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ECOLOGY OF FOREST INSECTS

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To my Professor, doctor honoris causa of the
Agricultural University of Warsaw, MARIAN NUNBERG,
on the 60th anniversary of His scientific work

The Author

Introduction

Few branches of the biological sciences have developed to such an extent as has ecology in the recent decades. The successful development of this science is directly related to need to create a sound scientific basis by which we can control our diminishing natural resources and integrate this with the control of biological systems of the component species.

Studies on the bioenergetics of ecosystems, as well as on the homeostatic mechanisms functioning at the populations and biocenoses levels are of great importance in this respect. The results of these studies are very significant in forestry management which deals with multiannual tree communities – forest stands. It is particularly important in this respect for economic planning, in view of the necessity for the possible prolonged maintenance of forest biocenoses as stable systems. Neither in the present nor in the immediate future can be protection of forest ecosystems consisting of natural plant and animal communities be achieved by the cultivation of resistant forms or the intensification of chemical intervention.

Historical experience indicates that, besides the main factors determining the turnover of matter and energy flow in forest ecosystems, the mechanisms regulating the size of populations of various insect species are the most decisive element of stability of exploited forest associations securing also a favourable course of timber production, lasting forest exploitation and permanence of the forest as a component of the natural landscape. This is due to the fact that communities of forest insects, formed in the course of many centuries within the process of development of forest formations, are particularly susceptible to external stimuli and readily react to changing environmental conditions in the form of changes in their numbers. Under definite conditions many phytophagous species, in dissipating their enormous reproductive potential, may rapidly reach such enormous numbers that their nutrient requirements exceed the efficiency of the given phytocenosis. This leads to a change in the rate and direction of the circulation of matter and energy and even to a collapse of the entire ecosystem.

These circumstances seem to justify the need for a detailed understanding of the ecology of forest insects which should supply certain data for correct forest management, particularly in the field of forest protection and shaping of the environment.

The ecology of forest insects as a scientific branch connected with forest ecology and entomology includes:

1) studies on the dependences of individual insect species on various factors of the forest environment, which frequently change under the influence of management practices, as well as the elucidation of the causes and regularities of occurrence of definite insects in the forest due to these dependences;

2) studies of the influence of the forest environment on the changes in the abundance of individual species and their contribution to the turnover of matter and energy flow in forest ecosystems;

3) studies on the conditions and regularities of the structure of multispecific communities of organisms, particularly insects in various forest types under different geographical conditions, and upon the application of various forest management methods as well as the recognition of the homeostatic mechanism of these communities.

The influence on communities and functions of forest insects of anthropogenic activities not connected with forest management, as for example industrial pollution or agricultural utilization of forest soils, etc., is an important aspect of the study of the ecology of forest insects.

The aim of these studies is to create an ecological basis for the planning and realization of protective methods as well as biological recultivation of areas requiring afforestation. A study of ecology of forest insects should establish the rules governing insect numbers and by forming the forest environment should raise the resistance of forest stands. Such a study should also indicate the natural and, in particular, the entomocenotic consequences of forest management as well as the influence of other anthropogenic factors.

Contents

1 Species and populations of insects and their basic associations with the forest environment

So far, about one million species of insects have been described and this number is constantly increasing as a result of recent intensified research in the tropical regions. In Poland alone, the number of known species amounts to about 27 000. The specific differentiation of the forest entomofauna is directly correlated with the environmental variability. The greater the number of ecological niches available, the greater the number of species which may occur in a given biotope. In a single habitat type in the Biała Forest, in the litter of a rather poor pine forest, there are 120 species of staphylinid beetles alone. These account for about 10% of all the species of *Staphylinidae* recorded in Poland (Szujecki, 1966b). Just under 400 species of *Chalcidoidea* have been recorded in Tilio-Carpinetum typicum and stachyetosum in the Białowieża National Park (Szczepański, 1970) and a total of 364 insect species of various orders have been found feeding on heather in the forests around Jędrzejów (Karczewski, 1967a). Finally, 700 species of poplar-feeding insects and 800 species of oak-feeding insects have been recorded.

Each species represents a complex biological system consisting of numerous individuals exhibiting a unique group character determined by its occurrence in time and space and by its specific genetic structure. The consolidation of individual properties of the species is determined by intraspecies systems as the structure of the sex ratio, the protection of progeny, possibilities of creating different aggregations of individuals and the existence of interdependencies between individuals. Such interdependences have no significance when looked at in isolation but together are important for the species as a whole. They include coincidence of sexual maturation, synchronization of life-cycle and intraspecific competition. The number of individuals between which these intraspecific phenomena occur may vary widely according to species and may also vary in time. In many insects, large numbers are particularly evident when conditions favour their reproductive activity (outbreaks of foliophages) or when a stable food supply is available in the ecosystem (soil saprophages). For example, in ca. 50-year-old oak stands over 6.5 million caterpillars of *Lymantria dispar* (L.) hatch per hectare every fifth year of its outbreak (Rafes, 1964).

Ecological populations are formed by individuals occupying a particular environment which is usually of a uniform nature as, for example, the occurrence of *Tomicus piniperda* (L.) in pine forests. Such populations constitute the main object of ecological studies. The borders of such populations are rarely distinct and are dependent on the physiography of the area under consideration. Each ecological population possesses its own characteristic life-cycle, in balance with its environment, and constitutes a discrete but concrete element of the biotope. The distribution of individuals within a population is also species-specific and possesses a definite structure, this being the expression of the population's adaptations to the particular environmental conditions. Such adaptations determine the nature of the spatial distribution of individuals and the occurrence of elementary family, group or colony structures in some species. These structures are characterized by the nature of the contacts between the individuals composing such a unit. Family associations exist in many species of insects and not only in those exhibiting a social mode of life. Larvae as well as adults of *Scolytidae* occurring in a particular gallery-system constitute such a family grouping in which the protection of the progeny is sometimes observed, e.g. the cleaning of larval galleries of excrement by the female of *Xyleborus dispar* (F.) (Fig. 1.1). The occurrence of numerous feeding sites of *Xestobium rufovillosum* (De Geer) in the dead wood of single old oaks occurring in pine forest stands, indicate the formation of typical colonies of this insect within the range of which all life processes of these small internal structural units of the species occur.

Many ecological populations may constitute geographical populations (Naumov, 1955), which form the next structural unit of a species and which occur in a definite geographical region. A geographical population has a uniform life-cycle and exhibits no essential morphological differences from the neighbouring geographical populations. Inter-breeding occurs in the course of migration of individuals from one geographical (and ecological) population to another. Populations of insects isolated from other populations of the same species by a different developmental cycle exhibit unique characters. They rarely occur together in a

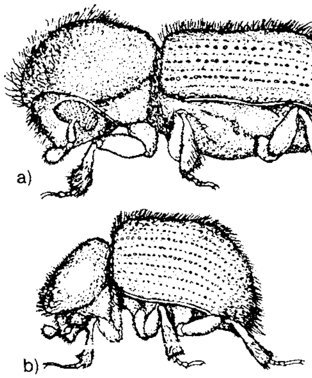

Fig. 1.1 Xyleborus dispar (F): a) female, b) male

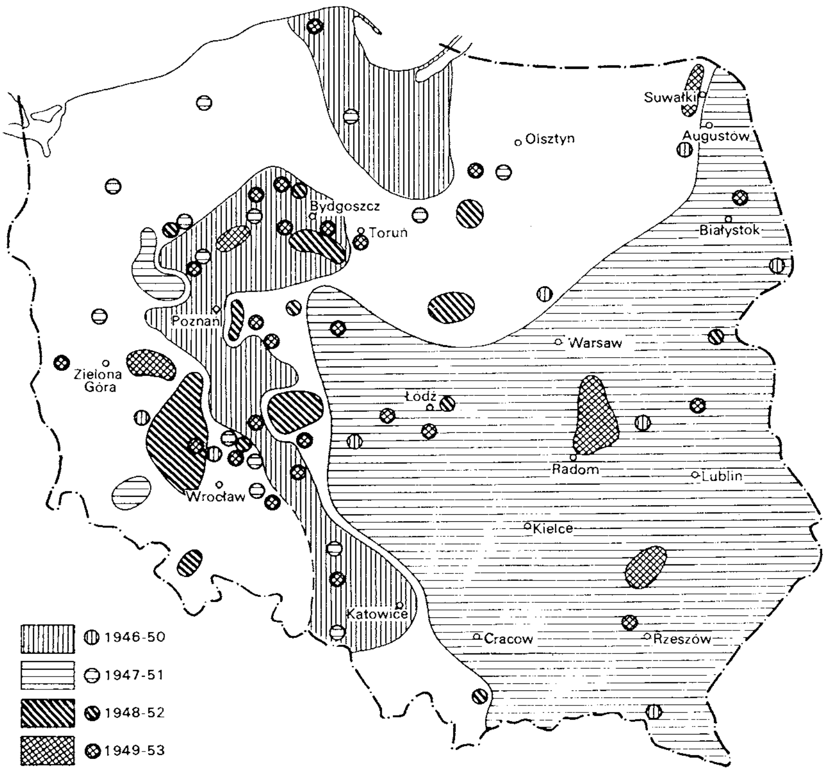

Fig. 1.2 Occurrence of nuptial flights of tribes of *Melolontha melolontha* (L.) in Poland in 1946–1953 (after Nunberg, 1951b)

common area and thus may be readily distinguished and their geographical distribution determined (Fig. 1.2). Since, however, abiotic factors (particularly temperature) determining the time of individual development vary in time and space, the developmental cycles of such populations are not stable (Figs. 1.3 and 1.4). In his analysis of the occurrence

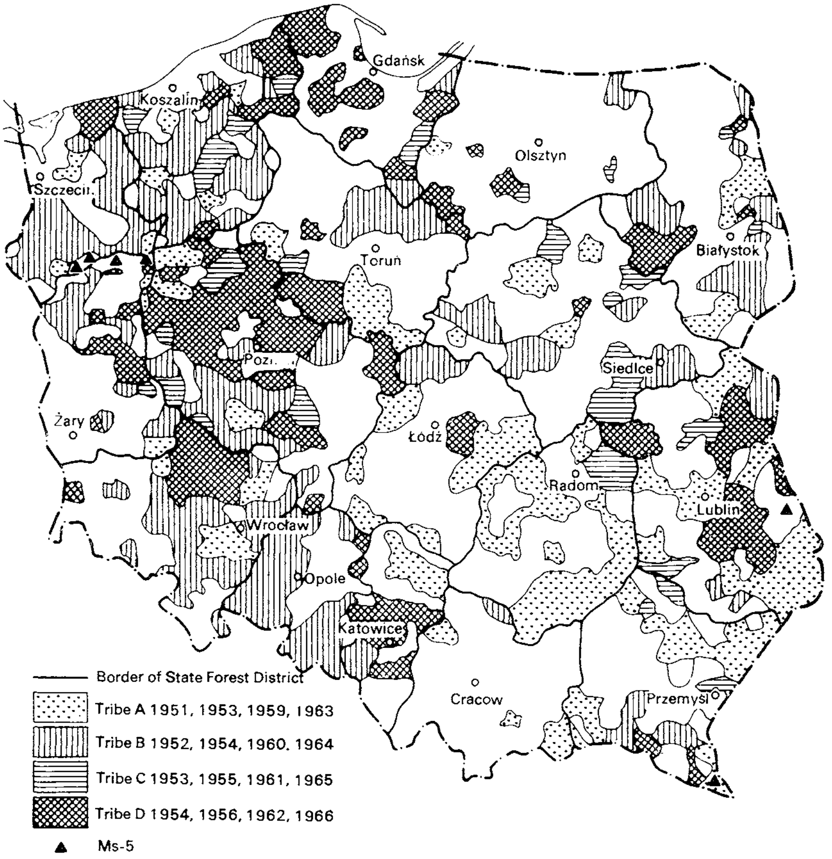

Fig. 1.3 Occurrence of nuptial flights of main tribes of *Melolontha melolontha* (L.) in Poland in 1951–1966 (after Karlikowski, 1965)

of populations of *Melolontha melolontha* (L.) and *Melolontha hippocastani* F. in Poland in the period 1951–1960, Karlikowski (1965) advanced the theory that changing meteorological conditions in the given area and not the mean temperatures in monthly or annual cycles are the main

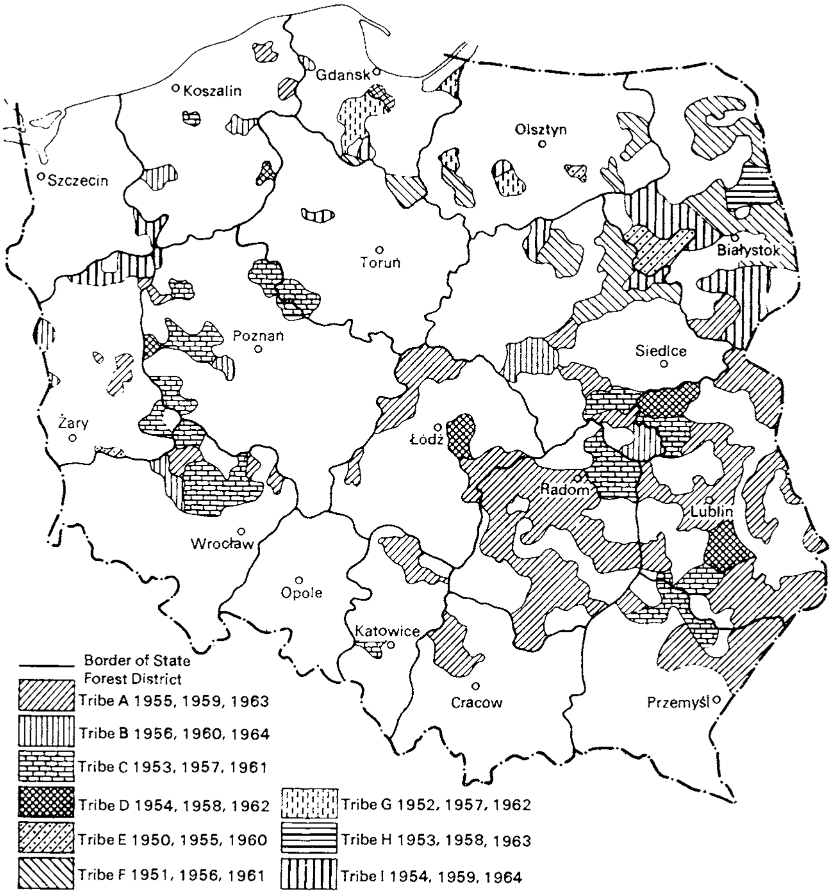

Fig. 1.4 Occurrence of nuptial flights of main tribes of *Melolontha hippocastani* F. in Poland in 1951–1964 (after Karlikowski, 1965)

cause of changes in the distribution of "tribes" of these insects, i.e. populations with the same developmental cycle.

Geographical populations can be a subspecies in the taxonomic sense and in such cases they differ morphologically and are generally isolated from populations of the typical form by geographical barriers such as mountains, water bodies, steppes or deserts. Forests can also constitute such a barrier, separating populations of a given species not suited to the forest habitat.

A subspecies may be regarded as an expression of the geographical variability of a species and appears as a result of differences in environmental conditions in various parts of the area occupied by the species. For example, the litter-inhabiting subspecies *Xantholinus azuganus trellai* Szujecki occurs in the western Bieszczady Mts on the periphery of the area of the typical form *X. azuganus azuganus* (Reitter) which is distributed throughout the eastern and southern Carpathian Mts and in the neighbouring mountain massifs. Subspecies differ from one another by stable but not very distinct morphological features and often also by biological and ecological ones. Transitional forms develop on the borders of the areas occupied by subspecies. The appearance of subspecies is not a rule but, on the contrary, is generally only observed in widely distributed species or when the area of a certain species includes regions separated by natural geographical barriers providing possible isolating mechanisms for parts of the population.

Further examples of the polytypic character of a species, i.e. the occurrence of intraspecific forms such as ecotypes, ecological races and alimentary races of insects, are very interesting and important from the standpoint of forest protection.

An ecological race develops as the result of a species' adaptation to new environmental conditions and new localities. Unlike subspecies, ecological races occur in small, ecologically similar areas and exhibit no or only weak morphological differentiation. The polytypic character of *Formica rufa* L. and *Trichogramma embryophagum* Hartig under various environmental conditions is an example of the occurrence of ecological races, though the opinions of zoologists-taxonomists and ecologists can differ widely as regards the taxonomic rank of the intraspecific unit.

Many species with a meridional distribution exhibit different behaviour patterns in the northern and southern extremities of their range. Their populations may be treated there as separate ecological races or, where there are distinct morphological differences, as subspecies.

Alimentary races exhibit no morphological differences but have different food requirements. For instance, one race of *Galerucella lineola* (F.) living in the Baltic drainage area feeds on leaves of the black alder while another feeds on willows and occurs throughout Europe and Asia. They differ biologically in their phenology and attitude to the aspen as a supplementary host plant. The willow-form can feed and successfully develop on aspen while the alder-form, when obliged to feed aspen leaves, perishes in the first larval instar. Laboratory breeding of several generations of these forms failed to demonstrate the actual food requirements of these species. Two genetically different and sexually isolated races of *Zeiraphera griseana* (Hübner) have been found on larch and on pine respectively in the same area (Bovey & Maksymov, 1959).

In view of the ability of individual populations of the given species to adapt to various environmental conditions, and thus develop new characteristics, a number of terms have been proposed to describe the environmental peculiarities of the species. Besides the concept of the "gradocene", advanced by Schwerdtfeger (1941) (see later discussion), which leads to the idea of the "unrepeatability" of the mass-appearance phenomenon, the concept of a "life system" (Clark *et al.*, 1967) is also particularly noteworthy. The life system of a species consists of a given population and its effective environment, i.e. all the factors, anthropogenous ones included, which exert an influence on the survival of individuals and on the size of the population (Fig. 1.5).

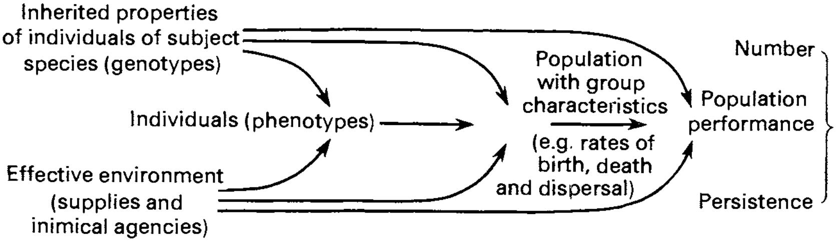

Fig. 1.5 Components of the life system of a species (after Clark *et al.*, 1967)

The occurrence of intraspecific forms or the polytypic nature of a species should not be confused with the variability in the appearance of individuals within the population which is frequently observed, i.e. polymorphism. Polymorphism usually consists of the variability of colours and structures described in taxonomy as variation (aberratio, varietas[1]). Sexual and seasonal polymorphism are also distinguished.

Sexual polymorphism consists of the morphological variation of representatives of various sexual forms of the same species. In social insects such as ants, males, females and workers (sexually immature females)

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[1] Colour aberrations occur particularly often in the chrysomelids. Typica for *Linaeidea* (*Melasoma*) *aenea* (L.) is the green form, although its blue-purple aberration known as *Linaeidea aenea* ab. *haemorrhoidalis* (L.) is observed more frequently. To the better known forest insects in which colour aberrations occur belongs *Tomicus piniperda* (L.) the aberration of which *Tomicus piniperda* ab. *rubripennis* (Reitter) resembles in its colouring *Tomicus minor* (Hartig). If the individual variability concerns changes in shape, it is generally referred to as *varietas* (variety).

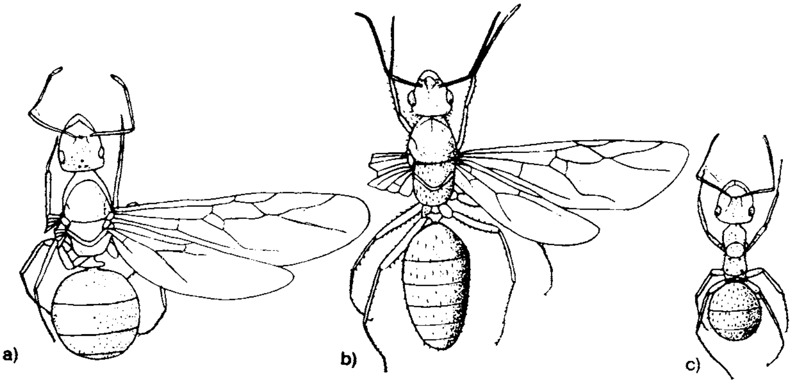


Fig. 1.6 Polymorphism of *Formica rufa* L. (after Dlusskii, 1967): a) female, b) male, c) worker

can be distinguished (Fig. 1.6). When the morphological differences concern only the secondary sexual characters of the males and females, they are referred to as sexual dimorphism (Fig. 1.1). Finally, some species which have two generations per year, e.g. *Araschnia levana* (L.) may exhibit different forms according to the season (seasonal dimorphism).

Although a species may constitute a biologically discrete unit, its genetical structure endows it with a wide range of internal variation, especially when the species has an extensive geographical distribution. Such variation makes it difficult for man to execute measures of control in forest-protection, especially those involving the regulation of the abundance of the populations of insects concerned. This is because the populations of any given species occupying different ecological situations have different biological values and react differently to control measures.

An insect's environment consists of all of the factors which influence its chances of survival and reproduction. The general environment consists of the immediate surroundings (in the widest sense) and those environments of direct importance to the organism. The environment is continuously changing and so, therefore, is its influence upon the organism. The relationships between an organism or association of organisms and the environment are:

1) specific for each organism;
2) continuous – the organism remains in the environment for life;
3) mutual – the environment and the organism influence one another reciprocally;
4) unseparable – separation of the living organism from the environment is impossible (Schwerdtfeger, 1963).

The environment of any organism consists of abiotic and biotic factors. Abiotic factors include temperature, light, water, humidity, soil, air and air pressure, etc. Biotic factors consist of interdependences between individuals of the same species, i.e. homotypical dependences (e.g. reproduction) as well as heterotypical dependences, i.e. various kinds of associations between populations and individuals of different species including exploitation (e.g. parasitism, predation), competition, paratrophy and commensalism, etc.

The effects of the various ecological factors on insects vary in time and space. Each living organism can only tolerate a certain amplitude of change of any individual factors. Thus the existence of an organism depends on the intensiveness of the action of environmental factors necessary for its survival. If environmental factors are deficient or in excess of the requirements of species, they can serve to limit the occurrence of this species. The amplitude of change of any factor which can be resisted by an organism is termed the limit of tolerance of this organism (to the given factor) and is determined in points of the ecological minimum and maximum of its activity (Fig. 1.7). The optimum action of factors may be very narrow or very wide as compared with the amplitude of oscillations of the factor within the limits of its minimum and maximum. In *Lymantria monacha* (L.) the optimum rate of development of eggs occurs between 20 and 25°C and their survival optimum between 10 and 22°C at 100% relative humidity, whereas the total temperatures range within which egg development may take place lies between 4 and 30°C.

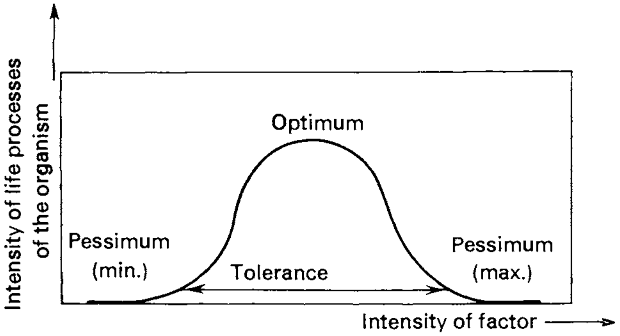


Fig. 1.7 Scheme of the limit of tolerance of organisms to an environmental factor

The limits of tolerance of an organism to environmental factors are denoted by the prefix eury (wide) or steno (narrow). For instance, species able to occur and develop in stable or slightly varying thermal conditions at exclusively low, high or mean temperatures are called stenothermal, whereas those which may occur within a wide range of temperatures, both low and high are called eurythermal species. Analogously those occurring in a single or in a number of biotopes are called stenotopic or eurytopic species respectively.

In order to determine the optimum value of a given factor, a three-grade scale is applied in which the prefix oligo (scanty) indicates an organism requiring low values of the factor discussed, the prefix meso (mean) indicates an organism requiring mean values and the prefix poly (many) indicates that the organism requires high values of the factor. Species of noxious insects feeding on a number of different tree species, e.g. *Lymantria dispar* (L.) are called polyphages whereas insects feeding only on closely related plant species are termed oligophages. *Chrysomela populi* L., which feeds only on various species of two genera (poplar and willow), is an example of an oligophage. The prefixes indicating the range of tolerance and those determining the requirements concerning the given environmental factor can be combined together as well as with the name of the factor discussed. For instance, a species requiring a high, stable temperature may be referred to as polystenothermal. Other dependences of this type are given in Fig. 1.8.

The tolerance of insects to definite environmental factors invariably changes at various stages of their development and may depend on their sex. For instance, the adult form of *Ergates faber* (L.) exhibits far higher temperature requirements than its larva which feeds in pine stumps. Moreover the degree of tolerance depends on the physiological conditions and the geographical origin of the given individual. Caterpillars of *Cossus cossus* (L.) successfully resist low temperatures beneath −20°C in winter but in spring they perish at −17°C. Caterpillars of *Lymantria monacha* (L.) originating from the Masurian forests reared on leaves of trees growing in the environs of Berlin exhibited a higher mortality than those fed on the same food from the original source of the caterpillars (Schwerdtfeger, 1963).

No environmental factor influences the forest insects in isolation from the others. Particularly many examples of this can be quoted as regards the combined influence of temperature and humidity. Insects may exhibit a wide range of tolerance to one factor and a narrow one to another, but where the environmental conditions are not optimal in

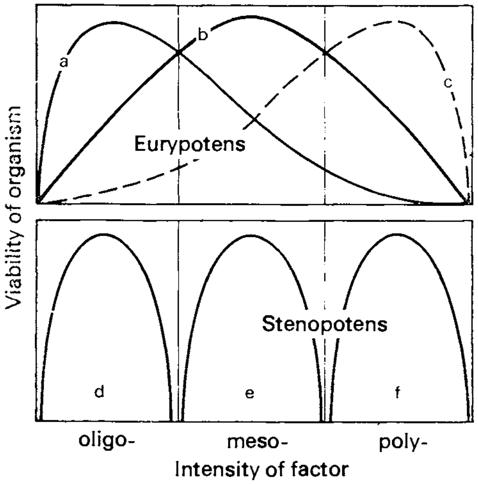


Fig. 1.8 Scheme of the limit of tolerance of organisms belonging to various ecological types to an environmental factor (after Schwerdtfeger, 1977)

respect to one factor the tolerance of species to others may be limited. For instance, larvae of *Melolontha* sp. in Poland avoid humid areas with a high ground water level, while in south-western Europe they can exist under such conditions. It appears that low soil temperatures in winter are the main factor limiting the occurrence of the larvae in Poland since these determine the depth at which the larvae hibernate in the soil. Thus, in Poland the grubs hibernate several dozen centimetres deeper than in south-western France where the winters are less severe, and therefore in Poland they cannot occur in soils with a high ground water level. In this case, low soil temperatures in Poland have reduced the limits of tolerance of *Melolontha melolontha* (L.) to the ground water level and soil humidity.

It seems that the most critical period in the lives of insects is that of reproduction and it is at this time when the environmental factors are most limiting. In view of this weather conditions prevalent at the time of the nuptial flights can exercise a decisive influence on the abundance of the progeny and thus on the resultant damage to forest stands.

Insects exhibiting a wide range of tolerance to many environmental factors invariably have the most widespread distributions. On the other hand, experimentally determined optima of definite physical or chemical factors are rarely sufficient to provide the conditions most favourable to development. Biotic factors such as competitors, predators and parasites are also very important in the natural environment since they limit the extent to which a population of any given species may take advantage of the optimal abiotic environmental conditions (Fig. 1.9).

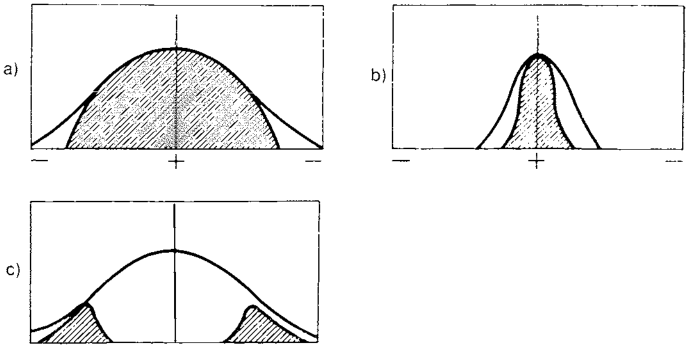


Fig. 1.9 Schematically presented concepts (a–c) of the dependences between the ecological and biocenotic optima of occurrence of insects (after Dylis, Tselnikov & Karpov, 1964): perpendicular line marked (+) indicates the optimum of habitat and nutrient conditions of occurrence of the species; (–) indicates extremal conditions; the curve indicates the ecological range of the species (possible in the case of absence of enemies and competitors); shaded surface indicates the biocenotic range, i.e. actually realized range in the presence of antagonistic species

Situations exist in nature in which one limiting factor can be substituted by another, particularly when many factors influence an organism. Because of this the mechanisms of the actions of limiting factors do not sufficiently explain the geographical distribution of any given species or the course of changes in the abundance of forest insects. Such mechanisms consider only the most simple ecological situations and do not take into account the effects of concomitant populations and biocenotic systems.

2 Influence of abiotic environmental factors on forest insects

Influence of solar radiation and atmospheric factors

2.1. Light

Light rays of different wavelengths exercise various direct or indirect influences on insects. Besides visible radiation ($0.4 < \lambda \leqslant 0.7$ μm), there are invisible infra-red rays of wavelengths exceeding 0.7 μm, which provide heat and thus increase body temperature, as well as ultraviolet rays of 0.4–0.003 μm wavelength, which may have important chemical, and consequently biological, effects on living protoplasm.

Light plays an extremely important role in the life of insects. It directly influences the body structure, activity, diurnal rhythm, development, sex determination, reproduction, physiological processes and behaviour. Indirectly, it influences the food-plants of insects, because plants can only assimilate carbon dioxide in light (photosynthesis).

2.1.1 Influence of light on behaviour

Light is an indispensable factor in the life of the majority of insects, the only exceptions being the few species living in deep caves (troglobionts) and those permanently inhabiting deeper soil levels (geobionts).

Many forest insects spend at least one stage (and usually most) of their life-cycle in darkness. The eggs, larvae and nymphs of *Xyleborus* and *Trypodendron* live in wood, just as those of *Melolontha* sp. occur in the soil, whilst the adult stages of these insects live on the soil surface or on trees and are often exposed to the direct effect of light rays.

Light has a direct influence on the activity of insects. A particular structural modification of the body or light-avoidance reactions protect them from excesses of light. Light-avoidance usually involves the adoption of nocturnal habits or the colonization of poorly illuminated sites. The 24-hour activity pattern is a biologically complex phenomenon since it also depends on other factors such as temperature and humidity. Nevertheless, because of its stability, light is the main regulator of the daily activities of the majority of species. Insects may be classed as either diurnal, crepuscular or nocturnal. Numerous forest insects, particularly large ones, are only active as adults at twilight or at night when they are less exposed to attack by predators. The onset of the night flights of *Melolontha* sp., *Geotrupes mutator* (Marsham), *Panolis flammea* (D. & S.) is determined by the time of sunset, and thus its timing varies somewhat, particularly if the period of nuptial flight, for example, lasts a number of days (Fig. 2.1).

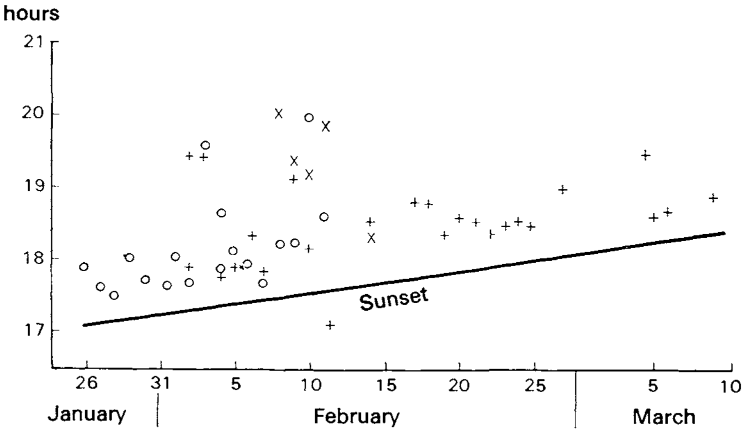


Fig. 2.1 Beginning of evening activity of *Carabus cancellatus* Illiger in dependence on time of sunset (after Weber, 1966)

The 24-hour light-dependent rhythm is called the exogenous rhythm (originating from external causes). In many species, however, the 24-hour rhythm adapted to the light conditions of day and night is not determined by the light stimulus, but takes place independently in an endogenous way and therefore is called the endogenous rhythm (originating from internal causes). For instance, the common forest litter-species *Pterostichus vulgaris* (L.) (*Carabidae*) exhibits normal nocturnal activity both when kept in complete darkness and when reared under full light for several weeks. In many insects an exoendogenous 24-hour rhythm occurs due to both kinds of stimuli.

The light orientation (phototaxis) of insects is associated with their activity and photokinesis (motions induced by light). Phototaxis is a reaction to the intensiveness and quality of light as well as its direction. Some species exhibit positive phototaxis (moving towards the source of light) whereas others react negatively (moving away from light). For some species only light waves of a particular length, mostly ultraviolet and yellow-green rays of the spectrum, are of significance; for other species the light intensity also plays an important role in phototaxis. Caterpillars of *Lymantria monacha* (L.) about to feed in the tree crown exhibit a positive phototaxis, but at the moment when they actually start to feed they become phototactically neutral. *Carabus nemoralis* Müller ignores the whole scale of light intensity and chooses the darkest or poorly illuminated sites with about 1 lx whereas in an analogous situation *Geotrupes stercorosus* (Scriba) prefers sites with 3–60 lx illumination (Schwerdtfeger, 1963). All soil insects are photophobic and exhibit a negative phototaxis.

The reaction of insects to light varies according to their stage of development and state of sexual maturity. *Tomicus piniperda* (L.) exhibits a stronger photopositive reaction in the spring, when it is sexually mature, than in the autumn. The males of the serious pest of Canadian forests, *Choristoneura fumiferana* Clemens in definite life periods exhibit a positive phototaxis, whereas the females show a negative one. Teneral *Dendroctonus ponderosae* Hopkins individuals as well as those capable of flight exhibit a positive phototaxis, whereas egg-laying females present a negative phototaxis. They exhibit no reaction to polarized light (Shepherd, 1966). Temperature may have a significant influence on the course of phototaxis. Larvae of some *Neodiprion* sp., for example, are photopositive at low temperatures and photonegative at high ones.

Many insects, such as *Lasius fuliginosus* (Latreille), exhibit a space orientation based on sun illumination, particularly on the incidence of the sun's rays. Individuals of this species returning to their nest on a sunny day placed for half an hour in darkness and then released on the same site choose a direction to the ant-hill differing from the original one by the angle by which the sun has moved across the sky.

A similar compass-type orientation based on the incidence of light rays and supplemented by the orientation based on the nest's scent and the individual's own tracks is observed in caterpillars of *Yponomeuta*.

Another mode orientation depends on the differentiation of light and dark backgrounds (scototaxis). *Coccinella* sp., when placed on a surface covered with light and dark strips moves only on the white strips.

Pityokteines curvidens (Germar) locates tree trunks in the same way. The phenomenon of scototaxis has been utilized in the construction of devices for catching *Dendroctonus ponderosae* on the basis of olfactory stimuli in which black and white screens were used (Vité & Gara, 1962). Many of the more highly organized insects such as *Apidae*, *Ichneumonidae* and *Diptera* can distinguish the colours of visited flowers, as can adults of *Anthaxia* and *Leptura* (*Cerambycidae*) feeding on pollen (Fig. 2.2).

Fig. 2.2 Leptura maculicornis (De Geer) on flowers of *Umbelliferae* (photo by T. Bojasiński)

Some *Ichneumonidae* can also distiguish more "white" tints than the human eye. Finally, many soil insects living on the surface exhibit a visual orientation in that they orientate by the shape of objects or the appearance of the landscape, etc., and not by the light intensity. Such orientation behaviour is observed in *Cephenemyia stimulator* (Clark), a parasite in the larynx of the European roe-deer, which recognizes its host by its silhouette.

Tree selection by *Scolytidae* may be stimulated by the shape of weakened trees (e.g. deprived of needles or wounded), and especially by their dimensions. In the latter case the beetles proceed to the largest and darkest objects visible on the light background. These are the highest or, if the trees are of equal height, the thickest trees (Shepherd, 1966; Hopping & Beall, 1948). In this way the highest concentration of beetles over the largest area accessible for settling is achieved (Isaev & Girs, 1975).

