differentiate in callus of injured roots *(Shepherdia argentea, Elaeagnus angustifolia, Ulmus laevis, Malus silvestris).*

Sarmentation, as one mode of vegetative propagation, often gives a species a leading position among plant groups and has great adaptive significance (in forest renewal, reconstruction of meadow grass cover, turf formation on moving sands and ravines).

Particulation (Latin *particula* — particle, part) is longitudinal cleavage, mainly of subterranean plant organs (caudex, vertical rhizome, main root, caulorrhizous tubers) into separate living parts (particles), which are able to develop independently after separation.

This phenomenon was described for the first time by Jost (1890), who observed longitudinal splitting of root and rhizome in *Aconitum lycoctonum, Gentiana cruciata* and other plants. The term was introduced by Vysotsky (1915), who studied vegetative propagation in herbaceous perennials from the Middle Russian plain.

Particulation occurs in the wild in many representatives of Ranunculaceae, Papaveraceae, Fabaceae, Crassulaceae, Apiaceae, Gentianaceae, Convolvulaceae, Plantaginaceae, Polygonaceae, Chenopodiaceae, Asteraceae and other families differing in ecology and life forms. Among them are taproot, racemose, bunchgrass, short rhizome and tuberous perennial herbs, semishrubs and subshrubs, small shrubs and shrubs with sympodially growing shoots, and cushion-shaped plants. It is especially common among plants of the steppe and prairies (Shalyt, 1950, 1965; Golubev, 1962), semideserts and hot deserts (Korovin, 1934; Rachkovskaya, 1957), and mountain semideserts and deserts (Raykova, 1930; Stanyukovich, 1949; Sabardina, 1951) and among some representatives of alpine flora (Daubenmire, 1941; Mikeladze, 1960; Barykina *et al*, 1991). Much more rarely it can be found in typical forest mesophytes.

Particulation can be complete and incomplete, obvious and latent. In most cases, the capacity for particulation is a species-specific feature. In evolutionary terms, particulation in flowering plants is a comparatively late phenomenon. More primitive taxa of higher plants apparently do not have it (Shalyt, 1965).

The biological meaning of particulation still remains questionable. Several points of view, sometimes opposing, are expressed (Basargin and Gorovoy, 1972). Some authors (Korsmo, 1930; Zakrzhevsky and Korovin, 1935; Troll, 1935; Novikov, 1943; Prokofyev *et al*, 1954; Chernyaeva, 1960; Lyubarsky, 1961; Voskanian, 1973; Barykina, 1995a) consider particulation accompanied by splitting of maternal plant into several daughter plants to be a special type of vegetative propagation (see Vegetative propagation). However, it is not accompanied by considerable expansion of the territory occupied by the species and as a rule does not involve noticeable rejuvenation of vegetative offspring. Although it does not play an essential role in self-maintenance of populations, particulation has adaptive significance. It prolongs the life of the clone and helps the species retain a territory (Golubev, 1962). This mode of propagation is the most effective in conditions with a mobile substrate. For taproot representatives of *Carum caucasicum, Taraxacum stevenii, Plantago saxatilis* and other alpine plants, particulation is the main mode of propagation because their seed propagation is much less effective than their vegetative propagation (Mikeladze, 1960).

Other researchers (Jost, 1890; Vysotsky, 1915; Nechaeva, 1949; Kozlova, 1953; Gordeeva, 1957; Kazaryan and Balagedyan, 1960; Shalyt, 1965; Poshkurlat, 1975), on the basis of morphological analysis of dwarf semishrubs and taproot and racemose root herbaceous mesophytes, interpret this phenomenon, which can be usually revealed only with plant transition to generative period of development, as one of the features of its slow dying off, i.e., they consider it to be purely an aging phenomenon without biological significance. It is senile disintegration of the plant.

Some botanists (Radkevich and Shubina, 1935; Vasilevskaya, 1950) connect particulation in xerophylous shrubs and desert subshrubs not with plant age but with exceptionally tough climatic conditions. These authors suppose that the sharper the contrasts between spring period of maximum precipitation and summer drought are, the earlier particulation starts in ontogenesis and the more intensively it proceeds. The influence of sharply continental climate on the process of particulation was also mentioned for some herbaceous plants. For example, some populations of *Taraxacum kok-sagyz* in Tien Shan spurs propagate vegetatively by disintegration into independent individuals (Kudryashova, 1958).

Rabotnov (1969a,b), identifying particulation with vegetative propagation, divides it into three types: **normal** particulation is propagation of plants by specialized, non-dispersed organs of vegetative propagation; **traumatic** particulation is formation of new individuals by separation (by humans or animals) of non-specialized organs of vegetative propagation from the maternal plant: **senile** particulation is disintegration of aging individuals into several independent plants (proper particulation). Many scientists agree with this classification (Levina, 1981; Zhmelev *et al.*, 1993, also see Serebryakova and Sokolova, 1988).

Particulation in different species in accordance with their life forms does not happen identically, as partly illustrated by Vysotsky (1915). It occupies a different place in the individual life cycle and has different structural basis caused by anatomo-morphological peculiarities of axial vegetative organs and their transformation in ontogenesis. Changes in microstructure of particulating plants were mentioned by many researchers starting from Jost (1890). Particulation in some herbaceous mesophytes and also sympodially growing desert shrubs, semishrubs and subshrubs begins with necrosis of some shoot and root tissues connected with natural seasonal die-off of shoots and their periodical renewal (Radkevich and Shubina, 1935). The process of die-off spreads along the branch scar down, moves from the shoot, caudex or rhizome to the root, creating structural precondition of its splitting. In this way, living tissues are separated from dead tissues by the layers of periderm. Particulation in this case is the plant reaction to the die-off of some epigeal organs independently of the nature of factors causing it (biological or ecological).

However, particulation is not always linked with branch scar die-off. For example, Vysotsky connected particulation in taproot semishrubs with uneven secondary thickening of root and rhizome. More detailed description of anatomical changes preceding longitudinal splitting of subterranean organs of plants from different ecological groups and life forms is given in a number of works (Pfeiffer, 1926; Rudenskaya, 1941; Bulgakov, 1944; Barykina *et al.*, 1976,1977; Mikhaylovskaya, 1976). Early activation of lateral meristems (in high-mountain plants in their second or third year of life), typical for herbaceous forms, is mentioned in them. In rhizome, particulation starts with isolation and accretion of vascular cambium arcs around the groups of xylem tracheal elements (one to three bundles next to each other) till they

completely or almost completely join into a circle. As a result, numerous centres of local secondary thickening appear.

Sometimes, for example in some species of *Taraxacum*, representatives of *Convolvulaceae* (De-Bari, 1880) with tuber-like thickened roots and tuberous species of *Aconitum* (Kumazawa, 1937), in the zone of hypertrophic root growth, groups of thin-walled parenchymal cells from the central part of the organ and also from primary *(Aconitum)* or secondary phloem *(Taraxacum)* become meristematic. They divide, forming areas of small-celled tissue differentiating in additional conductive bundles (amphicrybral, collateral or incomplete). In the cambial zone of some open bundles, primordia of lateral or adventive roots are initiated. On the surface of the outlined particles, phellogen forming phellem differentiates as a result of cell division in phloem and xylem parenchyma. An external feature of the atypical thickening is the slightly ribbed surface of the organ. Subsequent die-off and lysis of interfascicular parenchyma results in the separation of the particles (Fig. 46). High activity of lateral meristems (phellogen and cambium) causing particulation is apparently determined by the dynamics of physiologically active matter (Mikeladze, 1960); finding out the nature of this matter is the task for the future.

In the bundles of separated particles the work of cambium continues for two or more years (20-25 in *Anemone protracta* — Barykina, 1995a), which leads to increase and renewal of parenchymatized or mainly secondary phloem or xylem. According to Rudenskaya (1941) and Bulgakov (1944), in the root particles of *Taraxacum kok-sagyz* (appearing in consequence of atypical secondary thickening), formation of lacticifers intensifies, increasing rubber-bearing ability of the roots and the plant in general. Consequently, when particulation of subterranean organs starts at the early stages of ontogenesis and is accompanied by intensive preliminary formation of local plots of secondary thickening, it must apparently be regarded as one of the manifestations of adaptive specialization of the plant.

Bud (Latin eguivalent *gemma)* is a monopolar structure presented by a primordial shoot or a part of it. It consists of an axis with an apical cone (apex s.l.) and leaves of various ages that cover the axis and each other, and sometimes also with primordia of axillary buds, flowers and inflorescences. External (lower) leaves in the bud rise and bend over the apex due to irregular growth. This phenomenon of leaves in the bud is called **acrovergence.**[1] As a result of acrovergence, a dark wet chamber develops inside the bud where the apical meristem is disposed and first stages of shoot morphogenesis as well its initial growth take place. Thus, external coat of the bud protects the youngest and most vulnerable parts of primordial shoot from unfavourable external factors, primarily desiccation. Origination of buds in the process of evolution is considered an important aromorphosis that allowed angiosperms to cope with the whole diversity of conditions of life in the above-ground environment (Serebryakova, 1978b, c).

Buds ensure lengthening and branching of shoots. All this leads to an increase of the plant photosynthetic surface. The reproductive organs, flowers, are initiated inside the buds as well. The ability of buds to remain in the state of growth dormancy for a long time allows plants to endure unfavourable conditions (prolonged drought, cold winter). After termination of an unfavourable season, growth is recommenced, the buds explode and give rise to new shoots.

[1]Greek *akros*—upper, terminal and Latin *vergens*—reversed, directed.

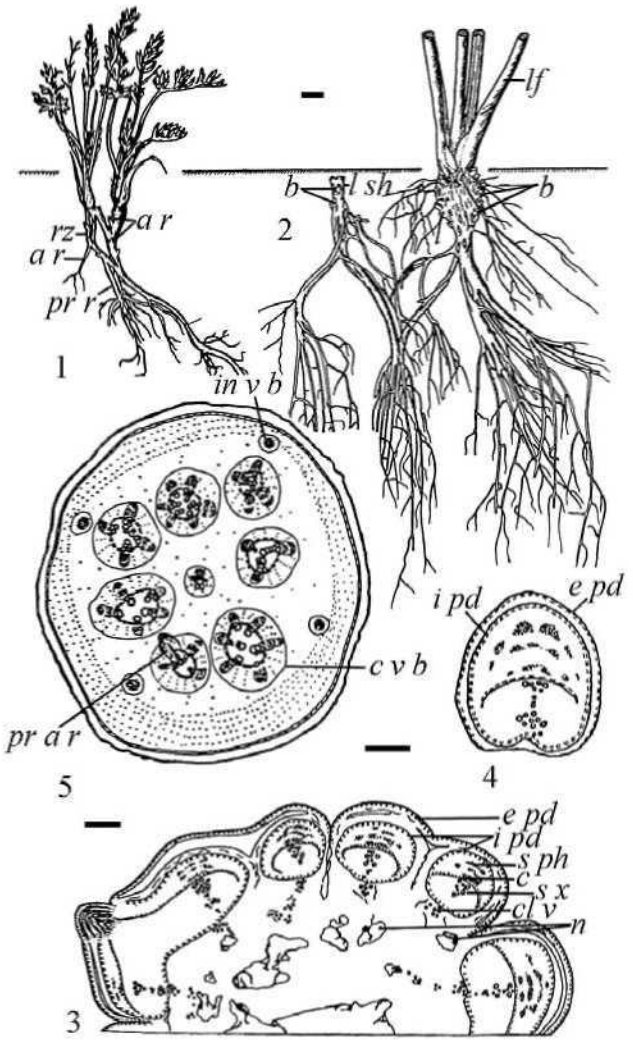


Fig. 46: Particulation (after Barykina, orig. data).

1—five-year-old immature plant of *Pulsatilla violacea* with particulating subterranean organs, 2-4—particulation in *Aconitum orientale:* 2—separating fragment of perennial particulating vertical rhizome with developed lateral shoot and dormant buds, 3—anatomical structure of particulating rhizome, 4—one-f ascicular particule separated from rhizome, 5—cross-section of one-year shoot-root tuber of *A. confertiflorum* possessing latent particulation and atypical thickening (3-5—schematic); *a r*—adventive root, *b*—bud, c—cambium, *cl v*—closed vessels, *c v b*—circular vascular bundle, *e pd*—external periderm, *in v b*—incomplete vascular bundle, *i* pd—internal periderm, *If—leaf, I sh*—lateral shoot, n—necrotic centres, *pr a r*—primordium of adventive root, *pr r*—primary root, *rz*—rhizome, *sph*—secondary phloem, s x-secondary xylem. Scale: 2—10 mm, 3-5—1 mm.

Buds may have storage functions as well; in that case they are modified often. An example of a highly metamorphosed bud is a head of cabbage. The storage function is clearly expressed also in winter buds of some water and riverside plants such as arrow-head, frog-bit and water-soldier. These winter buds are called **hibernacles.**[2] They serve for vegetative propagation, overwintering, and regeneration of plants. Sometimes buds are specialized as organs of vegetative propagation related to so-called viviparity, for example, brood buds of *Bryophyllum, Dentaria, Polygonum viviparum* (see Viviparity; Brood Bud).

The term "bud" is used in both broad and narrow senses. The broad sense includes both dormant buds and tips of growing shoots (Troll, 1937, 1954; Serebryakova, 1971; Halle *el ah,* 1978). In the narrow sense, only structures that are in the state of relative dormancy are called buds (Fedorov *et ah,* 1962; Romberger, 1963).

Buds are classified on the basis of various characters. According to the type of primordia, they are divided into **vegetative** buds that contain metameres of vegetative shoots, **generative** (floral) buds with primordia of flowers and inflorescences, and mixed **(vegetative-generative)** buds with primordia of reproductive and vegetative organs. A bud that contains the primordium of a single flower is called a button (Serebryakova, 1978c).

On the basis of the nature of protective structures, buds are divided into **covered** buds having specialized bud scales—leaves of basal formation, or cataphylls (e.g., in *Populus, Padus, Convallaria)* — and **open** (naked) buds having no bud scales. Open buds may be surrounded by primordia of photosynthetic leaves (e.g., in *Viburnum lantana, Myrtus communis),* by paraphylls of quite developed middle leaves *(Ficus elastica,* species of *Trifolium, Alchemilla),* by expanding green leaves (plantain, elodea and all growing tips of shoots). Thus, open buds are morphologically protected by various coats.

According to the position on the plant, **terminal, lateral** (axillary) and **adventive** buds are distinguished. Terminal buds develop on the tips of shoots, and axillary buds develop in leaf axils. Both are initiated in primary apical meristems. Sometimes (e.g., in linden), the shoot tip dies in the process of shoot growth, and it is replaced by ultimate upper axillary bud that becomes situated on the end of the shoot and is called end bud, or pseudoterminal bud.

Axillary buds are formed as meristematic protuberances exogenously by means of divisions of surface cells most commonly in the axils of third to fifth leaf primordia from the shoot tip. As a rule, a single axillary bud is initiated in the axil of a leaf; occasionally a few buds are initiated. In the latter case, **accessory buds** are formed having no cataphyllary leaves of their own. Accessory buds occur as a result of prolonged activity of the axillary meristems and may be situated vertically, one above another, or horizontally, side by side. Vertically situated buds are called **serial buds** (honeysuckle, blackberry), and horizontally situated ones are called **collateral buds** (garlic, *Ornithogalum caudatum).* Collateral buds are characteristic of plants having leaves with broad bases, primarily monocots.

In some plants, branching occurs inside the bud, i.e., daughter second-order buds develop from axillary primordia inside the first-order maternal bud, and grand-daughter third-order buds are formed inside these daughter buds. In that way,

[2] Latin *hibernaculum* — a winter lodging.

cluster buds develop, for example, in tubers of *Solatium tuberosum*, shoots of *Acer negundo*, species of *Prunus* and *Vitis* (Kostina, 1997). Cluster or branching buds differ from accessory buds in that every bud is in the axil of its own cataphyll. Daughter and grand-daughter buds may have the same degree and rate of development as those of the maternal bud or even more, as for instance in species of *Camellia* (Mikhalevskaja *et ah*, 1988) where flowers develop from the daughter buds while the maternal buds remain vegetative.

Adventive buds develop not from primary apical but secondary lateral and wound meristems or as a result of dedifferentiation of cells (more often parenchymatous) of the permanent tissues. In contrast to axillary buds, adventive buds are initiated both exogenously and endogenously (i.e., in the inner tissues) and develop on the stem internodes, leaves and roots. Adventive buds have the same structure and functions as the terminal and axillary ones. Moreover, they ensure **vegetative propagation** in the root-sucker plants (European aspen, *Sonchus arvensis*, sorrel dock) and **regeneration** of shoot systems in cases of breakage, cutting, mowing, etc.

According to duration of the growth dormancy and apparent growth periods, **regular renewal** buds (overwintering), **dormant** buds, and **permanently growing** buds are distinguished (Serebryakova, 1978b,c). Regular renewal buds are the terminal and axillary buds in a state of growth dormancy for not more than one year. In the temperate latitudes, after overwintering, these buds explode and give rise to new shoots (renewal).

Dormant buds persist in the dormant state for several years. According to their origin, they may be axillary, accessory and even terminal buds (in *Pittosporum* — Mikhalevskaja, unpublished data). In the dormant bud, the apical cone produces yearly primordia of a few shoot metameres, and some of the external scales die. As a result, the bud axis gives yearly an increment of 1-2 mm (sometimes more) that is usually equivalent to the thickness of annual ring of the xylem. Dormant buds ramify often and make clusters on the surface of stems, branches and roots. Dormant buds arise in case of plant injury and ensure renewal (regeneration) of the shoot systems, for instance, formation of the stump sprouts (Serebryakov, 1952; Lyashenko, 1964; Kozlowski, 1971) and secondary crowns (Smirnova, 1994).

Permanently growing buds are the open terminal buds of certain tropical plants *(Tradescantia, Zebrina, Lodoicea maldivica,* etc.) as well as some temperate herbaceous perennials with monopodial growth *(Plantago, Veronica nemorosa, Geum, Oxalis)* having a forced winter growth stoppage. In the permanently growing buds, leaves are usually initiated and expand in concord, so that the number of leaf primordia remains constant; for example, it is always three in *Tradescantia* (Serebryakova, 1978c).

Bud morphogenesis includes several stages. Usually, four stages are distinguished: bud initial, bud primordium, immature bud, and mature bud. The **bud initial** (Shilova, 1967) is a smooth meristematic protuberance developing as a result of anticlinal and periclinal divisions of superficial cells of a meristem. In the **bud primordium,** first metameres of a shoot (i.e., leaf protuberances and nodes of the future stem) are initiated. At this stage histogenesis is not observed yet, and procambial bands are not visible (Hagemann, 1984). An **immature bud** includes metameres of different ages but is unable to explode and form a shoot because of its small capacity. **Bud capacity** refers to a number of metameres initiated in the bud (Serebryakova, 1971). In immature buds, acrovergence is just well expressed, and

histogenesis begins: primary tissues and procambial bands are differentiated. **Mature buds** have the maximum capacity. All bud scales are just formed there (when it is a covered bud) and in many cases all the metameres of the future shoot are just initiated. Mature buds usually switch over to active growth (Serebryakova, 1959, 1961,1971).

Thus, buds are in constant flux in terms of their capacity and structure. Even if a bud is in the state of so-called growth dormancy, there may be growth inside the bud, i.e., initiation of new metameres and reproductive organs. The inside-bud growth runs at a steady pace because formation of every new metamere diminishes volume of the apex, and some time is required to recover it. The period of time between formation of two successive metameres on the apex is called a **plastochron** (Askenasy, 1880). Duration of plastochrons in different species, in the same species in different conditions, and even in the same shoot in different periods of its life is unequal. For example, in the period of active shoot growth during spring and summer, the value of plastochron in hazelnut, birch and oak is 2-3 days and in maple 12 days, but in spruce it is only 4-5 hours (Serebryakova, 1978b).

The inside-bud growth of shoots has multi-stage rhythms that are expressed not only in plastochrons but also in growth periods and growth beats. **Growth period** is a time of initiation of a portion of metameres that corresponds to one or several cycles and is equal to the denominator in the leaf arrangement formula. When the formula is 1/3, the cycle includes three primordia, when it is 2/5 there are five primordia, and when it is 3/8 there are eight. **Growth beat** is a temporal interval between initiation of repeated leaves of different cycles (i.e., leaves lying on the same orthostichy). The single-beat periods are distinguished when a single cycle of metameres is initiated; in two-, three- and many-beat periods, metameres of two or more cycles respectively are formed (Shilova, 1988). The inside-bud growth of shoots and the apparent growth often run asynchronously and differ in both number and duration of periods and beats (Shilova, 1967,1974,1984,1988). For instance, in the majority of tundra plants, inside-bud growth is much more prolonged than apparent growth (respectively, 6-8 and 2-4 weeks) and is often composed from several periods, while apparent growth includes only one period. Temporal and structural organization of inside-bud growth is an important form of plant adaptation to environmental factors.

The structure and capacity of buds change with shoot development and its switching over from the vegetative to the generative phase. Monocarpic (single-fruiting) shoot begins its development from an **initial** bud, which is as a rule an axillary vegetative bud. An **intermediate** bud is situated on the top of a monocarpic shoot in the course of its vegetative growth. In plants with polycyclic shoots, for example, in shinleafs, this bud may remain vegetative for several years. When monocarpic shoot passes to flowering, a **final** terminal bud is formed (a generative bud as in shinleafs, or a vegetative-generative as in some grasses such as *Deschampsia caespitosa, Festuca ovina).* The initial bud in plants with monocyclic shoots *(Asarum, Corydalis, Orchis)* may be the final one simultaneously when it contains all parts of the shoot including flowers and inflorescences (Serebryakova, 1983).

Leaf primordia are initiated in buds in the form of meristematic protuberances that grow at first evenly in all directions and then in height. In monocots, leaf primordia have the appearance of falculate crests that grow in width, subsequently enveloping the whole circumference of the apical cone. The primordia are divided into lower and upper parts just at the early phases. The lower part forms the base of a

leaf (a leaf sheath in monocots) and paraphylls, the upper part forms the leaf blade and petiole. The paraphylls arise very early as lateral outgrowths of the base and quickly increase their sizes by means of lateral growth (Serebryakov, 1952). In the bud, the paraphylls are often larger than initial leaf blades and give them additional protection. At first, the leaf blades are formed by growth of the general vein and basal lateral veins in length but this growth soon ceases, and subsequent formation of leaf blade is due to marginal growth; in monocots it is due to intercalary growth that continues through the post-bud phase (Serebryakova, 1978c). The form of packing of leaf blades in the bud is called **vernation.** The relative position of leaves to one another in the bud is called **aestivation** (bud leaf connexion).

The bud scales of closed buds are of different morphological nature in different plants. They may be the bases of leaves (lily-of-the-valley, Solomon's seal), paraphylls *(Corylus, Quercus, Fagus),* or whole leaves *(Daphne, Vaccinium myrtillus).* The buds situated in the axils of bud scales are called **scale axillary buds.**

According to the extent of shoot formation in the bud, Serebryakov (1947,1952) distinguished three plant groups: (1) the whole shoot is initiated, including flowers and inflorescences *(Anemone, Corydalis, Ficaria verna);* (2) only vegetative part of a shoot is initiated but flowers and inflorescences are formed during the post-bud developmental phase *(Tilia, Geum, Veronica nemorosa);* (3) only a part of vegetative shoot is initiated *(Chamerion angustifolium, Solidago virgaurea, Angelica sylvestris).* Later on, the first variant of shoot development was named "preformation", and an additional initiation of metameres during the post-bud developmental phase was named "neoformation" (Halle *et al.,* 1978). The preformed buds were detected to initiate not only all the metameres of the future shoot but also a part of bud scales of the future terminal bud. In the case of neoformation, the long shoots (for instance, in poplar) have morphologically different early leaves developed from preformed primordia and late leaves arisen from neoformed primordia (Critchfield, 1960,1970, 1971; Kozlowski, 1971; Macdonald *et al.,* 1984).

A plant bears diverse buds that differ in morphogenetic phases, position, size, structure and function. This is the basis of high plasticity of plant shoot development and allows optimal adaptation to the environment by changing size and shape of shoot systems. One of the most popular classifications of plant life forms, the system of Raunkier (1934), uses the position of resting buds in relation to the soil surface as the main criterion.

Brood Bud is the specialized organ of vegetative propagation and dispersal of flowering plants **(Plate X).** In the process of brood bud development, its bipolarity is established (adventive roots are laid down) and a new individual is formed.

Originally, the term "brood bud" was applied to the identification of uni- and multicellular formations providing vegetative propagation in thallophytes (algae, liverworts) (Goebel, 1908; Buch, 1911; Schuster, 1969). The structures fulfilling this function are also typical of the higher sporiferous plants (mosses, horsetails, club-mosses, ferns) and of some flowering plants (Kerner, 1896, 1898; Levina, 1961; Vassilyev *et ah,* 1978; Schuster, 1984). The notion of "brood bud" in flowering plants belongs to a broader notion of "propagule",[3] which is the general term for indicating organs and parts used for vegetative propagation (Kirpichnikov and Zabinkova,

[3]Propagule, from Latin *propago* - offset, descendant.

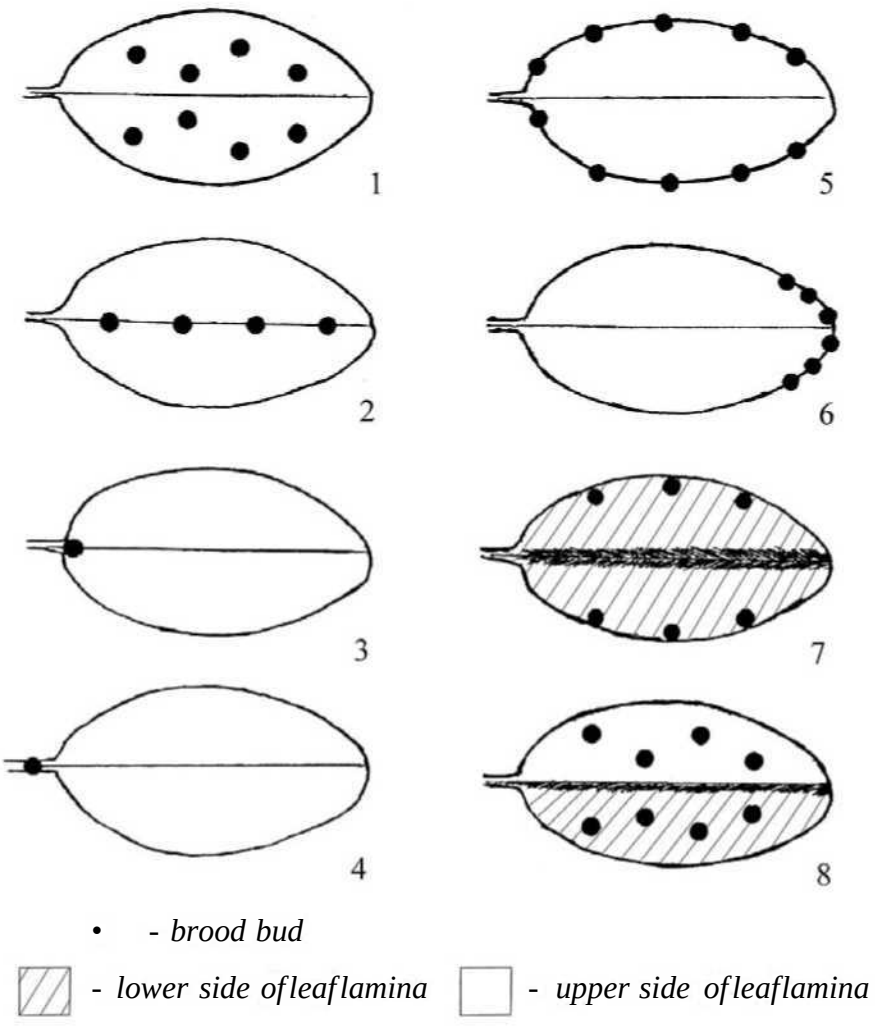


Fig. 47. Arrangement of brood buds on the leaf (after Bragina, orig. data).
1—all over the surface of the upper leaf lamina *(Arabis pumila, Drosera intermedia, D. rotundifolia,), 2* — along the main nerve of leaf lamina *(Hyadnthus pouzolsii),* 3 — in the base of leaf lamina *(Cardamine mathioli, C. pratensis, Nymphaea guineensis, N. micrantha, Pinellia tuberifera),* 4—on leaf petiole *(Pinellia tuberifera),* 5—through the margin of leaf lamina *(Bryophyllum daigremontianum, B. pinnata),* 6—through the margin of apical part of leaf lamina *(Bryophyllum tubiflora, Hammarbya paludosa),* 7—on the lower side of leaf lamina, on a short distance from the margin *(Ceraptopteris thalictroides),* 8—all over the surface of the upper and lower sides of leaf lamina *(Ornithogalum salloides).*

1977). Brood buds may be of different structure: non-metamorphosed axillary or adventive buds with adventive root, bulblets and tubercles (Vassilyev *et al.*, 1978) (see Bud; Bulblet and Bulbil).

Brood buds arise on a plant in large number and then fall from it like seeds and spores; the resemblance is greater in that the plants formed from the shedding buds are considerably rejuvenated and look like seedlings or young gametophyte.

Brood buds are called **leaf, stem and root brood buds** depending on where on the plant they arise. The location of initiation and structure of brood buds are taxon specific (Kerner, 1898; McVeigh, 1937; Kultiasov, 1953; Zhukovsky, 1964; Schuster, 1969; Haccius and Lakshmanan, 1969; Haccius and Hausner, 1975; Longton and Schuster, 1983).

Among flowering plants, 446 species are known to be able to form buds of different types on leaves (Haccius and Hausner, 1975). In some species these buds are believed to be brood buds (Fig. 47). **Leaf brood buds** arise from leaf cells, usually in the region of veins. In many cases the separation of leaf from stem is the necessary condition for bud development. Brood buds on leaves were described in Amaryllidaceae *(Curculigo)*, Araceae *(Atherurus ternatus)*, Brassicaceae *(Arabis pumila, Brassica oleracea, Cardamine pratensis, C. silvatica, C. uliginosa, Nasturtium officinale, Rorippa palustris)*, Crassulaceae *(Echeveria, Rochea falcata)*, Droseraceae *(Drosera anglica)*, Gesneriaceae *(Chirita scinensis, Episcia bicolor)*, Liliaceae *(Allium, Fritillaria, Gagea sinensis, Hyadnthus, Ornithogalum)*, Nymphaeaceae *(Nymphaea guianensis)*, Papaveraceae *(Chelidonium majus)*, Pinguiculaceae *(Pinguicula backeri)* and others (Kerner, 1898; Goebel, 1908; Sinnott, 1960). Morphogenesis in the species mentioned was fragmentally investigated.

Among orchids the development of leaf brood buds is noted only in *Hammarbya paludosa* (Dickie, 1875; Kerner, 1898; Gustafsson, 1946; Summerhayes, 1951; Taylor, 1967; Bragina *et al.*, 1996; Batygina and Bragina, 1997). Brood bud in this species is formed exogenously, owing to proliferation of cells in the upper leaf or bract epidermis. The brood bud consists of the leaf enveloping the inner part of the propagule, which has a shoot apex with primordia of three leaves. The adventive root is laid down after the brood bud separates (Batygina and Bragina, 1997; see Viviparity).

The formation of brood buds on the leaf margin and in its axil is characteristic of the species of *Bryophyllum* genus (see Viviparity). Some authors considered these structures the adventive buds (Levina, 1961; Vassilyev *et al*, 1978). However, detailed investigations of their morphogenesis revealed that brood buds differ in origin and differentiation: non-metamorphosed bud, in which the adventive roots develop (B. *crenatum)*, and embryoid (B. *pinnatum)* (Yarbrough, 1932,1934; Batygina, 1989a,b,c, 1990; Batygina *et al.*, 1996; see Embryoidogeny). In B. *daigremontianum*, the brood bud appears to be the transitional form between non-metamorphosed bud and embryoid. Brood buds are formed at the definite stage of maternal leaf development from cell groups (Berger, 1877; Yarbrough, 1932,1934; Batygina, 1989a,b,c, 1990). These cell groups ("dormant meristem") are derivatives of marginal leaf meristem and retain the capacity for further development for a long time. The cells produced are referred to as stem cells (Batygina *et al.*, 2004).

Kerner (1898) noted the interesting fact of buds appearing on the carpels in *Crinum* and *Amaryllis*. When they got into damp soil, new plants developed from them.

Stem brood buds[4] are produced on the hypocotyl *(Anagallis phoenicea, Euphorbia peplus, E. helioscopia, Linaria vulgaris),* in leaf axiles *(Dentaria, Lilium, Ranunculus ficaria)* or on the inflorescence *(Allium, Poa, Polygonum viviparum, Titanotrichum oldhami)* (Fig. 48). In P. *viviparum,* the brood buds (tubercles) are formed in the axiles of inflorescence bract leaves. The basic mass of the brood bud is formed by the basal internode or hypopodium and is partly due to the thickening of upper internode axis. The terminal tubercle bud and after it the lateral axile buds begin opening even on the maternal plant, forming a rosette of two or three green leaves. In such condition the tubercles fall on the ground and take root, producing new plants (Serebryakov, 1952).

There are data on the production of brood buds (bulblets) in the panicle of viviparous and semiviviparous forms of *Poa bulbosa* (Popolina, 1960,1962a,b; see Viviparity). Bulblet formed consists of shoot apex, surrounded by young leaves, shortened stem (collum), primordia of adventive roots, leaf-like formations (five to seven) developing instead of flower parts, and spikelet scales. In the beginning of

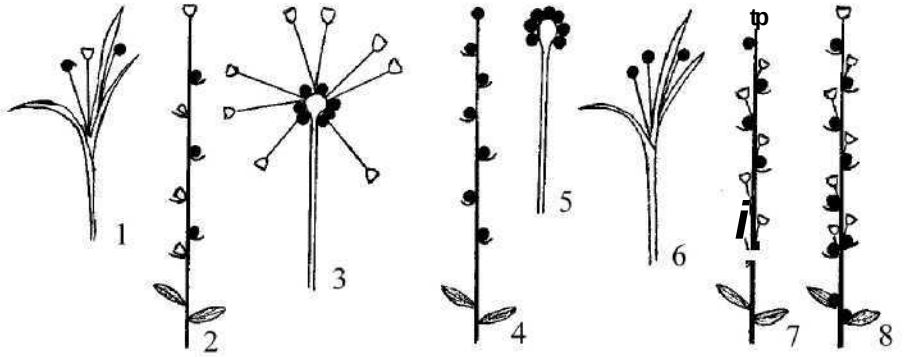


Fig. 48: Brood buds on inflorescence (after Bragina, orig. data).

1—brood buds in the lower part of inflorescence *(Gagea arvensis),* 2, 3—throughout the inflorescence, alternating with the flowers in *Polygonum viviparum* (2), *Allium senescens, A. oleraceum* (3), 4-6—the inflorescence has only brood buds in *Polygonum viviparum* (4), *Allium vineale* (5), *Gagea liotardi* (6), 7—brood buds throughout the inflorescence in bract axiles together with flowers in *Dentaria bulbifera, Gagea bulbifera, Lilium bulbiferum, L. landfolium, L. tigrinum, Saxifraga bulbifera, S. cernua, Sparaxis bulbifera,* 8—brood buds throughout the inflorescence in bract axiles together with flowers and in leaf axiles in *Dentaria bulbifera, D. triphylla, Dioscorea batatas.*

[4]The brood buds of ferns originate from the stem as the frond represents the phylloclade (Kerner, 1898). Among 140 species of ferns capable of bud formation on fronds, there are species in which they appear constantly *(Asplenium celtidifolium, A. flagelliferum, A. bulbiferum, A. viviparum)* (McVeigh, 1937). Brood buds form in different parts of the frond: on the surface of green frond lobes (in the species mentioned), on petioles of certain frond lobes *(Ceratopteris thalictroides),* in the frond fork *(Gleichenia alpina)* or on the top of the frond (A. *cirrhatum, A. flagellifolium, A. rhachirhizon, A. adgeworthii).*

brood bud development, spikelet scale primordia are formed and then acropetal initiation of the primordia of leaf-like formations is observed. Spikelet scales and the first pair of leaf-like formations fulfil assimilative and protective functions in the period of panicle throw out. The second and third pairs of leaves have the lamina, fulfilling assimilative function, and the sheath, in the tissues of which nutrients accumulate (starch grains and hemicellulose). In the sheath part of the leaf the mechanical tissue is considerably developed. In epidermal, subepidermal and parenchymal cells of sheath, the anthocyan, used for bulblet protection in the period of dormancy, is accumulated.

Adventive roots form on the bulblet axils. Root primordia penetrate the parenchymal tissue of the scales and remain there till germination. Thus, the bulblet has all the organs required for the normal development of a plant. Sometimes, in the axils of certain lower scales in the bulblet, the daughter bud is formed, consisting of three or four leaves (Popolina, 1960,1962a). The matured bulblet separates from the maternal plant and germinates when it lands on soil under particular conditions (low temperature and sufficient moisture), giving rise to an independent plant. The roots appear first and then the leaves appear.

The unique morphogenesis of the brood bud formed on the inflorescence was described in *Titanotrichum oldhamii* (Gesneriaceae) (Wang and Cronk, 2003). The flower meristem of T. *oldhamii* is able to produce the flower, brood buds (bulblets) or numerous bracts only. The flower primordium separates two bracteole primordia and three additional meristems. From these meristems and from new meristems arising in bracteole axils, numerous bulblets develop. In the form having brood buds, one floral primordium, which usually produces one flower, gives nearly 50-70 brood buds owing to repeated subdivision of the meristem. The formation of brood buds increases in the end of the flowering period, which lasts from July till the end of September. The brood bud consists of the small part of the stem (bract stem), covered with two bracts, that comprises the apical meristem. The adventive root develops from the side of the bract stem. The rate and percentage of germination of bulblets (95%) is shown to be higher than that of seeds (75%).

Brood buds (hibernacles) in *Sagittaria, Stratiotes* and *Hydrocharis* originate from the stem. They peel off rotted maternal plants in autumn, pass the winter in silt, and in spring give new plants (Vassilyev *el ah*, 1978; see Bud; Reproductive strategy in Ceratophyllaceae).

The examples given above testify to the polymorphism of brood buds (Fig. 49). Brood buds also differ by the character of interaction with the maternal plant and by the occurrence of dormancy period. Brood buds germinating on the maternal plant are considered one of the structural units in viviparity (see Viviparity).

In order to determine the morphogenesis pathway (gemmorhizogenesis or embryoidogenesis) for brood bud, it is reasonable to compare it with "the typical" bud and with the somatic embryo (embryoid). "The typical" bud is the specialized part of the plant that develops into the new organ. Depending on the location, there are **terminal** and **lateral (axile and adventive)** buds. The axile buds regularly arise exogenously, in the form of meristematic protuberances in the axils of young leaf primordia, near the top of the maternal shoot. The meristem of axile bud is derived generally from the apical meristem of the main shoot. The arrangement of axile buds directly corresponds to the leaf arrangement (Esau, 1977; see Bud).

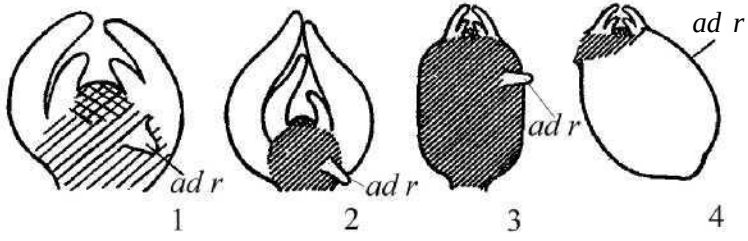


Fig. 49: Types of brood buds (after Vassilyev *et ah,* 1978).
1—non-metamorphosed axillary or adventive bud with adventive root, 2—bulblet, 3—tubercle of stem derivation, 4—tubercle of root derivation; *ad r*—adventive root, the shoot axis is shown shaded and the shoot apex chequered.

The lateral buds, which arise from more or less mature tissues owing to without apical meristem, are considered to be adventive ones (Priestley and Swingle, 1929; MacDaniels, 1953; Haccius and Lakshmanan, 1969; Haccius and Hausner, 1975). According to the origin, they may be exogenous or endogenous (Priestley and Swingle, 1929; Thompson and McLean, 1943-1944). Frequently, adventive buds show no regularity in their arrangement (Vassilyev *et al.,* 1978).

The resemblance between the brood bud and the "typical" bud lies in their origin, location on plant and structure (occurrence of shoot apex). **The differences between them** concern **the level of organization** and **the functions.** The brood bud is an individual with a bipolar structure, with shoot and root apices, but the typical bud is part of an organism and has monopolar structure, with the shoot apex only. The brood bud provides vegetative propagation of a plant, while the typical bud usually serves for vegetative renewal of a plant and the formation of reproductive structures.

The morphogenesis of embryoids forming under natural conditions is known to vary greatly (Batygina and Zakharova, 1997; Batygina, 1998,1999a,b. Polymorphism of sexual and somatic embryos as manifestation of their developmental parallelism under natural conditions and in tissue culture; see Vol. 2).

In origin, location, structure and functions, the brood bud manifests a great resemblance with the embryoid developing on vegetative organs. However, there are certain differences between them **concerning morphogenesis pathways** (the development of brood bud proceeds according to gemmorhizogenesis pathway with the lack of stages typical to the embryoid, i.e., globular, heart-shaped and torpedo-shaped) and **the time of initial arising of the adventive root.**

Variable character of brood bud organization is explained to a considerable extent by the species ecology and by the mode of laying down of brood bud initials (endogenous or exogenous).

A high rate of rejuvenation, which is observed also in axile shoots to a considerably lesser extent, is considered to be the species (or genus) feature for plants producing brood buds. Aging in such plants is also greatly slowed, hi this sense, the brood buds have something in common with the embryos of seeds in a number of physiological processes (Krenke, 1950).

Vegetative propagation by means of brood buds allows plants to quickly conquer local territories. Different agents successfully spread brood buds as well as

seeds over long distances (see Diaspore). The brood bud gives rise to a well-developed plant able to root immediately, which is especially important in regions in which the period favourable for propagation is rather short.

The capacity of most plants to produce brood buds is widely used in agriculture to obtain rejuvenated progeny (Kerner, 1896, 1898; Pravdin, 1938; Krenke, 1950; Lyubarsky, 1960; Shalyt, 1960; Haccius and Hausner, 1975).

Bulb (Latin equivalent *bulbus)* is a metamorphosed shoot (or its part) consisting of the short axis (the plate), storage leaf organs (scales) and buds **(Plate XI).** The roots are formed in the plate tissue. The bulb is the constant and perennial organ of vegetative renewal and propagation.

The bulb is the result of adaptation to unfavourable conditions, mainly to very hot and dry summer and cold winter. Bulbous plants generally inhabit the mountainous, desert, and semi-desert regions. Water and nutrient storage in the bulb keep the plant relatively independent of environmental factors.

There are 3,000 species of bulbous plants in the world. They belong to the monocot families, such as Liliaceae, Hyacinthaceae, Melanthiaceae, Calochortaceae, Amaryllidaceae, Iridaceae, Alliaceae.

The bulb consists of the short shoot or short part of the shoot, depending on the structure of the monocarpic (single-fruiting) shoot. The bulb of a plant with rosetted shoot comprises a short shoot, but the leafless scape of the shoot dies off after fruiting. Bulbs of plants with semi-rosetted and non-rosetted monocarpic shoots comprise only the short part of the shoot, but the leaf-bearing part of the shoot dies off after vegetation is completed (Fig. 50).

Bulbs are classified on the basis of duration of bulbous renewal, type of branching of the shoot, direction of growth of the shoot axis, and form, number and function of the bulbous scales.

Bulbous renewal can occur yearly (annual bulbs) or for some years (perennial bulbs). Annual bulbs are represented by only one shoot (or the short part of the monocarpic shoot), in other words, by the shoot of one year *(Tulipa, Allium, Calochortus).* Perennial bulbs are represented by a few short monocarpic shoots (from two to eight) or their short parts of some successive generations. Such perennial bulbs represent the shoot system *(Amaryllis, Lilium, Veltheimia).*

The duration of the renewal of perennial bulbs is determined by the number of short shoots in the bulb. The new shoot is annually formed from the renewal bud in the bulb and the outermost bulbous scales and part of the plate die annually too. The result is that the number of shoots in the mature bulb is kept constant.

Die-off of the scales and the plate occurs simultaneously, as a rule. But sometimes the scale die-off outstrips the plate die-off, and the naked plate (without scales) acquires the appearance of a rhizome. Such a rhizome can exist for some years with a living root system and axillary and adventive buds. This is the original biomorph "bulb on the rhizome". Such a rhizome is the complex of the plates of past generations *(Allium, Lloydia, Drimiopsis).* The **monopodial** bulbs form the new shoot from the terminal bud. In this case the terminal bud remains vegetative constantly but the flowering stem is formed from the axillary bud *(Narcissus, Leucojum, Galanthus).* **Sympodial** bulbs form the new shoot from the axillary bud, but the flowering stem is developed from the terminal bud *(Lilium, Erythronium, Fritillaria).* Perennial bulbs are the monopodial or the sympodial joined system of the shoots (or the parts of the shoots) of successive generations.

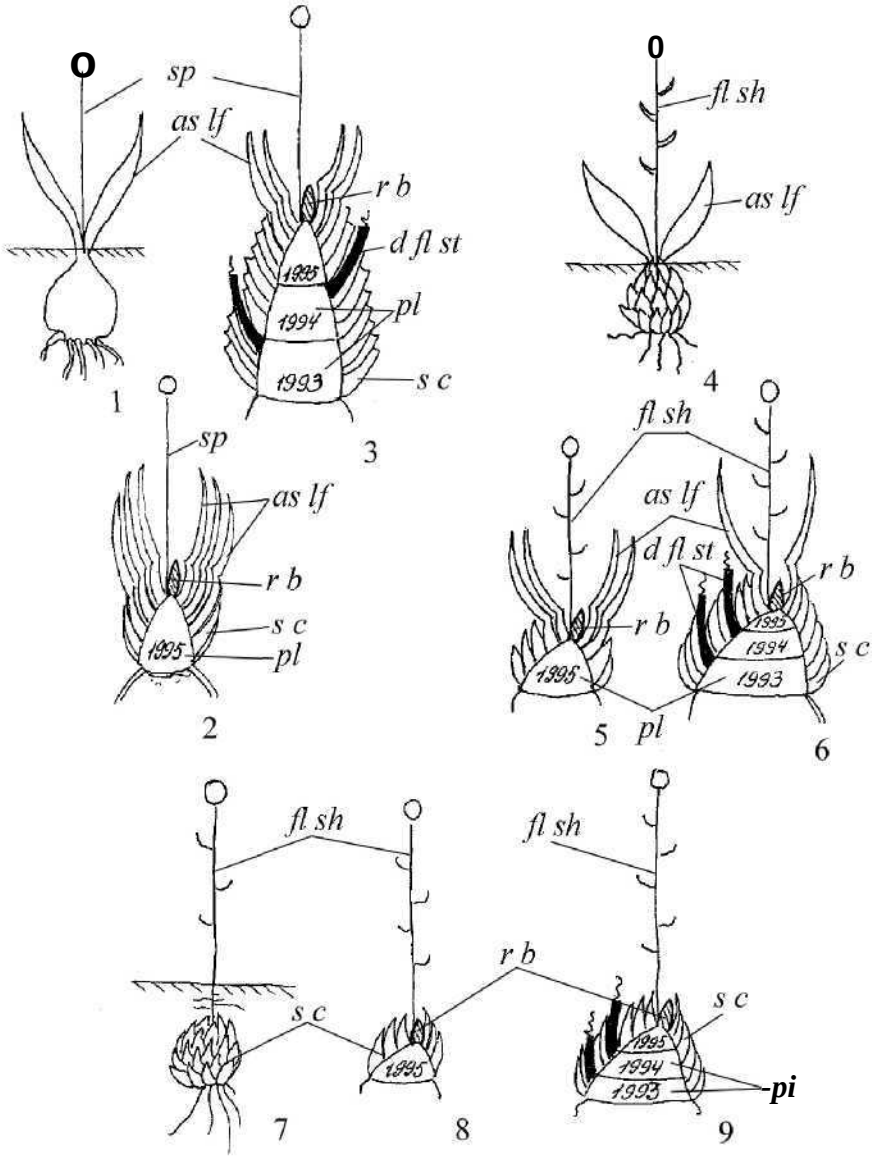


Fig. 50: Types of shoots in bulbous plants (after Baranova, orig. data).
1-9—rosetted (1-3), semirosetted (4-6) and unrosetted (7-9) types: 1,4, 7—a general view, 2, 5, 8 — structure of the annual bulb (yearly renewal), 3, 6, 9 — structure of the perennial bulb; *as* //—assimilative leaves, *A fl st* — dry flowering stem of the past year, *fl sh* — flowering part of the shoot, *pi* — plate, *rb* — renewal bud, *s c* — swollen cataphyll (scales), sp—scape.

There are **symmetrical** (equal-sided bulbs) and **asymmetrical** bulbs (slant bulbs). The direction of growth of the shoot axis defines the bulbous form (Baranova, 1981). Equal-sided bulbs *(Hyacinthus, Muscari, Eucomis)* are developed in the orthotropous direction of the axial growth, but slant bulbs *(Tulipa, Erythronium, Gaged)* are formed in the plagiotropous or the slant-orthotropous direction of the axial growth.

The bulbous scales are the modified leaves. They are distinguished by form, morphological peculiarities, life duration, and functions.

Bulbs are composed of three different types of scales: **imbricate, semitunicate** and **tunicate** (Fedorov *et ah,* 1962). The bulbs are named after the type of scales. Imbricate bulbs have narrow lanceolate scales: the edges of the scales do not touch each other *(Lilium, Nomocharis, Schizobasis).* Semitunicate bulbs are composed of wide scales, enveloping half or one-third of the circumference of the bulb. Tunicate bulbs have scales with united edges or scales united in the radial direction *(Tulipa, Brimeura, Erythronium).*

Scales can have different morphological structures: green leaf sheaths, cataphylls, sheathed scales, and special covering scales. Most plants have bulbs with different types of scales. However, the bulbs of some plants are composed exclusively of one type of scale: the bases of green leaves *(Ornithogalum caudatum, Albuca angolensis),* or cataphylls *(Lilium, Fritillaria, Nomocharis).* The green leaves of these plants are arranged on the flowering stem.

A particular number of bulbous scales are formed annually in the renewal bud (from 1 to 25). As already noted, bulbs of various plants are composed of one to eight short shoots of successive generations. So the number of scales in the bulb can reach 150 and more. Usually, the number of scales determines the size of the bulb. The biggest bulbs reach 20-30 cm in diameter and 3 kg in weight *(Urginea maritima, Bowiea volubilis, Lilium kesselringianum)* and the smallest bulbs (one-scaled bulbs) are 0.8 cm in diameter *(Litanthus, Gagea).* However, such dependence is not uniformly seen.

Bulbous scales are organs of **storage** and **protection.** The swollen bases of green leaves or cataphylls (special leaves without green plates) carry out the general storage function.

The covering and sheathed scales carry out the function of protection. Specialized covering scales are found very seldom in bulbous plants *(Tulipa, Notholirion).* Usually, the old, dry, outermost scales defend the bulb. Very delicate sheathed scales surround the young leaves near the bases, defending them from damage. Sheathed scales never become storage scales. They die right after they carry out their function.

Axillary buds (the future bulbils or organs of vegetative propagation) are developed in the axils of the bulbous scales. In some plants, axillary buds are initiated in the axils of the upper scales, near the renewal bud. The development and growth of the axillary and renewal buds are simultaneous in this case, and two or three equal bulbs are formed on the common plate as a result. Examples are species of *Zigadenus, Ledebouria, Barnardia* and some varieties of *Hyacinthus.* Such "pair-bulbs" are often among species of *Allium.* Most bulbous plants form buds in the axils of the outermost scales. Sometimes 10 and more buds are laid in the axil of one scale. They are arranged collaterally. Such axillary buds form the bulbils. Later, the bulbils are separated from the mother bulb and survive independently *(Ornithogalum umbellatum, Notholirion thomsonianum, Chionodoxa luciliae).* Sometimes the bulbils are developed on the stolons outside the mother bulb.

Some plants can develop **adventive buds** *(Fritillaria, Erythronium, Brimeura)* on the scales and on the leaves. They are formed from the secondary or wounding meristem. Such buds are very weak and die immediately. However, they can be used for microclonal propagation *in vitro.*

The determination of the life span of the bulb and the whole bulbous plant is an important biological problem. As already noted, the bulb is regularly renewed over 1 to 8 years, depending on the species. But the renewal of the bulb and the life span of the bulbous plant are different notions. The process of bulb renewal can be repeated many times during the plant life. This indicates that the bulbous plant can live for decades. There are known 50-year-old individuals of *Lilium martagon* and *Scilla sibirica,* 45-year-old individuals of *Tulipa borszowii,* and 30-year-old individuals of *Muscari neglectum* and *Gagea lutea* (Zalivskyi, 1955; Bochantseva, 1956; Golovkin, 1973). On the other hand, there are bulbous plants *(Lilium pumilum, L. buschianum, L. callosum)* that live no more than 4-5 years.

The bulb structure is constant for the species and can be used as the diagnostic sign. At the same time, one kind of bulb structure can characterize large taxonomic groups such as genera, subgenera and sections *(Fritillaria, Gagea, Ornithogalum, Allium).*

Most bulbous plants can regenerate from scales, leaves, and flowering stems. This peculiarity of bulbous plants is widely used in floriculture.

Bulblet and **bulbil** are modified buds comprising the swollen cataphylls (scales), the primordial green leaves and the short axis (plate) with the adventive roots; they are the special organs of vegetative propagation (Fig. 51). Such modified buds vary in structure and site of formation: buds on the above-ground part of the shoot are named bulblets and buds on the underground part of the shoot are defined as bulbils.

Bulblets are formed in the axils of green leaves *{Lilium lancifolium, L. bulbiferum, Gagea lutea, Calochortus luteus, Nomocharis mairei, Tulipa praestans, T. kaufmanniana)* or in the zone of the inflorescence when the flower formation is broken *(Allium caesium, Gagea minima, Lilium regale, L. bulbiferum).* Sometimes they develop from the adventive buds on the stem or on the leaves. Such buds are formed from the secondary lateral or wounded meristem *(Brimeura amethystina, Scilla leidieni, Fritillaria latifolia).* Bulblets may be green, brown or dark brown and consist of two to five swollen cataphylls. They are 0.5-1.5 cm in diameter. Bulblets of most plants have a prolonged dormant period that can last for some years. In some plants they have no dormancy and germinate on the mother plant right after formation (e.g., *Tulipa subpraestans* — Danilova and Silina, 1962; some varieties of *Lilium* — Baranova, 1973).

Bulbils are developed in the axils of bulbous scales *(Ornithogalum umbellatum, Tulipa kaufmanniana, T. bifloriformis, Muscari armeniacum)* or on the underground part of the flowering stem, in the axils of the slender scale-like leaves *(Lilium willmottiae, Nomocharis saluensis).* In the axils of the bulbous scales there are 1 to 20 buds forming the bulbils. They have a collateral arrangement and are separated from the mother bulb after the die-off of the outermost scales and begin independent life *(Chionodoxa luciliae, Galtonia candicans, Allium subhirsutum).* Some species form bulbils on the stolons, outside of the mother bulb (juvenile plants of *Tulipa praestans, Allium oreophilum, Notholirion thomsonianum, Muscari aucheri, Fritillaria uva-vulpis).* After the stolons perish the bulbils continue independent growth and development. The vegetative mobility of the species is realized in this way. There are species with

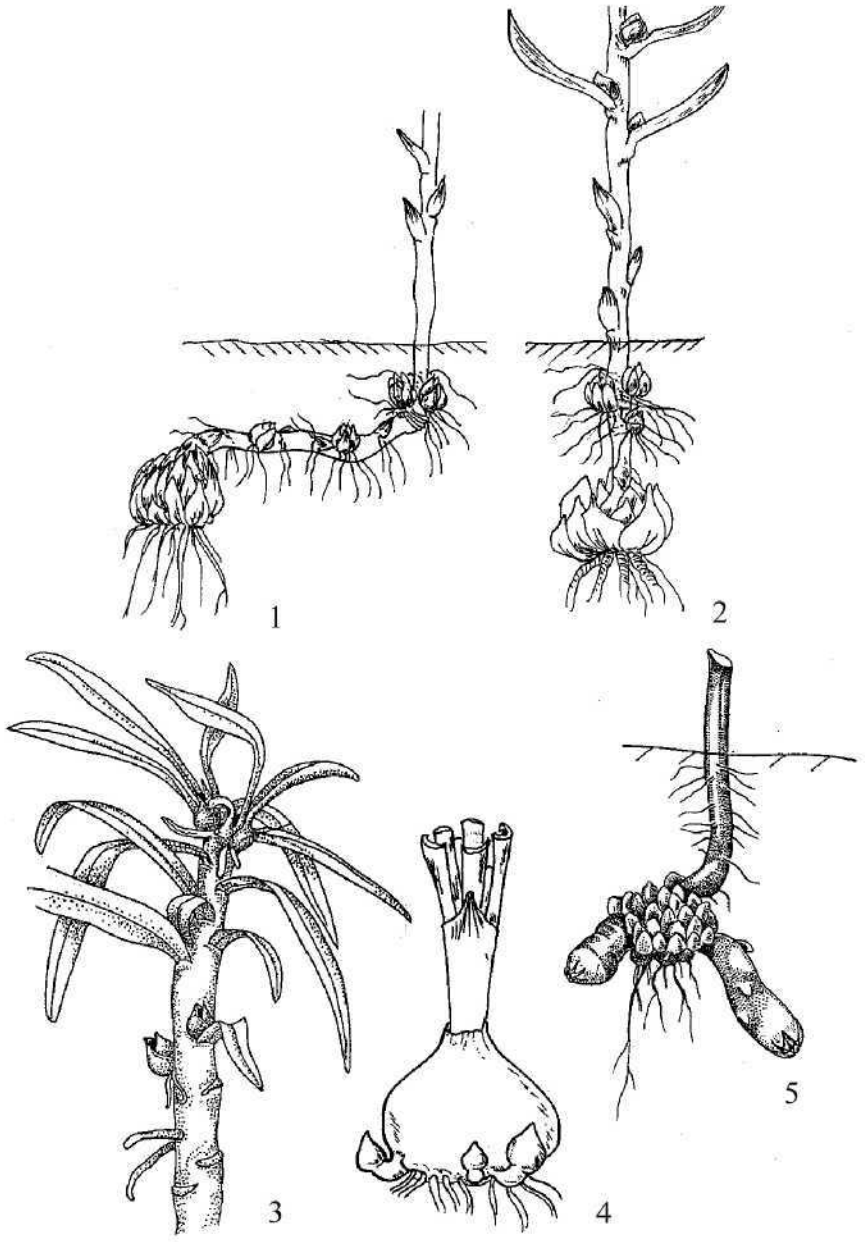


Fig. 51: Bulblet and bulbil (Baranova, orig. data).

1 — on underground part of the floriferous shoot in *Lilium pseudotigrinum,* **2 — on leaf axils in** *L. lancifolium,* 3 **—on inflorescence in** *L. regale;* 4, 5**—bulbils on bulb stolons in** ***Brimeura*** *amethystina* (4) **and** *L. canadense* (5).

stolons and bulbils that grow together with the bulbous scale *(Ornithogalum caudatum).* In such cases, the bulbils stay on the scales till they fully die off.

Only species of genera *Lilium* (L. *regale, L. willmottiae, L. lankongense, L. pennsylvanicum)* and *Nomocharis (N. saluensis)* are able to form bulbils on the underground part of the shoot. There the adventive roots are developed and the axillary buds are formed on the shoot nodes.

Bulbils can be developed from the adventive buds on the scales *(Fritillaria meleagris, Brimeura amethystina, Hyacinthoides hispanica, Erythronium sibiricum).* However, the buds are very weak and perish before the bulbils form completely.

Bulbils are larger than bulblets. They consist of three to six (eight) cataphylls, primordia of the green leaves, axis and roots. Their colour is white or like the mother scales. Bulbils have a short dormant period and germinate after separating from the mother plant. Only the bulbils of a few plants *(Notholirion thomsonianum, Cardiocrinum)* can germinate on the mother plant right after their formation.

Protocorm (Greek *protos*—primary, the first, and *cormos*—stem, shoot, tubercle) is a tuber-like seedling of orchids and some pteridophytes. Synonyms: embryonic tubercle, seedling.

The term "protocorm" was introduced by Treub (1890) for the tuber-like structure with hairs on the lower side that formed during club-moss embryo germination (Fig. 52). Balfour (1905, cited by *The Oxford English Dictionary,* 1989) was the first to use this term to designate the seedling in Orchidaceae.

In the early 20th century, the term "protocorm" was not widely used in descriptions of orchid plant development. Even in the works of the outstanding French botanist Bernard in 1909 it was not used. Later on by 1916, Bernard (1932) devoted a chapter to Treub's theory of "protocorm" and suggested the rightful use of this term for orchids also. Nevertheless, he underlined that the similarity in the structure of club-moss sporophyte and orchid seedling was connected with the mycotrophy phenomenon. He regarded the appearance of protocorm as an example of convergence but not as an example of the common origin of these plants or as an argument of ancient origin of orchids.

The term "protocorm" is used also in the broader sense, to include more than orchid and club-moss seedlings. Jacques-Félix (1958,1982) call the embryo proper of all angiosperms as protocorm.

In the opinion of the majority of modern investigators, the orchid protocorm is a seedling (Veyret, 1965, 1974; Batygina and Vasilyeva, 1980, 1983a,b; Batygina and Shevtsova, 1985; Batygina and Andronova, 1991; Vakhrameeva *et al.,* 1991; Vinogradova and Filin, 1993; Kulikov, 1995; Vinogradova, 1999). However, some researchers regard the structure forming during orchid seed germination as embryo (Teryokhin, 1977; Møller, 1987a-c, 1989). Thus, today the question whether the protocorm in orchids is seedling or embryo is still under discussion.

Views about the morphogenetic nature of protocorm organs and their interpretation are also contradictory. The borders of the protocorm stage in the life-cycle are defined differently (Vakhrameeva *et al.,* 1991; Vinogradova, 1996, 1999; Tatarenko, 1996; Batalov, 1998). The absence of consensus about the limits of the term "protocorm" can be explained not only by the peculiarity of protocorm structure, but also by the difficulties in the definition of age phases in orchids, such as seedling or juvenile plant.

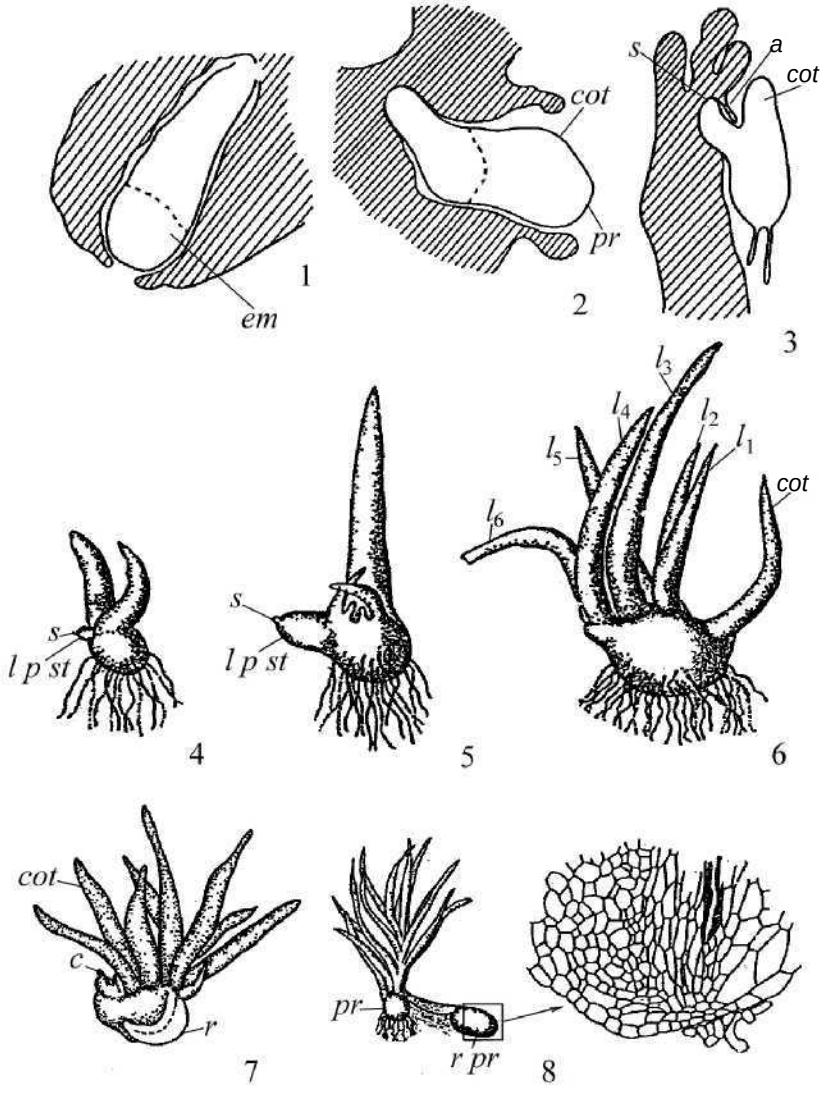


Fig. 52: Seedling development in *Lycopodium cernuum* (modified from Treub, 1890).
1 — embryo in the prothallus at early stage (schematic), the border between its upper and lower parts is shown as dotted line; cotyledon and embryonal tubercle arise from the upper part, while "foot" (it persists in the prothallus) is formed from the lower part; 2,3 — seedlings at the stage of emerging prothallus, cotyledons and embryonal tubercle with hairs are differentiated (schematic); 4-6—seedlings with forming leaves; 7—seedling with the first root; 8 —seedling with tubercle (protocorm) forming on the first root; *a* — archegonium, *cot*—cotyledon, *em —embryo, $l_r l_e$—iirst* and subsequent leaves, *I p st*— lower part of the stem ("foot"), *pr* — protocorm, , *r*—root, *r pr*—root protocorm, s — suspensor.

As is known, in most species of the family Orchidaceae studied, embryogenesis ends with the formation of the embryo, which is not differentiated into organs. The embryo germination subdivides into several stages. In the first stage embryo swells and its volume increases significantly. The seed coat ruptures and the protocorm appears from it. The protocorm shape varies: inverted egg-shaped, oval, elongated, disc-like, branched, thorny, globular, spindle-shaped (Veyret, 1965, 1974; Batygina and Shevtsova, 1985; Clements, 1995, cit. after Cribb, 1999; Vinogradova, 1999). This feature is taxon-specific. The protocorm in all orchid species studied usually has radial symmetry in the early stage (see Embryogenesis in Orchidaceae, Vol. 2). As the shoot organs form, it can preserve symmetrical structure *(Bletilla, Dactylorhiza)* or can become asymmetrical *(Calypso bulbosa).* In some species protocorm acquires dorsoventral structure *(Phalaenopsis).*

The basal part of protocorm consists of large parenchymal cells and functions as a "storage organ". At the protocorm apical pole made by small cells the shoot apex with the leaf primordia differentiates. The leaf primordium in the early stage of development is usually like a closed (in *Listera ovata)* or unclosed (in *Dactylorhiza baltica)* ridge (Batygina and Andronova, 1991). With the growth of primordium in these species, the "hole" delineated by edges of the ridge gradually shifts to the lateral position. The primordium acquires a conical form. In a number of cases the edges of this hole join completely.

The first leaf organ in orchids is called either cotyledon (Burgeff, 1936; Teryokhin, 1977) or true leaf (Batygina and Vasilyeva, 1983a,b). In the opinion of Teryokhin and Nikiticheva (1968), both the first and the second appendiculate organs formed on the *Thunia* protocorm are cotyledons.

The term "cotyledon" itself remains under discussion. Most investigators consider cotyledons to be modified leaves, which are initiated at the embryonic stage of flowering plant sporophyte development. In connection with the fact that leaf organs in the majority of orchids appear at the protocorm stage of post-seminal development, it is not accurate to call them cotyledons or leaf-like organs (Batygina and Andronova, 1988,1991). They represent real seedling leaves, and the embryo itself has no cotyledons.

In some orchid species, in the embryo apical part (in longitudinal section) a hillock can be seen, which was called "cotyledon" *(Arundina graminifolia*—Rao, 1967; Nishimura, 1991; *Bletilla striata*-Bernard, 1909; Tohda, 1968; Nishimura, 1991; *Dendrochilum glumaceum*—Beer, 1867, cit. after Nishimura, 1991; *Epidendrum vitellinum, Polystachya microbambusa*—Veyret, 1965,1974; *Sobralia macrantha—Treub,* 1879; Nishimura, 1991; *Thunia alba*-Teryokhin and Nikiticheva, 1968; Teryokhin, 1977,1991,1997; Nishimura, 1991).

Embryo development was studied in detail only for some so-called "cotyledonous" species. Reinvestigation (with the help of scanning electron microscope) of the embryo and protocorm in *Bletilla striata* and *Thunia alba* (Andronova and Batygina, 1992) has shown that in these species structures quite different in morphology and genesis are formed, although in the literature they are all called "cotyledon". In *B. striata* the appendiculate organ in the form of sickle-shaped ridge is formed in the embryo apical part. The embryo of *Th. alba* has no primordium of such organ and when germinating in the protocorm apical part the hillock is formed; the latter consists of several cells. The structure described can be found only in the early stage of protocorm development; in the course of cell division in the apical domain it gradually disappears.

Initiation of the leaf organ in *Th. alba* occurs at the protocorm stage by means of the formation of ridge, as in species without cotyledon (Batygina and Andronova, 1991; Andronova and Batygina, 1992; Andronova, 1997a). The hillock appearance in the axial part of the germinating embryo in *Thunia* is evidently determined by the peculiarities of growth processes and by the laws of cytomechanics. Study of the architectonics of the surface layer and inner tissues of embryo in mature seed has revealed the presence of large, pyramidal cells in the axial zone in embryo apical part; the latter preserve their shape and sizes during germination. These cells enter the mitotic cycle later than other cells in the apical and middle embryo parts.

From the above it can be concluded that the embryo shape in longitudinal sections cannot in itself be a reliable criterion for resolving whether or not the embryo has cotyledon, i.e., the primordium of the leaf-like organ. Data on the absence of appendiculate organ in *Th. alba* testify in favour of the exclusion of this species from the list of "cotyledonous" plants.

In the basal part of protocorms, the embryo root meristem does not form. The roots in orchids appear after differentiation of the shoot organs and are adventive (Veyret, 1965,1974; St.-Arnaud *et al.*, 1992; Barabe *et al.*, 1993; Andronova, 1997a,b).

Seedling growth and initiation and development of the shoot organs are realized on account of nutritive substances accumulated in the protocorm basal organ (Ricardo Alvarez, 1971; Raghavan, 1976; Batygina and Vasilyeva, 1983b). This organ usually functions till adventive roots appear on the protocorm. Its life span varies in different species, and also within a single species. Data obtained from *in vitro* culture show that the "storage organ" of the protocorm degenerates at once after first root formation {*Angraecum maculatum*—Veyret, 1965; *Dactylorhiza maculata* — Batygina and Vasilyeva, 1983b). In the case of *D. baltica* the basal part of protocorms dies out immediately after appearance of the first root or persists for a much longer time and can be observed even at the stage of seedling with several developed roots (Andronova, 1997a).

There are two points of view concerning morphogenetic nature of the basal protocorm organ in orchids. According to some investigators, it is a hypocotyl (Nishimura, 1991; Teryokhin, 1997; Clements, 1995, cit. after Cribb, 1999). According to others, the basal organ of the embryo and protocorm of orchids has the characteristics of root, and the presence of epidermal hairs points to this (Bernard, 1909; Veyret, 1965,1974).

It is difficult to define the border between the hypocotyl and the root in the embryo of flowering plants. It can be easily found in the seedling by the presence of epidermal hairs, which are characteristic of root and, as a rule, absent in the hypocotyl. This is connected with the differences in epidermis differentiation in two different seedling organs, which are characteristic of most flowering plants studied (Duckett *et al.*, 1994). Unlike in flowering plants, during orchid protocorm formation, practically all parts of the epidermis (with the exception of shoot apex) acquire the ability to form epidermal hairs. Thus, basal and middle protocorm parts are covered by the hairs and represent a unified organ by exterior and interior structure (parenchymal tissue).

The type of hairs formed at the protocorm and the root is similar: one-row *(Coeloglossum, Dactylorhiza, Gymnadenia, Orchis)* or multi-row *(Bletilla, Dendrobium phalaenopsis, Phalaenopsis, Thunia).*

In adult orchid plants, trichomes can be found not only at the roots, but also in the other organs, which to varying degree take part in mycorrhiza formation: in the root-stem tuberoid and in the underground shoot part lower than leaf node (Pridgeon, 1994). Thus, the trichomes in orchids cannot serve as a feature pointing to the root nature of the organ, as was considered earlier. Apparently, the basal organ of the embryo and protocorm in orchids is not a root by nature, but it is homologous to the hypocotyl of embryo and seedling of other flowering plants (Teryokhin, 1977; Clements, 1995, cit. after Cribb, 1999).

Reproduction and propagation in orchids, both in natural conditions and in culture *in vitro,* regardless of structure type (generative or vegetative) and the mode of reproduction (sexual or asexual), is connected with the formation of protocorms and protocorm-like structures (Shevtsova *et ah,* 1986; Batygina, 1987a,b). The authors consider the appearance of the protocorm in orchid ontogenesis as the necessary stage in the transition from sexual to asexual mode of reproduction. The vegetative propagation of orchids in asymbiotic culture can be realized whether in the form of "budding" of protocorms or by the initiation of several points of growth on one protocorm; this can be considered one of the reserves of the orchid reproduction system (Batygina and Vasilyeva, 1980,1983b; Batygina and Shevtsova, 1985).

Embryoidogeny is a New Type of Vegetative Propagation

Batygina was the first to propose the term "embryoidogeny" as a new category of vegetative propagation; she also considered the role of this phenomenon in the reproductive system of flowering plants (Batygina, 1987,1989a,b, 1990,1993a,b, 1994, 1996) (Table 21, Fig. 53).

Embryoidogeny (Greek *embryon*—embryo, *oidos*—view, *genus* - origin) is one of the two types of homophasic reproduction of flowering plants *in situ, in vivo* and *in vitro,* the elementary structural unit of which is an embryoid (somatic embryo).

The tendency toward somatic embryo formation exists at all stages of plant ontogenesis, beginning with the zygote. Embryoids can arise on different structures and organs of plants growing in various ecological zones.

While categorizing embryoidogeny into types of reproduction and propagation, we used **two criteria: ontogenetic** (homophasic reproduction with no meiosis or gamete fusion, i.e., asexual mode of new generation formation; uniparental heredity) and **morphological** (bipolar organization of the structure with shoot and root apices and new polar axis). As for **embryogeny** (heterophasic reproduction), the formation of a new individual is a result of sexual process, i.e., meiosis and gamete fusion (biparental heredity).

The main thesis of the conception of embryoidogeny is believed to be the universality of the morphogenesis of embryoids (as well as sexual embryos) developing in natural conditions and in experimental culture *in vitro* (Batygina, 1996,1998; Batygina and Zakharova, 1997a,b).

Embryoid forms **exogenously** or **endogenously,** usually from one somatic cell, rarely from embryonal cellular complex. An embryoid is characterized by the formation of its own **new axis** (in relation to the maternal organism), joining polarly developing shoot and root apices. As a rule it does not have a vascular system in common with that of maternal organism (close radicular pole). Genesis of embryoid,

Table 21. The ways and types of reproduction and propagation in flowering plants.

With a alternation of generations			Without a alternation of generations										
Sexual			Asexual										
Seed propagation			**Vegetative propagation**										
Gamospermy		Agamospermy	Aspermy										
Amphimixis		Gameto-phytic apomixis	Amixis										
Embryogeny			**Embryoidogeny**						**Gemmorhyzogeny**				
			Floral		Vegetative				Floral	Vegetative			Sar-menta-tion	Particu-lation
			Embryonal (cleavage)	Ovular (nucellar, integu-mentary)	Foliar	Cauli-genic	Rhizo-genic			Foliar	Cauli-genic	Rhizo-genic		
Cap-sella, Pisum	*Avicen-nia, Rhizo-phora*	*Antenna-ria, Hiera-cium, Ta-raxacum*	*Erythro-nium, Orchis, Paeonia*	*Allium, Citrus*	*Bryophyllum, Ranunculus*	*Crassula,*			*Allium, Fes-tuca, Poa*	*Hammarbya, Lilium*			*Ajuga, Paris, Sta-chys*	*Aconitu Carum, Plantag*
	Vivi-pary		Vivipary											
Embryogenic			**Embryoidogenic**						**Gemmorhizogenic**					
TYPES OF REPRODUCTION														

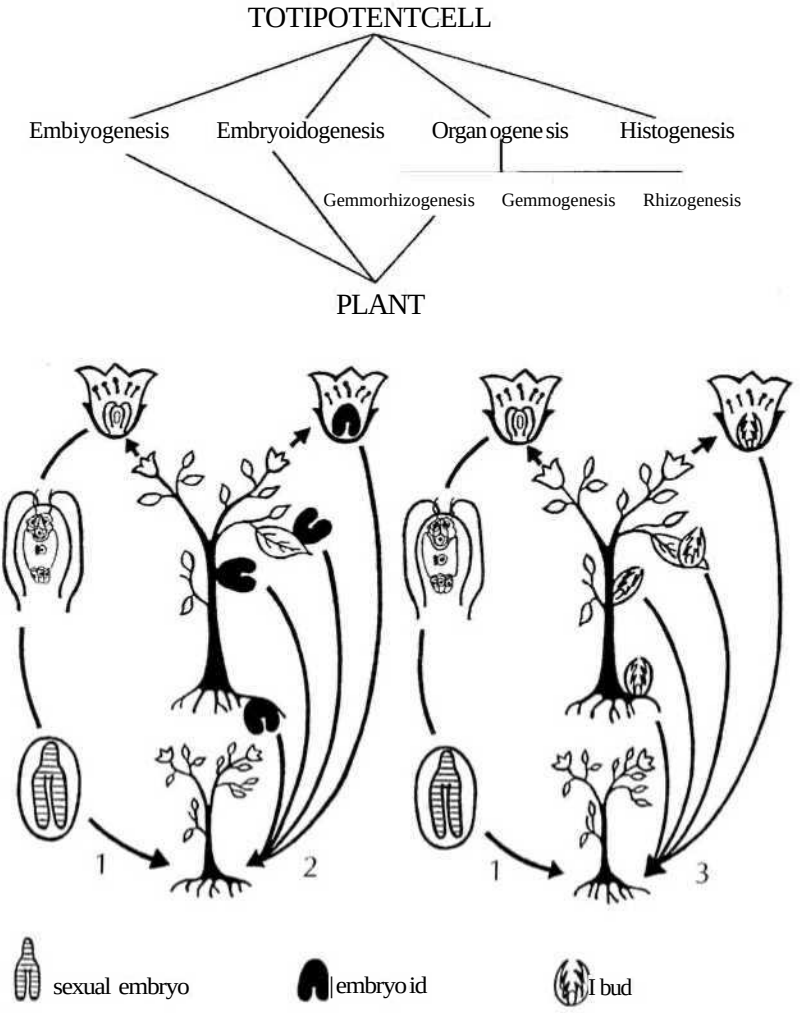


Fig. 53: Modes of morphogenesis leading to the formation of a new organism. 1—embryogenesis, 2—embryoidogenesis, 3—gemmorhizogenesis.

as well as its shape and size, is taxon-specific. **The main features established for sexual embryos (e.g., polarity, cellular and histogenous differentiation, autonomy)** are typical for embryoid. During embryoid germination a new individual is "born" (Batygina, 1987c, 1989a,b), and in some species a short contact with the maternal organism is noted. The duration of contact and the stage at which this contact is realized differ in various plant species.

Forms of embryoidogeny. Depending on the origin and location of somatic embryos on the maternal plant, **two main forms of embryoidogeny** can be distinguished: **reproductive (floral) and vegetative** (Fig. 54).

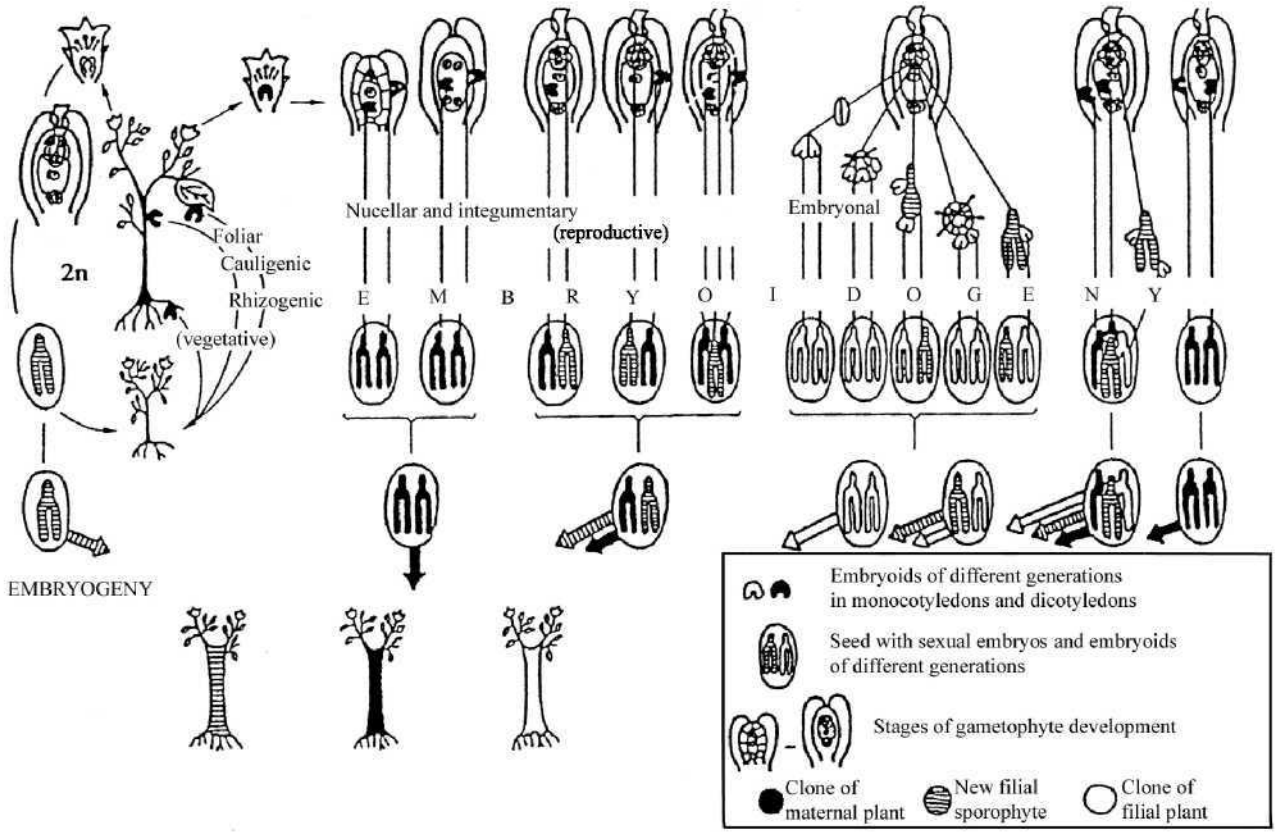


Fig. 54: Various patterns of embryoidogeny resulting in seed heterogeneity.

Reproductive (floral) embryoidogeny is the formation of embryoids in the flower and seed. It may be **embryonal**[5] (monozygotic cleavage), on the base of zygote or embryo, or **ovular** (integumentary and nucellar), from the cells of ovule integument and nucellus.

Monozygotic cleavage embryoidogeny was revealed in *Loranthus* (Loranthaceae), *Erythronium*, *Tulipa* (Liliaceae), *Limnocharis* (Orchidaceae) (Ernst, 1918), *Lobelia* (Lobeliaceae) (Cŕeťe, 1938), Papaveraceae (Ilyina, 1968), Poaceae (Erdelská, 1996) and many other species of flowering plants. Gymnosperms are also inherentinthisphenomenon:*Sciadopitys*(Buchholz,1931),*Cryptomeria*,*Chamaecyparis* (Buchholz, 1932a,b), *Cupressus* (Doak, 1937), *Sequoia* (Buchholz, 1939), *Juniperus* (Cook, 1939; Mathews, 1939) and *Saxegothea* (Doyle and Looby, 1939). In the representatives of Orchidaceae family *(Eulophia epidendrae* - Swamy, 1943), several embryoids can form in the same embryo sac, developing either from the zygote or from somatic cells of sexual embryo (suspensor or proper embryo) (Fig. 55).

A special type of cleavage embryoidogeny is observed during embryo development in the genus *Paeonia* (Fig. 56). According to Yakovlev, the sexual embryo at coenocyte-cellular developmental stage is formed by "the budding" of numerous embryo-like structures, one of which is modified into the sexual embryo (Yakovlev, 1951,1983; Yakovlev and Yoffe, 1961). According to our concept, these structures are **the somatic embryos, arising from epidermis cells of sexual embryo.** This is one of the forms of monozygotic embryoidogeny (Batygina, 1987a,b, 1989b, 1992; Brukhin and Batygina, 1994). In mature seed, only one embryoid remains as a result of competing development; the rest die at different developmental stages. The sexual embryo also degenerates and is destroyed at different stages of seed development in various peony species. In this case **the organism is cloned at the first stages of its development** (embryo) and in the mature peony seed there is, as a rule, **a single somatic sexual embryo** (embryoid), representing the clone of sexual embryo but not **a proper sexual embryo,** as Yakovlev considered earlier (Yakovlev and Yoffe, 1961; Yakovlev, 1983). This is believed to be a striking example of **transition from one mode of sporophyte formation, sexual (n+n), to another, asexual (embryoidogenesis, 2n=2n). In** the process of evolution, the representatives of one taxon probably acquired the capacity for homophasic reproduction **(sporophyte to sporophyte)** at the very early stages of ontogenesis; vegetative propagation by cloning therefore takes place (uniparental heredity). Thus, in the developing seed **two types of embryos, successively forming** and differing in **origin,** can be observed: **sexual** embryo, not differentiated on organs, which stops developing and is replaced by the **somatic embryo,** differentiated on all general organs (shoot and root apices, cotyledons). It should be emphasized that although mature peony seeds contain only somatic embryos, the plants arising from them develop in natural conditions without abnormalities.

Some experimental data concerning the influence of various factors (radiation, morphactins etc.) on the development of sexual embryo in culture *in vitro*, e.g., in *Eranthis* (Haccius, 1965b), are compatible with the phenomenon described for peony (Batygina, 1992). Stress situations probably induce the formation of somatic embryos on the base of dying sexual embryo in nature as well. In *Paeonia* this process is fixed in

[5]The terms "embryonal" and "ovular" are used to identify not only embryoid origin (from somatic cells of embryo or ovule), but also the embryogenesis stages at which they form.

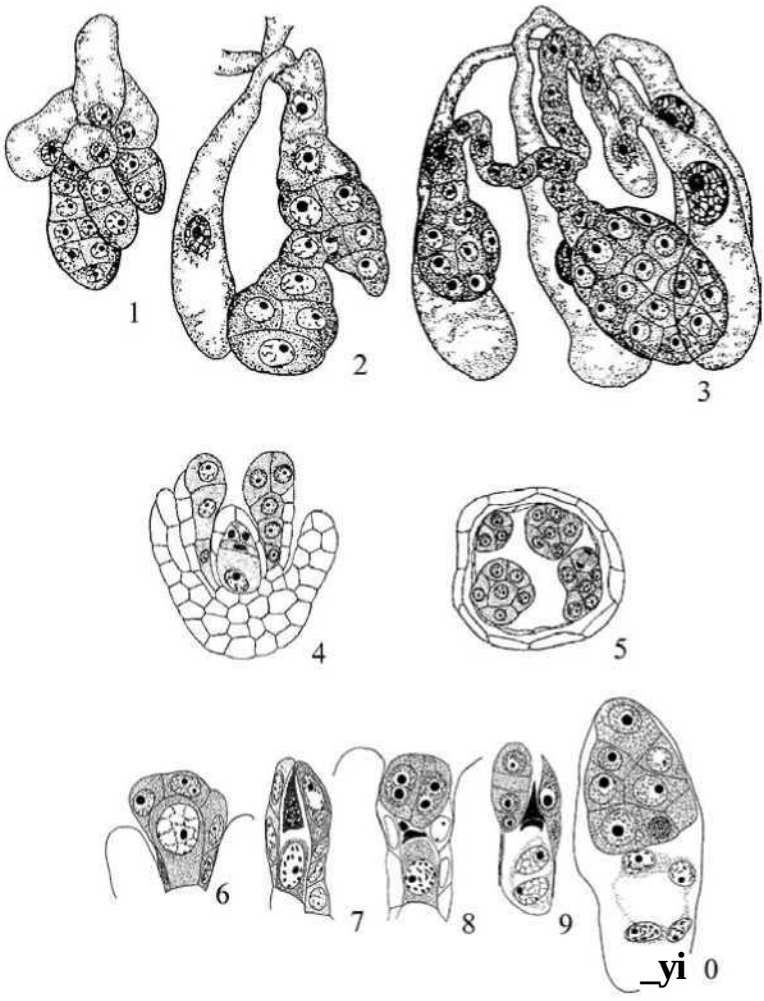


Fig. 55: Forms of embryoidogeny in orchids.

1-3—polyembryony in *Eulophea epidendraea:* 1—three cells produced by a zygote developed embryoids as a result of divisions, 2—"bud" on the right side of a sexual embryo, 3—two embryoids formed by the cleavage of one sexual embryo (large vacuolated cells belong to the embryo suspensor); 4, 5—integumentary embryos in *Spiranthes cernua* at the stage of T-shaped tetrad of megaspores (4) and four-nuclear embryo sac (5); 6-10—formation of somatic embryo (embryoid) in *Nigritella nigra* at the early stages of ovule development: 6—nucellus with megaspore mother cell, 7—subsequent stage (degenerating micropylar cell of dyad), 8—two-celled embryoid and vital megaspore with the remnants of the degenerated megaspore, 9, 10—many-celled adventive embryos, located over top of two- and four-nucleate embryo sac, correspondingly; 1-4, 6-10—longitudinal section, 5—cross-section.

1-3 - after Swamy, 1943; 4,5 - after Swamy, 1948; 6-10 - after Af zelius, 1928.

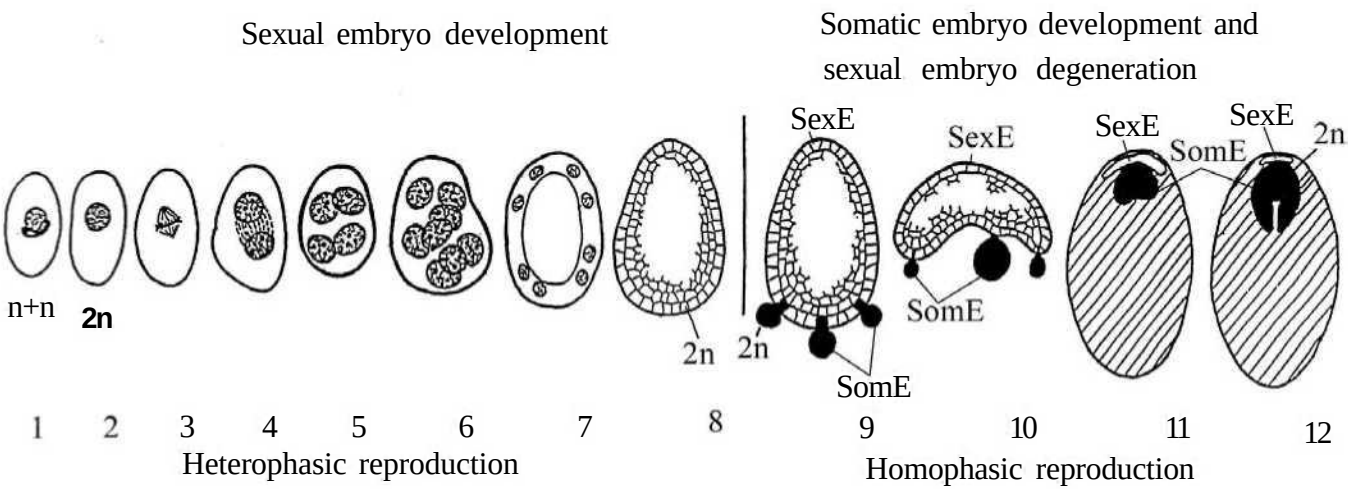


Fig. 56: Switching of the reproductive programme from heterophasic to homophasic pattern in the seed of *Paeonia.*

1-8 — development of sexual embryo (from zygote to the coenocyte-cellular stage)—heterophasic stage of reproduction: 1—fertilization, 2 zygote, 3-7—development of coenocytic embryo, 8—formation of epidermis at coenocyte-cellular stage; 9-12—formation of somatic embry and degeneration of sexual embryo: 9,10 — several somatic embryos appear on the sexual embryo, 11 — maturating seed, 12 — mature se with one somatic embryo, the remnants of a zygotic embryo are seen. Sex E —sexual embryo, Som E —somatic embryo.

the course of evolution; in *Eranthis* the embryoidogenous morphogenesis pathway is realized sporadically, in stress situations.

Nucellar and integumentary embryoidogeny was noted in more than 250 plant species (Webber, 1940; Maheshwari, 1950; Lakshmanan and Ambegaokar, 1984; Naumova, 1992). There is vast information on nucellar embryoidogeny in fruit trees such as *Citrus*, *Mangifera* and *Eugenia.* The number of nucellar embryos in the seeds varies in various species: in *Citrus microcarpa* the seed usually produces 21 seedlings, whereas in C. *unshiu* it produces about 40 (Maheshwari and Rangaswamy, 1958).

Nucellar and integumentary embryoidogeny is also observed in some orchid species *(Nigritella nigra, Spiranthes cernua)* at different stages of ovule development, often just before embryo sac formation (Afzelius, 1928; Swamy, 1948).

Embryoids are able to arise from somatic cells of nucellus and integuments by different modes and at different stages of ovule development (Modilewsky, 1931; Button *et ah,* 1974; Batygina and Freiberg, 1979; Batygina and Mametyeva, 1979; Batygina, 1991b). In *Poa pratensis,* for example, the embryoids form on the base of stem cells, either from a single cell of nucellus dormant meristem, or through embryonal cellular complex as a result of proliferation of nucellus cells (Fig. 57). However, in this species, seeds with sexual and nucellar embryos are observed together with agamospermous seeds.

Irrespective of the mode of embryoid formation, in the mature seed at nucellar and integumentary embryoidogeny one is dealing with the clone of the maternal plant presented by somatic embryos. Nucellar embryoidogeny is given attention for various reasons. One of them is the ability to produce plants without viruses. In conventional vegetative propagation, cuttings are often infected by pathogens, whereas nucellar embryos and seedlings planted from them are free of viruses. Some authors explain this by the fact that the nucellus and neighbouring tissues do not have contact with each other through the vascular system.

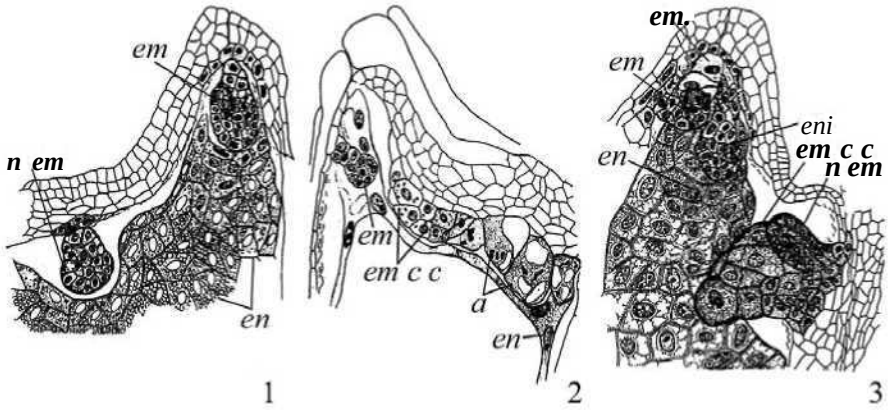


Fig. 57: Two modes of somatic embryo formation in *Poa pratensis* (after Batygina and Freiberg, 1979).

1—from one cell, 2,3—from a group of cells of embryonal complex, *a* — antipodals, *em* — embryo, *en* — endosperm, *nem* — nucellar embryo, *emc c*—embryonal cellular complex.

Geneticists and plant breeders use the high capacity of some plant species *(Mangifera, Citrus)* to form nucellar embryos as the main criterion of genotype selection for cross breeding, thereby ensuring diversity in generation. Nucellar embryoids result in "rejuvenated" seedlings, which resemble those arising from sexual embryos. Maheshwari (1950) emphasized that seedlings of *Citrus,* forming from vegetative buds on sporophyte, develop without spines, whereas seedlings from nucellar embryos develop into plants with spines, similar to seedlings from zygotic embryos. Clones of *Citrus,* always vegetatively propagated (by cuttings), finally become weak and sterile. Gardeners renew *Citrus* clones using nucellar seedlings, which develop better than plants obtained from cuttings.

There are cases in which in the same seed the formation of embryoids proceeds parallel to embryogenesis (e.g., *Citrus).* We use the term "clone" for embryoids and seedlings arisen from them. It should be noted that in some representatives of angiosperms (Citroideae, Orchidaceae, etc.) two different clones of two generations can form in the same seed: the clone of the maternal plant (by means of nucellar and integumentary embryoidogeny) and the clone of the daughter plant (by means of cleavage embryoidogeny). Foliar, cauligenous and rhizogenous embryoids and related seedlings represent clones of the maternal organism at later ontogenesis stage (in comparison with monozygotic embryoids).

When **embryoids of different** origin, from **maternal plant (ovular) and** from **new daughter (embryonal),** exist in the same seed, plants of two genotypes develop in the population. This is the prerequisite to create **heterogeneity of seeds,** which together with vegetative embryoidogeny ultimately results in **genetic heterogeneity of population** (see The genetic heterogeneity of seeds. Polyembryony).

Vegetative embryoidogeny is the formation of embryoids on vegetative organs; it includes foliar embryoidogeny (on leaf), cauligenous embryoidogeny (on stem) and rhizogenous embryoidogeny (on root). The arrangement of embryoid formation with respect to the particular vegetative organ is taxon-specific.

Foliar embryoidogeny. Because of incomplete data on morphogenesis of structures arising on vegetative organs, there is no common terminology for their identification. The structures formed on the leaf in different *Bryophyllum* species (Crassulaceae) are referred to as "buds" (Howe, 1931; Serebryakova, 1978c), "embryos" or "leaf embryos" (Naylor, 1932; Yarbrough, 1932; Warden, 1968), "leaf pseudobulblets" (Johnson, 1934; Resende, 1954), or "embryoids" (Batygina, 1987b,c).

The results of investigations of *Bryophyllum calycinum* and B. *daigremontianum* (Bragina *et ah,* 1995; Batygina *et ah,* 1996) testify in favour of the last term. In the species studied the leaf structures (embryoids) are formed endogenously, from the meristem, which Yarbrough (1932) called "dormant meristem". It is unknown whether they arise from one or several cells of dormant meristem. Therefore, one can speak of the resemblance of these structures with sexual embryo only at later developmental stages. The sexual embryo of dicot is known to undergo globular, heart-shaped, and torpedo-shaped stages and the stage of maturation. The same stages can be distinguished in the development of leaf structures in two species of *Bryophyllum,* but the"globular" stage differs in morphology from classic globular stage of sexual embryo. The formation of "cotyledons" in these structures occurs in common with sexual embryos of dicots. In both species, one "cotyledon" is usually smaller than the other at early developmental stages. Later they become equal in size. The leaf structures of B. *calycinum* and B. *daigremontianum* are characterized by the

lack of apical meristem of the main root, instead of which the system of adventive roots is formed.

Comparative morphological and histogenic analysis of vegetative structures allows one to consider these structures as somatic embryos (B. *calycinum)* or as a transitional form between embryoid and bud (B. *daigremontianum).* Such features as the origin from dormant meristem, the proceeding of main developmental stages inherent in sexual embryo (globular, heart-shaped, torpedo-shaped), the presence of cotyledons and well developed plumule, and bipolarity of their development could be regarded as arguments in favour of that view. The formation of adventive roots on the base of dormant meristem derivatives is the specific feature of these foliar embryoids. Short-term connection of embryoid with the conductive system of leaf still does not justify considering this structure to be the bud.

In another representative of the Crassulaceae family, *Crassula multicava,* the formation of embryo-like structures from the derivatives of epidermis cells in leaf or petiole (i.e., **exogenously)** was described (McVeigh, 1938). These bipolar structures as in the case of B. *daigremontianum* and B. *calycinum* stay in contact with the mother plant for a long time. Comparative analysis of the morphogenesis of some sexual embryos, somatic structures on leaves as well as embryoids formed in culture *in vitro* suggests that the notion "embryoid" for vegetative structures in different *Bryophyllum* species and in C. *multicava* may be more correct than other terms. We are of the same opinion as Naylor (1932), Yarbrough (1932) and McVeigh (1938), who suggested that new vegetative structures formed on leaves be referred to as "leaf embryos" or "embryos", but not as buds. These authors did not use the term "embryoid", which was introduced later.

Most investigators **compare "leaf embryos" with seeds** (Yarbrough, 1934; Serebryakova, 1978c). Dispersal of vegetative diaspores on different distances from the maternal plant depends on the mode of their formation and the character of development. Seedlings from these leaf embryos look like tumbleweed.

Cauligenous embryoidogeny was first described in detail in *Ranunculus sceleratus in situ* and *in vitro* (Konar and Nataraja, 1965; Konar *et ah,* 1972). The embryoid of this plant, as in C. *multicava,* forms exogenously from the derivatives of epidermis cells; its development proceeds similarly to that of sexual embryo (Onagrad-type of embryogenesis). Cauligenous embryoids do not connect with the conductive system at any stage of their development, unlike the foliar embryos of *Bryophyllum* and *Crassula.*

Rhizogenous embryoidogeny. There are only fragmentary published data on this subject, which requires additional investigation.

Embryoidogeny as a type of propagation. Comparative analysis of results on somatic embryo formation in natural conditions and in tissue culture permitted us to formulate the notion of **embryoidogenesis as a process, the basis of asexual mode of new sporophyte formation (i.e., without participation of gametes and fertilization),** and of **embryoidogeny as a special type of vegetative propagation.**

It is in conformity with the opinion of Winkler (1934), Battaglia (1963) and Grant (1981) that adventive embryony and viviparity (homophasic—T.B.) are forms of vegetative propagation. The propagation in this case is realized either by proper embryoids or by tiny seedlings developing on the plant from embryoids or by the seeds where embryoids are formed.

Embryoidogeny represented by different forms is of a greater adaptive significance for flowering plants than another type of vegetative propagation, gemmorhizogenous. The evolutionary origin of embryoids was likely conditioned by such advantages as a shorter and consequently more energy-efficient pathway to formation of numerous new individual initials with uniparental heredity (together with sexual embryos). The formation of different vegetative and generative diaspores, especially seeds containing the sporophyte initials of new daughter sexual generation (biparental heredity) and "old" maternal generation (uniparental heredity), i.e., the formation of gamoagamic complexes, obviously improves the potential for success in the struggle for existence, due to which these processes were followed by natural selection and became the central force in preserving biological diversity of plants. Another advantage of embryoidogenous propagation is in that the initial of a whole organism, forming in the seed or on the vegetative organs, is the unit of propagation, not part of the organism (or its separate organs such as bud or root), as appears at gemmorhizogeny. In the latter case, particular conditions and time are required for regeneration of the part to a whole individual. A full-value bipolar organism forming at embryoidogeny in some plant species is immediately able to root and also to disperse like seeds by wind and water over small and large distances.

Such established forms of embryoidogeny as ovular (nucellar and integumentary), embryonal (monozygotic cleavage) and vegetative (foliar, cauligenous and rhizogenous) are believed to be the elements of a single common propagation type — embryoidogenous. The exclusive property of the plant cell, its totipotency, is the basis of the phenomenon described above. The role of embryoidogeny phenomenon in evolution is not completely established because of poor research of its different forms.

It is hard to agree with some authors that particular forms of embryoidogeny have a special role in the reproductive system of flowering plants. That position is not quite correct. Every form of embryoidogeny must be considered in comparison and in interaction with the other forms and also with embryogeny, gemmorhizogeny and gametophytic apomixis.

The following original investigations of different aspects of embryoidogeny are more satisfactory in stating the concept (Brukhin and Batygina, 1994; Batygina *et al.*, 1996; Batygina and Bragina, 1997; Batygina and Zakharova, 1997a,b; Batygina, 1998, 1999a,b). A definite parallelism in the development of sexual and somatic embryos was revealed. It manifests in the resemblance of main morphogenetic regularities (polarity, symmetry, ability to proliferate), high polymorphism of those and others, occurrence of transitional forms and abnormalities. The main difference between sexual and somatic embryos lies in their origin: heterophasic and homophasic, respectively. However, irrespective of origin and conditions of development *(in situ* or *in vitro),* both embryo types are bipolar structures, representing the initial of a new individual (not of its part as in the case of the bud). Their role in the reproductive system is also the same: they are elementary structural units of propagation.

Another important aspect of the characteristics of embryoids as original formations is the comparison of their development with bud production. The resemblance between embryoid and bud lies first in the mode of formation, homophasic reproduction. Besides that, both are elementary structural units of vegetative propagation. The main difference between these structures is that an embryoid, as well as a sexual embryo, represents the initial of a new individual, with

bipolar structure (cotyledons, shoot and root apices are present), but the bud is part of a whole organism, monopolar, with shoot apex alone and without cotyledon formation; only in the process of its development and root formation does it become bipolar.

Because embryoidogeny is considered a new category of vegetative propagation, we look briefly at the history of its discovery. Since the investigations of Reinert (1958) and Stewart and colleagues (1958), the embryo-like structures found in culture *in vitro* in *Daucus carota* became the subject of research. The similar formations are observed not only in experimental conditions, but also in conditions of natural propagation of plants (in monozygotic cleavage embryony) (Batygina *et ah*, 1978; Batygina and Butenko, 1981; Batygina, 1987b,c, 1989).

Vasil and Hildebrandt (1966) suggested using the term "embryo" only for structures of sexual origin, and the term "embryoid" for structures similar to the embryo but forming in the process of asexual (vegetative) reproduction (e.g., nucellar embryos, foliar embryos) or arising in culture *in vitro*. Haccius and Lakshmanan (1969) and Haccius (1971) first discussed the criteria for distinguishing embryoids. They came to the conclusion that this term could be applied to all formations, including "adventive" embryos, characterized by closed radicular pole, situated opposite to the shoot pole, as well as to embryo-like structures found in culture *in vitro*.

Haccius (1965a,b) and also Vasil and Hildebrandt (1966) recorded the resemblance in the peculiarities of the development and structure of embryoids obtained in culture *in vitro* and embryos arising in nucellar and integumentary embryony. On the other hand, Haccius and Lakshmanan (1969) for the first time discussed the resemblance and differences of embryoids and "bud-like" structures in culture *in vitro*. Haccius (1971) and Swamy and Krishnamurty (1981) examined in detail the morphological nature of embryoids and came to contrary conclusions. According to Haccius, despite definite differences in the development of sexual ("zygotic") embryos and embryoids, the notion of "embryonal" character of development and organization is applicable to both these structures. Nevertheless, as the author noted, embryoids differ from sexual embryos in most angiosperms by delayed differentiation and in this respect are similar to the embryos of gymnosperms with so-called "irregular" mode of differentiation.

It should be noted that Haccius and Hausner (1975) considered that the main criterion for distinguishing sexual embryos and embryoids, on one hand, from adventive (as well as axile) buds, on the other, is not the difference in their origin but the fact that embryos are not part of the plant (they are original individuals of the next generation) and they are not in contact with the maternal plant through a common conductive system. They are characterized by the formation of a new axis, connecting polar shoot and root apices (presence of hypophysis and epiphysis — Batygina, 2004). However, this observation, correct in general, is not absolute. For example, in *Crassula multicava*, temporary connection of the new bipolar sporophyte with the mother plant is observed. In mammals, the offspring is also usually temporarily connected with the maternal organism by the navel.

Swamy and Krishnamurty (1981) concluded that embryoids have few common features with "zygotic" embryos and in the character of development are more similar to adventive buds. They suggest, therefore, that the term "embryoid" be

rejected or that it be distinctly emphasized that embryoids are not in essence common with sexual embryos.

Some authors consider that embryoids never arise in nature and that it is incorrect to compare nucellar and integumentary embryos with embryoids forming in tissue culture (Oryol and Lodkina, 1988; Naumova, 1992). The main argument of these authors is "the place of origin" and "the place of development": for nucellar and integumentary embryos it is the embryo sac, which is absent in culture *in vitro*. However, it is hard to agree with this. First of all, the occurrence of embryo sac does not determine the genetic nature of adventive embryos, as it has already been conditioned by their sporophytic origin (2n=2n). Besides that, there are some plant species in which the embryos develop outside embryo sac (e.g., in the members of Podostemaceae family).

Ontogenetic and morphological criteria proposed by us for distinguishing embryoidogeny make it possible to refer to embryoids as a special class of "the initials" of new individuals, and embryoidogenesis as a special, asexual mode of new individual formation that cannot be turned to parthenogenesis or to apogamety. It is impossible to delimit the term "embryoid" because somatic embryos (cleavage, nucellar and integumentary, foliar, cauligenous and rhizogenous), being formed from the somatic cells of mother and daughter sporophyte, have a number of peculiarities (e.g., the mode of formation, the lack of generation alternation) that prevent this formation from being categorized with zygotic or gametophytic embryos.

Embryoidogeny cannot be applied to traditional categories of vegetative propagation (particulation, sarmentation, etc.). "Cleavage" somatic embryos, as well as nucellar and integumentary ones, represent the elementary structural units of vegetative propagation. Here we are faced with a kind of "rejuvenation" of the process of vegetative propagation, a kind of neoteny.