2.1.2 Influence of light on reproduction and development

Light influences the reproduction of insects in three ways:
1) by affecting the endocrine system, i.e., the secretion of hormones and the development of sexual glands;
2) by affecting the nutrition factor, namely, in suitable light feeding is more intensive and the sexual organs develop better;
3) by increasing general activity, and hence also sexual activity.

In general, reproduction is influenced by light in all three ways, but not only by the intensity of illumination but also by the varying time of daylight which determines the reproductive cycle.

For example the intensity of illumination may determine the time of the day when the nuptial flight takes place, whereas the duration of daylight determines the season of the year at which it will occur. In this way *Serropalpus barbatus* (Schaller), a pest of spruce and fir, undertakes its nuptial flights only at night, whereas the parasite of *Lymantria dispar* (L.) and other *Lepidoptera*, *Meteorus versicolor* (Wesmael), only does so in full sunlight. Individuals of the latter species reared in isolation from the sun rays reproduce parthenogenetically, and thus only males develop from the eggs laid. The females of *Ergates faber* (L.) lay their eggs only in stumps on illuminated forest edges or in clearings. In some *Lepidoptera* the number and weight of the eggs, as well as the weight of the larvae and pupae, depend on the colour of the light under which development took place. Eggs of *Dendrolimus pini* (L.) develop equally as long in light as in darkness. Caterpillars of *L. dispar* pupate earlier when kept in the dark, whereas mortality is higher in those reared in the light.

The duration of daylight is one of the main regulators of the seasonal developmental cycles of insects and has a significant effect on the course of diapause. The mechanism of the influence of light on reproduction and the development of insects is a complicated physiological process. In general it can be said that, by way of the nervous system, the light stimulates the endocrinal glands (e.g. the *corpora allata* and *corpora cardiaca*), the hormones of which activate the sexual or moulting glands. The changes in day length act as signalling factors, their significance being their constancy of occurrence under natural conditions in the temperate zone, as opposed to temperature and humidity changes. This ensures that mating and the development of the immature stages take place at the most favourable time.

In many species the endocrinal control of reproduction is very significant and, since it is associated with the periodical nature of biological processes in the living organism, it causes the developmental cycle to be independent of light conditions. This particularly affects insects with a poorly differentiated seasonal cycle such as the house-fly or insects with generations lasting many years, the development of which is strictly determined and stable as in *Melolontha* sp. On the other hand, day

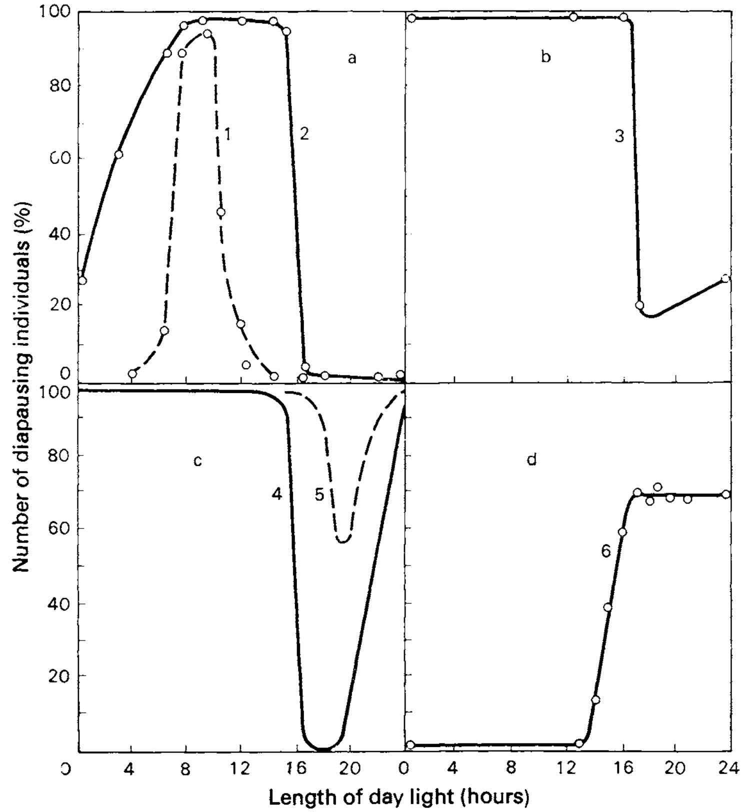


Fig. 2.3 Types of photoperiodic reaction (after Gorishin, 1966): a and b — long-day reaction, c — photoperiodic reaction of intermediate type, d — short-day reaction; 1 — *Pieris brassicae* (L.), 2 — *Acronycta rumicis* (L.), 3 — *Leptinotarsa decemlineata* (Say), 4 — *Euproctis similis* (Fuessly), 5 — *Leucoma salicis* (L.), 6 — *Bombyx mori* (L.)

length, i.e. the phenomenon of photoperiodism, is very important for the development of insects which have two or more generations per year and exhibit a differentiated seasonal cycle.

Photoperiodism is particularly significant at the onset of diapause. The day length initiating diapause differs not only between species but also between populations of the same species. It has been proved experimentally that it is not so much the light itself, but the rhythmical succession of light and darkness and particularly the variability of these factors which affects the insects. Moreover the insects react differently to rays of different wavelengths. The short-wave section of the spectrum is most effective in this respect whereas most insects exhibit no reaction to red light. Under laboratory conditions, diapause may be induced in some insects by artificially changing the day length at any season of the year. This indicates that the light condition is a more important external factor than temperature or even nutrition.

Under temperate climatic conditions long-day photoperiodism is the more commonly observed phenomenon, diapause being induced by shortening the day length to below 18–14 hours. Short-day photoperiodism is rarely observed in this climatic region but it does occur, for example, in *Dasychira pudibunda* (L.) where diapause occurs at day lengths above 14–18 hours (Fig. 2.3). The photoperiodic reaction only occurs within a definite temperature range which varies between species independently of light intensity. However, the threshold of light intensity at which individual species commence diapause also varies. Larvae of

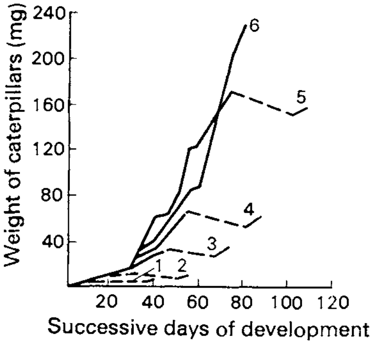


Fig. 2.4 Occurrence of diapause in caterpillars of *Dendrolimus pini* (L.) in dependence on the moment of beginning of short day (after Gorishin, 1966): 1 – from egg stage, 2 – from stage I of caterpillar, 3 – from stage III of caterpillar, 4 – from stage IV of caterpillar, 5 – from stage V of caterpillar, 6 – at long day. Period of diapause denoted by dashed line

Dendrolimus pini (L.) start their diapause by descending into the litter when the day length is reduced to 9 hours and the lowest diurnal temperature falls below 0°C (Figs. 2.4 and 2.5). It is noteworthy that light conditions are more significant at the onset of diapause when the temperature range is wider. Generally speaking, at higher temperatures the light stimulus (length of daylight) must be shorter in order to induce diapause. Finally, the photoperiodic reaction is dependent on the quality of food (Fig. 2.6) and also exhibits geographical differences.

The period between the light stimuli and the beginning of diapause differs in individual species. Pupal diapause is determined by the light conditions occurring in the egg phase or during feeding period of the larva. In extreme cases it may even be determined by the light conditions occurring at any stage of the development of the preceding generation. Besides its decisive role in the initiation of diapause, the day length may affect the development in other ways and can also influence the morphological appearance of insects. Insects which occur at definite seasons of the year have formed and stabilized their requirements (through evolution) in association with a definite length of daylight. If some deviations occur they affect the duration of the developmental period. For example, in an experiment under conditions of a long, 17-hour daylight, the developmental period of *Panolis flammea* (D. & S.) was shorter by 3 days than that in individuals of the same species reared under conditions of a short, 5-hour daylight. Larvae of *Bupalus piniarius* (L.) developed more rapidly under short daylight, whereas under long-day conditions they all died in the 4th instar.

The seasonal colour dimorphism of the butterfly *Araschnia levana* (L.) is not caused by temperature as it was once believed, but can be induced

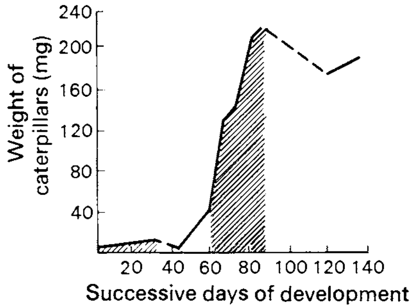


Fig. 2.5 Experimental evoking of repeated diapause in caterpillars of *Dendrolimus pini* (L.) (after Gorishin, 1966): dashed line – period of diapause, shaded surface – influence of short day

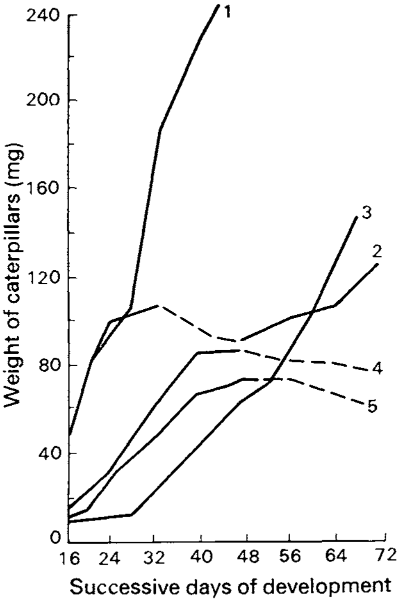


Fig. 2.6 Growth and diapause of caterpillars of *Dendrolimus pini* (L.) under various illumination and feeding conditions (after Danilevskii, 1961): 1 – food constantly accessible under constant illumination, 2 – food constantly accessible under short (12 hour) day, 3 – food accessible 12 hours per 24 hours under constant illumination, 4 – food accessible 12 hours in dark period of short day, 5 – food accessible 12 hours in light period of short day; continuous line – active development, dashed line – diapause

by a suitably long daylight period, independent of the season. Under long-day conditions *ab. prorsa* (L.) (the summer form – black with white spots on the wings) develops, and under short day the typical, spring form (light with black spots) develops from the hibernating nymph.

In many aphid species the length of daylight influences the appearance of winged or wingless and bisexual or parthenogenetic forms. In species in which the change from parthenogenesis to normal sexual reproduction occurs in the autumn, bisexualism may be induced as early as May by exposure to a 7–8 hour day.

2.2 Temperature

Environmental temperature plays an important role in the life of insects since it affects, either directly or indirectly, their development, survival, abundance and reproduction. Insects, like most animals, are poikilothermic, and therefore their body temperature depends on that of the environment. Thus all of the organism's metabolic processes occur at a rate dependent on the environmental temperature. The opinion that insects cannot regulate their body temperature, however, is wrong.

2.2.1 Regulation of body temperature

The simplest method of regulating body temperature is to move from one place to another. Individuals of *Pyrrhocoris apterus* (L.) cluster on insolated tree trunks, particularly those of lime-trees. *Hylobius abietis* (L.) adults migrate at 35°C from sunlit to shaded parts of plantations, i.e. to sites where the temperature on the soil surface is 15–20°C lower, or crawl into moss and hide under plants of the herb layer and return to the trees only at 13–18°C and an air humidity of 74–100%. If it is cool in May, *Melolontha hippocastani* F. lays most eggs in insolated plantations, whereas on hot days it mainly populates the interior of forest stands and this therefore determines the extent of the damage produced by its grubs in the following years (Schwerdtfeger, 1977).

The choice of the site of optimum thermal conditions for a given species (i.e. of the specific thermal preference) does not occur within a stable temperature range but differs according to the developmental stage and environmental conditions, the most important of which is air humidity. It also depends on the "introductory temperature", i.e. the temperature in which the insect remained before this choice. The thermal preference may differ at various times of the day, as well as during various periods of the vegetation season.

Interesting studies in this respect have been carried out on the thermal preference of *Harpalus rufipes* (De Geer) (= *Pseudophonus pubescens* (Müller)) in the environs of Leningrad. It was found that the preference oscillates within the limits of 20–30°C. In spring, after abandoning their winter lair, the beetles exhibit a slight variation of preference at different times of the day, with a rising tendency between 10 a.m. and 1 p.m. This reaction changes radically after reaching sexual maturity and is expressed by a rhythmical expansion and contraction of the preference amplitude at various times within 24 hours (Fig. 2.7).

The highest temperature is chosen during the day and the lowest at night. The studies showed that the 24-hour rhythm of the thermal preference remained even when the beetles were reared at a constant temperature for one month. A variability of the thermal preference was also

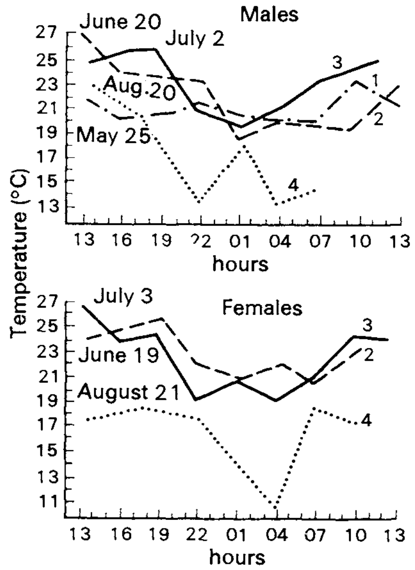


Fig. 2.7 Diurnal dynamics of thermal preference of adult individuals of *Harpalus rufipes* (De Geer) (after Yakhontov, 1964): 1 – period of spring feeding, 2 – period of sexual maturation, 3 – period of copulation and egg laying, 4 – period preceding hibernation

observed within the vegetation season (Fig. 2.8). Maximum thermal requirements occurred in males around June 20 and in females around July 2 (after Yakhontov, 1964).

Mature forms of *Phyllodecta vitellinae* (L.) are characterized by a mean diurnal thermal preference varying in different seasons of the year. In late summer it amounts to 22.0±0.26°C, whereas in autumn it is 16.2±±0.31°C and 20.4±0.74°C in spring. The variation curve of the preference of this species exhibits one maximum, falling to midday and the early evening hours, with minima at night and in the morning. On the other hand, in September *Agelastica alni* (L.) exhibits the maximum thermal preference at 9 a.m. (20.3°C) and the minimum at 6 p.m. (15°C) (Kadłubowski & Dudik, 1968).

The regulation of body temperature may be primarily achieved by changes in the intensity of oxygen uptake and water evaporation. The body temperature rises and falls with increasing rates of respiration and water evaporation respectively, so that the body temperature is higher in humid air than in dry at the same air temperature. It has also been established that certain insects occurring in sunlit areas have a body

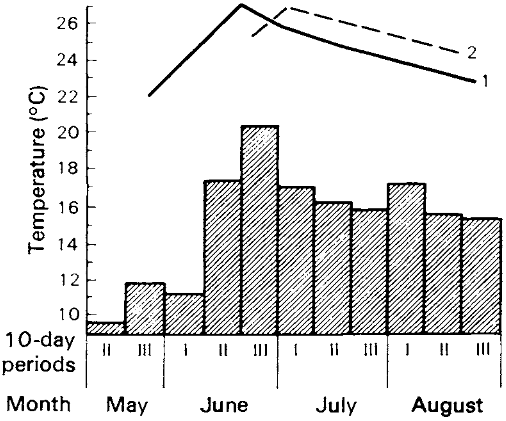


Fig. 2.8 Seasonal dynamics of thermal preference of adult individuals of *Harpalus rufipes* (De Geer) (after Yakhontov, 1964): 1 – preference of males, 2 – preference of females

temperature 2–9°C lower in living as compared to dead individuals. This indicates that temperature regulation is taking place in the living organism as a result of intensive water evaporation.

Another way of regulating body temperature involves chemoregulation, due to intensive muscular activity. This is observed particularly in insects performing long flights. In *Hyloicus pinastri* (L.), rapid wing motion increases the body temperature by over 10°C, whereas in running individuals of the genus *Carabus*, the body temperature may rise by 2°C. It should be stressed that the chemoregulation of body temperature is the more distinct when the environmental temperature is lower (within certain limits) than that required by the given species.

The intensity of heat exchange between the organism and the environment depends on the size, form and colour of the body of the organism. Since heat is released by the body more or less in proportion to the value of the ratio between the surface and the volume of the body, small insects lose heat more rapidly than large ones. Because of this small larvae of *Dendrolimus pini* (L.) descend earlier in the autumn from the trees than larger individuals and return later to them in the spring. Dark colours favour heat adsorption from the environment. Thus, tropical day-active insects frequently exhibit bright colours whereas nocturnal species or those inhabiting the far north and the alpine zone of mountainous regions generally exhibit dark colours. In high peatland areas, metallic coloured *Carabidae* inhabit high, intensely sunlit peat tufts whereas black forms are mostly found in cold depressions.

In this discussion on dependence of the colour of insects on thermal conditions it should be remembered that, as mentioned above, the day length at which development occurred has a considerable influence on the variation of the colours of individuals belonging to the same species, as seasonal forms for example.

Besides regulation of body temperature by particular individuals there is also a phenomenon of temperature regulation by groups of individuals. Ants of the genus *Formica* regulate the temperature in their nest by the construction of ant-hills of various heights and selection of sites in forest stands of varying density, thus obtaining a larger or smaller quantity of heat from the Sun's rays. Ant-hills in dense spruce stands are invariably higher than those in insolated pine forests (Fig. 2.9). The difference between the temperature within the ant-hill and that of the surrounding air reaches up to 13°C, and because of this the temperature within the nest remains at the level of 20°C, securing normal reproduction and developmental processes. At night the temperature within the nests of *Eriogaster lanestris* (L.) remains 13–15°C higher than that of the surrounding air. The larvae abandon the nest only when the air

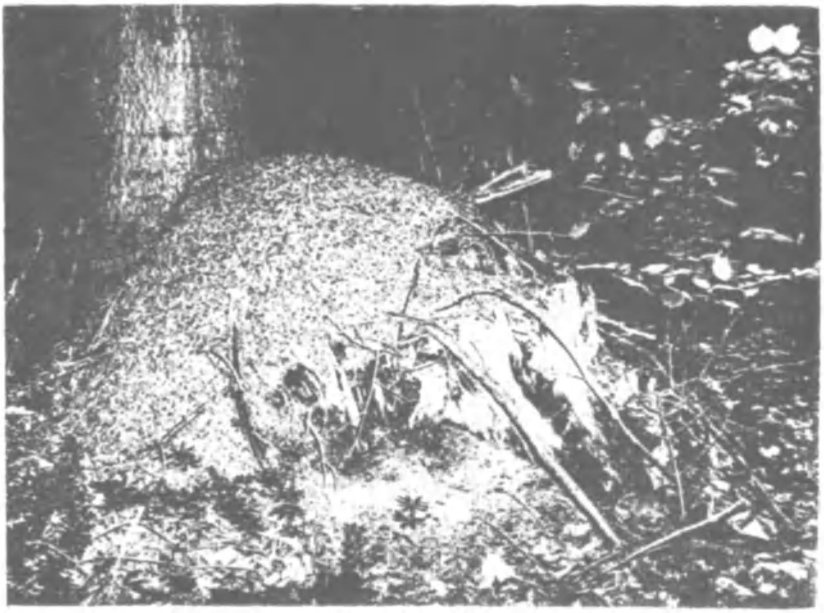


Fig. 2.9 Ant-hill of *Formica rufa* (L.) in shaded mixed forest stand (photo by T. Bojasiński)

temperature rises to the level of that within the nest. Wasps living in communities are able to raise the temperature within their nests by muscular activity to as much as 31°C. Hibernating congregations of insects, such as *Ichneumonidae* living under detached bark of stumps or chips may exhibit a temperature considerably higher than that of the surrounding air.

Thus, social insects exhibit a capacity to partially regulate their immediate microclimate and, due to their communal activity, they become facultatively homoiothermal. On the other hand, however, the regulation of their own body temperature at high environmental temperatures is greatly limited.

2.2.2 Thermal tolerance

The upper thermal limit at which the insects can exist, as in other animals, is associated with the resistance of proteins to coagulation. This depends on the content of water and mineral salts in the body. In general, insects can resist high temperatures oscillating between 55 and 65°C, i.e. higher than the mean temperature of protein coagulation. However, larvae of the genus *Scatella* (*Ephydridae*) living in the hot springs of Iceland and Kamchatka are exceptional here. The upper lethal temperature (that at which 50% of individuals perish) is considerably lower for forest insects, and is even lower than that for desert and steppe insects. Larvae of *Buprestidae* living under the bark of insolated trees survive a temperature 15–20°C higher than that of the air due to heating of the tree trunks. This indicates that the larvae can resist temperatures of 50–52°C. Most species living on the soil surface perish at 45–48°C, but *Aphidoidea* perish as soon as temperatures exceed +35°C and the lethal temperature for soil insects is considerably lower.

The lethal temperature varies for the same species depending on its developmental stage, sex and nutritional condition. The time of exposure of insects to high temperature affects the death rate, though not always proportionally, and frequently it increases along an S-shaped curve (Fig. 2.10).

The lower thermal limits at which insects can exist are more variable than the upper ones. When the body temperature falls, death may be caused by the formation of ice crystals, dehydration or destruction of intracellular and intercellular structures. The resistance of insects to low temperatures depends on the species, geographical conditions, developmental stage, sex and physiological condition determined by nutrition and thermal conditions occurring before the temperature fall. For instance, larvae of *Melolontha* perish at −4°C and pupae of *Hyloicus pinastri* (L.) at −12°C. Caterpillars of *Rhyacionia buoliana* (D. & S.) hibernating in pine buds perish in Poland at −27°C, in Ukraine at −12°C and in Syria at several degrees below 0°C. Tropical insects perish at +7°C, whereas the entire life cycle of *Astagobius angustatus* (Schmidt) is accomplished in ice caves at temperatures oscillating within the limits of −1.7 to +10°C. The adults of *Ips typographus* (L.) are more resistant to frost than the larvae and pupae. Caterpillars of *Lymantria* *monacha* (L.) are resistant down to a temperature of −40°C and, under laboratory conditions, even −70°C but in spring they perish at −23C°,

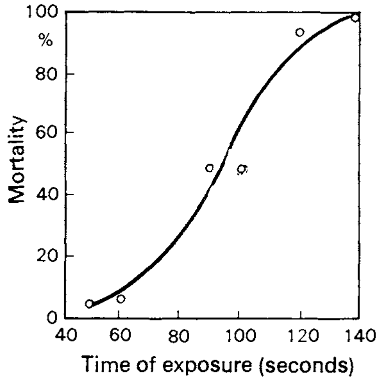


Fig. 2.10 Mortality of pupae of *Tribolium confusum* (J. du Val) under the influence of temperature of 58°C (after Schwerdtfeger, 1977)

The resistance of two individuals of the same species and developmental stage and living under the same conditions may depend on their physiological condition. The latter depends on the water content of the body and its association with colloids as well as on the concentration of solutions and glycogen (animal starch) and fat content.

The lower the content of free water and the higher that of bound water, mineral salts (in the tissue fluids), glycogen and fat, the higher the resistance of insects to low temperatures.

In species hibernating on uncovered or poorly covered sites, the resistance to cold depends to a great extent on glycogen content in the body. During diapause the content of glycogen in the haemolymph amounts to 9% and, sporadically, even to 40–50%. In insects hibernating in environments in which frosts do not occur, or where the temperature only falls slightly the fat as well as glycogen content plays an important role in their resistance to cold. Beetles of the genus *Plagionotus* contain up to 14% of fat and survive at −7°C, whereas larvae of *Melolontha* containing only 6% of fat perish at −5.75°C and 74% of water freezes in their tissues.

The phenomenon of supercooling, originally studied by Bakhmatyev (1901), plays an important role in the resistance of insects to the cold. It centres on the fact that water in the insect's body colloidally bound with proteins freezes at temperatures considerably lower than 0°C, e.g. about −5.3°C in *Scolytus* larvae. Let us follow this phenomenon in the classic example of the pupae of *Hyloicus pinastri* (L.) (Bakhmatyev, 1901). The body temperature of these insects falls in line with the drop in the environmental temperature until the critical point, −12°C (Fig. 2.11), is reached. At this point, colloidally bound water passes into the intercellular spaces. This produces an increase in body temperature due to the short-lasting balance between the heat released by freezing and the radiation of heat to the direct environment. The temperature remains at this level until the heat released by freezing completely dissipates. The body temperature then falls once again, attaining a stable balance with the environment. This phenomenon is called supercooling and during its course the insect remains in the condition of anabiosis. In the process of intensive cooling, a fluid acquires the form of an amorphous vitreous mass and this phenomenon is called vitrification. Vitrification is characterized by an irregular dispersion of particles of the given substance. Due to the rapid change from the liquid to the solid state, the substance can by-pass the crystalline stage and pass directly to the vitreous stage.

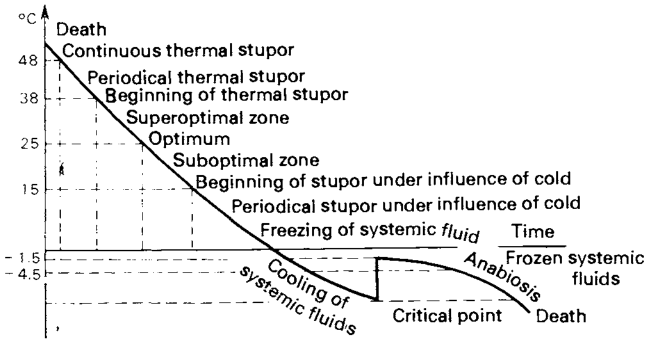


Fig. 2.11 Bakhmatyev's curve

During anabiosis the life process is latent but the insect can survive even after remaining at low temperatures for long periods. The temperature of freezing (lethal temperature) of the body of an insect is neither directly associated with the limit of fluid supercooling nor with the temperature at which the supercooled fluid transforms to ice under the influence of the heat of freezing.

Two types of reaction to cold may be distinguished. The first concerns particularly resistant insects enduring both supercooling and freezing, perishing only in prolonged frost or at sudden temperature changes. The second type concerns insects exhibiting a low resistance to cold, incapable of hibernating and perishing even without freezing.

All of the forest insects occurring in Poland belong to the first category. Most of them perish when ice crystals form in the cell fluid, far earlier than the point where the body temperature regains the critical level (e.g. species of the genus *Melanotus*), i.e. earlier than as described by Bakhmatyev (1901).

On the other hand, there are examples where insects endure complete freezing of the cell fluid (e.g. larvae of *Cossus cossus* (L.)). It was mentioned above that the moment of death of the insect, i.e. the critical point, varies widely not only between various species but also within the same species and even the same developmental stage (Fig. 2.12). Individuals which have succeeded in completing their feeding period and have accumulated sufficient fat and glycogen stores before cold late autumn period are resistant, whereas underdeveloped or starved ones deprived of fat perish before the onset of frost.

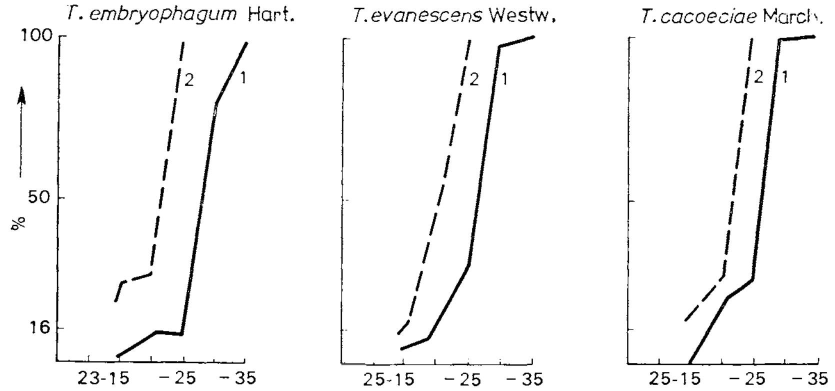


Fig. 2.12 Curves of mortality of larvae of *Trichogramma* sp. under low temperatures (after Kot, 1964): 1 – diapausing individuals, 2 – active individuals

A larger or smaller temperature interval at which individuals of a given species can exist occurs within the upper and lower lethal temperature levels. This interval is called the vital zone. It is not identical for both sexes, females generally being more resistant than the males.

2.2.3 Influence of temperature on activity and orientation

The activity of insects starts above a definite temperature threshold, which is characteristic for a given species. There is also an upper thermal threshold of activity. The mobility due to temperature is called thermokinesis. This mobility includes the abandonment of the hibernation site and moulting as well as activity connected with various life stages.

Caterpillars of *Dendrolimus pini* (L.) abandon the litter when the soil temperature rises to 4°C. *Trypodendron lineatus* (Olivier) starts mating in early spring, immediately after the thawing of the soil at 10–12°C, whereas other bark beetles remain in the resting phase during this period. *Pityogenes chalcographus* (L.), for example, starts its activity only at a temperature exceeding 15°C. In most insects movements associated with moulting occur only above a definite temperature threshold. The periods of nuptial flights and oviposition are determined by definite temperature levels, often varying between competitive species or species exhibiting exploitation of one another. Temperature conditions the rate of movement of insects (this rate is frequently a simple function of temperature), their capacity to attack their prey or their own susceptibility to the attack of predators. The activity of *Tabanidae* in attacking cattle

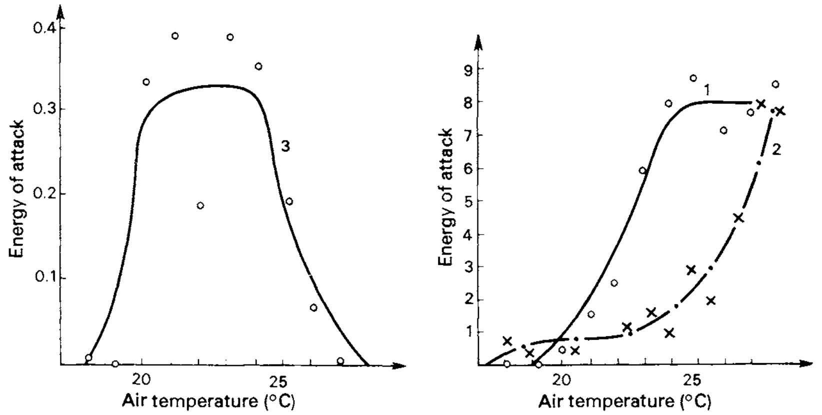


Fig. 2.13 Diurnal activity of *Tabanidae* (after Trojan, 1975): 1 — *Haematopota pluvialis* (L.), 2 — *Tabanus bromius* (L.), 3 — *Tabanus maculicornis* (Zetterstedt)

or horses depends directly on the air temperature (Fig. 2.13). On hot days this activity is so intense that the tabanids can render the work of horses in the forest impossible (Trojan, 1975).

The limits of activity may vary for the different sexes and developmental stages of insects. For instance, first instar larvae of *Melolontha* exhibit a threshold of activity above 0.5°C, whereas those of the third instar have a threshold within the limits of 1.2–2.5°C. The limits (i.e. the upper and lower thresholds) of activity also depend on the adaptation temperature occurring before the introduction of the insect into the limiting temperature. Different effects are also produced by the application of variable temperatures. In general, with wider changes of temperature insects are more active than in stable temperatures.

The 24-hour activity of insects depends less on temperature than on light. Nevertheless, temperature, particularly when combined with changes in the relative air humidity, plays a definite role in the determination of the specific composition of insects appearing at given hours of the day and night. The activity of ichneumonids visiting the flowers of *Peucedanum oreoselinum* (L.) exhibits two frequency peaks depending on temperature and relative air humidity. One of them occurs at 16–19°C and 90–95% R. H., whereas the second is observed at noon at 23–27°C and 50–65% R. H. (Figs. 2.14 and 2.15; Sawoniewicz, 1973).

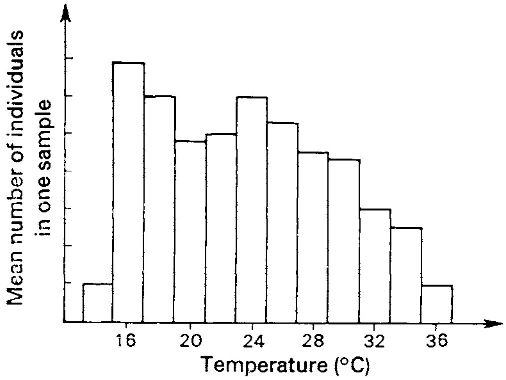


Fig. 2.14 Abundance of *Ichneumonidae* on flowers of *Peucedanum oreoselinum* (L.) in dependence on air temperature (after Sawoniewicz, 1973)

A change in the 24-hour rhythm may occur with the change of temperature at various seasons of the year. *Carabidae* living in Finland on lake banks are active in early summer only during the day, whereas in

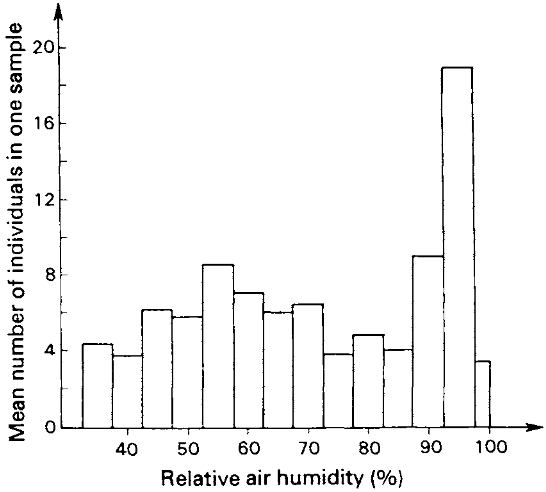


Fig. 2.15 Abundance of *Ichneumonidae* on flowers of *Peucedanum oreoselinum* (L.) in dependence on relative air humidity (R.H.) (after Sawoniewicz, 1973)

late summer they are also active at night (Krogerus, 1948). Frequently the 24-hour rhythm is determined by the combined influence of light and temperature.

2.2.4 *Influence of infra-red radiation on behaviour and orientation*

It is possible that certain species of phytophagous insects find suitable trees for dwellings by the intensity of infra-red radiation. This may be due to the varying intensity of heat adsorption and emission by trees in various physiological conditions. The damage and loss of the assimilation apparatus (e.g. leaves) due to the feeding of various insects, inhibit water flow in tree trunks and cause an increase in their temperature thus limiting heat emission. The damage of tree trunks due to forest fires increases their temperature owing to higher heat adsorption by the darker, smouldered bark. According to the studies of Girs (1967) (cit. after Isaev & Girs, 1975), the temperature of the phloem of Siberian larches damaged by fire differs during the day by 3–15°C from that of undamaged trees and the analogous temperature of the bark surface is higher by 2–23°C. It has also been established that dying trees inhabited by xylophages exhibit higher 24-hour temperature amplitudes than healthy ones (Powell, 1967). Insects such as *Melanophila acuminata* (De Geer) inhabiting burnt forest stands react to heat radiation of 6 μm wavelength via thoracic and antennal receptors which are sensitive to heat and infra-red radiation of 0.8 µm wavelength respectively. The heat receptors detect the fire at a distance of 5 km, whereas the infra-red radiation receptors enhance the orientation of insects at shorter distances. It is noteworthy that the reaction of *M. acuminata* and other species of *Melanophila* depends not on the burning material but on the intensity of the fire. These beetles react to the intense fires of oil wells at a distance of 50 km (Evans, 1962; Evans, 1966; Wright, 1964; Isaev & Girs, 1975). The possibility of the use of infra-red radiation in the orientation of insects has also been established by Dyachenko (1957), and Dyachenko & Glushenko (1967) (cit. after Isaev & Girs, 1975), in his studies on *Monochamus galloprovincialis* (Olivier). Further studies on the influence of the factor under consideration on the behaviour of insects, for instance locating objects of interest, should elucidate to what extent infra-red radiation plays a decisive role in orientation and to what degree its function in this respect is combined with other factors such as temperature and aromatic factors stimulated by temperature.

2.2.5 Dependence of growth and development on temperature

The intensity of metabolism is directly dependent on the body temperature which, in poikilothermic animals, is associated with the temperature of the environment. Attempts were made to fit this phenomenon into the thermodynamic law of Van't Hoff according to which temperature rise of 10°C is accompanied by a 2- or 3-fold acceleration of chemical processes. This proved wrong, however, since the acceleration of chemical processes in living organisms oscillates within the limits of 0–7.4 times. Frequently the rise of temperature is accompanied by a decreased rate or even inhibition of biological processes. The disagreement of this phenomenon with the law of Van't Hoff is attributable to the complex nature of the biochemical processes taking place in a complex colloidal system.

Insects start to develop and grow after reaching a definite temperature called the developmental threshold, biological zero or zero point of development. This point varies for different species and also depends on the developmental stage. In Poland's climatic conditions, for example, it oscillates within the limits of 5–8°C. The zero point for first instar larvae of *Lymantria monacha* (L.) is 3.2°C, with 5.7°C for the second, 7.2°C for the third, 7.6°C for the fourth and 7.8°C for the fifth. That of the pupae, which occur in June, is 8.4°C. The biological zero for eggs of *Bupalus piniarius* (L.) is 8°C, for second instar larvae – 7.3°C, for fourth instars – 5.3°C and for fifth instars (occurring in late autumn) – 2°C (Schwerdtfeger, 1963).