The peculiar features of such original embryoidogenous reproduction (unlike the usual forms of vegetative propagation such as particulation or sarmentation) are the same as for propagation by seeds with zygotic embryos: a large number of new individual initials and their capacity for near and distant dispersion. Besides that, as is mentioned above, embryoidogeny essentially extends the range of seed heterogeneity. In consideration of polyembryony phenomena and its different forms (monozygotic cleavage embryoidogeny, gametophytic apomixis, nucellar and integumentary embryony), four types of genetic heterogeneity of seeds could be distinguished (Batygina, 1999a,b; see Genetic heterogeneity of seeds. Polyembryony). Apart from general seeds (only with the sexual embryo), there are seeds in which different modes of new individual formation, sexual and asexual, occur "hand in hand". Here, often no single mode of reproduction is clearly represented. For example, the sexual process precedes the arising of "monozygotic twins" (twins, triplets, etc.). In some cases, before clearly "agamospermous" seeds were formed, i.e., containing only somatic embryos, the seeds were "gamo-agamous" during the developmental process, i.e., they could contain nucellar, integumentary embryos and heterozygote, which subsequently could produce enzygotic twins by asexual mode, by cloning (cleavage monozygotic embryoidogeny).

All these complex, multistage processes taking place in the seed ensure the capacity for reproduction and propagation of new daughter individuals (or new generation) with different genotypes, either uniparental or biparental heritability (in the case of sexual embryo formation).

Thus, the new conception of "embryoidogeny" makes possible a non-traditional view of the reproductive system of flowering plants. So, there are: two modes of new individual formation, sexual and asexual; three pathways of morphogenesis in individual formation, embryogenesis, embryoidogenesis and gemmorhizogenesis; two forms of reproduction, heterophasic (embryogeny, gametophytic apomixis) and homophasic (reproductive and vegetative embryoidogeny, gemmorhizogeny — particulation, sarmentation and vegetative viviparity); and two types of propagation, seed (gamospermy, agamospermy and gamo-agamospermy) and vegetative (including gemmorhizogenous and embryoidogenous modes of propagation).

In conclusion, it should be mentioned that the concept of embryoidogeny, a new, highly specialized form of vegetative propagation, unites phenomena earlier thought to be isolated, such as monozygotic cleavage, nucellar and integumentary embryoidogeny and "foliar embryos".

Phytomer Conception and the Higher Plant Evolution

Specimens of the higher plants are complex; they usually do not have a constant shape and size, unlike specimens of higher animals (vertebrates and arthropods). The basic constituent parts of their body, shoots consist of more or less repeated structures called **phytons** or **phytomers,** by analogy with metameres of animals (Gray, 1879). Every phytomer consists of the leaf with the internode below it; the base of the internode can have the bud situated in the leaf axil of the preceding phytomer (Serebryakova, 1971).

Phytomers often are given only ontogenetic importance as the units of growth and development of shoots, which are considered unified integrated structures (Arber, 1950). Indeed, the shoots of most higher plants from modern positions look unified. However, using a phylogenetic approach, it is easy to ascertain that in origin the phytomers correspond to sterilized specimens reproducing by budding, like some colonial animals (Rytova, 1984; Tzvelev, 1993a).

The most primitive fern phytomer is represented by only one frond, which both photosynthesizes and has reproductive organs, sporangia, on the underside; this can be found in some genera of annuals. In the course of evolution the functions have been divided: the single frond has divided into two parts, one photosynthesizes and the other produces sporangia. The stages of this division of the bi-functional frond into two mono-functional fronds can be observed in the extremely original order Ophioglossales; probably, this order has come to us as a relic of gymnosperm ancestors (Kato, 1988).

Polymerization of the sterilized photosynthetic frond-phytomers leads to the formation of the rosette shoot, highly characteristic of many ferns. In this shoot the numerous photosynthetic fronds are followed by fronds with reproductive organs; the latter are able to photosynthesize at first, but in the course of further evolution they lose this ability. The expediency of such polymerization is quite easy to understand: it allows accumulation of more nutritive substances for the development of the reproductive organs, and this is particularly important in less favourable habitats. Also, it reveals wide possibilities for evolution in the direction of increasing plant size.

The rosette shoots of ferns are still very primitive, because their stem parts, consisting of the frond-phytomer bases, are very short and weakly integrated. Such shoots are considered to be "proshoots", as distinct from the true shoots of gymnosperms and angiosperms (Khokhrjakov, 1982). In our opinion, the differences between them are not great.

The peculiarities of the typical shoot are manifested already in the feebly integrated rosette shoots of the ferns. The principal part of the latter is the phytomer, the sterilized or sporiferous frond. The greatly shortened internodes of the axial part of the shoot, the stem, are formed on account of the frond petiole bases. In the upper part of the internodes the bud (the next frond initial) develops endogenously.

The primitive shoots are still unable to lengthen the internodes and have only the apical meristem. Meristems with activity leading to internode lengthening and lateral bud formation appeared much later in the course of evolution.

It should be noted that the growth of the primitive fern shoot (as, incidentally, of any shoot with alternate leaves) proceeds sympodially. The sympodially appearing apical meristem of the shoot is significantly stronger than the true apical meristem, which gives rise to the leaf part of the frond. In any shoot, the meristem, which is stronger and forms the greater quantity of organs, always becomes apical whether it is primary or secondary in evolution (Grassl, 1967).

During further evolution of the shoots in gymnosperms and angiosperms, the leaf and the stem parts of the vegetative phytomers increasingly differentiate from one another, the stem parts being integrated more and more, thus forming the highly organized shoots. The internodes of the latter can lengthen and still later form axile buds and lateral branches.

Every phytomer composing the higher plant shoots is as if biaxial (Rytova, 1984) One axis, which terminates in the top of the frond or leaf and has limited growth, can be named vegetative. The other, principal axis, though it appears sympodially, is reproductive, because it is intended for the formation of reproductive organs, but often via the whole row of polymerized vegetative phytomers.

The vegetative phytomers can alter variously. Their leaf parts can turn to scales or cataphylls, which protect the young buds from external influences. As a result of adaptation to xerophyllous conditions, the leaf parts of all phytomers (e.g., in *Asparagus* and *Ruscus)* turned to scales, and their stem parts, internodes, became phytosynthetic. In some representatives of the genera *Juncus* (e.g., /. *effusus)* and *Schoenoplectus* and other monocotyledons, the rosette leaves became scale-like, and the single strongly elongated vegetative phytomer has both functionally and anatomically almost indistinguishable stem and leaf parts. These parts can be distinguished only by the position of the clearly lateral inflorescence. In the duckweeds (Lemnaceae), the leaf parts of all phytomers are completely reduced, and the very weakly integrated stem parts of phytomers, fronds (reproduced by budding and easily separated from each other), became photosynthetic.

During evolution, phytomers have acquired the ability to polymerize not only in the different tiers along the shoot axes, but also in the same tier. The consequence of this was the transition from more primitive alternate leaf arrangement to opposite or verticillate one. The stem parts of two or more phytomers unite in these cases, while their leaf parts, phyllomes, remain free. Such one-tiered polymerization has taken place in gymnospermous plants also; here it appeared to be also secondary.

Monocotyledonous plants are characterized by alternate position of phytomers (and absence of axile buds in stem leaves) and in this aspect they are more primitive than dicotyledons, which can have up to 20 and more phytomers in one tier or node *(Hippuris).*

The fertile or reproductive phytomers also are able to polymerize and oligomerize in different ways. These are the stamens and carpels of angiosperms, which constitute the reproductive shoots, flowers with different structure. In flowers there are often more or less modified vegetative phytomers. Incidentally, the reproductive phytomers also can be sterilized and be part of the perianth (in many Ranunculaceae).

Noting the metamere shoot structure in higher plants, Rytova (1984), not without reason, finds in these shoots much in common with some colonial animals; she therefore advises for the phytomers the less formal name "phytoids". However, when homologating the vegetative phytomers of the shoot with sterilized specimens, it is impossible not to forget that in the course of long evolution the shoot consisting of phytomers has become an integrated structure, and nowadays it cannot be considered a simple colony of phytomers. Perhaps only in duckweeds can the phytomers, fronds without leaf parts, form groups very similar to budding colonies.

With the appearance of the axile meristem, axile buds and branching, the more evolutionary young coloniality of the second order has developed: shoots consisting of phytomers are becoming repeating structures (Tzvelev, 1993a,b), because every lateral shoot is homologous to the primary shoot, which is formed from the embryonic bud (Rytova and Tzvelev, 1982). In this case "the specimen" (e.g., in *Quercus)* is a very complicated system, which consists of repeated structures of different orders.

It was proposed that these structures be called "modules" (White, 1979). However, the introduction of this technogenic term into biology was not at all successful, though it would be useful to have a common accepted term for the repeated structures of different orders. Other authors have offered the "complementary" models of the shoot structure (Gatsuck, 1995; Kusnetzova, 1995). The conception expounded in this article corresponds to the metameric or phytonic shoot model (Gray, 1879).

The relatively great primitivity of the vegetative organs in monocotyledons in comparison with dicotyledons has already been noted. Probably, the presence of only one cotyledon in the embryo is also the more primitive peculiarity of the monocotyledons. This cotyledon (scutellum in grasses) together with other embryonic parts represents one phytomer, which can be called primary. Like vegetative phytomers of the shoots, the primary phytomer forms the plumule, which gives rise to the primary shoot. The formation of the embryonic bud on the mother plant is a peculiar "viviparity" and probably can be considered the secondary feature, because there are no such structures in the seed of gymnosperms. Therefore, the weaker development of the plumule in some families of angiosperms could be considered a primitive feature, inherited from gymnospermous ancestors. The absence of the plumule and the very weak differentiation of the primary phytomer or embryo in the family Orchidaceae may also be primitive signs. In spite of their very high flower specialization and mycotrophy, the orchids are undoubtedly one of the most ancient angiospermous groups (their modern distribution testifies to this), and as a result of mosaic evolution very primitive features were preserved in this group.

The phytomer nature of the embryo carries its ability for unitiered polymerization like shoot phytomers. This suggests the primary but not the secondary nature of the monocotyledonous embryo, in comparison with the polycotyledonous (including dicotyledonous) embryo (Grassl, 1967; Tzvelev, 1993a). The ability of the cotyledons to modify into the photosynthetic above-ground organs, peculiar to the dicotyledons (probably the secondary feature) agrees with the phytomer nature of the cotyledons. The idea of the primary nature of the dicotyledonous embryo is widespread, and from this the monocotyledonous embryo is drawn via "syncotyly" or "heterocotyly"; however, these last two possibilities have little probability (Tillich, 1992). The usual presence of two or more cotyledons in gymnosperms was one of the arguments for the primary dicotyly, though it is obvious enough that modern gymnosperms have no relation to the ancestors of the angiosperms.

With the unitiered polymerization of "leaf part" of the primary phytomers the dicotyly of the embryo turned out to be more advantageous in evolutionary terms, because the plumule passes from lateral to apical position and is protected by cotyledons from both sides. It is interesting that in the duckweeds the weakly differentiated embryo, the primary phytomer, evidently, is also deprived of its upper, "leaf" part; instead of the plumule, one or two young fronds are formed on it, which are easily detached from the maternal frond or embryo (Iliyna, 1990). It is quite possible that the proembryo, and not the differentiated embryo, mostly corresponds to the primary phytomer.

Thus, the phytomer (phyton, or phytoid) concept offers a new approach to the solution of some controversial questions of the evolution and phylogeny of higher plants, and also to the evaluation of the primitive or advanced nature of some features. It should be noted once more that in the course of the long evolution of higher plants the stem parts of the phytomers, the internodes, are increasingly integrated up to the formation of the thick woody trunks of trees, and their leaf parts or phyllomes are increasingly separated from them. The phytomers are able to polymerize not only in different tiers, but also in one tier or node; the result of this is the opposite or verticillate leaf arrangement (probably the secondary sign). Undoubtedly, the phytomer capacity for internode elongation and lateral bud formation (the branching) is secondary. Embryo of the seed is the primary phytomer, which is able to form lateral buds as the shoot phytomer does; these buds during the primary phytomer polymerization in one tier become apical. It follows that embryos with two or more cotyledons, as well as embryos with well-developed lateral plumule, are to be considered more advanced than the monocotyledonous embryos.

PART FIVE–MOLECULAR-GENETIC ASPECTS OF REPRODUCTION

FLOWER DEVELOPMENT GENETICS

One of the most convenient models for studying morphogenetic processes in plants is the flower, because it contains a number of diverse structures despite the short time of its development. It is very important that the alternation of gametophytic and sporophytic generations, characterizing the specifics of angiosperm life cycle, occurs during development of these organs. Processes such as micro- and megasporogenesis, pollination and fertilization, embryo development, and finally seed and fruit formation take place in the flower.

One of the widely used models in flower development genetics is the annual plant *Arabidopsis thaliana.* The *Arabidopsis* flower, as in many other Cruciferae is characterized by actinomorphic structure and contains four sepals, four petals, six stamens (four long and two short ones) and one pistil, formed by two joint carpels. The initiation of these organs proceeds in a strictly determined order. Initially the sepals and primordia of the first petals form. The young petals stop developing before the primordia of gynoecium start growing. Stamens begin to develop only after all these events. The long (internal) stamens develop first and short (external) ones afterward.

Flower development in *Arabidopsis* proceeds through several stages:

— formation of vegetative apical shoot meristem,

— transformation of the vegetative into the generative apical meristem (the inflorescence meristem),

— formation of floral meristems,

— initiation of flower organs.

The genetic control of flower development was studied through large-scale works on breeding and detailed investigation of defective mutants in various stages of regeneration. Such works are being undertaken on *Arabidopsis* and *Antirrhinum.* Despite the taxonomic distance of these species they appeared to have generally the same scheme of genetic control of flower development, and many genes involved in this control are homologous (Schwarz-Sommer *et ah,* 1990; Coen, 1991; Coen and Meyerowitz, 1991; Weigel and Meyerowitz, 1993). Similar results were accumulated for many other species of dicotyledons and monocotyledons, suggesting the high evolutionary conservatism of the mechanisms of genetic control of flower development.

Floral induction or triggering of flowering programmes causes the transformation of the vegetative meristem into the generative meristem and is regulated by various exogenous as well as endogenous factors. The factors significantly influencing floral induction in *Arabidopsis* are day length and temperature conditions (Bernier *et ah,* 1993). Long day (more than 14-16 hours) is favourable for early transition to flowering, whereas short day (8-10 hours) retards floral induction. Short-term treatment of seedlings with low temperature (vernalization) is also favourable for early flowering. A number of mutants were obtained possessing altered reaction to these environmental factors. Some of these mutants *(fca, fd, fe, fha, fie, fpa, ft, foe, fwa, fy* etc.) are insensitive to long day and low temperature, whereas others *(elfl, elfl, elf3,* em/1, em/2, *spy, tfl* etc.) are able to flower early regardless of day length (Weigel, 1995a,b).

Early flowering is caused by mutations in genes EARLY FLOWERING *(ELF1,* 2, 3), EMBRYONIC FLOWER *(EMF1,* 2) and TERMINAL: FLOWER *(TFL).* Later flowering is caused by mutations in genes *CO, FCA, FD, FLA, FE, FPA, FRI, FT, FVE, FY, GI. LD, GAL*

Formation of a single flower almost immediately after seed germination is characteristic of *emfl* and em/2 mutants (Coupland, 1995). Judging by the fact that almost the entire vegetative stage of development is omitted in these mutants, the normal *EMF* gene product is required to suppress the generative programmes, so that the plant will have enough time to pass through a long vegetative stage. A model was proposed to describe the transition to flowering. The main role in this model is played by the repressor, blocking the switch from the vegetative to the generative developmental stage. The main candidates for the role of the repressor are the *EMF1* and *EMF2* genes. The *EMF2* gene belongs to transcriptional factors, and the protein coded by this gene has the domain of "zinc finger" type. This protein is structurally homologous to the protein of *FLS2* (FERTILIZATION INDEPENDENT SEED) gene, classified as belonging to polycomb family of genes. The function of the protein coded by the *EMF1* gene is unknown, but it is also classified as a transcriptional factor based on its structure. The *EMF1* and *EMF2* genes thus play the key role in the transition to flowering. The *API* and *AG* genes express ectopically in the seedlings of em/mutants, suggesting they serve as the negative regulators of later genes of flowering (Leyser and Day, 2003). The *tfll (terminalflower)* mutations also cause the generative meristem to be formed earlier, shortening the vegetative phase significantly (Shannon and Meeks-Wagner, 1991). The long vegetative stage of development in plants is therefore provided by active suppression of the generative programmes. External factors (long day and short treatments with low temperature) seem to be able to relax this suppression in favour of earlier flowering.

The formation of the floral meristem is just another change in the meristem functional type. In this case, the inflorescence meristem is transformed into floral meristem. The formation of the floral meristem depends much less on environmental factors and is much more strictly controlled by plant genotype than floral induction. A number of mutants were obtained in *Arabidopsis* and *Antirrhinum,* which are defective in some elements of flower meristem formation up to its complete absence (Table 22). Genetic analysis of these mutants allowed identification of specific genes controlling the floral meristem formation.

The *Ify (leafy)* mutants (Fig. 58) are unable to form normal meristems of flowers; secondary inflorescence meristems are induced instead (Coen *et ah,* 1990; Irish and Sussex, 1990). It should be noted that secondary meristems of inflorescences arise in *Arabidopsis* under normal conditions only at the lowest (and earliest-formed) part of the inflorescence. At the same time, the floral meristem formation in the *Ify* mutants appears to be shifted toward the upper (and later-formed) zones of the inflorescence, and the flowers initiated retain a number of features inherent to the inflorescence: the floral bracts develop, which are formed in inflorescences and are absent in flowers of wild type; the organs of the flower are arranged in spiral order; the distance between the organs in the flower is much greater than in normal flowers.

The *ap* mutations have quite similar manifestations. In the plants homozygous in the mutant allele *apl-1* (Fig. 59), the flowers contain secondary floral meristems, initiated in sepal axils. The tertiary floral meristems develop similarly inside these secondary flowers. So the floral meristems in *ap* mutants are able to form the floral

Table 22. The main genes controlling flower development in *Arabidopsis thaliana* (1) and *Antirrhinum majus* (2).

Stage	Gene		Mutant phenotype	Gene function	Gene product
	1	*2*			
Flower-bearing stem proliferation	*TFL1* *TFL2*	*CEN*	AM transformation into FM; early flowering	Maintenance of AM activity	Protein with unknown function
FM formation	*LFY*	*FLO*	FM transformation into shoot meristem (for *Ify* partial)	Primordia transformation into FM; positive regulation of homeotic genes	Transcriptional factor
FM formation	*UFO*	*FIM*	First flowers replaced with secondary inflorescences; change in flower organ size and number	FM formation; positive regulation of homeotic genes	Cell cycle regulating protein
FM formation; setting direction of differentiation in organs of whorls I and II	*API*	*SQUA*	Sepals replaced with leaves and petals replaced with stamens (or absent); formation of secondary flowers in axils of whorl I organs	Participation in FM formation; function A	Transcription factor containing MADS-domain
FM formation	*CAL*	-	The *cal* mutants have normal phenotype, but the double *apl cal* mutants show FM transformation into inflorescence meristems	Partly compensates API gene function in *apl* mutants (the homologue of API gene)	Transcription factor containing MADS-domain
FM formation; setting direction of differentiation in organs of whorls I and II	*AP2*	-	Sepals replaced with carpels or leaves and petals replaced with stamens (or absent)	Participation in FM formation; function A; negative regulation of *AG* gene	Transcription factor containing domain AP2

Table 22 *(Contd.)*

Setting the direction of differentiation in organs of whorls II and III	*AP3*	*DEFA*	Petals replaced with sepals and stamens replaced with carpels	Function B; positive *PI* gene regulation	Transcription factor containing MADS-domain
Setting the direction of differentiation in organs of whorls II and III	*PI*	*GLO*	Petals replaced with sepals and stamens replaced with carpels	Function B; positive *AP3* gene regulation	Transcription factor containing MADS-domain
Setting the direction of differentiation in organs of whorl IV	*SUP*	-	Carpels replaced with stamens	Negative regulation of class B genes expression in whorl IV	Transcription factor containing "zinc finger domain
Setting the direction of differentiation in organs of whorls III and IV	*AG*	*PLENA*	Stamens replaced with petals and carpels replaced with sepals; prolonged FM proliferation	Function C; negative API and *AP2* genes regulation in whorls III and IV; FM proliferation restriction	Transcription factor containing MADS-domain
Regulation of FM size and number of organ primordia in the flower	*CLV1* *CLV2* *CLV3*	- - -	Similar phenotypic manifestation; increase in sizes of all meristem types, formation of large number of flowers and separate flower organs	Suppression of cell divisions and transition to differentiation	Products of three genes form CLV-complex, suppressing *WUS* expression; CLV1 is transmembrane proteinkinase; CLV2 forms receptor comple with CLV1 gene produ CLV3 is the extracellul protein capable of secretion

Note: AM, apical meristem; FM, floral meristem.

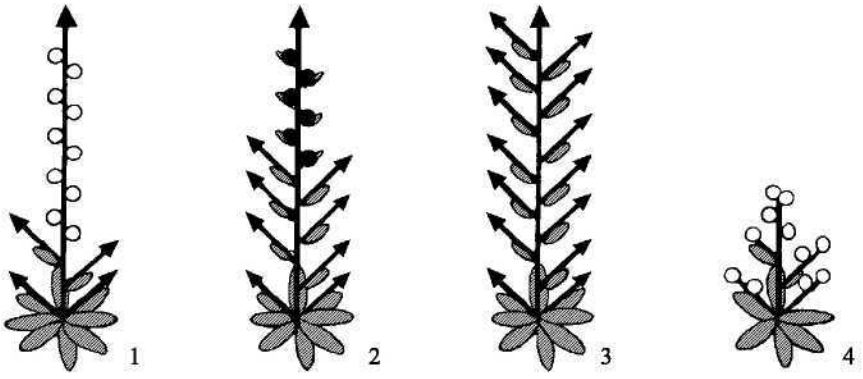
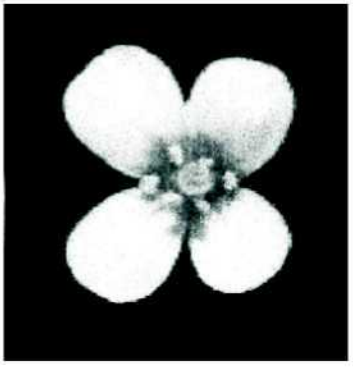
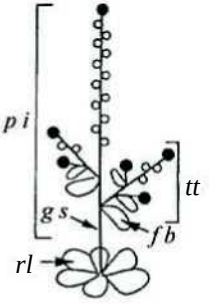


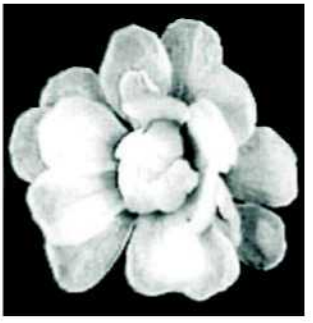
Fig. 58: Schematic representation of wild type *Arabidopsis thaliana* plants and mutants at the floral meristem identity genes. The arrows mark the inflorescence meristem, the light circles indicate normal flowers, the dark ones indicate abnormal flowers.
1 - wild type; 2 - *leafy;* 3 - *leafy, apetalal;* 4 - *terminal flowerl.*





Wild type

lfy



Agamous

Fig. 59: The *Arabidopsis thaliana* mutants at the flower organs identity genes.

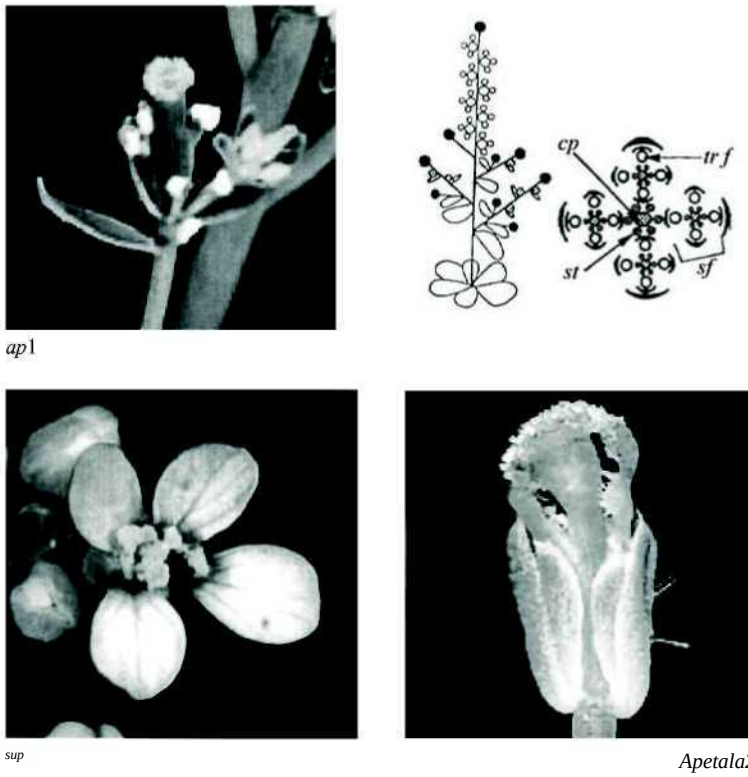


Fig. 59 *(Contd.)*

r I - rosette leaves, *g s* - generative shoot, *p i* - primary inflorescence, s *i* - secondary inflorescences; the floral bracts *(f b)* are situated at the base of inflorescences; the leaves and flowers are arranged in spiral order; the flowers are shown as white circles, the inflorescences as black ones, sf - stamens, *cp* - carpels, *sf*- secondary flowers; the tertiary flowers *(trf)* develop inside the floral bracts of the secondary flowers.

meristems again, suggesting their functional similarity with the inflorescence meristems.

Judging by the phenotype of the dual mutants *Ify apl* (the complete transformation of inflorescences into vegetative shoots), the products of the corresponding genes control some parallel and partly overlapping pathways leading to floral meristem formation (Fig. 58). Similar results were obtained for the mutations *flo (floricaula)* and *squa (squamosa)* in *Antirrhinum.*

The genes *LFY* and *API* from *Arabidopsis* and also *FLO* and *SQUA* from the *Antirrhinum* were cloned and sequenced (Coen *et ah,* 1990; Mandel *et ah,* 1992; Weigel *et ah,* 1992). The results of the molecular-genetic analysis showed that the *FLO* and *LFY* genes encode homologous proteins with proline-enriched parts, which are characteristic of the transcriptional factors. The idea that the product of the *LFY* gene is the transcription regulator gets indirect support from data about the localization of

this protein inside the nucleus (Weigel and Meyerowitz, 1993). The results of API and *SQUA* genes analysis supported their homology to each other and allowed their classification as members of the family of MADS transcriptional factors, widely known in many organisms. Moreover, it was shown that all four genes are expressed at the earliest stages of floral meristem development, that is in conformity with the putative role of their products as factors defining the development of the floral meristem (Coen *et al*, 1990; Weigel *et al*, 1992).

Other genes also participate in floral meristem formation. The effect of *ap* mutations was dramatically enhanced in the presence of mutant alleles of the CAULIFLOWER *(CAL)* gene. At the same time, *cal* alleles have no independent phenotypic manifestation or influence on the degree of *Ify* mutation manifestation (Bowman *et al*, 1993). The effects caused by the mutant alleles *ap* or *Ify* could be enhanced by mutations in *ap2 (apetala.2)* and *clvl (clavatal)* genes, which also do not influence floral meristem formation. Thus, not only *LFY* and API genes, coding key regulatory molecules, participate in floral meristem formation in *Arabidopsis*, but also a number of another genes, demonstrating noticeable influence in the absence of one of the main factors. Reaching the threshold level of *LFY* gene expression is the critical factor for floral primordium formation.

Unlike the genes considered above, coding the positive regulators of floral meristem formation, the product of TFL1 (TERMINAL FLOWER 1) gene suppresses the transformation of inflorescence meristem into the floral meristems. The mutants on this gene form small inflorescence carrying just a few flowers and ending with the terminal flower (Fig. 58). The secondary inflorescence meristems do not form at all and the terminal flower consists of two or three incomplete flowers. Thus, the secondary inflorescence meristems normally initiated in wild type plants are in *tfl* mutants replaced with the meristems of single flowers. The primary inflorescence meristem in these mutants undergoes transformation into two or three closely arranged floral meristems, whereas the primary inflorescence meristem under normal conditions in this species potentially is not restricted in growth and is never transformed into the floral meristem. The product of TFL1 gene is probably the antagonist of products of *LFY* and *API* genes and able to suppress their activity in the primary inflorescence meristem. According to this, the manifestation of *tfll* mutation is caused with extension of the activity zones peculiar to the *LFY* and API genes (Weigel *et al*, 1992; Bowman *et al*, 1993; Weigel and Nilsson, 1995). One of the main functions of *LFY*, *API* and *CAL* genes is the initiation of transcription of the main genes controlling flower organ formation (Leyser and Day, 2003).

The formation of flower organs. The floral meristem of *Arabidopsis*, as in many other angiospermous species, forms four types of organs, characterized by their circular arrangement in the flower. The relative order of the whorls formed by the organs of each type always stays unchanged: the first (external) whorl occupied by the sepals, the second one by the petals, the third one by the stamens, and the fourth (central) whorl by the carpels. At the same time, a number of mutant forms were obtained with changed sequence of whorls in the flower (Fig. 59). The main feature of such mutant forms is the aberrations in two neighbouring whorls simultaneously. The homeotic genes API, AP2, AP3, *PI* and *AG* are of special interest. The mutations in these genes cause some flower structures to be replaced with others (Bowman *et al*, 1991a,b; Coen and Meyerowitz, 1991; Meyerowitz *et al*, 1991; Fig. 58). So, sepals are replaced by carpel-like structures and petals by stamens in the mutants in APETALA

1 and 2 (API and *APT)* genes. The mutants *apl/ap2* as a result have the following order of organs in the flower: carpels, stamens, stamens, carpels. The mutations in APETALA 3 (AP3) gene cause the transformation of petals into sepals and of stamens into carpels. The same effect is caused by the mutations in PISTILATA *(PI)* gene. That is why the flowers of *ap3* and *pi* mutants have the following organ order: sepals, sepals, carpels, carpels (Bowman *et ah,* 1989). In case of mutation in AGAMOUS *(AG)* gene, stamens are transformed into petals, and carpels are transformed into sepals. Moreover, the mutants in *AG* gene are characterized by the undetermined development of the floral meristem, which is why the flower of *ag* mutants contains numerous repeating sequences of organs: ..., sepals, petals, petals, sepals,....

All data listed above were generalized in 1991 into a working hypothesis explaining interaction between the homeotic genes of the flower. This hypothesis was called the "ABC" model or "war of the whorls" theory (Coen and Meyerowitz, 1991). The main principles of this hypothesis are the following:

1. The floral meristem during its development is subdivided into four concentric areas, conventionally referred to as "whorls" and numbered from the first to the fourth from the periphery toward the centre of the flower.
2. The three types of activity are expressed in the different whorls: activity A in whorls I and II, activity B in whorls II and III, and activity C in whorls III and IV. Activities A and C are antagonists and each suppresses the activity of the other.
3. The destiny of each primordium in the flower is defined by the combination of activities expressed in the corresponding whorl. Activity A causes the sepals to arise, the interaction of activities A and B causes petal formation, the interaction of activities B and C causes stamen formation, and the carpels arise as a result of activity C.

According to this scheme, the defect of activity A causes activity C to be expressed in all four whorls. Thus, the localization of activities in the floral meristem will be C BC BC C, which results in the formation of a flower containing carpels, stamens, stamens, carpels. Such a flower has absolutely no petals. That is why the corresponding genes are named APETALA 1 and 2 (API and AP2). The mutations affecting activity B lead to the following distribution of the activities in the floral meristem: A A C C. This scheme of development provides the formation of flowers with complete absence of petals and stamens and with additional whorls of sepals and carpels instead. It was revealed that such plants with flowers containing sepals, sepals, carpels, carpels could arise because of mutation in two genes, named APETALA 3 (AP3-without petals) and PISTILLATA *(PI*-multipistillous). The mutations disturbing the activity C cause the antagonistic activity A (the product of AP2 gene) to be present in all four whorls. Thus, the following type of the floral meristem is characteristic for the corresponding mutants: A AB AB A (sepals, petals, petals, sepals). Such mutants are totally lacking in flower generative structures (stamens and carpels), so the gene is named AGAMOUS (AG) — asexual. It should be noted that the *ag* mutants are characterized by undetermined floral meristem development and for this reason the flowers contain numerously repeating whorls of sepals and petals.

The "ABC" hypothesis is in good conformity with phenotypes of the multiple mutants. So the double mutants *ap2 api/pi* (C C C C) have flowers consisting of carpels only. The undetermined flowers of the double mutants *ap3/pi ag(AAA* A) contain only sepals. The double mutants *ap2 ag (-* B B -) have only undetermined

flowers, containing leaf-like organs and distorted structures resembling petals and stamens at the same time. Finally, the triple mutants *ap2 ap3/pi ag* (——) are characterized by transformation of the flowers into the undetermined analogues of vegetative meristems with the spiral order of the typical leaf-like structures. This fact convincingly suggests that the flower is really the modified shoot.

The ABC model was later slightly modified in consideration of new data on the genes of flower organ identity and products of their interaction. The additional component of activity A was revealed, which is coded by *API* gene, and its expression in whorls III and IV is negatively regulated by the *AG* gene (Mandel *et al.,* 1992). At the same time, the AP2 gene product in whorls I and II negatively regulates the *AG* gene itself.

The phenotypes of the mutants on *API, AP3, PI* and *AG* genes suggest a number of functions these genes serve. First, they all participate in the identification of the flower organs. Second, the changed number of the organ primordia in the mutants' *ap2* and *ag* flowers (two carpels instead of four sepals and six stamens instead of four petals in case of *ap2* and the opposite relation in case of *ag)* indicate the influence of these genes on initiation of the flower organ primordium. Finally, yet another function of the *AG* gene product is the establishment of the determined type of floral meristem development.

It is significant that activity of the flower organ identity genes is regulated with *LFY* and *API* genes (Weigel and Meyerowitz, 1993), which express not only at floral meristem initiation, but during flower development as well (Mandel *et al.,* 1992; Weigel *et al.,* 1992). In particular, the products of *LFY* and *API* genes activate the expression of *AP3* and *PI* genes and regulate the character of *AG* gene expression. Thus, the processes of floral meristem initiation and establishment of flower organ identity are closely related.

As was noted before, the product of AGAMOUS gene is the key molecule controlling the development of the reproductive organs of the flower (stamens and carpels). At the same time, this gene provides the determined type of floral meristem development. Judging from the fact that all known *ag* mutants show simultaneous disturbance of both functions, the corresponding active centres of the molecule are either overlapping or unable to function separately. At the same time, three types of transgenic plants were obtained after the treatment of normal *Arabidopsis* plants with antisense copies of *AG* gene, linked with the strong constitutive promoter 35S-CaMV: transformants of type I, similar to *ag* mutants; transformants of type II, forming undetermined flowers with partly modified reproductive organs; transformants of type III, forming undetermined flowers with normally developed stamens and carpels. Such flowers form the new whorls of the stamens and carpels inside their gynaeceum, and were called "mutreshkas" for this reason.

Thus, the separation of two AG protein functions is possible and requires a certain level of their expression. The number of AG molecules upon such expression level is probably quite enough for normal reproductive organ development but not enough for floral meristem determination.

The *AG* gene is one of a family of genes coding AG-like transcriptional factors. These genes are called *AGL* (from AGAMOUS-like). There are presently more than 20 AGL genes described in *Arabidopsis.* Six of them are characterized in detail. As their transcription proceeds in the apical meristem after its differentiation into floral meristem, the corresponding proteins probably are also components of the regulatory

cascade. Indeed, the *AGL5* gene contains in its promoter region the area for the specific recognition of MADS-proteins and does not express in *ag* mutants. In opposition, the *AGL6* gene transcription is increased in the same mutants. Thus, the AG protein is able to influence directly or indirectly the transcription of other MADS-genes. On the other hand, the AGL14 gene expression proceeds long before the beginning of the *AG* gene transcription.

The product of the *AG* gene appears to be able to form dimers with some AGL family proteins. This was concluded on the basis of results obtained with the yeast dihyhrid system. It turned out that the K-domain of the AG protein is able to interact efficiently with K-domains of the AGL2, AGL4, AGL6 and AGL9 gene products. Thus, it is quite probable that the AG protein normally forms not only the homodimeric complexes, but also the different types of heterodimers.

For the successful termination of the floral meristem the activity of at least several genes *(AG, FON, CLV* and *SUP),* revealed by the analysis of the *Arabidopsis* mutant forms, is necessary.

The *CLAVATA, SUPERMAN* and *FLORAL ORGAN NUMBER* genes regulate the quantity of primordia in the flower, and also the determination of the floral meristem.

The several *CLAVATA* genes *(CLVl, CLVl* and *CLV3)* with the similar phenotypic manifestation of mutations are described (Leyser and Furner, 1992; Clark *et al.,* 1993, 1995). The mutants analysed especially completely are those with aberrations in *CLVl* and *CLV3* genes. Such plants are characterized by enlarged sizes of all types of apical shoot meristems: vegetative meristem, inflorescence meristem and floral meristem. The enlarged apical meristem contains a larger number of the actively dividing undifferentiated cells, which causes the formation of larger number of flowers (in case of inflorescence meristem) or separate flower organs (in case of floral meristem). The mutant phenotype *clvl* shows the development of the additional carpels inside the gynoecium. However, even with the most sharply pronounced mutant alleles *(clvl-1* and *clvl-4),* the growth and development of the additional carpels are restricted and do not cause the fracture of the gynoecium walls (Clark *et al.,* 1993). The size of the apical meristem is generally supported by the activity of two main genes *WUS* and *CLV.* The function of the WUS gene is to support stem cell proliferation, whereas the products of the *CLV* genes family suppress cell division and activate their transition toward differentiation. The control for this process is provided by the negative feedback mechanism. The product of the *CLV3* gene is the extracellular protein, capable of secretion. After secretion it forms a complex with the heterodimeric protein, which arises from two proteins, coded by the *CLVl* and *CLV2* genes. Thus, the *CLV3* gene product is the signal molecule, and the *CLVl* and *CLVl* gene products form the receptor complex. The complex, formed as a result of expression of *CLV* family genes, restricts the WUS gene expression. On the other hand, based on the mechanism of feedback inhibition, the WUS gene itself controls the *CLV3* gene expression, facilitating the *CLV* complex formation. The *CLVl* gene regulates the synthesis of the typical transmembrane protein kinase (Brand *et al.,* 2000; Trotochand *et ah,* 2000). The mutations in *CLV* genes thus cause increase in the flower organ number and the slowed-down termination of the floral meristem due to increased size of the meristem itself.

The other mechanism of increase in number of flower organs and establishment of non-determined floral meristem development is the prolongation of meristem activity, which continues after formation of the first three flower organ primordia

whorls. The flower organs increasing in number are only the stamens and carpels in mutant on *FON* gene (Haughn and Sommeville, 1998).

The analysis of the double mutants on *CLV1* and *FON* genes showed that these genes control the development of the floral meristem in different ways. Indeed, the *clvl fonl* and *clv3 fonl* double mutants are characterized by more pronounced aberrations of the floral meristem determination and increase in flower organ number as compared with the single gene mutants on these genes. A much larger number of stamens and carpels therefore develop in flowers of the double mutants than in flowers of *CLV1* or *FON* single gene mutants. At the same time, the double mutants *clvl-4 fonl-1* show much more intensive growth and development of the additional carpels inside the ovary than the single *clvl-4:* mutants. The internal carpels in some flowers break the ovary wall and develop into additional pistils. In double mutants of the *clv3-2 fonl-1* genotype in some flowers, the floral meristem cells continue their divisions after flower organ formation, forming a mass of undiff erentiated cells inside the ovary instead of additional carpels.

Thus, *CLV1* and *FON* genes activity is necessary for successful termination of the floral meristem, and these genes use independent means of meristem development control and different mechanisms of meristem activity restriction.

The gene *SUPERMAN (SUP)* also belongs to genes controlling the number of organs in the flower (Schultz *et al,* 1991; Bowman *et al,* 1992). The mutant phenotype *sup* shows the formation of several stamen whorls, with number varying from 8 to 26 (Bowman *et al,* 1992). The most obviously manifested alleles, such as *sup-1,* show significant increase in stamen number in the flower, usually accompanied by loss of carpels. Analysis of the double mutants *sup ap3* and *sup pi s*nowed that the product of the *SUP* gene negatively regulates the expression of *AP3* and *PI* genes in the fourth whorl of the flower organs. Accordingly, the mutant phenotype arises owing to expansion of expression of genes *AP3* and *PI,* normally expressed only in second and third whorls, to the fourth whorl. The *SUP* gene does not define the identity of flower organs in the second and third whorl, but its activity is important at more advanced stages to maintain the border between these whorls (Sakai *et al,* 1995). At the same time, the formation of several additional whorls of stamens on the floral meristem suggests indeterminacy of the floral meristem in mutants at *SUP* gene.

Floral meristem termination could be disturbed also if the meristem returns to its earlier programme of development. Such a phenomenon is caused by aberrations in maintenance of floral meristem identity. Available data (Mokamuro *et al,* 1996) suggest that maintenance of floral meristem identity requires the activity of at least two genes providing other important regulatory functions. Such conclusions are based on the analysis of some cases of floral meristem reversion, i.e., return of the flower meristem to functioning like the vegetative meristem. Such reversions, causing development of the vegetative shoot from the flower, could be induced by manipulating the photoperiod in plants mutant at the *AG* gene, and also in heterozygotes at *LFY* gene. As was noted before, the *AG* gene is necessary for establishing flower generative organ identity and termination of the floral meristem, whereas the *LFY* gene defines the identity of the floral meristem during its formation and regulates the activity of some homeotic genes.

It is not surprising that the gene *WUS (WUSHEL)* also plays an important role in the regulation of flower development. It is expressed in the centre of floral meristem and is necessary for support of its activity. *WUS* codes the homeodomain, containing

the transcriptional factor, which can be bound with the regulatory sequence of the *AG* gene's second intron. The transcriptional factor coded by the *LFY* gene is also bound with this area of *AG* gene. Thus, the WUS and *LFY* genes activate *AG* gene expression in the centre of the flower (Leyser and Day, 2003).

The analysis of double *ag wus* mutants and *wus* mutants showed that WUS is required for undetermined development of mutant *ag* flowers. These results imply that the *AG* gene inhibits the WUS gene in the centre of the floral meristem. The WUS and *AG* genes are thus components of the integrated system of negative regulation in which the *WUS* gene activates the *AG* gene at the formation of flower organs, and at a later stage the *AG* gene inhibits the WUS gene, making the flower meristem determined (Leyser and Day, 2003).

Thus, the process of floral meristem termination is related closely with other aspects of flower development and a number of multifunctional genes participate actively in its control.

Molecular mechanisms of flower development. One of the most important factors established by investigations into genetic control of flower development is that many of the genes described above belong to the conservative group of transcriptional factors, presented not only in plant genomes, but also in other groups of living organisms.

The products of *API, AP3, PI* and *AG* genes are the transcriptional factors. The protein *API* is the original type of the transcriptional factors, whereas the products of *AP3, PI* and *AG* genes contain the highly conservative DNA-binding domain (MADS-domain). This domain of 56 amino acids is named for the first letters of four genes coding the transcriptional factors with the highly homologous DNA-binding domains (Schwarz-Sommer *et al,* 1990; Yanofsky *et al,* 1990):

MCM1 is the yeast gene, controlling the number of copies of mini-chromosomes in the cell; *AGAMOUS* is the homeotic gene of *Arabidopsis; DEFICIENS* is the homeotic gene of *Antirrhinum* corresponding to the AP3 gene; *SFR* is the human gene coding the regulatory factor of the serum.

The characteristic of the MADS-genes products (MADS-proteins) is not only the presence of the conservative DNA-binding domain, but also the similarity of their general structure. Each of them consists of five domains: N-end, MADS- (necessary for specific DNA-binding; Yanofsky *et al,* 1990), I- (slightly conservative and providing the protein dimerization), K- (containing sequences similar to keratins and also responsible for protein dimerization; Ma *et al,* 1991; Jack *et al,* 1992) and C-end domain (slightly conservative and necessary for functioning). All MADS-proteins are dimers. Here, the products of *API* and *AG* genes form exclusively homodimers, whereas the *AP3* and *PI* proteins function only as heterodimeric complexes. That is why the *ap3* and *pi* mutants show similar phenotype.

All MADS-proteins contain the highly conservative DNA-binding domain and can be bound by the oligonucleotide motif $CC(A/T)_6GG$, which is named CArG-box (Pollock and Treisman, 1990; Wynne and Treisman, 1992). Indeed, various MADS-proteins of *Arabidopsis* compete successfully with each other *in vitro* to bind with the same sequences of the nucleotides (Mueller and Nordheim, 1991; Huang *et al.,* 1993; Shiraishi *et al.,* 1993). At the same time, the quite autonomous transcription activity is doubtless characteristic for each type of MADS-protein. Chimerical constructions were created to resolve this paradox. In these constructions, the C-end parts of *API,*

AP3, *PI* and *AG* genes (including their I-, K- and C- domains) were linked with the MADS-domains of *SRF* and *MEF2* genes of the animals. Despite the slightly different DNA-binding abilities of *SRF* and *MEF2* proteins, the products of both chimerical constructions are the full functional analogues of normal API, AP3, PI and AG proteins (Riechmann and Meyerowitz, 1997). Thus, it is not only the DNA-binding domains of MADS-proteins that define the specificity of their action. Furthermore, it was shown that the products of *AP3* and *PI* genes, as well as products of their homologues from *Antirrhinum (DEFA* and *GLO,* respectively) are unable to bind DNA separately, but after heterodimer formation they could successfully bind the target sequence (Schwarz-Sommer *et ah,* 1992). Molecular investigations have shown that the active form of all MADS-gene products is the homo- or heterodimer, and MADS-domain is responsible for the dimerization (Riechmann *et ah,* 1996a,b; Riechmann and Meyerowitz, 1997).

The analysis of various *Arabidopsis* mutants showing certain anomalies in the flower development thus allow us to propound a theory about the cascade regulation of this process at the transcriptional level. In particular, the investigation of homeotic *Arabidopsis* mutants led to formulation of the "ABC" model. The analogous mutants were obtained in another model, which is quite distant taxonomically from the Cruciferae. This fact suggests that the genetic control of flower development is obviously universal (Schwarz-Sommer *et ah,* 1990; Coen, 1991; Coen and Meyerowitz, 1991; Weigel and Meyerowitz, 1993).

As a result of the investigations into genetic control of flower development, it becomes clear that these processes are controlled by a large number of regulatory proteins forming a highly complicated network of closely interacting elements. Each element of this network can control several different processes at the same time. Many genes, particularly TFL1 and API, participate in more than one stage of flower development, suggesting that the same regulatory protein could interact with different genes at different stages of development. According to this, mutations affecting different parts of the same regulatory gene could show quite different manifestation. Thus, detailed investigation of such gene functions is impossible without analysis of as wide a range as possible of mutations affecting various aspects of flower development.

Genetic Analysis of Ovule Development (Plate XII)

In contrast to the tremendous knowledge about ovule morphology of a vast number of species (see Vol. 1), little was known until recently about the genetic and molecular mechanisms controlling its development. The situation has changed with the use of *Arabidopsis thaliana* as a model system to study plant development at the genetic and molecular level. This is accompanied by a growing interest in ovules in the context of flower evolution (see review Endress, 1997). Thus, we will focus largely, though not entirely, on a summary of our knowledge about the genetic and molecular control of *Arabidopsis* ovule development.

Ontogenesis of the *Arabidopsis* ovule. A number of laboratories contributed to the investigation of *Arabidopsis* ovule development at the cellular and sub-cellular level (Webb and Gunning, 1990; Mansfield *et ah,* 1991; Robinson-Beers *et ah,* 1992; Modrusan *et ah,* 1994; Schneitz *et ah,* 1995; Christensen *et ah,* 1997) and a convenient staging system has been established (Schneitz *et ah,* 1995).

Stage 1 defines the early initiation and outgrowth phase of ovule ontogenesis. About 40-60 ovules per gynoecium originate as finger-like protrusions along the placenta. At early stage 2 the archesporial cell becomes visible as a subepidermally located enlarged cell at the apex or nucellus. The archesporial cell directly gives rise to the megaspore mother cell, which will eventually undergo meiosis at the end of stage 2.

Gametophyte formation takes place during stage 3 following the Polygonum-type from the bottom-most megaspore of the tetrad (Willemse and van Went, 1984). The mature embryo sac consists of the two synergids and the egg cell at the micropylar end, the large two-nuclear central cell, and three antipodal cells at the chalazal pole.

During early to mid-stage 2, the inner and outer integuments are initiated from the epidermal cell layer flanking part of the subnucellar region (chalaza). The integuments eventually envelop the nucellus, leaving open only a small cleft, the micropyle, through which the pollen tube enters during the fertilization process. The outer integument experiences asymmetric growth with the posterior (abaxial, see below) side undergoing more extensive cell division and elongation. The ovule therefore will exhibit a characteristic kink (anatropy) with the micropyle situated next to the developing funiculus (Gifford and Foster, 1989). Within the funiculus the vascular strand develops.

In summary, the ovule of *Arabidopsis thaliana* is tenuinucellate and carries a Polygonum-type embryo sac. It is bitegmic and campylotropic at fertilization. The campylotropy changes to amphitropy during the early post-fertilization phase.

Fundamental processes controlling ovule development. It has been reasoned that, for ovule development to occur, several processes have to take place: initiation and outgrowth, specification of identity, pattern formation and eventually morphogenesis (Schneitz *et ah,* 1995). One can formally regard them as independent processes. However, they obviously also have to be coordinated in a spatial and temporal manner, and they can take place a number of times.

In this context it is worth mentioning that growth control is of particular importance in plant organogenesis (Meyerowitz, 1997). As a rule, cells or cell populations in plants do not move relative to each other. Thus, the size, pattern and shape of the ovule will be largely achieved through regulation of the timing and spatial patterns of cell divisions and cell shape changes. This is also reflected by the results of the genetic analysis.

Identity. Culture experiments in tobacco indicated that the commitment to ovular fate undergoes sequential restrictions from first gynoecial to second ovular fate (Evans and Malmberg, 1989), and that commitment takes place after the primordia are detectable but before morphological signs of nucellus and integument development emerge.

As is the case for other floral organs (Coen and Meyerowitz, 1991; Ma, 1994; Weigel and Meyerowitz, 1994), genes encoding MADS-domain transcription factors regulate ovule fate (Angenent *et ah,* 1995; Colombo *et ah,* 1995). In *Petunia,* simultaneous co-suppression of two probably redundant genes, *floral binding protein 7 (FBP7)* and FBP11, results in carpelloid tissue in place of ovules (Angenent *et ah,* 1995). Ectopic expression of FBP11 suffices to lead to the occurrence of ectopic ovules in certain regions of the perianth (Colombo *et ah,* 1995). It was also observed that

ectopic expression of C function activity (regulating carpel identity — Coen and Meyerowitz, 1991; Weigel and Meyerowitz, 1994) in tobacco can lead to the development of carpelloid tissue from the placenta (Mandel *et al,* 1992). Taken together, these findings suggested the possibility that genes like FBP7/11 regulate ovule fate by repressing carpel identity genes in the ovule. However, the two C function genes of *Petunia,* FBP6 and *pMADS3* (Angenent *et al,* 1993; Tsuchimoto *et al.,* 1993), are also expressed during wild-type ovule development and seem not to be under the control of FBP7/11 (Angenent *et al.,* 1995). It was therefore suggested that the balance of C function and FBP7/11 activities is critical (Angenent *et al.,* 1995). In this context, one possibility includes competition between the proteins (Angenent *et al.,* 1995). On the other hand, MADS domain proteins form dimers or heterodimers (Mueller and Nordheim, 1991; Schwarz-Sommer *et al,* 1992; Tröbner *et al,* 1992; Pellegrini *et al,* 1995; Shore and Sharrocks, 1995), and certain heterodimeric combinations are unable to bind DNA *in vitro* (Riechmann *et al,* 1996). Thus, the phenotype following overexpression of C function genes could be due to excess amounts of C function factors simply titrating out ovule identity factors such as *FBP7* and FBP11 by forming non-functional heterodimers.

Several MADS box genes are expressed in the ovule (Ma *et al,* 1991; Rounsley *et al,* 1995; Savidge *et al,* 1995), but true *Arabidopsis* orthologues of *FPB7* and FBP11 have not yet been isolated. However, the floral homeotic gene *APETALA2 (APT)* may contribute to the control of ovule fate because carpelloid outgrowths, in place of ovules, occur in particular *ap2* mutants (Modrusan *et al,* 1994). The AP2 locus encodes another putative transcription factor with two so-called AP2 domains (Jofuku *et al,* 1994; Weigel, 1995a,b).

The ovule is a modular structure (see below) and the identity of certain elements of the ovule appears to be regulated separately. Evidence comes from the phenotype of mutants defective in BEL1 function (Robinson-Beers *et al,* 1992; Modrusan *et al,* 1994; Schneitz *et al,* 1997). The primary defect in *bell* mutants is restricted to the chalaza. In *bell* mutants no inner integument develops and instead of the outer integument a collar-like protrusion forms, indicating that BEL1 controls outer integument identity. The outgrowths can develop carpelloid features at very late stages expressing the *Arabidopsis* C function gene *AGAMOUS (AG)* (Modrusan *et al,* 1994; Ray *et al,* 1994). It was therefore suggested that BEL1 exerts a cadastral function and prevents the misexpression of *AG* in the ovule (Modrusan *et al,* 1994; Ray *et al,* 1994). However, the situation is again more complex. *AG* is expressed in the ovule throughout its development. Its RNA expression pattern overlaps with that of BEL1 (Bowman *et al,* 1991a; Reiser *et al,* 1995), indicating that BEL1 is not a transcriptional regulator of *AG*. The BEL1 locus encodes a putative homeodomain transcription factor (Reiser *et al,* 1995). It is still possible that the BEL1 and *AG* proteins interact, as do other MADS domain and homeodomain transcription factors (Gehring *et al,* 1994; Shore and Sharrocks, 1995). It is, however, unclear whether *AG* plays a role in ovule development after all, because ovules develop in *ap2-2 ag* double mutants (Bowman *et al,* 1991b), and overexpression of *AG* does not lead to the formation of carpels in place of ovules (Mizukami and Ma, 1992).

Initiation and outgrowth. In *Arabidopsis,* the *AINTEGUMENTA (ANT)* gene controls floral organ initiation, growth and shape in general (Elliott *et al,* 1996; Klucher *et al,* 1996; Baker *et al,* 1997; Schneitz *et al,* 1997). The *ANT* locus encodes a putative transcription factor with two domains that share homology with AP2 (Elliott

et al, 1996; Klucher *et al,* 1996). In *ant* mutants the number of ovules per carpel is reduced by half and the ovules are separated by wider spaces. This indicates that *ANT,* besides its other functions, is required for ovule primordium initiation and/or outgrowth. The ovules that are produced form a nucellus, chalaza and funiculus but lack integuments and an embryo sac. Because such a phenotype is produced even by putative null-alleles (Elliott *et al,* 1996; Klucher *et al,* 1996), it suggests that partly redundant factors regulate this process.

It has recently been shown that the *HUELLENLOS (HLL)* gene (Schneitz *et al,* 1997) encodes such an ovule-specific redundant function (Schneitz *et al,* 1998). The phenotype of *hll* mutants is restricted to the ovule and is not identical but very similar to that of *ant* mutants. The analysis of *hll ant* double mutants reveals best a function of *HLL* in ovule primordium outgrowth. The number of ovules in plants defective for *HLL* and *ANT* activities is not obviously different from *ant* single mutants. However, the double mutants bear ovules that are drastically reduced in their longitudinal axis. The effect is restricted to the subnucellar region (see also below). It implies that within this domain *HLL* and *ANT* control ovule primordium outgrowth in a partly redundant fashion. This is supported by *in situ* hybridization studies that indicate that *HLL* does not act as a transcriptional regulator of *ANT.* It is possible that in the absence of *HLL* a threshold level of required *ANT* activity is higher. Alternatively, the two proteins may interact directly.

Pattern formation. Pattern formation controls the spatial arrangement of distinct regions with different cell fates (i.e., pattern elements) within an organ or an entire organism (Waddington, 1962,1973; Wolpert, 1971).

One can discriminate several such elements, based on morphological criteria, along a longitudinal or proximal-distal axis of the ovule (Schneitz *et al,* 1995). Distally, the nucellus is characterized by the presence of a megaspore mother cell, and eventually a tetrad and embryo sac. Centrally, the chalaza is recognized as the region that initiates the two integuments at its flank. The funiculus, as the proximal element, harbours the vascular strand. This linear arrangement of at least three distinct morphological units along the proximal-distal axis is obviously not unique to *Arabidopsis* but is a typical feature of a generalized ovule (Esau, 1977; Bouman, 1984; Gifford and Foster, 1989). Therefore, it was suggested that they actually correspond to distinct proximal-distal pattern elements (Schneitz *et al,* 1995). These elements are recognizable by early to mid-stage 2; hence, they must be laid down during stage 1. It is noteworthy that an implicit consequence of this hypothesis is the concept of an ovule as a modular structure.

There is also an anterior-posterior axis (adaxial-abaxial), perpendicular to the proximal-distal axis, as indicated by the mode of integument initiation and the unequal distribution of growth along this axis within the ovule and the outer integument (Gaiser *et al,* 1995; Baker *et al,* 1997). Furthermore, the vascular strand is placed more anteriorly within the funiculus. Interestingly, all the ovules within a carpel are oriented with their anterior side pointing towards the stigma, suggesting that the establishment of the anterior-posterior axis requires cues from outside the ovule.

Progress on the identification of genes that directly function in the establishment of the pattern elements has been scarce. However, indirect evidence for a pattern formation process is accumulating. For example, the *BEL1* expression pattern provides molecular evidence for the existence of the central or chalazal element

(Reiser *et al*, 1995). At late stage 1 it becomes restricted to a band located at the centre of the primordium. In addition, the region-specific defects of many early-acting ovule genes argue in favour of the presence of such a patterning process (Schneitz *et al*, 1997). The analysis of *INNER NO OUTER (INO)* suggested the presence of a fourth element along the proximal-distal axis (Baker *et al.*, 1997). In *ino* mutants, outer integument development does not proceed beyond the initial subepidermal cell divisions and epidermal cell enlargements. In addition, they occur at the anterior side as opposed to the normal posterior side. Because of this polarity shift in the mutant, *INO* could play a direct role in establishing the anterior-posterior polarity of this pattern element. In addition, mutations in *SUPERMAN (SUP)* (Bowman *et al*, 1992; Sakai *et al*, 1995), also known as *FLOW* (Schultz *et al*, 1991), specifically lead to a defect in the anterior domain of the outer integument (Gaiser *et al*, 1995).

The polarity of pattern formation. As outlined above, the *Ml ant* double mutant specifically fails to form the subnucellar region. More specifically, the funiculus is always absent, the chalaza is variably affected and the nucellus is always present. This finding suggests a qualitative difference between these elements and supports the modular concept of an ovule (Schneitz *et al*, 1998). Interestingly, the nucellus is produced even in the absence of a funiculus and chalaza. This also indicates that the nucellus forms as an independent element.

What then regulates the formation of the nucellus? There is a separate process, regulated by the *NOZZLE (NZZ)* gene, which controls the formation of the nucellus (Schiefthaler, Redweik, Schneitz, orig. data).

Morphogenesis and cellular differentiation. A number of genes have been identified that seem to regulate growth and morphogenesis in response to specification and pattern formation. They primarily affect the integuments. Results indicate that at least two levels of control exist; some genes are required for the initiation of the integuments, some for subsequent steps of morphogenesis. With respect to the latter class of genes, analysis is still in its infancy and generalizations cannot be made yet. However, a complex scenario of multiple distinct steps controlling morphogenesis is suggested.

Several loci have an early central role in the initiation of the integuments. As already discussed, *HLL* and *ANT* are partly redundant factors that control ovule primordium outgrowth. They are also required for the initiation and/or growth of the integuments (Elliott *et al*, 1996; Klucher *et al*, 1996; Baker *et al*, 1997; Schneitz *et al*, 1997). In addition, both are necessary for the formation of the outgrowths in *bell* mutants (Klucher *et al*, 1996; Baker *et al*, 1997; Schneitz *et al*, 1998). It is therefore likely that both play a general role in cell proliferation processes in the ovule.

Mutations in three genes lead to the absence of specific structures within the chalaza. Besides the effects on the outer integument, *bell* mutants lack an inner integument. *ABERRANT TESTA SHAPE (ATS)* is responsible for the formation of the boundary region between the two integuments (Léon-Kloosterziel *et al*, 1994) and *INO* directly or indirectly for outer integument development (Baker *et al*, 1997; Schneitz *et al*, 1997). The *ino* phenotype indicates that inner integument development is independent of the presence of an outer integument. The existence of an inter-integumentary boundary region seems essential for this independence, because *ats ino* double mutants do not develop an inner integument (Baker *et al*, 1997).

Only one gene is known, *UNICORN (UCN)*, that seems to have a suppressory role. A small extra bump is formed in ovules of *ucn* mutants that could represent a partial supernumerary integument (Schneitz *et al*, 1997).

A number of loci are involved in the control of morphogenesis of the integuments themselves, where they regulate cell proliferation and/or cell shape (Robinson-Beers *et al,* 1992; Gaiser *et al,* 1995; Schneitz *et al,* 1997). Mutations in these genes do not result in the absence of integuments but rather in their altered shapes and sizes. Loci such as *STRUBBELIG (SUB), SHORT INTEGUMENTS* 1 (SIM), *BLASIG (BAG)* or *SUPERMAN (SUP)* most likely act after, for example, *HLL, ANT* or *INO.* In some instances this is corroborated by double mutant analysis (Baker *et al,* 1997). The defects may be quite specific, with respect to either the location or the process that is affected. For example, in the case of *sup* mutants only cell proliferation in the anterior domain of the outer integument is enhanced, leading to cup-shaped integuments (Gaiser *et al.,* 1995). *SIN1* specifically controls cell shape (Robinson-Beers *et al.,* 1992; Lang *et al.,* 1994), and *sinl* mutants carry ovules with drastically reduced integuments. The defects in *SUB* or *BAG* affect both cell proliferation and cell shape (Schneitz *et al,* 1997).

As might be expected for genes with a general function in morphogenesis, members of this class usually exhibit pleiotropic activities. A role for the zinc-finger putative transcription factor *SUP* in the control of cell proliferation is also assumed for its early function in floral organ specification (Bowman *et al,* 1992; Sakai *et al,* 1995). *SIN1* does not only appear to regulate cell shape in the ovule, but has a number of different functions as well (Ray *et al,* 1996a,b) including a possible role in cell-to-cell communication. In the case of *bag* or *sub* mutants, the entire plant is shorter and bushier (Schneitz *et al,* 1997). This again suggests similar functions for the two genes throughout post-germination development.

Gametogenesis. Compared to other areas of ovule development, little is known about megasporogenesis or megagametogenesis at the functional level.

As outlined above, megasporogenesis takes place in the nucellus (sporangium). A number of cells exist within the first subepidermal, or L2 (Satina and Blakeslee, 1941; Satina, 1945), cell layer. However, in most angiosperms only one of these cells will give rise to an archesporial cell, which then directly differentiates into the megaspore mother cell (Gifford and Foster, 1989). This cell will undergo meiosis and eventually generate the embryo sac. The first step of megasporogenesis thus consists of the singling out of the megaspore mother cell within a hypodermal cell population. A maize gene, *macl,* was recently identified that appears to control this process (Sheridan *et al,* 1996). In *macl* mutants, several hypodermal cells in the first subepidermal cell layer will develop into megaspore mother cells, which will also undergo meiosis. The *macl* locus is therefore likely to be a component of an inhibitory system, which suppresses the switch to the meiotic fate in all other L2 cells except the developing megaspore mother cell. An interesting aspect is that apparently most L2 cells, if not all, have the capacity to enter the meiotic pathway (Sheridan *et al,* 1996).

A number of mutants in other species have also been characterized to some degree, including mutants defective in meiosis or cytokinesis (Hanna and Powell, 1974; Kennell and Horner, 1985a,b; Benavante *et al,* 1989; Golubovskaya *et al,* 1992). A large number of mutations causing male and female sterility have recently been isolated in *Arabidopsis* (Schneitz *et al,* 1997). They also seem to be specific to spore formation, because the developmental block in all of them takes place at or before the appearance of the uninucleate embryo sac.

What about the female gametophyte? A large number of genes are apparently involved in its development (Patterson, 1994; Vollbrecht and Hake, 1995). In contrast,

there are very few reports on specific female gametophytic mutants in the literature. In *Arabidopsis*, one mutant, *gf*, has been described (Rédei, 1965) which carries a doublet of embryo sacs. A second female gametophytic mutation, *lethal ovulel*, is known from maize (Nelson, Clary, 1952). It disrupts the nuclear division cycle during embryo sac development (Sheridan and Huang, 1997).

An important question concerns the relative contribution of the gametophytic and sporophytic genomes to embryo sac development. There is genetic evidence that embryo sac ontogenesis is controlled by a combination of female gametophytically as well as sporophytically active genes. The integuments play a key role (Reiser and Fischer, 1993), but, regardless of the integuments, the sporophytic genome has an effect on gametophyte development. This is indicated by, for example, the *indeterminate gametophyte (ig)* mutant of maize (Kermicle, 1971; Lin, 1978; Huang and Sheridan, 1996), the *macl* mutant (Sheridan *et al.*, 1996), and the embryo sac-defective *(emd)* class of mutants in *Arabidopsis* (Schneitz *et al.*, 1997).

Much of the functional analysis has been carried out in *Arabidopsis*, but impressive results have also been obtained from studies of several other species, in particular *Zea* and *Petunia.* Taking into account the increased interest of plant systematists in ovules as well, we may be able to discern the fundamental properties of ovule development, shared by even remotely related species, in the not so distant future.

Gametophytic Mutations

Gametophytic mutations are a conventionally segregated group of mutations affecting micro- and/or megagametophyte features. Mutations affecting the stages of sporogenesis are also to be classified in this group since, as a rule, they result in structural or genomic changes of gametophyte. The extent of investigation of different gametophytic mutations is far from being evenly distributed.

Mutations affecting the sporocyte stage. Mutations have been revealed that caused mitotic disturbances followed by formation of sporocytes with altered chromosome number or with increased nucleus number. This class also includes mutations responsible for formation of additional sporocytes that are able to develop into embryo sacs. In particular, in *Nigella sativa*, an induced mutation was described that caused disturbance of mitoses in anthers. It results in chromosome mosaicism in the microsporocytes and, as a consequence, in disturbance of meiosis and formation of sterile pollen (Datta and Biswas, 1985). In *Hordeum vulgare*, mutation was induced that gave rise to formation of coenocytes in pollen mother cells of anthers of tip regions of the spike. Further development (sporogenesis and formation of pollen grains) was abnormal because of coenocytic or, if nuclei fused, polyploid cells. Meiotic anomalies resulted in complete pollen sterility (Sethi *et al.*, 1983). In *Zea mays*, formation of multinucleate micro- and megasporocytes caused by mutation *paml* was described; their further development was abnormal and resulted in male and female sterility (Golubovskaya *et al.*, 1994; Voronova and Batygina, 1997; Voronova, 1998, 1999). Another mutation *macl* (=Zar-487) in Z. *mays* is characterized by manifestation of multiple (up to 25) archesporium cells per ovule, which developed asynchronously into mono- or bisporic embryo sacs. One or two such embryo sacs reached the final stage (Golubovskaya *et al.*, 1993, 1995; Batygina *et al.*, 1994; Sheridan *et al.*, 1996;

Voronova and Batygina, 1997; Batygina and Voronova, 1999; Voronova, 1999). In a mutant line AS-1 of *Sorghum bicolor*, the nucellar cells or derivative structures, positioned close to the sporocyte, were able to develop into differentiated or coenocytic embryo sacs (Enaleeva *et al*, 1994). Apospory, characteristic of some apomictic species and manifested as inheritable ability of nucellar cells to develop into gametophyte, is referred to this class of mutation also (Nogler, 1984a).

Mutations affecting sporogenesis. A great many mutations responsible for alteration of cell division or chromosome behaviour at different stages of meiosis are known. These mutations are named meiotic or mei-mutations. In some species *(Zea mays, Secale cereale, Pisum sativum, Oryza sativa)*, a great many mei-mutations are known, and they are brought together into genetic collections (Gottschalk and Kaul, 1974; Golubovskaya, 1975; Kitada *et al*, 1983; Sosnikhina *et al*, 1994). In many other species, single mutations were induced similar to those described above.

With regard to their manifestation patterns, meiotic mutations were classified into groups: lack of meiosis, omission of the first or second meiotic division, chromosome adhesion, disturbances of chromosome pairing (asynapsis or desynapsis), cell division, etc. (Gottschalk and Kaul, 1974,1980a,b; Golubovskaya, 1975; Kaul and Murthy, 1985; Sosnikhina *et al*, 1994).

The most abundant phenotypic effect of mei-mutations consists in blocking or abnormal development of post-meiotic cell structures, which ultimately results in gametophyte degeneration (Gottschalk and Kaul, 1974; Golubovskaya, 1975; Kaul and Murthy, 1985). Another effect of mei-mutations is possibly an alteration of ploidy level of gametes, and occurrence of unreduced gametes. These mutations are of special interest: first, because they are widely used for production of "meiotic" polyploids, and second, because they are related to diplospory in apomicts. It was found that failure of reduction can result from mei-mutations followed by nuclear restitution at first or second meiotic division, as well as from mutations responsible for omission of the second division. Genetic peculiarity of 2n gametes depends on the mode of their origin. If the first meiotic division is followed by nuclear restitution, diploid heterozygous spores are formed, giving rise to 2n gametes genetically similar to the sporophyte. This occurs in some apomicts during megaspore formation. If crossing-over takes place, deviations from a genotype of the parental form are possible. Omission of the second meiotic division or nuclear restitution during second meiotic division results in formation of mainly homozygous diploid gametes (Hermsen, 1984; Werner and Peloquin, 1987). One more mechanism of nuclear restitution in species with simultaneous cytokinesis is related to parallel or tripolar spindles in anaphase II leading to formation of dyad or triad of microspores, respectively. Both spores of dyad are diploid; in triad, one spore is diploid. Unreduced gametes produced in this way are genetically equivalent to those originating after first division restitution. Mutations *(ps, rp)* affecting the division spindles are described in *Beta vulgaris* (Malyuta, 1980), *Trifolium pratense* (Parrott and Smith, 1984), *Medicago sativa* (Vorsa and Bingham, 1979), *Solanum tuberosum* (Conicella *et al.*, 1996), and *Lotus tenuis* (Rim and Beuselinck, 1996). Synaptic mutations can also result in nuclear restitution during the first meiotic division in both micro- and megasporogenesis (Hermsen, 1984).

Mutations causing omission of the second meiotic division and leading to formation of homozygous unreduced gametes were detected in many species. Among them, mutation *tri* in *Hordeum vulgare* (Finch and Bennet, 1979) and mutation

el in *Zea mays,* affecting only megasporogenesis (Rhoades and Dempsey, 1966), were revealed. In *Datura stramonium,* mutation *dy* responsible for omission of the second meiotic division displays similarly in micro- and megasporogenesis and gives rise to formation of embryo sacs and pollen grains of typical structure but with doubled chromosome number in their nuclei (Satina and Blakeslee, 1935). In *Solanum tuberosum,* clones were isolated with omission of the second meiotic division in megasporogenesis (Stelly and Peloquin, 1986).

Production of 2n- or in some cases of 4n-gametes may be determined by mutations giving rise to distortion of cytokinesis after the first or second meiotic division. In particular, such mutations (msl and ms4) were isolated in *Glycine max.* Failure of cytokinesis leads to formation of coenocytic microspores giving rise to giant pollen grains that are capable of germination (Graybosch and Palmer, 1985; Chen *et ah,* 1987). In *mslmsl* plants, failure of cytokinesis occurs in the female generative sphere too. It was detected that nuclei in coenomegaspores can merge and, further from such spores, diploid embryo sacs originate; some of them contain increased element number. Formation of diploid embryo sacs or embryo sacs with extra elements is the cause of appearance of polyploids, haploids and twins in their progeny (Chen *et ah,* 1985; Ñutter and Bingham, 1977; Kennell and Horner, 1985a,b). Similar mutations were isolated in *Medicago sativa (jp)* (McCoy and Smith, 1983; Pfeifer and Bingham, 1983; Mariani *et ah,* 1993; Calderini and Mariani, 1995), *Zea mays (va)* (Beadl, 1931), and *Kniphofia* (Moffett, 1939). However, in the two last cases, mutation was manifested only in microsporogenesis.

One of the genetic consequences of mei-mutations along with formation of unreduced or tetraploid gametes is aneuploidy. It was shown that aneuploids may arise in a progeny of synaptic mutants as a result of unequal chromosome distribution in meiotic divisions (Uchino and Tanaka, 1995). In mutants with distortion in a formation of synaptonemal complexes, abnormalities in embryo sac structure were revealed.

In particular, in an asynaptic mutant of *Glycine max,* embryo sacs were revealed to be of reduced size, had atypical structure of nuclei and cells, and degenerated (Benavånte *et ah,* 1989).

Mutations affecting microgametogenesis. A range of mutations has been found that affected development of pollen grains from the stage of tetrad of microspores to sperm cell formation. The best-known mutations of this type cause blocking of development at the stage of uninucleate microspore and their further degeneration. These mutations *(ms, rf)* manifest often in plants with certain type of sterile cytoplasm (S). This type of male sterility qualifies as nuclear-cytoplasmic sterility. A blockade of pollen development in this case usually occurs because of distortion of functioning of tapetal anther layer, though additional reasons are not ruled out (Gottschalk and Kaul, 1974; Frankel and Galun, 1977). Manifestation of male sterility phenotypically similar to that but without participation of S-cytoplasm (gene male sterility) was revealed in different species. These mutations usually are designated as *ms.* In *Zea mays* and *Lycopersicon esculentum,* nearly 40 such genes were revealed; in *Hordeum vulgare,* 19 genes were revealed (Reznikova, 1984). Such mutations may be induced by the action of different mutagen factors (Krupnov, 1973).

Since, in diploids, after completion of meiosis, microspore nuclei contain one set of chromosomes, expression of mutant genes occurs under hemizygous genotype condition; consequently, all mutations, including recessive ones, can be detected. In

Zea mays some mutations were revealed to be transcribed in the gametophyte; among them were *wx*, causing waxy pollen grains (Nelson, 1962), and *Adh-1* alcohol dehydrogenase (Freeling, 1977). Mutation *gaMS-1* is expressed during or immediately after the first microspore division and leads to the production of immature, non-functional pollen grains (Sarigorla *et al.*, 1996). Such characters of pollen grain as dimension, ability to germinate, pollen tube growth rate, and specific proteins were identified to be encoded by genes specifically expressed by the haploid genome (Johnson *et al.*, 1976). A series of S-alleles responsible for self-incompatibility of the gametophytic or gametophytic-sporophytic type was found in some species (Lewis, 1954). In *Solanum phureja*, a mutation was detected that prevented mitotic division of generative cell in pollen tube. This was followed by single fertilization and haploidy (Montelongo-Escobedo and Rowe, 1969).

Dimorphism of pollen grains for aperture number is likely explained by genetic variability. Thus, in diverse genotypes of *Nicotiana tabacum*, 3- and 4-aperturate pollen grains were detected (Till-Bottraud *et al.*, 1995). Pollen grains of tetrahedron form (as a result of junction of several microspores), which were produced under chemical mutagenesis in *Anethum graveolens*, seem to be caused also by particular genetic change (Raghuvanshi and Joshi, 1965).

A mutant line ZMS-8 of corn was obtained in which functional impairment (until then of unknown nature) of one or both sperm cells in pollen tube gave rise to failure of double fertilization. As a result, single fertilization (of egg cell or central cell) occurs in the embryo sac. In the latter case, endosperm developing normally stimulates parthenogenesis of the haploid egg cell (Tyrnov and Zavalishina, 1984; Enaleeva *et al.*, 1997).

Mutations affecting the megagametogenesis stage. Corn mutation *pam2*, responsible for cytokinesis following each mitotic division of megaspore, belongs to this group. As a result, haploid uninucleate cells are produced instead of eight-nucleate coenocyte. In male generative sphere, mutation *pam2* causes non-specific multiple abnormalities of meiosis (Golubovskaya *et al.*, 1994).

Mutation *ig* in corn was found, causing formation of anomalous embryo sacs. Among them, the most frequent were embryo sacs with increased cell number (Lin, 1978,1981). Multicellular embryo sacs were shown to arise through additional mitotic divisions at coenocytic stage; the latter in turn are caused by cytoskeleton impairment (Huang and Sheridan, 1996; Enaleeva *et al.*, 1998). Pleiotropic effect of *ig* mutation consists in male sterility, polyembryony, and production of haploids, mainly androgenic ones (Kermicle, 1971).

Several mutations affecting element number in embryo sacs were isolated in *Nicotiana tabacum*. One of them (the line BG-141.4) is characterized by development of uni- or bipolar embryo sacs with decreased nucleus and cell number. Frequency of mutant embryo sacs ranged from 0 to 72% per plant (Enaleeva, 1992,1997). In plants of the line M-2 in sequent generations, embryo sacs with increased cell number, due to extra mitotic divisions, were observed. Frequency of multinucleate embryo sacs per plant ranged widely; plants were found to have more than 70% of mutant embryo sacs. The lines M-3 and M-4 are characterized by high frequency (up to 90%) of coenocytic embryo sacs with decreased nucleus number (Enaleeva, 1992).

Mutation *Io2* in *Zea mays* arrests embryo sac development at one-, two- or four-nucleate stage and, in some cases, the nuclei enlarge dramatically (Sheridan and Huang, 1997). Mutations similar to that were identified in *Arabidopsis thaliana*.

Mutations *GF, gfal, gfa, feml, and fem3* arrest megagametophyte development at uninucleate stage (Christensen *et al,* 1997; Drews *et al,* 1998) and mutations *hdd* and pr/at two- and four-nucleate stage (Springer *et al,* 1995).

Trichosanthes lobata exhibited two embryo sac patterns: small (60 nm x 20 nm) and large (100 nm x 30 nm). Both types of embryo sacs were observed in the same ovary and even on either side of the same T-shaped placenta (Datham, 1974).

The category of mutations affecting the stage of the mature embryo sac can include mutations of premature division of the egg cell before fertilization. These mutations were revealed in the line RA91 of *Linum usitatissimum* (Huyghe, 1987; Secor and Russel, 1988) and in the line AT-1 of *Zea mays* (Tyrnov and Enaleeva, 1983; Enaleeva and Tyrnov, 1997). Both mutant lines exhibit high frequency of polyembryony of 2n-n type. This is due to the cells resulting from the first egg cell division (in flax) and from the second one (in corn). Occasionally these cells can function as autonomous egg cells that can be fertilized or divide parthenogenetically. Frequency of this phenomenon in flax ranged from 8 to 74%, in corn from 17.1 to 82.6%. The corn line AT-1 is characterized by autonomous endosperm formation (0-59.4%), which is arrested at early developmental stages.

In *Arabidopsis thaliana,* mutations *fie, fisl, fis2* and ^Is3 were induced, which caused autonomous endosperm development in the absence of fertilization (Ohad *et al,* 1996; Chaudhury *et al.,* 1997; Feldman *et al.,* 1997). In this species, mutations *gfal, gfa3* and *gfa7* also were found to prevent polar nuclei fusion (Feldman *et al,* 1997; Drews *et al,* 1998).

Variation of gametophyte patterns due to chromosomal, genomic, and cytoplasmic mutations. Aneuploidy causes alteration in vegetative and generative structures. Thus, there were revealed in aneuploids of *Beta vulgaris* arrest of embryo sac development at early stages and distortion of mitosis number and polarity (Zaykovskaya and Yarmolyuk, 1968; Yarmolyuk, 1972). In *Zea mays,* male gametophytes nullisomic for chromosome 2 or 6 can reach only the first mitosis, but those nullisomic for chromosomes 1, 3, 4, 7, 8, 9 or 10 do not reach the first division (Zhao and Weber, 1989). In monosomic and double monosomic of *Brassica carinata,* pollen fertility decreased for 17% and 53%, respectively (Serla and Raut, 1987). Failure of the chromosome 7A or 7D in *Triticum turgidum* var. *durum* prevented the normal course of megasporogenesis (Joppa *et al,* 1987).

Availability of B-chromosome(s) in the genome variously influences gametophyte development. As a rule, increase of their number is correlated with increase of male and female sterility, although, in some species, availability of single accessory chromosome can result in increase of fertility (Moshkovich, 1979). In diploid and tetraploid forms of *Impatiens balsamina,* B-chromosome attendance promoted faster pollen tube growth (Mahajan and Raghuvanshi, 1983). In *Aster novae-angliae,* B-chromosomes caused failure of cytokinesis in megasporogenesis, development of embryo sacs with increased nucleus number, formation of aposporic embryo sacs, and penetration of pollen tubes through chalazae (Kluska, 1986).

Polyploids are characterized by enlargement of mature gametophytes (Satoshi, 1980; Wafai and Koul, 1984) and decrease of fertility (Bormotov, 1972). The latter is connected mainly with formation of multivalents in the prophase I of meiosis and consequent development of gametes, unbalanced for chromosome number.

In the course of development of female gametophyte, distortions of polarity, of number of mitotic divisions and of cell differentiation were revealed (Dzevaltovsky,

1969; Molchova, 1970; Chechenova, 1977). Abnormality patterns in different polyploids had a wide range, and a level of male and female sterility in the same polyploid plants was often different (Kutty and Kumar, 1983). In self-incompatible forms of *Petunia hybrida* and *Pyrus communis*, transition to polyploidy was followed by ability to set seed under self-pollination (Lewis, 1954). In haploids, because of failure of homology, meiosis is greatly disturbed, resulting in nearly complete male and female sterility. Since meiotic distortion causes formation of spores unbalanced for chromosome number, anomaly patterns of haploid embryo sacs are similar to that described above for polyploids and aneuploids (Zverzhanskaya and Shishkinskaya, 1974).

Cytoplasmic mutations of sporophyte can also dramatically distort an exhibition of gametophyte features. Thus, along with the CMS effect described above, the following were recorded: alteration of callose deposition in microspore cell wall *(Petunia hybrida);* formation of anomalous tetrads of microspores *(Triticale);* fragmentation of nucleoli in microspores *(Zea mays);* origin of two-pore and very small pollen grains; inability of externally normal pollen grains to grow *(Nicotiana tabacum);* induction of parthenogenesis and polyembryony; selective fertilization *(Triticum);* formation of 2n-gametes *(Beta vulgaris);* capability of microspores in anther culture *in vitro* to morphogenesis *(Triticum* and *Triticale)* (Krupnov, 1973; Frankel and Galun, 1977; Davidenko, 1984).

Modifiable Variability of Gametophyte

Modifiable variability of gametophyte involves non-inheritable changes of its features effected by environmental factors.

Temperature, light, humidity, chemicals, irradiation, gravitation, and magnetic and electromagnetic fields are the environmental factors influencing gametophyte development. Various influences (beginning with temperature) are largely used to overcome self-incompatibility, restore fertility in CMS forms, and increase seed set under distant crossings.

Modifiable variability of sporogenesis. Extreme temperatures (high and low) were shown in different plant species to modify a course of meiosis or cause its entire suppression, omission of the first or second meiotic division, distortion of cytokinesis and chromosome distribution. In particular, meiosis in microsporogenesis was found to be entirely suppressed in *Triticum aestivum* at a temperature of 33°C (Bodanese-Zanettini *et al.,* 1979). Omission of meiosis and transformation of megaspore mother cell directly into uninucleate embryo sac was induced by high temperature in *Nicotiana tabacum* (Lobanova and Enaleeva, 1995). In *Ulmus laevis* at temperature 30°C, meiosis was replaced with mitotic divisions of the megaspore mother cell, giving rise to a row of three to six uninucleate cells that further degenerated (Hjelmqvist and Grazi, 1965). At low and high temperatures, entire or partial omission of the second meiotic division can also occur, resulting in formation of dyad or triad of microspores and megaspores (Barskaya and Balina, 1970; Karihaloo, 1991; Lobanova, 1992). In *Solanum phureja,* which is characterized by partial formation of diploid pollen, the percentage of the latter is greatly increased at low temperature because of destruction of spindle fibres in the second meiotic division (Mettale, 1983). Formation of 2n-gametes influenced by temperature may be related to omission of the first or second

meiotic division and dyad formation or to fusion of sister haploid nuclei in the course of the second meiotic division (Lutkov, 1937). Formation of 2n-gametes in some species was shown to be induced by high temperatures (> 30°C), and in other species by low temperatures (< 5°C) (Hermsen, 1984). Plants of a hybrid potato clone growing under different conditions differed by more than two times for frequency of 2n-megagamete formation (Werner and Peloquin, 1987). The possibility that diploid or even tetraploid pollen grains are induced by temperature stress was recorded in many early publications (Belling, 1925; Michaelis, 1926; Sakamura and Stow, 1926).

Distortion of cytokinesis due to environmental conditions usually is displayed as suppression of cell wall development after first or second meiotic division. As a result, two-, three- and four-nucleate spores are formed both in megasporogenesis (Hjelmqvist and Grazi, 1964,1965; Dharamadhaj and Prakash, 1978; Lobanova, 1992) and in microsporogenesis (Poddubnaya-Arnoldi *et al.,* 1934; Barskaya and Balina, 1970). However, in some cases, extreme conditions provoke the formation of cell walls in species with tetrasporic type of embryo sac. In *Tulipa* plants flowering during dry hot periods, for example, a triad of megaspores instead of four-nucleate coenomegaspore was developed because of cell wall formation after first meiotic division and after second division in micropylar cell of the dyad (Belyaeva, 1977). A consequence of cytokinesis distortion is the alteration of embryo sac spory. As a rule, spory increases at high temperatures (Hjelmqvist and Grazi, 1964,1965; Dharamadhaj and Prakash, 1978). For example, in *Nicotiana tabacum,* which is characterized by monosporic embryo sac, high temperature induces development of bi-, tri-, or tetrasporic embryo sacs (Lobanova, 1992). Spory was recorded to increase at lower temperatures (Sokolowska-Kylczycka, 1988).

Environmental factors can also modify the inheritable tendency for production of unreduced female gametes in apomictic species. In particular, alteration of light and temperature regime was established to increase or decrease an extent of apomixis manifestation due to change of frequency of diplosporic or aposporic embryo sac formation (Nogler, 1984a).

Chromosome behaviour in meiosis is significantly influenced by x-rays (Delone, 1960), low and high temperatures (Bleier, 1930; Altergot *et al.,* 1978; Bodanese-Zanettini *et al,* 1979; Gavrilenko, 1984; Eliseev and Gvassaliya, 1988; Karihaloo, 1991), illumination (Veselova, 1977), deficiency or abundance of soil moisture and mineral supply (Zavadskaya, 1959; Batygina *et al,* 1966; Skazkin, 1971; Caetanopereira *et al.,* 1995), treatment by HC1 (Konstantinov, 1970) and chloroform (Lutkov, 1937), and spaceflight conditions (Kuang *et al.,* 1995). Chromosome disturbances are displayed as formation of uni- and multivalents, chiasma frequency variation, diverse anaphase aberrations, chromosome adhesion, nucleus destruction, parallel or multipolar spindles, cytomixis, etc.

Distortions of chromosome segregations in meiosis cause formation of monads, dyads of different sizes, triads, irregular tetrads, polyads, and micronuclei in spores (Poddubnaya-Arnoldi *et al.,* 1934; Barskaya and Balina, 1970), which in turn results in development of anomalous pollen with unbalanced genome or in spore degeneration.

Modifiable variability of microgametogenesis. Microgametophyte development from microspore stage to spermiogenesis is affected to a large degree by environmental factors. Distortions of karyo- and cytokinesis arising at these stages (equal first division of microspore, additional nucleus and cell divisions) can be attributed to meiotic distortions. In the case of serious structural and functional

modifications, microspores usually degenerate at different developmental stages. In *Olea europaea* at high temperature, activation of mitotic divisions was recorded that resulted in formation of multinucleate pollen grains or pollen tubes with supernumerary sperm cells. Development of multinucleate pollen is also related to suppression of cytokinesis beginning from a two-nucleate stage (Sholokhova and Nikiforov, 1973). Such distortions were recorded in *Gossypium hirsutum* after gamma-irradiation (Rumy *et al*, 1973) and in *Scorzonera tau-saghyz* at low temperature (Poddubnaya-Arnoldi *et al.*, 1934). Formation of pollen grains with two vegetative and two generative nuclei was induced in *Triticum aestivum* by high temperatures (Altergot *et al.*, 1978).

The possibility of formation of abnormal pollen grains is largely used for haploid production in anther culture *in vitro* (Batygina, 1987a,b). Anomalous pollen development is caused by such factors as the following : temperature and length of photoperiod during growth of donor plants (Rashid, 1983; Sunderland, 1983); pretreatment of anthers at microspore stage by low or high temperatures (Sunderland and Huang, 1985; Li *et al*, 1988; Lazar *et al*, 1990); and cultivation conditions, that is, composition of nutrient medium, temperature, light, and CO_2 concentration (Chen *et al*, 1984; Reznikova, 1984; Heberle-Bors, 1985; Shimada, 1989).

Effect of stress factors on mature two-celled pollen grains can result in distortion of spermiogenesis in pollen tubes. Thus, under X-rays, mitotic divisions of generative cells were suppressed or defective, and sperm cells of unequal size and/or containing micronuclei were formed (Vassileva-Dryanovska, 1966; Rumy *et al*, 1973). Abnormal mitotic divisions of generative nuclei with formation of micronuclei were also effected by cold (Mo and Yang, 1992) and hydroxyurea (Khan and Ma, 1974). Besides, after cold treatment of pollen, equal and unequal amitotic divisions were observed (Mo and Yang, 1992). Arrest of mitosis occurs at high temperatures (Balina, 1974). Pollen development can be stopped at one- or two-nucleate stage by alteration of photoperiod (Zhukova, 1938). There is evidence that high temperature can induce embryo sac-like pollen grains (see Development of Embryo Sacs in Anthers, Vol. 1)

Modifiable variability of megagametogenesis. All of the key processes of megagametophyte development including initiation of functional megaspore, mitotic divisions, polarization, cytokinesis and cell differentiation are affected by environmental factors. The modifications that appear, as well as those in microgametophytogenesis mentioned above, can be attributed to meiotic disturbances.

Depending on environmental conditions, any megaspore (or simultaneously two, three or even four spores) of tetrad can turn into embryo sac mother cell(s). Tendency to development of several embryo sacs in a ovule is not always realized (Lobanova, 1992). Development of embryo sacs from several megaspores can be induced by temperature (Dharamadhaj and Prakash, 1978) and salt stress (Gounaris *et al*, 1991).

Coenocytic stage is also sensitive to environmental conditions. Mitosis number varies with temperature. For example, under increasing temperature in some species with tetrasporic embryo sac, Adoxa-type of development is replaced by Drusa- or Chrysanthemum-type (Hjelmqvist and Grazi, 1964,1965). In *Nicotiana tabacum*, the mitotic activity of nucleus in gametogenesis is promoted by high temperature (35-40°C) and is inhibited by low temperature (10-13°C); in the first case, embryo sacs with increasing nucleus number (9-48) are formed, and in the second embryo sacs

with decreasing nucleus number (1-7) are formed. At 40°C, amitotic divisions of nuclei were observed (Lobanova and Enaleeva, 1992,1995). Anomalous embryo sacs with different number of nuclei and cells were recorded to arise at stress temperatures in *Scorzonera tau-saghyz* (Poddubnaya-Arnoldi *et al*, 1934) and *Tulipa* (Belyaeva, 1977).

Cytokinesis in embryo sacs is also affected by temperature. In *Nicotiana tabacum* at temperatures 40°C and 10°C, the coenocytic embryo sacs prevailed, but at 37°C and 13°C the organized embryo sacs prevailed (Lobanova, 1992).

Among the factors causing alteration of size and shape of embryo sac and its development tempo are temperature (Belyaeva, 1977; Ormrod *et al*, 1967; Saini *et al*, 1983), soil water deficit (Skazkin, 1971), light quality (Ustinova, 1973), photoperiod (Knox, and Heslop-Harrison, 1963), salt stress (Gounaris *et al*, 1991), X-rays (Rumy *et al*, 1973), constant magnetic field (Kozlov and Kozlova, 1978), spaceflight conditions (Kuang *et al*, 1995), treatment by colchicine (Iarciniak, 1967), and complex variations of environmental factors in natural populations (Chernik, 1992; Geushova, 1992; Pfahler *et al*, 1996).

The influence of environmental factors on mature embryo sacs manifests in change of size, structure and vacuolization of cells, nucleus arrangement, condition of polar nuclei and filiform apparatus (Chebotaru, 1965; Gerassimova-Navashina *et al*, 1968; Lobanova, 1992). In some cases, divisions of cells of mature embryo sacs can be induced. Thus, in *Zea mays* at high temperature, the increase of nucleus number in antipodal cells occurs (Chebotaru, 1965). In a line of *Linum usitatissimum*, a frequency of autonomous division of egg cell resulting in formation of two egg cells increases from 31% to 52% with temperature rise from 16 to 28°C (Huyghe, 1987). Of special interest is the possibility that additional egg cells arise from additional nuclei in anomalous multi-nucleate embryo sacs or redistribution of nuclei; in the last case, decrease of number of antipodal cells and synergids is displayed (Chebotaru, 1965; Lobanova and Enaleeva, 1995). Such modifications of embryo sacs can cause polyembryony. Numerous data on parthenogenesis of egg cell under various environmental factors *in vivo* are generalized in a number of reviews (Kimber and Riley, 1963; Tyrnov, 1976a,b; Laptev, 1984; Kashin and Kupriyanov, 1993).

In *Zea mays* and *Panicum miliaceum*, apomictic development of embryo and endosperm occurs under treatment of ovaries by different chemical substances (Kashin and Kupriyanov, 1993). Retardation of pollination can be considered as a factor that induces parthenogenetic development of egg cell (Eenik, 1973; Tyrnov and Enaleeva, 1983). A possibility of inducing cell divisions in mature embryo sacs was demonstrated in experimental cultivation of unfertilized ovaries and ovules (Wu and Cheng, 1982; Yang and Zhon, 1982; Tian and Yang, 1983). In this case, inducing factors are composition of the nutrient medium, temperature, and light.

Plant Embryogenetics

The importance of embryology for solution of some fundamental and applied problems of modern biology is well known. Together with this, the possibilities of development control and synthesis of forms with desirable characters are connected with use of genetic methods and regularities. The need for unification of embryological and genetic data is therefore repeatedly noted.

This specific and complex problem in every respect can be solved only by means of development of the original direction of plant embryogenetics (Tyrnov, 1986a,b). Why is it embryogenetics, but not "genetic embryology" or simply "genetics of embryological characters"? The essence of the term is not its brevity or capacity (which is of no small importance in itself), but its integration (not simple summation) of two sciences and their influence against each other.

We understand embryogenetics as the discipline involving research on the following subjects:

1. mechanisms of genetic determination and regulation of embryological characters, processes and phenomena;
2. genetic consequences, conditioned by morpho-functional peculiarities of reproductive structures;
3. possibilities and ways of using reproductive structures for genetic engineering.

The scheme of genetic analysis of embryological characters looks like that for many other sporophyte structures, but there is its specificity, resulting in the following:

— different nature of control of some embryological characters (gametophytic, sporophytic);
— hemizygosity of gametes in diploids (with manifestation of all recessives) and its absence in polyploids;
— different ploidy level of female gametophyte components: egg cell, central cell, and also zygote-embryo and endosperm;
— maternal or hybrid nature of generative structures and seed elements;
— transmission of certain characters by both male and female gametophytes or by one of them;
— different time of arising of some characters (e.g., the different time of generative cell division, egg maturation in the different parts of inflorescence, polar nuclei fusion);
— presence of structures of "cell in cell" type.

As a subject for genetic investigation, such embryological processes as growth of pollen tubes, division of generative cell nucleus, fusion of polar nuclei, fertilization, cellularization of endosperm, and degeneration of antipodals have great significance.

Since the different processes are characterized by the significant variability in time, discovery of the genetic determination of the whole developmental pathway and its successive stages, studies are ongoing to determine the limits within which some conditions can be described as elementary discrete signs available for genetic analysis.

Apomixis, haploidy, polyembryony, and self-incompatibility can be related to the phenomena needed in genetic analysis. Their realization, as a rule, is connected with polygenic control, but sometimes mutation of one gene can induce the phenomenon (e.g., gene *IG*, provoking androgenesis in maize). Isolation of every phenomenon into a separate subject of genetic analysis is also advisable because equifinale (i.e., achievement of the same result by different ways) is characteristic of many of them. For example, haploidy can be a result of parthenogenesis (gynogenesis), hemigamy, elimination of chromosomes, and other factors. The final result is formation of sporophyte with "gametic" chromosome number. Sometimes

the same process can have different results. For example, diplospory can lead to apomixis and/or polyploidy.

The question of genetic consequences of embryological processes is conditioned by the fact that they, being themselves genetically predetermined, can raise a number of genetic phenomena with other regularities and possibilities (including evolutionarily and selectively significant ones) or influence significantly some other genetic signs. So, in some species the preservation or disappearance of mitochondria and plastids in male gametophyte was discovered, and due to this the possibility of uni- or biparental inheritance of cytoplasmic characters arises. Gynogenesis leads to introduction of nuclear and cytoplasmic material from paternal form without karyogamy in haploid egg cell. Atypical meiosis in haploids leads to translocations and aneuploidy. Triploids can arise in endosperm culture *in vitro*.

In embryogenetic engineering two directions can be noted:

1. use of genetic engineering for construction of forms with desirable **embryological characters** and
2. use of embryonic structures (gametophytes, sexual cells, zygote, proembryo, embryoids and others) for genetic construction and transmission of other **(not embryological)** characters.

Attractiveness of embryogenetic engineering is determined by the following. After different manipulations at cell level in most cases it is necessary to produce regenerant plants. This is achieved easily by using explants of the different embryonic structures. Besides that, for the purpose of experimental mutagenesis and cell selection, it is advisable to use haploid cells. Attempts to introduce DNA (genes) in pollen or to transmit certain paternal genes through irradiated pollen are known. With the aid of introduction of alien genetic material into embryoids and cells of embryogenic callus, transgenic plants of maize and rape were produced (Kuchuk, 1997). The results of gametic selection, based on use of pollen treated by action of different factors (high and low temperatures, toxins, herbicides, heavy metals, salts, ozone and others) are interesting and practically significant (Kilchevsky and Khotileva, 1997; Compendium of genes expressed specifically in pollen that have been cloned and characterized, Vol. 1; Gametophytic mutations; Modifiable variability of gametophyte; Genetics of flower development in this chapter).

The aims and expected results of researches are rather various:

1. **Creation of collection of embryomutants.** The use of genetic methods without solution of this question is practically impossible.
2. **The discovery of genetic grounds of similar characters in different taxa.** Such information is necessary for solution of many evolutionary and phylogenetic problems. It will allow us to estimate the perspectives of "interchangeability" of genes from the different species by methods of traditional selection or molecular biology, and the correct choice of the donors for appropriate genes.
3. **Control of morphogenesis pathways, their modification and reprogramming.** Questions connected with *in vitro* culture, interconversion in the "plant-cell-plant" cycle, and "gametophyte-sporophyte" will be most important for a long time. It does not exclude the necessity of investigation of *in vivo* development regularities, for example, conversion of somatic cells in embryo by adventive embryony, haploidization, absence of reduction.

4. **Temporal modification of embryological characters.** This will make it possible to solve the problem of experimental induction of many important phenomena, for example, sterility or restoration of fertility by temperature factor, morphogenesis *in vivo* and *in vitro*, polyploidization.
5. **Creation of organisms with planned, heritably fixed embryological characters and reconstruction of reproductive system.** Some characters are: removal of self-incompatibility, replacement of dioecy by monoecy, transition to apomictic mode of reproduction, intensification of regenerative potential *in vitro*.
6. **Management of phenomena having general biological and applied significance.** These include androgenesis, reproductive isolation, and embryogeny.
7. **Working out of principally new methods of selection** on the basis of embryogenetic approaches.

Modifiable variability must also be the subject of research, since it is necessary to discover factors that influence the gene expression and compensate for some of their defects. Compensation effects make clear physiological-biochemical and molecular mechanisms of gene action. With modifications, desirable results can be achieved without change in genetic grounds.

Objects of study must satisfy the following demands. They must be reckoned among classic genetic objects, be handy for embryological investigations, give more than one seed generation in a year, reproduce easily by vegetative mode and *in vitro* culture, and be true diploids with a rather low number of well-identified chromosomes, all or most of which control well-expressed marker characters. It will facilitate future works on localization of the genes controlling the reproductive sphere. The objects must be suitable for realization of different bio-technological and gene-engineering operations. Suitable objects, although not ideal, are maize and barley among monocotyledons, and tomato and petunia among dicotyledons. *Arabidopsis* is used in experiments on a broader scale owing to its short reproductive cycle, low chromosome number (n=5) and possibility of development *in vitro* in strictly controlled conditions (Smith, 1990; Ohad *et al.*, 1996).

Genetic Control of Apomixis

The role of the genotype in determination of plant capacity for apomixis is undoubted. This suggestion is supported by multiple apomictic forms that are shown to segregate the same trait in their progenies. It should be especially stressed that in progenies of all apomictic forms studied so far, irrespective of their taxonomic position, segregation of both sexual (normal) and apomictic organisms is obtained (see Nogler, 1994; Savidan, 2000). According to these data, all apomictic plants are likely to be heterozygotes in which the capacity for apomixis is controlled by some dominant allele(s), while sexual reproduction is determined by recessive one(s). This proposition is in good accordance with the fact that, in progenies obtained by selfing of obligate sexual plants, only the same mode of reproduction is usually found.

Because of the wide prevalence of apomixis (Asker and Jerling, 1992; Carman, 1995) and similar dominant character of this trait in different taxa, the scheme of its genetic control should be quite common and relatively simple in all flowering plants.

Nevertheless, segregation analysis of this trait has had few results. Such a situation is due to several problems.

First of all, although apomixis is found in many wild species, it does not occur in any of the major plant crops. Moreover, multiple attempts to transmit the capacity for apomixis from wild species to their crop relatives were not successful. So the studies are conducted entirely on wild species that are poorly genetically characterized, highly heterozygous and therefore unsuitable for segregation analysis.

Another problem consists in significant difficulties in testifying the plants for the trait studied. The fact is that even highly apomictic forms preserve at least a slight ability to reproduce sexually, so the trait usually shows incomplete penetration (Valle and Miles, 1992; Nogler, 1994; Savidan, 2000; Spielman *et al*, 2003). For example, the parent apomictic plants involved in segregation analyses by crossing with obligate sexual ones show rather high but not 100% frequency of apomixis. As a result, in the hybrid progenies obtained in such crosses, wide spectrum of segregants displaying various equilibria between sexual and apomictic modes of reproduction are usually found (Sherman *et al*, 1991; Valle and Miles, 1992; Lutts *et al*, 1994). It is very difficult to divide each progeny into several classes clearly differing in the mode of plant reproduction. So the capacity for apomixis often seems to be not a qualitative but a quantitative trait and therefore is quite difficult to analyse genetically.

Several attempts have been made to divide hybrid progenies in two clear phenotypic classes (Savidan, 1983; Nogler, 1984a; Leblanc *et al*, 1995a,b). In each of these cases, one phenotypic class was represented by obligate sexual plants and the other included all kinds of segregants possessing any, even very low, frequency of apomixis. However, such a qualitative approach also usually faces significant difficulties. The main difficulty lies in distinguishing the plants possessing zero and very low frequency of apomixis. Traditional methods for testifying the trait studied are based on either cytoembryological analysis of certain plants or detailed investigation of their individual progenies (Herr, 1982; Savidan, 1982a,b; Nogler, 1984b; Crane and Carman, 1987; Asker and Jerling, 1992). Unfortunately, both methods are quite complicated and scarcely useful for unravelling rare events or for large-scale analysis of each segregant. So a significant part of the progeny studied might be erroneously identified as obligate sexual plants because the frequency of apomixis is too low (Nogler, 1989).

One more problem impeding segregation analysis of this trait concerns significant diversity of the mechanisms of apomixis. Actually, the phenomenon studied may be the result of such different processes as adventive embryony and gametophytic apomixis including apospory and diplospory (Nogler, 1984a; Crane, 1989; Solntseva, 1989; Naumova, 1990; Koltunow, 1993). Each of these processes may have at least partly independent genetic control. Therefore, to make segregation analysis successful, parent plants should be identified and used that can undergo only a certain type of apomixis, for example, solely apospory or diplospory.

Segregation analysis of apomicts is also strongly impeded by their polyploidy. The fact is that almost all natural or artificially obtained apomictic plants appear to be either allopolyploids or various kinds of interspecific hybrids. So segregation analysis of the studied trait is traditionally based on the following main approaches (Nogler, 1994; Savidan, 2000):

1. intraspecific crosses between apomictic polyploids and obligate sexual diploids;
2. intraspecific crosses between apomictic and obligate sexual polyploids that possess the same level of polyploidy; and
3. interspecific crosses between apomictic and obligate sexual forms.

Each approach faces considerable problems. In crosses between plants of different ploidy (as a rule, 4n x 2n), the F_x hybrids obtained are usually unfit for segregation analysis because of their almost complete sterility. This inconvenience may be removed if the parent plants are of the same polyploidy level (for example, 4n x 4n or 6n x 6n). However, inheritance of the trait studied in polyploids should be quite complicated, thus impeding segregation analysis. Furthermore, the ratios obtained in crosses between different species are often distorted by meiotic imbalances in the hybrids. Finally, the general problem of all these approaches is significant heterogeneity of genetic background between the parent plants. So using traditional modes of segregation analysis to study the trait "ability for apomixis" may give only approximate data.

In spite of the high complexity of such approaches, significant data have been obtained for several species. These data allow some preliminary suggestions on the genetic control of apomixis in flowering plants. The genetics of adventive embryony is still very poor, so all progress has been achieved in the field of gametophytic apomixis.

The main developmental elements of gametophytic apomixis are apomeiosis and parthenogenesis (Grossniklaus *et ah,* 2001; Spielman *et ah,* 2003; see Parthenogenesis). In all the apomicts genetically investigated so far, both elements are shown to be dominantly inherited. In several species, namely *Poa pratensis, Taraxacum officinale* and *Erigeron annuus,* these elements have independent genetic control and could be segregated from each other (Barcaccia *et ah,* 1998; van Dijk *et ah,* 1999; Noyes and Rieseberg, 2000). However, in the majority of the apomicts studied, apomeiosis and parthenogenesis are strictly correlated.

In *Ranunculus auricomus,* tetraploid plants capable of both apospory and diplospory were described. According to the results of segregation analysis, the capacity for apospory in this species is controlled by a single locus A (Nogler, 1984b, 1989, 1995). It should be noted that normal (sexual) plants in *R. auricomus* are homozygotes for the recessive wild type allele (a^+a^+), while all aposporic tetraploids appear to be either simplex ($A''a^+a^+a^+$) or duplex ($A''A''a^+a^+$) heterozygotes. Complete absence of homozygous aposporic plants seems to be due to pleiotropic manifestation of the dominant A" allele resulting in some recessive lethal effect at the stage of gametophyte (Nogler, 1989). Thus, the A" allele could be transmitted to progenies only via gametes that simultaneously carry the wild type a^+ allele. Such a scheme corresponds well to the fact that aposporic *R. auricomus* plants are almost entirely polyploid.

Although the presence of a single allele A~ is quite sufficient for development of aposporic embryo sacs, the frequency of their formation depends on other factors. Among these factors are the dosage of the dominant allele as well as the time of aposporic programme induction (the last is controlled independently of the A locus). Therefore, some plants carrying the A" allele(s) but displaying late induction of apomictic programme could be misidentified as obligate sexual plants (Nogler, 1989).

The overwhelming majority of aposporic *R. auricomus* plants are simultaneously capable of diplospory. This suggests that both types of apomixis are under the same or very close genetic control. Meanwhile, using multiple backcrosses, a single trisomic plant (2n + 1 = 17) displaying high frequency of apospory but almost completely incapable of diplospory has been obtained. In this unique plant, the diplosporic mode of reproduction was shown to be retained but strongly suppressed (Nogler, 1989). So the capacity for diplospory in *R. auricomus* is controlled not solely by the A locus but in addition by some still unknown modifier(s).

Similar studies have been carried out with grass *Panicum maximum,* which is taxonomically far from Ranunculaceae. As was shown by precise cytogenetic analysis, normal (sexual) plants of this species are also represented by diploid recessive homozygotes (aa), whereas all apomicts appear to be tetraploids (Savidan, 1983). Among F_x hybrids obtained in crosses between apomictic and obligate sexual plants, the trait studied displays clearly monogenic 1:1 segregation. According to these data, apomictic mode of reproduction is determined in P. *maximum* by the genotype Aaaa. Moreover, as in *R. auricomus,* there is tight correlation between the capacities for apospory and diplospory. This could be regarded as additional support for similarity in genetic control of both types of apomixis.

Another grass, *Tripsacum dactyloides,* is also used in genetic studies of apomixis. Like *R. auricomus* and P. *maximum,* this species is known in obligate sexual diploid and apomictic tetraploid forms. Being the closest relative to the genus *Zea*, *T. dactyloides* successfully crosses with maize, which lacks any type of apomictic reproduction. Therefore, genetic studies in *T. dactyloides* attract not only purely fundamental but also strong applied interest.

F_x progeny obtained in crosses between maize and apomictic T. *dactyloides* plants shows clear 1:1 segregation for the mode of reproduction (Leblanc *et ah,* 1995a,b), thus resembling the monogenic scheme of inheritance supposed for *R. auricomus* and P. *maximum.* This progeny was studied by RFLP analysis using a set of T. *dactyloides*-specific probes. As a result, the locus controlling the capacity for apomixis has been linked to four molecular markers and thus mapped at T. *dactyloides* chromosomes (Grimanelli *et al.,* 1998). It should be noted that in normal (sexual) plants, these markers possess effective recombination, while in apomicts they strictly co-segregate like a single genetic unit. This unit comprises approximately 40 cM from the map developed for sexual T. *dactyloides* and probably contains no less than 100 genes. So although the capacity for apomixis is inherited monogenically, it may be controlled by multiple genes located within an extended chromosome segment that has strongly suppressed recombination (Grimanelli *et al.,* 1998, 2001).