The temperatures quoted above indicate that the biological zero is variable and adapted to mean thermal conditions of the periods at which the individual developmental stages of various species of forest insects occur.

There also exists an upper temperature limit called the upper threshold of development, but the levels for individual species of insects have not been precisely established.

The zone between the lower and upper temperature threshold is called the development zone of the given insect. Since only the temperature within this zone influences insect development, it is called the effective temperature. Its level is determined by the difference between the actual temperature of the environment and the temperature of biological zero of the given species and the given developmental stage of the insect. If the rate of development increases and the length of life decreases with the rise of temperature we can establish that each insect species must be subjected to a definite temperature for a suitable period or, more precisely, that it requires a definite amount of thermal energy in order to complete development. In order to illustrate this dependence, Sanderson & Peairs (1917) and Blunck (1923) proposed the following formula called the rule of the sum of heat:

$$C = (T^0 - t^0) \cdot D,$$

where T^0 = temperature of the environment (in °C), t^0 = temperature of development zero (in °C), D = time of development in days or hours, $(T^0 - t^0)$ = effective temperature.

It is obvious that the rule of the sum of heat may be applied only in the case when the temperature of the environment does not fall beneath the level of the biological zero (Table 2.1). On the basis of numerous

Table 2.1 Development of *Trichogramma evanescens* (Westwood) under laboratory conditions (after Kot, 1964).

Number of replications	Number of females per 1 replication	Temperature, °C	Length of development, days	Total of effective temperatures
3	200	16	26	156
3	200	20	16	160
4	400	25	10	150
4	200	30	8	160

experiments on the influence of temperature on the rate of development (over 400,000 individuals of various insect species were studied) Sanderson & Peairs established that the dependence of the length of development on temperature may be presented in the form of a hyperbolic curve (Fig. 2.16). In order to utilize the hyperbolic dependence, the time of development for at least two stable temperature levels must be determined experimentally (using a thermostat).

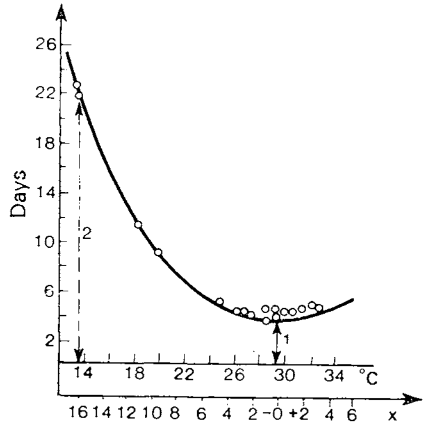


Fig. 2.16 Development of insects in dependence on temperature (after Janisch, 1925): 1 – shortest period of development, 2 – longest period of development

After marking the times of development obtained at the given temperatures on the diagram and connecting them with a hyperbolic line (the temperature level is marked on the axis of abscissae and the length of development in days on the axis of ordinates) we can read off the time of development for any given temperature.

This dependence, together with the knowledge of effective temperatures, is widely utilized for determining the approximate length of development at a given temperature of "quarantine" species. Where these may spread to new geographical regions, this knowledge may also be used to determine the number of generations per year.

The value of C is approximately stable for all individuals of a given species. If this value is known from laboratory experiments, the formula may be transformed and the time of development of the insect (or the given stage) may be calculated as follows:

$$D = \frac{C}{T-t}\,.$$

For the eggs of *Bupalus piniarius* (L.) the value $C = 180°\text{C}$ and the biological zero is 8°C. At a mean diurnal air temperature in summer of 18.5°C, the time of development of these eggs amounts to:

$$D = \frac{180}{18.5-8} = 17 \text{ days.}$$

The thermal requirements of insects determine the number of generations per year under the given climatic and geographical conditions. *Rhyacionia buoliana* (D. & S.) requiring a sum of heat of 3600°C has a single generation per year under the climatic conditions of Poland, whereas to the south of the 40th parallel of northern latitude, as in Syria, where the mean yearly temperature is 20°C, it has two generations per year. *Melolontha* has a 3-year generation in south-western Europe (where the mean yearly temperature exceeds 9°C), a 4-year generation in regions where the isotherm of summer months is 20°C and a 5-year generation to the north of this border.

Species requiring a high sum of heat invariably have a single generation per year (*Neodiprion sertifer* (Geoffroy), *Scolytus ratzeburgi* Janson, *Tomicus piniperda* (L.)) or the length of their development is independent of the rule of the sum of heat.

In many insects the number of generations is stable within various geographical latitudes. *Gryllotalpa gryllotalpa* (L.), for example, has a single generation both in the environs of Leningrad and in Central Asia. In many cases this is attributable to the inhibiting influence of diapause which neutralizes the influence of temperature.

It should be stressed that the values of the sum of temperatures are virtually very similar owing to the different values of biological zero of various developmental stages of the insects and to the action of variable temperatures in the course of 24 hours.

It is also noteworthy that the temperature of the insect's environment differs from the mean meteorological temperature. For instance, the rate of development of a parasite depends on the body temperature and rate of development of its host. *Trichogramma embryophagum* Hartig develops for 2–2.5 weeks in the eggs of *Panolis flammea* (D. & S.), whereas in the eggs of *Acantholyda posticalis* Matsumura (= *A. nemoralis* Thomson) the period of development is mainly much longer.

The intensity of an insect's metabolism is not always proportional to the rise of the environmental temperature, since, as mentioned above, insects are able to regulate their body temperature. Moreover, when we consider that a proportion of the individuals of a given generation can exhibit a different developmental time due to the onset of diapause (*T. embryophagum* in the eggs of *A. posticalis* remain in diapause for an entire year) or to individual properties (e.g. 1- or 2-year generations of *Dendrolimus pini* (L.)), we can understand the wide deviations from the time of development calculated either according to the rule of the sum of heat or by means of the hyperbolic curve. These methods cannot therefore be accepted as satisfactory for the forecast of the quantitative occurrence of forest insects of economic importance.

The experiments of Ludwig & Cable (1934) proved that the influence of changing temperatures on the development of insects is not uniform. The influence of these changes depends on their direction and amplitude as well as on the physiological condition of the individuals. Generally the development of insects is inhibited by temperature oscillations above the optimum level, whereas oscillations within the range between the optimum and the lower thresholds of development produce no distinct deviations from the standard rate of development. On the other hand, oscillations occurring between the optimum and values below the lower threshold of development cause a certain acceleration of development. Since the influence of temperature oscillations on development is slight, perhaps involving several hours and, rarely, several days, attempts have been made to elaborate improved mathematical and graphical methods for determining of the influence of temperature on the developmental time of insects (Janisch, 1925; Prokhonov, 1907, 1908, 1914, cit. after Yakhontov, 1964), (Fig. 2.17).

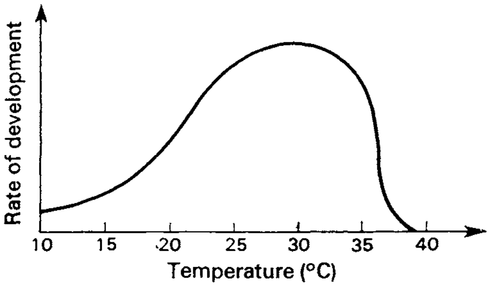


Fig. 2.17 Rate of development of insects in dependence on temperature (after Yakhontov, 1964)

Shelford (1929) introduced the index of the rate of development. He calculated it as the percentage of the entire duration of development according to the following formula:

$$V = \frac{100}{x}$$

where $V =$ rate of development in a time unit, e.g. per 24 hours, $x =$ duration of development of the given stage at a given mean temperature.

Thus, the rate of development is the reciprocal of the time of development determined by the hyperbolic curve ($C = xy$). Hence $c = x\frac{1}{y}$ or $c = x/y$, and this is a linear formula according to which the approximate dependence of the rate of development on temperature may be graphically determined (Fig. 2.18).

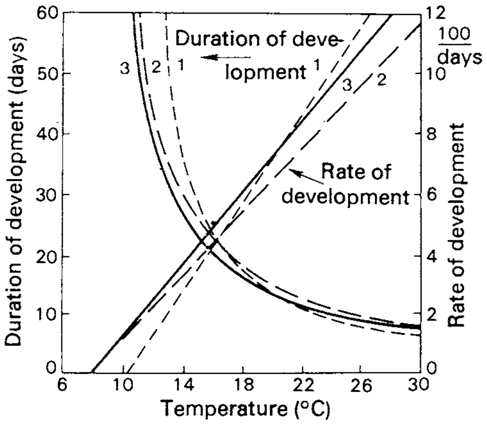


Fig. 2.18 Length and rate of development of eggs of *Dendrolimus pini* (L.) in dependence on temperature (after Schwerdtfeger, 1977): 1 — according to Prokhonov, 1908, 2 — according to Kojima, 1934, 3 — according to Schwerdtfeger, 1963

The rise of temperature accelerating the development of individuals is not always favourable for the development of the population and its later fate since it can lead to a discordance of the developmental rhythm with the general rhythm of seasonal phenomena. For example, in warm, long autumns the caterpillars of *Lymantria monacha* (L.) and L. *dispar* (L.), normally hibernating within their frost-resistant egg capsules, abandon them before winter and perish in large numbers when the temperature falls. On the other hand, in a cool vegetation period and early winter, some insects hibernating as adults may not complete their development in autumn and perish from frost in the larval or pupal stage (e.g. as observed in *Ips typographus* (L.) and *Pityogenes chalcographus* (L.)).

The influence of temperature on the development of a population is still more complex due to its frequently observed effects on sex determination, number of eggs laid and the course of the actual copulation

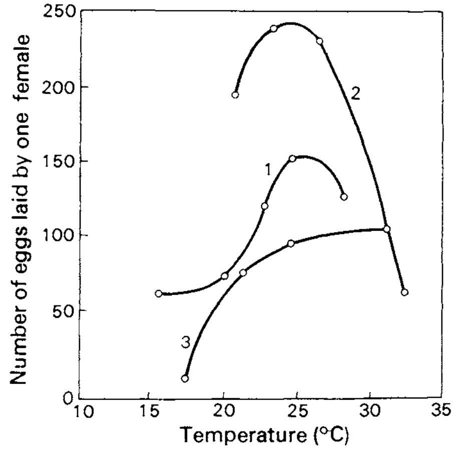


Fig. 2.19 Production of eggs by females of some *Lepidoptera* species in dependence on temperature (after Schwerdtfeger, 1977): 1 — *Lymantria monacha* (L.), 2 — *Malacosoma neustria* (L.), 3 — *Aporia crataegi* (L.)

process. These processes may take place only within definite thermal ranges. In *Formica rufa* L. only males hatch from eggs laid at temperatures below 20°C, whereas females hatch from eggs laid at higher temperatures (within a certain limit of course). Individuals of *Trichogramma cacoeciae* (Marchal) reared at temperatures beyond the range of 15–30°C were practically sterile. *Lymantria dispar* (L.) at 20–30°C produces a constant number of eggs, but produces considerably less at 32°C and more at 14–17°C. On the other hand, the behaviour of *Panolis flammea* (D. & S.) differs in that, at five constant temperature levels within the range of 8–27°C, it lays 186–219 eggs. The number of eggs laid by three species of insects according to the temperature is illustrated in Fig. 2.19.

It can thus be seen that insects exhibit a wide variation in their susceptibility to thermal stimuli depending on the species, sex, stage of development and physiological condition of individuals.

2.3 Humidity and precipitation

2.3.1 Water in the insect body

It is commonly known that water is indispensable in physiological processes taking place in the protoplasm of any organism. All chemical processes in living organisms can only take place in solutions, thus water is indispensable as the component of any organism and as the medium for the physical and chemical processes occurring in the organism. Moreover, water in various forms is an important component of the environment of any organism.

The amount of water in the body of animals generally exceeds 50%. In the larvae of some *Scarabaeidae* it amounts to 78% and up to 67% in the adults. There is a correlation between the water content of an insect's food and that of its own body.

Larvae of *Sitophilus* (= *Calandra*) *granarius* (L.) feeding on grain with a 9–10% water content, contain only 46–47% of water, whereas the larvae of a gelechiid (*Teleiodes* sp.), feeding on hazel leaves containing 71–73% of water, have a water content as high as 90–92%. It should also be stressed that the water content differs in the various organs of the body and is higher in the more metabolically active tissues.

Such figures indicate that food is the main source of the water indispensable for the functioning of any organism. Depending, however, on the species, development stage and site of occurrence of the individuals, water acquired in other ways and from other sources may play an important role in the life of insects. This concerns water absorbed from the environment, i.e. imbibed water and what may be termed metabolic water.

The absorption of water from the environment is a very frequent phenomenon in the forest. Eggs of *Melolontha* absorb water from the soil in amounts augmenting their original volume by a factor of three. Eggs of *Acantholyda erythrocephala* (L.) laid in incisions made in pine needles absorb water from the sap of these needles. Grasshoppers absorb water through their body cover directly from the humid air. Numerous insects drink water from small bodies of water, humid soil and sap secreted by fresh stumps or by wounded deciduous trees. These include numerous *Lepidoptera* and *Diptera* as well as some beetles such as *Lucanus cervus* (L.). Dew is also an important source of water available for insects in the forest.

Insects which live in dry environments, such as *Anobium punctatum* (De Geer) in dry wood, utilize water obtained by the oxidation of hydrogen contained in the food and in substances stored in the body tissues or liberated by the decomposition of sugars and other carbohydrates. This water is called metabolic water since it is produced as a result of metabolic processes.

Excess water in the organism of insects is eliminated with the faeces, by evaporation and, in some cases by glands. The water balance of the organism, i.e. the difference between the amount of water taken in and that eliminated, depends on environmental factors such as temperature, air humidity, air currents and the water content of the food, as well as on individual properties of the species such as its morphological structure, capacity for regulating its physiological condition and its ecological plasticity which may involve a change of environment at periods unfavourable for development.

2.3.2 Tolerance and adaptation

The loss of water by evaporation from the body is one of the most imminent dangers to insects, as in terrestrial animals in general. Insects are usually able to tolerate dessication within a loss of between 10 and 80% of its optimum body water content. Individual species and their developmental stages, however, differ widely in this respect. Eggs of *Melolontha* are polystenohygric and in general cannot tolerate desication since they remain constantly in the soil air saturated with water vapour. Eggs of *Diprion pini* (L.) are mesostenohygric and perish when the air humidity decreases from 80 to 60%. On the other hand, eggs of *Dendrolimus pini* (L.) (Fig. 2.20) and those of *Panolis flammea* (D. & S.) are euryhygric and resist very wide oscillations in relative air humidity (Fig. 2.21). Naturally this is due to the occurrence of various adaptations which protect the body against water loss or to the ability to endure states of semidrying. Even larvae of *Elateridae* normally breathing with air saturated with water vapour are able to endure a considerable water loss reaching, for example, 31% in *Prosternon tesselatum* (L.) (death occurring at a 32–49% water loss) and 52% in *Agriotes lineatus* (L.) (death occurring at a 53–57% water loss).

The time of occurrence of death under the influence of drying or, more precisely, the time between the moment of introduction of the insect into conditions of unfavourable humidity and the moment of loss of the amount of water indispensable for life, varies widely. This can be illustrated by the time of death of the small staphylinid beetles living in the litter of forest areas on lake banks subject to violent drying, the air being almost completely dried by concentrated sulphuric acid. For *Sipalia circellaris* (Gravenhorst) it was 4 hours, with 6–8 hours for *Stenus humilis* Erichson, 11.5 hours for *Philonthus nigrita* (Gravenhorst), 19.9 hours for *P. umbratilis* (Gravenhorst) and 38.3 hours for *Xantholinus tricolor* (F.). No dependence has been established between the rate of drying and the moment of death on the environment from

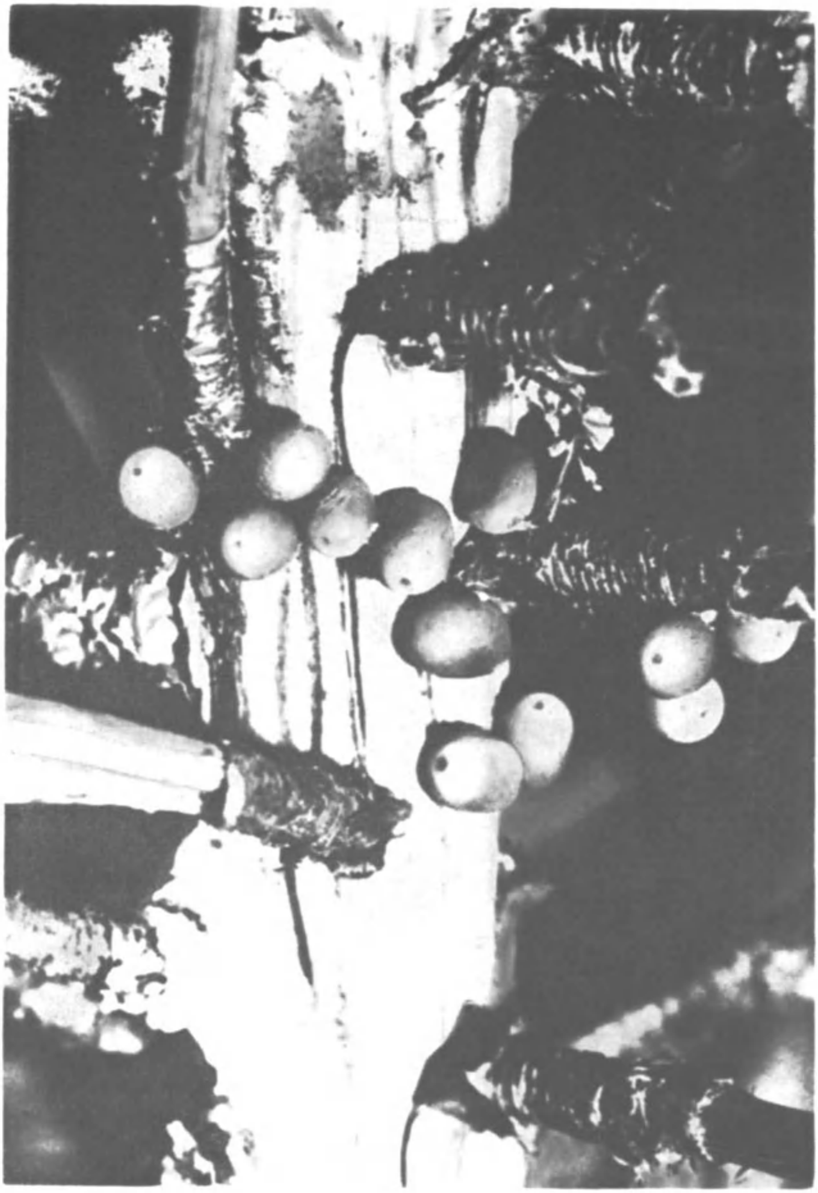


Fig. 2.20 Dendrolimus pini (L.), batches of eggs (photo by S. Kinelski)

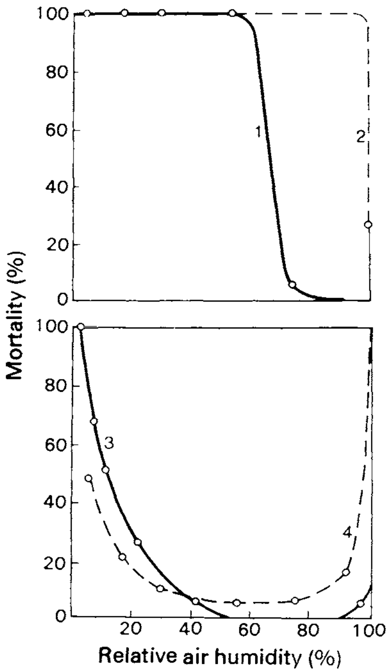


Fig. 2.21 Mortality of eggs of some insect species in dependence on air humidity (after Schwerdtfeger, 1977): 1 – *Diprion pini* (L.), 2 – *Melolontha melolontha* (L.), 3 – *Dendrolimus pini* (L.), 4 – *Panolis flammea* (D. & S.)

which the insects originated or on their size. However, it may be supposed that smaller insects are more susceptible to drying because of the unfavourable (higher) value of the ratio of body surface to volume (Szujecki, 1966b). At variable humidities in a stable temperature, the mortality is higher the wider the amplitude of humidity oscillations (Fig. 2.22). Larvae of *Diprion pini* (L.) reared for 15 days in air of stable and variable humidity exhibited the following percentages of mortality: 7% at a stable humidity of 55%, 10% at humidity changed every 24 hours within the amplitude of 0–100%, 12% at an amplitude of 20–100%, and 7% at an amplitude of 20–90%.

The adaptations which protect insects against drying may be of a morphological, biological, physiological or ethological nature.

Morphological adaptations include the structure of the cuticle whereby the external layer protects the body against evaporation, particularly if it is thick and covered with numerous setae, squamae or other formations. On the other hand, numerous experiments have proved that the

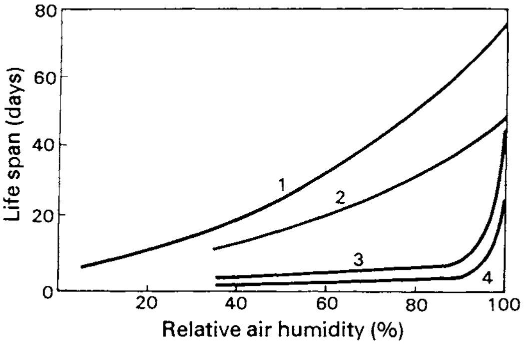


Fig. 2.22 Life span of some ant species in dependence on air humidity at 15°C (after Schwerdtfeger, 1977): 1 – *Leptothorax nigriceps* Mayr, 2 – *L. unifasciatus* (Latreille), 3 – *Tetramorium caespitum* (L.), 4 – *Lasius niger* (L.)

structure of the cuticle is not the only barrier which protects the body against drying. An important role in this respect is performed by the apparatus which closes the tracheae and regulates respiration by conveying and removing humid or dry air. Also sensory setae (hygroreceptors) found on the antennae or the legs of many insects may be classed as morphological adaptations. They provide the insect with information regarding environmental changes and thus warn the insect via the nervous system of any dramatic fall in the environmental humidity (Fig. 2.23).

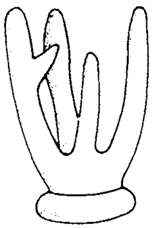


Fig. 2.23 Ramified humidity receptor on antenna of *Tribolium* sp. (after Chapman, 1969)

Among the biological adaptations we should mention the structure of various types of cocoon inhabited by pupae or larvae of insects such as the *Diprioninae* and *Coleophora laricella* (Hübner), coccoliths protecting lamellicorn pupae (Fig. 2.24), portable cases formed of excrement by larvae of *Cryptocephalus* and *Clytra* (*Chrysomelidae*) (Fig. 2.25)

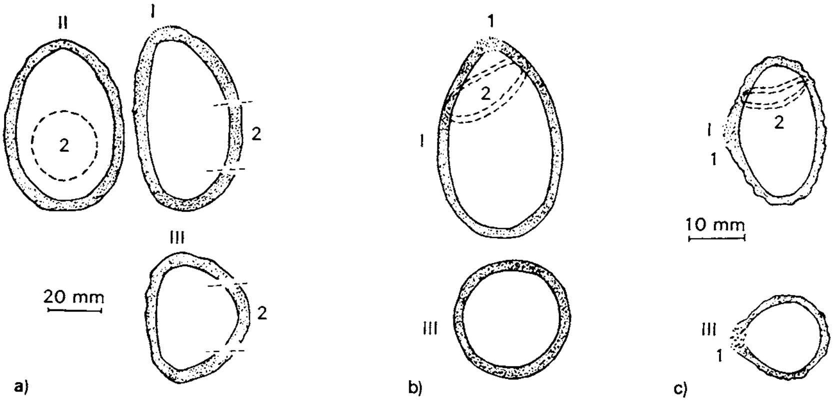


Fig. 2.24 Sections of coccoliths of *Lamellicornia* (after Pawłowski, 1961): a) shaving-shaped coccolith of *Lucanus cervus* (L.), b) coccolith of *Osmoderma eremita* (Scopoli), c) coccolith of *Liocola lugubris* (Herbst): 1 – air sieve, 2 – outlet, I – longitudinal section, II – horizontal section, III – cross-section

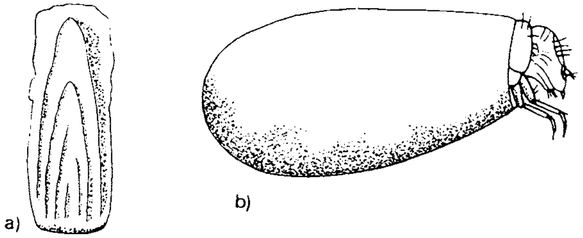


Fig. 2.25 Various types of protection of chrysomelid larvae and pupae against drying (after Ogloblin and Medvedev, 1971): a) scatoconcha of larva of *Clytra quadripunctata* (L.), b) larva of *Cryptocephalus* (Müller) in scatoconcha

as well as the production of foam from the sap leaking from shoots damaged by *Aphrophora* spp. (Fig. 2.26). It has been established that the larvae of *Malacosoma neustria* (L.) lose 9.4% of their weight in the course of 5 days after removal from their cocoon, whereas those remaining in the cocoons lost only 3.5%. Diapausing larvae of *Neodiprion sertifer* (Geoffroy) removed from their cocoons lost after 7 days 24% of their weight, whereas specimens remaining in their cocoons lost only 8% (Schwerdtfeger, 1963). Humidity is also regulated in the large nests of insects living in societies or groups, such as in ant-hills or hornet nests.

An important role is played, especially in insects living in dry environments, by those physiological adaptations which regulate the adsorption of water from food and those which control the functioning of the tracheal system by which metabolic water is produced by the oxidation of hydrogen within the organism. Moreover, the occurrence of rectal glands in the hind-gut aids the resorption of water from the faeces,

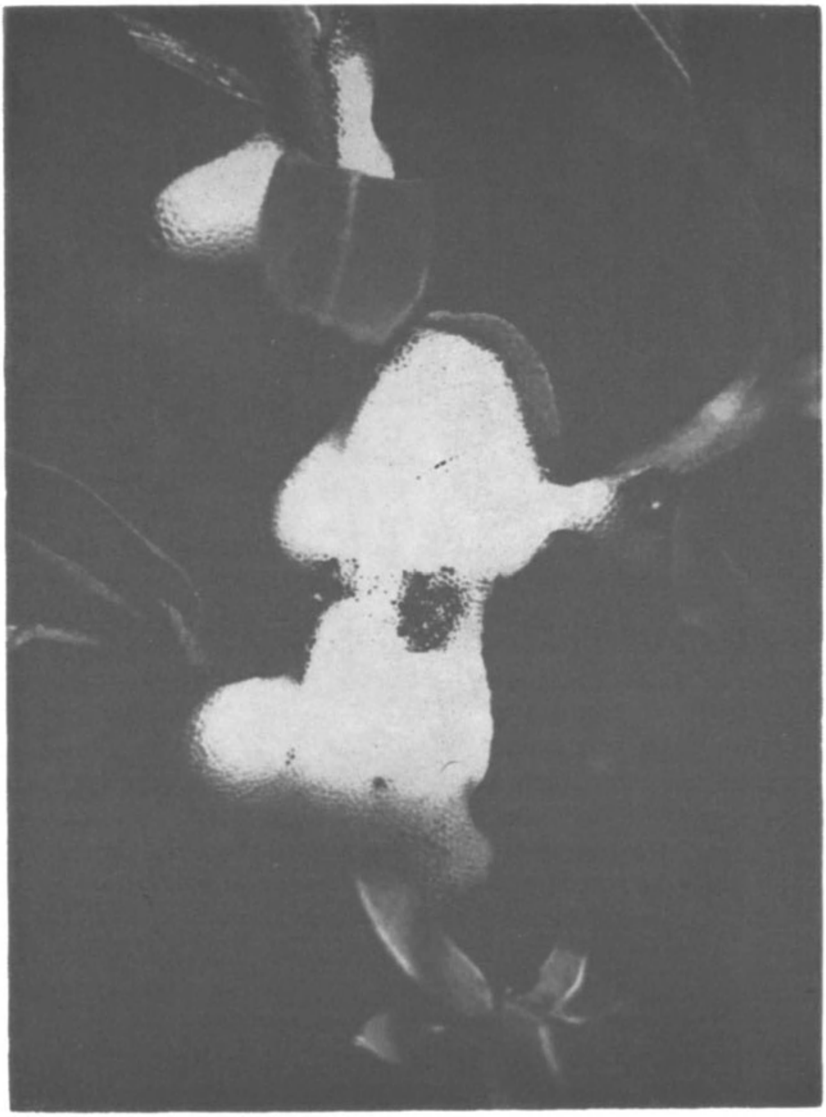


Fig. 2.26 Larvae of *Aphrophora salicina* (Goeze) on *Salix cinerea* (L.) (photo by W. Strojny)

which explains why the excrement of *Dendrolimus pini* (L.) caterpillars, as well as that of other caterpillars and larvae of *Symphyta* feeding on pine needles, are dry. Physiological adaptations also include mechanisms which induce aestivation under conditions of drought.

Ethological adaptations are most common. They involve changes in the behaviour of insects under the limiting influence of humidity deficiency.

When the soil is dry, many insects penetrate into the deeper layers or cease feeding on humus and penetrate into the roots of plants. A more pronounced migration of insects from dry areas to more humid biotopes also occurs, and this is facilitated by the presence of hygrotactic hairs. The course of the diurnal activity characteristic of many insects consists in the adaptation of a rhythmical character associated with the rhythmical changes in air humidity during the course of the 24-hour period. This does not necessarily indicate, however, that the 24-hour activity pattern is entirely dependent on the diurnal air humidity. A considerably more important influence in this respect is attributable to the competitive coactions and primarily to the light factor.

The negative influence of water excess in the forest environment can best be observed in inundated soil insects. Inundated larvae of *Melolontha hippocastani* F. increase their weight by 28–42% and perish after 2–10 days. Other soil beetles, particularly *Carabidae* and *Staphylinidae*, also suffer a high mortality from the effects of water excess and low temperatures.

2.3.3 Activity, orientation and preference phenomena

The activity of insects is often influenced by the humidity of the air. Caterpillars of *Dendrolimus pini* (L.) feed most intensely at 75% relative air humidity whereas those of *Panolis flammea* exhibit no correlation in this respect. The mobility of many insects is dependent on a definite air humidity so that the flight of some species only occurs in the evening. Such mobility due to humidity stimuli is called hygrotaxis. Positive and negative hygrotaxis may be distinguished. Many insects, such as the caterpillars of *Lymantria dispar* and *Dendrolimus pini* as well as the larvae of *Diprioninae* as compared with most soil insects, exhibit no directional reaction to humidity. Ants of the genus *Myrmica* distinguish humidity changes within the limits of 10% whereas larvae of *Agriotes obscurus* (L.) and *A. lineatus* (L.), by means of their antennal and palpal sensillae, can distinguish differences within the limits of 99.5 to 100%

air humidity, i.e. changes within the range of 0.5%. Due to this ability to distinguish changes in humidity conditions, numerous insects exhibit a distinct humidity preference. Many studies have been performed on the humidity preferences of soil insects. Laboratory experiments have shown that the preferences correspond approximately with the humidity conditions occurring in the insects' natural environments (Fig. 2.27).

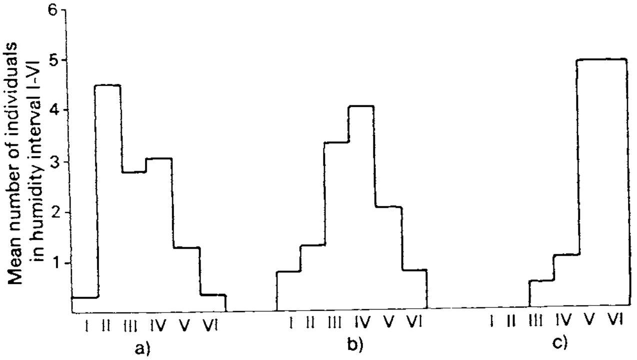


Fig. 2.27 Preference of soil humidity of some *Staphylinidae* (original): a) *Stenus clavicornis* (Scopoli), b) *Othius myrmecophilus* (Kiesenwetter), c) *Ochthephilum fracticorne* (Paykull). Ranges of substrate humidity in experiments: I – 0%, I – 1.25%, III – 2.5%, IV – 5%, V – 10%, VI – 20% (water-saturated sand)

The increases in the population densities of large *Carabidae* such as *Carabus arcensis* Herbst and *C. nemoralis* Müller in definite biotopes, which result from the influence of intensive precipitation, take different courses in each of these species. This is due to their different humidity requirements. *C. arcensis* normally occurs in a variety of biotopes but mainly in those of moderate humidity. *C. nemoralis*, on the other hand, is distinctly hygrophilous. The population of *C. arcensis* thus becomes denser with increased rainfall in the coniferous forest association on dry soils and considerably rarer in the more humid biotope of the mixed coniferous forest. The population of this species remains low on very humid soils of the transitional area between mixed coniferous forest and alder bog forest. Different phenomena are observed in *C. nemoralis* in that with intensified precipitation its population increases in the mixed coniferous forest habitat as well as in the transitional area to alder bog forest, whereas it remains very low in the pine forest biotope (Fig. 2.28).

These data correspond with the results of laboratory studies on the humidity preferences of these species (Grüm, 1971). Various developmental stages of certain species and individuals of different sex exhibit different preference ranges. The humidity preference may be largely de-

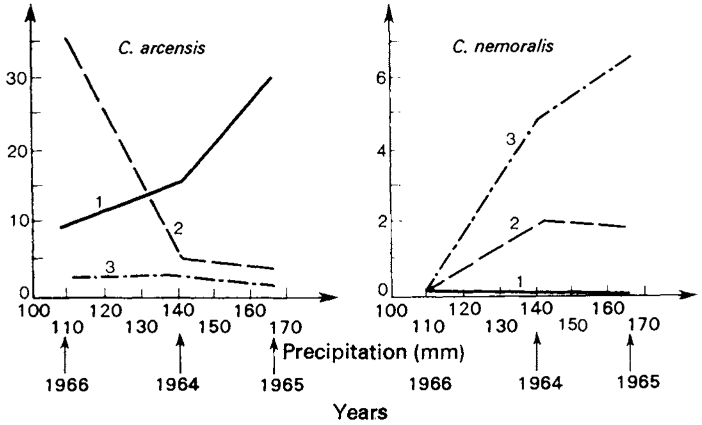


Fig. 2.28 Dependence between total precipitation in May and June and changes in the population density of *Carabus arcensis* Herbst and *C. nemoralis* Müller in three biotopes (after Grüm, 1971): 1 – *Pino-Vaccinietum myrtilli* (5.6% of water content in soil), 2 – *Pino-Quercetum* (8.4% of water in soil), 3 – ecotone between *Pino-Quercetum* and *Alnetum* (24.2% of water in soil)

termined by the current water balance. When its water content was artificially lowered, *Harpalus serripes* (Quensel) (*Carabidae*) became an outstanding hygrophil, but when reared under conditions of high humidity it behaved as a xerophil. The change from a humid environment to a dry one, as occurs for many litter insects of marshy coniferous forests in the autumn, is probably due to the tendency of the organism to drying and removing the superfluous or even noxious water excess which occurs in winter.

The changes in tolerance to humidity conditions in insects thus depend on the developmental stage, sex, physiological constitution, feeding conditions, season of the year and temperature.

2.3.4 Influence of humidity on reproduction and development

There is a certain amount of information in the literature on the influence of humidity on the course of copulation and oviposition in forest insects. Zwölfer (1931) reported that copulation in *Panolis flammea* (D. & S.) proceeds more favourably at a relative air humidity of 80–90% than at 100% humidity. The parasite of *Diprionidae*, *Dahlbominus fuscipennis* (Zetterstedt) lays more eggs at higher air humidities, the number of eggs laid decreasing with increasing humidity deficiency.

The developmental time of insects is considerably less dependent on humidity than on temperature, although both dependences vary for different species. The time required for the development of the embryo is only slightly dependent on air humidity, although it is generally somewhat shorter when humidity increases (*Lymantria monacha* (L.), *Dendrolimus pini* (L.), *Ergates faber* (L.), *Hylotrupes bajulus* (L.)). Under unfavourable humidity conditions the development of eggs may be completely inhibited. The time of development of larvae of *D. pini* is shorter at high humidity values (about 90%) than at lower ones. Other species, however, do not exhibit this dependence. It has been observed that in some species, such as those of the genus *Anthrenus*, the number of moults increased in dry air due to the prolongation of development. In general, the time of development of pupae decreases somewhat with an increase in humidity, although in *Carpocapsa* sp. a slight prolongation of development was observed when humidity levels were raised. The life span of adult insects increases with rising relative air humidity, although Zwölfer (1931) reported that the length of life of adults of *Panolis flammea* was considerably shorter under conditions of water-saturated air. This indicates that in general a higher humidity shortens the developmental period of insects and prolongs the life of the adults.

The correlation between the developmental rate of wood-feeding insects and environmental humidity may be readily established. It appears that the optimal rate of development of *Hylotrupes bajulus* takes place when the humidity of the wood is approximately 35%, and that of *Ergates faber* when it is about 60% (Fig. 2.29).

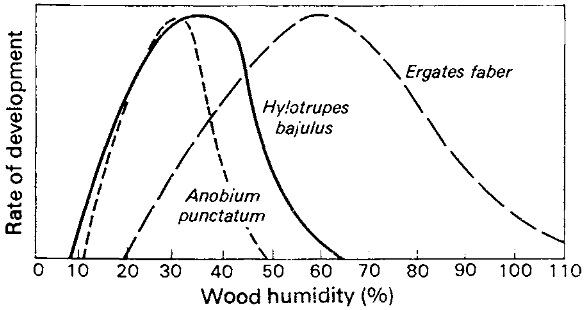


Fig. 2.29 Dependence of rate of development of larvae of xylophages on wood humidity (after Schwerdtfeger, 1977)

Decreasing the humidity of wood to 20% inhibits the development of larvae of numerous insects such as *Siricidae*, *Cerambycidae* and some *Scolytidae*.

2.3.5 Precipitation

The influence of air, wood or soil humidity on insects is frequently the indirect result of the amount of precipitation and its distribution during the course of the year.

The indirect influence of precipitation is very important. Precipitation affects insects not only through the humidity conditions discussed above, but also with respect to the food factor. Drought, for example, causes a lowering of the soil water level and in consequence changes the physiological condition of trees in such a way that feeding conditions for insects become more favourable. Also, damage to the root system of trees, due to the combined influence of intensive precipitation and wind, plays an important role in the development of secondary pests.

Precipitation also exerts a direct influence on the life of insects. Rainfall can disturb the reproductive cycle of pests or useful insects. Thus its influence on the frequency of these insects in this respect depends on whether rain occurs at the period of their nuptial flights (Fig. 2.30). In the case of forest pests, for example, the poorly flying *Bupalus piniarius* (L.) is particularly susceptible to rain. Intensive rains also inundate the

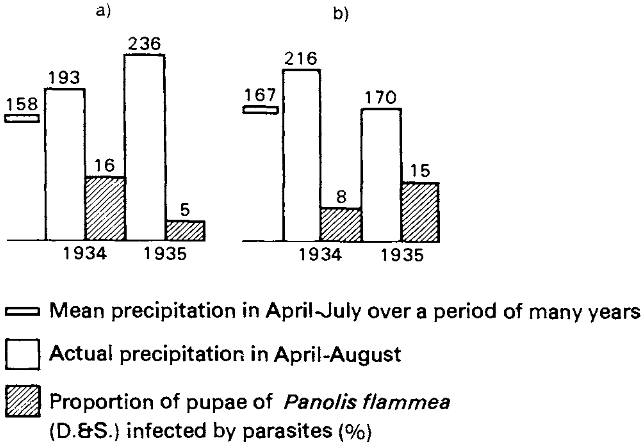


Fig. 2.30 Percentage of pupae of *Panolis flammea* (D. & S.) killed by parasites in dependence on the amount of precipitation (after Nunberg, 1937). Calculated for two groups of forest stands: a) on sites where precipitation exceeded the several-years' mean, b) on sites where precipitation was lower than the several-years' mean

galleries of some xylophages such as *Trypodendron*, thus killing the feeding larvae (Dominik, 1968b). In extreme cases intensive rain, and hail in particular, can mechanically destroy insects, especially their immature stages feeding on the surface of leaves or pine-needles. Rain occurring in winter is harmful to pests hibernating in litter, whereas snow is favourable for such insects because it protects them against low temperatures.

2.4 Air, atmospheric pressure and wind

In the part of the insect's environment above the ground, the composition of the air undergoes only slight changes and thus has hardly any influence on their life. On the other hand, the oxygen content of the air of forest soils may be a limiting factor. Insects suffer oxygen deficiency in the soil at periods of excessive humidity and this also limits their penetration to deeper levels.

It is noteworthy that the tolerance of insects to CO_2 excess is particularly high and only in exceptional cases may it become a limiting factor. Changes in atmospheric pressure, just like any intensification of air vibrations, may exercise a certain stimulative influence on the emergence of *Lepidoptera* and on the activity of certain *Diptera*. Schwerdtfeger studied the kinetic effect of air vibration on the adults of *Bupalus piniarius* which started to fly from tree trunks at toots of cars. An increased activity of insects such as dragon-flies was observed under the influence of rising air ionization.

The most important influence on the life of insects, however, is exercised by air currents, i.e. winds and ascending currents. The percentage of wingless insect species increases in sites where intensive air currents occur. In the European mountains the percentage of non-flying insects above the upper forest line is 70%, whereas on lowlands it is only 5%. Forest insects without strong wings, such as *Bupalus piniarius* fly almost exclusively in calm weather, whereas the strong-flying *Panolis flammea* utilizes weak air currents in its nuptial flights.

Taeniothrips laricivorus Kratochvil & Farsky abandons the branches of larches and takes cover in crevices of the trunk bark during strong winds.

The phenomenon whereby insects glide on air currents is called anemochoria. It may be the cause of the widespread dispersal of pests, particularly young caterpillars covered with long hairs (e.g. *Lymantria* *dispar* (L.)) and larvae producing gossamer (e.g. *Choristoneura murinana* (Hübner)). First instar larvae of *Lymantria monacha* may even be transferred by winds blowing with a velocity of 0.7 m per second.

The altitude to which insects are carried by ascending air currents may amount to several thousand metres. Air currents may even sweep up wingless insects and larvae. The wingless *Collembola*, as well as numerous *Thysanoptera*, *Diptera* and *Hymenoptera* were captured by means of special devices mounted on baloons and aeroplanes at the altitude of 4000 m. Invertebrates floating in the atmosphere are called aeroplankton.

Strong unidirectional and long-lasting winds may contribute to the long-distance flights of strongly flying insects. Butterflies of the genus *Danaus* fly from Mexico to Alaska, thus covering a distance of 4000 km. In some years, eastern winds in Poland facilitate the dispersal of *Aporia crataegi* (L.) butterflies flying from the east. Their caterpillars later feed on deciduous trees. Analogously *Lymantria monacha* is continuously carried from the continent to England. *Aphidoidea* found at Spitsbergen are transferred a distance of 1000–2000 km from Scandinavian regions.

The direct influence of air currents on the development of insects is slight. Strong winds render copulation impossible for many insects and impede oviposition, thus reducing their numbers. They also blow down larvae feeding in the crowns of trees and sometimes catch up great numbers of insects in the course of their nuptial flights and carry them to unsuitable environments or even cause their death by carrying them to bodies of water. Such a phenomenon was observed in the second half of 19th century when, during a mass appearance of *Lymantria monacha*, strong winds carried off millions of individuals above the coniferous forests of the Masurian Lakeland and drowned them in the Baltic Sea. The remains of the insects washed up by the sea onto the beaches formed a heap several kilometres long and in some places over 0.5 m high.

Under experimental conditions it has been established that weak winds with velocity of 0–2 m per second have hardly any influence on the development of *Lymantria dispar*, although they may slightly prolong the development and diminish the number of eggs laid and also diminish the weight of the pupae.

The indirect role of air currents in the life of insects consists primarily in the occurrence of definite weather types influencing the activity of insects and the physiological condition of the plants on which they feed. A certain influence is also exercised by winds through the motion of tree crowns and the consequent changes in illumination of the forest floor regulating the activity of insects such as *Larvaevoridae*. Furthermore, weak air motions are very favourable for the transference of certain odours which inform insects of the location of suitable food sources or which facilitate the congregation of individuals of a given species. In the case of forest insects such as *Scolytidae*, especially those belonging to the genera *Hylastes* and *Hylurgops*, as well as *Curculionidae* of the genera *Hylobius* and *Pissodes*, this phenomenon is particularly important since scent stimuli due to the presence of α-pinenes in the resin of coniferous trees facilitate the location of food and sites of reproduction. Air currents also carry the scents of pheromones which play an important role in communication between individuals of a given population. The pheromones may be released by individuals which have found trees suitable for feeding sites and thus attract other individuals of the population. Air currents also transfer the scents of glandular secretions characteristic of females of numerous species of butterflies and other insects. These female scents attract the males during the period of mating.

It is obvious that, in some cases, winds selectively affecting certain components of insect associations are able to change the quantitative proportions involved in these associations. This is principally due to the fact that factors which are harmful to species of differing abundancies and which are associated with functional dependences, reduce the number of predators and parasites to a higher degree than that of the more frequent hosts. This generally leads to mass outbreaks of phytophagous species.

2.5 Integrated action of climatic factors

Individual climatic factors affect insects as complex groups and not as separate individuals. There is much data available on the combined influence of temperature and humidity. The results of such studies on the development of insects at various temperature variants and constant humidity, as well as at various humidity variants and constant temperature, can be plotted on diagrams called thermohygrograms. These facilitate the estimation of the range of mortality distribution for various developmental stages of different forest insects. The limits of these mortality ranges determine the temperature and relative air humidity intervals at which life processes may occur. Figure 2.31 illustrates the ranges of the combined influences of temperature and humidity on the mortality curve of the eggs and first instar larvae of *Panolis flammea* (D. & S.).

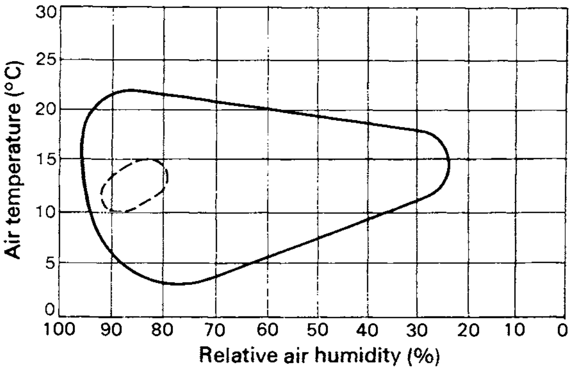


Fig. 2.31 Mortality curve of eggs (continuous line) and of first instar larvae (dashed line) of *Panolis flammea* (D. & S.) in dependence on temperature and relative air humidity (after Gusev *et al.*, 1961)

2.5.1 *Climograms, bioclimograms and hygrothermic coefficient*

Climograms are constructed by graphically plotting the mean monthly values of the temperature and relative air humidity (or amount of precipitation) occurring in a given locality. The mean monthly temperature values are marked on the axis of ordinates and those of humidity or precipitation on the axis of abscissae. Months are denoted by numbers beginning from January. The lines connecting the points determining the hygrothermal conditions of individual months form a dodecagon which represents the annual hygrothermal situation of the given locality. The plotting of such diagrams for areas in which the given pest exhibits a tendency of mass occurrence and their comparison with diagrams prepared for areas where the pest occurs but causes no damage, leads to the determination of which climatic factor has the most decisive influence on the mass development of the pest, and its time of occurrence (Fig. 2.32). The comparison of thermohygrograms plotted for individual developmental stages of a given insect with climograms prepared on the basis of data obtained at the periods when the successive stages occur, gives a more or less precise estimation as to whether the given species has a possibility of mass reproduction in the given geographical area. The use of climograms was originally introduced in 1910 by Boll and was later improved upon by other scientists.

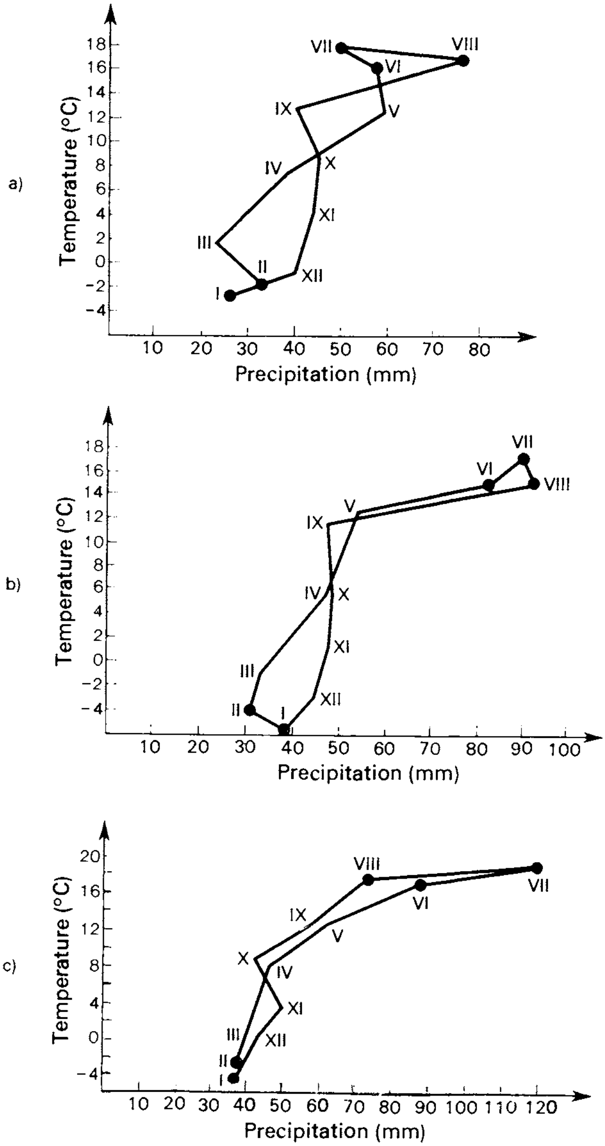


Fig. 2.32 Climograms for localities characterized by a various degree of invasion of pine plantations by *Rhyacionia buoliana* (D. & S.) (after Koehler, 1967): a) zone of mass occurrence (Krzyż), b) zone of sporadic occurrence (Suwałki), c) zone in which the insect occurs as result of influence of industrial pollution on pine plantations, ● months of particular importance for the course of population-dynamic processes (Roman numerals denote months)

Uvarov marked the lines on the climogram connecting particular months in which the development of a definite stage of a given species occurs with a colour or thickness differing from that of the lines connecting months in which other stages develop. Thus he plotted bioclimograms (Fig. 2.33). By drawing rectangles on the bioclimograms, the upper and lower borders of which determined the maximum and minimum lethal temperatures, whilst the lateral sides determined the analogous humidity values, it was possible to establish accurately whether the given insect had a chance of mass occurrence in the area studied. If the answer is positive the lines of the bioclimogram determining the development of a definite stage are included within the given rectangle, whereas in the case of negative answer they are beyond the rectangle. A similar method

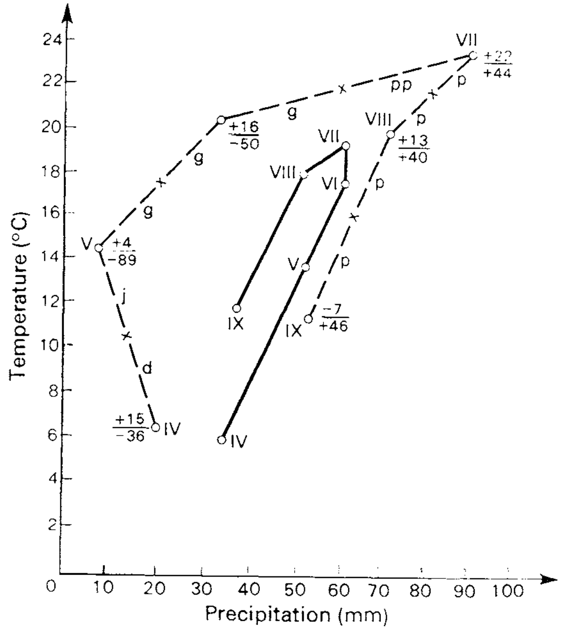


Fig. 2.33 Bioclimogram (after Ilinskii & Tropin, 1965): continuous line – several-years' mean, dashed line – mean of individual months in 1936; Roman numerals – months, fractions – deviations from several-years' mean (numerator – temperature, denominator – precipitation, mm); letters – successive development stages of *Panolis flammea* (D. & S.): d – adult, j – egg, g – caterpillar, pp – prepupal stage, p – pupa

gave an indication of the months in which the amount of precipitation or temperature level are decisive for the reproduction of the pest.

In order to obtain this information climatic data and requirements of the given species in years in which a mass occurrence of the pest was observed were compared with analogous data of years in which a quantitative depression occurred. The part of the diagram above the rectangle indicated temperatures too high, and that below the rectangle temperatures too low for the given species. Analogously the parts of the diagram on the right and left sides of the rectangle represented excessive and deficient precipitation respectively.

Comparison of climograms of years of outbreaks with those plotted using the mean values of a number of years allows one to establish which climatic factors during a given period differed most significantly from the yearly means and which had most influence on development.

The knowledge of hygrothermal requirements of individual species enables one to forecast the possibility of their appearance and reproduction in any year and under various geographical conditions. This is achieved by means of the hygrothermal coefficient calculated according to Rubtsov's formula:

$$Ah = \frac{R}{\sum (t-c)},$$

where Ah = the hygrothermal coefficient for the given year or vegetation period, R = the total precipitation during the course of the year or vegetation period, $\sum (t-c)$ = the sum of the monthly mean effective temperatures (c = lower development threshold).

When the hygrothermal coefficients are determined for various geographical localities it is possible to trace the limits of areas which are uniform with respect to the developmental conditions for any given insect species.

Climograms, bioclimograms and isopoids (curves connecting points with the same value of the hygrothermal coefficient) can provide data for the analysis of the possibility of mass occurrence of insects and also, in some cases, data for forecasts. At present, however, these data are mainly used for analyses concerning the introduction of species and the possibility of their occurrence under new geographical conditions.

Despite its popularity in the 1920's the method of climograms is rarely applied now. This is due to the fact that, although climatic factors influence the size of the population to a great extent, they are frequently not the only factors which have to be considered.

2.5.2 Influence of the forest mesoclimate on the distribution of insects

The mesoclimate of the forest is distinctly different from the climate of open areas. The differences increase with the increasing density of the forest stand and the increasing number of plant layers which occur in it. In this way each forest type exhibits a characteristic mesoclimate.

The particular elements of the forest mesoclimate have a complex influence on the distribution of insects within the forest. The temperature differences which occur between definite sites within the forest environment may be explained by the different amounts of sunlight received by each. Thus, the most insolated parts of the forest are also the warmest, though wide temperature amplitudes may occur here. On the other hand, temperature determines the relative air humidity. Because of this, the most insolated sites under the same soil conditions generally exhibit the driest air. This is particularly significant on eminences and their southern slopes as well as at the forest edges. On such sites photophilous and thermophilous insect species such as *Buprestidae*, *Panolis flammea* (D. & S.), *Dendrolimus pini* (L.) and *Ips acuminatus* (Gyllenhal) and ants are generally found (Fig. 2.34). On the other hand, hygrophilous species having lower temperature and light requirements such as *Hylurgops palliatus* (Gyllenhal) are grouped in depressions.

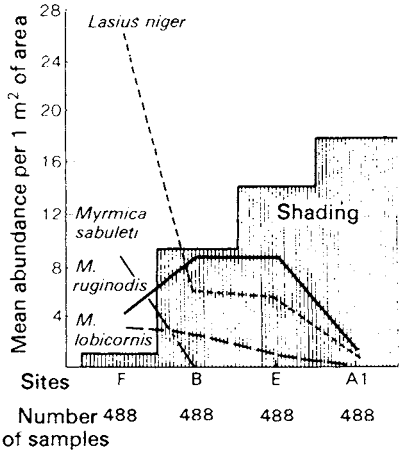


Fig. 2.34 Influence of shading of forest floor on occurrence of certain ant species (after Kaczmarek, 1953)

Buprestids are particularly susceptible to light intensity. Their development requires considerable amounts of heat and they are only active in full light. *Phaenops cyanea* (F.) occurs in pine forests growing in a wide variety of soil humidity conditions, but invariably on intensively insolated sites. It avoids very dense forest stands and those characterized by the occurrence of a rich undergrowth or a second tree layer. Species of the genus *Agrilus* occur in numbers on trees growing on insolated forest edges or stumps and snags in clearings.

Studies on the distribution of secondary spruce pests have shown that *Anthaxia quadripunctata* (L.) was predominant on the southern edges of a certain forest stand, whilst *Polygraphus poligraphus* (L.) was predominant 50 m deeper into the forest stand and was accompanied by *Orthotomicus laricis* (F.), *Tetropium* sp. and *Rhagium* sp. Transiently insolated sites were occupied by *Caenoptera* sp., *Pissodes harcyniae* (Herbst) and *Siricidae* (Vorontsov, 1960).

Projects of any cultivation measures or timber exploitation, as well as plans of forest management, should invariably consider the requirements of individual pest species as regards microclimatic conditions and should avoid forestry practices favourable for their development. The neglection of these rules of forest hygiene invariably leads to economic difficulties. Thus in the past the application of alternate strip cutting caused an intensified occurrence of *Ips typographus* because the forest light conditions were particularly favourable for its development. The microclimatic requirements of forest insects must also be considered in the course of the control of secondary pests since only by selecting suitable sites for traps may their efficiency be secured.

There are numerous examples which illustrate the protective role of the undergrowth and herb layers of forest stands or plantations undergoing attacks of photophilous and thermophilous insects. Dangerous poplar pests such as *Saperda carcharias* (L.) and *Sesia* (= *Aegeria*) *apiformis* Clerck attack the trees near their root necks. *S. apiformis* exclusively invades trees on which the illumination is at least 32,000 lx. By shading the lower parts of the poplar trunks, the trees are afforded a great deal of protection from the invasion of this pest.

It has frequently been observed that the pests generally invading the lower (but illuminated) parts of trees, such as *Cerambyx cerdo* L. on oak (Fig. 2.35) and *Poecilonota variolosa* (Paykull) on aspen, move from the region of the root necks to upper parts of the trunk when in the shade.

The temperature of the southern side of the trunk is considerably higher by 10–20°C than that on the opposite side, both in summer and in winter.

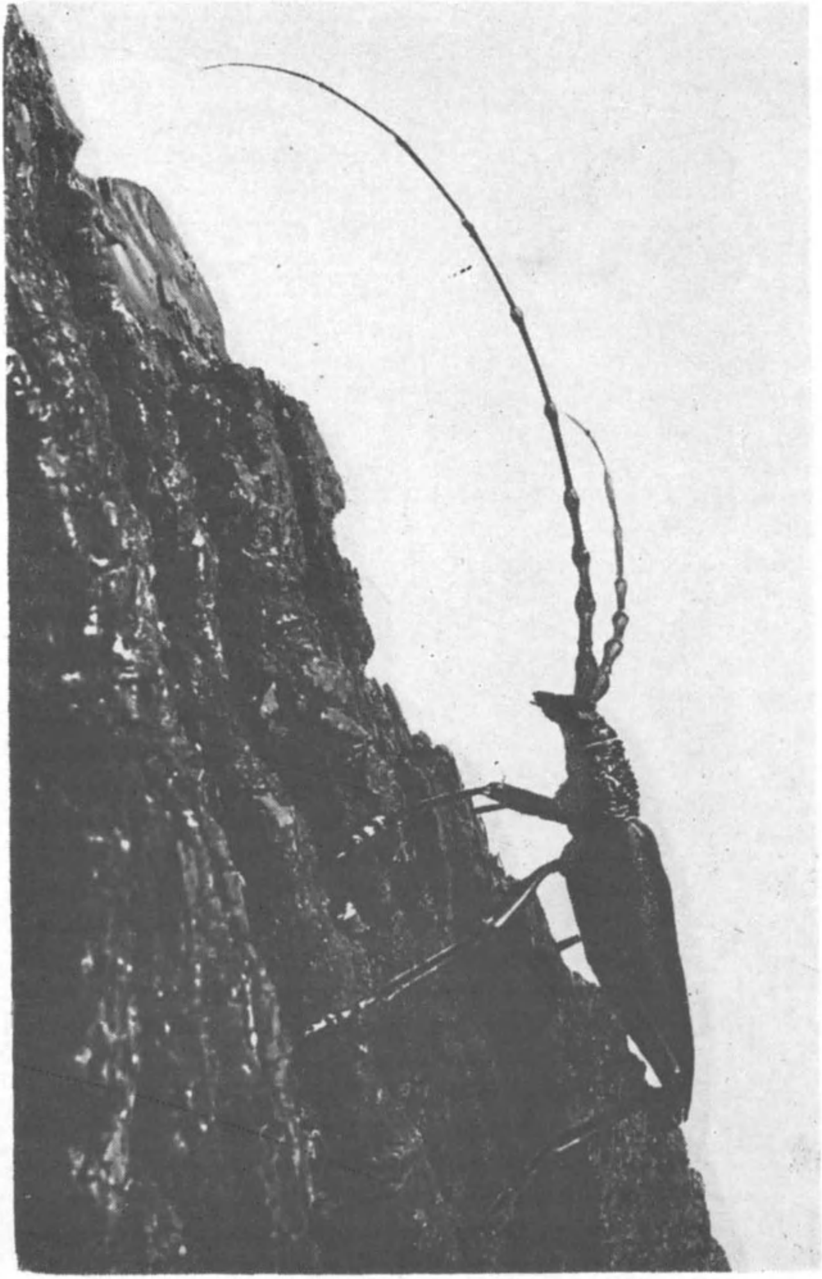


Fig. 2.35 Cerambyx cerdo L. (photo by W. Strojny)

Numerous species of *Scolytidae*, *Cerambycidae* and *Buprestidae* in particular invade the southern side of trunks if the trees grow within the forest stand. On the other hand, on southern forest edges and on solitary trees the most insolated parts of trunks are generally avoided by secondary pests since the high temperature occurring under the bark in June and July would lead to the death of larvae. The rapid drying or overheating of the cambium would also render the development of the insects impossible. Only some *Buprestidae* such as *Anthaxia quadripunctata* (L.) and *Phaenops cyanea* (F.) and sometimes also *Siricidae* are able to inhabit those sites. Felled trees are invaded by insects in an analogous way. Because of this, the exposure of logs to the intensive action of the sun's rays and their rapid drying can partly prevent their being attacked by *Trypodendron lineatum* (Olivier) and some other pests. The secondary pests occurring on trees lying on insolated sites prefer to invade the lateral, partly shaded sides, which is also associated with the humidity of these parts of the logs.

Individual parts of the tree crown are subjected to different amounts of insolation at different times of the day. This determines the distribution of insects occurring here. At an air temperature of 30°C the temperature of the leaves rises under the influence of the sun's rays to about 38°C, although this depends on many factors such as the inclination and superficial structure of the leaf, etc. At such temperatures the insects occurring on the leaves are obliged to migrate to other parts of the crown or to interrupt feeding. Because of this numerous species of *Chrysomelidae* (though belonging to photophilous and thermophilous insects) invariably feed and lay eggs on the lower side of the leaves of poplars and willows.

Striking examples of the influence of the mesoclimate on the distribution of insects are provided by observations on the entomofauna of clearings. Different species prevail near the southern borders of clearings whilst others prefer the northern side where the conditions at the foot of the insolated wall of the forest stand favour the occurrence of thermophilous insects.

The occurrence of *Dendroctonus micans* (Kugelann) constitutes the most outstanding example of the influence of environmental humidity on the distribution of insects. In Europe this species usually attacks spruces on the lower part of the trunk. In extreme cases, under conditions of dry soil and intensive insolation it feeds beneath the soil level on the root neck and on roots. On the other hand, in very dense humid spruce forests as well as in the mountains *D. micans* is more frequently observed on tree trunks at the height of above 2 m. In the north-western part of the USSR this species becomes a dangerous pest on peat-land where it attacks pines, invading their lower parts. The drying of peat-land protects the forest stands against this pest and liquidates the centres of its occurrence.

Thus the microclimate determines the general geographical distribution of a species, whereas the mesoclimate of the forest influences the local distribution. The variation of the mesoclimate in various forest environments makes possible the parallel occurrence of species developing under different climatic conditions, since their temperature and humidity requirements may be fulfilled and adequately synchronized during the course of their developmental cycles.

Influence of soil factors on insects

2.6 General characteristics of soil insects

Besides representatives of various animals such as *Protozoa*, *Nematoda* and *Annelida*, numerous *Arthropoda*, including representatives of 23 orders of insects, occur in the soils of Poland. Since it is difficult to abide always by a strictly systematic classification, a number of other classifications of the soil fauna have been advanced. These are generally based on the ecological specificity of the organisms and on the methods suited to the study of each particular group.

The most general classification is that of Jacot, in which all soil organisms, including insects, are grouped as follows: geobionts (associated throughout their life with the soil, e.g. *Collembola*), geophils (transient inhabitants of the soil, e.g. *Melolontha*) and geoxenic species (which treat the soil as a shelter during the pupal stage as in *Panolis flammea* (D. & S.), or as a site of oviposition as in *Barbitistes constrictus* Brunner von Wattenwyl and *Lochmaea caprea* (L.)).

Franz's (1950) classification is based on the specialized adaptations possessed by soil-dwelling organisms suiting them to this mode of life. He distinguished them as follows: those swimming in capillary soil water (e.g. *Turbellaria*), those creeping in free soil spaces (e.g. *Collembola*) and those rooting in the soil (e.g. tipulid and elaterid larvae).

From a practical standpoint it is often useful to apply the classification scheme proposed by Van der Drift (1951) who distinguished the following categories: euedaphon (fauna of deeper soil levels), hemiedaphon (fauna of superficial soil levels and litter) and epedaphon (fauna of the soil surface, sometimes also occurring sporadically in the superficial level).

The classification of Fenton (1947), based on trapping methods, distinguishes the following: microfauna (organisms of 0.002–0.2 mm body length, e.g. *Protozoa*), mesofauna (0.2–2.00 mm, e.g. *Apterygota*, mites, etc.), macrofauna (2–20 mm, e.g. most insects) and megafauna (> 20 mm, e.g. *Carabus* spp.).

McKevan (1962) classified soil animals according to their food specializations, dividing them into primary and secondary consumers. Primary consumers include phytophages (feeding on parts of living plants, e.g. older *Melolontha* larvae), xylophages (feeding on wood, e.g. larvae of *Spondylis buprestoides* (L.)) and saprophages (feeding on dead plant remains, e.g. larvae of various *Diptera* and some *Collembola*). Saprophages constitute 70–80% of the total mass of soil invertebrates.

Secondary consumers include predators (e.g. *Staphylinidae*), parasites (e.g. *Proctotrupoidea*), necrophages (feeding on dead animals, e.g. *Silphidae*), coprophages (feeding on the excrement of other animals, e.g. *Aphodius* (*Scarabaeidae*)) and microphages (feeding on soil microorganisms). Amongst the last category may be included those *Collembola* feeding on the bacterial slime covering particles of leaf litter.

Collembola, *Coleoptera* and *Hymenoptera* and the larvae of *Lepidoptera* and *Diptera* are the most important groups of insects which occur in the soil. About 5000 species of insects live at some stage or other, either continuously or periodically, in the forest soils of Poland.

Almost half of them belong to the order *Coleoptera*, of which the *Staphylinidae* are the most frequent totalling about 700 species. The number and composition of insect species depend on the type of soil, its physical, chemical and biotic (e.g. character of flora) properties. They also depend on the history of human management of the soil of the given area and environment.

2.7 Insects and physical soil properties

Physical properties of the soil include its structure and mechanical composition as well as humidity, thermal conditions, air and humus content.

2.7.1 Structure and mechanical composition

The soil structure affects the penetration and movement of insects. Small insects move in the soil taking advantage of minute fissures and free spaces. Insects belonging to the macro- and megafauna must push or root through the soil. *Coleoptera*, *Lepidoptera*, *Orthoptera* and *Diptera*

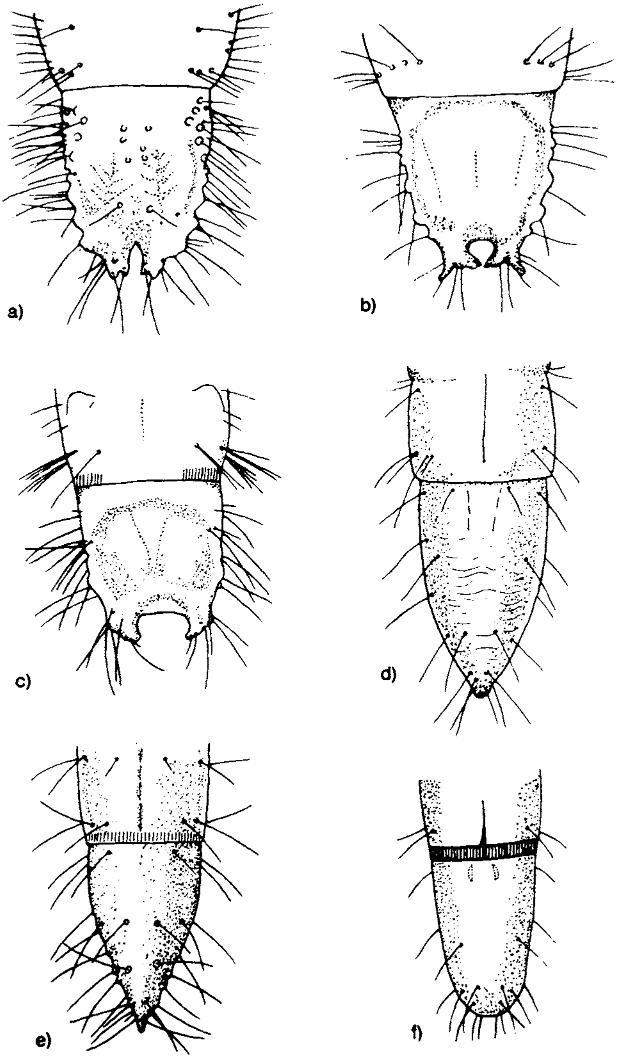


Fig. 2.36 Terminal segments of larvae of *Elateridae* (after Cherepanov, 1965): a) *Agrypnus murinus* (L.), b) *Athous subfuscus* (Müller), c) *Selatosomus aeneus* (L.), d) *Ectinus aterrimus* (L.), e) *Dalopius marginatus* (L.), f) *Sericus brunneus* (L.)

larvae, for example, push their way and squeeze between soil clods (*Tipulidae*, *Agrotis* spp.) or crumble the soil with their anterior body end and shift it backward (without forming a gallery). Wireworms (*Elateridae*) move in the last-mentioned way, using their well-developed rigid urogomphi of the terminal body segment as resistance organs aiding forward movements in light soils. In wireworms characteristic of heavy soils the terminal abdominal segment is invariably deprived of urogomphi since these larvae require no hard resistance organs because of the hardness of the soil (Fig. 2.36).

Melolontha larvae with their characteristic C-shaped bodies, move forward as if in a chamber, the anterior part of which is continuously widened by the mouth parts whilst the posterior part is filled in by soil being shifted backward and packed in. Thus, no empty gallery remains in the wake of the larva (Gilarov, 1949).

Larvae of various insects react to the higher CO_2 concentration surrounding the roots of living plants and in this way they are able to detect such roots.

Because of their distinctive structural and mechanical compositions, different soil types are inhabited by various characteristic insect species. It is commonly known that *Polyphylla fullo* (L.) occurs only in loose sands of inland or coastal dunes, whilst tipulid larvae inhabit humus soils, etc. Representatives of the genus *Harpalus* exhibit a distinct preference for soils of a definite mechanical composition. *H. rufitarsis* (Duftschmid) selects loamy or fine-sandy soils while *H. serripes* (Quensel) exhibits no specific requirements in this respect (Fig. 2.37).

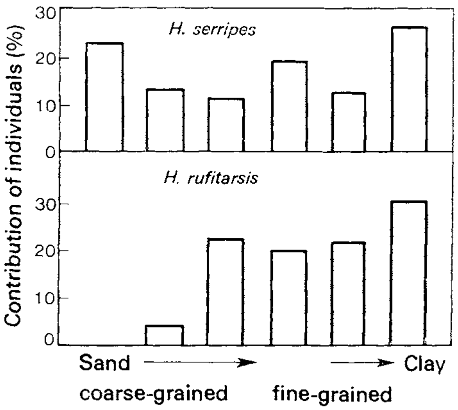


Fig. 2.37 Influence of mechanical soil composition on the distribution of *Harpalus serripes* (Quensel) and *H. rufitarsis* (Duftschmid) (after Lindroth, 1949)

In general it can be said that heavy soils are more rarely inhabited by root pests than sandy and sandy-clayey ones though within various parts of the inhabited area the same species can occur in soils with various physical properties. For instance *Melolontha hippocastani* F. in the northern range of its distribution inhabits dry and sandy soils of open areas, while in the south it prefers shaded, more humid soils containing more particles smaller than 0.02 mm (Fig. 2.38).