Very similar results have been achieved in other apomictic mono- and dicotyledonous plants, including *Pennisetum squamulatum* (Ozias-Akins *et al.,* 1998), *Cenchrus ciliaris* (Roche *et al.,* 1999), *Paspalum simplex* (Pupilli *et al.,* 2001) and *Erigeron annuus* (Noyes and Rieseberg, 2000). In each of these species, the apomixis-related locus is represented by a huge chromosome segment showing no recombination in the apomicts. However, on the basis of comparative mapping of several grass genomes, which are shown to be highly conservative in evolution, the apomixis-related loci from different species are not homologous with each other and thus should comprise distinct sets of genes (Pessino *et al.,* 1997; Grimanelli *et al.,* 1998; Pupilli *et al,* 2001). This may reflect that, in different plant phyla, the capacity for apomixis has arisen independently involving various segments of the genomes.

Unfortunately, no particular genes controlling the capacity for apomixis are known so far. The molecular basis of apomixis is also entirely hypothetical. Several mechanisms are usually mentioned. The first one is temporal or spatial miscoordination of some normal sexual reproduction developmental programmes as a result of complete or partial genome duplication as well as allopolyploidy (Carman, 1997; Grossniklaus et al, 2001; Grimanelli *et al,* 2001). Another mechanism implies molecular imprinting that affects some genomic regions in polyploids or mutants (Luo *et al,* 2000; Grimanelli *et al,* 2001; Spielman *et al,* 2003). In any case, the dominant inheritance of the capacity for apomixis reflects the regulatory character of the deviations, which are crucial for realization of this trait. Actually, on the basis of fundamental genetic ideology, dominant manifestation of a mutant allele is usually the result of such a molecular defect that retains the function of the gene product but leads it out from negative regulation of some repressor.

Progress in dissecting the molecular mechanisms of apomixis could be provided by detailed analysis of the genes, mutations in which were recently shown to stimulate fertilization-independent seed development (Grossniklaus *et al,* 1998; Luo *et al,* 1999; Ohad *et al,* 1999). Another intriguing and promising direction concerns the fact that in *Pennisetum squamulatum* some sequences from the apomixis-related locus are represented in hemizygous state (Ozias-Akins *et al,* 1998; Akiyama *et al,* 2004).

Genetic Heterogeneity of Seeds. Polyembryony

Seeds of flowering plants differ in morphological, biochemical, physiological and genetic characteristics (Table 23). **One of the most important signs of the seeds is their genetic heterogeneity, mainly related to the different origins of the embryos.** It is worth mentioning that, to some extent, the heterogeneity of seeds depends on the level of vegetative propagation in the population, which affects the quantity and quality of seeds produced by each plant.

Genetically diverse seeds may look phenotypically alike. However, in the case of xenia and metaxenia in maize seeds, for instance, when parental forms distinctly vary in phenotype, the genotypic and phenotypic heterogeneity of the seeds is obvious.

Genetic heterogeneity of seeds in flowering plants is not a novelty. While experimenting with *Hieracium,* Gregor Mendel failed to reproduce the type of segregation (3:1) he had revealed in *Pisum sativum.* Later, embryologists discovered the formation of embryos without fertilization (apomixis) in *Hieracium* seeds.

The genetic heterogeneity of seeds is based on diverse phenomena, such as embryogeny, embryoidogeny (ovular and embryonal) and gametophytic apomixis (see details, Embryoidogeny —a new type of vegetative propagation; Apomixis). Seeds may have zygotic embryos (gamospermy) formed as a result of sexual process involving meiosis and gamete fusion (n+n). This mechanism is the major source of gene recombination, bringing about hereditary variability. A new generation of plants may, however, develop from seeds, the embryos of which were formed without fertilization (agamospermy). There are various manifestations of agamospermy. This type of seed development is notable for the apomictic formation of embryos as a result of gametophytic or sporophytic apomixis comprising ovular (nucellar and integumentary) and embryonal (monozygotic cleavage) embryoidogeny.

Table 23. The criteria of seed heterogeneity (modified from Levina, 1981).

I. Quantitative	Size, weight
II. Structural	Morphological: shape, type of symmetry, colour, topography of surface, presence and type of appendages, extent of development of embryo, its position and shape Anatomical: histological characteristics of spermoderm, properties of endosperm (e.g., size and shape of cells, size of starch grains)
III. Biophysical	Electric and radioactive properties of seeds
IV. Biochemical	Composition of proteins, amino acids, and vitamins; composition and activity of enzymes; presence or absence of inhibitors of germination
V. Physiological	Permeability of seed covers, depth of dormancy, hydration of tissues, physiology of germination, longevity
VI. Ecological	Various requirements and tolerance to external factors of germination (e.g., water, temperature and light regime, aeration of soil, chemical composition of soil solution), modes of dispersion and germination
VII. Embryogenetic	Various forms of agamospermy on the basis of gametophytic apomixis (parthenogenesis, apogamety) or sporophytic apomixis (nucellar, integumentary, and monozygotic cleavage embryoidogeny)

Monozygotic cleavage embryoidogeny must be included with agamospermy, although it is not attributed to seed reproduction by many biologists (Battaglia, 1963; Grant, 1981; Nogler, 1984a,b). The main reason this phenomenon is ignored is apparently that it is poorly investigated in flowering plants. Lakshmanan and Ambegaokar (1984) attribute the development of additional embryos from the proembryo and its parts to sexual polyembryony. In our opinion, this phenomenon is a graphic example of the cloning of a new sporophyte in the early stage of its development, i.e., one of the modes of vegetative propagation (Batygina, 1992,1993a).

Various clones may arise in one seed: **clone of maternal organism** as a result of nucellar and integumentary embryoidogeny (2n=2n) and gametophytic apomixis (n, 2n, 3n etc.) and **clone of new daughter individual** in monozygotic cleavage embryoidogeny resulting in the formation of twins, triplets, etc.[1] In higher plants, twins, triplets, etc. with embryos differing in origin and genotype do occur. For instance, haploid-haploid twins are known in *Orchis maculata* (Hagerup, 1947), *Gossypium barbadense* (Beasley, 1940), and *Sesbania aculeata* (Haque, 1946). Haploid-diploid twins were found in *Lilium martagon* and L. *henryi* (Cooper, 1943) and diploid-diploid ones in *Asparagus officinalis* (Randall and Rick, 1945). Diploid-triploid twins occur in *Triticum* (Yamamoto, 1936). The triplets also differ genetically: diploid-diploid-diploid triplet in *Sagittaria graminea* (Johri, 1936) and haploid-diploid-haploid triplet in *Azadirachta indica* (Nair and Kanta, 1961).

[1]Twins, triplets, etc., can be of different origin, either enzygotic (from the same zygote) or fraternal (from zygote, synergid, nucellar cell, etc.).

Comparison of phenomena that are the basis of various modes and types of reproduction and propagation allowed us to develop a new scheme of the formation of genetic heterogeneity of seeds by embryo origin.

1. **Sexual embryos** (biparental inheritance) arise as a result of fertilization of egg cell (classical sexual process) or of synergids (or antipodals) that are past gamete differentiation. These processes are followed by recombination.
2. **Parthenogenetic embryos** (uniparental inheritance) are formed in different forms of gametophytic apomixis and different modes of embryo sac development:
   a) Some kinds of diplospory (Taraxacum- and Ixeris- types of embryo sac development) are characterized by a greater or lesser participation of meiosis and have a narrower reserve of variability than sexual reproduction;
   b) Apospory and some forms of diplospory (Antennaria- and Allium-types of embryo sac development) have maternal inheritance and are consequently like vegetative propagation proper.
3. **Somatic embryos** (uniparental inheritance) may arise in the following ways:
   a) From nucellar or integumentary cells; in this case the level of possible hereditary variability is equal to that of classic vegetative propagation—gemmorhizogeny.
   b) As a result of zygote or sexual embryo cleavage; monozygotic embryoids in respect of sexual embryo (from which they were formed) are the new daughter generation and have another genotype in comparison with ovule cells and tissues.

On the basis of embryo origin and inheritance character, the following types of genetic heterogeneity of seeds may be classified:

1. Seeds with a sexual (zygotic) embryo (n+n=2n), biparental inheritance.
2. Seeds with a hemigamous (chimaerous) embryo, biparental or uniparental inheritance.
3. Seeds with a parthenogenetic embryo, uniparental (maternal or paternal) inheritance:
   a) seeds containing diploid embryos (2n+2n) —non-reduced gynogenesis;
   b) seeds containing haploid embryos (n) —reduced gynogenesis;
   c) seeds containing haploid embryos (n) —reduced androgenesis.
4. Seeds with a somatic embryo (embryoid) (n=n, 2n=2n, 3n=3n etc.), uniparental inheritance:
   a) seeds containing nucellar embryoids;
   b) seeds containing integumentary embryoids;
   c) seeds containing monozygotic embryoids.
5. Seeds containing zygotic and parthenogenetic embryos and different embryoids in various combinations; in such heterogenous seeds the development of embryos and seedlings is competitive.

The proposed scheme of genetic heterogeneity of seeds does not consider hybrid seeds and seeds with sexual embryos and embryoids, which may form in different

sacs and ovaries. These aspects of seed genetic heterogeneity have been discussed (Asker, 1979; Lakshmanan and Ambegaokar, 1984; Nogler, 1984a).

As distinct from the usual seeds, containing only zygotic embryos, in heterogenous seeds sexual and asexual processes of individual formation occur side by side. The reproductive process is often not simple. For example, while forming enzygotic twins (or triplets, etc.), the sexual process precedes the asexual one (i.e., the developmental programme is switched). Theoretically, several types of embryos with different inheritance may develop in the same seed. Some of them—sexual and parthenogenetic embryos (Taraxacum- and Ixeris-types of embryo sac development)—are a significant resource of variability for new populations. Other apomictic embryos, which are formed in apospory and some kinds of diplospory (Antennaria- and Allium-types of embryo sac development), preserve a maternal genotype and are incapable (or poorly capable) of restoring the genetic diversity. For that matter, formation of these embryos can be considered vegetative propagation, although it occurs in the seed.

In this relation, it is interesting to cite the lines of Levina (1981, p. 12) that vegetative propagation ensures species renewal here and now, whereas seed propagation ensures it there and then.

Polyembryony. Development of several embryos in the same seed of flowering plants was called **polyembryony,** and the seeds themselves were called **polyembryonic** (Fig. 60). Although this phenomenon was discovered in plants by Leeuwenhoek as early as 1719, the essence of the term "polyembryony" is still discussed (Johansen, 1950; Maheshwari, 1950; Maheshwari and Sachar, 1963; Lakshmanan and Ambegaokar, 1984). The processes constituting polyembryony cause the appearance of different genotypes in the same seed and consequently the enhancing of genetic heterogeneity of seeds. The need to correct the concept "polyembryony" also arises from the fact that embryoids may be formed not only in the seed, but also on vegetative organs in flowering plants.

Irrespective of their origin, all somatic embryos produced by flowers or vegetative organs (stem, leaf, root) of the sporophyte, as well as the embryos formed from synergids and antipodal cells in the course of gametophytic apomixis, are actually adventive with respect to zygotic embryo. That is why the term "adventive embryony" should be considered in a broader sense and not reduced to nucellar and integumentary embryony or to nucellar embryony only, as some authors have done (Grant, 1981; Nogler, 1984a). In my opinion, polyembryony embraces embryogeny, reproductive embryoidogeny (monozygotic, nucellar and integumentary), gametophytic apomixis and vegetative embryoidogeny (homophasic viviparity). Polyembryony may be caused by hybridization, pollination, and physical and chemical and other factors. Development of additional embryos may be autonomous, sporadic or induced. At present, the morphophysiological and genetic reasons for polyembryony are unknown. One of the reasons appears to be a disturbance of the integrity of the embryo and surrounding structures that induces embryoidogeny. It is possible that, in the weakly integrated embryos of some animal species, another mode of cell division regulation arises that is designed to protect the embryo from an unfavourable environment. In these cases, some invertebrates were shown to begin somatic embryoidogenesis (Tokyn, 1987). It is very important that disintegration of the embryo or its parts is associated with the death of some cells (apoptosis), whereas, in other cells, dedifferentiation and proliferation processes start, thus leading to polyembryony (Tokyn, 1987).

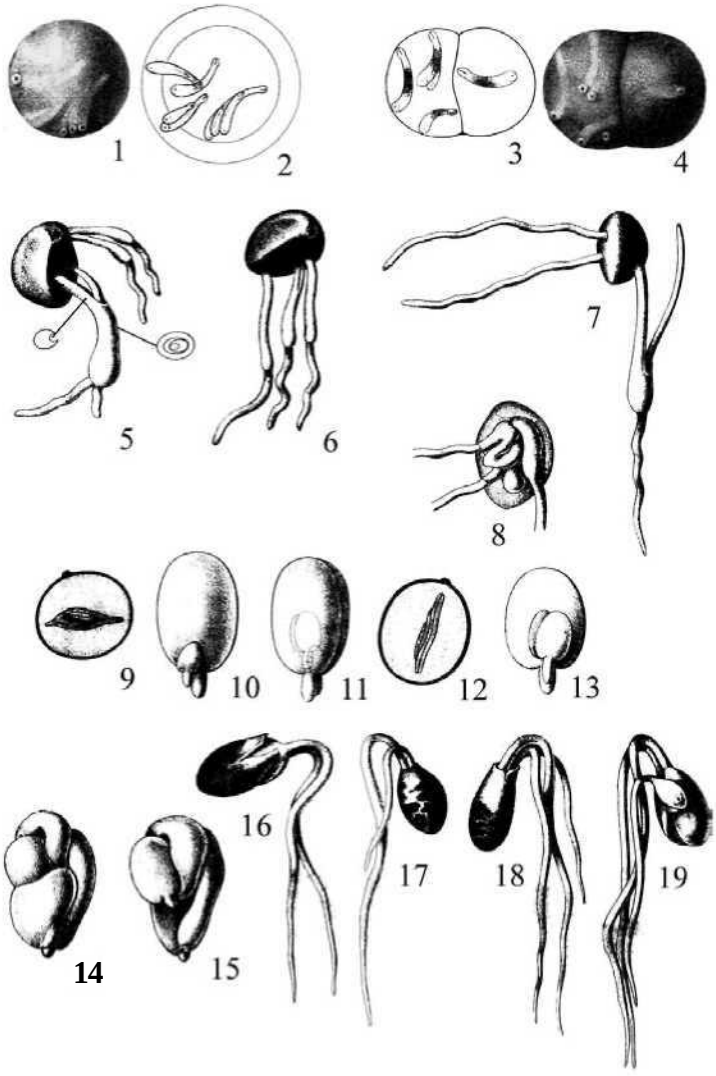


Fig. 60: Polyembryony in flowering plants (after Braun, 1859).

1-i—Ardisia polytoca: 1—exterior of seed with seven embryos, 2, 3—position of embryos within the seed, 4—two seeds from the same fruit, top view; 5-8—*Hemenocallis mexicana:* germinating seeds, with embryos emerging in different places (8—flexed cotyledons); 9-13,16-19—*Euonymus latifolius:* 9-11—three embryos in one seed, two smaller embryos are situated between the cotyledons of larger embryo (in 11 their size and position are shown by a dotted line), 12,13—seed with two embryos, 16,17—two seedlings emerging from one seed, 18,19—three seedlings emerging from one seed (in 19 testa is removed); 14,15—*Amygdalis communis:* two embryos in one seed, a small embryo is situated between the cotyledons (unequal in size) of a large one.

Some researchers believe that polyembryony is a recessive trait governed by a group of genes (Kappert, 1939; Maheshwari, 1950). Another hypothesis interpreting the formation of seeds with several embryos in terms of cytology (Rhoades, 1961) envisages that a certain chromosome balance between the embryo, endosperm, and maternal tissues (2:3:2) is a prerequisite for the development of additional embryos in the seed.

The ability of a plant to form embryoids at all developmental stages in both generative and vegetative organs together with the ability to reproduce sexually increases the flexibility and tolerance of reproductive systems. These are prerequisites to the development of populations heterogenous in both age and genetic material (Fig. 61).

Ecological and evolutionary role of seed heterogeneity. There is a relationship between the different forms of embryoidogeny, gametophytic apomixis and the geographic and climatic distribution of plants. Adventive polyembryony (nucellar and integumentary embryoidogeny) occurs in tropical and subtropical regions, whereas gametophytic apomixis is more often observed in boreal plants under more severe conditions (Grant, 1981). Asexual diploids more often occur in groups of plants exhibiting nucellar and integumentary embryoidogeny (e.g., many species of *Citrus)* than in groups with gametophytic apomixis (Gustafsson, 1946, 1947a,b; Stebbins, 1950).

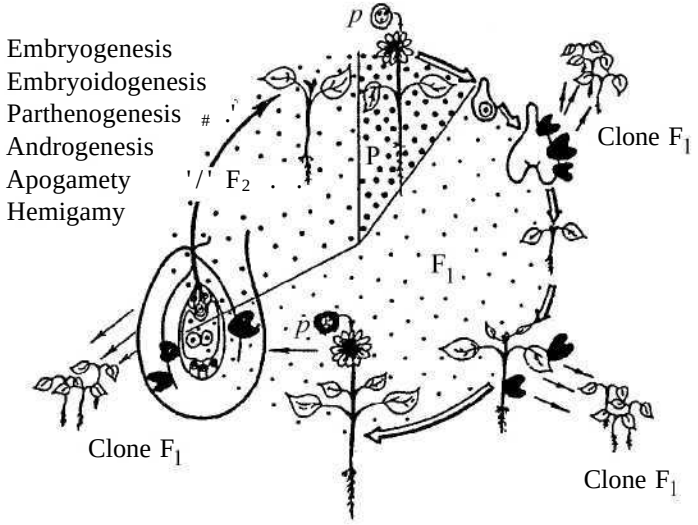


Fig. 61: Modes of individual formation in flowering plants influencing the composition of the population.

P—parent organism; F_1—first generation, F_2—second generation, *p*—pollen; zygotes and zygotic embryos of the first and second generations are shown white; somatic embryos (embryoidogenic type of reproduction) are shown black; white arrows designate the formation of the first generation from zygote to the development of reproductive organs (ovule, seed); long black arrow designates the development of the second generation in ovule and seed in the plant of the first generation. Possible modes of formation of new individuals of the first and second generations are listed in the left upper corner.

The influence of climate on polyembryony was also discovered in some gymnosperms. For instance, in northern autochthonous populations of Scotch pine, formation of polyembryonic seeds may be induced by low temperatures (Shimak, 1973).

Specific features of seeds such as dormancy, presence of embryos of different origin, reserve of stored materials, and rigid coats provide for the existence of seed bank in the soil. Homeostasis of species, population and coenosis largely depends on the soil stock of seeds. According to Levina (1981), the seed bank in soil is essentially the "embryonal population" of the species, its "long-term reserve".

One may assume that, owing to cleavage embryoidogeny and viviparity only (see Viviparity), it is possible to observe a genetically homogeneous population comprising individuals of different ages during the same growing season (Fig. 61). At the same time, nucellar and integumentary embryoids derived from the same zygote as the embryoids formed by cleavage embryoidogeny or viviparity preserve the parental genotype in population during several growing seasons and even several years. It is worth noting that in the same seed, along with nucellar and integumentary embryoids, a zygote may be formed, which will produce genetically new progeny in the population. One should not forget about various manifestations of gametophytic apomixis (parthenogenesis, apogamety, hemigamy and androgenesis), which also increase the genetic heterogeneity of seeds. Thus, the presence of sexual embryo and embryoids of various origin in the same seed results in great genetic heterogeneity of seeds, i.e., heterogeneity of the "embryonal population". This phenomenon often takes place in nature. However, it is usually underestimated.

When different types of reproduction are compared, the degree of transformation of genetic material in successive generations gradually decreases in the following order: gamospermy (cross-pollination), gamospermy (self-pollination), agamospermy (gametophytic apomixis), agamospermy (monozygotic, nucellar and integumentary embryoidogeny), and aspermy (foliar, cauligenic, and rhizogenic gemmorhizogeny or embryoidogeny).

In this series, the role of meiotic transformations gradually becomes less important, and seed propagation is replaced with vegetative propagation. The change in the reproductive patterns and the combination of the propagation types in one life cycle appear to depend on environmental conditions. Unlike cross-pollination, more limited transformations of genetic material (e.g., as a result of apomixis) do not elevate the adaptive potential of the organism. All the trends mentioned above may be expressed simultaneously and fixed in the progeny. Reproduction by seeds simultaneously containing the primordia of individuals with different inheritance (i.e., sexual and somatic embryos) may serve as an example.

In completely agamospermic reproductive systems, sporophytes of different origin (with different maternal inheritance) may be reproduced in seed: monozygotic, nucellar, and integumentary embryoids, as well as the embryos formed as a result of gametophytic apomixis (parthenogenesis, androgenesis, hemigamy and apogamety).

The study of gamo-agamic complexes is of interest for understanding that agamospermy is a special form of seed propagation and plays a role in microevolution. In addition, these investigations are very important for better insight into the cytogenetics of apomixis in relation to breeding. The families with agamospermic species occupy different positions in the phylogenetic system. This

appears to reflect an evolutionary parallelism widely known in flowering plants by numerous morphological characteristics.

The genetic heterogeneity of seeds arises even as a result of autogamy owing to meiosis. The seed progeny produced genetically differs from the mother plant, which is never observed in a clone in the course of vegetative propagation. In cross-pollinating populations, allogamy leads to a high level of heterozygosis, thus producing a large pool of recessive genes "for manoeuvrability".

The study of the genetic heterogeneity of seeds and populations is very important for the development of reproduction theory and the practice of producing new species and cultivars of plants. This problem is undoubtedly related to the preservation of biological diversity on our planet.

The variety of modes of reproduction within one life cycle in flowering plants seems to be of adaptive significance because they ensure the survival of the species under normal and stress conditions. The systems of plant reproduction should be considered at the levels of individual, population, and ecosystem, as well as from the evolutionary point of view.

PART SIX–POPULATION AND ECOLOGICAL ASPECTS OF REPRODUCTION

Phytocoenosis (Greek *phyton*—plant, *koinos*—common) is a site of vegetation with relatively homogeneous pattern, floristic composition and abiotic environment (Shennikov, 1964). Phytocoenosis is one of the basic subjects of geobotany (phytocenology).

There are different definitions of phytocoenosis but they differ in form only. Homogeneity of floristic composition is accounted as a main character (Kylin, 1926; Braun-Blanquet, 1951). To this, Sukatchev (1935) added interrelations among plants. Ellenberg (1956,1968) emphasized the role of competition among plants. Nitzenko (1953,1963) wrote that the necessary degree of homogeneity was not pointed out in Sukatchev's definition. This makes it possible to distinguish phytocoenosis from non-phytocoenosis but not different types of phytocoenosis.

The shortcoming of the definition consists in the inclusion of two different criteria: interrelations among plants and spatial homogeneity of species composition and species abundance. Neither criterion was defined exactly.

Interactions among plants do not promote spatial homogeneity of phytocoenosis and do not create a united system of plant interactions. Every plant changes its environment, forming a zone of influence (phytogenic field, after Uranov, 1965). The area of the zone is usually not large. It does not exceed the area of the crown and roots. Every plant interacts with neighbouring plants only and remote parts of a phytocoenosis hundreds of square metres or hectares in area are fully independent of one another. A spatially homogeneous environment can define a spatially homogeneous phytocoenosis but only in the case of similar history of colonization and vegetation development. Otherwise, different phytocoenoses can occupy one ecotope. Unevenness in diaspore supply in different parts of the ecotope can define significant differences in vegetation.

Interactions among plants are not less intensive on the boundaries of phytocoenoses than within them. When analysing different definitions of phytocoenosis, Ipatov (1966) concluded his notion of coenocell was more correct, i.e., the set of directly interacting plants, and that the phytocoenosis is a unit of regionalization.

Norin (1968, 1974) believed that phytocoenosis must have an **edificator,** i.e., environment-forming species that affects the abundance and frequency of all others. In fact, he considered as phytocoenoses only forest and moss-dominated mire communities.

Species composition in every spot of vegetation is determined by environment and plant interactions. It is known that the interrelations are very important for abundance and performance of plants in more or less closed vegetation cover. Only neighbouring plants interact but homogeneous sites of vegetation can occupy a very large area. Phytocoenosis is not a system of interacting plants but a spatially homogeneous patch of vegetation (Vasilevich, 1983; Ipatov and Kirikova, 1997).

Within phytocoenosis, there are often spots with distinct species composition. They are the result of the influence of one or a group of plant individuals on the environment. In forest phytocoenoses they occur under the crown of a single tree or in a group of tree saplings. In herbaceous phytocoenoses, microcoenoses are infrequent. They arise in consequence of vegetative enlargement or higher frequency of the

species in a more favourable environment. Heterogeneity in incoming propagules is important in creating the vegetation pattern.

Rabotnov (1972) distinguished the following types of vegetation mosaic: episodic or related to propagule distribution, ecotopic, phytogenic, clonal, and anthropogenic. As microcoenoses one has to consider only regularly occurring species groups with enough dissimilarity from others.

It is necessary to distinguish spatially homogeneous and clinal phytocoenoses (Vasilevich, 1967). Within spatially homogeneous phytocoenosis, vegetation does not change in any direction. The spatially homogeneous phytocoenoses occupy usually spatially homogeneous abiotic environment (ecotope).

Clinal phytocoenosis is characterized by continuous change in species composition in any direction. The abundance of one species increases and that of another decreases, but it is impossible to draw a boundary within clinal phytocoenosis. When clinal phytocoenosis is extensive, its two ends may be very dissimilar in species composition. They may even be included in different plant associations.

Vegetation classification is not classification of phytocoenosis, as many believe. In reality, all vegetation classifications are based on description of plots that represent only definite parts of a phytocoenosis. They must be larger than a representative area. They must include a sufficient number of species and give mean species abundance scores smoothing random variation.

Ecological niche is the position of a species in an ecosystem, its relationships to environmental factors, to other species and to resources consumed. American ornithologist Grinnell (1917) was the first who used the term "niche". He described the ecological niche of California tracher *(Toxostoma redivivum)*. He characterized its food and foraging method, place of sheltering and nesting, and its relation to climatic factors and to plant communities. Grinnell did not differentiate between ecological niche and ecological range, which is still a source of confusion.

Elton (1927) defined ecological niche as an animal's place in biotic environment and its relations to food and enemies. He believed that niches are only smaller subdivisions of conceptions such as "carnivore", "herbivore", or "insectivore". Different species can occupy the same niche in different communities. Hutchinson (1957) introduced the notion of multidimensional ecological niche as hypervolume in multidimensional space in which every axis is an ecological factor influencing the species. Minimal and maximal factor scores permitting a species to survive and reproduce are the boundaries of the ecological niche of a species. It is a fundamental niche. As a result of interspecific competition the species may be excluded from any part of the fundamental niche. The residual part of the niche is the realized niche. The principle of competition exclusion (Gause, 1934) states that species that occupy the same ecological niche compete intensively and cannot coexist permanently.

When all factors important to an organism are included in an ecological niche, many believe ecological niche and ecological range are synonyms (Savage, 1958). In this connection it was proposed to distinguish the following: (1) functional or resource niche that characterizes resources consumed by species, and differences in these resources can exclude interspecific competition for species that exist in one community; (2) habitat niche, i.e., species distribution along environmental gradients; and (3) niche as junction of the two (Whittaker, 1972; Whittaker *et al.*, 1973).

Odum (1971) wrote that the habitat is the address of a species and the ecological niche is its profession.

Differentiation of ecological niches excludes interspecific competition only when niches do not overlap on all consumed resources. All autotrophic plants consume the same resources: solar radiation as source of energy for photosynthesis, water, and nutrients (macro- and microelements). The same nutrients are necessary for every plant but in different quantities. Differentiation of ecological niches of plant species is possible for every resource but only to a limited degree.

Plants under a closed spruce layer use light that penetrates through tree crowns. There is no competition for light since undergrowth plants cannot intercept light that reaches spruce trees. But such differentiation with respect to light is not complete in relation to plant populations. Every plant begins life as a seedling and its available light depends on all the mature plants around it. Crown competition among neighbouring plants cannot be excluded.

Water is a more complex factor. It can enter the community from above as precipitation, from below as ground water, and from the side as surface and ground outflow. It is possible that a plant community would have two groups of plants independent with respect to water sources. Phreatophytes consume deep ground water and ombrophytes consume precipitation. When precipitation does not make contact with the ground water, as in arid regions, the differentiation of ecological niches can be complete. But seedlings of all plants are ombrophytic. This does not exclude competition for water between phreatophytes and ombrophytes.

Plants require a large number of nutrients but they do not differ significantly in the set of necessary nutrients. The differences are mainly quantitative. It is impossible to imagine that neighbouring plants might have independent sources of nutrients. Thus, **complete differentiation of ecological niches for autotrophic plants within the plant community is impossible with respect to any resource.**

The vegetation pattern within a community is often a consequence of environmental change by plants. This phytogenic pattern creates differentiation of plant species in different microsites. It can cause differentiation of ecological niches of some plant species and can exclude interspecific competition. Phytogenic pattern develops usually in communities with strong edificator species that do not create a closed canopy or some edificator species intermingled in a closed canopy.

Effective separation of ecological niches is possible in relation to place and time only. The basic parameters of ecological niche are **space, time** and **food** (Pianka, 1974). Food specialization is absent in autotrophic plants.

Plant ecologists estimate differentiation of plant ecological niches in different ways. Rabotnov (1950a,b) and Shennikov (1964) believed that every sinusia in a plant community has a separate ecological niche. Later Rabotnov (1973) wrote that every plant species has a separate niche but they overlap.

Whittaker (1972) considered that ecological niches of all plant species differ in the position of their centres along environmental gradients. In the Sonora desert, niches differ in the height at which plant species bear the greatest part of their foliage, in the seasonal time of plant growth and development, and in different solutions to the water problem (Whittaker, 1975). But these factors are not sufficient for significant differentiation of all ecological niches of species in the community. There is differentiation of plant species in growth time. The temporal sinusia exist in desert

and nemoral forests. Spring ephemeroid sinusia end growth before the beginning of development of summer herbs. This sinusia has a separate ecological niche but many species occupy it.

Ecological niches of plant species greatly overlap or coincide completely but there are multispecies plant communities with dozens of species. These communities are stable in many cases. This contradicts the principle of competition exclusion at first sight. However, there are a number of circumstances that prevent competition exclusion. Plants are sessile organisms and they influence only the limited area around them. During their lifespan plants can exclude neighbours from an area that is slightly larger than their crown and root area. Competitive exclusion can be successful only in the case of great advantage in the competition ability of one species in relation to others. But in a speciation process that runs independently in different taxa, many species originate with approximately equal competition ability. These circumstances prevent competition exclusion (Vasilevich, 1979).

Unlike plants, animals are strongly differentiated with respect to food. Their resource niches can be absolutely different.

Population (Latin *populus-a* large number) is the set of individuals of one species within which there is relatively free gene flow. As a result, all individuals in a population are genetically similar. It is a minimal group of organisms that can reproduce, exists in any territory for a long time in evolutionary terms, and is greatly isolated from analogical groups of organisms (Yablokov, 1987).

Spatial boundaries of plant populations usually are weakly manifested and delimitation of natural populations is very difficult task. A small gene flow is sufficient to account for similarity of genetic structure of two populations. Plant population area is defined by distance of pollen and diaspore dispersal. It was shown that a great part of intraspecific genetic variation concentrates within populations, and geographically remote populations can have very similar genetic structure. Genetic differences of the populations do not correspond in many cases to geographical distance.

Plant ecologists define plant population the set of individuals of the species in the phytocoenosis. This population was named coenopopulation (Petrovsky, 1961). A more reasonable viewpoint regards coenopopulation as a part of population (Rysin and Kazantseva, 1975; Uranov and Serebryakova, 1976). Boundaries of populations do not coincide with phytocoenosis boundaries. Some hindrances to gene flow can appear on phytocoenosis boundary, for example, differences in flowering time (Falinska, 1974). In many cases the abundance and performance of species changes only on the boundary of phytocoenosis. Pollen and diaspores can disperse from one phytocoenosis to another of the same community type when they are placed a short distance away. This provides gene flow among phytocoenoses. A population must exist over many generations in one place but many phytocoenoses are short-lived. Vegetation successions proceed quickly and many species exist on the site for just one or a few generations. Ruderal species occupy the territory very quickly and are not able to stay on it a long time. Populations of many plant species can occupy a large territory but they exist as a number of short-lived dems (Schwarz, 1969; Timofeev-Resovsky *et ah*, 1973), which shift from one place to another. Owing to pollen and diaspore dispersion and seed bank these populations exist continually. They are metapopulations (Husband and Barrett, 1996).

Life form is an appearance or habit[1] of a plant, including its epigeal and hypogeal organs, arising in harmony with the environment. Synonym: biomorph (Greek bios—life, *morpha-iorm).* The theory of life forms is called biomorphology (Khokhrjakov, 1975; Yurtsev, 1976; Zhmelev *et al.*, 1993).

The term "life form" (German "Lebensform") was proposed by Warming (1884). As applied to plants, this term is used in two senses: (1) as a convergent resemblance of habit in members of different systematic groups affected by the same life conditions (a **classificational approach)** and (2) as a combination of adaptive characters of a particular organism at every moment of its individual life (an **individualistic approach).**

The **classificational approach** was applied for the first time by Humboldt (1806) who distinguished 16 (later 19) **"general forms"** of plants based on the resemblance of external, i.e., habitual, morphological traits. The combination of certain "general forms" is characteristic of the physiognomy of the plant cover in various climatic regions of the Earth.

For a long time, only the classificational approach existed in plant life form studies. It was used widely (and is used now) in geographical, phytogeographical, geobotanical and systematical works.

According to the classificational approach, the **life form** is the appearance of the adult plant living in the typical environment of this species. Life forms have developed over a long-term evolutionary process and are determined genetically. However, they may change when affected by environmental factors (particularly unfavourable factors) showing a certain range of variation, a peculiar norm of reaction. For instance, *Tilia cor data* is a single-trunk tree in the central parts of its area in the European broad-leaved and mixed forests. In the same area, in clearings it may form shrub-like stump sprouts. This species acquires the appearance of a stunted patch-forming tree with numerous trunks at the northern boundary of its area in the zone of taiga and an appearance of elfin wood in mountains at the tree-line (Chistjakova, 1988; Smirnova, 1994).

The **individualistic approach** to the analysis of life forms was realized much later than the classificational one. It was Warming (1884) who founded this approach. He considered **life form** to be the form in which the plant vegetative body exists in harmony with the environment during its whole lifespan, from seed to death. Although changes of the habit of every organism are evident during its individual life, these ideas were not accepted for a long time. Only in the mid-20th century did Serebryakov (1962), his students and followers demonstrate that plants change their life form in the course of ontogenesis. These ontogenetic changes of biomorphs were named "phases of morphogenesis" (Shafranova, 1967; Gattsuk *et al.*, 1974; Zhmelev *et al.*, 1993). The ontogenetic successions of life forms were described in different taxa (Khokhrjakov, 1975,1978,1981; Serebryakova, 1983). These life forms were named "ontobiomorphs" (Mazurenko, 1986; Zhmelev *et al.*, 1993).

At present, classificational and individualistic approaches develop in close interrelation especially in works on the problems of morphological evolution and biomorphological plant classification (Serebryakov, 1962,1964, 1968; Serebryakova, 1971,1972,1974,1983; Khokhrjakov, 1975,1978,1981; Mazurenko, 1986).

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[1] *Habitus,* Lai—an appearance.

Classifications of biomorphs are based predominantly on the structural characters of vegetative organs and reflect the parallel and convergent ways of ecological evolution. Like all ecological classifications, they are numerous and depend on the approaches and aims of the investigations.

One of the most popular classifications was proposed by the Danish botanist Raunkiaer (1905,1934). It is based on an extremely important adaptive character, the position of renewal buds in relation to the substrate and the kind of protection they have during the season unfavourable for growth (cold or dry). According to this character, five large groups of life forms are distinguished.

1) **Phanerophytes** (Greek *phaneros*—open, apparent, *phyton*—plant): the buds are situated high above the ground, i.e., in the aerial space. They are trees, shrubs, woody lianas, and epiphytes, i.e., plants living on the branches and trunks of trees.
2) **Chamaephytes** (Greek *chamae—low,* on the ground): the buds are situated not more than 20-30 cm above the ground surface and are protected by snow cover in winter. They are dwarf shrubs, semishrubs and dwarf semishrubs, creeping perennial herbs, cushion plants.
3) **Cryptophytes** (Greek *cryptos*—hidden): the buds are hidden either in the soil depth (geophytes—Greek *geo*—earth, they are bulbiferous, bulbotuberous, a number of rhizomatous plants) or in the peat and reservoir substrate (helophytes—Greek *gelos*—mire, i.e., mire plants), or in the water thickness (hydrophytes—Greek *hydor*—moisture, i.e., water plants).
4) **Hemicryptophytes** (Greek *gemi*—half): the buds are situated on the surface of the soil or in its uppermost layers and are protected by dead plant material (forest litter, mulch in grasslands). Most temperate herbaceous perennials are hemicryptophytes.
5) **Therophytes** (Greek *theros*—summer) are the annuals that die completely at the end of the vegetative season. The next year, they arise from the seeds that persist in the soil or on its surface.

Raunkiaer subdivided these groups of life forms further according to various characters, including plant size, features of the bud coats, and lifespan of leaves. On the basis of his classification, the biological spectra of the floras (ratio of species with different life forms) are composed for various natural zones and areas of the Earth. It was shown that certain life forms predominate in each climatic zone: phanerophytes prevail in areas with wet tropical climate, hemicryptophytes in the temperate zone, therophytes in hot deserts with seasonal rainfall.

A detailed ecological morphological classification of the life forms of angiosperms and conifers was elaborated by Serebryakov (1962, 1964, 1968). The classification includes the names of biomorphs that are widely used in everyday life: trees, shrubs, dwarf shrubs, herbaceous plants. The classification considers in the first place the appearance of plants that is in close relation with lifespan and pattern of change of skeletal axes. The skeletal axis is called a perennial shoot system often having the form of a stem with crown and developing from buds on near-ground and below-ground parts of a plant (Serebryakov *et ah,* 1954; Zhmelev *et ah,* 1993). Serebryakov's classification is a hierarchical one and includes six to eight biomorphological units of different ranges from the largest (divisions and types) to the smallest (subgroups and the biomorphs proper). Four divisions are distinguished:

woody and **semi-woody plants, terrestrial** and **water herbs. Woody** plants have perennial lignescent epigeal skeletal axes with aerial renewal buds (phanerophytes and chamaephytes according to Raunkiaer). **Semi-woody** plants have both perennial woody and annual herbaceous shoots. The uppermost, usually small, parts of shoots die yearly but the lowermost parts with renewal buds are included in the system of skeletal axes 5-20 cm in height (chamaephytes). **Herbaceous** plants differ from the woody and semi-woody in that their erect above-ground shoots are always annual (more precisely, one-season) but skeletal perennial parts bearing renewal buds are always below-ground (geophytes) or near-ground, i.e., hidden in the litter (hemicryptophytes). Annual herbs have no renewal buds at all (Serebryakova, 1978a).

The division of woody plants includes **three biomorph types: trees, shrubs,** and **dwarf shrubs. Trees** have well-expressed main trunks (seldom several trunks), which persist throughout their life. **Shrubs** possess a number of smaller trunks replacing one another and having a limited lifespan that varies from 2 *(Rubus idaeus)* to 40-60 *(Caragana arborescens)* years. **Dwarf shrubs** are 20-50 cm high, woody plants (chamaephytes) with above-ground shoots forming numerous relatively short-lived (5-10 years) tufts that are connected by long below-ground rhizomes.

Semi-woody plants include **two biomorph types:** relatively higher semishrubs with skeletal axes 20 cm and longer (e.g., *Artemisia)* and shorter dwarf semishrubs (skeletal axes not longer than 20 cm) *(Thymus, Lavandula, Salvia).*

Types of woody biomorphs, i.e., trees, shrubs and dwarf shrubs, are divided into classes, subclasses, sections and groups of biomorphs depending on the structure and shape of the crowns, stems, root systems, lifespan of leaves, and other characters.

Terrestrial herbaceous plants are divided into **two biomorph types: herbaceous polycarpics,** i.e., perennial plants, fruiting many times through their life (the predominant majority of temperate species) and **monocarpic** herbs, i.e., plants fruiting only once in their life and dying completely after seeding. Monocarpics are all annual and biennial herbs as well as some perennials (e.g., *Carum carvi).* Monocarpics are known not only among herbaceous plants but also among woody ones. For instance, the palm *Corypha umbraculifera* (Arecaceae) lives 40-70 years but flowers only once and dies after fruiting.

The classification of biomorphs of terrestrial polycarpic herbs includes several classes, subclasses and groups based on such characters as structure of root system (taprooted and fibrous-rooted), presence of metamorphosed organs (rhizomatous, stoloniferous, bulbiferous, etc.), mode of vegetative propagation (root-sucker, long-rhizomatous), or pattern of tillering (densely tufted and loosely tufted).

The biomorphs of monocarpic herbs are divided into four classes: "common" (with assimilative non-succulent-type shoots), succulent, lianoid, semiparasitic, and parasitic. Classification of biomorphs of aquatic herbs is not elaborated in the Serebryakov system at all.

Serebryakov (1962, 1964, 1968) considered the term "life form" from an evolutionary point of view that was reflected in his classification. The main so-called descending row of biomorphs demonstrates the general direction of life form evolution in angiosperms: **from trees to shrubs, dwarf shrubs, semi-woody plants, perennial and annual herbs.** Moreover, the rows of biomorphs are distinguished that arose in extreme environmental conditions (for instance, succulents, elfin woods, cushion plants) as well under the pressure of phytocoenotic selection (lianas).

Biology and biomorphology of annual and oligennial plants (i.e., those living a few years) are of special interest (Harper, 1977; Begon *et al.*, 1986; Markov, 1986,1990, 1992). The fact is that this group, which was attributed by Serebryakov to the biomorph type of monocarpic herbs, plays an increasingly important role in the present plant cover because of widespread anthropogenic disturbance. Oligennial and annual herbs were shown to be highly heterogeneous in both structure of vegetative organs and lifespan which ranges from 1.5-2 years in winter (winter-annual) plants to several weeks in ephemers. The shoots of these plants may be rosette, semirosette, erosulate (elongated), erect, prostrate, or climbing; root systems may be taprooted and fibrous-rooted.

Plant life forms are also studied from the standpoint of **phytocoenotic analysis.** In this case, the life form is considered the form of coexistence of plants with their neighbours and environment (Tikhomirov, 1963). Several plant biomorph classifications were developed on the basis of phytocoenotically important characters. One of the earliest classifications is that of Vysotskii (1915), who divided the steppe herbs into groups depending on the structure of hypogeal organs and degree of vegetative mobility. He distinguished taprooted, densely tufted, rhizomatous, and bulbiferous plants. He named the first two groups "sitters", emphasizing that these individuals practically do not move throughout the area of coenosis. There is an original biomorph system of Zozulin (1961, 1968, 1976) considering the ability of plants to regenerate after destruction of their epigeal parts and to retain and broaden their areas in the community.

The biomorph system reflecting the structure of phytogenous fields of plants is widely used in phytocenology and especially in plant population biology. It is based on the concept of the phytogenous field being a space whose parameters are modified by the vital activity of a plant (Uranov, 1965). The degree of change of the general parameters (light, strength of wind, composition of litter, etc.) characterizes the tension of the phytogenous field.

Taking into account the tension of phytogenous field, **mono-, poly-** and **acentric biomorphs** are distinguished (Uranov and Serebryakova, 1976; Shorina, 1981; Smirnova, 1987,1994; Palenova, 1993; Zhukova, 1995).

Monocentric biomorphs are vegetatively immobile and have only a single centre of action on the environment. They are trees, taprooted, and densely tufted herbaceous perennials, and annual herbs. Polycentric biomorphs are vegetatively mobile and have several centres of intense action on the plant community. They are dwarf shrubs, many shrubs, root-sucker, long-rhizomatous, stoloniferous plants. Their above-ground parts are presented by bunches, scions and shoots relatively distant from one another, having communication organs, and creating centres of high tension of phytogenous field. Above-ground parts of acentric biomorphs are presented by summer leaves and ephemerous generative shoots and below-ground parts by a dense net of interlacing rhizomes (e.g., in *Trifolium repens).* These biomorphs have no centres of long-term phytocoenotic activity, and their phytogenous fields are characterized by relatively homogeneous tension.

Thus, the classificational systems of plant biomorphs reflect the principles adopted by modern ecology of plurality and complementarity of classifications.

Plant life forms are to be distinguished from **ecological groups,** which account for **the adaptation of plants** to **separate ecological factors** but not to the whole

complex of environmental conditions. Ecological groups are distinguished on the basis of moisture conditions (xero-, **meso-, hygro-, hydro-** and **hydatophytes),** light availability **(helio-** and **sciophytes),** and mineral nutrition **(oligo-, meso-** and **eutrophic plants).** The same life form may belong to different ecological groups. For example, among trees there are both heliophytes (light-requiring) and sciophytes (shade-tolerant). Also, a single ecological group may include different life forms, for instance, the ecological group of eutrophic plants, i.e., plants requiring high level of mineral nutrition, is presented by trees *(Alnus glutinosa)* as well as shrubs *(Rubus idaeus)* and herbs *(Urtica dioica).*

Diaspore (Greek *dia-preiix* with the sense of the through movement, *spora-*spore, seed) is the dispersal unit representing part of the plant (or the whole plant) with various morphological nature and naturally detaching from the maternal plant **(Plate XIII).** Synonym: disseminule.[2]

The term "diaspore" was advised at first by Sernarder (1927). He defined the diaspore as a structure containing the rudiments of the new organism and serving for the propagation and distribution of plants. According to this author, diaspores that spontaneously detach from the maternal organism are the **primary diaspores.** In the process of dissemination they can disintegrate into **secondary diaspores.** Sernarder described the whole morphological diversity of the primary diaspores in flowering plants and divided them into two groups, **generative** and **vegetative,** and several types. On the basis of these groups, van der Pijl (1969,1982) later suggested his own classification of diaspores: A, spores (in the lower plants); B, haplonts[3]; C, new diplonts[4] with envelopes (usually indicated as generative units); and D, vegetative parts of the old diplont. Unlike Sernarder's classification, here there is no diaspore subdivision into primary and secondary, and the systems of the branches with fruits or collective fruits are not considered diaspores. Besides, van der Pijl includes in the diaspore classification the seed of gymnospermous plants and assesses the number of ovaries forming the fruit.

Generative diaspores. Van der Pijl divides **generative diaspores into seven types:** (1) nude embryo; (2) nude seed itself (gymnosperms and some angiosperms); (3) seeds liberated from dehiscent fruits (with or without arillode); (4) fruits (simple, from one ovary, or aggregate, from many ovaries in one flower); (5) spurious fruits or pseudocarps (from one ovary + other parts); (6) multiple or collective fruits from the inflorescences (syncarps); and (7) seed contained in whole plant or part thereof (e.g., tumbleweeds).

According to Levina (1981), there are only two morphological types of generative diaspores: the nude seed itself and the seed surrounded by the pericarp (one-seeded fruit or fruitlet, mericarp, eremus, articule, joint, stone, collective fruit). Such division of diaspores is most general and **focuses on the seed as a dispersal unit.**

We suggest the generative diaspores be classified into six types taking into consideration the morphological unit that separates from the maternal plant:

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[2]The term was introduced by Clements (1904).

[3]The haplont (Greek *haploos-single,* simple and on-creature) is an organism in which all cells contain the haploid chromosome set, and only the zygote is diploid.

[4]The diplont (Greek *diploos*-double and on-creature) is an organism in which all cells except gametes are diploid.

collective fruit *(Tilia, Morus, Ficus, Loncera alpigena, Arctium),* **fruit** *(Betula, Ribes, Quercus, Corylus, Fragaria),* **fruit part** *(Acer, Cynoglossum, Rhaphanus),* **seed** (most flowering plants), **embryo** *(Inga feuillei, Enhalus acoroides),* and **seedling** *(Rhizophora, Bruguiera, Kandelia, Ceriops).*

Fruits differing in morphology and inner structure (see Heterocarpy) and seeds containing embryos of various origin (see Heterospermy; Genetic Heterogeneity of Seeds; Polyembryony) may form in a single specimen.

Vegetative diaspores differ in morphological nature: **rhizome** (or its part) *(Agropyrum repens, Asarum europaeum, Carex hyperborea, Cypripedium calceolus, Geum urbanum, Pulmonaria obscura, Tussilago far/am);* **tuber** *(Chaerophyllum bulbosum, Corydalis solida, Ranunculus bulbosa, Sedum maximum, Solanum tuberosum, Trientalis europaea);* **bulb** *(Allium, Crocus, Lilium, Tulipa;* see also Bulb; Bulblet and Bulbil); the various **transitional forms** between them *(Adoxa moschatellia, Allium montanum, A. angulosum, Dentaria digitata, Epilobium palustre, Lathraea squamaria)* (Serebryakov, 1952; Lyubarsky, I960), **bud** *(Tolmieia menziesii)* (Sernarder, 1927; Serebryakov, 1952; Levina, 1961, 1981), **embryoid** (or seedling) *(Ranunculus sceleratus),* and the **transitional form** between embryoid and bud *(Bryophyllum daigremontianum)* (Batygina, 1987b, 1989a,b,c, 1993a).

Vegetative diaspores are formed **in gemmorhizogenic vegetative propagation** (wherein the structural unit is the bud) **and in embryoidogenic vegetative propagation** (wherein the structural unit is the embryoid or seedling) (see Vegetative Propagation; Embryoidogeny is a New Type of Vegetative Propagation).

Depending on the plant organ in which they are formed, **root, stem** and **leaf** diaspores can be distinguished (Sernarder, 1927). The distinct *(Saxifraga flagellaris)* and non-distinct *(Scirpus alpinus)* diaspores are separated by the length of the shoot axis, and by proximity to the soil surface: **above-ground** *(Fragaria vesca)* and **underground***(Epilobiumpalustre)*diaspores.

In some cases in gemmorhizogenic vegetative propagation, the diaspores are similar to the other parts of the maternal plant in outer appearance and structure (e.g., the shoots of *Elodea, Lemna, Opuntia, Sempervivum).* These shoots detach themselves from the maternal plant, spread by water or wind, and then root.

Brood buds also belong to the vegetative diaspores (see Brood Bud).

Depending on the stage of diaspore development when it detaches from the maternal plant, there can be distinguished **dormant** and **germinating** diaspores (Levina, 1981).

Almost all flowering plants are able to form vegetative diaspores. In some plants this ability manifests itself constantly and in others only when the plant is damaged or when the external conditions change (Rabotnov, 1974; see also Particulation).

It should be noted that there are units of dispersion that represent the plant or its parts with fruits or collective fruits. Such diaspores occupy the intermediate position between vegetative and generative ones.

In some cases the diaspore of one plant species can include the diaspores of another species and later on they can develop together (e.g., orchid seeds containing mycogenous hyphae).

The morphology and anatomy of diaspores is closely connected with the mode of their distribution (Linnaeus, 1751; Hildebrand, 1873; Sernarder, 1901, 1906, 1927;

Ilyinsky, 1945; Levina, I960, 1981; van der Pijl, 1969, 1982; Stebbins, 1971a). The process of diaspore distribution is called **dissemination**[5] or **dispersal.**

Modes of dissemination. Diaspore distribution can occur without the participation of agents **(autochory)** (Clements, 1904) or with the participation of external agents **(allochory)** (Sernarder, 1901). Autochory includes **barochory** (the spontaneous shedding of mature diaspores) and **automechanochory** (active seed dispersal on dehiscence of fruits). The following modes of allochory are distinguished depending on the dissemination agent.

Anemochory is diaspore transfer by air currents (Dammer, 1892; Massart, 1898). Wind-borne diaspores have small mass and/or parachute devices. They may have wings. All wind-borne diaspores have streamlined form. They can be transported along the surface of the soil or water or along ice-encrusted snow. Diaspores distributed by the wind are characteristic for the following plant groups (Levina, 1981):

1) woody anemochores (diaspores with wings, adapted for soaring flight);
2) species of marsh and beach and steppe, and weed species (fruits and seeds with crests or parachutes);
3) anemochores of sphagnous marshes and of the grassy tier in coniferous woods (diaspores are small dusty seeds);
4) plants of the sandy deserts (diaspores of the balloon or the air-turbine type).

Hydrochory is the distribution of diaspores by water (Dammer, 1892; Massart, 1898). Such diaspores are not moistened with water, they acquire floating properties and remain viable during their long stay in the water.

Zoochory is the distribution of diaspores by animals (Dammer, 1892; Massart, 1898; Sernarder, 1906; Levina, 1981). **Endozoochoory** (distribution of seeds that pass undamaged through the digestive tract of the animal) is characteristic for plants of the woods, sphagnous marshes and tundra and the diaspores are juicy fruits. **Epizoochory** (the passive delivery of diaspores on the animal body) is noted in ruderal plants, facultative weed species and desert plants. **Synzoochory** (the active distribution of diaspores connected with storage of food by animals) is noted in the principal forest-forming stocks *(Quercus, Fagus, Pinus sibirica).* **Anthropochory** is diaspore distribution with human help (Heintze, 1932).

Distribution of underground vegetative diaspores may also occur on dislocation of soil layers (during avalanches or landslips).

The mode of dissemination depends not only on the diaspore structure, but also on the biological peculiarities of the specimen in which they are formed (e.g., the form of growth, height, inflorescence morphology, position of diaspores on the plant, or time of maturation) (Levina, 1981). Similar diaspores can be distributed in different ways, depending on the biotope. Sometimes the same diaspores are successively distributed by two or more agents (van der Pijl, 1969).

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[5]It was Linnaeus (1751) who called the process of seed scattering "dissemination". The terms "dispersal", "dispersion" and "dissemination" are used to describe the scattering and distribution of seeds, fruits, plant vegetative rudiments, pollen and spores (Jackson, 1916; Henderson, 1953). Praeger (1923) suggested the term "dispersal" to designate the active (dynamic) process of diaspore transport and "distribution" to designate the passive (static) state. Van der Pijl (1969,1982), like Linnaeus, used the term "dissemination" only for the seeds.

The appearance of various types of diaspores in flowering plants during evolution has secured their dominant position among the other plants and their widespread distribution.

Population and Coenotic Regulation of Reproduction

The specific feature of plant reproduction is its dependence on processes taking place at the level of populations, phytocoenoses, and ecosystems, not only separate individuals.

The reproductive process is regulated by various population and coenotic factors that are studied in different degrees (Table 24). The main information about their role in plant reproductive process is provided by different quantitative parameters (Table 25).

Population regulation. Sufficiency of pollination, which is interlinked with a number of structural features of the plant population, is in the forefront among the factors of reproduction control in many cases. Only 2.5% of ovules develop into mature seeds because of the lack of pollen (Fenner, 1985).