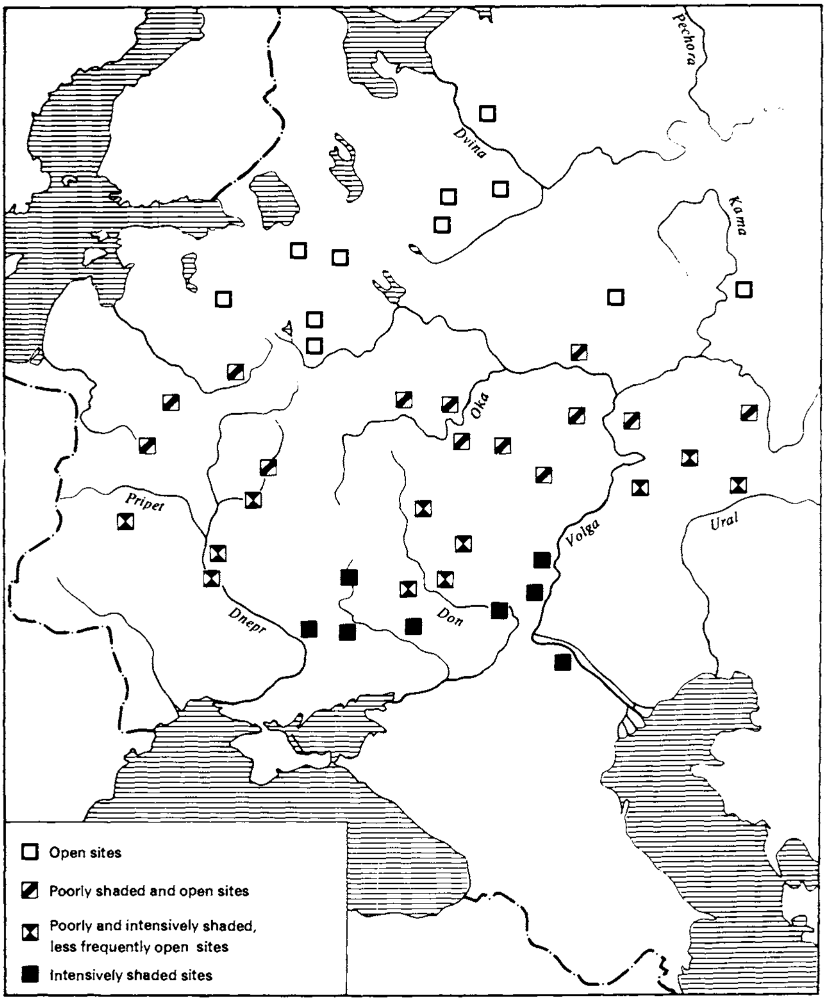


Fig. 2.38 Influence of geographical conditions on invasion of various soils by *Melolontha hippocastani* F. (after Berezina, 1960)

2.7.2 Humidity

Humidity is the most important factor affecting the distribution of soil insects. This is probably due to the fact that soil humidity determines the development of insects in one or more of their life stages (e.g. eggs of *Melolontha* or larvae of *Elateridae*) since they adsorb water from the soil through their skin. On the other hand, excessively humid, wet soil adhering to the body of soil insects hinders their respiration and can even cause their rapid death.

In general it can be stated that gravitation water is noxious and capillary water favourable for soil insects, although the mesofauna is not susceptible to general water excess in the soil since invariably small air bubbles occur in the capillaries. Also in summer at higher temperatures numerous insects such as wireworms cannot withstand submersion in water. They exhibit a higher resistance to submersion in cool seasons than in hot ones when the oxygen requirement is high but its content in water is low.

The damage caused by wireworms of the genus *Athous* and others in soils rich in humus depend on humidity. Generally these insects feed on decomposing plant tissues, but at periods of drought they feed on the roots of living plants and thus considerably augment any damage occurring in forest nurseries. Species continuously feeding on roots are less susceptible to drought than saprophages whose food can consequently become deficient.

The geographical and environmental limits of the distribution of *Melolontha* depend on the depth of the ground water level and air temperature in winter. It has also been established that numerous soil insect species occur in soils with a definite level of ground water (Fig. 2.39).

Soil humidity can play an important role in the occurrence of mycosis of insects hibernating in the litter. The percentage of *Melolontha* larvae infected by *Beauveria tenella* Siemaszko, for example, is higher in humus and more humid soils than in sandy ones.

The complexity and variety of the ways in which soil humidity influences insects is not yet fully known. One way of investigating its effects, however, is by studying the distribution of insects in various soils arranged according to their humidity gradient. It appears that there is a correlation between this gradient and the changes in the entomofauna in which there is a gradual succession of species in soils of different humidity (Fig. 2.40). Soil humidity combined with temperature and oxygen content influences vertical and horizontal migrations of insects. At

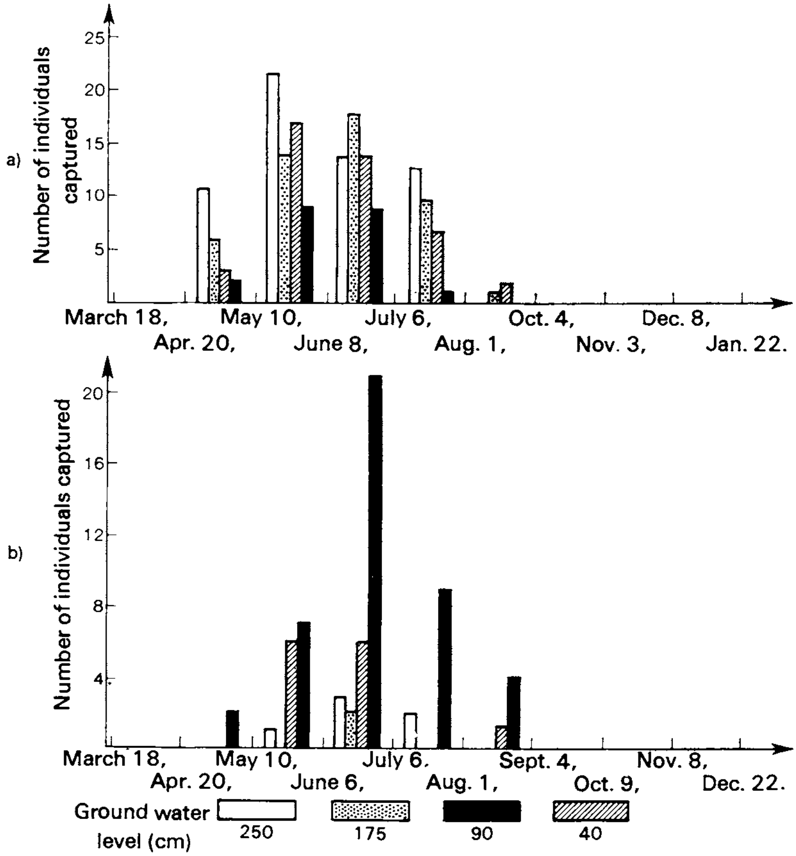
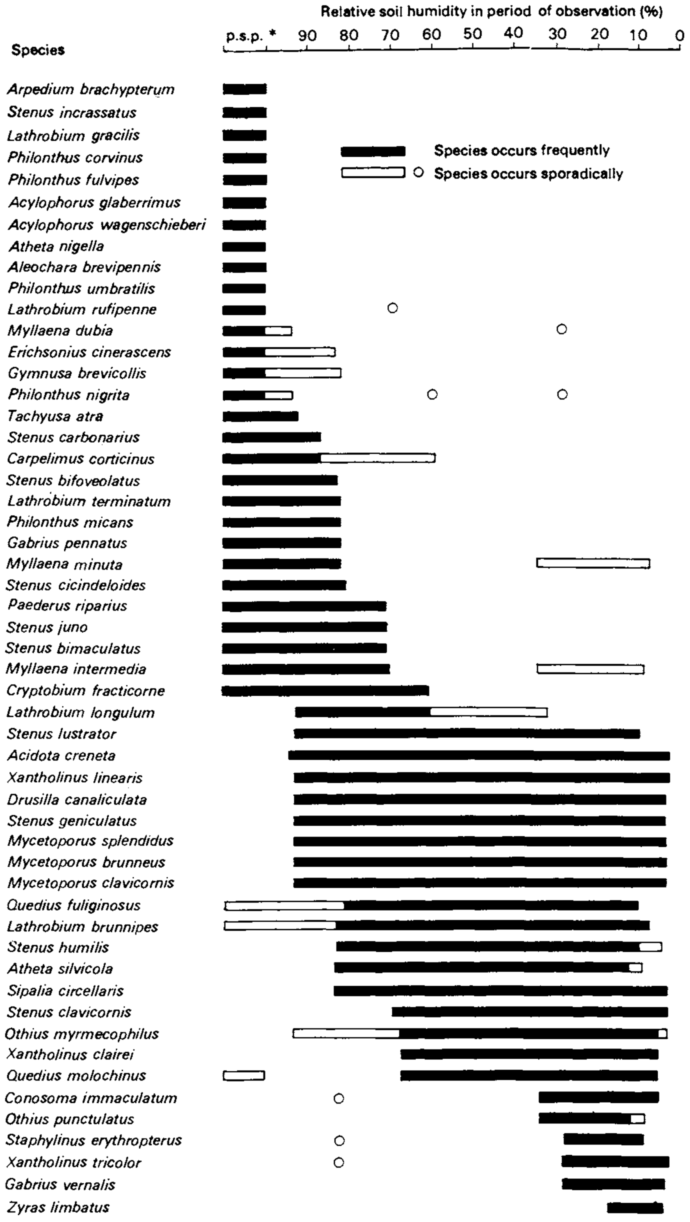


Fig. 2.39 Dependence between the ground water level and activity of two forest species of epigeic *Coleoptera* (after Niemann, 1963): a) *Carabus arcensis* Herbst (mesohygrophilous species), b) *Staphylinus (Platydracus) fulvipes* Scopoli (hygrophilous species)

periods of drought larvae of *Tipulidae* migrate horizontally to more humid sites.

2.7.3 Thermal conditions

The influence of soil humidity is closely connected with that of temperature, although its influence cannot be always distinguished from that of other factors. As mentioned above, the distribution of *Melolontha* depends on the depth of the ground water level and air temperature in winter which determine the "obligatory" vertical migration of larvae in the



* Partly submerged plants

Fig. 2.40 Distribution of more important *Staphylinidae* species in dependence on humidity of superficial soil layer (according to Szujecki, 1966b) soil. These larvae are susceptible to low temperatures, they enter dormancy at 6°C and perish at −5°C. A high ground water level renders impossible their deeper penetration into the soil where they would be protected from the harmful influence of low temperatures. In view of this, it is interesting to note that larvae of *Amphimallon solstitialis* (L.) are more resistant to cold since they begin to move at an environmental temperature of 1°C. Because of intensified respiration, their body temperature increases at this time and amounts to 9°C.

Elaterid larvae are active at soil temperatures of 8–20°C. At 6°C they cease feeding and enter dormancy at 0°C. In general they show little resistance to low temperatures.

The air temperature of a given vegetation season has a significant effect on the course of mating and oviposition in soil insects. It has been observed that low air temperatures in May cause increased forestry damage due to *Melolontha* larvae in the ensuing years. This is because, during low temperatures, the females lay eggs in open areas such as forest nurseries and plantations while in years when May is warm most eggs are laid under the forest canopy.

The temperature tolerance ranges of soil insects and other *Arthropoda* vary widely in different species. In numerous species active life is possible at temperatures of only a few degrees above zero.

The thermal preference of soil *Collembola* such as *Onychiurus armatus* (Tullberg), oscillates between 11 and 19°C, that of *Sinella coeca* (Schött) between 16 and 24°C (Berestyńska-Wilczek, 1963 after Wojtusiak, 1971), whilst that of *Orchesella flavescens* Bourlet which is found on snow varies between 6 and 12°C (Wolska, 1957).

Besides *Collembola*, many other insects such as *Boreus hyemalis* (L.) (*Mecoptera*) (Fig. 2.41), abandon the soil on sunny winter days and copulate on snow patches, which appear to have dark stains due to the large concentration of these insects. The thermal preference of *B. hyemalis* lies between the limits of +2.5 to −3°C with a maximum at +0.12°C. (Wojtusiak, 1971). When the temperature rises by a few degrees these insects perish from the heat.

A total of 66 species of insects exhibiting activity on snow have been observed in the Wielkopolski National Park (Szulczewski, 1947).

Vertical migrations of the fauna occur in places where the soil undergoes considerable temperature changes during the course of the day. High temperatures during the day, associated with a decrease in humidity, force the insects to penetrate into the deeper layers while the coolness of the night allows them to migrate back up into the superficial layers.

Fig. 2.41 Boreus hyemalis (L.) on snow (photo by T. Bojasiński)

In mountains and in certain regions of northern Europe, the soil temperature is considerably higher than that of the air. The rule of zonal change of habitat is associated with this phenomenon. Insect species with a meridional distribution occur in drier and warmer soils in the northern parts of their range than those in the southern parts. This can be explained by the results of Palmen's (1954) studies based on the beetle

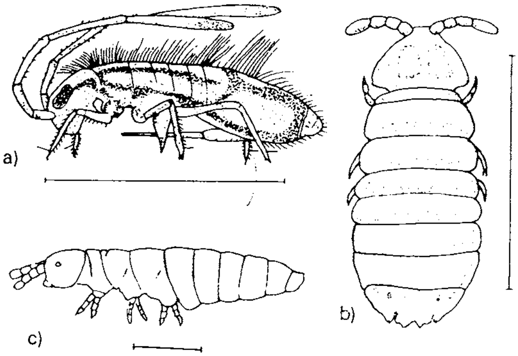


Fig. 2.42. Intensity of pigmentation of *Collembola* living in soil environment at various depths (after Dunger, 1964): a) *Entomobrya muscorum* (Nicolet) (epedaphon), b) *Tetrodontophora bielanensis* (Waga) hemiedaphon), c) *Willemia anopthalma* Börner (euedaphon)

Dyschirius thoracicus (Rossi). He showed that the beetle's requirement of a drier soil were correlated with its preferences for lower temperatures and higher relative air humidity.

2.7.4 Light

Light generally penetrates into the soil to a depth of 1–2 cm. The activity of the soil fauna may be inhibited under the influence of excessive light, especially ultraviolet rays. The lower the insect's pigment content in the cuticle, the more susceptible it is to the influence of light. Thus soil insects inhabiting the deeper layers are less heavily pigmented than those at the surface (Fig. 2.42).

2.7.5 Soil air

The proportion of water to air contained in the soil varies in different soils. It is most favourable in fine-grained soils. As mentioned above, the air content may be insufficient at high soil humidities, particularly when water fills all the spaces between the soil particles. The oxygen requirements of soil insects are associated with the depth of their occurrence in the soil profile and they can either inhibit or favour vertical migrations. *Gryllotalpa gryllotalpa* (L.) living directly beneath the soil surface, adsorbs 53 cm^3 of oxygen per 1 g of body weight per hour. Wireworms adsorb about 22 cm^3, whereas *Melolontha* larvae living deep in the soil at certain seasons adsorb 13 cm^3.

It has been mentioned above that CO_2 content is only rarely a limiting factor. The forest soil contains most CO_2 in spring and in autumn in proportion to the content of organic particles. In sandy forest soils

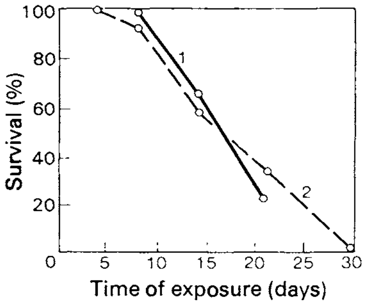


Fig. 2.43 Survival of grubs of *Melolontha melolontha* (L.) (1) and wireworms of *Selatosomus aeneus* (L.) (2) in CO_2 atmosphere (after Schwerdtfeger, 1977)

the CO_2 content is about 0.38% in the subsoil, 1.3% in the superficial layer and 5.43% in humus soil. The CO_2 content in the soil increases considerably under the snow, particularly in spring when an ice crust forms on the snow. Soil animals belonging to the euedaphon are most resistant to CO_2 concentration in soil air. Euedaphon *Collembola* (e.g. *Onychiurus armatus* (Tullberg)) resist CO_2 concentrations of up to 35%, whereas epedaphic representatives of this order such as *Orchesella villosa* (Geoffroy) and *Tomocerus vulgaris* (Tullberg) show symptoms of intoxication at a concentration as low as 1–2%.

The survival of larvae of *Melolontha melolontha* (L.) and *Selatosomus aeneus* (L.) in a CO_2 atmosphere is illustrated in Fig. 2.43.

2.7.6 Humus content

Humus content influences the frequency of organisms in the soil. Generally the frequency of insects occurring in the forest litter is inversely proportional to its degree of decomposition and in the soil is directly proportional to its humus content. It was found that the frequency of *Apterygota* per 1 kg of the fir-beech litter in Czechoslovakia oscillated from 3905 in poorly decomposed litter (weighing 0.1 kg per 1 dm^3), through 600 in fairly decomposed litter (weighing 0.27 kg per 1 dm^3) to 50 individuals in intensively decomposed litter (weighing 0.44 kg per 1 dm^3) (Nosek, 1954).

The quantitative dependences described above are indicative of tne contribution of the soil fauna to the decomposition of organic matter in the forest.

In fact the total biomass of litter saprophages increases with the decrease of the C:N ratio in the litter and the increased rate of litter decomposition (Table 2.2). On the other hand, the annual average pro-

Table 2.2 Occurrence of macrofauna in dependence on the C:N ratio, C contribution and rate of litter decomposition in three forest associations of the Kampinos Forest (after Zimka and Stachurski, 1976).

Forest association	Biomass of litter macrofauna, kg per 1 ha	Percentage of predators in macrofauna	C:N in fallen leaves	Percentage of C in A_1 and A_2	Rate of litter decomposition
Mixed forest	10.1	41	64.9	1.1	0.50
Oak-hornbeam-linden forest	12.3	27	31.9	5.3	0.61
Alder forest	23.7	19	18.7	22.7	1.14

duction of *Carabidae* predators is only slightly correlated with the trophic capacity of the insects' habitat, which is determined by the amount of organic nitrogen in the fallen leaves of trees, undergrowth and herb layer plants in various forest associations. A dependency exists, however, between the production of biomass of litter *Carabidae* species and the nitrogen access to the forest litter. This regularity does not concern epigeic species active on the surface of the litter (Fig. 2.44).

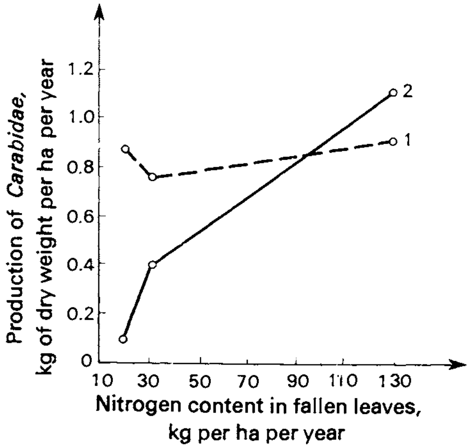


Fig. 2.44 Biomass production of epigeic and litter *Carabidae* in dependence on nitrogen content in fallen leaves (after Grüm, 1976): 1 — epigeic species, 2 — litter species

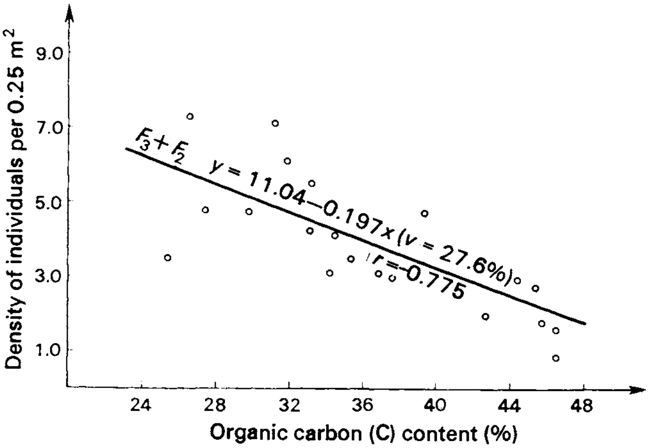


Fig. 2.45 Dependence between organic carbon (C) content in sublayer A_1 (litter) and density of forest *Staphylinidae* species (F_3+F_2 — fidelity classes) (after Szujecki, 1978)

The abundance of other litter predators such as staphylinid beetles under the same habitat conditions in fresh pine forests, exhibits an inverse correlation with the humus content (determined by the amount of organic carbon in the superficial litter layer) and no correlation at all with the nitrogen content (Fig. 2.45).

This leads to the conclusion that the humus content of forest soils and the nitrogen circulation in forest ecosystems determine the abundance and biomass of saprophages. On the other hand, the occurrence of predators depends on the frequency of saprophages, and thus indirectly on the general abundance of organic matter undergoing decomposition.

2.8 Influence of chemical properties of the soil

Acidity, salinity and calcium content, as well as the content of other elements or chemical compounds, constitute the chemical properties of the soil.

Soil acidity depends mainly on the direction of aerobic or anaerobic processes and is thus very variable. From the experimental standpoint it is difficult to distinguish the influence of acidity from that of other soil factors on the distribution of insects. However, it has been established that such an influence often plays a decisive role. In general it can be said that less animals occur in acidic soils than in alkaline or neutral ones. On peatland on the shores of forest lakes of the Pisz Forests, where the acidity amounts to pH 2.35, only 12 species of *Staphylinidae* were found, whereas on sites of similar soil humidity where the acidity is pH 5.7, the number of staphylinids recorded was 58 (Szujecki, 1966b).

On the other hand, it cannot be established whether the number of insects occurring in less acidic soils invariably increases with the decrease of soil acidity. For instance, in acidic soils where the pH oscillates within the limits of 4.7–5.5, many wireworms occur which only perish when the acidity is pH 1.9. Some wireworms, such as species of the genus *Limonius*, only occur in alkaline soils of pH 8, whereas *Selatosomus latus* (F.) is most abundant in heavy soils of pH 6.5. Among soil *Staphylinidae*, *Acidota crenata* (F.) occurs in soils the pH of which does not exceed 4.9, regardless of their humidity, and *Stenus humilis* Erichson occurs exclusively in soils with pH not exceeding 4.4. The largest number of cocoons of *Pristiphora abietina* (Christ) was found in acidic soils where the pH oscillated between 3.1 and 4.8.

Soil acidity is thus an important limiting ecological factor but in many cases its effect is secondary to that of the decisive influence of soil humidity and fertility. The distribution of *Agriotes obscurus* (L.) larvae depends on humidity and not on the acidity of soil. Most larvae of this species occur at a humidity of 80% while soil pH oscillates within the limits of 5.6–8.1. The content of calcium in the soil not only determines its alkalinity, but can also affect the fauna in other ways by influencing the structure and chemical composition of the soil as well as the presence of microorganisms. Some species occur exclusively in calcareous soils. Liming of the soil causes distinct changes in its fauna. Liming under spruce forest stands over a four year period resulted in the appearance of *Lumbricidae* species formerly absent from the site and limited the occurrence of spiders and *Myriapoda.* Liming of the soil can also limit the occurrence of *Collembola* and *Acarina* in the humus layer and increase their frequency in the mineral soil level.

The salt content of the soil affects the water balance of soil insects by changing the osmotic and chemical pressure and is usually toxic. Insects and other organisms occurring in salinic soils are called halophilic. Halophilic species are not common in Polish forests but they can occasionally be found in forest stands, particularly in plantations in the vicinity of the Baltic Sea on sea-coast dunes.

Salt was used in the control of pupating larvae of *Bupalus piniarius,* wireworms and larvae of *Melolontha.* Positive effects were obtained only with very large doses which caused a distinct increase of soil salinity.

Mineral fertilizers such as phosphates, potassium salts, nitrates and calcium exercise an important influence on the composition of the soil fauna. They also indirectly affect the abundance, fertility and development of insects feeding on tree crowns by way of their action on the insects' food plants. This will be discussed in further chapters.

3 The role of nutrient factors in the life of forest insects

3.1 General characteristics of trophic relationships

The nutritional relationships of forest insects are among the most important ecological factors determining the development and distribution of species. This is because food is indispensable for the successful course of growth processes, development of reproductive organs and the functioning and locomotion of the organism in general. Food influences, directly or indirectly, the fertility, rate of development, activity and abundance of insects as well as the characters of groups formed by them.

Insects can be classified according to their nutritional preferences as follows: phytophages, saprophages, zoophages, necrophages and coprophages. Phytophages feed on living plants or their secretions, zoophages on other living animals (and can be classified as parasites and predators), saprophages on the remains of dead plants, necrophages on the bodies of dead animals and coprophages on the excrement of other animals.

It is obvious that the classification of insects according to nutrient groups as given above, is only schematic and not entirely clear-cut. Many insects can assimilate both animal and plant food or can utilize different food sources at various stages of their development. For example, some parasites of the family *Larvaevoridae* are zoophages in their larval stage, while as adults they become meliphages, i.e. they feed on flower nectar and pollen. Coprophages such as *Geotrupes* sp. may often be classed as saprophages as well, since they can feed on the remains of non-digested plants occurring in the excrement. Finally, some predators of the genus *Staphylinus* can facultatively feed on carrion and thus may be regarded as necrophages.

Environmental factors play an important role determining the nature of the food assimilated, and can obliterate the boundaries between the nutrient groups of insects mentioned above. Young wireworms and grubs at a suitable soil humidity are typical saprophages feeding on humus, but in periods of drought they switch over to plant food and thus become phytophages like the older individuals. During extreme drought they may also feed on other animals and thus become facultative zoophages. For example, some wireworms penetrate into the cocoons of *Diprionidae* occurring in the forest litter, whereas larvae of *Melolontha* may, under certain circumstances, devour other individuals of the same species. The latter form of predation is called cannibalism. The classification given above does not take into account certain specialized nutrient dependences such as feeding on honeydew produced by aphids (trophobiosis). Neither are symbiontophages feeding on lower organisms occurring in the alimentary tract of insects included.

Trophic specialization can be characterized by the number of different food-types assimilated. The following groups are distinguished from this point of view: monophages (feeding only on one kind of food, e.g. phytophages feeding on plants of a single species or parasites feeding on insects of a single species at a definite development stage); oligophages (feeding on systematically related plants or animals usually belonging to a single genus); polyphages (feeding on plants or animals belonging to different systematic groups) and pantophages (feeding on both living and dead plant and animal food).

The boundaries between these groups are not always distinct. Some insects may thus be described as having either a narrow nutrient specialization (stenophagy) or a wide nutrient specialization (euryphagy). The evolution of the trophic dependences of insects is considered to have proceeded from panto- and polyphagy to monophagy, which occurs at the threshold of oligophagy.

Though monophages are considerably more frequent among insects than in other animal classes, at least in the temperate climate they do not constitute a dominant group. *Cephenemyia stimulator* (Clark), parasitizing the European roe-deer, and *Panolis flammea*, feeding on pine, are representatives of this group. Obviously oligophages (e.g. *Chrysomela* = *Melasoma populi* L. feeding on various poplar and willow species) and polyphages are more numerous in the Polish fauna. Polyphagy is particularly characteristic of the temperate and arctic climatic zones in which abrupt changes can occur in the nutrition resources of insects. Many insects of the Polish fauna belong to polyphages, e.g. *Lymantria dispar* (L.) the larvae of which can feed on 477 plant species. Polyphagy should not be considered to be the same as absolute euryphagy. From a wide variety of host-plants, *Lymantria dispar* (L.) chooses those most suitable as regards chemical composition and other properties. Pantophagy is a rare phenomenon among insects. Within the Polish fauna, for instance, it is exhibited by some *Dermaptera* and *Blattaria* which can consume both plant and animal food as well as the remains of dead organisms.

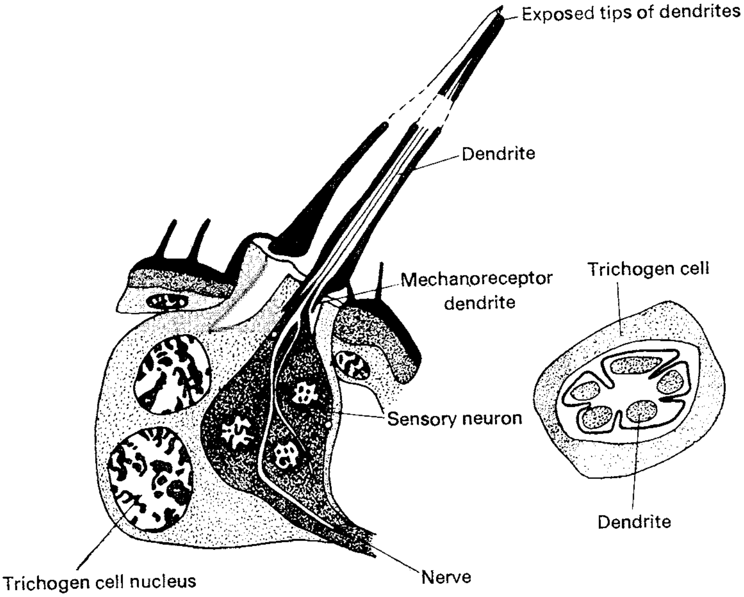


Fig. 3.1 Diagram of chemosensory trichoid sensillum. Such sensillae occur on mouthparts and legs of *Phormia* sp. (*Diptera*) (after Chapman, 1969)

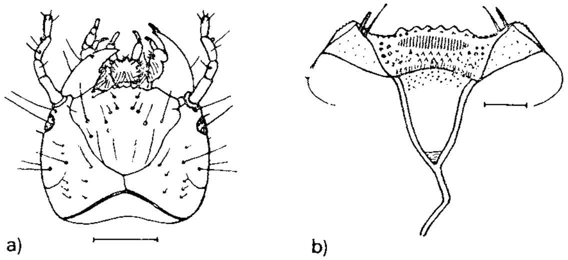


Fig. 3.2 Amara pseudocommunis Burakowski (*Col. Carabidae*) (after Burakowski, 1967): a) head, b) dorsal view of hypopharynx modified as a filter-feeding organ in predaceous, soil-inhabiting larvae

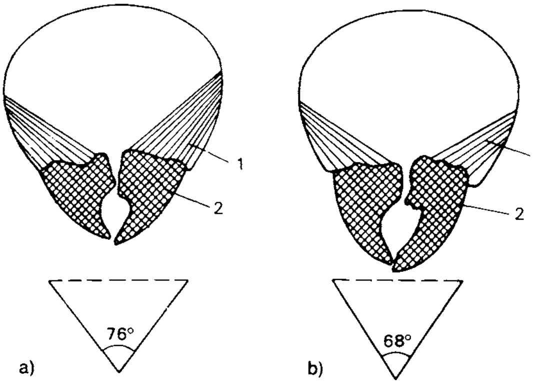


Fig. 3.3 Diagrams of structure and function of mandibles (after Pawłowski, 1959): a) *Sinodendron cylindricum* (L.) feeding in hard wood, b) *Ceruchus chrysomelinus* (Hochenwarth) feeding in soft wood; 1 – muscles, 2 – mandibles

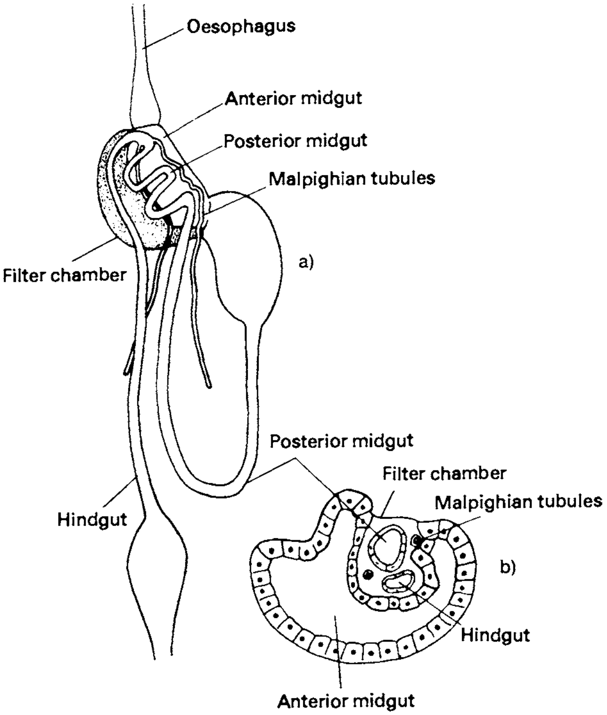


Fig. 3.4 Scheme of structure of alimentary canal of *Homoptera* (after Chapman, 1969): a) general view, b) cross-section of filter chamber

Nutrient specialization has determined the development of morphological and physiological adaptations particularly with respect to the structure of sensory organs, the mouthparts and the alimentary tract (Figs. 3.1, 3.2, 3.3 and 3.4).

3.2 Nutrient relationships of phytophages

3.2.1 Nutrient specialization

The nutritional scope of phytophages is based on the biochemical similarity of the host plants, and particularly the homology of proteins and some special substances such as tannins and salicylic acid. Tannins, for example, stimulate the consumption of leaves by *Melolontha* adults, whereas the oligophagy of *Chrysomela* = *Chrysomela populi* L. is due to the utilization of salicylic acid contained in poplar leaves for the deterrent secretion of the insect's dermal glands.

Insects feeding on trees usually specialize on a particular component of the tree such as the flowers, fruits, seeds, leaves, buds, shoots, trunk wood, cambium or bark.

Specialization of this type is primarily the result of selecting that part of the tree having the optimal food requirements as regards its biochemical properties. The cambium, seeds and fruits, for example, contain most proteins, whereas the leaves contain most carbohydrates. The physiological condition of phytophages is virtually dependent on the biochemical composition of their food which thus determines their fertility and survival.

The trophic adaptations of phytophages attained during the course of their evolution determine the dynamics of accumulation and utilization of resources, and consequently induce specific requirements as regards the selection of food, which often differ for the various developmental stages or successive generations of the insects.

The stabilization of food requirements has been realized by means of the single mechanism of a preference for the trees on which the insects hatched as the site for oviposition. A restriction of requirements as regards the range of host plants frequently had to occur in the course of this selection. A similar rule accompanies to some extent the phenomenon of the adaptation of insects to feeding on local populations of host plants which have specific biochemical properties, generally connected with the genetic properties of trees or with the environment. For instance a different trophic utility of Douglas spruces originating from various North-American sources for *Gilletteella cooleyi* (Gillette) was observed in Europe (Teucher, 1955). Observations on many *Chrysomelidae*, particularly of *Chrysomela lapponica* (L.) feeding on *Salix caprea* (L.) and *Ch. vigintipunctata* (L.) feeding on *Salix alba* (L.) demonstrated that the adaptation of local populations of these species to their host plants is so strong that in the course of a number of years they do not move away from the originally inhabited willows despite the vicinity of other willows apparently identical and occurring in the same habitat (Szujecki, 1966a).

On the other hand, the territorial vicinity and the consequent facility of settlement is of great importance in the formation of the food plants ranges of insects. In natural pine-spruce forest stands the phytophages normally feeding on spruces frequently occur on pines and vice versa (Fig. 3.5). Beyond the area of these two species the entomofauna of each is quite different from some distance. This is also observed in the entomofauna of other related trees, i.e. pine and larch or larch and fir.

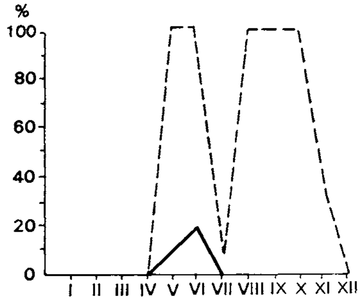


Fig. 3.5 Frequency of *Ips typographus* (L.) on pine and spruce in various forest types in the Białowieza National Park (after Karpiński, 1933): continuous line – pine, dashed line – spruce; I–IV – pine forests, V–VII – pine-spruce and mixed coniferous forests, VIII–XII – oak-hornbeam-linden forests and alder carrs

When suitable food sources are scarce or unavailable, phytophages can switch over to feeding on plants of other species or other parts of the same nutrient plants.

Switching from one host plant to another generally occurs during outbreaks of a phytophage feeding on tree leaves or needles. When the suitable food resources are exhausted the larvae abandon the trees and start feeding in the herb layer but this often results in a high mortality and a decrease in the fertility of the resultant adults. Monophagous species have no substitute host plants and thus perish when the original host is unavailable. Other species may become weak and readily succumb to infection due to bacteria, viruses and fungi.

Beside "forced" changes of host plants, some species switch food sources as a matter of course. Such changes are due to the following: i. different food requirements of individual developmental stages; ii. different food requirements of successive generations; iii. the dispersal of a monophagous species beyond the limits of the range of the host plant and iv. the introduction of a new plant of potential use as a food source into the range of a monophagous species.

The differentiation of the food requirements of various developmental stages of certain species of insects is a very common phenomenon and is usually associated with different morphological adaptations of the mouthparts in the various stages. Young larvae of *Panolis flammea* (D. & S.) feed in May on the delicate shoots and developing buds of pine, whereas the older larvae prefer the needles of the previous year. Grubs of *Melolontha* sp. feed initially on humus and roots of grasses and subsequently on the roots of young trees, whereas the adults feed on young leaves, particularly those of the birch and oak. Many *Lepidoptera* larvae feed on leaves while the adults imbibe flower nectar. Changes of host plants by successive generations of the same species are frequently observed in aphids. *Adelges* sp. (including the subgenus *Cnaphalodes*) feed successively on spruces and larches, etc. This phenomenon is considered to constitute an evolutionary adaptation serving as a protection against unfavourable feeding conditions at the period of migration which proceeded and proceeds from philogenetically older plant species to philogenetically younger ones.

Changes in the geographical ranges of phytophages or their host plants have increased considerably as a result of human activities including the development of transcontinental transport from the 18th century onwards. During the present day, however, in spite of the intensification of the transportation of plants and animals, the acclimatization of unwanted pest species in certain regions has decreased due to the efficiency of quarantine services in many countries. On the other hand, however, attempts to acclimatize introduced foreign tree and shrub species have increased. In the 1920's *Hyphantria cunea* (Drury) was accidentally introduced into Hungary from North America and here began to feed on European species of deciduous trees. Studies carried out in central

Poland showed that local phytophagous pests of pine and spruce became adapted to feeding on conifer trees such as Douglas spruce and Weymouth pine brought in from North America (Dominik, 1966–68). In other regions of Central Europe it was observed that the larch monophage *Coleophora laricella* (Hübner) adapted to feeding on Douglas spruce. Such feeding of insects on unsuitable plant species and of entomophages parasitizing unsuitable hosts, is called xenophagy.

The differentiation of the trophic possibilities of insects leads to the development of biological races as has been mentioned above. Persistent trophic changes have also been observed in other forest insects. For example, in some regions of Central Europe, the common beetle *Lagria hirta* (L.) feeds on gorse while on other regions where this plant is absent it lives on willows. In this case, however, no additional biological characteristics were observed which would justify the distinction of two trophic races. Such a situation does occur, however, in the case of *Dendroctonus micans* (Kugelann). According to some entomologists, individuals of this species feeding on Sitka spruces constitute a different ecological race since they are larger and lay more eggs than those feeding on the common spruce.

3.2.2 Selection of the host plant

The selection of the host plant by insects rarely takes place randomly, that is by trial and error, but is usually due to the attraction exerted by the food. The host plant influences the insect by visual stimuli, such as colour or reflected light intensity, as well as by tactile, chemical, odour and taste stimuli. These stimuli usually act singly, but together they may form complex conditioning systems. The mechanism of host plant location is made up of the following components: random movement, directional movement, gnawing or puncturing of food, feeding and, finally, dispersal. The reaction of insects to chemical compounds contained in plants, either by their taste or smell, is assumed to be the main factor determining the selection of a suitable host plant. Insects may be particularly susceptible when the sensory organs are adapted to the reception of a particular chemical compound (Dąbrowski, 1974).

The synchronization of the insect's life-cycle with the phenology of the host plant so that a suitable food source is available at just the right time is very important in the procurement of food.

The role of scent as a means of transmitting information regarding the availability of food to other members of the population is at present receiving a great deal of attention from entomologists, especially as to its practical and economic significance.

The absence of any ability to receive scent stimuli in primitive insects such as *Thysanura* and *Archaeognatha* is due, in part, to their restricted occurrence and parthenogenetic habits, whereby individuals do not need to come together for reproduction to take place. The evolution of cuticular specializations of the body integument, as well as the development of wings and sensory organs capable of detecting chemical odours, has enhanced the ability of insects to select suitable sources of food and to locate other individuals of the same species. In most insects, xylophages in particular, tree selection is the result of "secondary scent attraction".

Two main stages can be distinguished in the process of tree selection. The first stage is the attraction of the insect to a tree by the "primary attractant" secreted by the tree itself. The second stage is the attraction of other insects (of the same species) to the tree by a "secondary attractant", or pheromone, emitted by the insect already on the tree. "Secondary attraction" is closely associated with the suitability of trees as hosts for phytophages since pheromone activity can increase or decrease depending on the quality of the food and on their combination with the "primary attractants".

"Primary attractant" phase. The resin of conifers, by virtue of its volatile aromatic constituents, is an important attractant for many insects, particularly those invading tree trunks, and gives information regarding the identity of the tree species and its physiological condition. Those substances responsible for attracting particular species of insects have been identified using the technique of resin extraction. The most important compounds belong to the monoterpenes such as α-pinene, limonene, β-pinene, camphene, etc. (Table 3.1). For *Scolytidae*, the maximum alluring effect takes place at a monoterpene concentration of 0.01–0.05%. *Ips typographus* (L.) invades living trees at a monoterpene concentration of 0.03–0.05%, *Hylurgops palliatus* (Gyllenhal) attacks very weak trees at a concentration of 0.02–0.03%, whereas *Dryocoetes autographus* (Ratzeburg) attacking dead trees reacts to the lowest concentration oscillating between 0.01–0.02% (Chararas, 1959, after Isaev & Girs, 1975).

Insects orientate towards an odour source by an anemotropic reaction, taking advantage of the direction of air currents carrying the odour. It should be stressed that the reaction of different insects to the same type of resinous compounds varies a great deal. Each species' reaction depends

Table 3.1 Some monoterpenes content in the pine (*Pinus silvestris* L.) (after Hiltunen, Schantz & Löyttyniemi, 1975) and in the Siberian larch (*Larix sibirica* Ledebour) after Isaev & Girs, 1975).

Compound	Monoterpene content (%)			
	Pinus silvestris (resting period)			*Larix sibirica* vegetation period
	phloem	shoots	needles	phloem
α-Pinene	50.1	22.6	43.4	39.0
Camphene	0.9	0.4	4.0	0.6
β-Pinene	4.1	7.9	2.5	14.2
Myrcene	0.5	0.8	+	–
Δ^3-Carene	20.7	30.1	15.1	30.5
α-Terpinene	0.2	0.5	0.1	5.3
Limonene	3.6	13.1	1.4	5.3
β-Phellandrene	2.3	11.2	0.7	5.4
γ-Terpinene	0.3	+	0.2	1.3
Terpinolene	2.1	1.5	0.2	1.3

on the concentration of these compounds in the air as well as their synergetic activity. The scope of the attractive activity of fragrant substances can be determined by their composition, the quantitative proportions of individual constituents, and their threshold concentration. The latter is that concentration which has the minimum active effect and may be determined experimentally by the emission of standardized quantities of essential oils from a point capillary source under conditions of immobile air. It has been found that the synergetic activity of fragrant substances is decisive in determining their value as attractants.

The attraction of pine for *Tomicus minor* (Hartig) is determined by the synergetic activity of the principal monoterpene attractant, α-terpineol, as well as *trans*- and *cis*-carveol which on their own do not act as attractants (Kangas, 1968). It is supposed that carveol is formed in the phloem of weakened trees as the product of the acidification of limonene and that at a definite concentration it becomes the catalyst of the attractive activity of α-terpineol (Oxanen *et al.*, 1968).

Most studies on the attractive activity of monoterpenes have been carried out on scolytids. An attractive activity of α-pinene has been established for *Hylobius abietis* (L.) (*Curculionidae*) and a positive chemotropism to α-pinene, β-pinene and Δ^3-carene has been observed in *Hylotrupes bajulus* (L.) and *Ergates faber* (L.).

As mentioned above, monoterpenes are only active as attractants within definite concentration limits. Beyond these they either have no effect at all on insects or else may have a distinct repellant action. When the concentration of the active constituent rises above the threshold of the receptive capacity of the antennal sensillae, these activate a response termed the "general chemical susceptibility", the occurrence of which is invariably associated with a negative reaction from the insect. Even a high concentration of α-pinene (which is usually an attractant) in such situations acts as a repellant on *Scolytidae* (Chararas, 1960; Isaev & Girs, 1975).

The double nature of these chemicals as conveyers of information is very important in the orientation of *Scolytidae* during the selection of hosts because, in addition to their active properties as attractants or repellants, they exhibit toxic contact and gaseous properties. Insects may thus be exposed to a certain amount of danger when invading "resistant" trees due to the high concentrations of volatile oils in the resins of such trees.

Besides terpenes, other chemical compounds, particularly fatty acids contained in the resins such as palmitic, stearic, oleic, linoleic and linoleic acids and their methyl esters, may act as chemical attractants. Effective concentration values of these acids oscillate within the limits of 10^{-6} to 10^{-9} and those of esters between 10^{-8} and 10^{-12} (Merker, 1960). *Hylobius abietis* can detect a 10^{-7} concentration of the methyl ester of linoleic acid from a distance of 1 m (Schwerdtfeger, 1963).

For scolytids and curculionids, as well as some cerambycids such as *Spondylis buprestoides* (L.) (Fig. 3.6), benzoic acid is an effective attractant, as are vanillin and some aldehydes produced as a result of the acidification of lignin in deciduous trees for *Scolytus multistriatus* (Marsham). The fragrant specificity of even closely related species of trees can be distinguished by some insects such as *Pityokteines curvidens* (Germar), *Tomicus piniperda* (L.) and *Pristiphora abietina* (Christ). *P. abietina* locates suitable sites for oviposition by means of the scent of spruce shoots in May.

The volatile fractions of resins may also serve as attractants to insects predacious on xylophages, whereas parasites are generally attracted by the host's pheromones such as those secreted by fertilized female scolytids (Kharitonova, 1972).

"Secondary attractant" phase. Tree invasion by scolytids consists of several distinct stages. These include searching for suitable tree hosts

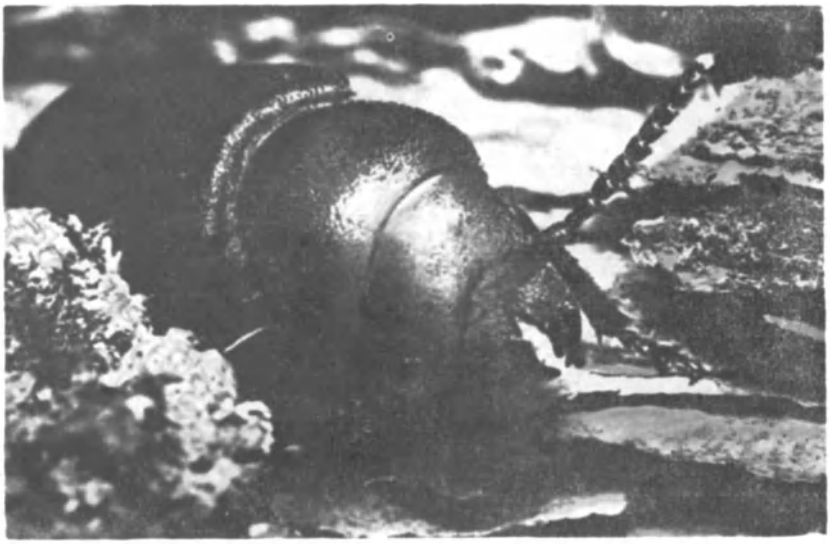


Fig. 3.6 Spondylis buprestoides (L.) (photo by T. Bojasiński)

by solitary individuals, orientating towards weakened trees and the mass assembling of other individuals of the same species on the selected trees. The first two stages may result from the direct action of the resin attractants as described above, whereas the third (and also partly the second) stage depends on the emission of pheromones from the early invaders. The phenomenon of "secondary attraction" was first reported by Anderson (1948) and since then fundamental works on the subject have been published by Wood & Vité (1961), Rudinsky (1963) and others in the USA, Chapman (1966) in Canada, Bakke (1967) in Norway, Chararas (1966) in France and Isaev (1967) in the USSR.

"Secondary attractants" or pheromones (sexual attractants) emitted by some beetles act as signals indicating the suitability of food to other individuals of the same species (and usually population). The increase in the attractiveness of the host tree is proportional to the number of beetles which originally invaded it and to their reproductive capacity. In polygamous scolytids such as *Ips*, *Pityokteines*, etc. the males produce the pheromones whereas in monogamous genera such as *Scolytus*, *Dendroctonus* and *Trypodendron* they are emitted by the females. In *Dendroctonus pseudotsugae* (Hopkins), pheromones are only produced by non-fertilized females (Rudinsky, 1963) whereas in *Ips subelongatus* (Motschulsky) they are produced by both mature and immature males alike (Isaev & Girs, 1975). In *Ips confusus* (LeConte) the intensity of pheromone secretion depends on the frequency of contact with the opposite sex and decreases after each act of copulation (Borden, 1967). The pheromones in this case have their main effect on members of the opposite sex, although individuals of the same sex may be affected to a lesser degree.

Pheromone production also depends on the physiological condition of the host tree and its secretion is usually initiated as soon as the insect starts to feed. Higher contents of carbohydrates, particularly glucose, as well as higher osmotic pressure in the tree stimulate increased pheromone production. The timing of pheromone emission also depends on the biology of the scolytid species involved. For example, in the monogamous *Trypodendron lineatus* (Olivier), pheromones are secreted by nonfertilized females, their production ceasing as soon as fertilization takes place. The phenomenon of "secondary attraction" usually occurs a few hours after the initial invasion and reaches its maximum within 24 hours. It diminishes rapidly as soon as the males appear but, nevertheless, may persist for about two weeks. In *Ips subelongatus* pheromone activity starts after 4 to 6 hours, achieves its maximum after 1 or 2 days and finally disappear after 2 weeks (Fig. 3.7) (Isaev, 1967). The limitation of the period of pheromone activity prevents overdensity of population on the same trees which would eventually result in an increased mortality.

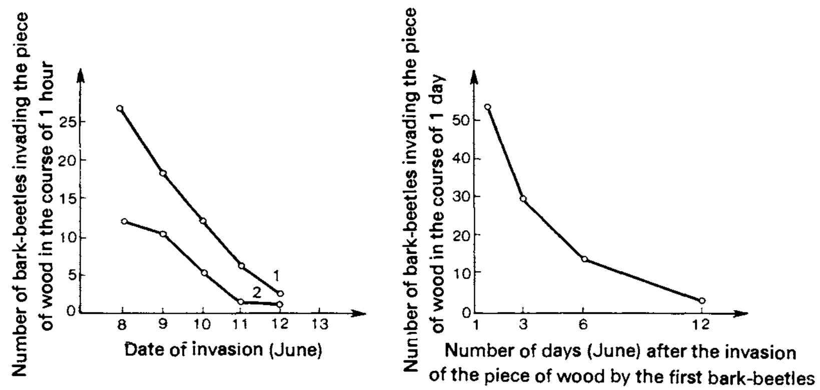


Fig. 3.7 Attractiveness of pieces of Siberian larch trunks for *Ips subelongatus* (Motschulsky) in dependence on the abundance of bark-beetles (left) and on the date of initial invasion by this bark-beetle (right) (after Isaev & Girs, 1975): 1) piece of wood on which 75 beetles were initially introduced, 2) piece of wood on which 20 beetles were initially introduced

The presence of pheromones in air currents can be perceived at a distance of 1 km and favours the focal nature of the method of tree invasion by scolytids (Maslov *et al.*, 1973). Pheromones are highly specific in xylophagous species but may also serve as attractants for parasites and predators by virtue of this specificity. The pheromones of *Ips subelongatus*, for example, attract *Tomicobia seitneri* (Ruschka) and *Thanasimus rufipes* (Brahm) (Isaev & Girs, 1975). Sawdust invaded by *Tomicus piniperda* (L.), and which probably contains pheromone residues, is attractive to the staphylinid *Phloeonomus pusillus* (Gravenhorst) which is often found in association with the feeding site of late instar *Tomicus* larvae. The predator *Rhizophagus depressus* (F.), on the other hand, invades quite fresh feeding sites of *Tomicus* and does not react to the sawdust. It is probably attracted by the smell of resin (Mazur, 1974).

In addition to the olfactory stimuli described above, visual stimuli such as the shape and colour of plants and also phototaxy are both very important in the location of suitable food sources by phytophagous insects. Larvae of *Lymantria monacha* (L.) are positively phototactic on hatching and thus make their way to the tree crown where, on encountering the food source (i.e. the pine needles) they immediately become phototactically neutral. In general, when insects have located their food, they test it mechanically at first by shaking, striking or just touching the plant surface and then test it chemically (i.e. they taste it). If the plant is found to be chemically suitable, feeding proceeds and may be enhanced by substances in the food as in *Melolontha*, for example, where the tannin content of leaves stimulates their increased consumption.

3.2.3 Food value

Synchronization of the life-cycle of an insect with the phenology of its host plant (e.g. adult tachinids, sarcophagids and *Cetonia aurata* (L.) feeding on the pollen of the flowers of suitable plants; Fig. 3.8, Table 3.2) ensures that food is available at the correct time. The season when the leaves of a particular plant develop may be particularly important in the life of a phytophage, especially when the latter has very specific requirements. Spring leaves are generally richer in water and proteins but have lower sugar content, but later these proportions change to such an extent that in autumn stored compounds (especially starch) are predominant. Larvae of *Lymantria monacha* (L.) were reared on leaves collected, and suitably preserved, at different times of the year. Their percentage mortality was as follows: 7% on spring leaves, 12% on summer leaves and 80% on autumn leaves.

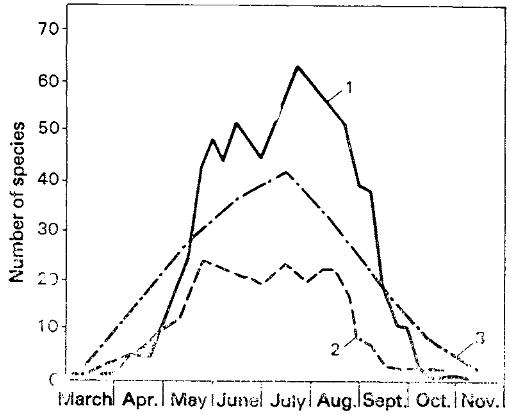


Fig. 3.8 Synchronization of appearance of *Diptera* of the family *Tachinidae* (1) and *Calliphoridae* (2) and abundance of flowering plant species (3) (after Karczewski, 1967b)

We can distinguish the following five groups of insects according to the stage of development of the leaves on which they feed:

1) insects feeding exclusively on spring leaves and completing their development in the first months of the vegetation period (*Lymantria dispar* (L.), *Operophthera brumata* (L.), *Tortrix viridana* (L.), *Malacosoma neustria* (L.), etc.);

2) insects feeding on leaves in summer (*Phalera bucephala* (L.) (Fig. 3.9), *Cerura* (= *Dicranura*) *vinula* (L.));

3) insects feeding on leaves in summer and autumn (*Bupalus piniarius* (L.));

4) insects feeding on leaves in the summer-autumn period and in spring (*Euproctis chrysorrhoea* (L.));

5) insects feeding on leaves throughout the entire vegetation season (*Dendrolimus pini* (L.)).

The varying nutritional value of the food at different seasons of the vegetation period causes differences in food requirements. Insects completing their larval development in autumn (and even in summer) invariably require more food per body weight unit. In species having two generations per year the larvae feeding in spring generally have a shorter development period. The development of caterpillars feeding on leaves of plants of the genus *Stigmella* in spring lasts several days whilst in autumn it extends to several weeks. In absolute values, food requirements are characteristic for each particular species and depend on the

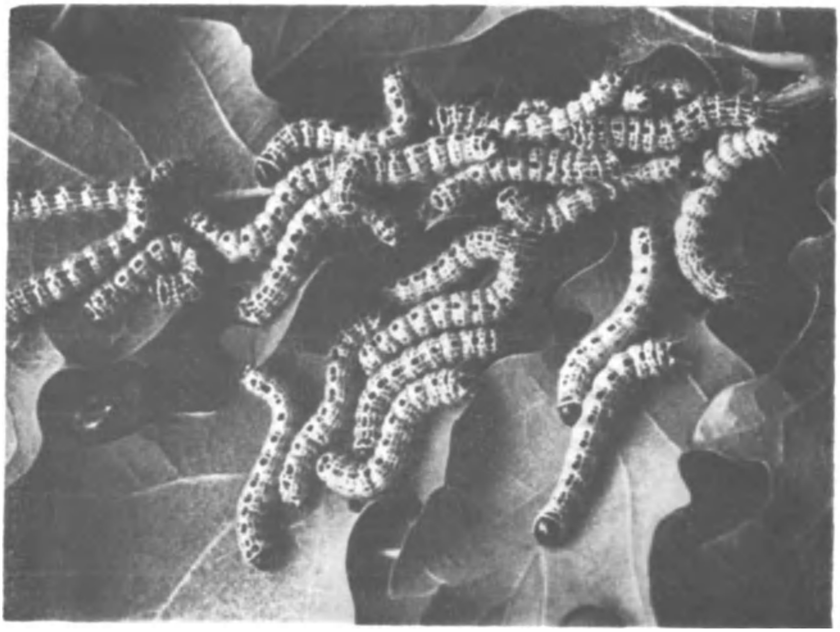


Fig. 3.9 Phalera bucephala (L.) on the cak (photo by W. Strojny)

natural size of the insect. For instance, between hatching and pupation *Bupalus piniarius* (L.) consumes 1.2–2 g of pine needles, *Panolis flammea* (D. & S.) 7 g and *Dendrolimus pini* (L.) 15–20 g. The amount of food assimilated by the larvae of future females is invariably higher than that consumed by the larvae of males. This is due to the generally larger body size of females of many phytophagous insects. The weight of male and female pupae is as follows: in *Tortrix viridana* (L.) – 30 and 45 mg, in *Bupalus piniarius* (L.) – 105 and 146 mg, in *Hyloicus pinastri* (L.) – 2004 and 2181 mg respectively.

In general we can say that in most phytophagous insects the daily food requirements oscillate within the limits of 50–150% of their body weight (Reichle & Crossley, 1967).

The nutritional value of leaves fluctuates not only during the course of the vegetation season but also in the course of 24 hours because of the varying content of starch, sugar, protein and water at various hours of the day and night. It can also change according to the age of the tree. The leaves of younger plants are more valuable, and hence, for example, *Chrysomela* larvae feed only on young poplars or the offshoots of old trees.

Immature insects appear to utilize more nutritive food than do the adults. This may be proved by comparing the ratio of the weight of food assimilated to the weight of faecal matter produced during the life of any given individual as well as by the fact that the food requirements change with the insect's growth (Figs. 3.10 and 3.11).

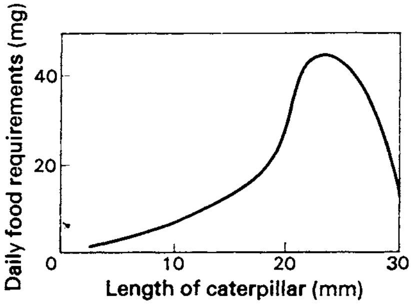


Fig. 3.10 Daily food requirements of ***Bupalus piniarius*** (L.) caterpillars in dependence on their length (after Schwerdtfeger, 1977)

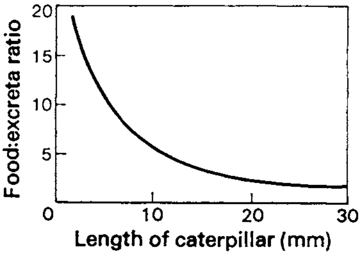


Fig. 3.11 Ratio of daily consumption to excrements in caterpillars of ***Bupalus piniarius*** (L.) in dependence on their length (after Schwerdtfeger, 1977)

For phytophagous insects, under natural conditions, food is usually available in excess and the phenomenon of hunger is rare. The resistance of insects to hunger varies. In general, the older larval stages are invariably more resistant than the younger stages. Larvae of females, particularly immediately after moulting, are more susceptible to hunger. Progressive, regressive and casual food deficiency may be distinguished. Progressive deficiency occurs after the consumption of all the leaves on the trees, i.e. after exhaustion of the food stock. Regressive deficiency is observed in the case of asynchronization in the development of the phytophage and its host plant, such as been observed in *Tortrix virida-*

na (L.) when the larvae hatched early, before the oak leaves had developed. Repeated casual lack of food occurs, for example, when insects are expelled from their host plants by wind or rain.

Progressive food deficiency often leads to a "forced" change of host plant which is generally to the detriment of the insect. Just as in regressive food deficiency, this results in a higher mortality of the insect.

Food thus plays a very important role in the course of all biological activities of insects and their ultimate survival.

3.2.4 Influence of food on reproduction and development

The influence of food on the fertility of insects is rather variable. In insects which do not feed as adults, fertility depends on the feeding conditions during their larval stages. *Panolis flammea* (D. & S.), feeding in a non-damaged forest stand, laid 150–160 eggs whereas individuals feeding in a severely damaged forest stand (i.e. under conditions of food deficiency) produced an average of 79 eggs. The heavier the female pupa the more eggs the mature adult lays. This is what is called "pupa–egg" dependence which has been verified in *Bupalus piniarius* (L.), *Panolis flammea* (D. & S.), *Lymantria monacha* (L.), *L. dispar* (L.), *Dendrolimus pini* (L.), and in some diprionids, in which the width of the cocoon indicates the number of eggs to be laid (Fig. 3.12).

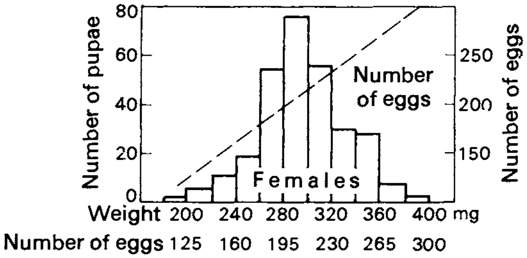


Fig. 3.12 Weight of pupae of females of *Panolis flammea* (D. & S.) and number of eggs laid by one female (line) (after Schwerdtfeger, 1979)

In insects which also feed in the adult stage, the number of eggs laid may depend on the amount of food consumed during the course of supplementary (i.e. adult) feeding. Oak leaves containing greatest amounts of nitrogen compounds, particularly proteins and tannins, are the most valuable source of food for *Melolontha*, for example, and give rise to the most fertile and viable adults (Fig. 3.13).

Fig. 3.13 Oak with leaves devoured by *Melolontha melolontha* (L.) (photo by W. Strojny)

Table 4.4 Age-specific life table of *Phytodecta olivacea* (Forster) populations (after Dempster, 1975).

X	$d_x F$	1954				1955				1956				1957				1958			
		l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x
Adults		11 820				16 184				17 027				6 393				6 759			
	sex ratio: percentage of females	47.4				56.5				50.0				58.3				56.5			
	fertility (eggs per 1 female)	82.1				72.1				82.4				54.1				32.7			
Eggs and larvae		460 169				659 554				701 563				201 760				125 039			
	non-fertilized eggs		46 927	10.2			39 573	6.0			25 256	3.6			9 866	4.9			10 003	8.0	
	parasites of eggs and larvae		51 539	11.2			60 019	9.1			41 392	5.9			7 263	3.6			3 238	2.6	
	predacious arthropods and unknown factors		297 754	64.7			422 352	64.0			627 775	89.5			139 805	69.3			101 344	81.0	
				86.1	86.1			79.1	79.1			99.0	99.0			77.8	77.8			91.6	91.6
Pupae		63 939				137 610				7 140				44 826				10 454			
	predators and unknown factors		29 884	46.7			99 766	72.5			1 843	25.8			37 482	83.6			5 098	48.8	
				46.7	92.6			72.5	94.3			25.8	99.2			83.6	96.4			48.8	95.7
Adults before hibernation		34.055				37 844				5 297				7 344				5 356			
	Periletus		4 836	14.2			3 747	9.9			1 398	26.4			1 292	17.6			268	5.0	
	Beauveria		3 916	11.5			7 190	19.0			122	2.3			0	0.0			193	3.6	
	transferred to laboratory and unknown factors		11 787	34.6			14 860	39.3			938	17.7			1 171	16.0			2 153	40.2	
				60.3	97.1			68.2	98.2			46.4	99.6			33.6	97.6			48.8	97.8
Adults after hibernation		15 516				12 047				2 839				4 875				2 742			
Adults surviving from former year		2 668				4 980				3 554				1 884				1 258			

The duration of development in insects depends to a certain extent on the quantity and quality of the food. When the food available is abundant the time of development is somewhat longer. As stressed above the quality of food distinctly affects the time of development. Caterpillars of *Lymantria monacha* (L.) reared at 27°C develop more rapidly when they feed on deciduous leaves than when they feed on coniferous needles. They achieve the fourth moult within the following time intervals: after 12 days on beech, after a longer period on hazel, apple, pine and larch and after the longest time (21 days) on spruce. Polyphagous species taking a varied diet appear to develop more rapidly than those species feeding on a single though favourable type of food. The quality of the food also influences the mortality of phytophages. The mortality of *Lymantria monacha* (L.) caterpillars is highest on alder (86% perish at stage IV), followed by fir (78% at stage IV), and finally pine (20% at stage II). Among caterpillars feeding on spruce only 1% perishes and these only at stage V. This indicates that this tree species is the best food source for *L. monacha* (L.), although its development on spruce is slow and the number of eggs laid by individuals feeding on it is not the highest (alder – 68, fir – 86, pine – 160, spruce – 195, beech – 227, apple-tree – 238, larch – 261, oak – 269) (Schwerdtfeger, 1963).

3.2.5 Influence of the physiological condition of the host plant

The quality of food depends not only on the species of the host plant of the phytophage but also on its physiological condition. This was proved long ago in studies on the biology of secondary pests. More recently, similar results have been obtained in studies on insects gnawing or sucking leaves previously regarded as being primary pests. Physiological differences between individuals of the same plant species depend on the habitat (soil and climate) and on the course of meteorological conditions as well as on the influence of other living organisms and on the plant's own history. As mentioned above the physiological condition of plants varies with time both during the day and throughout the year.

The content of water and nitrogen in the soil exercises a very important influence on the physiological condition of a tree. According to Schwenke (1963):

1) Soil humidity is indispensable since it takes into solution those nutrient compounds vital to the survival of the plant and activates the microorganisms which break down acidic humus and the soil fauna which transfers the humus into the mineral soil layer.

2) Long-standing water deficiency impairs the respiration of plants thus increasing the sugar content in leaves as well as the osmotic pressure.

3) Sufficient water supply to woody plants enables the water to transfer from colloidal bodies to the cell sap and secures an adequate content of nitrogen compounds, particularly protein, in living cells. Assimilation and transpiration increase. Thus, the soil humidity serves to limit the relative sugar content and, since sugar deficiency as well as nitrogen excess diminish the value of leaves as food for insect larvae, it inhibits their development.

Conversely, when water supply is insufficient, the increased sugar content of the leaves favours the development of phytophages, lowers their mortality and increases the percentage of females and their fertility.

The weakening of trees can be due not only to the deficiency or excess of water but also to the lack of mineral compounds indispensable for the nutrition of plants and to anthropogenic causes such as the cultivation of forest trees outside of their natural range.

Authors agree that insects feeding on weakened trees or cut shoots exhibit a lower mortality than those feeding on healthy trees. However, divergences in their observations exist as to the size and fertility of insects. Khanislamov *et al.* (1962) observed that caterpillars of *Lymantria monacha* (L.) and *L. dispar* (L.) feeding in the crowns of weakened trees exhibited a lower mortality while their pupae were heavier on healthy trees. Analogous results were obtained by Schwenke (1963, 1964) who found that individuals of *Diprion pini* (L.) were larger and the percentage of females was higher in pine forest stands on poor and dry soils. On the other hand, Grimalskii (1964), in his studies on the pupae and fertility of *Dendrolimus pini* (L.) and Merker (1961, 1963) in his studies on the size of pupae of *Lymantria dispar* (L.) obtained different results. Namely that the parameters mentioned above were greater on fertilized soils and on healthy trees.

These divergences are associated with the differences in results obtained by studies on the biochemical characteristics of leaves and needles of diseased trees as compared with those of healthy ones. Particular divergences occurred as regards the content of total and protein nitrogen as well as that of soluble sugars.

The higher mortality of insects feeding on healthy trees is usually attributed to the more intensive secretion of essential oils, alkaloids and resins by the latter.

According to the investigations of Krushev (1966), a sufficient content of nutrient compounds in the soil exercises a decisive influence on the resistance of pines to *Rhyacionia buoliana* (D. & S.). For this reason, pine plantations growing on poor sandy soils are most susceptible to pests. The outstanding thermo- and photophilicity of *R. buoliana* also enhance the damage caused by this pest. Pines growing on sandy soil secrete small amounts of resin and are readily damaged by insects. The intensity of resin secretion is not stable. Under uniform growth conditions of trees the resin secretion depends on pressure determined by the ratio of water uptake to output in the tissues surrounding the resin ducts. In pines illuminated with diffuse light the intensity of resin secretion from shoots is considerably higher than that in trees exposed to the direct activity of the Sun's rays. Lateral shoots exhibit a higher rate of resin secretion than the central one. In periods of dry, sunny weather pines growing in normal groups exhibit a higher intensity of resin secretion than solitary trees.

This explains Krushev's observation that free cultures from seeds are less susceptible to *R. buoliana* than planted seedlings. In the former case, as opposed to the latter, the trees are distributed in groups. They shade each other, therefore their transpiration organs develop poorly and this diminishes evaporation. The microclimate in groups is more humid. In planted tree cultures analogous conditions develop only when the stand becomes dense and then the numbers of *R. buoliana* decrease. Young caterpillars of *R. buoliana* are particularly susceptible to resin secretion since they are able to penetrate into the bud and shoots only when this secretion does not exceed a certain minimum. Pines exhibiting an intensive resin secretion from the needles, e.g. Crimean pine are resistant to this pest. The fact that resin ducts on the tips of the shoots of the Crimean pine *Pinus palasiana* L. have already developed by May also limits the feeding of this pest. In the common pine these ducts develop later. It should be remembered that caterpillars of *R. buoliana* select the tips of shoots as the site of initial feeding.

Biochemical analyses of needles from poorly growing 15–40-year-old pine forest stands in Ukraine (old farm land, fallows) showed that their nitrogen content is very low and that in appearance they differ from needles of natural forest stands by their smaller dimensions and weight as well as by their paler colour. When damaged, these needles secrete small bubbles of resin. It has been established that the mortality of caterpillars of *Dendrolimus pini* (L.) and other pests is considerably higher when they feed on needles of healthy trees actively secreting resin.

Grimalskii (1964, 1966) claims that the pine is sufficiently resistant to the feeding of needle pests when the length of the needles is not less than 6–7 cm and their average weight not less than 4–5 g. If we accept a four grade scale for the size of resin bubbles secreted by the damaged needles (0–1–2–3), the pine is resistant to the pest when the contribution of damaged needles secreting resin is not less than 40–50% and the resin bubbles are not smaller than 1.4–1.5 according to this scale. According to Grimalskii, a content of essential oils exceeding 0.8 mg per 100 g of air-dry needles is toxic for young caterpillars of *Dendrolimus pini* (L.). The contact of the caterpillars' mouthparts with resin drops is also toxic. A considerably higher mortality of caterpillars of *Panolis flammea* (D. & S.) has been observed on trees the needles of which were actively secreting resin than on trees exhibiting weak resin secretion (Schwerdtfeger, 1963). It was later shown that the essential oils of the resin secreted by pine needles contain 47 components, 10 of which (constituting 90–95% of the oil mass) have been identified by chromatographic techniques. An interesting dependence has been also detected where the resistance of forest stands to *Rhyacionia buoliana* (D. & S.) was proportional to the content of γ-terpinene in the oils. In dying down foci of this pest, pine needles contained 6–7% of γ-terpinene, in developing foci, 2.2% and in foci with a low frequency of the pest, 4.2% (Rudnev *et al.*, 1970). Thus, the index of resistance of pine forest stands can be determined according to the following formula:

$$U = \alpha + l + \Delta^3 + \gamma - \beta$$

where U = the index of resistance, and α, l, Δ^3, γ, β = the content of essential oils α-pinene, l-limonene, Δ^3-carene, γ-terpinene and β-pinene in percentages respectively.

The plantation is resistant to *R. buoliana* when $U > 60\%$ (for needles) or $U > 70\%$ (for shoots).

3.3 Feeding relationships among zoophages

Two basic forms of zoophagy can be distinguished – predation and parasitism. Predators include insects which attack other (mostly smaller) insects. Their development requires more than a single prey and the contact between the predator and the prey is short-lasting. Very frequently predators, e.g. *Thanasimus formicarius* (L.) (Fig. 3.14) kill more victims than they need for their food requirements. During the course of its larval development and adult life, *Calosoma sycophanta* (L.) de-

Fig. 3.14 Thanasimus formicarius (L.) attacking *Tomicus piniperda* (L.) (photo by S. Kinelski)

stroys about 550 caterpillars of *Lymantria dispar* (L.) whereas a coccinellid (ladybird) of the genus *Hyperaspis* devours over 3000 individuals of coccids in the course of its larval development alone (Sweetman, 1958). Unlike predators, parasites spend most of their life either on or in the host's body. The entire development of the parasite occurs to the detriment of the invariably larger host. The effect of parasitization is extended over a period of time and is sublethal for the host and has long-lasting consequences. The physiological functions, feeding, time of development, growth and endocrine gland functions of the host are disturbed prior to its death. Göpfert (1934) observed that caterpillars of *Panolis flammea* (D. & S.) parazitized by larvae of *Ernestia rudis* (Fallén) produce 2–3 times more excrement than healthy ones. Other authors have observed the opposite dependence in caterpillars of *Lymantria monacha* (L.). Those invaded by *Parasetigena silvestris* (= *P. segregata*) (Robineau–Desvoidy) produce 60% of the amount of excrement produced by healthy ones. Despite the attack of parasites, larvae of the host sometimes pupate and the subsequent pupae do not die until the parasite's development is complete.