The main prerequisite of viable pollen supplied to flowers is the simultaneous blooming of all specimens in a population. Competition for pollinators is also significant. It is known that larger flowers and individuals are more attractive to pollinators. That is why redundancy of flowering in a population is neither harmful nor erroneous. It provides for pollination of a greater number of flowers and increases seed output. Besides, such "barren flowers" act as pollen producers. The years of abundant flowering ("seed years"), recorded for many trees, shrubs and even herbs,

Table 24. Main factors regulating plant reproduction at the level of populations and communities.

Factors	
Population level	
Population size	+
Spatial distribution of individuals	++
Degree of isolation of population	+
Population density	+++
Individual differentiation in population	
• % according to age status	+++
• % according to vital status	++
Coenotic level	
Resource accessibility and availability of conditions necessary for reproduction	+++
Level of interspecific competition	+++
Location in food chains of ecosystem	+
Availability of microhabitats promoting preservation and germination of seeds	++
Anthropogenic pressure on communities	+++

+++ well studied, ++ satisfactorily studied, + poorly studied.

Table 25. Main reproductive parameters of plant populations.

Factors	Units of measure and parameters
Pistil reproductive success	The number of pistils per unit of area
Stamen reproductive success	The number of stamens per unit of area
Fruitfulness	The share of fertilized ovules out of their total number
Reproductive pressure of the population	Total number of seeds produced by the population
Seed production of the population	The number of seeds per unit of area
Seed distribution in population field	Indexes of uneven distribution
Soil seed bank	The number of viable seeds in soil bank

are very useful, because phytophages leave a large quantity of flowers and seeds undamaged in these years.

Spatial arrangement of a population is important: higher population density and short distances of seed dispersion create prerequisites for repollination of closely related plants, which decreases the viability of descendants (Willson, 1984). On the other hand, groups of growing plants that appear in the so-called contagious spatial distribution of individuals in a population greatly increase the quantity of fruit set at the time of flowering, as was shown by the example of many plant species (Krannitz and Maun, 1991). This might be connected not only with visual attractiveness but also with higher concentration of odorous substances that are appealing to many insect-pollinators (Robacker *et al.*, 1988).

The structure of a population is important for seed production (Zlobin, 1989a,b, 1996). Individuals in a population are known to be unequal in seed output. The reproductive pressure of a population on the coenosis depends on the share of its generative individuals and their vital status. Large individuals produce many seeds, but there are few of them in a population. Small specimens have lower seed productivity, but produce the most seeds due to their numerical superiority. Such seeds may be overloaded with genetic defects and be less viable. Old individuals are known to produce seeds of low quality. The part played by individuals in producing the total quantity of seeds in a population remains little studied.

With increase in population density, the share of organic compounds carried from the leaves to reproductive organs declines and seed production drops noticeably (Snaydon, 1984; Zimmerman and Weis, 1984). In small populations it is often a consequence of simple shortage of pollen (Agren, 1996); moreover, according to Zhilyaev (1996), most pollen in herbs disperses at a radius of not more than 3-5 m from the donor plant, and mainly within one clone in clonal plants. In some species this causes flower drop and in others the inflorescence size is reduced or seed set is destroyed. According to the so-called Oily rule (Lekyavichyus, 1986), there are two groups of plants distinct in character of reaction to population density: the first shows inverse dependence of reproduction on population density; in the second, propagation peak falls at intermediate density. The hierarchy of individuals in seed productivity magnitude often happens to be most evident in areas with high population density.

Seeds, no matter how they are dispersed, tend to concentrate near the mother plants. Here reproductive pressure of species population is at its maximum. But in many cases an inhibitory action of maternal plant cover on seed germination and sprouting is observed (Rai and Tripathi, 1985).

Thus, peculiarities of population organization affect a number of important phases of reproductive process acting as controlling mechanisms over quantity and quality of diaspores produced.

Coenotic regulation. In coenotic regulation of reproduction there are both mutualism and competition, the combination of which influences all phases of this process (Silvertown, 1982).

The main mechanisms of coenotic regulation of reproduction are linked with the level of diffusive competition in phytocoenosis and neighbourhood of individuals entering a reproductive cycle. These effects manifest themselves in changes of the vital status of individuals, which is apparently correlated with plant reproduction. The effect of certain forms of competition on reproduction are yet little studied. On the whole, parent strategy of *Angiospermae* is oriented towards protecting reproduction from stress factors (Lloyd, 1979) and is in itself the result of a long evolution process.

In conditions of multi-species communities, the competition for pollinators often becomes sharp and ecosystem relations of such kind appear very important (see Faegri and van der Pijl, 1980). For successful pollination of entomophilous plants, a synchronization of flowering and pollinator activity are necessary. A dense one-species thicket of plants attracts more pollinators and, in this way, contagious type of individual distribution turns out beneficial for both entomophilous and anemophilous plants and should be maintained by selection (Klinkhamer and Jong, 1990). Larger individuals bearing more flowers have the best opportunities for pollination (Pleasants and Zimmerman, 1990).

Seed death peaks during the time seeds stay in soil and germinate. The loss of seed viability in this period is caused mainly by soil phytophages, pathogenic fungi and abrupt changes in moisture and soil temperature regimes. Allelopathic effects remain debatable but they are proven to exist, though they do not play a critical part in reproduction of a number of plant species.

The concept of safe habitat (Harper, 1977) and reproductive niches (Grubb, 1977) determines that coenosis area is not of equal value in the last phase of reproduction. Regeneration takes place in areas where there are stimuli to interrupt seed dormancy and optimal conditions for germination as well as resources necessary for growth of seedlings. Such microhabitats are called safe or regeneration niches. Ecosystem relations are multisided in this situation. *Opuntia engelmannii* and *Prosopis glandulosa* increase the resource flow from reproductive sphere to vegetative in excess moisture conditions (Windberg, 1997). Seeds of many species germinate and sprouts are rooted only in areas of plant cover damage. But there are species that regenerate better under the cover of maternal plants (e.g., *Calluna vulgaris)* or under the cover of nursing plants (Zlobin, 1993a,b). Direct dependence of seed germination on the size of glade was observed in *Amaranthus retroflexus* (Fenner, 1985).

The successional status of the community also affects reproduction. In serial communities the reproduction peak is connected with the period of species dominance. In climax communities it is maintained at the intermediate level. On the

whole, the results of reproduction as population and coenotic process are determined by its synchronization within a particular species population and by correlation with the seasonal dynamics of development of other species in the community.

Population and Coenotic Aspects of Research on Plant Reproduction in Arctic Conditions

Plant reproduction is a complex process consisting of successive stages that are influenced by diverse biotic and abiotic factors. This process comprises different levels of plant life organization: cell, individual, species, population, coenosis and region.

The problem of plant cover preservation in the Arctic has now become urgent in connection with global climate change and also with intensive human impact on plant cover. One of the important aspects of the problem is the stability of populations and the preservation of plant cover, which is closely connected with life-history strategies of the components of the plant cover.

There are many conceptions of plant life-history strategies. According to Rabotnov (1975), plant life-history strategies comprise the co-adaptations that determine the place of the population in the biocoenosis. In later studies, they were defined as long-term adaptive behaviour of a species population that is determined by genetic potential of the species and by the modes of its realization in particular ecology-coenotic conditions (Grime, 1979; Stearns, 1980, Smirnova, 1987; Khodachek, 1995). According to the widely accepted theory of r/K selection (MacArthur and Wilson, 1967; Pianka, 1970) and the Ramensky-Grime classification of plant life-history strategies (Ramensky, 1938; Grime, 1979), arctic plants are categorized as extreme K-strategists (Eriksen *et ah*, 1993; Molau, 1993) or ultra-persistent, according to Ramensky (Yurtsev, 1986). It is assumed that typical K- and r-strategists (stress tolerators and ruderals respectively, according to Grime's approach, 1979) differ in their most basic reproductive traits (Pianka, 1970). Many arctic species apparently possess features of both r- and K-strategists. The indices of arctic plant reproduction suggested in this paper may be included among the list of criteria for the categorization of a species as using one strategy or another.

Plant cover in the Arctic is formed under the influence of extreme environments. In these conditions persistence of the plant cover is closely connected with reproduction of its components. We studied arctic plant cover in three tundra subzones (southern, typical and arctic tundras) of the Taymyr Peninsula and polar deserts (according to the Aleksandrova approach, 1977) of the Severnaya Zemlya archipelago (Khodachek, 1995,1997). In each of these areas for three years the plant seasonal development, biology of flowering and fructification, pollination modes, seed productivity, seed banks, seed germination and seedling establishment were studied in zonal and some intrazonal conditions for widespread species (Table 26).

The most specific characteristics of plant reproduction in the Arctic include the following: formation of flower buds during the previous season; ability to flower at very low temperatures (in the polar deserts as low as -6°C); wide extension of various forms of self-pollination (including cleistogamy, geitonogamy, contact autogamy), apomixis and parthenocarpy; and the ripening of seeds in winter or during the following season. These characteristics facilitate seed propagation, renewal of plant

Table 26. Indices of seed productivity of plants in Western Taymyr.

Plant species	Seed productivity			Fruit-flower ratio (%) on generative shoot
	Potential	Conditional-real	Real	
Hierochlo^paudflora	6-8	1-5	0-5	12-68
Alopecurus alpinus	42-52	0-7	0-7	0-18
Arctagrostis latifolia	36-54	0-24	0-4	0-20
Trisetum sibinˆcum ssp. *Htorale*	108-124	94	82	0-74
Koeleria asiatica	124-147	8-19	4-18	6-18
Poa arctica	7-23	0-11	0-4	0-67
P. alpigena	21-23	4-18	0-8	0-40
P. glauca	13-16	-	-	0-74
Dupontia fisheri	5	1.6	1.6	31
Festuca cryophila	21-37	3.2	2.5	0-26
Eriophorum medium	59	0-13	0.5-7	22
Carex chordorrhiza	10-19	5-12	0-12	50-80
C. stans	65-197	11-130	1-18	16-59
C. ensifolia ssp. *arctisibirica*	35-49	12-30	0-2	34-75
Juncus biglumis	90-114	26-62	0-62	33-66
Luzula confusa	48-90	30-83	25-79	83-93
L. nivalis	32-60	16-33	4-27	57-100
Lloydia serotina	51	0-33	0-28	100
Salix polaris	25-186	5-15	2-12	0-81
S. arctica	180-1008	0-107	0-51	0-79
S. reptans	48-160	0-138	0-74	52-93
S. pulchra	400-1535	0-140	0-72	0-93
S. lanata	2310	-	-	-
Betula nana	38-90	27-87	12-65	76-97
Claytonia joanneana	23-30	20	15	-
Cerastium maximum	496-792	10-200	0-165	9-67
Melandrium apetalum	220	160	110	-
Minuartia macrocarpa	28-34	18-22	17-18	100
M. arctica	33-38	10-20	6-15	100
Calthaarctica	421	-	-	-
Ranunculus nivalis	24	20	14	100
R. borealis	12-72	40-93	0-29	100
Papaver pulvinatum	1400-1500	192-276	0-216	100
Eutrema edwardsii	27-33	14-24	11-23	100
Erysimum pallasii	372-576	100-516	0-320	80-100
Parrya nudicaulis	19-110	9-10	2-9	0-61
Draba pilosa	20-41	10-36	6-35	100

Table 26 *(Contd.)*

D.oblongata	18	15	15	100
D.micropetala	34	30	23	100
D.macrocarpa	10	7.5	7.0	88
D.fladnizensis	33	32	30	100
Saxifragapunctata	513-1100	80-433	53-304	40-96
S . nivalis	885	0-340	0-210	-
S.hieradfolia	944-2700	102-836	93-710	0-100
S. hirculus	600	45-80	28-73	70
Potentillastipularis	84-168	6-90	0-62	100
Dryaspunctata	5-54	0-45	0-33	0-100
Astragalussubpolaris	7-15	2-15	0-2	0-44
Oxytropisadamsiana	85-220	0-63	0-41	0-62
0. middendorffii	150-210	0-70	0-27	0-83
Hedysarumarcticum	15-26	0-8	0-2	0-47
Pachypleurumalpinum	226-316	24-127	0-31	15-71
Cassiopetetragona	160-220	0-85	0-85	0-90
Androsacebungeana	20-30	0-3	0-1	0-45
A.septentrionalis	80-100	24-52	22-52	98-100
Armeriaarctica	42	29	22	60
Polemoniumboreale	90-120	20-89	22-71	17-64
Myosotisasiatica	44-96	3-24	0-10	11-84
Eritrichium villosum	37	0	0	-
Pedicularisvertidllata	676-768	0-105	0-92	8-88
P.sudetica	565	187	160	73-91
P. hirsuta	240-415	0-172	0-86	77-98
P.oederi	660-800	78-91	0-56	-
Tripleurospermumphaeocephalum	550	490	-	90
Arnica iljinii	60-65	60-65	0-58	100
Senecioatripurpureus	136	124	54	92

cover and survival of flowering plants even at the extreme borders of their areas (polar deserts and arctic tundra).

Potential seed productivity (PSP) to a great extent is determined by the genetic programme and particularly by the type of gynaeceum, the number of ovules in the ovary and the number of flowers on a generative shoot (Khodachek, 1974,1978). **Real seed productivity (RSP)** is the value that determines the resumption of species in phytocoenosis and it is influenced by the whole complex of biotic and abiotic factors. It is more a biocoenological characteristic of species than a biological one (see Potential Seed Productivity; Real Seed Productivity).

Besides potential and real seed productivity it is expedient to distinguish the intermediate term **"conditional-real seed productivity" (CRSP),** which includes all seeds irrespective of their quality: unripe or underdeveloped (weak) and seeds

damaged by insects and fungi (Khodachek, 1970,1974,1978). Whereas PSP is only a theoretical value, CRSP characterizes the real capacity of a species for the formation of seeds. The ratio of CRSP and PSP shows the proportion of ovules that develop into seeds. This value directly depends on the factors of pollination, nutrition and biological features of the species that influence fertilization (e.g., the quantity and quality of pollen, the rate of the pollen tube growth, state of stigma at the moment of pollination, dichogamic or homogamic development of the flower). The study of CRSP in different years and in different ecological and phytocoenotic conditions makes it possible to determine the maximum quantity of ovules that develop into seeds for each species. Their maximal values and ratio of CRSP and PSP can be regarded as biological characteristics of a species. The CRSP value characterizes the role of a species in phytocoenosis; it shows the place that the species occupies among the components of a coenosis. It is the quantitative characteristics that along with phytomass, intensity of photosynthesis and various biochemical and physiological parameters determine the importance of a species as an edificator. Ignoring this parameter and using RSP alone may give an incomplete or even incorrect notion of the fruiting character, reproductive potential and modes of propagation of a species. In case seeds do not ripen or they are intensively damaged by insects and fungi, an incorrect assessment may be made about the inability of the species to propagate through seed though in other climatic conditions this species forms fully ripened seeds not damaged by insects or fungi. Besides, the CRSP value does reflect the effect of the pollination factor on seed reproduction. The ratio CRSP:PSP shows which of the pollination modes are the most effective for seed formation.

For evaluation of seed reproduction it is important to use not only absolute values but also relative ones. The following coefficients can be proposed: **Cs — coefficient of seed formation** (the ratio of CRSP:PSP), which shows what part of the ovules develop into seeds; **Cr—coefficient of ripening** (the ratio of RSP:CRSP) expressing the proportion of seeds that achieve ripeness; **Cv — coefficient of viability,** which shows the proportion of viable seeds in the total number of ripe ones (Khodachek, 1993a,b, 1994,1995,1997,1998).

With the aim **of characterizing the reproduction process as a whole** we suggest an integral index, **the generative activity of a species (R):**

$$R = No/N \times d \times Cs \times Cr \times Cv,$$

where N is the observation period in years, No is the number of fruitage years within that period, d is the number of generative shoots per m^2, and Cs, Cr and Cv are coefficients.

This index includes the main characteristics of the reproduction process (Table 27). In particular, the ratio No/N shows the regularity of fruiting; Cs reflects the summary result of the all seed formation stages; the expression d x Cs characterizes the success of seed bearing in a population; and the coefficients Cr and Cv are the qualitative characteristics of seeds as a result of the effect of biotic and abiotic factors on seed reproduction.

An index R, characterizing the reproduction process as a whole, reflects genetic capabilities of a species for seed propagation, and the modes of their realization in certain ecological-coenotic conditions. An integral index R can serve for comparison of seed propagation in different species, populations, coenoses within one vegetation climate zone or different zones, comparative evaluation of reproductive process of

Table 27. Generative activity (R) of Western Taymyr plants.

Species	Cs	Cr	Cv	d	**No/N**	R
Hierochlöepaudflora	0.4	0.8	0.5	144	2/3	15.0
Trisetum sibiricum ssp. *litorale*	0.8	0.9	0.7	5.0	1	2.5
Poaalpigena	0.4	0.4	0.6	10.0	1	1.6
P.arctica	0.4	0.4	0.6	10.0	1	1.6
Carexchordorrhiza	0.6	1.0	0.1	32.0	1	1.9
*C.ensifolia*ssp.*arctisibirica*	0.5	0.5	0.1	27.0	1	1.0
Juncus biglumis	0.4	0.7	0.5	0.2	1	0.03
Luzula nivalis	0.5	0.6	0.5	0.2	1	0.03
Salixarctica	0.1	0.5	0.7	18.0	1	1.0
S.reptans	0.7	0.5	0.6	0.2	1	1.9
S.pulchra	0.1	0.5	0.6	0.4	2/3	0.01
Cerastium maximum	0.2	0.8	1.0	45.0	1	7.2
Minuartiaarctica	0.4	0.7	0.4	0.1	1	0.01
Papaverpulvinatum	0.2	0.8	1.0	45.0	1	7.2
Erysimumpallasii	0.6	0.5	0.8	0.2	1/3	0.02
Drabapilosa	0.7	0.8	0.2	0.05	2/3	0.01
D.micropetala	0.9	0.8	0.2	0.05	2/3	0.01
D.macrocarpa	0.8	0.9	0.2	0.05	2/3	0.01
Parryanudicaulis	0.1	0.6	0.2		2/3	0.01
Potentillastipularis	0.5	0.6	0.9	25.0	1	7.9
Dryas punctata	0.7	0.7	1.0	30.0	1	14.7
Oxytropisadamsiana	0.2	0.7	1.0	20.0	1	2.8
0. middendorffii	0.2	0.4	1.0	20.0	1	1.6
Cassiopetetragona	0.2	1.0	1.0	65.0	1	13.0
Androsaceseptentrionalis	0.4	1.0	1.0	1.7	1/3	0.2
Polemoniumboreale	0.6	0.8	1.0	17.0	1	8.2
Myosotisasiatica	0.5	0.5	1.0	30.0	1	7.5
Arnica iljinii	1.0	0.9	0.7	20.0	1	12.6

species in different parts of a wide geographical area. This index may be used for the attribution of a given species to a certain life-history strategy type, for example, to K- or r-strategy. Among the arctic plant species, the highest R (7-15) values were recorded for *Dryas punctata, Cassiope tetragona, Potentilla stipularis, Hierochlo, paudflora, Cerastium maximum, Papaver pulvinatum, Polemonium boreale, Myosotis asiatica, Arnica iljinii;* moderate R values (1-6) were recorded for *Poa arctica, P. alpigena, Trisetum sibiricum* ssp. *litorale,* and species of genus *Carex, Salix,* and *Oxytropis.* Species of low R (< 1) include *Juncus biglumis, Luzula nivalis, Salix pulchra, Minuartia arctica, Androsace septentrionalis, Parrya nudicaulis,* and species of the genus *Draba.*

Stability of the plant cover depends on the vegetative mobility of its components. The behaviour of species in given ecological-coenotic conditions is determined to a

great extent by the ratio of seed and vegetative propagation. According to this index, arctic plants can be divided into the following groups:

1. Generatively labile plants; these are species that have generative organs with quick reaction to changes in climatic conditions, thanks to special mechanisms such as autogamy, geitonogamy, cleistogamy, apomixis, parthenocarpy, a secondary flowering, transition from dichogamy to homogamy, to viviparity. They possess a low vegetative mobility, if any, and propagate principally by seed *(Saxifraga hieradfolia, Salix arctica, Minuartia macrocarpa, Juncus biglumis, Draba micropetala, Pedicularis hirsuta, P. oederi,* and species of the genus *Luzula).*
2. Vegetatively mobile plants; their propagation is basically vegetative (most grasses, sedges, some species of the genus *Salix, Eriophorum,* and such species as *Pyrolagrandiflora,Ramischiaobtusata* and *Stellariaciliatosepala).*
3. Stable species; these are plants that have a mixed nature and combine both the previously mentioned propagation types (e.g., *Betula nana, Carex ensifolia* ssp. *arctisibirica, C. starts, Cassiope tetragona, Cerastium maximum, Draba pilosa, Dryas punctata, Hierochlo, pauciflora, Salix reptans).*

Plants with sufficiently high generative activity (R) are capable of active propagation by vegetative means also. They build up a considerable bank of seeds that are able to germinate in a wide range of conditions. Such plants possess the greatest tolerance in environments of the Arctic (Khodachek, 1993a,b, 1985). Generative activity and vegetative mobility of species provide population stability: the first facilitates the renewal of genofond, the second the wide spread of species and their preservation in the plant cover.

Multiplicity of Vegetative Propagation and Expansion in the Ranunculaceae

Tendency to intensification of perennial plant mobility and to formation of various specialized organs of vegetative propagation can be distinctly traced in morphological evolution of Ranunculaceae (Barykina, 1975,1995b). The adaptive role of these structures becomes particularly clear when seed propagation is lowered or for some period of time completely depressed. Levina (1981, p. 12) is quoted as figuratively saying that vegetative propagation is "the most important reserve of species existence".

Ranunculaceae possess almost all modes of natural vegetative propagation known in *Angiospermae,* including sarmentation, particulation, and vegetative diaspory; the former predominates.

In the simplest case, vegetative propagation happens without formation of specialized organs by means of fragmentation of creeping or layering monocarp shoots, typical for herbaceous polycarpics (e.g., species of *Ranunculus)* and also liana-formed shoots of shrubs such as *Clematis brevicaudata,* trailing and rooting in nodes when touching wet soil. In epigeal creeping forms *(R. jlammula, R. reptans)* growing on mobile wet substrate, branch orthotropic rooting rosetted shoots appear from axillary buds of the braking zone (Troll, 1964) on floriferous shoots. Passing the winter, they give new plants repeating the developmental cycle of the mother plant. Typical of water representatives of *Ranunculus (R. circinatus)* and also the amphiphyte *Caltha palustis* is reproduction by isolation of separate parts of layering and rooting

generative shoots, which then sink to the bottom of the reservoir at the end of the vegetative period. Monocarpic shoots change function: after blossom and fruitage part of their metamers participate in vegetative propagation and plant expansion.

In an overwhelming majority of cases the plant vegetative mobility is connected with the development of specialized structures, mainly of shoot origin. They differ by a series of biomorphological features caused by different functional loads, type of growth, renewal and duration of existence. In stoloniferous vegetative short-lived plants (Vysotsky, 1915) timed for wet or redundantly moist habitats with loose soil, individual number increases by means of sarmentation. Epigeal plagiotropic, short-lived lashes or stolons with assimilating leaves are formed. They deviate from rosette zone of innovation of orthotropic semirosette maternal shoot and regularly form rosette shoots with sylleptic rooting. Plants of *Ranunculus repens* grown from seeds may propagate with the help of stolons even from the second year of life (Golubev, 1961; Barykina and Pustovoytova, 1973). The apex of stolon becomes orthotropic at the end of the season and finishes development by formation of terminal rosette. All rosette plants separate in autumn. Because of more specialized epigeal stolons bearing leaves only of the lower formation and therefore not taking part in photosynthesis, species of *Halerpestes* quickly seize territory and disseminate daughter plants.

High vegetative productivity of *Ranunculus lapponicus* and *R. lingua* is achieved by development of intensively branching fragile hypogeal stolons with assimilating *(R. lapponicus)* or scale-shaped *(R. lingua)* leaves. While growing stolons form numerous rosette branch shoots quickly breaking connection with the maternal one, adventive roots initiating early at the rosette base prepare their transition to independent existence. Quick cloning and high speed of vegetative propagation increase general longevity of seed-origin individuals, although particles themselves live only for one to four years.

Elongated metamorphosed plagiotropic shoots of epigeal creeping and hypogeal stolonate forms of herbaceous polycarpics are formed in different ways but enable a similar strategy of quick and active seizure of new habitats, brief retention of those habitats, and considerable rate of displacement.

Further specialization of reproductive organs in Ranunculaceae is connected with the reduction of stolons accompanied by tuberous accretion of their terminal buds. Stoloniferous forms of *Ranunculus* (Barykina and Chernyakovskaya, 1986) and stolono-tuberous forms of *Delphinium* and *Aconitum* (Barykina *et ah*, 1977) propagate by relatively short (1-2 metamers), hypogeal stolons ending by orthotropically oriented renewal buds with thickened axis and bundles of adventive roots at their base.

In tuberous, vegetative, short-lived plants (species of *Aconitum, Delphinium),* facultative vegetative propagation occurs usually in the generative period. It is achieved by simultaneous opening of several quickly rooting dormant buds or buds of renewal on the perennial maternal tuber. Their hypopodium and mesopodium are often stretched stolon-like, and subsequent shortened internodes grow in width, forming cauline and cauline-rhizous daughter tubers. In due course they separate, giving rise to new plants. During the life cycle, several generations of vegetative descendants are formed. Tubers exist for one or more years. The settled vegetative life of tuberous forms, according to Lyubarsky's (1967) terminology, along with weakly

expressed vegetative propagation, keeps them in the same place in the community for a long time.

In Ranunculaceae, the most typical mode of vegetative propagation is formation of rhizomes. Short-rhizome species of *Actaea, Enemion, Ranunculus* and others possess weak vegetative mobility, the increase of individual number is achieved as a result of simultaneous development of two to four anisotropic, rooting, later separating, metamorphosed shoots of innovation. Slow seizure of the territory by vegetative means is typical of them; daughter plants remain close to each other.

In long-rhizome herbaceous, shrubby and mainly forestry species of *Anemone, Clematis, Coptis,* and *Thalictrum,* branched hypogeogenous (initially of hypogeal origin) rhizomes (xylorhizomes) from time to time form numerous rooting epigeal shoots, later separating into independent individuals as a result of die-off of older, connecting parts of the rhizome. Species with clearly expressed dimorphism of rhizome can also be placed in this group. The rhizomes bear different functions: vertical shortened epigeogenous (epigeally born) rhizomes with bundles of adventive roots serving as peculiar "centres of fixing" (Smirnova, 1974) and developing from their basal adventive buds vertical "communicating" hypogeogenous rhizomes serving for quick and intensive seizure of new places within the territory occupied by the species. The appearance of hypogeogenous rhizomes on the base of epigeogenous in ontogenesis essentially changes the plant life strategy; the extensive character of this new formation intensifies vegetative mobility. Vegetative propagation in long-rhizome plants quite often starts at the end of the virginal period and is accompanied only by partial shallow rejuvenation of descendants. The life cycle of long-rhizome species is 70-150 or more years (Rabotnov, 1946,1950a; Serebryakov, 1952).

Soboliferous forms are known in a comparatively small number of species belonging to three genera: *Anemone, Clematis* (Chubatova, 1989) and *Delphinium* (Ziman, 1985). They are obligatory soboliferous plants. Primordia of adventive buds in *A. dichotoma* and *A. sylvestris* are clearly noticeable in two-year-old plants first on the main, lateral and then on thin, superficial, horizontal adventive roots. They initiate in the cambial zone, usually close to dying sucking branch roots; the accumulation here of root decay products and inflow of nutrients favour the formation of meristem centres. In generative (4- to 5-year-old) individuals of *A. dichotoma* up to 30 and in *Clematis recta* up to 50 root shoots can be found, ranging from new growth to flowering shoots. By the depth of rejuvenation and speed of transition to reproduction the soboles do not differ from juvenile or immature plants of seed origin. Adult soboles form adventive buds on their own cauloborne horizontal roots, which adds to the lifespan of the clone. At the same time, soboles having a root system, like partial shoots of long-rhizome forms, have a high physiological autonomy increasing with their development till at last all connections with the mother plant come to an end. High vegetative productivity in soboliferous species is accompanied by strong suppression of seed propagation.

The fact that some Ranunculaceae possess some specialized diaspores of shoot origin is worth special attention. These diaspores are easily separating tuber-like axillary buds on the rhizome of *Anemone flaccida* (Potapova, 1988) and tubers of more complicated morphological structure forming in the axillary complexes of rosetted and stem leaves of phytophilous monocarpic shoot of *Ficaria verna* (Tsyrina, 1930; Metcalfe, 1938), which we proposed to call gemmarhizous tubers (Barykina and

Gulenkova, 1990; Barykina, 1995a). Their development is based on the same mechanism as that of hypogeal tubers in species of *Aconitum.* It manifests in early rooting of buds of innovation and subsequent accretion of root as the main nutrient depository. It is interesting that in *Ficaria verna* the number of tubers appearing is considerably greater than the number of annually unfolding leaves. This is caused by branching inside buds bringing about formation of numerous buds of different order in the axil of the cataphyllary leaf. In this species of *Ficaria* tubers are formed regularly, but mature fruits appear only sporadically; seedlings and sprouts are found only in well-lit and moist habitats.

Development of metamorphosed vegetative primordia with nutrient supply, such as brood buds (vegetative diaspory), provides not only quick propagation of *A. flacdda* and *F. verna* within the coenosis (where they do not become strong competitors with others because of their ephemerality) but often also active intrusion into another coenosis. One can note deep rejuvenation of vegetative descendants starting their life cycle from juvenile phase.

Separation of rhizome or shoot particles is a peculiar mode of vegetative propagation in some high-mountain species of *Aconitum, Delphinium, Anemone, Paraquilegia,* and *Pulsatilla* (Barykina and Gulanyan, 1974; Barykina *et al,* 1976,1991; Barykina and Potapova, 1994; Barykina, 1995b). Their formation starts at early stages of ontogenesis and is accompanied by atypical secondary thickening (Kumazawa, 1937; Tamura, 1964; Barykina *et al.,* 1977). First features of particulation can be revealed outwardly in 3- to 4-year-old immature plants of *Anemone fasciculata, A. protracta* and *A. speciosa* beginning to blossom only in the 18th to 20th year of their life (Rabotnov, 1950b). Presence of the dormant bud on particles of shoot origin, ability to form roots and often functioning of the already well-developed root system determine weakly expressed vegetative propagation after complete separation of particles in the conditions of the mobile substrate. Particulation does not bring about sufficiently strong rejuvenation of daughter plants but helps to prolong clone life.

The multiplicity of modes of vegetative propagation among the Ranunculaceae demonstrates a wide spectrum of species adaptations to habitat conditions, different strategies of territory seizure ("stayer" and "sprinter", after Yurtsev, 1986), different speeds of movement and peculiarities of cloning taking into account rejuvenation of vegetative descendants.

Similar specialized organs of vegetative propagation in different taxa are the result of convergent evolution. The modes of vegetative propagation are as a rule specific for every species. Each species is characterized by one mode of vegetative propagation; only in a few cases are various specialized structures formed. For example, vegetative mobility is provided by epigeal stolons or soboles along with rhizomes and creeping shoots. Such a multiplicity of modes of vegetative propagation within the species appears to be one of the mechanisms formed during evolutionary transformations in the family and providing population self-maintenance especially in the changing living conditions. A great variety of modes of vegetative propagation and expansion along with other biomorphological peculiarities allowed representatives of Ranunculaceae to assimilate ecological niches sharply differing from each other and made possible their essential role in plant cover in the modern geological epoch.

Ontogenesis in *Ferula* L. (Apiaceae)

The genus *Ferula* is represented by mono- and polycarpics. Fourteen western Tien-Shan species of the genus were studied for their ontogeny in the borders of their area (monocarpics — F. *diversivittata, F. kuhistanica, F. samarkandica, F. ugamica;* polycarpics — F. *akitschkensis, F. ferganensis, F, karatavica, F. lapidosa, F. leucographa, F. pallida, F. penninervis, F. prangifolia, F. tenuisecta, F. tschimganica)* (Vasilchenko, 1941; Nikolaeva, 1948; Fedorov *et al.,* 1962; Golubev, 1965; Melibaev, 1977; Rahmankulov and Melibaev, 1981).

The latent period lasts from 6 months (Markova and Medvedeva, 1968) to 2-4 years (Momotov *et al.,* 1989). The virgin (pregenerative) period in monocarpics lasts for 8-10 years, and in polycarpics 4-7 years.

Representatives of the Apiaceae are characterized by low germination capacity, slow germination and deep dormancy of seeds. In laboratory conditions (at temperature 0 to +4°C) the germination percentage of the freshly gathered seeds increased to 70% for monocarpic species and 76% for polycarpic species. The germination of monocarpics was 17-42% and that of polycarpics 43-75% after 8 years of storage. The seed longevity testifies to the great potential of *Ferula* species in the struggle for survival in conditions of the arid zone of Middle Asia.

Field germination of the seeds of monocarpics and polycarpics is on average 74% and 64%, respectively. The value varied in different species (40-86%) and within the same species in various points of its distribution area.

Epigeal germination is characteristic of all species. The radicle is the first to appear, and it quickly penetrates the soil; the hypocotyl appears later. It straightens completely and brings above the surface of the soil two cotyledons or three (in 0.3% of cases). The cotyledons are leaf-like, linear, and often naked. After 30 days of seedling appearance the middle length of cotyledons is 18.0 mm and the width is 2.9 mm, in monocarpics; and the length and width are 17 mm and 1.9 mm in polycarpics (the ratio of these values is 6:1 and 9:1, respectively). The average duration of cotyledon life is 42-48 days. The moderate growth tempo of the radicle is characteristic of all species; 30 days after germination the root penetrates the soil to a depth almost equal to the cotyledon length.

Juvenile state. The cotyledons wither after two or three seedling leaves unfold and the plant becomes juvenile. The first leaf appears at the end of March; at the beginning of April, the average duration of its life is 46-48 days. The second leaf appears on the 24th to 30th day; the average duration of its life is 56 days. The appearance of the third leaf was noted for 75% of cases; the duration of life was 45-55 days. The size of leaves during the season increases three-fold in monocarpics, and in polycarpics it increases five-fold.

The immature state is absent in species of *Ferula* genus, because they do not form vegetative shoots (Rabotnov, 1983; Zhukova, 1988).

Depending on the habitat, the transition from virgin period to generative occurs in monocarpics after 8-10 months and in polycarpics after 4-7 months. During this period only the rosette leaves grow and the root elongates; later on the generative shoot forms.

The generative period in monocarpics constitutes several months and in polycarpics 8-14 years.

The *Ferula* monocarpics are the classic example of plants with a slow rate of pregenerative growth, that is to say, only rosette leaves grow rapidly and the root thickens every year. After 8-14 years the generative shoot forms and the generative organs develop. Depending on meteorological conditions the plants begin to blossom after 25-30 days (Rahmankulov and Melibaev, 1981; Momotov *et ah,* 1989; Bogdasarova, 1990). The growth of the reproductive shoot is due to internode elongation. In the year in which individuals enter the generative state (March-April), the vaginae of the stem leaves closely cover the inflorescences and form a "green bud"; this "green bud" with the stem growth increases because of loosening of the umbels and umbellulae, which grow intensively, and straightening and growth of the vaginae; the structure of the vaginae is a reliable diagnostic feature of the species. They differ in shape, size, consistency, pubescence and mode of attachment to the stem.

The flowers open acropetally. The opening mechanism of the flowers is similar for different sexual forms (uni- and bisexual) but there are some differences in their flowering biology. The bisexual flowers on the central umbels of paracladia open from 6 a.m. till 10 p.m. The blossoming peak is 7-10 a.m. The duration of the blossoming of bisexual flowers is 6-13 days.

Within the inflorescence the continuation of the blooming is different, but the common regularity was found: the blooming is longer at the lower paracladia than at the higher ones.

The seed productivity of the species depends on the quantity of generative shoots, paracladia, umbels, and umbellulae, and also on the ratio of bisexual and male flowers on a single individual. The number of bisexual flowers is half that in polycarpics. The monocarpics have male flowers, almost five times as many as the polycarpics; the ratio of male flowers to female is, respectively, 1:3 and 1:2.

The senile (postgenerative) period for monocarpics is absent. For polycarpics this period begins after 6-8 years of vegetation. One of the senile features for the individual is the tissue dying off in the basal part of the central cylinder of the main root, and this leads to the formation of a hollow, the depth of which after 4-6 years of blooming reaches 10 cm. The longer the individual blooms, the more hollows form at the shoot-root and the deeper they are; however, no particulation was found for any of the species studied. Another feature of the senile period is the formation of shortened vegetative shoots (during the next 3-6 years) only and after this the individual dies. Hence, the more shortened vegetative shoots and hollows in the root there are, the older the individual is.

Thus, the ontogeny of the *Ferula* species (both monocarpics and polycarpics) is characterized by the lack of immature period in the development. The longer period in monocarpics is the pregenerative period; the generative period with only blooming and fruitage is relatively short. There is no senile period, because immediately after fruitage the plant dies.

PART SEVEN–EMBRYOLOGICAL BASES OF REPRODUCTIVE STRATEGIES

Adaptive Possibilities and Reproductive Strategy in Trapaceae (Plate XIV)

The Trapaceae family is represented by the single genus *Trapa* (water chestnut), which includes many forms with vague taxonomic rank. The water chestnut is a rare tertiary relict, being at the same time a valuable food and fodder crop (Vassilyev, 1960; Takhtajan, 1981, Red Book of RSFSR, 1988). According to Kozo-Polyansky (1931), relict species are "living fossils", the evidence reflecting separate stages and the whole history of flora establishment in a region. In modern times, relicts often find themselves in quite a different environment from what they inhabited in the remote past. That is why the study of limits of plasticity and tolerance in their reproductive systems, and their development of living strategies in the course of settling of various ecological niches, are of interest from the point of view of general biology and merit the working out of approaches to study them.

A vast though interrupted range in Eurasia and Africa is characteristic of the genus *Trapa* (the separate races were brought also into North America and Australia). Its representatives are members of various plant communities, forming associations with different species of other aquatic macrophytes (e.g., Ceratophyllaceae, Nymphaeaceae, Potamogetonaceae, Najadaceae, Hydrocharitaceae). They are surrounded by various land vegetation, from dark-coniferous taiga, steppes and forest steppes in the northern hemisphere to tropical woods of the southern hemisphere. Water chestnut inhabits fresh and, as a rule, stagnant or slow-running, well-warmed reservoirs of eutrophic type (lakes, former river-beds, ponds, river backwaters and so on) with silt or sand bottom at a depth of 0.5 to 4 m and neutral or weakly alkaline (pH 6-8) mild water with a slightly high content of ferrum (Apinis, 1940; Vassilyev, 1960; Shilov and Mikhailova, 1970; Dubyna, 1982). This plant has been known to grow in dystrophic lakes (Martynenko and Kaim, 1977) and also in cold lakes with intensive ground nutrition (Shilov and Mikhailova, 1970).

The representatives of the genus are aquatic rooted grasses and belong to the group of hydatophytes (according to the classification of Uranov, 1974). The upper, floating generative part of the shoot is thickened and carries a rosette of rhombic leaves with long petioles. Large bubble-like swellings on the petioles support the plant at the water surface. The submerged, vegetative part of the shoot (0.5-4.0 m long, depending on reservoir depth) has long internodes and leaves, which fall early. Long photosynthetic organs, dissected into lobes, are formed in every internode. The nature of these organs is debated: metamorphosed adventive roots (Flerov, 1925; Zitek, 1955; Timonin, 1984) or modified stipules (Vassilyev, 1978). The plant is fixed in the bottom substrate by adventive root system; these roots form in the region of the long hypocotyl and lower shoot nodes.

The formation of terrestrial forms was described for some species of *Trapa*. These forms have roundish instead of rhombic rosette leaf blades, shortened petioles without bubble-like swellings, no submerged leaves and assimilating stipules (roots) in their nodes. So, these forms could be recognized as different species (Chernov, 1939; Smirnova-Garaeva, 1972; Dubyna, 1982).

The ability of *Trapa* (T. *europaea, T. longicarpa* and T. *brevicarpa)* to germinate and develop subsequently in the aerial environment was also demonstrated

experimentally (Jankowič and Blazenčič, 1968). In this case the plants differed significantly from the control ones (grown from the fruits in water) both in physiology of development (accelerated passing of the ontogenetic phases) and in morphological and anatomical features (morphological dwarf, appearance of the features of the terrestrial plants in the anatomical structure of the stem and leaves).

Water chestnut is commonly considered an annual plant (Takhtajan, 1966; Cook, 1987; Agarwal and Mohan Ram, 1995). However, there are data to suggest that in certain conditions it can be perennial (Paillieux and Bois, 1888, Halácsy, 1901; Gams, 1925; Flerov, 1902,1925,1926). According to Vassilyev (1960), water chestnut is a potentially perennial plant by its nature. This is argued from the duration of its blossoming and fruiting, which in moderate latitudes are abruptly ended by cold. This supposition is evidenced by the developmental peculiarities of T. *astrachanica* and *T. europaea* plants, introduced from Volga delta region (Astrakhan state reservation) into conditions enabling longer vegetation (Tashkent Botanical Garden, Uzbekistan). Such plants were characterized by the change of growth and developmental cycles in shoots (their secondary growth, flowering and fruiting), and also a better-expressed ability for vegetative propagation (Murdahaev, 1975).

Thus, water chestnut is an annual monocarpic in moderate latitudes, and in subtropical and tropical regions the existence of perennial (more primitive) species with protracted or repeated fruiting is possible.

Vegetative propagation. The stem in *Trapa* can branch repeatedly at different stages of ontogenesis, forming lateral shoots in the leaf axils. As a result, several rosettes of various age form on it during the vegetation season. Still, in the embryo the lateral buds are initiated in the cotyledonary axils besides the main bud, and lateral stems forming from them can give new plants (Raimann, 1898; Vassilyev, 1960). Such lateral stems develop only at shallow depth (not more than 2.5 m); otherwise the stems stop developing and die (Murdahaev, 1975; Titova, orig. data).

The lateral rosette formation can be also observed later; on the vegetative and generative parts of the main shoot, branching can be rather abundant. For example, a specimen of T. *astrachanica* 8.6 m long with 26 big rosettes of leaves was found (Karshina and Trofimov, 1951). The lateral rosettes may be separated from the main stem as a result of mechanical damage or aging (basal part of the stem dies) (Gibelli and Ferrero, 1891; Vassilyev, 1960; Murdahaev, 1975). This means that one sample divides into several, and autonomous daughter plants can take root with the help of adventive roots or can freely float at the water surface (traumatic and senile particulation, according to Rabotnov, 1950a,b, see Particulation).

The capacity of various *Trapa* species to form lateral shoots is used for their artificial vegetative propagation (Fu Ka-shui, 1954).

It should be mentioned that the role of vegetative propagation in reproductive system of *Trapa* is still not significant. According to some authors (Cook, 1987), *Trapa* lacks natural vegetative propagation because of its strongly expressed apical dominance. This made it necessary to work out the modes of artificial propagation of this plant *in vitro* (Agarwal and Mohan Ram, 1995).

Seed propagation. The dissemination unit of *Trapa* is a one-seeded, drupe-like fruit with characteristic horns, terminating in long, sharp thorns or harpoons. The massive pericarp consists of a green fleshy outer layer (exocarp + mezocarp) and black-brown lignified inner layer (endocarp). The fruits are unusually variable in

form and surface sculpture; this can be determined by ecological-geographical factors, by adaptation to distribution by certain species of animals (Vassilyev, 1960; Tzvelev, 1964), and also by introgressive hybridization between separate species. The last is affirmed by embryological data and data of biometric fruit analysis (Staszkiewicz and Wojcicki, 1979; Titova, 1988).

The seed, flattened like a heart, occupies the whole fruit cavity. The embryo appearing as a result of sexual process is pseudomonocotyledonous. It consists of a massive cotyledon, long hypocotyl and main bud with several leaf primordia, covered by a peculiar scale-like organ (second rudimentary cotyledon); in the cotyledon axils and scale-like organ axils the lateral buds are initiated; the main root is reduced. The thin seed coat is formed by the derivatives of both integuments (Kolesova (Titova), 1996; Titova, 2000).

Besides sexual reproduction, *Trapa* also has asexual reproduction. In T. *natans* var. *japonica*, the possibility of apomixis was demonstrated experimentally, but its form was not established (Kadono and Schneider, 1986). The appearance of zygote-like egg cells with the lack of pollen tubes in the embryo sac of T. *astrachanica* suggests the presence of parthenogenesis in this species (Titova, 1988).

Seed productivity and factors that determine its level. Genetic factors. At the early developmental stages in the half-lower bilocular ovary of *Trapa*, two ovules are initiated (one in each loculus). However, one of them always degenerates, regardless of whether fertilization has occurred. The probability of degeneration of the right and left ovules with respect to the plant axis is approximately similar (Titova, 1988). Thus, when one of the ovules in the ovary perishes, there is a decrease of real seed productivity (RSP) to half that of potential seed productivity (PSP). However, in isolated cases in some species (T. *longicarpa*—Yankowič and Blazenčič, 1961,1973; T. *manshurica*—Titova, orig. data), the development of both ovules and formation of dispermous fruits were found.

Climatic and coenotic factors. The productivity of water chestnut greatly depends on the vegetation duration, average temperatures, and solar radiation intensity. It increases from 1-2 to 15-20 fruits per plant with movement of species from the north to the south of Russia (Chernov, 1939; Mikhailova, 1940; Vassilyev, 1960; Belavskaya and Seraphimovich, 1977; Chernaya, 1988). The fruit number varies also depending on the state of the plant itself (e.g., from 4 till 100 and more fruits to every plant in T. *astrachanica*—Vukolov, 1932; Karshina and Trophimov, 1951).

Factors that limit water chestnut reproduction are the following: frequent summer freshets, causing significant disturbances in the development of plants and even death of the population (Sorokin, 1988); inhibiting influence of other members of the community (water lilies, duck-weed, and elodea) and also riverside plants (reed mace, sedgecane, reed, cane, lotus etc.) (Korzhinsky, 1887; Selling, 1940, Vassilyev, 1960; Belavskaya and Seraphimovich, 1977). However, there are contrary data about high competitiveness of the water chestnut and its peaceful coexistence with those plants (Wenner, 1939-1940; Shilov and Mikhailova, 1970).

The data of different authors concerning water chestnut yield even in the same region are rather contradictory. According to Vassilyev (1960), this is caused by flaws in the methods for crop counting, not by alterations in the limits of the population or individual.

The PSP and RSP in T. *natans* in the northern border of its range (Pskov region, Lake Vorokhoby) were estimated by a specifically developed method. The method

showed that with insignificant variation in the PSP, the values of RSP and, consequently, the productivity index altered significantly in some years and as a whole were notably lower than values of PSP (Titova and Batygina, 1997) (Table 28 and Fig. 62). Increase in RSP from one year to another was evidently determined by favourable weather conditions (e.g., relatively high average monthly summer temperatures, insignificant rainfall). Abundant rains, especially at the period of mass flowering, led to submerging of plants and sharp intercalary growth of internodes (including generative part of the shoots), and thus to extinction or retardation in development of flower buds. The consequence of this was decrease in fruit setting. Thus, redundant precipitation, causing abundant freshets, is really a limiting factor for *Trapa* reproduction in the North-Western region of Russia, which has a wet sea climate.

The values of PSP and especially RSP in the association T. *natans* + *Nymphaea Candida* were substantially lower than those of T. *natans purum* (Table 28). Overall plant development, formation of lateral rosettes, and development of buds were prevented as well.

Anthecological factors The flowers of water chestnut are small, single, white, monoecious, actinomorphic and tetramerous; they develop in the leaf axils. The androecium consists of four stamens, the anthers are tetrasporangiate, lartrorse, situated in the bud approximately at the same level as the style, a bit inclined to it, touching the stigma. The gynoecium is formed by two carpels, the ovary is half-inferior, the long style is of closed type; the capitate stigma is covered with slightly elongated, papilla-like cells, which secrete a substance of mucopolysaccharide nature.

The main mode of pollen transfer is self-pollination, supplied by the movement of perianthium parts and anthers relative to the stigma surface (Gibelli and Buscalioni, 1893; Mikhailova, 1940; Ram, 1956; Kadono and Schneider, 1986; Grevtzova *et ah*, 1987b). It is possible via contact and non-contact autophyly (Titova, 1988). The same mechanism is the basis for ecological cleistogamy, which is characteristic of *Trapa:* in the cloudy weather and also at the end of the vegetation period, the flowers often do not open completely, but pollination and fertilization can

Table 28. Potential (PSP) and real (RSP) seed productivity in *Trapa natans* L. in the various associations (Lake Vorokhoby, Pskov region).

Association	Year of observation	Number of individuals	PSP	RSP	Productivity index, %
Trapa natans purum	1990	24	95.76	0.46	0.48
	1991	100	82.34	5.65	6.82
	1992	100	99.40	7.49	7.53
T. natans + *N. Candida*	1990	-	-	-	-
	1991	64	64.24	2.41	3.75
	1992	100	62.70	5.82	9.28

Average value of PSP and RSP (per individual) was defined by the number of traces of fertile and sterile fruits on the generative part of the stem at the end of vegetation season, after fruits fell down from the mother plant; the traces of fertile fruits were significantly more salient and larger than those of sterile ones (see Fig. 62).

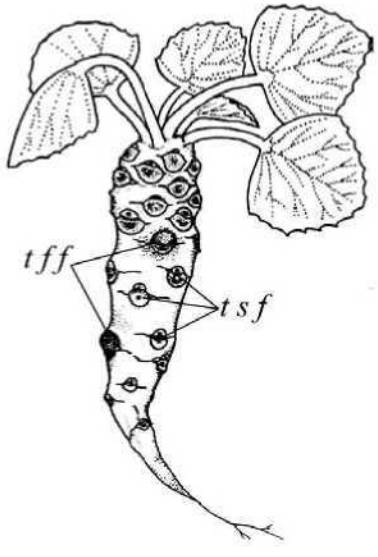

Fig. 62: Generative part of the *Trapa* shoot after falling from mother plant with traces of fruit stalks differing by form and size, f//—traces of fertile fruits, *t s f*— traces of sterile fruits.

occur. In T. *astrachanica*, the germination of pollen in the anthers was noted even before bud opening, though the penetration of pollen tubes into embryo sac and fertilization were not observed (Titova, 1988).

Cross-pollination by insects in *Trapa* has an accidental character (Mikhailova, 1940; Vassilyev, 1960; Kadono and Schneider, 1986). Both geitonogamy and xenogamy are possible because of simultaneous flowering at several rosettes of the same plant or formation of two flowers at one rosette, which happens quite often.

Cross-pollination in *Trapa* has probably played an important role in the past. The evidence of this is the presence of a special disc near the pistil in the lower part of the ovary; in this region nectar was found (Ohtaki and Joshido, 1980). Ram (1956) and Kadono and Schneider (1986), who observed pollen germination at the disc surface, supposed that it secretes a special substance that promotes pollen germination at the stigma. The cells of the disc contain a large quantity of starch, which after fertilization quickly disappears (Titova, 1988). This testified the possible role of the disc as a source of nutritive substances for fertilization. The presence of abundant starch in the disc attracts leaf-cutting insects (beetles), which damage the fruits and decrease the seed productivity of water chestnut.

Although the self-pollination mechanism in *Trapa* provides pollen transfer at the stigma even when pollinators are missing or avoid flowers opening in unfavourable conditions, fertilization is rare and a great number of aberrant ovules and seeds are formed. The success of fertilization is greatly influenced by the climatic conditions, pollen and ovule quality, their ratio and other factors (see Population aspects of sex determination; Population and coenotic aspects of plant reproduction research in Arctic conditions; Aberrant ovules and seeds: structure and diagnostics).

Optimal conditions for *Trapa* flowering are water temperature 18-20°C and high illumination (Mikhailova, 1940; Vassilyev, 1960; Kadono and Schneider, 1986; Titova, 1988). This helps the flower to reach the water surface in the day time. In T. *natans* in the Pskov region, flowers can rise to the water surface and flower over a large time interval, from 11 a.m. to 11 p.m. (Titova and Batygina, 1997). It is connected with increase in light day duration in the northern latitudes and, apparently, promotes fruit set, especially in the period of mass flowering. The most favourable combination of conditions for pollination and fertilization, still water and sufficient illumination to warm it, is achieved in that region in the evening hours. In the conditions of the northern border of the range, with short vegetation period, this factor may compensate partly for the limited time for fruit ripening. In T. *natans* var. *japonica*, separate samples were found to flower up to 11 p.m. and flowering did not show clear connection with radiation intensity. The nature of this phenomenon in the conditions of the Far East region is not quite clear (Kadono and Schneider, 1986).

Special studies of pollen and ovule quality in various *Trapa* species were not conducted. However, in a number of species (T. *astrachanica, T. manshurica),* a high rate of anomalies was observed in the development of pollen grains and embryo sacs (see below). These can lead to change in pollen-ovule ratio and, consequently, to decrease in RSP.

The specificity of embryonal processes. The embryological characteristics of various species and forms of water chestnut are sufficiently similar (Gibelli and Ferrero, 1891, 1895; Ram, 1956; Davis, 1966; Corner, 1976; Trela-Sawicka, 1978; Poddubnaya-Arnoldi, 1982; Batygina and Kolesova, 1985; Grevtsova *et ah,* 1987a,b; Titova, 1988, 2000; Kolesova (Titova), 1996; Titova *et al,* 1997; Zakharova, 1998). The anthers are tetrasporangiate; mature pollen grains are bicellular. Ovule is anatropous, crassinucellate, bitegmic, archesporium is more often unicellular, tetrads or triads of megaspores are linear as a rule and more seldom isobilateral and T-shaped. Embryo sac is of modified Polygonum-type; fertilization is porogamic; endosperm is represented by a single cell with hypertrophied nucleus, which degenerates early. Embryogenesis type is Solanad *(T. bispinosa)* or Onagrad *(T. astrachanica, T. manshurica).* Some differences in the character of embryonal processes are found at the population and species level.

The RSP of water chestnut can be influenced by various anomalies in the development of embryonal structures, such as forming of abnormal tetrads (T. *bispinosa*—Ram, 1956), high percentage of disturbances during the meiosis in micro- and megasporocytes and the formation of pollen grains and embryo sacs. This leads to the formation of a great amount of sterile pollen and ovules (T. *astrachanica*—Titova, 1988; T. *manshurica*—Titova and Zakharova, orig. data). Substantial disturbances of the morphology of pollen grains (e.g., the character of furrows and crests, aperture number) were mentioned in *T. astrachanica, T. natans* (Titova, 1988), T. *conocarpa,* and T. *szaferi* (Piorecki, 1980). They can be caused by a high level of aquatic pollution or introgressive hybridization between different species.