In practice there may not always be a distinct differentiation between predators and parasites. For example the larvae of some *Hymenoptera* destroy an entire batch of the host's eggs and therefore doubts arise as to whether they are external parasites or predators of the eggs. There are also some coccinellids which reach the adult stage at the cost of just one coccid individual and thus, according to the definitions given above, may be classified as parasites.

Finally, certain developmental stages of a given species may behave as predators whilst others act as parasites. The adults of *Aleochara bilineata* Gyllenhal (*Staphylinidae*) are predators, attacking larvae and other developmental stages of *Diptera* in the soil, whereas the first and second larval instars parasitize the pupae of *Diptera.*

The range of feeding preferences of zoophages can be either very narrow or very wide. As well as monophages, oligophages and polyphages have also been observed. Polyphagous entomophages readily adapt to new victims or hosts when they come into contact with them, as when a new host species is introduced into the range of the predator or parasite or vice versa. In general, it can be said that despite the considerable food specialization of many parasites the range of trophic tolerance of predators is not wider than that of parasites. It seems, however, that the environment and behaviour, and not biochemical features, are the main factors of food selection of predators. On the other hand, in the case of parasites, the biochemical properties of the hosts play an important role in food selection in addition to the environmental and behavioural factors. Insects parasitic on polyphagous hosts thus frequently exhibit a varying rate of development and survival depending on the host plant of the phytophage, the nutritional value of which is also determined by the existing trophic association. Factors of the abiotic environment, such as temperature and humidity, which alter the activity of the components of the trophic association can also influence the selection of prey by polyphages, entomophages and predators in particular.

3.3.1 Predators

The contribution of animal food to the diet of predators is variable. Species which feed exclusively on animal food are called euzoophages, those with a varied diet are known as hemizoophages, whereas those eating "meat" only casually are called parazoophages. Either larvae or adults, or both of these stages in a given insect species can be predators. In cases where the adults are not predators they generally feed on light plant food such as flower pollen and nectar as well as honey-dew and sap – only exceptionally do they feed on leaves or other green parts of plants. Only rarely are the adults alone predaceous and then in these instances the larvae are generally saprophages and rarely phytophages.

Sweetman (1958) distinguishes the following three types of predators according to the site of oviposition: i. eggs laid in the direct neighbourhood of the prey; ii. eggs laid within the environment surrounding the prey, and iii. eggs laid independently of the character of the prey and its environment.

A further sub-classification of these developmental types is based on differences in the behaviour of the larvae and imagines: a. only larvae are predators (some *Chalcidoidea* (i), *Rhagionidae* (ii)); b. both larvae and adults feed on prey belonging to the same taxa (most *Chrysopidae* (i), numerous *Coleoptera*, *Heteroptera*, etc. (ii), some *Orthoptera*, *Coleoptera*, *Heteroptera* (iii)); c. both larvae and adults are predators but their prey belong to different systematic groups (some *Muscidae* (i), *Myrmeleon* (ii), some *Elateridae*, *Raphidioptera* (iii)); d. only adults are predators (*Empididae* (i)).

Synecthry is a particular case of predation. Synecthrans are predatory cohabitants of ants' nests. These species mostly inhabit peripheral parts of the nest or its close vicinity. Usually at night, when the temperature is low, they creep into the ant-hill and attack the ant eggs and larvae. The activity of synecthrans can lead to the degradation of ants and create difficulties in the colonization method used. Among synecthrans are included *Quedius brevis* Erichson and *Gyrohypnus atratus* Heer (*Staphylinidae*).

The food specialization of predators is determined by the size and hardness of the prey's integument, the environment, the behaviour and particularly the season of occurrence and activity of the prey.

Owing to the active mode of life of predators due to the necessity of finding their prey, their larvae exhibit better developed sense organs than those of parasites. Also a definite rhythm of activity is displayed by predators. In many diurnal species the sense of vision plays an important role. *Cicindela hybrida* L. (Fig. 3.15), for instance, as well as *Staphylinus dimidiaticornis* Gemminger, react only to live prey and exhibit no reaction to dead or immobile food. As compared with most adult parasites, many predatory insects are active during the night. Nocturnal species, e.g. *Chrysopa*, are generally directed by typochemical senses while the sense of vision plays a secondary role in their life (Kawecki, 1932). Even within the same taxonomic group the 24-hour activity pattern can vary widely and thus a "continuous functioning" of

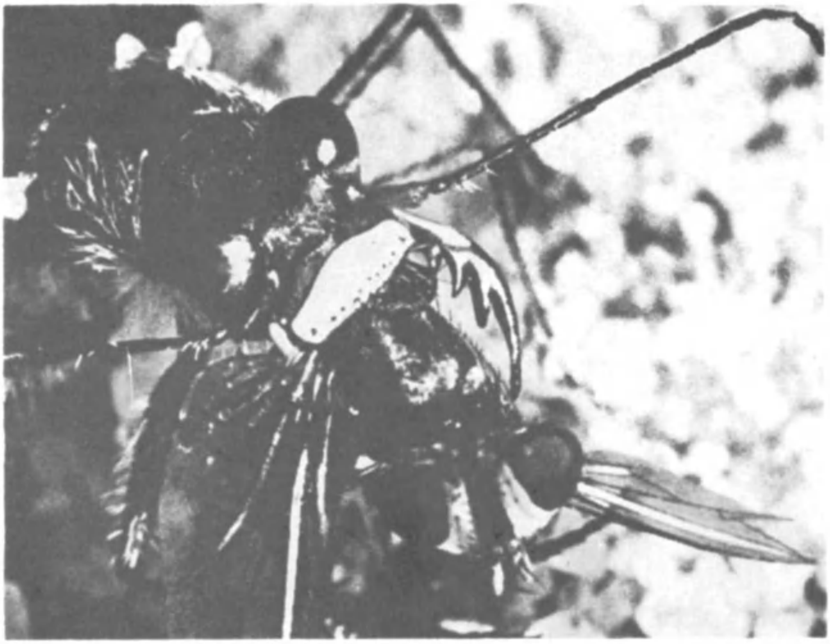


Fig. 3.15 Cicindela hybrida L. devouring a fly (photo by T. Bojasiński)

predators in the biocenosis is secured. Within the *Staphylinidae* the following three groups of predators are distinguished according to the character of their activity (Tikhomirova, 1967): i. species belonging to the subfamilies *Oxytelinae*, *Tachyporinae* and *Aleocharinae* characterized by a low 24-hour activity and a low degree of specialization in the selection of the site of activity; ii. certain species of the subfamilies *Paederinae* and *Steninae* exhibiting a high activity with long intervals of resting periods; iii. species of the subfamily *Xantholininae*, as well as most *Paederinae*, exhibiting a high activity uniform throughout the 24-hour period.

Not only the time intervals between prey capture, but also the index of prey mortality due to reduction by other predators depends on the degree of activity of the predatory insect in question (Grüm, 1975).

3.3.2 Parasites

Parasites are classified as either external (ectoparasites) living on the surface of the host's body and feeding on its fluids (haemolymph) and products of tissue decomposition, or internal (endoparasites) living within the host's body and destroying its tissues. Endoparasites parasitic in their larval stage within various animals and particularly other insects are the most common. Larvae of flies of the family *Gastrophilidae* are endoparasites of vertebrates. Ectoparasites include both parasites of insects and insect parasites of homoiothermal animals, e.g. lice, bird lice, fleas and larvae of some *Diptera* invading the superficial body layers of forest vertebrates (*Hypodermatinae*) or their air passages (*Oestrinae*). *Hippoboscidae* and *Nycteribiidae* (the latter specializing in parasitizing on bats) are also ectoparasites of mammals. There are rare instances of adult beetles with ectoparasitic habits, such as *Platypsyllus castoris* Ritsema (*Staphylinoidae*: *Leptinidae*) which is parasitic on the beaver. Parasites of eggs, larvae, pupae and adult insects may be distinguished. On occasions a parasite lays an egg in the larva of its host which then develops inside the host larva and completes its development in the pupa of the host. A particularly interesting life-cycle is seen in species of the genus *Ibalia* (Latreille) (Fig. 3.16), parasites of *Siricidae*, which lay their eggs in the host's eggs and complete their development in the host's larva.

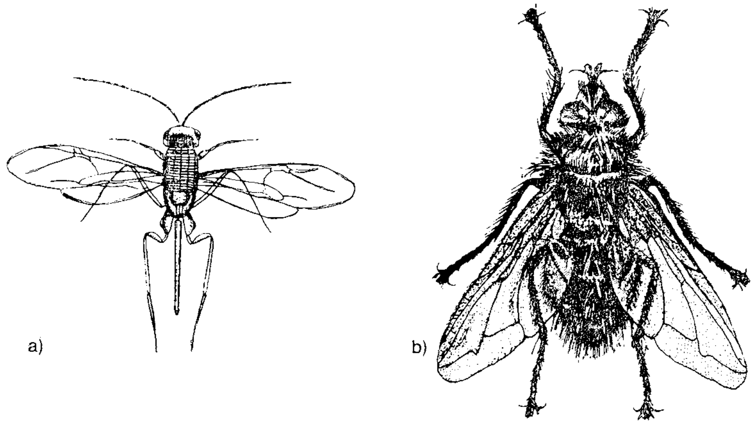


Fig. 3.16 Parasitic insects: a) *Ibalia leucospoides* (Hochenwarth), b) *Ernestia rudis* (Fallén)

Numerous species of parasites produce several generations per year so that when conditions are favourable their frequency rapidly increases. Each parasite species usually has more than one host species, although only one of these is the main host and the others are either supplementary or facultative ones. The development of monophagous parasites must be synchronized with the biology of a single host. Oligophagous or polyphagous parasites can develop their several generations on transitional or supplementary hosts (Fig. 3.17).

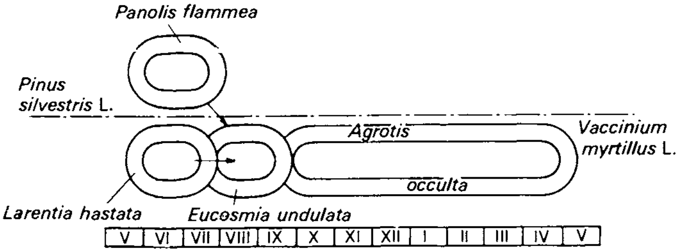


Fig. 3.17 Development of *Meteorus gyrator* (Thunberg) (= *scutellator* (Nees)) in annual cycle on successive hosts connected with the pine and the blueberry (after Karczewski, 1962). Roman numerals denote months

Primary parasites, parasitic on insects which are neither parasites nor predators can be and frequently are attacked by secondary parasites. Most secondary parasites belong to *Ichneumonidae* and *Chalcidoidea* (*Hymenoptera*). One of the most important peculiarities of secondary parasitism is the lack of specific specialization, i.e. the same species can parasitize primary parasites belonging to various species, particularly when they are readily available. There also exist parasites of secondary parasites, i.e. parasites of the third order (III) and also rarely parasites of the fourth (IV) and fifth (V) order. It is obvious that parasites of orders I and III (eventually V) are useful whereas parasites of orders II and IV are noxious from the standpoint of human economy.

The infection of insects with secondary parasites is sometimes quite intense and greatly limits the effects of primary parasites, although generally this influence becomes perceptible only in the form of retrogradation of the pest.

There are two further terms connected with parasitism, namely superparasitism and multiparasitism. Superparasitism occurs when the host is facultative and the number of parasite individuals developing within it exceeds the normal level. As a result of competition, most or even all of the parasites fail to complete their development. Multiparasitism or multiple parasitism occurs when several parasitic species attack the host almost simultaneously. In such cases the most specialized parasite generally eliminates the other competitors. Adults of parasites mostly feed on flower nectar, honey-dew or fluid organic substances such as sap flowing from wounded trees, etc. Some parasites feed on the host's haemolymph which flows from wounds produced by gnawing or by perforation with the ovipositor. Numerous *Hymenoptera*, particularly *Chalcidoidea*, and some *Diptera* feed in this way. In cases where the host stays in a puparium or cocoon, some parasites form a delicate tube through which they suck the haemolymph from the otherwise directly inaccessible food. Feeding on the haemolymph increases the fertility of females of the parasite.

Selection of the host and specialization of the parasite. The following three phases of achieving contact with the host by the parasite may be distinguished: perception, selection and accessibility of the host. The perception of the host is confined to the detection of a suitable environment and site of occurrence for the host (Fig. 3.18). Sometimes the host plant plays an important role in such environmental selection. For instance, the smell of volatile pine oils can repel the ichneumon *Pimpla ruficollis* (Gravenhorst) (a parasite of *Rhyacionia buoliana* (D. & S.)) before it achieves sexual maturity. Later the volatile oils of the resin become attractive for individuals of this species, and thus these individ-

Fig. 3.18 Female of *Ephialtes manifestator* (L.) seeking larvae of xylophages (photo by S. Kinelski)

uals fly towards pine shoots damaged by *R. buoliana* (Sweetman, 1958). *Itoplectis conquisitor* (Say) also parasitizes *R. buoliana* more intensely when the latter feeds on the Scotch pine rather than on *Pinus resinosa.* This is due to the smell of the Scotch pine which is more attractive to the parasite (Arthur, 1962). The selection of the host can be determined by both smell and visual stimuli (including the shape and colour of the host as well as its movements). The smell of the excrement of *R. buoliana* can provide the stimulus for host selection by some parasites of this species (Koehler & Kolk, 1972). In other cases the pheromones of the host act as scent stimuli.

Generally parasites avoid invading hosts previously infected by larvae of other parasitic species. Parasites can distinguish infected hosts from healthy ones by means of chemoreceptors located on the ovipositor. However, cases in which the opposite effect occurs have also been observed. For example, the infection of caterpillars of *R. buoliana* by either *Orgilus obscurator* (Nees), *Temelucha interruptor* (Gravenhorst) or *Pristomerus orbitalis* Holmgren is intensified by the earlier infection by any one of the other two species. In such cases scent stimuli originating from the parasites which infected the host earlier also serve to attract other parasites (Koehler & Kolk, 1972).

Shape and colour play a particularly important role in the selection of a host. Parasites of eggs, or of larvae and pupae which are enveloped in symmetrical cocoons or freely distributed on the plants where they may be readily perceived, proceed towards the host by means of visual stimuli (Fig. 3.15). The accessibility of the detected host leads to its infection. The infection by various parasitic species takes place in different ways. Endoparasitic ichneumons perforate the host's cuticle (and sometimes also the wall of the cocoon, the bark and wood, etc.) with their ovipositor and lay eggs in the host's body. *Larvaevoridae* which do not have a proper ovipositor attach their eggs to the cuticle of the larvae or deposit them on the leaves of the host's food plant. Some *Larvaevoridae* inject their eggs into the oral cavity or onto the mouthparts of feeding caterpillars while others deposit the eggs inside the host's body by cutting through the cuticle with special spines. Finally, some larvaevorids lay eggs on leaves and when the larvae hatch they locate their caterpillar hosts and bore into their bodies.

Frequently the dispersal of parasites is due to phoresis, i.e. to their transfer by the hosts.

Ectoparasitic ichneumons which attack larvae hidden in cocoons or crevices in wood (Fig. 3.19) paralyse the hosts by piercing them with

Fig. 3.19 Larva of *Ephialtes* sp., the ectoparasite of *Cerambycidae* larvae (photo by S. Kinelski)

their ovipositor before laying eggs. The initial paralysing of the host is a necessity because otherwise the eggs run the risk of being crushed by the movements of the host.

When their development is complete the larvae of parasites pupate either inside the body of the dead host or near it.

The character and degree of self-defence exhibited by the host against parasites and predators is very important in the complex of agents determining the effectiveness of entomophages. Such defences may consist of a divergence of ecological requirements, which serve to keep the potential host beyond the reach of the aggressor, and of physiological adaptations such as the encapsulation of the eggs of endoparasites (in which a layer of tissue is formed enveloping any foreign body in the body of the organism).

Pathogeny, i.e. diseases of insects due to microorganisms such as viruses, bacteria, fungi, protozoans and nematodes constitutes a specific form of parasitism.

3.4 Characteristics of saprophages

As opposed to biophages which feed on living plants (phytophages) or animals (zoophages), saprophages are animals which feed on dead organisms. Most saprophages feed on dead plant remains and include humusophages and karyophages. Necrophagy and coprophagy are specific forms of saprophagy. Saprophages include animals which live in the soil (mainly humus) and in dead wood (xylophages and karyophages) although many saprophages occur in specific habitats such as birds' nests on trees, human buildings and other constructions, etc.

The feeding of saprophages is associated with two of the four basic processes of decomposition of organic substances which are dependent on thermal and humidity conditions as well as on the activity of living organisms. These two processes are humification and decay. The contribution of saprophages to the two other processes of decomposition, i.e. mould and peat formation is slight. In temperate climates humification takes place only when there is sufficient availability of humidity and oxygen. The gradual transformation of the forest litter during the course of the successive phases of humification leads to the production of mineral compounds. The activities of organisms decomposing the litter, i.e. consumers (humusophages) and destructors (saprophagous and saprophytic microorganisms) are closely associated and interdependent. In the process of humification, saprophagous insects feed on plant remains which have undergone preliminary decomposition by microorganisms. An important factor in the feeding of saprophages is that the dead organic matter is utilized in successive phases each of which is the result of the actions of different groups of animals and microorganisms.

Various organic compounds are presented in the plant remains occurring in litter. These include those that may be readily assimilated by organisms, such as sugars and amino acids (constituting 5–15% of the litter mass), proteins (5–8%), waxes, tars, tannins (5–20%) and cellulose, hemicellulose and pectins (40–50%). These are all broken down in the alimentary canal of insects. Lignin constitutes about 30% of the litter mass although it is not, however, utilized as food but is excreted and subjected to the action of microorganisms. According to many authors, the "liberation" of lignin, which later becomes the main component of humus, constitutes the most important contribution of the soil saprophagous fauna to the soil-forming process (Musierowicz, 1960).

Larvae of *Diptera* belonging to the families *Bibionidae*, *Tipulidae* and *Sciaridae*, as well as those of *Coleoptera* (e.g. some *Scarabaeidae* and *Elateridae*, etc.), are the most important insects belonging to the group of macrohumusophages. Among insects, most microhumusophages belong to the order *Collembola*.

Decay occurs in compact humid organic matter under conditions of light and oxygen deficiency. It is mainly due to the decisive contribution of specific microorganisms and involves the breaking down of both plant and animal remains. The decay of plant debris in the forest environment may take place under compact deciduous forest stands on humid impermeable soil where larvae of *Diptera* and some *Coleoptera* contribute to the processes of decay after the preliminary activity of anaerobic bacteria and microfauna.

In the vegetation period the rate of decay of animal remains, consisting mainly of proteins (e.g. corpses of forest animals) is high. It starts with an intensive development of anaerobic bacteria followed by an invasion of nematodes feeding on these bacteria. *Diptera* larvae then appear, secreting substances inhibiting the development of bacteria and they are finally followed by predatory and necrophagous *Coleoptera* (Górny, 1975b). Larvae of *Diptera* belonging to the families *Calliphoridae* (e.g. *Lucilia* and *Calliphora*) and *Sarcophagidae* (e.g. *Sarcophaga carnaria* (L.)) as well as beetles (various species of *Necrophorus*) are the most frequent necrophages.

The amount of food available for larvae of *Necrophorus humator* (Gleditsch), *N. germanicus* (L.) and *N. vespillo* (L.) influences (within certain limits and in direct proportions) the weight of their pupae as well as the frequency of the next generation (Spičarová, 1973).

4 Intraspecific relationships of forest insects

Integration of populations

An aggregation of individuals belonging to the same species and inhabiting the same area is called a population. It constitutes the third principle grade in the organization of the biosphere (after the cell and the organism) and exhibits a definite ecological structure. Characteristic demographical phenomena occur in the population and are determined by the fertility and mortality of individuals, as well as their age distribution and quantitative sex proportion. These phenomena are manifested by changes in the abundance of organisms. The processes of reproduction and mortality are the basic components of the dynamics of the population size and determine its existence. They also must be strictly regulated within the system in order to unify the individuals within the population.

Some of the mechanisms which enable the population to maintain its individual character in the presence of other organisms will now be discussed. It is known that the limits of a population are not strictly defined and it is difficult to find integrating systems within their range. This particularly concerns insects which exhibit no distinct group organization. This conclusion can be illustrated by the comparison of the behaviour of predatory forest *Diptera*, such as the *Asilidae* (Fig. 4.1), which are outstanding "solitary hunters" with that of socially living ants (e.g. *Formica rufa* L.) in which the function of each individual can be readily detected and in which the action of the individuals are closely interdependent (Fig. 4.2).

Most mechanisms integrating a population are centred around the reproductive and behavioural activities of the given species. The exchange of genetic information is particularly effective when individuals are able to discern members of their own species and of the opposite sex. The sex instinct is particularly strong and is based on numerous mor-

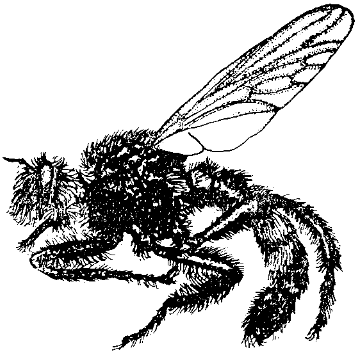


Fig. 4.1 Representative of the family *Asilidae*

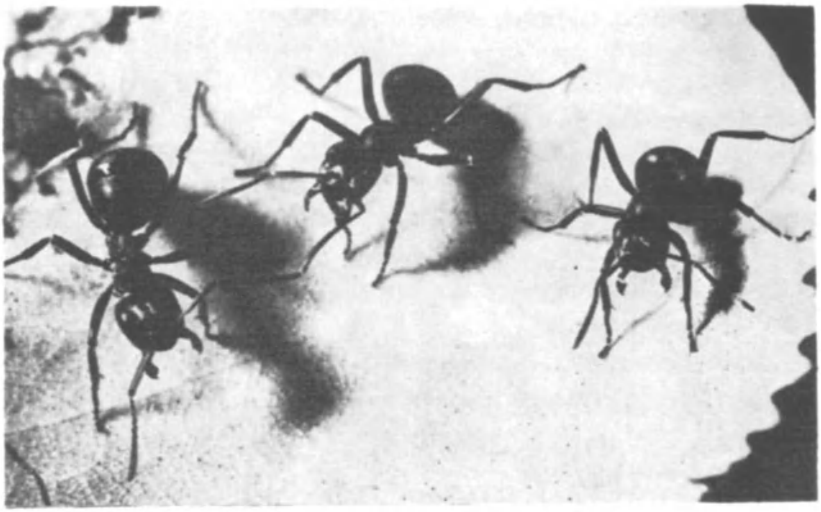


Fig. 4.2 Group of individuals of *Formica rufa* L. (photo by T. Bojasiński)

phological and ethological adaptations which make possible the rapid and certain mutual detection of sexes as well as the protection of the progeny.

4.1 Sexual life and protection of progeny

In insects the occurrence of males and females is determined by the annual developmental cycle of the species and depends on many agents, particularly light and temperature. Many species reproduce at strictly determined and rather stable periods of the year. The nuptial flight of *Panolis flammea* (D. & S.) occurs during the first half of April, whereas that of *Dendrolimus pini* (L.) in the beginning of July, etc. In other species the period of mating distinctly depends on the course of the meteorological conditions in any given year, as well as on the microclimatic conditions of individual forest stands and may be signalled by pertinent phenological phenomena.

Males usually appear somewhat earlier than the females (protoandria) although in rare instances they emerge somewhat later (protogynia). The phenomenon of protoandria is due to the more rapid development of males. The male caterpillars of *Lymantria monacha* (L.) undergo five moults whereas female caterpillars have six. The males thus pupate 2–5 days earlier. A similar course of development is observed in *Bupalus piniarius* (L.).

The actual sexual contact of forest insects occurs in flight, on plants, in the litter or on other sites. Invariably the scent of secretions of the abdominal glands of females (Fig. 4.3) is the attractant stimulus in insects. The males of *Lymantria dispar* (L.) are able to detect females in

Fig. 4.3 Sesia apiformis (Clerck) – individuals copulating on a poplar stump (photo by W. Strojny)

this way from a distance of 3.5–3.8 km. This capacity has been put to a practical use in the prediction of the appearance of this moth. Individuals of the opposite sex may locate one another not only by scent, but also by visual (e.g. the luminescence of female of glow-worms) or acoustic (e.g. the chirp of crickets) stimuli.

The recruitment of individuals of the opposite sex takes place by administering stimuli which may be tactile (mostly by means of antennae), acoustic (e.g. *Orthoptera*), olfactory, visual (particularly when sexual dimorphism occurs), gustatory (before copulation the male of *Panorpa communis* L. presents a salivary secretion to the female which the latter eats) or motor (e.g. contests between *Lucanus cervus* (L.) males and between *Bystiscus* sp. males, the assumption of characteristic postures by various insects, etc). Haber (1953) presented an interesting and detailed description of the mating behaviour of *Barbitistes constrictus* Brunner von Wattenwyl in which the males attract the female with acoustic, olfactory and motor stimuli. During the late evening, the male proceeds slowly, moving its wings and delivering short chirps with 1–2 minute intervals, and then performs several vibrations with its entire body. At this moment the female approaches the male, which stands parallel to the female's body and stops chirping but continues to move its wings. The female stretches its palpi towards the male and moves its antennae and sometimes also its wings. When touched by the female's antennae, the male stands astride with its foremost legs, bends the front of its head and leans it against the substrate, stretches its antennae forward and then straddles and bends its second pair of legs. The female touches the tergites of the male with its palpi and finally settles on the male and consumes drops of fluid from the bristles on its body surface. In addition the female may frequently bite the margins of the male's wings which are saturated with the secretions of scent glands. Finally, in this position copulation occurs and eggs subsequently are laid by the female.

After the mating and egg-laying period the parental individuals of most forest insects are not interested in each other nor in their progeny although some exceptions do occur.

The oviposition habits vary as to the degree of the provision of food and security for the future progeny. Eggs are invariably laid in protected places (under stones and bark scales, in niches, etc.). They may be covered with setae from the female's abdomen, secretions of sexual glands, sawdust (Fig. 4.4), plant material, etc. Insects usually place their eggs near food e.g. *Lochmaea caprea* (L.) oviposits in the soil beneath the host plant *Salix caprea* (L.) and *Rhyacionia buoliana* (D. & S.)

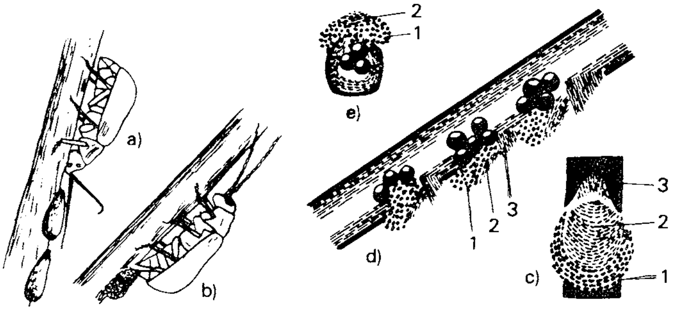


Fig. 4.4 Oviposition by *Pyrrhalta viburni* (Paykull) (after Horion, 1949): a) female gnawing out an egg niche, b) female covering an egg batch, c) protection of eggs (dorsal view), d) longitudinal section of a twig with egg batches, e) cross-section through a twig egg batch; 1, 2 and 3 – successive layers of excrements and wood-dust covering egg batch

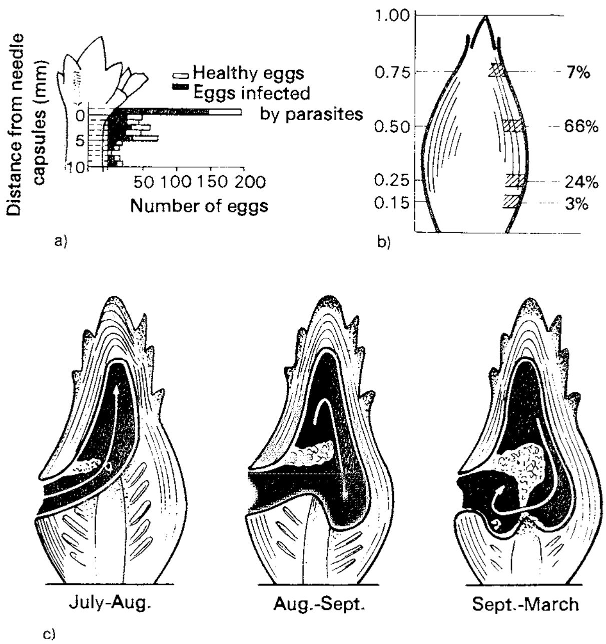


Fig. 4.5. Phyacionia buoliana (D. & S.) (after Koehler, 1967): a) Oviposition site on pine top shoot, b) distribution of inlets of caterpillars, c) scheme of feeding of caterpillars.

around buds (Fig. 4.5), on food (e.g. *Bupalus piniarius* (L.) on pine needles) or in food (e.g. *Ips typographus* (L.) under the bark of spruces).

The total number of eggs laid by a single female depends on the probability of their survival and may vary widely even between closely related species. Species making more provision for the safety of their eggs produce less eggs than those laying them "carelessly".

At the moment of oviposition many insects prepare food for the future larvae in a specific way. *Attelabidae* incise leaf petioles and lay eggs into the furled leaves thus deprived of turgor, such leaves serving as food for the larvae. *Geotrupes stercorosus* (Scriba) oviposits in agglomerations of mouldering leaves which it then buries in the soil and sphecid wasps accumulate paralysed caterpillars and other invertebrates in special chambers. A very interesting adaptation is seen in the lymexylid beetle, *Hylecoetus dermestoides* (L.) in which the female possesses a modification of the terminal genital duct by means of which the eggs are provided with mycelial spores when laid. The larvae, which occur in decaying wood, feed on the resultant fungal growth.

Parental care is better developed and more complex in social insects such as ants and bees which possess a distinct division of labour (Fig. 4.6).

Fig. 4.6 Protection of progeny by *Tetramorium caespitum* (L.) (photo by T. Bojasiński)

The larvae are reared on specially prepared food and more, provided with suitable thermal conditions, not to mention the protection they receive from being inside the nest. In *Formica rufa* (L.) for example, the larvae are carried in the morning to the upper parts of the ant-hill where they receive the warmth of the Sun's rays. Then, when conditions become too hot, the larvae are transferred to the deeper layers of the nest.

Insects may occasionally lay their eggs in sites prepared by other species. For instance *Rhynchites sericeus* Herbst lays its eggs in leaves furled by *Attelabus nitens* (Scopoli), the larvae of both these species hatching and developing in the same leaf.

4.2 Collective life of insects

In rare instances, some non-social insects exhibit some degree of parental care. The egg batches of *Forficula auricularia* L. are protected by the female until the larvae hatch. The female of *Xyleborus dispar* (F.) (*Scolytidae*) removes the excrement of larvae from the galleries. Females of the pentatomoid bugs *Elasmucha grisea* (L.) and *E. ferrugata* (F.) lay only 40 eggs in a batch and then take care of them, covering them with their abdomen and thus protecting them against parasites. Eggs lying on the periphery of the batch may not always be covered by the female's abdomen and are sometimes parazitized but those in the centre of the batch are invariably healthy (Bilewicz-Pawińska, 1961).

Such sub-social habits are not restricted to parental care but may be evident, for example, in the congregation of larvae on a common feeding site as in some chrysomelids (e.g. *Phyllodecta* sp.). Such groupings constitute the most primitive form of "family" life amongst insects.

Besides family groupings, higher social associations may also be observed in insects. These include the common hibernation of numerous individuals of certain species (e.g. ichneumonids under the bark of rotten stumps, caterpillars of *Euproctis chrysorrhoea* (L.) in leaves joined with threads of silk) and the processionary formations of the caterpillars of species of *Thaumatopoea.*

Colonies develop when many individuals remaining in family groups inhabit a common area. Colonies may be formed by numerous soil insects inhabiting the borders of bodies of water (e.g. *Bledius* (*Staphylinidae*)) and steep walls of gorges (e.g. colonies of wasps), as well as by bark beetles. As described earlier (3.2.2) the first individuals of the species to locate a suitable host tree inform the other members of the population by means of pheromones. Consequently the tree becomes covered with numerous "feeding grounds", each supporting a distinct family group which has usually been derived from the same batch of eggs (as in *Dendroctonus micans* (Kugelann), for example).

Social and sub-social communities only occur in nature when they confer distinct advantages on the individuals involved. Some means of communication between individuals is necessary, however, so that these advantages may be realized and made available to the other individuals. Pheromones here play a very important role and serve to transmit information concerning the whereabouts of food sources, the breeding site and, in some cases, large but sporadically occurring sources of food. For example, the honey-bee informs other worker-bees in the hive of any new discovery of plants in flower so that they may locate such flowers themselves and collect the nectar and pollen rapidly and efficiently. Needless to say, there must be many as yet undiscovered systems of communication between individuals of the same population.

The collective life of insects can, on the one hand, stimulate the favourable course of developmental processes and protect the individuals against enemies, etc. On the other hand, however, it can lead to intraspecific competition for food supplies or space. Such competition is discussed briefly below.

The optimum temperature for the development of larvae is maintained in ant-hills and hornet nests by the direct or indirect efforts of the adults. Analogously *Eriogaster lanestris* (L.) moderates the amplitude of temperature oscillations in its nests. Both these and other similar phenomena have been described in the chapter concerning the influence of temperature on the life of insects. A group of individuals is, of course, not only larger than a single individual but also distributes a greater number of sense organs over a larger area. A solitary individual must frequently interrupt food procurement to protect itself against antagonists, while members of groups can more effectively perform their life activities as it is sufficient that only some of them guard the entire group (as seen in termites for example).

It has been established that the space orientation of groups of *Pieris brassicae* (L.) caterpillars is based on a memory record whereas that of solitary caterpillars of *P. rapae* (L.) has compass-like character based on the direction of the sun's rays. As soon as the group instinct begins to decline in *P. brassicae* caterpillars, so does the memory-based orientation mechanism leaving only a compass-like, monotactic, unidirectional mechanism. This indicates a more efficient use of the senses in such collectively living insects.

The positive aspects of collective, or group life seem to compensate for the disadvantages associated with the exploitation of a single food source and the limitations of living within a restricted space. With so many individuals involved there is the danger that there will be insufficient food or space for each. A certain amount of competition for food does occur, for example, amongst bark beetles and, occasionally amongst caterpillars feeding in tree crowns. In some instances, such intraspecific competition for food and space may serve to regulate the population density.

Structure and function of the population

A population is characterized on the one hand by the biological properties common to its individuals and, on the other hand, by features unique to the group and not possessed by each component member.

The exclusive group properties are mainly statistical in nature and thus the biological features of organisms at the population level may be expressed in the form of statistical functions.

Values characterizing the structure of a population (abundance, density, spatial distribution, age distribution and sex ratios), as well as its functions (reproductive capacity, mortality, mortality index, growth curve, etc.), belong to such parameters.

4.3 Abundance and density

The abundance of a population represents the total number of its individuals without reference to a definite unit of space, whereas the density of a population is the abundance expressed in terms of numbers per given unit of area.

Ecological and forest protection studies are often concerned with elucidating the population dynamics of insects, particularly their densities and density regulating mechanisms. As mentioned above, density is expressed in numbers per unit area as, for example, the number of pupae of *Panolis flammea* (D. & S.) occurring in late autumn under the canopy of a single pine (calculated during the search for primary pine pests), or the number of grubs of *Melolontha* sp. found in the soil dug up from a control excavation about 1 m^3 in volume, etc. Sometimes, particularly when the density is difficult to measure, the abundance or relative abundance is determined as in the evaluation of the general danger to the forest stand of a particular potential. Abundance may be expressed, for instance, as a definite number of adults of *Lymantria dispar* (L.) captured per time unit with the use of an m.v. light-trap.

Relative abundance is expressed in the form of various indexes mostly representing the quantitative characteristic of a population in percentages. An example of this is the index of stability which represents the percentage of samples collected in which the species involved was observed (e.g. the percentage of poplars damaged by *Saperda* in a selected row).

Sometimes also the intensity of the abundance of a population may be distinguished. This denotes the number of individuals per definite number of leaves, buds or other plant organs on which the insects feed. Obviously, the density of a population may undergo considerable changes at a stable intensity of abundance, due to the growth of the forest stand and the development of the tree crown.

In view of this it is necessary to distinguish the intensity of abundance from the density of a population. An underestimation of this difference can lead to a misinterpretation of the true situation. For example, the mass appearance of *Agrilus viridis* (L.) in 1946–1951 in FRG was brought about by dry weather condition which weakened the trees. In 1952 excessive rainfall caused a distinct decrease of the abundance of this species due to the restored defence reactions of the trees. Schwerdtfeger (1958) considers this case as an example of the influence of the regulative activity of climatic factors on the density of the population. On the other hand, Klomp (1962) rightly remarked that Schwerdtfeger actually observed the number of individuals on the tree organs serving as their food (intensity of abundance) which was the controlled value in the conditions studied, instead of considering the absolute density of the population as conditioned by the total supply of suitable food (number of weakened trees).