In some species or populations, the tendency to form so-called duplicating structures in the ovule can be observed (see Ovule and Seed Viewed from Reliability of Biological Systems, Vol. 1, p. 214). For example, in *T. bispinosa* (Ram, 1956), T. *europaea, T. conocarpa* (Grevtzova *et ah,* 1987b) and T. *astrachanica* (Titova, 1988), sporadic formation of the multiple archesporium and additional embryo sacs were mentioned. In T. *manshurica* this feature is rather stable (Titova and Zakharova, orig.

data). In this case part of the archesporial cells develop into megasporocytes, which enter meiosis and later form additional embryo sacs. Fertilization can sometimes occur in these sacs and several embryos can develop in one seed (polyembryony). For T. *natans* (Lake Vorokhoby, Pskov region) the formation of homopolar megaspore tetrads and the simultaneous development of several megaspores are typical. However, practically this did not influence the RSP in the given population, because such megaspores ceased developing at the early stages and, as a rule, they did not develop into additional embryo sacs capable of fertilization. The mentioned peculiarity of development, evidently, is connected with the establishment of the micropylar pathway of metabolite transport in the ovule of *Trapa* and of the embryo sac of Oenothera-type in the evolutionary line Lythraceae—Trapaceae—Onagraceae (Titova *et al,* 1997).

Dissemination. As a fruit matures, the detachable layer forms at the border of fruit and fruit stalk. After that the fruit falls to the silt bottom of the reservoir. The outer pericarp is destroyed and the fruit enters dormancy, which in temperate latitudes lasts till spring. Sometimes, as is mentioned for the Kansk district of Siberia, the final development of the fruits can occur at the bottom of the reservoir, because the nuts develop here in late autumn, when the lakes are covered with ice (Vassilyev, 1947). In some *Trapa* species the fruit falls together with the fruit stalk; in this case the fruits float on the water surface owing to bubble-like swellings on the fruit stalks and can travel by water to significant distances (Fedchenko, 1925; Rusanov, 1957; Murdahaev, 1975).

The modes of dissemination of *Trapa* are still not fully understood. Some authors consider hydrochory characteristic of *Trapa* (Tanfilyev, 1890). Others believe that dissemination is realized via zoochory, and the agents of fruit distribution are large fishes (Ascherson, Jaeggi, 1884), birds (Nathorst, 1884) or small animals (Vassilyev, 1960; Senyaninova-Korchagina, 1961). In the opinion of Tzvelev (1964), the presence of serrate little harpoons at the end of fruit horns is an adaptation to distribution with the help of large animals (wisent, elk, buffalo); the disappearance of those animals in the temperate part of Eurasia was the main reason for the extinction of *Trapa* species in this region.

Germination. The water chestnut belongs to the group of recalcitrants: if fruits are stored at temperature lower than 8-10°C and dry quickly (after 10-12 days), they lose the ability to germinate (Agarwal and Mohan Ram, 1995). However, there are data about the ability of *Trapa* fruits to germinate, though very slowly (for 4 years, 61%), when fruits are stored dry for 6 months (Sedelnikov, 1907, Nikolaeva *et ah*, 1985). The necessary conditions for germination are scarification, cold stratification (Kinzel, 1913; Nikolaeva *et al.,* 1985), and temperature not lower than 12°C (Mikhailova, 1940; Troitzky, 1947; Vassilyev, 1960).

The laboratory germinating power of T. *astrachanica* fruits stored in wet conditions for 7 months was 75-100%, depending on the year (Mikhailova, 1940); for T. *natans* fruits the rate was 54-78% (Titova, orig. data); most of the fruits germinated in 10-12 days. This fact is evidence of the high energy of their germination and can be regarded as compensation for the relatively low RSP. It is characteristic that some fruits (e.g., 2-3% in T. *natans* from Lake Vorohoby) never germinate the first year after dissemination, though their ability to germinate is conserved and realized during several subsequent years (Fischer-Sigwart, 1901, Vassilyev, 1960; Sorokin, 1988; Titova and Batygina, 1997). This feature of the *Trapa*, peculiar also to many other

plants, plays an important role in the creation of a bank of viable seeds in the soil and for survival in unfavourable conditions. For the water chestnut, which is propagated entirely by seeds and is generally an annual plant, it has special significance, because it renews the population following catastrophic disturbances of fruit maturation under the influence of unfavourable factors. The most ruinous of such disturbances are mass destruction of the fruits by humans, animals or birds, low temperatures, and strong summer freshets.

The germination symbolically can be considered hypogeal, though only one large cotyledon remains in the seed and another cotyledon, rudimentary, goes out together with hypocotyl and plumule and defends the latter when going through the silt (Raimann, 1898; Gibelli and Buscalioni, 1893; Nakano, 1913; Gams, 1925; Mikhailova, 1940; Kolesova (Titova), 1996). The evolutionary establishment of this unusual mode of germination and pseudomonocotyledonous embryo is connected with a peculiar type of indehiscent fruit, no doubt the consequence of adaptation of this plant to aquatic life.

Thus, water chestnut is characterized by the ability to propagate by seed and vegetatively. Evidently, seed propagation is predominant and can be realized via gamospermy (the majority of species) and agamospermy (some species) (see Reproduction, propagation and renewal; Apomixis). Vegetative propagation (senile and traumatic particulation) is more peculiar to species growing in the warm southern latitudes. Surprising plasticity of the organization of vegetative and generative spheres of water chestnut (formation of perennial and annual, aquatic and terrestrial forms, differences in the diurnal rhythm of flowering, formation of duplicating structures and variety of modes of propagation) has made their reproductive systems highly reliable. This gives water chestnut the ability to adapt to most conditions of environment and has made possible its survival to the present.

Reproductive Strategy in Ceratophyllaceae (Plate XV)

Representatives of the monotypic family Ceratophyllaceae are submerged aquatic plants (hydatophytes, by Uranov, 1974). They can be found in fresh water all over the world and usually grow in former riverbeds at moderate depths or along the shores of shallow ponds and lakes. They form associations with *Butomus umbellatus, Myriophyllum spicatum, Phragmites australis, Potamogeton pectinatus, Sagittaria sagittifolia,* and *Typha angustifolia* (Dubina *et al.,* 1985). *Ceratophyllum demersum* is the worldwide species.

The species of the family Ceratophyllaceae form an important component of the freshwater ecosystem (Kaden, 1953a; Gaevskaya, 1966); they are one biological means of preventing over-growth of aquatic reservoirs (Kogan and Chinnova, 1972). Besides, they can accumulate radioisotopes (Chebotina and Lubimova, 1981).

A number of peculiarities of reproductive biology are characteristic of the Ceratophyllaceae. They are perennial monoecious aquatic rootless herbs embedded in the soft mud by lower leaf whorls ("peculiar rhizoids"). They have unisexual flowers, segmented stems and whorled leaves that are divided into linear lobes. Stomata are absent, and xylem is reduced. Ceratophyllaceae species reproduce both by seeds and vegetatively.

In connection with high specialization, associated with aquatic mode of life, and practical importance of these plants the study of their reproductive strategy is of great interest. Primarily, this concerns pollination ecology, fruiting, seed germination and ratio of different types of propagation in the life cycle.

The Ceratophyllaceae species are widely distributed but they blossom and bear fruits only in particular **ecotopes.** Most researchers explain the rare flowering and fruiting of these plants by their need for high temperature (Arber, 1920; Muenscher, 1940; Kaden, 1953b; Wood, 1959). Besides, flowering is observed when the plants grow in stagnant water (Muenscher, 1940) and are fixed in the bottom substrate (Meissner, 1954).

Seed propagation. Plant reproductive processes are connected with energy expenditure for production of diaspores (fruits, seeds, seedlings) (see Reproductive Effort; Reproductive Success).

The species of Ceratophyllaceae studied have a similar number of male and female flowers on the plant, 10-12 at the beginning of flowering and 25-30 in a mass flowering. In the male flower 15 sessile stamens are usually formed (Shamrov, 1981, 1983b; Wilmot-Dear, 1985). One orthotropic crassinucellate unitegmic ovule develops in the ovary (Shamrov, 1997b). The mature fruit is a one-seeded nutlet. The principal portion of the seed is occupied by a large, well-differentiated embryo with green plumule (see Possibility of Classifying Flowering Plants According to Occurrence of Chlorophyll in Embryo, Vol. 2) consisting of 12-14 whorls of leaves and a few lateral buds. The number and form of the plumule are taxon-specific (Shamrov, 1982; Les, 1985). The endosperm is cellular with chalazal haustorium consisting of four large cells. The single integument shrivels up during the embryo development and mature seed is devoid of a typical seed coat. Endosperm and integument are preserved as a film. Thick-walled cells of nucellar epidermis with epistase formed at the micropylar pole and preserving layers of chalaza, podium and hypostase cells serve a protective function (Shamrov, 1997b). Although potential seed productivity is high, the number of mature fruits on one plant is not great and varies with growing conditions. For example, there are from four to five mature fruits in C. *pentacanthum* (Leningradskaya region, the ponds of Pavlovsk park) and C. *demersum* (Charkovkaya region, river Uda, near Pesochin settlement), from five to six in C. *submersum* and 13-17 in C. *demersum* and *C. pentacanthum* (Voronezhskya region, Choper nature reserve).

Insufficient seed set can be determined by a number of factors. One of them is the presence of **sterile** pollen grains (20 % in C. *pentacanthum* and 15% in C. *submersum);* among them were observed large **abnormal** grains, and their structure was like embryo sacs (sometimes up to 30-35% in C. *pentacanthum)* (Shamrov, 1983a).

Another reason is an imperfect **means of pollen transfer.** For *Ceratophyllum* species, self-pollination is characteristic and the plants grow predominantly in monoclonal populations. This is affirmed by low genetic diversity, heterozygosity and capacity for intra- and inter-specific crosses (Les, 1991). At the moment of pollination air cavities are formed in the anther. The stamens with mature pollen lose touch with the receptacle and rise to the water surface. The abscised stamens remain floating for 6 to 24 hours and then dehisce to liberate the pollen. The points of dehiscence are always turned into the water. So, as there are no fibrous thickenings in the anther wall, dehiscence occurs, probably, on account of the difference in tension between dry upper and wet lower stamen surfaces. The released pollen appears directly in the water, slowly comes down to the stigma, which looks like a groove, and

then gets into the stylar canal (Shamrov, 1983a; Wilmot-Dear, 1985; Endress, 1994b). It should be mentioned that the stigma surface, with the exception of apical zone, can perceive pollen beginning from the stage of binucleate embryo sac to the first stages of embryogenesis. In case there are several female flowers ready to pollinate, they stay in various planes relative to each other, so they increase the probability of pollination (Shamrov, 1983a).

Pollination is also influenced by the **specificity of ecotope.** Stagnant water and high density of plants in the given habitat are favourable to pollination. Thus, the lack of strict pollinators (pollination is abiotic), unfocused dispersal of pollen in the water, and "imperfection" of the apparatus to perceive pollen, together with the above-mentioned peculiarities in anther development, prevent pollination of some of the female flowers and lead to their gradual degeneration.

Rare fruiting can be connected also with **the lack of optimal conditions for pollen germination.** In experimental conditions pollen grains failed to germinate at temperature 18°C, and pollen tubes began to form only at 22-25°C (Shamrov, 1983a).

Ecological factors also determine the difference in fruit number for species and separate populations. In the Choper reserve, where there is a large accumulation of Ceratophyllaceae, fixed in the bottom substrate, stagnant water of temperature 22°C and sufficient illumination during the day are characteristic of their habitats during flowering. The ecotopes of *C. pentacanthum* in the Leningradskaya region and C. *demersum* in the Charkovskaya region, with longer flowering period, are characterized by less illumination and colder water until flowering. Probably, different species need different optimal conditions for flowering and pollination. For example, in the Pavlovsk ponds (Leningradskaya region), flowering and fruiting of C. *demersum* is not observed. However, the same habitats are favourable for flowering and fruiting of *C. pentacanthum.*

The main and final indicator of reproductive success at the population level is the number of seedlings and their fixation in the coenosis (Zlobin, 1989b). In the Ceratophyllaceae, the seedlings develop in the upper layers of mud and it is difficult to find them (Strasburger, 1902; Arber, 1920, Muenscher, 1940; Kaden, 1953b; Seghal and Mohan Ram, 1981). It must be considered that aquatic birds, fishes and some molluscs consume fruits as well as vegetative plant parts. Therefore, only a small quantity of forming seeds grow to the seedling stage.

In experimental conditions, the bulk of seeds germinate three or four months after maturing. The mature fruits leave the mother plant and fall to the bottom. The horns on the fruit surface permit fruits to anchor themselves in the silt substrate. The germination is **hypogeal** and starts when the fruit wall splits open along the abdominal seam into two halves. The embryo goes out through the fissure by its lower end (radicle is weakly differentiated; there is hypocotyl- root axis). Later, cotyledons and plumule appear. The tops of cotyledons remain inside the fruit for a long time. They are curved like hooks in different directions. Once they emerge, they help the seedling fix itself in the substrate.

Vegetative propagation. In habitats with unfavourable conditions for flowering and pollination (swift water flow, great depth, insufficient warmth), Ceratophyllaceae reproduce **only vegetatively.** Flowers are formed in small numbers or not at all, and on the stem there are many vegetative buds. The vegetative propagation is realized by the formation of unspecialized organs or "hibernacles" (see Bud; Particulation; Brood Bud). In such case, the stem divides into pieces with one or

two whorls of green leaves, in the axils of which one or several vegetative buds are present (Seghal and Mohan Ram, 1981). Such stem parts survive the winter and produce new plants in the next year.

Populations of Ceratophyllaceae can be **renewed** by combining **seed** and **vegetative propagation.** In the ecotopes of the Charkovskaya region, fruiting accompanied by the formation of hibernacles was observed (Shamrov, 1980). These peculiarities of reproductive biology of Ceratophyllaceae permit them to survive during unfavourable times under the crust of dry plants and silt that appears consequent to drying of the reservoir.

Thus, the reproductive strategy of the Ceratophyllaceae includes the realization of two developmental pathways:

1) combination of **sexual** and **asexual** (gemmorhizogenic) modes of reproduction and, respectively, of **seed** and **vegetative** types of propagation;
2) only asexual (gemmorhizogenic) reproduction and vegetative type of propagation.

The choice of one or another reproductive system depending on ecological factors (illumination, water temperature until the time of flowering, rate of water flow) and mechanisms of population-coenotic regulation maintain Ceratophyllaceae populations at a relatively stable level.

Reproductive Strategy in Nelumbonaceae (Plate XVI)

The monotypic family Nelumbonaceae is represented by two very close species: *Nelumbo nucifera* Gaertn. and *N. lutea* Willd. They are ancient plants and their fossils are known from Upper Cretaceous sediments (in Greenland and southern France), Miocene in Europe, and Tertiary sediments in North America (Chugunova-Sakharova, 1924; Snigirevskaya, 1964).

Nowadays, lotus is mainly distributed in the tropical and subtropical regions of Central and North America *(N. lutea)* and in Southern and South-Eastern Asia (N. *nucifera).* It can also be found in the temperate latitudes in the Volga delta, Trans-Caucasus, the Far East *(N. nucifera),* and the Tennessee River valley *(N. lutea).* Its characteristic habitats are shallow bays of the coastal waters, coastal lines of rivers and small lakes. Here lotus usually grows together with other hydromacrophytes, including *Ceratophyllum, Trapa, Potamogeton, Butomus,* and *Lemna* (Palibin, 1904; Sohmer and Sefton, 1978). Lotus plants can grow in various hydrological conditions (weak and strong water flow, at depths of 0.5-2.2 m, and so on).

The character of the lotus habitat evidences its high demands of oxygen, nutritive substances and NaCl (Chugunova-Sakharova, 1924). The significance of these factors was confirmed experimentally, as well as the plant's ability to stand great alterations of pH, from 4.5 to 9.0 (Meyer, 1930).

From observation of *N. nucifera* behaviour in ecological conditions with different soil pH, water level, illumination and temperature, three ecotypes of this species can be distinguished: deep-water, shallow-water and green-housed basins (Zhao Jiarong, 1985).

Nelumbonaceae have a great practical significance. They decorate natural and artificial reservoirs and are cultivated in almost all botanical gardens. In India and

China, lotus is used as a food and medicinal plant. Recently, *N. nudfera* varieties were obtained that have potential use in cleaning sewage (Sun *et ah,* 1987; Tang *et ah,* 1990). Together with other aquatic plants and microorganisms they are able to remove more than 70% of various pollutants from the treated waters (heavy metals, organic components of pollution). Along with wide cultivation and use of lotus, in some cases methods of control and restriction of plant growth are applied (cutting of leaves, herbicide treatment) (Hall and Penfound, 1944). This is connected with the fact that the habitats of lotus have favourable conditions for malarial mosquito development.

The need to protect and artificially reproduce this rare plant is underlined by its value for scientific, practical and educational aims (lotus is mentioned in the Red Book of RSFSR, 1988).

The representatives of Nelumbonaceae are large perennial grasses with long rhizome (hydrophytes, according to Uranov, 1974). In the nodes of the rhizome, leaves, flowers and adventive roots are initiated. The roots with strongly branching rhizome keep the plant in the bottom substrate. Two types of rhizomes are distinguished: thin rhizomes (6-8 mm) in the upper soil layers and thick ones (8-20 mm) in the deeper layers; the rhizome forms a complicated underground net, with a total length of up to 72 km over an area of 0.4 ha *(N. lutea* — Hall and Penfound, 1944). The leaves are also of two types: the first is submersed, fleshy and scale-like (cataphylls) and the second is peltate, floating and aerial. *Nelumbo* has a unique type of phyllotaxis: triads of leaf structures, two cataphylls without green colour and one green peltate leaf, divided by internodes, are disposed along the rhizome (Esau and Kosakai, 1975). The leaves have simultaneously xeromorphic features (thick cuticle, wax film, thorns on the petiole) and features of hydrophytes (many aerial cavities in all organs) (Snigirevskaya, 1964, Chen Wei-pei and Zhang Si-mei, 1988). The flowers are large, solitary and monoecious with strongly overgrown receptacle, on the long pedicel, which is covered by small thorns. In the tubers, rhizome and seeds there is plenty of starch.

Three developmental phases of lotus plant are distinguished: seedling, juvenile shoot and annual shoot (= generative shoot) (Wang Hsi-Ching, 1956).

Seed propagation. The fruit in Nelumbonaceae is a **submerged polynutlet** (Snigirevskaya, 1964). The broadened inverse conical receptacle takes part in the forming of it. One-seeded nutlets have hard pericarp, which consists of exo-, mezo- and endocarp (Wettstein, 1888; Wigand and Dennert, 1888; Ohga, 1923; Fenton, 1929; Snigirevskaya, 1964; Kolesova (Titova) and Batygina, 1988).

The seed is oval, thickly surrounded by pericarp; the seed coat is like a dry, thin brown film including pressed remnants of both integuments. The remnants of endosperm are like a thin dry film surrounding the plumule. **The embryo** is large and elongated and takes up almost the whole seed cavity; it has two massive cotyledons, green plumule, short hypocotyl and greatly reduced main embryo root. In the course of embryogenesis root apex is submerged into the folds of the embryo body (peculiar coleorhiza); during germination it does not develop and is replaced by the system of adventive roots, which are initiated in the base of petioles of the plumule leaves.

The morphological nature of a number of structures and organs of embryo and seedling in *Nelumbo* is under discussion. *Nelumbo* embryo is interpreted as dicotyledonous (Schaffner, 1904; Gupta and Ahuja, 1967,1969; Ito, 1982; Batygina *et al.,* 1983; Yan Su-zhen, 1986; Lodkina, 1988; Snigirevskaya, 1992) or monocotyledonous (Lyon, 1901,1905; York, 1904; Haines and Lye, 1975; Titova and

Batygina, 1996). The interpretation of the *Nelumbo* embryo as a monocotyledonous one is based on the mode of cotyledon initiation, with the formation of a single primordium that "bifurcates" as it develops. According to Lyon (1901), this means of cotyledon initiation is the result of schizocotyly of the original single cotyledon. However, it seems more likely that it is the result of partial unimarginal congenial fusion of two original cotyledons, due to which *Nelumbo* embryo acquires a structure intermediate between di- and monocotyledonous (Titova and Batygina, 1996; Titova, 1999, see also Syncotyly, Vol. 2). Original views on the morphological nature of cotyledons in *Nelumbo* were suggested by Lodkina (1988) as result of their laying down alternately, and by Snigirevskaya (1992, see below) as modification of the lancet phyllomes.

The plumule of lotus has an unusual structure: besides four alternate peltate leaves there are peculiar scale-like organs, which are formed at the base of the second, third and fourth leaves (Wigand and Dennert, 1888; Lyon, 1901; Wang Hsi-ching, 1956; Wang Hsi-ching and Yu-Bing-sheng, 1966; Snigirevskaya, 1964, 1992; Gupta and Ahuja, 1967; Titova, 1988). Most authors consider the scale-like organ in *Nelumbo* embryo a variety of stipule (Trecul, 1854a,b; Gwynne-Waughan, 1897; Lyon, 1901; Wang Hsi-ching and Yu-Bing-sheng, 1966; Chen Wei-pei and Zhang Si-mei, 1988; Titova, 1988) or a peculiar developmental type of leaf sheath (Gupta and Ahuja, 1967). According to these authors, the scale-like organ is formed from adaxial meristem in the basal part of leaf primordium, being the derivative of it, and is disposed in the same plane with the foliage leaf, that is, in concordance with alternate position. Thus, it has the same origin as the stipules. Snigirevskaya (1992) considers the nature of scale-like organ in the plumule from the point of view of leaf dimorphism and unique phyllotaxis type, which are peculiar to the lotus shoot in the adult state; she considers it to be a lanceolate leaf (cataphyll). As this author points out, the presence of clearly expressed sheath and parallel venation are characteristic of scale-like leaf, unlike true peltate leaf, which has palmate venation and no broad sheath. The type of primary mutual disposition on the seedling stem of peltate and also scale-like leaves and cotyledons is cross-opposite. The similarity of the development of scale-like leaf and cotyledons in the embryo (e.g., peculiarities of venation, sheathing type of base) as well as their position on the axis in one plane allowed Snigirevskaya to conclude that the morphological nature of these organs is common and to interpret *Nelumbo* cotyledons as modified lancet phyllomes. Obviously, this important problem merits further investigation.

Seed productivity in Nelumbonaceae varies with the species and place of growth. The nutlet number in the fruit varies from 8 to 25-30 in *N. nucifera* (Snigirevskaya, 1964; Collinson, 1980; Titova, 1988; Vasilyeva, 1992) and from 12 to 25 in *N. lutea* (Pearl, 1906; Hall and Penfound, 1944). The average number of nutlets in the fruit of *N. nucifera* is 15-17 in Astrakhan State reservation (delta of Volga) and up to 35 at the Lake Khanka.

Real seed productivity depends on climatic, anthecological, genetic and other factors. Processes of flowering and fruiting may be negatively influenced by long droughts, floods and storm winds (Chugunova-Sakharova, 1924; Hall and Penfound, 1944). According to some data (Dobrokhotova, 1938), lotus withstands temporary drying.

One causative factor in the decrease of seed formation in Nelumbonaceae is the disturbance of pollination and fertilization due to lack of pollination agents, the changing of normal ratio for pollen and ovules and other conditions.

Nelumbo is characterized by preferential cross-pollination with the help of insects mainly; the flowers of both species are protogynous and the time of flowering varies from 3 to 5 days, depending on conditions (Miyake, 1898; Chugunova-Sakharova, 1924; Dobrokhotova, 1938; Snigirevskaya, 1964; Sohmer and Sefton, 1978; Schneider and Buchanan, 1980; Titova, 1988). On the first day of anthesis the flowers open only slightly early in the morning and close at midday. The anthers do not open. The stigmata can receive the pollen, but only from other flowers (xenogamy and geitonogamy). On the second day the flower opens completely and the dehiscence of anthers occurs; the stigmata are receptive to pollen only for some time (in the morning) and then wither quickly. Owing to this, self-pollination (autogamy) is possible only for a very short period.

In both species the embryological processes proceed uniformly enough: anthers have four loculi, mature pollen grains are bicellular, ovule is anatropic, crassinucellate, bitegmic, archesporium is unicellular, the embryo sac develops by Polygonum-type, endosperm is cellular, embryogenesis is of Asterad-type (Lyon, 1901, 1905; York, 1904; Khanna, 1965; Gupta and Ahuja, 1967, 1969; Gupta and Ahluwalia, 1979; Batygina *et al.*, 1982,1983; Ito, 1982; Yan Su-zhen, 1986; Kolesova and Batygina, 1988; Titova, 1988; Titova and Batygina, 1996). However, for some populations, anomalies were noted in micro- and megasporogenesis and development of embryo and endosperm. These anomalies lead to pollen viability reduction and formation of abortive ovules and defective fruits. For example, in *N. nudfera* growing at Astrakhan State reservation, the degeneration of microsporocytes (separate cells or their bundles) and microspores caused by lack of contact with tapetum surface or disturbances of the tapetum development was observed. Formation of polynuclear pollen grains and others was also often observed.

In a number of cases the process of syngamy was absent, because one of the sperms was delayed in the synergid and the result was the formation of seeds with endosperm but without embryo. The characteristic anomaly is the formation of monocotyledonous embryos, the number of which was approximately 4% of the total number of embryos investigated (Titova, 1988; Vasilyeva, 1990/1992). When cotyledons are fused along their whole length, plumule is underdeveloped and embryo is unable to germinate (Snigirevskaya, 1992).

Some deviations can increase **the level of seed productivity** in Nelumbonaceae. Of special interest in this context is the fact that in *N. nudfera* from different habitats (Volga delta, Russian Far East, and India) unreleased tetrads were found (Khanna, 1965; Kupriyanova, 1976, 1979; Kupriyanova and Aleshina, 1978; Titova, 1988; Batygina *et al.*, 1991; Titova *et al.*, 1993). An especially high percentage of unreleased tetrads is characteristic of *N. nudfera* from Lake Khanka. The presence of the pollen tetrads contributes to increase in pollination efficiency and, consequently, seed productivity. The microspore tetrads in *N. nudfera* from Astrakhan State reservation and Lake Khanka are chiefly tetrahedral, and more seldom isobilateral and crosswise; in *N. nudfera* from India, isobilateral tetrads dominate. The microspores united in tetrads, unlike solitary three-sulcate ones, often have only one circular furrow lying equatorially. Solitary pollen grains with a single circular furrow or a furrow or with some other structure also can be found in *N. nudfera* from Lake Khanka. Such pollen grains are rather similar in structure to mono-sulcate pollen grains of Nymphaeales s.s., which probably are distant relatives of Nelumbonaceae (Takhtajan, 1980a; Snigirevskaya, 1992). This may be a key to understanding the mechanism of

appearance of mono-sulcate pollen from three-sulcate pollen (see Kupriyanova, 1976, 1979).

In some populations the tendency for formation of double structures in the ovule was found (see Ovule and Seed Viewed from Reliability of Biological Systems, Vol. 1, p. 214). For example, in *N. nucifera* from Astrakhan State reservation, along with one-celled archesporium (approximately 30% of the studied ovules), the formation of multi-cellular archesporium (two to three archesporial cells) was found. However, additional archesporial cells as a rule develop till the stage of meiosis and usually degenerate before its beginning (Titova, 1988). In some nutlets additional embryos (embryoids) were found; they were situated between the cotyledons of the larger sexual embryo (Snigirevskaya, orig. data). In *N. nucifera* from India (Khanna, 1965) and *N. lutea* from North America (York, 1904) the formation of additional embryo sacs was noted.

Dissemination and germination. With maturity the receptacle dries, the fruit-stalk fades, and as a result the receptacle from vertical position turns "head down". Nutlets leave the receptacle tissues, fall into the water and float far from the mother plant, sometimes giving rise to new thickets. Wild boars and large birds such as geese or swans also serve as agents of distribution (Dobrokhotova, 1938).

Germination in both species of *Nelumbo* occurs similarly and only when the pericarp has not begun to dry (Dobrokhotova, 1938; Hall and Penfound, 1944; Snigirevskaya, 1964; Shafranov, 1958). When the pericarp dries, it becomes very hard and impenetrable to light, air and water. The seed turns to exogenous dormancy, which can last for an extremely long time, hundreds and thousands of years (Ohga, 1923, 1927; Libby, 1951; Krishtofovich, 1957; Yanishevsky and Pervukhina, 1941). Lotus fruits over 1000 years old found in a peat layer in Northern China retained their ability to germinate (Ohga, 1927).

There maybe several reasons for lotus seed longevity: peculiarities of embryo structure, the great store of nutritive substances, including low molecular proteins in the large cotyledons, well-developed green plumule, which can quickly begin to grow in favourable conditions, a solid pericarp impenetrable to water and air. But the main reason, probably, is the specific hormonal status: there are no germination inhibitors (abscisic acid) or cytokinins in the mature nutlets (Morozova and Vasilyeva, 1993).

Fruitlets with undried pericarp fall to the reservoir bottom but within several hours again rise to the surface and float away. The rising to the surface is, evidently, connected with the release of a great amount of hydrogen and other gases, which are intensively produced during germination, as was established experimentally (Toyoda, 1958,1960). The gases probably fill the cavities inside the nutlet. According to the data of Hall and Penfound (1944), 90% of nutlets come to the surface with stigma downwards. Such a position is maintained by the presence of a small cavity located in the lower part of the fruitlet, between seed and fruit envelope. This cavity also plays an important role in the dissemination of nutlets by water (Ohga, 1927; Hall and Penfound, 1944; Snigirevskaya, 1964, Titova, 1988).

In this connection, one point of great interest is a peculiar structure in *Nelumbo* pericarp, a "protuberance" or "spiracle", in its upper part near the stigma on the outer abaxial side. According to Ohga (1927), the cavity of this organ serves as a reservoir for oxygen, which is necessary for fruit germination in anaerobic conditions at the

bottom. Snigirevskaya (1964) considers that it supplies water entering into it during germination. However, the presence of multilayered epidermis and palisade layer and cell walls saturated with suberin, and absence of stomata in the epidermis (Ohga, 1927; Fenton, 1929; Kolesova and Batygina, 1988; Titova, 1988) are evidence for the isolation of the spiracle cavity from the environment and for its possible function of enabling fruitlets to float during dissemination and germination. After they come to the surface for some time (12 hours in *N. lutea* — Hall and Penfound, 1944) fruitlets go to the bottom again, and there they begin to germinate.

The germination is hypogeal and rather singular: neither cotyledons nor hypocotyl with radicle go out from the pericarp; only epicotyl appears through the fissure, which forms as a result of longitudinal rupture of fruit envelope (Wigand and Dennert, 1888; Turdiev, 1960; Snigirevskaya, 1964; Haines and Lye, 1975; Ito, 1982). This rupture often occurs near the spiracle, indicating its possible role in the dehiscence mechanism of the f ruitlet during germination. In connection with this, the accumulation of a large amount of druses of calcium oxalate in the cells covering the spiracle cavity probably provide an explanation. The fruit envelope ruptures after 5-6 days and the epicotyl emerges after 10-12 days. The germination accelerates at high temperatures (20-30°C) and is slowed at low temperatures (less than 15°C).

The young seedling has direct (orthotropic), zig-zag shoot with four floating peltate leaves, short internodes between them, and adventive roots in every node, initiated in the embryonic period. The fruitlet with young plant becomes lighter as the starch in the cotyledons is consumed and again comes to the surface. The young seedlings float for some time and later root in more shallow places.

The transition from germination to juvenile plant is very quick (Wang Hsi-Ching, 1956). The internode bearing vegetative bud elongates considerably, becomes horizontal and forms a plagiotropic rhizome. On the dorsal side of the rhizome in every node leaves are formed and on the ventral side adventive roots are formed. With the coming of the cold season the last two or three rhizome internodes of juvenile plant form a winter tuber with apical bud, which will develop in the following spring.

The annual lotus plant is similar to the juvenile plant in morphology, with the exception that its vegetative organs are larger and, besides vegetative buds, it forms also mixed buds (i.e., vegetative and generative buds). The rhizome of the annual plant branches extensively and forms the system of shoots. The structure of the rhizome has features that clearly show adaptation to amphibian mode of life. All hibernacles at the annual shoot are mixed. It should be noted that the data about the duration of ontogenetic phases and the time of initiation of mixed buds in *Nelumbo* are somewhat contradictory (Meyer, 1930; Hall and Penfound, 1944; Chen Wei-pei and Zhang Si-mei, 1989).

When the fruit coat manages to dry before the fruitlet appears in the water, germination can occur only if the coat is damaged. In artificial conditions, this can be done, as a rule, by mechanical or chemical treatment (concentrated H_2SO_4) of fruitlets (Ohga, 1923,1927; Meyer, 1930; Hall and Penfound, 1944; Shafranov, 1958; Toyoda, 1958). Damage of the fruit coat leads to elimination of the surfacing phase and acceleration of germination (to 1-2 days). In natural conditions only a very small percentage of fruitlets germinate and, moreover, factors and agents that cause fruit coat damage are practically unstudied (Hall and Penfound, 1944).

Vegetative propagation in natural conditions. *Nelumbo* seed propagation in natural conditions is rather difficult because of the above-mentioned factors and renewal more often occurs vegetatively (gemmorhizogeny) by formation of tubers, which withstand winter (Heritage, 1895; Meyer, 1930; Dobrokhotova, 1938; Snigirevskaya, 1964). For vegetative propagation in lotus the unfavourable factors are the same as for seed propagation: drought, floods and strong winds. For drought years in the Caspian Volga region, the drying of root system in *N. nucifera* was observed, and after this tubers were not formed in autumn (Chugunova-Sakharova, 1924); floods and droughts lasting more than two weeks caused the death of the major part of rhizomes of *N. lutea* in the Tennessee River valley (Hall and Penfound, 1944).

Artificial vegetative propagation. In botanical gardens lotus is usually reproduced from a section of rhizome with the apical bud, taken in spring (Fomin, 1905; Dobrokhotova, 1938). As a rule, in the first year of planting *N. nucifera* tubers there is no flowering. The tubers of *N. lutea,* being cultivated, usually form the flowering plant during one season, while seedlings from seeds require two to four years (Meyer, 1930). The use of rhizome cuttings in pot and vat cultures promotes the increasing of the flowering period (Deng *et ah,* 1990). Plants grown in basins demonstrated normal development, similar to those in natural conditions. The features of growth and development of embryonic structures, the dynamics of soluble carbohydrates in them in the early stages of seed formation, the type of anomalies (e.g., seeds without embryo but with endosperm, embryo with anomalous structure of cotyledons) were similar for *N. nucifera* growing in natural conditions and in greenhouse culture (Titova, 1988; Vasilyeva, 1990/1992). However, in greenhouse cultivation, seed productivity tended to increase (12-31 fruitlets in one receptacle, in comparison to 8-22 in natural growth conditions).

Artificial seed propagation has special interest for lotus selection, making it suitable as an indoor plant (Zhao Jiarong, 1988). Cross-pollination and artificial cross-breeding resulted in 12 new Chinese varieties of *N. nucifera.* These plants were not tall (8-20 cm in comparison with parent forms of 10-130 cm), they had flowers of unusual shape and colour and they could be grown in tubs. Pot and tub culture of lotus is widespread in China. Its selection is well developed; 70 lotus varieties are numerically classified, including the hybrid *N. nucifera* x *lutea* (Zhong Yang and Zhang Xiaoyan, 1987). The high seed productivity of various lotus forms was usually correlated with low decorative quality of the flower and edible quality of the rhizome. However, some varieties obtained by Chinese breeders had both high ornamental quality and nutritive values and sufficient seed production (Chang Sing-yen and Wang Chi-Chou, 1966).

A promising technique for preservation and propagation of lotus is embryoculture (Ta-Chu Liu, 1948; Vasilyeva and Batygina, 1981; Batygina and Vasilyeva, 1987; He Zican and Liu Shijita, 1987).

Thus, we can make the following conclusion. **Reproductive strategy of Nelumbonaceae** is characterized by a complex of features, including ability to self-pollinate, longevity of seeds, great energy and high rate of growth, ability to spread quickly over large territories, and tolerance of some kinds of pollution. Reproductive strategy includes **simultaneous realization of sexual and asexual (gemmorhizogenic) modes of reproduction** and, consequently, of **seed and vegetative propagation.** In certain stages of ontogenesis, however, one or another generative developmental programme may dominate. In this case, a close correlation

is observed between the development of the organs of sexual and asexual reproduction. Only rhizome nodes in which flower bud is not initiated thicken and form organs of vegetative propagation, or tubers (Wang Hsi-Ching, 1956).

The sexual reproduction greatly depends on pollen transfer by insects and, since the greater part of the lotus population is clonal, inter-population crosses help to shorten the seed formation period (Sohmer, 1977). If vegetative propagation promotes the preservation and renewal of the given lotus population in a certain habitat, seed propagation has a greater advantage in a strategic plan to expand and create a bank of long-lived seeds.

Seed Propagation and Vegetative Propagation in *Vaccinium myrtillus* L. (Ericaceae)

Vaccinium myrtillus (bilberry) belongs to the group of repent and vegetatively mobile dwarf shrubs (Serebryakov, 1962). This species dominates the grass and dwarf shrub layer in many plant communities in light and dark coniferous forest zone, as well as small-deciduous forests. *Vaccinium myrtillus* is a valuable food and medicinal plant.

Both seed and vegetative propagation are characteristic of bilberry. The biology of seed propagation is not completely investigated, and quite often the available data are contradictory. Fourteen months pass from the moment of flower initiation till the complete fruit maturation of bilberry, that is the development of reproductive organs spreads over two vegetative periods. During the first vegetative period the flower initiation in the renewal buds occurs, and during the second one flowering, fertilization, formation and maturation of fruits occur (Fig. 63). The dates of initiation and the rate of renewal bud formation depend heavily on meteorological conditions during the vegetative period (Tyak, 1984).

Generative individual numbers of bilberry vary in different phytocoenoses. For example, in the Carpathians the figures vary: in the bilberry fir-forest there are 1-2 units/m^2, in the green moss forest 196 units/m^2, and in the blueberry forest type of bilberry 62 units/m^2. In all populations the number of flowering plants is smaller, because some of them are temporarily in a non-flowering state (Uranov and Serebryakova, 1976; Zhilyaev, 1989).

In the pine forests of Leningrad region (Russia) 8.7 ± 1.5 flowers, 6.5 ± 0.7 fruits and more than 350 seeds formed on one partial shrub (Maznaya, orig. data). The reproductive structures develop asynchronously. Usually 10 stamens with 2500-4600 pollen grains in each are formed in the flower. The anther dehisces by apical pore. The mature pollen grains are bicellular, and they are preserved in tetrads. Quantity of viable pollen varies from 0.38% to 50.9%. Numerous ovules (86-95 in one ovary) develop at sutural-angular placentae in the five-celled ovary (Anisimova, 1997; Anisimova and Shamrov, 2000). The formed ovule is ana-campylotropous, tenuinucellate and unitegmic (Fig. 64).

The development of the reproductive structures is characterized by the presence of anomalies. They are displayed first of all in the degeneration of pollen grains, embryo sacs, egg apparatus elements, embryos and endosperm in various stages of development, and the disturbance of cellularization during endosperm formation. The formation of additional (synergid) embryos was noted in some cases (Anisimova, 1997,1998).

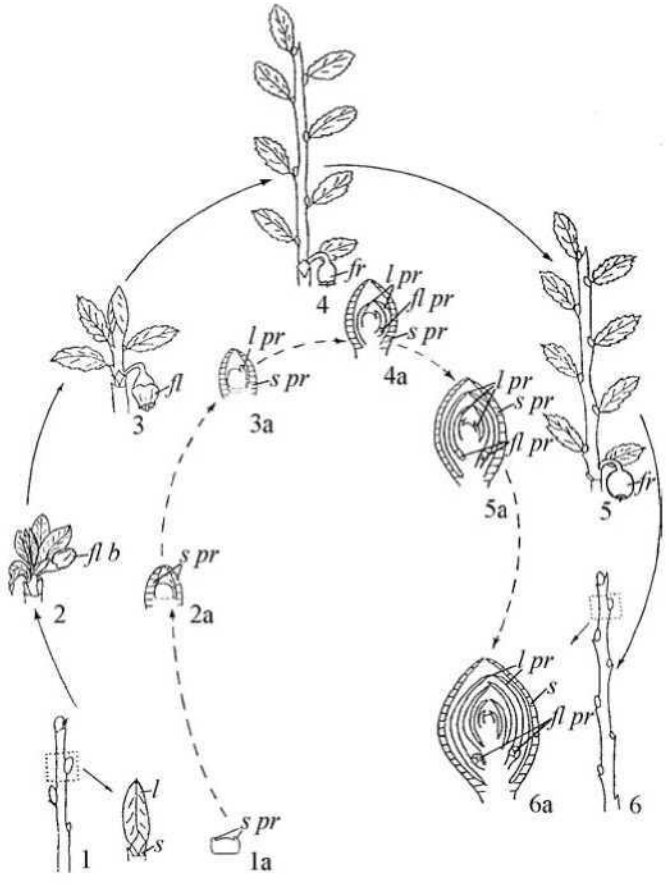

Fig. 63: Development of year-old shoot (outer circle) and renewal bud of mixed type of following vegetation year (inner circle) in *Vacdnium myrtillus* (modified from Tyak, 1984). 1 — the beginning of annual shoot growth, la — initiation of the first pair of scales in renewal bud; 2—flower bud stage, 2a—formation of the second pair of scales; 3 — flowering stage, 3a — appearance of the first leaf primordium; 4—fruiting stage, 4a — initiation of meristematic shoot apex of following vegetation year; 5 —stage of fruit maturation, 5a — initiation of new leaf and flower primordia; 6—fall of leaves and fruits, 6a — completion of renewal bud formation of following vegetation year; *fl*—flower, *fib* — flowerbud, ^I*pr*—flowerprimordium, *fr*—fruit, *I*—leaf, *Ipr*—leafprimordium, s—scale, s *pr*—scaleprimordium.

Bilberry is an obligatory entomophilous plant; it is pollinated by bumblebees. In investigated Carpathian populations the strict order of pollinator visits is determined by the number of flowering bilberry individuals, the distance between them, and the order of anthesis on the generative shoot (Zhilyaev, 1989). The neighbouring flowers of one shoot are pollinated first, and then the flowers of the neighbouring individuals are pollinated, and so on. This mode of pollination is conducive to the appearance of

inbred lines and the formation of subpopulations within all the individuals of the species in a community. In cases where the system exists during many generations, the local panmixia leads to the formation of homozygotic massives. In some cases (3-5% of flowers), autogamy was noted.

Heterogeneous seeds are found in bilberry fruits gathered during the dissemination period. These seeds can be divided into three fractions by morphology, biometrics (size) and quality (form, the degree of embryo and endosperm development): large, medium and small. The seeds of the large fraction (1.2-1.8 x 0.5-0.9 mm) are pointed-oval or lens-like. They contain abundant endosperm and direct or slightly curved cylindrical embryo, which occupies approximately 0.75 of seed length. The embryo is differentiated into two short cotyledons, shoot apex, hypocotyl and radicle. The seed coat consists of outer epidermis (radial and inner tangential cell

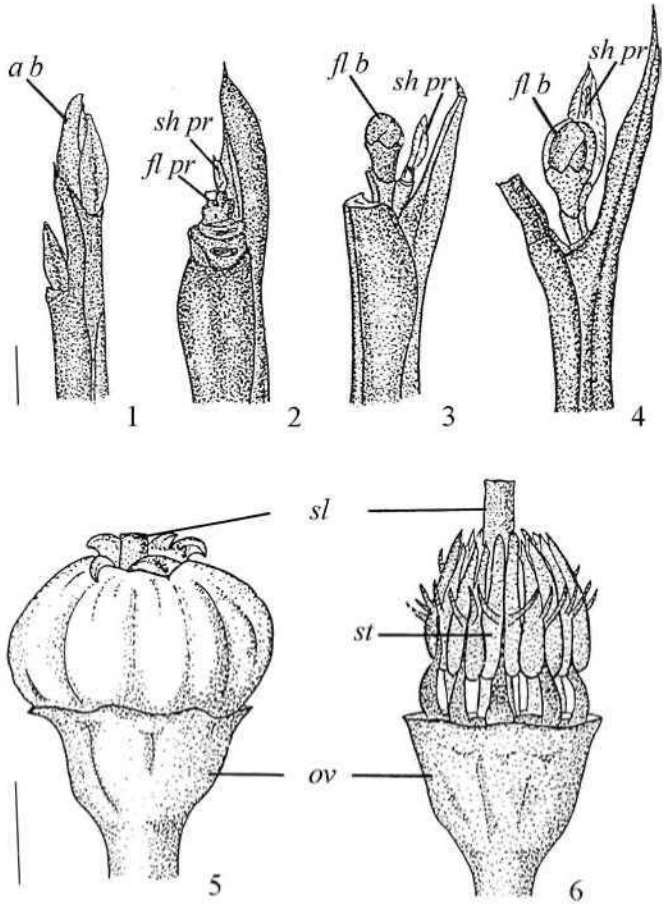

Fig. 64: Development of flower in *Vacdnium myrtillus* (after Anisimova, orig. data).
1-4 — development of apical bud of mixed type; 5 — general appearance of flower; 6 — flower without corolla.

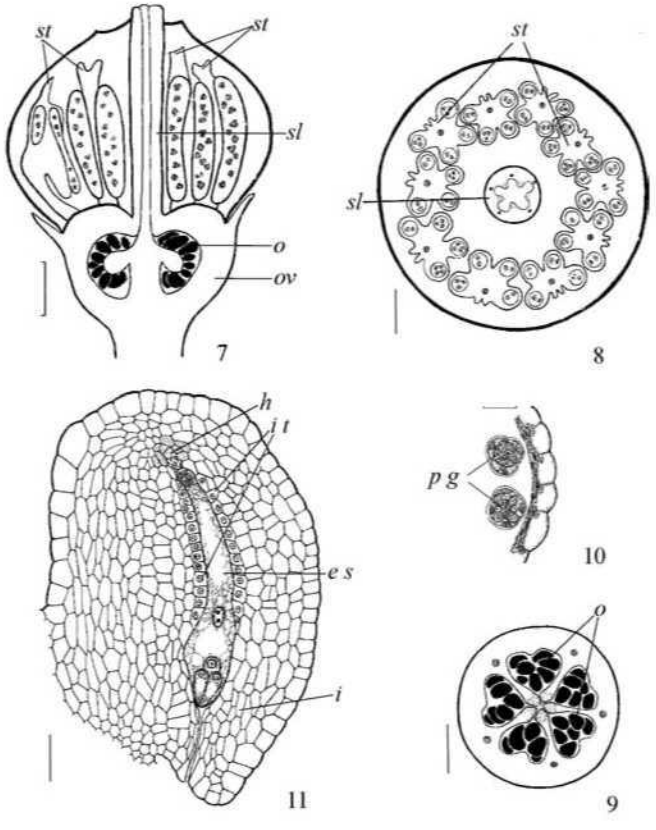

Fig. 64 *(Contd.)*

7, 8—flower structure, longitudinal (7) and cross-section (8); 9—upper part of ovary, cross-section; 10 — fragment of mature anther wall (cross-section), pollen grains in tetrads are seen; 11 —ovule at the stage of mature embryo sac, longitudinal section, *a b*—apical bud, *e s* — embryo sac, *fl b* — flower bud, *fl pr* — flower primordium, *h*—hypostase, *i* — integument, *i t*—integumentary tapetum, *o*—ovary, *ov*—ovule, *p* g—pollen grain, *sh pr*-shoot primordium, *si*—style, sf—stamen. Scale: 1-9 — 0.3 mm, 10,11 — 0.03 mm.

walls of it are irregularly thickened and have pores) and thickened parenchyma cells. Seeds with underdeveloped embryo were found in a few cases. The seeds of the middle fraction (0.6-1.1 x 0.3-0.5 mm) are oval, oval-pointed, lens-like, flattened, slightly curved, sometimes with folds; they are deprived of embryo, the endosperm is weak or absent. The seeds of the small fraction (0.2-0.6 x 0.1-0.2 mm) are oblong and flattened, they often keep the form of the ovule, they do not contain embryo or endosperm. They are represented by exotesta and sometimes by the remnants of the integumental and chalazal middle layers (Chernyakovskaya, 1992; Anisimova, 1997, 1998). The ratio of the large, medium and small seeds in the fruit of the North-Western Russian regions is 74:24:2 (Murmansk region), 30:45:25 (Leningrad region) and 56:43 (Karelia) (Maznaya and Lyangusova, 1995,1997; Lyanguzova *et al.*, 1999).

It is known that many factors, including habitat conditions, influence seed formation (see Real seed productivity; Reproductive success; Population and coenotic regulation of reproduction). The significant variation of the formed seed number and their mass in one fruit appear to be connected with this. In the pine phytocoenoses of the Russian North-West the seed quantity in one berry varies from 17 to 112 (Maznaya and Lyanguzova, 1995,1997; Anisimova, 1997; Lyanguzova *et al*, 1999), in Western Siberia from 8 to 50 (Timoshok and Parshina, 1990) and in the Ukrainian Polesie from 18 to 72 (Kondratjuk and Shabarova, 1968). Thousand-seed weight in the pine phytocoenoses of North-Western Russia is 200-288 mg (Maznaya and Lyanguzova, 1995,1997; Lyanguzova *et al*, 1999). The potential and real seed productivity of one partial shrub of bilberry in the Western Siberia, depending on phytocoenosis type and altitude, is, respectively, 67-574 and 47-189 (Timoshok and Parshina, 1990). Evidently, the seeds of the middle and small fractions are not viable, and it is important to consider this fact when evaluating seed quality. From the seeds formed in one berry, not more than 16% germinate (Maznaya, orig. data). The laboratory germination of the seeds gathered in various years and from different parts of bilberry area varies from 32% to 96% (Shabarova, 1968; Krasnov, 1978; Alekseeva, 1990; Maznaya and Lyanguzova, 1995,1997; Timoshok, 1998; Lyanguzova *et al*, 1999). However, soil germination of seeds does not exceed 30%; the seeds germinate slowly, the first shoots appear on day 15-19 of the experiment (Koziratski, 1975; Maznaya and Lyanguzova, 1995). Soil germination of the bilberry seeds can reach 80% after nine-month stratification (Stačkiavičene and Bucktus, 1983).

The potential of the bilberry for effective seed propagation is not completely realized in nature. The reasons for this may be connected with the quick loss of viability, which is caused by high activity of soil microorganisms (Kamenetzkaya, 1969; Karpov, 1960; Levina, 1981; Petrov V., 1989; Komulainen *et al*, 1994). Besides, the seedlings quickly perish in the moss-lichen layer because the bilberry shoots are very small and require peculiar conditions for their successful development (e.g., constant soil humidity, indirect insolation, presence of mycorrhiza, absence of competition). The most favourable conditions for their growth are in places with disturbed moss cover (e.g., on old bonfire sites, elehills, along old forest roads) and on rotten stumps and logs (Avdoshenko, 1948; Solonewitch, 1956). In such places, high soil humidity and the least root competition are noted, and also richer mineral composition of soil. This mineral content is formed on account of wood decomposition or the flow of minerally rich precipitation along the tree stems, a layer of ground litter and better aeration of substrate, and higher soil temperature in the layer with roots. Seeds appear at these places thank to birds and animals for which bilberry fruits are the main nutrition. In such cases the age of seeded bilberry individuals varies, which testifies to the repeated drift of seeds to these places (Timoshok, 1998). Usually the bilberry shoots are found in groups, seldom singly. Moreover, younger individuals are found in larger groups (Avdoshenko, 1948).

The most detailed description of bilberry morphogenesis from seed germination to the formation of clones was given in the works of Serebryakov and co-authors (Serebryakov and Chernyshova, 1955; Serebryakov, 1962). Bilberry seed germination is epigeal (Avdoshenko, 1949). During the first years the shoots grow slowly, at five years they reach a height of 5-8 cm. By year 8-10 the bilberry shoot forms an evergreen dwarf shrub, so-called primary (maternal) shrub (Fig. 65). Subsequent growth of the shrub is accompanied by the formation of assimilating shoots as well as of long

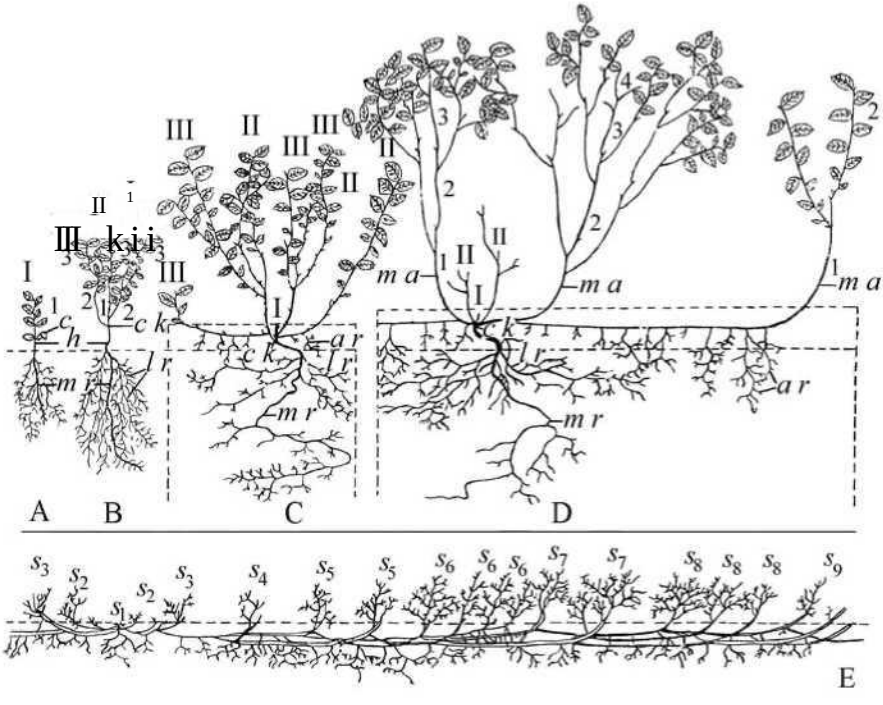

Fig. 65: Formation of partial shrub system in *Vacdnium myrtillus* (after Serebryakov and Chernyshova, 1955).

A-C—seedlings: A—year-old plants, B—three-year-old plants, C—7-8-year-old; D—formation of new partial shrubs after death of primary shrub, E—system of partial shrubs (up to nine orders); I—main axis, II and **III**—lateral axes, 1, 2, 3—annual increase, *a r*—adventive root, c—cotyledon, *c k*—cotyledonary knot, *h*—hypocotyl, *I r*—lateral root, *m a*—main axis of partial shrub, *m r*—main root, s_p s_2 ...—partial shrubs of the first, second and subsequent orders.

underground repent shoots. These shoots are formed from the resting buds situated at the basal part of the main axis, and also from shoots of the second order belonging to the primary shrub, which by this time are covered by forest litter or moss. At first these shoots grow horizontally, moving away from the primary shrub in different directions, and reach a length of 30-40 cm in the friable forest litter. The tops then acquire orthotropic direction, emerge from the soil surface and continue to grow as assimilating shoots. As a result of this shoot branching the partial shrub is formed. This is a part of the maternal plant and differs from the latter in its greater size. The system of partial shrub clones with maternal primary shrub in the centre gradually forms (Serebryakov and Chernyshova, 1955).

The intensive growth of underground repent shoots enables quick vegetative growth of clones in radial directions. The quickness of bilberry clone growth can be judged from, for example, parterres of bilberry in the fir-forests of Moscow region, which are 5-8 m in diameter and consist of several hundreds of partial shrubs. All

these shrubs in the young clones of bilberry are able to grow vegetatively (Zlobin, 1961; Gedyh, 1979). However, as the clones grow, this ability in older partial shrubs diminishes. It is practically impossible to determine the clone lifespan, because it is difficult to identify their borders, since clones penetrate each other and maternal shrubs die off. Clone lifespan appears to be 100 or more years (Avdoshenko, 1949; Serebryakov, 1962). When the system of the main root and then the whole maternal shrub die, the bilberry clones divide into separate parts (particles), which suggests that bilberry can be considered a vegetative mobile plant (see Particulation; Vegetative propagation). Another opinion about bilberry propagation, according to Timoshok (1998), is that *V. myrtillus* does not reproduce vegetatively. The author considers that this is determined by bilberry growing in colonies. In this case partial shrubs do not separate and exist in this colony system during their lifetime.

Thus, the reproductive strategy of bilberry includes sexual and asexual reproduction modes, seed and vegetative propagation. However, the data about the ratio of these types of propagation are contradictory (Kujala, 1926; Sinskaya and Shenkova, 1928; Avdoshenko, 1948; Solonewitch, 1956; Mazurenko, 1982; Deeva, 1988; Timoshok, 1998).

Reproductive Strategy of Viviparous Plants

It is known that every species has a peculiar reproductive system, which by its possibilities, plasticity and tolerance ensures the maintenance of the species. The modes, calendar dates or rhythm of reproduction and also quantitative and qualitative parameters of species productivity may be changed under the influence of meteorological or biotic factors within the same phytocoenosis peculiar to this species. These changes occur at the individual level as well as at population level (Levina, 1981).

Reproduction and propagation of plants, particularly viviparous plants, occur via formation of various generative and vegetative diaspores (see Diaspore). Viviparous plants have seed or vegetative propagation or their combination.

For many mangroves *(Rhizophora, Ceriops, Kandelia, Bruguiera),* **obligatory generative viviparity** is characteristic, that is, propagation with the help of seedlings. These seedlings develop from generative diaspores with sexual embryo (see Viviparity). Vegetative propagation in these species was not noted.

Some plants from the family Cucurbitaceae display the capacity for **facultative cryptoviviparity** in stress conditions (e.g., abrupt change in air humidity).

The greatest diversity of reproductive systems can be found in plants with characteristic vegetative viviparity, gemmorhizogenic or embryoidogenic.

For example, the species of *Festuca* genus from high altitudes reproduce only via gemmorhizogenic viviparity (Fernald, 1933; Scholander, 1934). However, at the southern border of the area the combination of seed and vegetative propagation is characteristic for the viviparous fescues (Turesson, 1926-1931; Wycherley, 1953; Siplivinsky, 1973). The quantity of plants and degree of modification of spikelets in *F. vivipara* vary with plant group, plant habitat and seasonal conditions (Salvesen, 1986). The plants differ also in the number of fertile flowers. Tetraploids from coastal population produce more fertile flowers than those from alpine population (Salvesen, 1986). In inflorescences of *F. rubra x vivipara* hybrid, some spikelets are regularly

transformed into air bulblets and the remaining flowers appear to be sterile (Elven, 1978,1980; Salvesen, 1986).

In the reproductive system of *Poa bulbosa, P. alpigena* and P. *sublanata* various ways of new individual formation are successfully combined: with the help of seeds, bulbils in the inflorescence and bulbs at the stem base. The quantity of value seeds in P. *alpigena* and P. *sublanata* can be compared with the quantity in seed forms, and germinating power is even higher than normal. These species, which grow in different habitats, differ in the quantity and quality of vegetative diaspores produced. *Poa alpigena* forms many small diaspores, which quickly lose germinating power and they occupy small free spaces in the mass of grass closed sinusia; they do not travel substantial distances. On the other hand, the large propagules of P. *sublanata* with a long period of viability can travel far along the shores of Ob Bay (Karskoe Sea in the Arctic) (Sarapultzev, 1998). Some forms of viviparous grasses are able to produce several fertile panicles (F. *vivipara),* usually at the very end of the vegetation period (Hunger, 1887; Schuster, 1910; Exo, 1916).

It is known that the system of seed propagation in flowering plants includes mechanisms taking part in the formation of initial cells of sexual and somatic embryos and in the formation of seed and fruits. These mechanisms can alone or in combination support the existence of a population in long generations (Levina, 1981; Kupriyanov, 1989; Batygina, 1998, 1999a,b). According to Kupriyanov (1989), the main parameters of seed propagation are the mechanisms or elements of the reproductive system, which influence the genetic structure of the species population. For the viviparous representatives of genus *Allium,* partial disturbances in meiotic course during both micro- and megasporogenesis were revealed. These disturbances determine to a large degree the sterility in these species (Ustinova, 1944). According to the authors' opinion, the reason for these anomalies is the development of little bulbs (bulbils—T.B., E.B.) in the inflorescence; their removal stimulates the formation of normal flowers. Thus, onions present all the transition forms, from inflorescences consisting of flowers only (A. *decipiens, A. aflatunense)* to inflorescences with flowers and bulblets (A. *senescens, A. oleraceum)* and inflorescences with bulblets only (A. *proliferum).* Ustinova divides viviparous onions into three groups according to their ability to form bulblets and the degree of seed sterility: (1) flower bud number in the inflorescence is equal to or slightly less than bulblet number, the seed fertility is 0.5-1.5% (A. *coeruleum, A. oleraceum);* (2) bulblets dominate in the inflorescence, the seeds are sterile (A. *carinatum, A. scorodoprasum);* (3) in the inflorescence there are only bulblets usually and very seldom flowers, the seeds are sterile (A. *proliferum).*

The variations in the ratio of seeds and vegetative diaspores (little tubers) are noted for dicotyledonous viviparous plants also, particularly for *Polygonum viviparum.* A cytological study of P. *viviparum* taken from five different points in the distribution area has shown that in Iceland it is heptaploid, in the Faroe Islands octaploid, and in Greenland, England and the Czech and Slovakia Republics nonaploid (Engell, 1973). The plants differed in spike length, size of spike part where flowers were replaced by small tubers, and morphology of leaves bearing tubers. The little tubers from five habitats differed in size and colour (see Bulblet and Bulbil). In central Norway, among P. *viviparum* plants from 12 habitats the majority had a prevailing tendency to substitution of tubercles for flowers (Law *et al.,* 1983).

The formation of seedlings at the leaf or in the leaf axil *(Cardamine, Nymphaea, Bryophyllum, Hammarbya paludosa)* (see Viviparity; Bulblet and Bulbil) is characteristic

of some viviparous plants. Depending on the environment (e.g., day length, temperature, humidity), genotype and age, viviparous plants can produce seeds, vegetative seedlings, or both types of diaspores simultaneously. On the other hand, unlike plants with characteristic floral gemmorhizogenic viviparity, the formation of vegetative seedlings at the leaves and in leaf axils is not connected with the development of inflorescence. This permits some autonomy during formation of bulbils and, consequently, greater plasticity in new plant formation.

The plants capable of **facultative gemmorhizogenic viviparity** in stress conditions (e.g., sharp increase in air humidity) can produce additional progeny *(Cymbopogon*-Dutt and Bradu, 1973; Naveen *et al.*, 1977).

The viviparous populations are heterogeneous in genotype and age because of the combination of various modes of reproduction and propagation and time of appearance of progeny.

Reproductive Strategy of Orchids in Temperate Zone

Orchids of the temperate zone representing a diverse group in systematical and biomorphological aspects have obviously penetrated these regions at different times and in various ways. Their adaptations to existence in a temperate climate are various and determine features of their reproductive systems, along with mycotrophic mode of life, common for all representatives of the family Orchidaceae.

Among the orchids of the northern temperate zone the three most numerous groups differ from one another primarily in the structure of underground or above-ground reserve organs. The representatives of the genera *Cypripedium, Cephalanthera, Epipactis, Listera* and *Neottia* belong to the **rhizomatous geophytes.** The reserve organs, tuberous roots (root-stem tuberoids, according to Dressier, 1981), are characteristic for group **tuberoid-forming geophytes.** This group includes subtribe Gymnadeniinae *(Platanthera, Coeloglossum, Gymnadenia, Dactylorhiza,* etc.) with fusiform or palmate tuberoids, distributed in more humid northern and mountain areas of a temperate zone, and subtribe Orchidinae *(Orchis, Ophrys, Himantoglossum, Serapias, Anacamptis,* etc.) with spherical or ovate tuberoids, which is the more specialized group adapted to conditions of the Mediterranean climate with dry summers and mild winters. The major part of the evolutionary history of these **primary-ground orchid groups** is connected to temperate regions, and the adaptations to a temperate climate have been imposed on the overall biology of their representatives. The third large group among the orchids of a temperate zone is represented by **secondary-ground hemicryptophytes** with reserve organs of above-ground tuberidia (settling in moss layer or in friable forest litter) or pseudobulbs (representatives of the subfamilies Epidendroideae and Vandoideae). Species of this group, growing in habitats with well-developed moss cover (bryophytes), are closely related to tropical epiphytes. The last group is the most numerous in the flora of areas with humid oceanic climate (East Asia, eastern North America) and in Europe and Siberia is represented by few species (from the genera *Calypso, Hammarbya, Liparis, Malaxis).*

Reproductive systems of non-tropical orchids differ from each other by a number of significant characters. In primitive rhizomatous geophytes (Cypripedioideae and Neottieae-Limodorinae) the features of **patient** (according to Ramensky, 1938), or

stress-tolerant (after Grime, 1979) living strategy are most clearly expressed, i.e., resistance to abiotic environmental factors, long lifespan, low rates of seed renewal (Zaugolnova *et ah,* 1992). The vegetative propagation by rhizome branching in adult plants with the subsequent isolation of particulae, i.e., normal particulation (Serebryakova and Sokolova, 1988), is a prevalent mode of self-maintenance of their populations. Seed crop in the populations, depending mainly on number and activity of pollinators, can be both stably low *(Cypripedium guttatum),* and rather high (C. *macranthon, Epipactis* spp.). The seed renewal, however, even in the latter case has low efficiency compensated by the long lifetime of clones (in C. *calceolus* the age of clones can achieve almost 200 years, see Kull, 1988) and their ability to spread significantly. The main reason for low efficiency of seed propagation is the difficult germination of seeds, caused mainly by structural peculiarities. In seeds of this plant group there is a cutinized internal layer of testa, which densely adjoins to embryo and prevents the entry of water into it (Lucke, 1981,1982a,b; van Waes and Debergh, 1986a,b). Besides, in seeds of this group the presence of abscisic acid is established, which, as is known, is an inhibitor of seed germination (van der Kinderen, 1987). Apparently, seeds of *Cypripedium* and Neottieae, in comparison with seeds of other orchids, remain viable longer in soil. The presence of compatible mycosymbiont is not a sufficient condition for seed germination in species of this group (Kulikov and Philippov, 1998). Probably, the germination is stimulated by the influence of non-symbiotic soil microflora or physical factors (change of redox potential of environment, etc.; see Weinert, 1990). As the combination of conditions favourable to germination occurs rarely, the percentage of germinating seeds is usually insignificant. The seedlings are strongly mycotrophic and develop rather slowly (e.g., in *Cypripedium* the first above-ground organs are formed usually in year three or four). The degree of mycotrophy in adult plants changes from high *(Cephalanthera rubra)* to insignificant *(Epipactis palustris).*

In tuberoid-forming geophytes from the tribe Orchideae the patient living strategy prevails. However, a number of features characteristic of explerents (ruderal strategy, after Grime, 1979) are peculiar to it, such as short lifespan, strong dynamic pregenerative fraction of populations in connection with renewal fluctuations, high seed productivity, and poorly expressed period of aging (Zaugolnova *et ah,* 1992). Vegetative propagation does not play an essential role in self-maintenance of populations of species of this group (with rare exceptions, such as *Herminium monorchis, Platanthera hologlottis),* which thus completely depend on seed renewal. In species from subtribe Gymnadeniinae, adapted to conditions of a humid climate, the seeds have no dormancy (Kulikov and Philippov, 1998) and germinate at once after hitting the soil. Only a small number of germinating seeds come into contact with compatible mycosymbiont and thus find favourable conditions for further development. However, protocorms in soil are more numerous than juveniles, which in turn are more numerous than adult plants in a population, which testifies to the death of the majority of seedlings at underground developmental stage (Möller, 1987a; Batalov, 1998). In connection with the absence of adaptations preventing premature seed germination and short seed viability (no more than one year), species from subtribe Gymnadeniinae, obviously, are incapable of forming even a short-term seed stock in soil. The significant fluctuations of the proportion of juvenile plants in populations, i.e., waves of renewal (Vakhrameeva *et ah,* 1987), are characteristic of the representatives of this group. This is probably due to the alternation of the periods favourable and unfavourable to survival of protocorms in soil.

The representatives of subtribe Orchidinae, many of which on a seasonal rhythm of development come nearer to ephemeroids, have time to flower and to disseminate prior to the beginning of a summer drought. Their seeds have dormancy (though less deep than in rhizomatous orchids) that allows them to avoid premature germination in the period of water deficiency. In the representatives of this subtribe the reproduction especially strongly depends on a degree of drying in the soil top layers during the summer; this is why the majority of formed protocorms die off and there are sharp fluctuations of renewal (Möller, 1987a-c). The rates of seedling development are probably higher than was considered earlier, and in conditions of the Mediterranean climate the duration of underground developmental stage does not exceed one year (Möller, 1987a,c). The degree of mycotrophy among the representatives of subtribe Orchideae is high in the early stages of ontogeny and in most cases kept significant during the entire life cycle of a plant. However, its fluctuations within this group are rather significant, from high mycotrophy *(Neottianthe cucullata* and *Orchis ustulata)* to practically complete autotrophy in adult condition *(Dactylorhiza incarnata).*

In populations of northern secondary-ground hemicryptophytes the seed and vegetative propagation can be submitted approximately to the same extent (e.g., in *Calypso bulbosa,* see Kulikov, 1997) or seed propagation prevails *(Malaxis monophyllos).* The seed productivity is usually high, though it can be limited to activity of phytophages (as in *Calypso bulbosa).* The seeds of Epidendroideae have no structural features limiting germination and have slightly expressed dormancy (Kulikov and Philippov, 1998). The seed viability is short (less than one year) and, therefore, species of this group cannot form seed stock in soil. The duration of the underground phase, apparently, is insignificant. The absence of attributes of seasonal periodicity of growth in C. *bulbosa* underground protocorms (Vinogradova and Filin, 1993) and also high rates of seedling development in this species under asymbiotic conditions *in vitro* - formation of primary shoot with a green leaf and pseudobulb for 9-10 months (Kulikov and Philippov, 1998) — testify to it. The ability of protocorms in tribe Malaxideae to turn green in light testifies to an opportunity for germination on a soil surface, though in the wild their seeds probably germinate in a thick layer of moss cover, under conditions of uniform humidity. The degree of mycotrophy at a protocorm stage in C. *bulbosa* is probably significant, whereas in tribe Malaxideae, as in the majority of the tropical orchids with chlorophyll-forming protocorms, obligatory mycotrophic phase of development is rather short.

For seed renewal of tuberoid-forming geophytes from tribe Orchideae, disturbed habitats creating free space for seed posterity and limiting competition from more active components of phytocoenosis are favourable or even necessary. The secondary-ground hemicryptophytes from subfamily Epidendroideae, in contrast with the tuberoid-forming geophytes, do not have such express features of explerent living strategy. They are connected usually with more stable plant communities and do not require disturbances of plant cover for successful seed renewal. Because they have little tolerance of competitors they always grow on sites that do not have close grass cover because of strong development of moss cover, with which they are closely connected during the entire life cycle.

Thus, the reproductive systems of the main groups of orchids characteristic to the temperate zone essentially differ from each other in a number of attributes (e.g., ratio of reproduction types, rates of ontogeny) and adaptations to a seasonal climate

(presence or absence of seed dormancy, seasonal periodicity of growth in seedlings) that determines their living strategy.

Problems and Perspectives of *In Vitro* Seed Propagation in Orchids of Temperate Zone (Plate XVII)

Representatives of the family Orchidaceae have long attracted attention in connection with conservation of rare and disappearing species. The asymbiotic and symbiotic cultivation *in vitro* of the immature and mature seeds (and embryos) are broadly used for the propagation of northern orchids; symbiotic growth in natural conditions is limited by different biogenic factors (the presence of the specific fungus) and abiogenic factors.

Asymbiotic cultivation of immature seeds. The seed germination percentage of northern orchids in asymbiotic culture varies significantly within the species (Arditti, 1982). Seeds isolated from immature fruits germinate better, as a rule (Burgeff, 1936; Fast, 1978,1982; Batygina and Vasilyeva, 1980,1983; Lindén, 1980; Arditti, 1982). **The stage of seed and embryo development at the moment of sowing can be the determining factor for obtaining the maximum quantity of seedlings** *in vitro*. Seeds of *Dactylorhiza baltica, D. maculata, D. flavescens* and *D. incarnata* isolated 40-50 days after flowering outset (DAF) germinated well, while seeds at earlier developmental stages (20-30 DAF) germinated very poorly (Table 29). The mature seeds from the dehisced fruits (60 DAF) of D. *baltica* and D. *flavescens* had very low germination percentage, and seeds of *D. incarnata* did not germinate at all.

In seeds of D. *baltica* at 40-45 DAF, the following processes were observed: cessation of cell division and the beginning of reserve material accumulation in the embryo, complete degeneration of the inner integument and the beginning of outer

Table 29. The seed germination percentage of *Dactylorhiza* species in asymbiotic culture depending on developmental stage at the moment of isolation (after Andronova, 1988).

Plant species	Nutritive medium*	Developmental stage of seeds (days after flowering outset)						
		20	30	35	40	45	50	60
D. baltica	BM	0		0	4		5	2
	BM+hormones	4		60	100		33	2
D. flavescens	BM		3		30		0	0
	BM+hormones		5		100		75	10
D. incarnata	BM					10	0	0
	BM+hormones					50	30	0
D. maculata	BM					-		0"
	BM+hormones					100		56"

*BM, basal medium, modified Knudson medium; BM+hormones, basal medium supplemented with kinetin 0.5 mg/1, IAA1 mg/1, and adenine, 0.5 mg/1.
**Seeds isolated from unriped fruits.

integument degeneration. This indicates the transition of the seed to maturation. With the course of seed maturation (45-60 DAF) **the inhibiting mechanism of the germination is developed; this is the reason for the diminishing of seed germinability in the asymbiotic culture.**

The capacity of the seed for asymbiotic germination *in vitro* was investigated also in other species representing the main systematic groups of northern terrestrial orchids (Andronova, 1988; Kulikov and Philippov, 1998). It was demonstrated that the optimal stage of seed development for cultivation is 90 days after pollination for *Bletilla striata,* 35-40 DAP for *Calypso bulbosa,* 45-50 DAP for *Liparis loeselii,* 30-35 DAP for *Cypripedium calceolus,* 35-50 DAP for C. *macranthon,* 20-25 DAP for *Orchis militaris,* and up to 20 DAP for *Lister a ovata.* These data testify that the developmental stage of embryo and surrounding seed structures that is optimal for germination is species-specific.

In the course of the investigation, a correlation was found between seed germinability and the state of the seed coat cells. For example, in C. *calceolus* 35-40 DAP the cells lose their contents, the seed coat becomes dark brown, and the seed's ability to germinate *in vitro* is entirely lost. In C. *macranthon* some cells of the seed coat remain alive till 50-55 DAP. The seeds of this species conserve partial ability to germinate *in vitro* till the late stages of maturation.

Asymbiotic cultivation *in vitro* of immature seeds at certain species-specific stages proved to be the effective way to obtain seedlings for the majority of species studied, especially those with the most difficult seed germination (the species of the genera *Cypripedium* and *Orchis, Epipactis palustris, Listera ovata, Dactylorhiza incarnata)* (Kulikov, 1991,1995; Kulikov and Philippov, 1991,1998; Pauw and Remphrey, 1992; Wagner and Hansel, 1994; Philippov, 1997). However, for some species — *Cephalanthera longifolia, Epipactis helleborine, E. atrorubens, Neottia nidus-avis, Hammarbya paludosa, Epipogium aphyllum,* and *Corallorhiza trifida* - the method of asymbiotic cultivation of the immature seeds *in vitro* has not given positive results. This may be due to insufficient knowledge of reproductive biology, type of seed dormancy and nutritive needs of the developing seedlings in these species.

Asymbiotic cultivation of mature seeds. As was already mentioned, **one of the main problems of the propagation of northern orchids is the fact that with maturation the seeds lose the ability to germinate in the asymbiotic culture *in vitro*.** Two inhibiting mechanisms of the mature orchid seed germination are possible: (1) accumulation of the germination inhibitors, for example, of abscisic acid (van Waes and Debergh, 1986a,b; van der Kinderen, 1987; Semenova *et ah,* 1992) and (2) impenetrability of the seed coats (Burgeff, 1936; Veyret, 1974; Lucke, 1981,1982a,b).

To remove the physiological inhibiting mechanism of germination, seeds can be soaked for a long time in water or sterile nutritive solution (Kano, 1968; Fast, 1982) or be subjected to long stratification at low positive temperatures after being sown in the medium (Borriss and Albrecht, 1969; Ballard, 1987; Semenova *et al.,* 1992; Kulikov, 1995; Philippov, 1997). These methods can help to stimulate germination in *Epipactis palustris* and *Cypripedium reginae,* but for the other species they gave no positive results (Lindén, 1980; Lucke, 1981; van Waes and Debergh, 1986a,b; Riether, 1990). That is why the supposition is legitimate that the germination-inhibiting mechanism in orchids is not only determined by the presence of germination inhibitors, but can be of more complicated nature.

One effective way to stimulate germination of resting seeds of orchids is considered to be the long treatment of seeds with solution of calcium or natrium hypochloride, which simultaneously sterilizes the seeds and increases the penetrability of the seed coat (Lindén, 1980; Lucke, 1982b; van Waes and Debergh, 1986a,b; Riether, 1990).

However, germination of *Cypripedium calceolus* and *C. macranthon* appeared possible only with a combination of long pretreatment of mature seeds with hypochloride (up to complete bleaching of the seed coat) and subsequent cold stratification of the seeds sown in the nutritive medium. This affirms the proposal that such seeds possess combined dormancy, i.e., physical dormancy connected with water impermeability of the coats and physiological dormancy connected with physiological germination-inhibiting mechanism.

Other promising methods leading to increase in mature seed germination are mechanical isolation of the embryos from the seeds and treatment of the seeds with hydrolytic enzymes, which destroy the seed coats, before sowing (Andronova, 1986, 1988; Lindén, 1992).

Pretreatment of mature seeds with cytase has stimulated germination twice in D. *baltica* and promoted the appearance of solitary protocorms in D. *incarnata* (Table 30). Soaking of mature seeds of *D. incarnata* for 4-5 weeks also promoted germination (Kulikov, 1995; Philippov, 1997). These data affirm indirectly the presence of the particular envelope around the embryo in the mature *D. incarnata* seed (Lucke, 1981, 1982b). It is conserved during mechanical isolation of the embryo and becomes more permeable only after enzyme action (Andronova, 1986,1988). This envelope appears to prevent water entry into the embryo cells; mature seeds and embryos isolated surgically fail to germinate.

Results of studies of the asymbiotic *in vitro* germination of mature seeds in more than 30 species of orchids from the flora of Russia (Kulikov and Philippov, 1998) have shown that the ability to germinate differs significantly in the different systematic groups. For the primitive rhizome orchids, subfamily Cypripedioideae and tribe

Table 30. Germination of mature seeds and embryos of *Dactylorhiza baltica* and D. *incarnata* in asymbiotic culture* (after Andronova, 1988).

Plant species (explant)	No. of **explants** sown	No. of **explants germinated**	**Germination** (%)
D. baltica			
embryos	20	1	5
seeds	120	13	10
seeds treated with cytase	210	44	21
D. *incarnata*			
embryos	25	0	0
seeds	300	1	0
seeds treated with cytase	260	13	5

*Modified Knudson medium without hormones. Seeds were stored 2 months at 8°C till sowing.

Neottieae, and also subtribe Orchidinae *(Orchis, Ophrys)* — the group originally adapted to Mediterranean summer drought conditions — impeded germination is characteristic. Mature seeds of the representatives of the subtribe Gymnadeniinae (with the exception of *Dactylorhiza incarnata)*, which are distributed preferentially in the wetter regions of the Northern hemisphere, germinate more or less easily. Mature seeds of *Goodyera repens*, indeciduous representative of the group with mainly tropical plants, also germinate easily; the seeds of secondary-terraneous representatives of the subfamily Epidendroideae *(Calypso bulbosa, Liparis loeselii* and others) appear to be able to germinate, but the germination is weaker and slower than in immature seeds. Mature and immature seeds of holomycotrophic species without chlorophyll *(Epipogium aphyllum, Corallorhiza trifida, Neottia nidus-avis)* failed to germinate on the nutritive media used (Kulikov, 1995).

The influence of exogenic growth regulators on seed germination in asymbiotic culture *in vitro*. The influence of growth regulators on *in vitro* germination of seeds of different orchid groups differs significantly. For *Dactylorhiza maculata* and *D. fuchsii* with seeds that do not have deep dormancy, the presence of growth regulators in the medium does not increase the percentage of mature germinating seeds. Higher concentration of growth regulators (kinetin, 4 mg/1) caused noticeable decrease in generation (from two to five times) (Figs. 66 and 67). At the same time, the growth regulators contribute to significant acceleration of seedling development. On the contrary, *Cypripedium calceolus* and C. *macranthon* seeds cannot germinate in the medium without growth regulators. The addition of auxin or kinetin to the nutritive medium at a concentration of 0.5-2 mg/1 stimulated seed germination substantially (20-76%) (Figs. 68 and 69). Kinetin turned out to be more effective than NAA. However, the significant majority of the protocorms formed stopped growing at an early stage, and to obtain the greatest output of seedlings the simultaneous presence of auxin and cytokinin in the medium was necessary.

Absence of phytohormones in the nutritive medium slows seedling development in the majority of the studied species of boreal orchids. Application of exogenic auxins and cytokinins makes the rate of growth of asymbiotic seedlings comparable to that observed in the symbiotic culture (Harvais and Hadley, 1967; Hadley and Harvais, 1968; Borriss and Voigt, 1986). It was shown for four species of boreal orchids that plants obtained in asymbiotic culture of seeds undergo the first ontogenetic stages more rapidly than in nature and may achieve the generative state 5-6 years after seed germination (Zakharova and Batygina, 1996; Batygina *et al.*, 2003).

Symbiotic cultivation of seeds *in vitro*. The first investigators of post-seminal development in orchid considered that infection with mycorrhizal fungus was necessary for seed germination in natural conditions (Bernard, 1909; Burgeff, 1936). Other authors were of the same opinion (Warcup, 1973; Clements and Ellyard, 1979; Filipello Marchisio *et al.*, 1985; Clements, 1988). Symbiotic fungi are regarded as deliverers of the exogenous phytohormones necessary for seedling development (Hadley, 1970; Stoutamire, 1974). However, **there are serious grounds for considering the two processes—seed germination and establishment of symbiotic relations—to be independent of one another.** It is known that in some orchids the initial germination processes—water uptake, increase in embryo size and use of stored nutritive substances (proteins and lipids)—can occur without fungal contamination in nutritive media without sugars or simply in distilled water (Eiberg, 1969; Stoutamire, 1974; Fast, 1978,1982; Hadley, 1982; Smreciu and Currah, 1989).

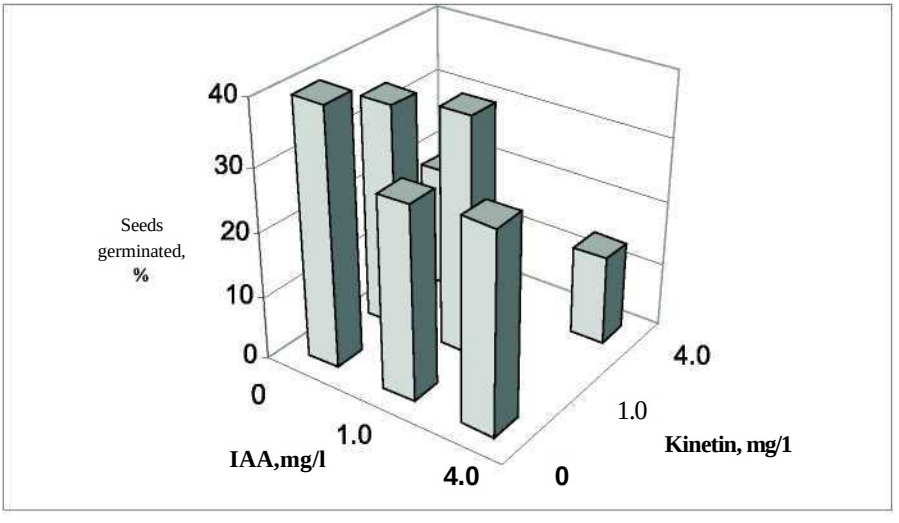

Fig. 66: *Dactylorhiza maculata* seed germination in asymbiotic culture *in vitro* in the modified nutritive medium of Harvais with different contents of auxin and cytokinin (by Philippov, 1997).

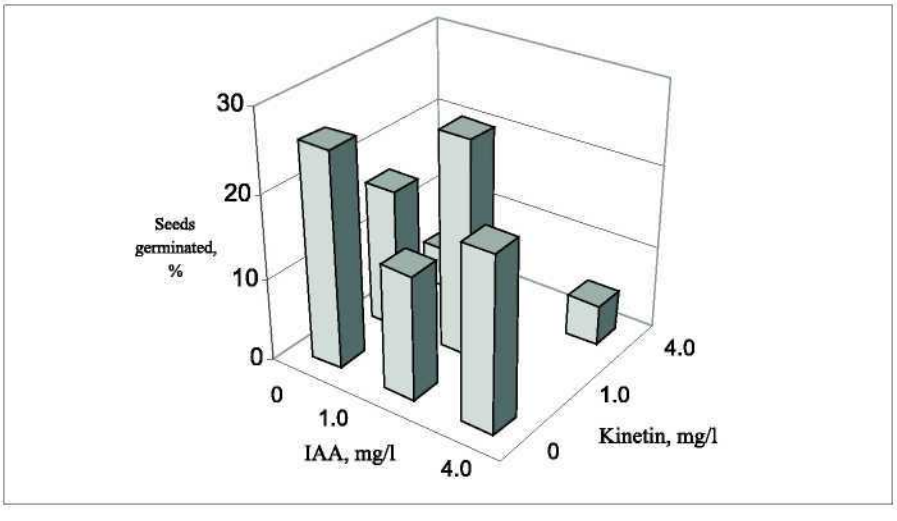

Fig. 67: *Dactylorhizafuchsii* seed germination in asymbiotic culture *in vitro* in the modified nutritive medium of Harvais with different contents of auxin and cytokinin (by Filippov, 1997).

However, in this case the protocorm stops growing at the early stage of development; growth is renewed after the compatible mycosymbiont penetrates the protocorm cells. Besides, in orchid species with the inner layer of the seed coat made of cutin,

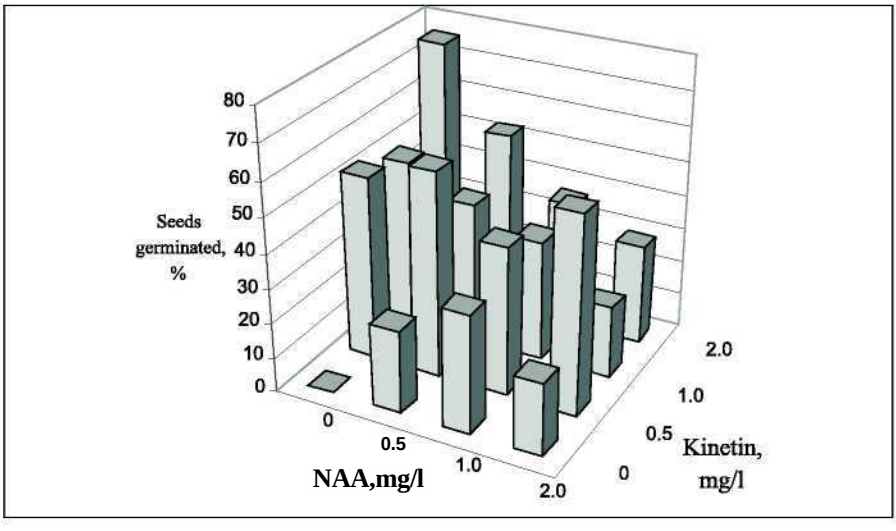

Fig. 68: *Cypripedium calceolus* seed germination in asymbiotic culture *in vitro* in the modified nutritive medium of Harvais with different contents of auxin and cytokinin (by Kulikov, 1995).

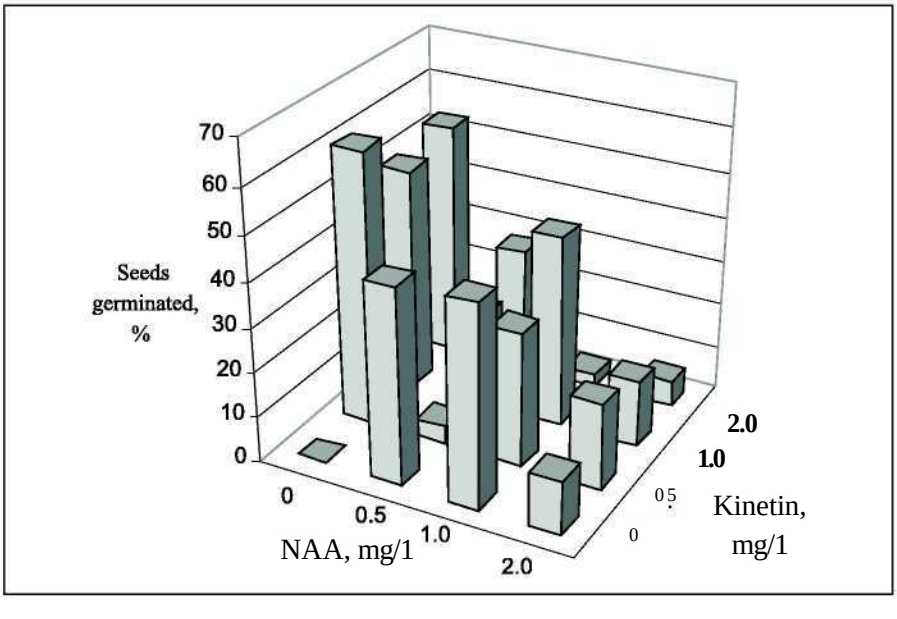

Fig. 69: *Cypripedium macranthon* seed germination in asymbiotic culture *in vitro* in the modified nutritive medium of Harvais with different contents of auxin and cytokinin (by Kulikov, 1995).

seed germination cannot be stimulated by symbiotic fungi, because the fungi cannot split cutin (Lucke, 1981). On the other hand, non-symbiotic soil microflora can stimulate the germination of resting seeds on account of secretion of enzymes and phytohormones or change in the physical-chemical parameters of the medium (in particular, redox potential) (Weinert, 1990).

It is easy enough to obtain symbiotic germination *in vitro* of mature seeds of *Dactylorhiza metadata, D. fuchsii, Neottianthe cucullata, Platanthera bifolia, Gymnadenia conopsea, Coeloglossum viride, Goodyera repens* and *Malaxis monophyllos* (Kulikov and Philippov, 2003). Among the species with mature seeds that do not germinate in the asymbiotic culture, symbiotic germination was obtained only for D. *incarnata* and in isolated instances, for *Epipactis palustris.* We did not manage to obtain seed germination for *Cypripedium* and tribe *Neottieae* with their own endophytes (though some of them stimulated the growth of protocorms in *Cypripedium* grown beforehand in asymbiotic culture), or with active mycosymbionts of species with easy germination. In these cases some fungi obtained from the seedlings of species with difficult germination of mature seeds (C. *calceolus, C. macranthon)* were able to stimulate germination and seedling growth in species with easy germination *(Neottianthe cucullata).*

The degree of specificity of mycorrhizal symbiosis in orchids alters over a broad range (Curtis, 1939; Harley, 1959; Harvais and Hadley, 1967; Dijk, 1988). Though a number of examples with highly specific symbiosis are found (Warcup, 1973; Ramsay *et ah,* 1986), as a whole the specificity can be observed usually not at the species level, but at the level of larger systematic groups (Clements *et ah,* 1986). Among the species studied, a rather high degree of symbiosis specificity was found in *Goodyera repens, Platanthera bifolia,* and *Coeloglossum viride.* The seed germination and seedling development of these plants were stimulated mainly by their own endophytes or by fungi with the same typical appearance, which were extracted from the seedlings of other species (Kulikov and Philippov, 2003). *Neottianthe cucullata* and *Dactylorhiza incarnata* in natural conditions, evidently, have highly specific symbiosis also, but the seed germination *in vitro* and seedling growth can be stimulated also by fungi extracted from the other orchids and in outward appearance absolutely unlike their natural symbionts. Finally, *Dactylorhiza maculata* has the smallest symbiotic specificity among species studied: abundant seed germination and successful seedling development in this species were obtained with fungi of rather diverse appearance, which were extracted from the 10 orchid species. The contents of the natural symbionts of D. *maculata* were also varied in different habitats.

Seed germination efficiency and the rate of seedling growth in symbiotic culture vary greatly in different species. The use of most active fungal isolates can increase the rate of seedling development several times in comparison with asymbiotic culture. For example, the symbiotic seedlings of *Neottianthe cucullata* and *Gymnadenia odoratissima* after two months of cultivation had already unfolded green leaves and roots and begun to form renewal shoots, where the tuberoids were soon formed. The seedlings of those species in asymbiotic culture developed much more slowly (6-12 months).

Heterospermy. The percentage of germination in orchid seeds seems to depend not only on the conditions of cultivation, but also on the share of viable seeds in the samples. In some species seeds without embryo can be observed **(Plate XVII).** The number of such seeds gathered from plants of *Dactylorhiza maculata* s.l. introduced in

botanical gardens was 88.4% (Andronova, 2003c) and from D. *incarnata* it was 60% (Vinogradova *et al,* 2003). In seed samples from one natural population the share of seeds without embryo out of the total amount of seeds in fruit altered in D. *fuchsii* from 6.5 to 24% (Andronova *et al.*, 2002) and in *Corallorhiza trifida* from 0 to 21.4% (Vinogradova and Pegova, 2002). The share of such seeds in samples of D. *incarnata* gathered in the different populations varied and was 17% in Karelia, 35% in Sverdlovsky region, and 42% in the Mordovian republic (Vinogradova *et al.,* 2003). If the share of seeds without embryo is very high in the samples, then the percentage of seed germination is significantly decreased and does not reflect the true germination picture. Seed germination in *Dactylorhiza maculata* s.l. *in situ* was 6% of the quantity of seeds of normal size and 39% of seeds with embryo (Andronova, 2003b).

Seedling morphogenesis *in vitro* **and in nature.** The morphogenesis of seedlings of boreal species of orchids has been studied since the mid-19th century (Irmisch, 1853). However, the peculiarities of their development from seed germination to the formation of juvenile plants in natural habitats are insufficiently studied (Møller, 1987a-c). Asymbiotic cultivation of seedlings *in vitro* makes it easier to study the early ontogenetic stages of orchids from temperate zone (Veyret, 1974; Batygina and Vasilyeva, 1981, 1983). However, the conformity of morphogenetic processes occurring in asymbiotic culture to those occurring in natural conditions is still under discussion.

At present, much factual material has been accumulated about protocorm development of boreal orchids *in vitro* (see Embryogenesis in Orchidaceae Vol. 2; Protocorm). The results point to the similarity of protocorm morphology *in situ* and *in vitro* at the early developmental stages (Batygina and Andronova, 2000). However, the conditions of growth in asymbiotic culture can cause the appearance of post-seminal developmental forms that differ from the forms observed in nature (Möller, 1987a; Kulikov, 1995; Philippov, 1997; Kulikov and Philippov, 2003).

In asymbiotic seedlings of *Dactylorhiza* and *Cypripedium,* the formation of the secondary protocorm-like structures, several points of growth at one protocorm and the callus can be observed. That is not characteristic of seedlings developed in natural habitats. In later stages of development, asymbiotic seedlings of *Cypripedium* and *Lister a ovata* differ from those observed in nature by a substantial increase in the number and size of adventive roots developing at the primary shoot till this shoot turns to the formation of the above-ground assimilating leaves, and also by the tendency of the primary shoots to branch (Kulikov and Philippov, 2003).

In the asymbiotic seedlings of *Calypso bulbosa* the shoot with a single green leaf and tuberidium is formed quickly, and after this the basal part of the protocorm begins to spread. This expansion leads to the formation of a coral-like structure (Kulikov and Philippov, 1991). In natural conditions a coral-like spreading (branching, according to Vinogradova and Filin, 1993) of protocorm precedes the development of the above-ground shoot.

Seedling development of the representatives of the tribe *Orchideae in vitro* is similar to that in nature (Batygina and Andronova, 2000). Sometimes, the protocorms are found to grow very long; this was not observed in natural conditions (Kulikov and Philippov, 2003). In later stages of development, such seedlings differ by an increase in number and size of adventive roots at the primary shoot, a delay in the unrolling of the assimilating leaves, and breaking of formation or complete lack of tuberoids. Instead of this, the adventive roots developed at the primary shoot thicken and

acquire the appearance of storage organs. The seedlings growing asymbiotically show more continuous monopodial growth of the primary shoot and the delay or complete absence of the transition to sympodial growth.

According to Vinogradova's data (1999), the apical bud of the two-year seedlings at the stage of one green leaf in D. *maculata* growing in nature becomes the renewal bud. Evidently, the primary shoot at least for 2-3 years can develop monopodially, without transition to sympodial growth (Vinogradova, 1999; Vinogradova and Andronova, 2002). Monopodial shoot growth, which is characteristic of seedlings cultured *in vitro,* is preserved for several years in young plants of *Dactylorhiza* introduced into nature (Andronova, 2003a,b). This testifies that monopodial growth of the shoot is characteristic of the early stage of development of those plants and probably is not connected with the cultivation conditions.

For the majority of the studied species of the northern orchids (with the exception of *Spiranthes amoena* and *Goodyera repens*—subfamily Spiranthoideae), the distinct periodicity of growth *in vitro* is characteristic. However, the developmental rhythm in seedlings in conditions *in vitro* was not found to coincide with that observed in natural habitats. The seedlings of *Cypripedium* and some representatives of tribe *Orchideae* developing *in vitro,* after formation of the bud with the primordia of above-ground assimilating leaves, remains at rest. After 3-4 months at low temperature (2-5°C), the seedlings unfold green leaves and form renewal buds at the primary shoots. From these buds after the second period of rest the shoots of the next generation are developed and, thus, the transition to the sympodial growth occurs. Sometimes the shoot growth can be stimulated without the cold period by passage to the fresh medium, but such seedlings do not pass to normal alternation of growth and rest periods. In a number of species *(Calypso bulbosa, Liparis loeselii, Malaxis monophyllos),* the shoots do not need low temperatures for passing the dormancy period and conserve normal growth periodicity at constant room temperature. Thus, for representatives of the primary terrestrial orchid groups, whose evolutionary history is most closely connected with temperate zone, the need for low temperatures during dormancy is characteristic, while representatives of the tropical groups conserve the seasonal growth rhythm at high temperatures or have uninterrupted growth.

Action of Herbicides and Other Factors on Embryogenesis of *Striga hermonthica* (Scrophulariaceae)

Striga species, especially *S. hermonthica* and *S. aspera,* have a devastating effect on food crops in the semi-arid tropics, with great economical impact. Innumerable tiny dark seeds are spread on the soil in the fields: a single dehiscing fruit produces 400 to 1000 seeds; each spike produces 50 to 70 fruits, and there are several (10-100 or more) *Striga* for one host plant.

Owing to the ravages caused by *Striga* species on food crops, we directed our effort in the area of embryology to obtain more information to contribute to the resolution of this important agronomical problem.

The evidence, although consistent, was rudimentary and our embryological position may stimulate further research in this neglected area (Pare´*et al.*, 1991; Paré, 1992). Our hypothesis is that embryological mechanisms can be defined to give a basis for controlling *Striga* by disrupting the process of reproduction (Paré *et al*, 1995).

Using this approach we have developed an effective assay to refine the mode of treatment with herbicide and also to test the utility of biological control with the use of insects.

Embryo development is of Qnagrad-type. In the cylindrical zygote the formation of two poles results in differentiation causing symmetry, which is essential for subsequent division and proembryo formation. The first wall in the zygote is horizontal; this brings about the formation of two superposed cells: a long and filamentous basal cell *(cb)* and a very small apical cell *(ca)* with a high cytoplasmic density. As a result of the vertical division of *ca* in two juxtaposed cells and the transversal compartmentalization of *cb* in two superposed cells *(m)* and *(ci)*, a T-tetrad is built up. Furthermore, arising from the division of the upper elements of the tetrad, four quadrants *(q)* are arranged about an axis in a horizontal plane. Their equatorial compartmentalization results in octants with two superposed fundamental tiers each of four cells (/, /'). In the tiers / and /', protoderm (dermatogen) is formed. Tangential divisions of inner cells allow the edification of the plerome and periblem. The intermediate cell of the tetrad *(m)* divides into two superposed elements; the upper element behaves in the same way as the hypophysial cell while the adjacent cells contribute to the formation of the filamentous suspensor. The hypophysial initial divides, giving rise to initials of the root cortex and the root cap. The significant role of the suspensor, particularly at the early stages, and its capacity for progressive change during embryogeny play an important part in the formation of the embryo proper and at a later stage in that of the young plantlet.

The cellular endosperm develops before the zygote divides. Five to six tiers of small endosperm cells surround the suspensor; the external cell, the nearest from the exit point of the micropyle, ends in a vesicle of haustorial character. The endosperm cells of this area become progressively larger in transition with the endosperm cells surrounding the embryo.

Action of herbicides. Some plants are totally destroyed by the action of herbicide; generally only some part of the inflorescence is sensitive to the action of the herbicide, especially the meristematic apical part.

The first-formed fruits escape destruction. The seeds are embryologically normal and able to germinate (Ouedrago, 1995).

Our studies have demonstrated that the early differentiation of the embryo and the stability of the structure of endosperm and seed offer possibilities of adjustment of structures and functioning, which reduce the success of treatment. The herbicides were used at different concentrations, in one or several treatments (Paré, 1994).

When the herbicide has a direct action on the seed, we can observe the necrosis of the haustorial vesicles. The membranes of the cells, which make up the micropylar area, are destroyed. We can also observe diverticuli from the haustorium worming their way into the seed coat in the micropylar area.

Striga hermonthica seems to be sensitive to the treatment only during a short period. Before fertilization and in the early stages of embryo development, we suggest a precocious treatment; to be sure to treat the vegetative plant, before the appearance of flower buds, it is better to treat two or three times to kill the parasite, taking into account the different stages of development in the fields. Use of less herbicide is better for the environment.

Impact of insect. Until now, the various methods used against *Striga* have been inefficient in the African countries. The possibility of using an insect, *Smicronyx* (Curculionideae), as a means of control in the biological fight against *S. hermonthica*, by using its ability to induce galls in the fruits of the *Striga,* appeals to researchers. The *Smicronyx - Striga* biology has been fully investigated from an en-tomological point of view (Traore *et ah,* 1991) but still there are many questions concerning the action of larvae on the mechanism of seed production. This research consists of a synthesis of recent data concerning the synchronism between the life cycle of *Striga hermonthica* and that of *Smicronyx.* It thus reveals the impact that the galls induced by the larvae have on the production of *Striga* seeds.

From the egg of *Smicronyx,* deposited in the deep epiderm of the young ovary at the moment of anthesis, the larva develops. In galls and seeds, the embryos develop normally. But the larva grows concurrently and progressively migrates inside the ovary, between the seeds. These seeds and most of the ovary tissues are destroyed, eaten by the larva. Ultimately the larva fills the gall completely and all the seeds are destroyed. There is a kind of synchronism between the development of *Smicronyx* and the fruit of *Striga.*

In research that has been undertaken until now in *Striga* biocontrol, the results are promising. It may be practical to use *Smicronyx* in a biological control agent against *Striga hermonthica* and its seed production and combine it with another method of combat, which would, in a short space of time, allow an increase in the yield of the parasite-infected crop.

Effects of Environmental Pollution on Plant Reproduction

The reactions of the reproductive structures and processes to various kinds of pollution are still not sufficiently studied.

Plant reproduction can be presented as a simplified scheme comprising flower, seed, seedling, juvenile plant and adult plant. Reproductive success is determined by a number of **internal** (biological) factors, which are expressed at the different levels of bioorganization, and **external** (ecological) factors. External factors such as the **type of pollution** (acid, alkaline, mixed), the **concentration and** form of pollutants (gaseous, liquid, solid; available or not available to plants), and the **duration of influence** play a critical role in regulation of the reproductive process.

It is known that the flower with all its elements is the organ most vulnerable to unfavourable environmental factors. Atmospheric pollution (by SO_2, NO_2, HFO_3, etc.) and acid rain influence both the development of the flower itself (size, colour, form, number of flowers) and the separate elements of the flower. For example, air pollution influences the size, form and chemical contents of pollen, the quantity and form of apertures, the sculpture of the pollen grain, pollen germination and pollen tube growth. It should be noted that *in vitro* a more substantial effect was observed than *in vivo* (Wolters and Martens, 1987; Bessonova *et al.,* 1997; Dzuba, 1997).

Comparison of sensitivity of pollen from different woody plants to acidification has shown that pollen of deciduous trees (e.g., *Acer saccharum* and *Betula allghaniensis)* is more sensitive to pH than pollen of conifers (Cox, 1988).

It was proved experimentally that the relative success of pollination (percentage of pollen germination and pollen tube growth) in the presence of heavy metals

decreases (Searcy and Mulcahy, 1985a,b; Cox, 1988). Correlation was found between meiotic aberration, pollen sterility, change in pollen grain size and accumulation of heavy metals in flower buds. This suggests that the pollen of a number of plants (e.g., *Armeniaca vulgaris, Betula pendula, Inpatiens balsamina, Lathyrus odoratus, Tanacetum vulgare)* can be used as bioindicators of heavy metal pollution of the environment (Bessonova, 1994; Veselova *et al*, 1996; Bessonova *et al*, 1997). Natural deviations in the development and structure of anther and pollen grain may add to the disturbances caused by the environment.

The scrappy data available on the influence of environmental pollution on the formation and maturation of fruits and seeds do not completely reveal its impact on potential and real seed productivity. One example can be found in data on the developmental disturbances of the seeds in parasitic plant *Striga hermonthica* under the influence of herbicide treatment (see Action of Herbicides and Other Factors on Embryogenesis of *Striga hermonthica* (Scrophulariaceae)). The progamic phase of fertilization and early embryogenesis appeared to be most sensitive to the treatment. Wolters and Martens (1987) reviewed data on the decrease of the number, weight and size of seeds and fruits under the influence of gaseous pollutants and acid rain. Tkachenko and Korobova (1995) noted some diminishing of these parameters in urban conditions.

At the same time, the analysis of seed mass and productivity in 16 species of herbaceous plants from meadows, edges of forests and glades did not show substantial changes of these parameters 3 years after the Chernobyl atomic station accident (Popova *et al.,* 1992). In cases of pollution by metallurgical complexes, the variation of such parameters as seed number in one berry and thousand-seed weight in representatives of *Vaccinium (V. myrtillus, V. vitis-idaea, V. uliginosum)* and *Empetrum hermaphroditum* is determined by intrapopulation variability and is not connected with the environmental pollution level (Lyanguzova and Maznaya, 1996; Maznaya and Lyanguzova, 1997; Lyanguzova *et al.*, 1999). Further investigations of seed productivity of plants are necessary to study the exposure of sensitive and tolerant species to various types of environmental pollution.

Seed propagation of plants is impossible without successful seed germination. The direct influence of environmental pollution on this process cannot always be seen. For example, the laboratory germination of seeds of plants near metallurgical works differed according to plant taxonomic position.

The seeds of *Vaccinium myrtillus, V. vitis-idaea, V. uliginosum, Arctostaphylos uva-ursi,* and *Chamaenerion angustifolium* had high germination power, which did not differ from the control. The germinating power of *Empetrum hermaphroditum* and *Solidago laponica* was significantly lower than the control, and the seeds of *Eriophorum polystachion* did not germinate at all (Lyanguzova and Maznaya, 1996; Maznaya and Lyanguzova, 1997; Lyanguzova *et al.*, 1999).

Similar data were obtained for germinating power of seeds of ruderal and trivial plant species growing in an urban environment. The laboratory germinating power of seeds of *Anthemis tinctoria, Capsella bursa-pastoris, Arctium tomentosum, Chamomilla suaveolens, Leucanthemum vulgare, Melilotus albus, M. officinalis, Polygonum aviculare,* and *Veronica nemorosa,* which were gathered on the borders of St. Petersburg, was lower than that of seeds from natural populations. The germinating power of seeds of *Plantago major* and *Rumex confertus* from urban and natural habitats did not differ. And a sample of *Tripleurospermum inodorum* gathered 15-20 m from a petrol station

showed the greatest germinating power among all the investigated samples of this species (Tkachenko and Korobova, 1995). The germination of seeds of *Acacia senegel*, *Haloxylon recurvum* and *Prosopis juliflora* was stimulated in polluted water and in contact with the extracts of polluted soils, while laboratory germinating power of the seeds of *Suaeda monoica* sharply decreased in such conditions (Iqbal and Qadir, 1973). It was noted that species with epigeal germination have greater sensitivity as a whole to environmental pollution than do species with hypogeal germination (Smith, 1981).

The distinctions in the reaction of different reproductive structures to environmental pollution can be connected not only with plant species peculiarities, but also with the formation of stable populations.

The formation of metal-tolerant populations in conditions of natural dressing with heavy metals was found for *Agrostis tennis, Salvia stepposa* and others (Gregory and Bradshaw, 1965; Karataglis, 1980). It has been shown in laboratory conditions that the progeny of *Bromopsis inermis* populations growing in compounds of metallurgical and coke-chemical works was more tolerant to the increased content of sulphur dioxide in the atmosphere and copper and zinc in the soil (Korshikov, 1996). Study of the natural vegetation on the ash slag-heaps near thermal power stations in the Urals has shown that cenopopulations of the pioneer species from Chenopodiaceae *(Chenopodium album, Atriplex nitens)* are characterized by significant diversity of individuals in mode of living. This appears to be the consequence of the polymorphism of seeds formed in these conditions (Seraya, 1979).

The plants have several protective systems that prevent toxic substances from entering them: these form barriers between soil and root, root and leaf, and plant and reproductive organs. The content of heavy metals in the seeds of both cultural and wild species is significantly lower than in the other plant organs. Therefore, one possible reason for plant generative sphere stability under the influence of heavy metals may be the limitation of pollutants entering the reproductive organs, specifically in seeds.

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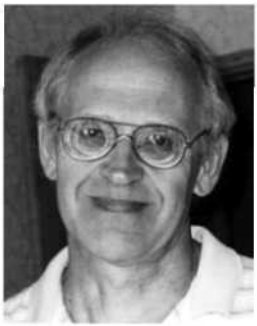

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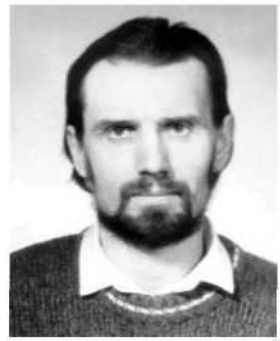

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