It should be remembered that the term "abundance of population" is frequently used in the literature as a synonym of density since invariably the abundance is related to a definite space in view of the small size and great number of individuals of various insect species. These two terms are commonly synonymized, particularly in discussions on the problems of dynamics of the abundance of insects.

4.4 Spatial distribution

The irregular distribution of individuals in space constitutes one of the basic problems arising in attempts to determine the density of a population (Fig. 4.7). An insufficient number of samples collected for the determination of population density can lead to completely erroneous conclusions as regards this value. In many instances the low effectiveness of the method of the "autumn search for primary pests" has failed to predict the sudden population explosions of *Diprion pini* (L.) which exhibits a distinct group mode of feeding and hibernation of larvae. Attempts to estimate the density of individuals of *Formica polyctena* (Foerster) in a pine forest would encounter great difficulties while the study of the distribution of their nests and the estimation of the number of their inhabitants can be more easily accomplished.

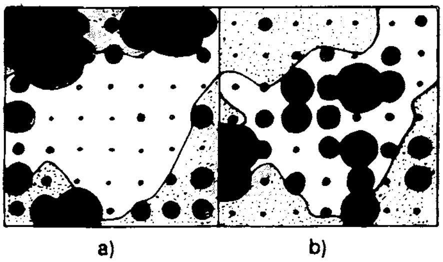


Fig. 4.7 Spatial distribution of two species of *Carabidae* on the forest floor (after Schwerdtfeger, 1979): a) *Abax parallelepipedus* (Piller & Mitterpacher), b) *Calathus piceus* (Marsham). White colour indicates sites covered with litter, grey colour – sites with more exuberant herb layer, black colour – distribution of insects

Three types of spatial distribution may be distinguished – uniform, random and clumped (Fig. 4.8).

Uniform distribution may occur when there is keen competition for space and food between individuals as observed, for instance, in web spiders.

Random distribution is rarely observed in nature and occurs only in very uniform environments and in species exhibiting no group tendencies. Studies on the fauna of the forest floor indicate that only spiders exhibit a random distribution.

Random distribution may be expressed mathematically by Poisson's formula, according to which the number of samples (of identical indi-

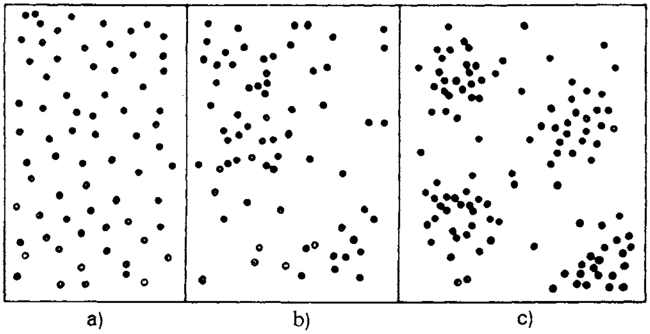


Fig. 4.8 Types of spatial distribution of individuals of a population (after Macfadyen, 1963): a) uniform, b) random, c) clumped

viduals collected from a population) containing 0, 1, 2, 3, 4 ... *n* individuals is determined by the following sequence:

$$N_e^{-m}\left(1, m, \frac{m^2}{2!}, \frac{m^3}{3!}, \ldots, \frac{\mathrm{m}^n}{n!}\right),$$

where m = the mean number of individuals per sample, e = the base of natural logarithms, N = the total number of observations.

The peculiarity of Poisson's distribution is due to the fact that the dispersion of the number of individuals per sample (i.e. the mean square of deviation of each observation from its mean value) is equal to the mean number of individuals.

It invariably results, however, that the dispersion is considerably larger than the mean and this indicates that the dispersion of the size of the samples exceeds the expectation, thus the population is distributed in clumps.

In insects, the occurrence of distinct groups is the most frequently observed distribution pattern. This tendency to form groups is due to the activity of environmental and, in particular, intraspecific factors. These include the irregularity of food distribution, the occurrence of sites unsuitable for invasion by the given species within the population's range (e.g. *Monochamus sartor* (F.) cannot invade free spaces between spruce logs), the deposition of eggs in clusters and the weak mobility of larvae hatched from these eggs (e.g. the larvae of many soil inhabiting flies or chrysomelid larvae on the leaves of poplars), and active tendency to form groups (e.g. ants), and so on.

The distribution of individuals of a given species cannot be considered as stable. Frequently, as the numbers of a population increase, the spatial distribution may undergo changes from clumped through random to uniform. Detailed studies on the spatial distribution of insects also indicate that frequently, although a random distribution is not exhibited by individuals of the population, it may be detected by considering pairs or groups of individuals.

As described above the formation of groups is generally advantageous to insects, although it can increase the competition between individuals. Both the extent of the concentration within the group and the general density, on which the optimal growth and survival of the population depend, change according to the species and conditions. Deficient and excessive densities can both limit the population of a species. In certain populations growth and survival rates are higher when the populations are small, while in others, as a result of intraspecific conditions, the optimum rates occur at a mean population size.

The knowledge of the type of spatial distribution of an insect species may be very important in the choice of methods of their capture as well as in the application of the appropriate statistical formulae for the interpretation of results. In practice, it is particularly important in the selection of suitable methods for the control of the pest. This has been mentioned above in the discussion of the causes of errors in the prognosis of the occurrence of *Diprion pini* (L.). It should here be stressed that on areas under the forest canopy, caterpillars of *Dendrolimus pini* (L.) exhibit a clumped distribution around tree trunks, whereas those of *Panolis flammea* (D. & S.) exhibit a distribution approximating that of a uniform or random nature.

4.5 Age distribution

The age distribution of a population characterizes the quantitative proportions between simultaneously occurring individuals of different ages (Fig. 4.9). Studies on age distribution of forest insects are scarce and doubtless this is one of the causes of the gaps in the theoretical interpretations of the phenomena of population explosions. Obviously the quantitative proportions within the range of each age class (e.g. the developmental stages of insects) vary in different species depending on the life-span of each individual stage, the number of generations per year, the percentage of time of the individual's life devoted to development, the reproductive and post-reproductive periods, as well as on the course of mortality. The overlap of successive generations is a necessary condi-

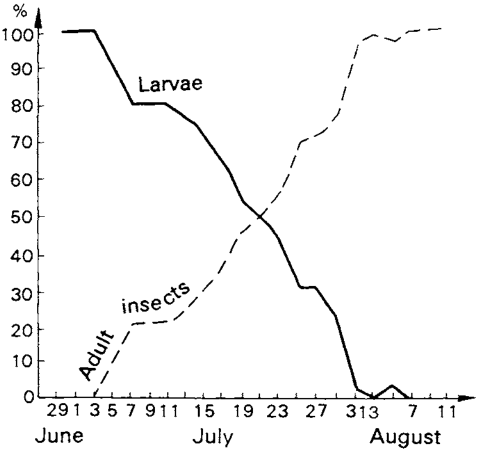


Fig. 4.9 Contribution of larvae and adult insects to a population of *Aradus cinnamomeus* (Panzer) in summer months (after Schnaider, 1968)

tion of the occurrence of a differentiated structure of age classes. This takes place, for example, when the length of life of the adults of a given species exceeds that of the period of reproduction. In addition, the length of the reproductive period and the rate of development of the progeny are very important in insects since they result in the overlapping of individual stages and the consequent differentiation of the age class structure.

This problem can be illustrated by the example of *Panolis flammea* (D. & S.). The population of this pest remains in the pupal stage, and therefore in the same age class, from the end of July to April. From about mid-May onwards, the proportions of the age classes begin to vary. At this time adults of the previous generation, as well as eggs and first instar larvae of new generation, are simultaneously observed. Around June 10 the caterpillars of stages I, II, III and IV may all be found feeding together on the host plant owing to the non-uniform development of individuals and to the non-simultaneous deposition of eggs in particular. Thus, the longer the period of reproduction the more differentiated is the distribution of age classes (Fig. 4.10). This phenomenon is particularly distinct in *Ips typographus* (L.) during mass outbreaks and periods of irregular meteorological conditions when, for most of the vegetation period, all developmental stages of this species may occur under the bark. The adult forms of this species can live for up to three years and the females can lay eggs several times (after regeneration

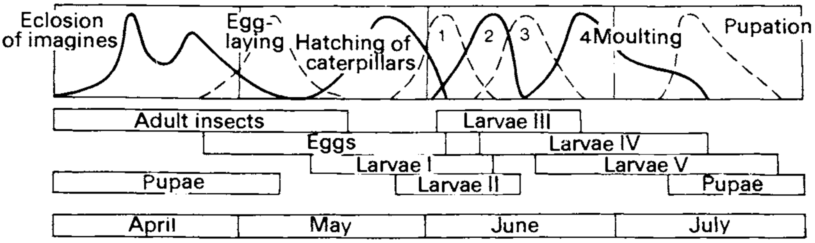


Fig. 4.10 Distribution of age classes of *Panolis flammea* (D. & S.) (after Schwerdtfeger, 1979)

feeding). Because of the decrease in the numbers of each generation as they advance in age, the population is at its maximum number during the egg stage. In the weevil *Cryptorrhynchus lapathi* (L.), for example, the population at the beginning of May consisted of larvae of stage III (24%), stage IV (40%) and stage V (36%). On the other hand, on June 20, larvae of stage V constituted 10% of all individuals, pupae 74% and adult beetles 16%.

As the adult stage of *Lymantria monacha* (L.) dies off, the population consists almost entirely (99%) of eggs due to the relatively short reproductive period in comparison with the long period of egg development.

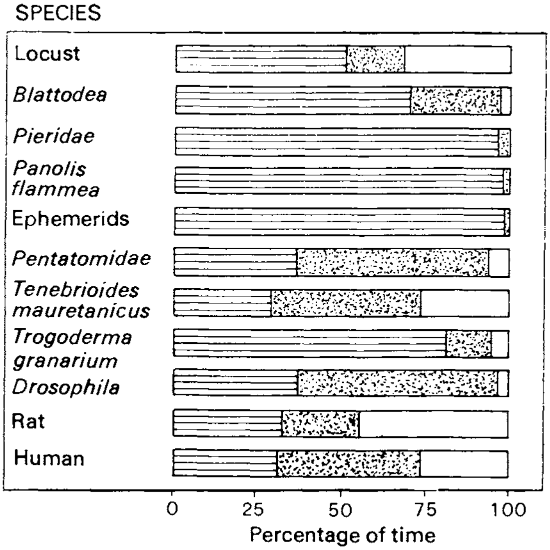


Fig. 4.11 Time (%) utilized by various animals for development period — hatched field, reproductive period — dotted field, post-reproductive period — white field after Allee *et al.*, 1950)

The ratios of the durations of the reproductive, developmental and post-reproductive periods vary widely between different species, and even between closely related members of a genus. On the other hand, the percentage of time (of the total life-cycle) devoted to the reproductive period in the ostomid beetle *Tenebroides mauretanicus* (L.) is most similar to that of man than to any other insect, such as *Panolis flammea* (D. & S.) for example (Fig. 4.11).

4.6 Sex structure

Insects as a rule are dioecious and frequently exhibit sexual dimorphism, i.e. morphological secondary sex features differentiating males from females. Copulation is the act which normally initiates the development of the next generation. Frequently, however, fertilization does not constitute a necessary condition of reproduction and the development of non-fertilized eggs takes place by way of parthenogenesis.

Parthenogenesis may be constant (as in the case of *Gilletteella cooleyi* (Gillette) which in Europe invariably exhibits parthenogenetic reproduction and males do not occur), almost constant (in *Xyleborus* sp. males are very rare and the new generation develops from non-fertilized eggs), sporadic (*Lymantria dispar* (L.) generally reproduces bisexually but under certain circumstances becomes parthenogenetic) or cyclic, consisting of a succession of bisexual and parthenogenetic generations (This phenomenon, known as heterogeny, is common in aphids). In the case of sporadic parthenogenesis males almost exclusively develop from the non-fertilized eggs (arrhenotokia).

It is thus evident that the male : female ratio in a given population may vary widely according to species, and even within a population at different times of the year. In extreme cases, as seen in some aphids, completely monosexual generations may occur.

The properties of reproduction are not the only factors determining the sex ratio observed in nature. This ratio also depends on the developmental cycle of the species (and of each sex) as well as on the feeding conditions of the larvae and the characteristics of the population. It may also vary in different parts of the species' geographical range and even in different parts of the biotope inhabited by a single population.

During the early part of the flight period *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson), males prevail in the population or, more precisely, in its "active" part. They wait for the females on pine trunks. In starving populations the number of females developing from larvae feeding in unfavourable conditions decreases. In *Melolontha melolontha* (L.), after the initial period of oviposition in clearings, the number of females increases in the population with the increasing distance from the forest stand and decreases during the initial period of the nuptial flight (Fig. 4.12).

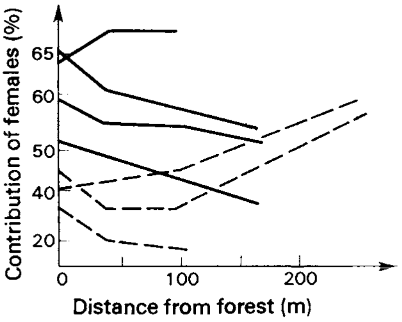


Fig. 4.12 Contribution of females of *Melolontha melolontha* (L.) on a cutting area during various periods of oviposition (after Schwerdtfeger, 1979)

Under the same geographical conditions the sex ratio in populations of *Pterostichus oblongopunctatus* (F.) depends on the habitat and specific composition of the forest stand. In relatively poor habitats of fresh pine forests males predominate, while in rich habitats of mixed or mixed coniferous forest females prevail (Fig. 4.13).

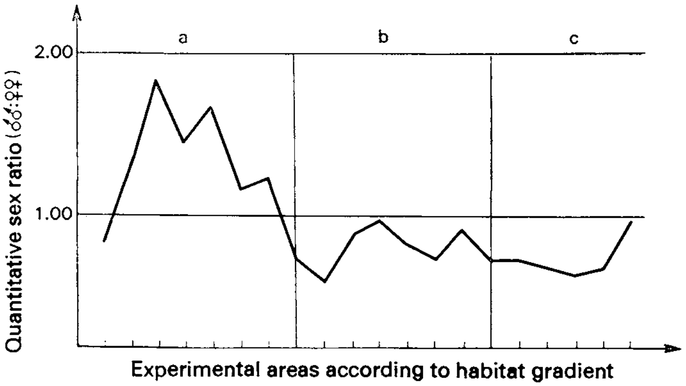


Fig. 4.13 Quantitative sex ratio in *Pterostichus oblongopunctatus* (F.) in dependence on the type of habitat (after Szyszko, 1976): a – fresh pine forests, b – mixed pine forests, c – mixed forests (mixed coniferous forests)

Apart from periods of dramatic quantitative changes in the population and the possibility of quantitative variability of the sex ratio, it appears that in many species this ratio is relatively stable. For example, in *Melolontha melolontha* (L.) it is 1:1; in *Bupalus piniarius* (L.), 2:3 in favour of males; in *Pristiphora abietina* (Christ), 3:2 in favour of females; and in *Diprion pini* (L.), 3.7:1.3, also in favour of females.

During outbreaks of *Lymantria monacha* (L.) in 1933–1937 in the Masurian forests, the percentage of females in the population diminished from 56 to 20%. In some cases this phenomenon may be due to the higher mortality of caterpillars of future females during periods of famine, whereas in other cases it may result from the activity of natural enemies, many of which (particularly predators) prefer the female caterpillars.

Thus, even in closely related insects, the sex ratio may differ considerably (Table 4.1).

Table 4.1 Contribution of males and females of some *Chalcidoidea* species caught in pine plantations in the Experimental Forests of the Agricultural University of Warsaw (tabulated according to the data of Szczepański, 1968).

Species	Males	Females	Sex ratio
Tetrastichus turionum Hartig	1	22	1:22
Tetrastichus pausiris Walker	31	32	1:1
Tetrastichus charoba Walker	36	99	1:3
Tetrastichus gaus Walker	5	45	1:9
Trichomalus perfectus Walker	–	54	0:54
Trichomalus campestris Walker	3	18	1:6
Trichomalus lepidus Foerster	11	20	1:2

4.7 Reproductive potential

Reproductive potential is the innate capacity for growth (i.e. numerical increase) of a given population. We can distinguish between the maximum reproductive potential of the population (also referred to as the absolute or physiological reproductive potential) and its actual, or ecological, reproductive potential. The first term indicates the theoretical maximum number of individuals produced under ideal conditions without the influence of ecological limiting agents. The latter concerns the reproductive potential of a population under strictly defined environmental conditions, and therefore is not stable for the given population and oscillates according to the size and composition of the population, as well as on environmental agents.

Apart from the phenomena of migration and mortality, changes in abundance are dependent on the reproductive potential and thus primarily on the fertility of the females.

It should be stressed that the number of eggs laid by the female is generally lower than the total number produced. This is due to the fact that a considerable percentage of eggs (oocytes) remains in the female's ovaries. The percentage of eggs laid depends on environmental conditions such as air humidity and temperature and wind force.

Contrary to earlier opinions, fertility only changes slightly during the successive phases of mass emergences, i.e. the changes in fertility are totally independent of the course of the quantitative variations (abundance) of the population (Table 4.2). On the other hand, however, fertility does appear to depend on food and meteorological conditions. The intensity of feeding, the weight of pupae, the proportion of females in the population, the activity during the nuptial flight and the number of eggs laid all increase under favourable meteorological conditions.

Table 4.2 Fertility of *Lymantria dispar* (L.) in the course of 6 years in Bashkiria – USSR (according to Khanislamov, 1958, after Vorontsov, 1963).

Year	Successive outbreak stages	Number of eggs laid by 1 female (mean in Bashkiria)
1952	explosive	257
1953	explosive	395
1954	critical condition	340
1955	retrogradation	362
1956	normal condition	277
1957	preliminary stage	304

The influence of food on the reproductive potential has been discussed above. It need only be added that the quality of food affects the fertility of both phytophages and zoophages. For example, *Dendroctonus micans* (Kugelann) lays 50–60 eggs when feeding on Norway spruce and 80–90 eggs when feeding on the Sitka spruce. The fertility of *Trichogramma embryophagum* Hartig is higher when it parasitizes the eggs of *Panolis flammea* (D. & S.) than when the host is *Bupalus piniarius* (L.) (Schwerdtfeger, 1968).

An important influence on the production of eggs is exercised by the feeding conditions occurring during the larval stage in those insects which do not feed as adults, as well as the conditions of supplementary feeding in those insects which are not sexually mature at the onset of the adult stage.

Despite the existing differences in fertility observed in many species, it would appear that, in general, reproductive potential is less variable than mortality.

4.8 Mortality

Mortality denotes the number of individuals dying during the course of a definite period and is expressed as a percentage of the initial size of the population. Sometimes it is also expressed as a percentage of the average size of the population, particularly when the density of the population undergoes considerable changes during the course of measurements.

Physiological and actual (or ecological) mortality may be distinguished.

Physiological mortality indicates the number of individuals of the population dying under ideal conditions, i.e. when limiting agents exercise no influence. In this case, individuals die naturally due to age and this depends on the physiological (not ecological) length of life. Actual mortality denotes the decrease in the numbers of individuals under the given environmental conditions. It undergoes greater changes than does the reproductive potential as a result of the influence of variations within the population and in external factors.

The mortality of a population is very important since it has a significant influence on the population size and the dynamics of its abundance. Mortality is generally presented in the form of life tables (Tables 4.2 and 4.3). Time-specific life-tables (Table 4.3) are drawn for animals exhibiting a relatively stable distribution of age classes and a mortality

Table 4.3 Time-specific life table (after Dempster, 1975).

x	l_x	d_x	q_x	e_x	L_x	T_x
1	1000	550	550	1.21	725	1210
2	450	250	556	1.08	325	485
3	200	150	750	0.80	125	160
4	50	40	800	0.70	30	35
5	10	10	1000	0.50	5	5

increasing with increasing age, as in long-lived mammals for example. These tables include the following indices:

x the pivotal age for the age class in units of time (days, weeks, etc.),
l_x the number of individuals surviving at the beginning of age class x (out of a thousand originally born),
d_x the number dying during the age interval x (out of a thousand),
q_x the mortality per thousand alive at the beginning of the age interval $(1000.d_x/l_x)$,
e_x the expectation of life remaining for individuals of age x.

In practice, time-specific life-tables include two further indices facilitating the calculation of e_x:

L_x the number of animals alive between age x and $(x+1)$, if the age intervals are reasonably small then: $L_x = (l_x - l_{x+1})/2$,
T_x the total number of animals x age units beyond the age x, which is given by: $T_x = L_x + L_{(x+1)} + L_{(x+2)} + \dots + L_{(x+n)}$, therefore $e_x = T_x/l_x$.

Because of the different mortality of insects at various developmental stages, the application of time-specific life tables to this group of animals may only supply data concerning the influence of various mortality agents on the population trends. Studies on the mortality factors of insects for purposes of forest protection must be more precise. This is achieved by the use of age-specific life-tables which enable one to evaluate the comparative significance of each agent causing mortality. They also indicate the critical periods occurring during the course of development of each generation which determine the course of the dynamics of abundance and the population. Age-specific life-tables include the following indices:

x the age classes expressed in units of time or as discrete developmental stages,
$d_x F$ factors of mortality (change of abundance)
l_x the number of individuals at the beginning of the given developmental stage,
d_x the number of individuals dying in successive developmental stages,
$100d_x$ the index of mortality in developmental stages successive to the abundance of the population at the beginning of the given stage,
$100q_x$ the accumulated index of mortality in successive developmental stages calculated against the original abundance of the population.

The indices given above should be summarized in life-tables for a number of successive generations of the insect species studied (Table 4.4).

Graphs plotted in the form of curves, traced using the data contained in the life-tables, are particularly interesting. When the data from column l_x are marked on the diagram in which the age classes (x) are marked on the horizontal axis and the number of surviving individuals (l_x) on the vertical axis we obtain the survivorship curve. This is simply "the fall-off of numbers in time". Species with widely differing lengths of life may be compared on such diagrams by applying a semi-logarithmic scale, with age classes marked on the arithmetic horizontal co-ordinate and expressed in percentages of the average life span, the vertical co-ordinate (l_x) being logarithmic.

At the point of the mean physiological length of life the curve is distinctly convex and then it declines abruptly with increasing age. When the mortality index is stable for all of the developmental stages (age classes) survivorship curve takes the form of a straight line running diagonally, whereas when mortality is particularly high in the earlier stages the curve is concave. For most insects, survivorship curves are generally concave.

The density of a population influences the shape of the survivorship curve. Generally the curves are more concave in populations exhibiting a higher density than in those of low density.

In forest *Carabidae* the profiles of the survivorship curves are associated with the developmental type of the species. The density of a population whose development occurs in the spring (*Carabus arcensis* Herbst, *C. nemoralis* Müller, *Pterostichus oblongopunctatus* (F.)) may be reduced to 13.2–32.9% of the density occurring at the egg stage within just 50 days (i.e. at the third instar). On the other hand, populations belonging to the autumn type of development (*Carabus glabratus* Paykull, *C. hortensis* L., *Pterostichus niger* (Schaller)) are reduced to a similar extent (7.4–26.5% of the density at the egg stage) in as much as 280 days (the third instar). Thus the survivorship curves of species of the early (spring) type of development are more concave than those of species belonging to the autumn type (Fig. 4.14).

Survivorship curves for a number of forest insects are illustrated in Fig. 4.15.

Survivorship curves are also called "l_x curves". Analogous mortality curves, or "d_x curves", may be plotted. The availability of a series of life-tables prepared for several successive generations of a given species is an indispensable for the correct interpretation of the abundance of a population and the contribution of individual mortality factors to this abundance. A number of different techniques have been elaborated for the analysis of data summarized in life-tables (Southwood, 1966). The method elaborated by Varley & Gradwell (1960) known as the "analysis of key factors" (*K*-factor analysis) is the most commonly applied.

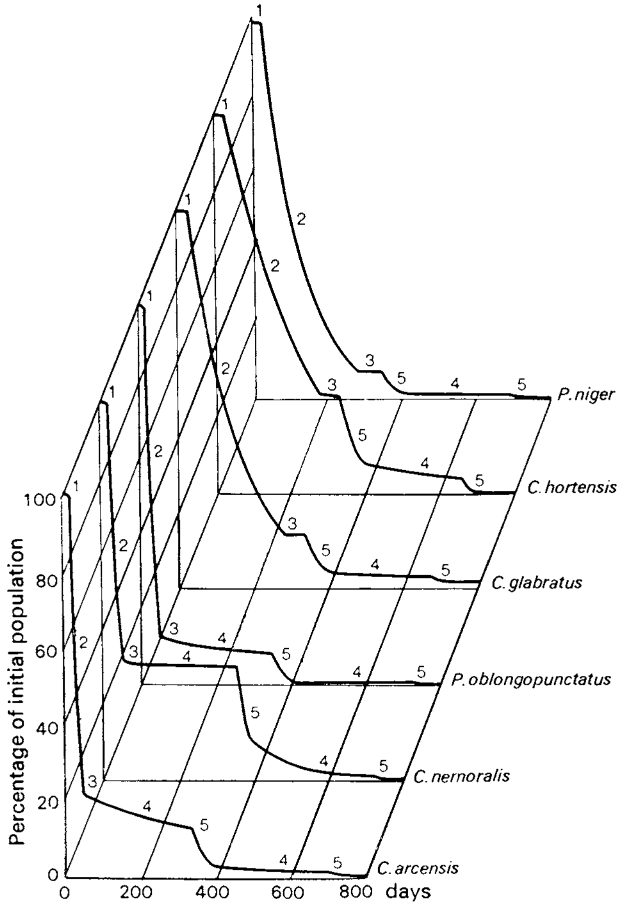


Fig. 4.14 Survivorship curves of some *Carabidae* species: 1 – hatching, 2 – development of larvae, 3 – prepupa and pupation, 4 – hibernation of adults, 5 – reproductive period (after Grüm, 1975)

This technique enables the establishment of the following: i. the key factor or factors determining the population trend (i.e. factors which give the most precise prediction of the abundance of the next generation); ii. the influence of changes in natality and mortality on populations, and iii. any density-depending relationship which may exist.

To illustrate the technique of calculating the value of *K*, the analysis of the life-table of ***Phytodecta olivacea*** (Forster) will be explained (Table 4.4) using the data obtained by Richards & Waloff (1961). *P. olivacea* occurs commonly on broom in western and central Europe, and in

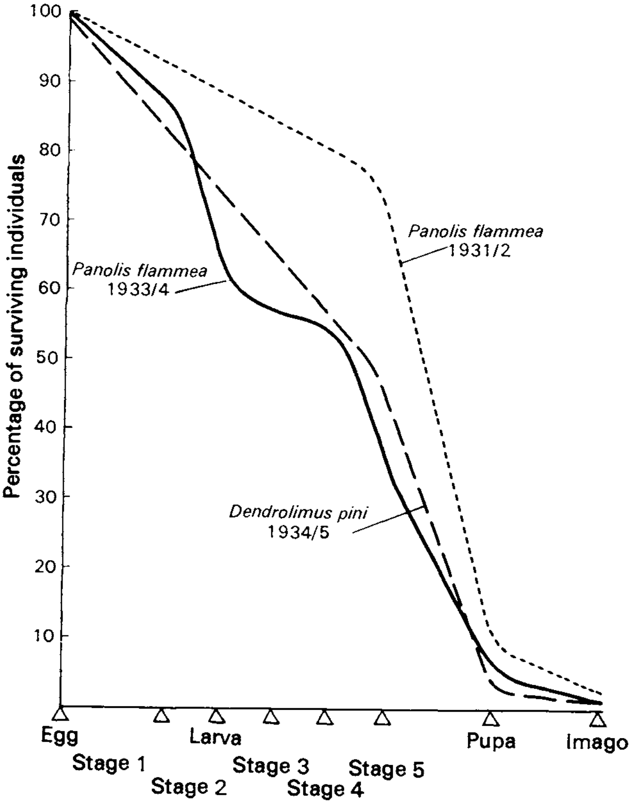


Fig. 4.15 Survival curve l_x (original according to data from Semevskii, 1964, Vorontsov, 1963 and Schwerdtfeger, 1968)

Poland mainly in the south-west. Richards & Waloff (1961) studied a population in England and found that the species here has one generation per year. Adults hibernate in the litter under broom plants and appear in the spring. They feed and oviposit on the broom leaves until the end of August and then either perish or return to the litter to hibernate. The larvae also feed on broom and pass through three instars before pupating in the soil. The resultant adults emerge from August to October but are not sexually mature. They only attain this condition the following spring on emergence from hibernation. Adults may live up to two years.

During the course of a 5-year study on a site occupying 0.8 ha, three major variations in the abundance of the adults at the beginning of the mating period were observed. Also, the number of eggs laid per female ranged from 32–82 whereas under laboratory conditions the number was in the region of 250–300. This was due to the fact that under natural conditions many females were killed by disease or parasites. Each year a large percentage of eggs and young larvae (60–90%) were destroyed in early summer by predatory insects, particularly *Heteroptera* (*Miridae*, *Anthocoridae* and *Nabidae*). The proportion of non-fertilized eggs amounted to 4–10% and 1% of the eggs were infected by parasites. A certain number of larvae were attacked by *Tachinidae*, mainly *Meigenia mutabilis* (Fallén). The mortality at the pupal stage was mainly due to predatory soil *Carabidae* and amounted to 25–84% in the course of 5 years. Hibernating adult insects were destroyed by the parasite *Perilitus dubius* (Wesmael) (*Braconidae*) and by mycosis caused by *Beauveria bassiana*.

In order to evaluate the key k-factors, the maximum reproduction potential of *Phytodecta olivacea* (Forster), is first calculated for each generation. It is obtained by multiplying the number of females in the reproductive period (found from the life-tables) by the number of eggs which a female is capable of laying. In 1954 this value was $11\,820 \times 474 \times \times 250 = 1\,400\,670$.

Then the logarithm of this number (6.1463) is recorded in the table of analysis of key factors (k_0). Similarly, the logarithms of the initial abundances of the successive age classes (eggs, larvae, pupae, adults before hibernation and adults after hibernation) are recorded. The mortality undergone in each generation (the value k and its relationship with the mortality μ being: $k = \frac{1}{\log_{10}(1-\mu)}$) can be calculated as the difference of two successive logarithms $k_i = \log N_i - \log N_{i+1}$. These represent the values of k for each age class. The total "mortality" of the generation is calculated as the sum of the successive k values: $K = k_0 + k_1 + k_2 + + k_3$ (Table 4.5).

The value k_0 does not actually represent the mortality but the reduction of the population due to the fact that the female does not lay all the eggs which she is capable of producing (i.e. the maximum natality).

The key factor or factors which determine the trend of the abundance of the adults from one generation to the next can then be established.

Table 4.4 Age-specific life table of *Phytodecta olivacea* (Forster) populations (after Dempster, 1975).

X	$d_x F$	1954				1955				1956				1957				1958			
		l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x	l_x	d_x	100 d_x	100 q_x
Adults		11 820				16 184				17 027				6 393				6 759			
	sex ratio: percentage of females	47.4				56.5				50.0				58.3				56.5			
	fertility (eggs per 1 female)	82.1				72.1				82.4				54.1				32.7			
Eggs and larvae		460 169				659 554				701 563				201 760				125 039			
	non-fertilized eggs		46 927	10.2			39 573	6.0			25 256	3.6			9 866	4.9			10 003	8.0	
	parasites of eggs and larvae		51 539	11.2			60 019	9.1			41 392	5.9			7 263	3.6			3 238	2.6	
	predacious arthropods and unknown factors		297 754	64.7			422 352	64.0			627 775	89.5			139 805	69.3			101 344	81.0	
				86.1	86.1			79.1	79.1			99.0	99.0			77.8	77.8			91.6	91.6
Pupae		63 939				137 610				7 140				44 826				10 454			
	predators and unknown factors		29 884	46.7			99 766	72.5			1 843	25.8			37 482	83.6			5 098	48.8	
				46.7	92.6			72.5	94.3			25.8	99.2			83.6	96.4			48.8	95.7
Adults before hibernation		34.055				37 844				5 297				7 344				5 356			
	Perilctus		4 836	14.2			3 747	9.9			1 398	26.4			1 292	17.6			268	5.0	
	Beauveria		3 916	11.5			7 190	19.0			122	2.3			0	0.0			193	3.6	
	transferred to laboratory and unknown factors		11 787	34.6			14 860	39.3			938	17.7			1 171	16.0			2 153	40.2	
				60.3	97.1			68.2	98.2			46.4	99.6			33.6	97.6			48.8	97.8
Adults after hibernation		15 516				12 047				2 839				4 875				2 742			
Adults surviving from former year		2 668				4 980				3 554				1 884				1 258			

Table 4.5 Key factors analysis elaborated on the basis of life-data (Table 4.4) of *Phytodecta olivacea* (Forster) populations (after Dempster, 1975).

	1954	1955	1956	1957	1958
Log. of maximum reproductiveness (number of females × 250)	6.1463	6.3591	6.3279	5.9693	5.9788
k_0	0.4833	0.5398	0.4818	0.6645	0.8828
Log. of number of eggs and larvae	5.6630	5.8193	5.8461	5.3048	5.0970
k_1	0.8572	0.6807	1.9924	0.6532	1.0777
Log. of number of pupae	4.8058	5.1386	3.8537	4.6516	4.0193
k_2	0.2736	0.5606	0.1296	0.7857	0.2904
Log. of number of imagines (autumn)	4.5322	4.5780	3.7241	3.8659	3.7289
k_3	0.4014	0.4972	0.2709	0.1778	0.2908
Log. of number of imagines (spring)	4.1308	4.0800	3.4532	3.6881	3.4381
K	2.0155	2.2783	2.8747	2.2812	2.5417

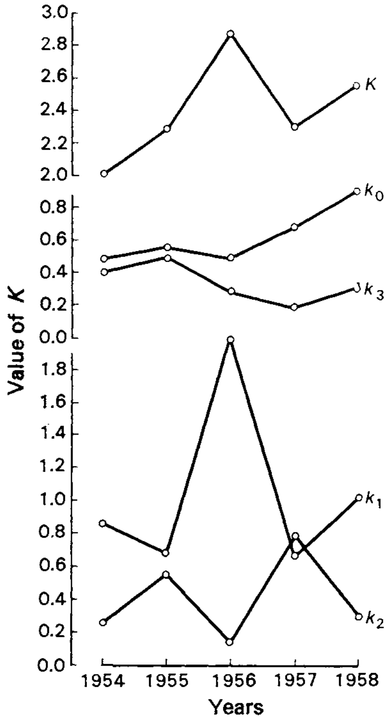


Fig. 4.16 Diagram of analysis of influence of key factors in the population of *Phytodecta olivacea* (Forster) (based on data in Table 4.4; according to Dempster, 1975): k_0 – limited reproduction (failure to reach maximum fecundity), k_1 – egg and larval mortality, k_2 – pupal mortality, k_3 – adult, winter mortality, K – total mortality

This is done by comparing the K value for successive generations after comparing it with the k values. To do this a diagram is prepared representing the course of the $(k_0-k_3(k_n))$ values and K in successive years of observation (Fig. 4.16).

It appears that the mortality factors acting on the eggs and larvae (k_1), the course of which coincides with that of curve K, play the most important role in determining the abundance of successive generations. These are polyphagous predators which may be assumed as a key factor in the determination of the abundance of the population in successive years. This observation can be verified by calculating the coefficient of correlation between the given key factor and the total K. In this case K shows a high correlation with k_1 $(r = 0.8605)$. The mortality of pupae k_2 seems to be inversely proportional to k_1. This, however, was not proved statistically. Thus the observation of various mortality factors in successive developmental stages allows a precise determination of the factor which is decisive for the final abundance of successive generations.

The mode of influence of each key factor may be established if we know its dependence on the logarithm of the initial density with which it can be equalized. By joining the points marking the successive relationships between k and the logarithm of initial density (in successive observations) we get a characteristic outline, the shape of which indicates the kind of dependence of the studied factor on the density of the population (dependent, delayed-dependent, inversely dependent, independent) (Fig. 4.17).

It is not easy, however, to be certain that the influence of the given factor depends on the density. This is due to the fact that, in the system discussed, the population cannot always be treated as an independent variable due to intraspecific competition if nothing else. Moreover, the assumption that the independent variable of a given population has been precisely established can also be questioned in view of the possibility of errors in its measurement. Finally, regression analysis depends on linear relationships which may not be representative of the true situation, especially when complex associations between living organisms are involved, since this dependence may have an exponential course.

In view of the difficulties mentioned above and described in detail by various authors, Varley & Gradwell (1968) proposed the test of "two-way regression" for the determination of values depending on the density of the population. The dependence on density may be considered as existing if the straight line of the regression of the initial density from the final density of the population ($\log N_i$ from $\log N_{i+1}$) as well as the

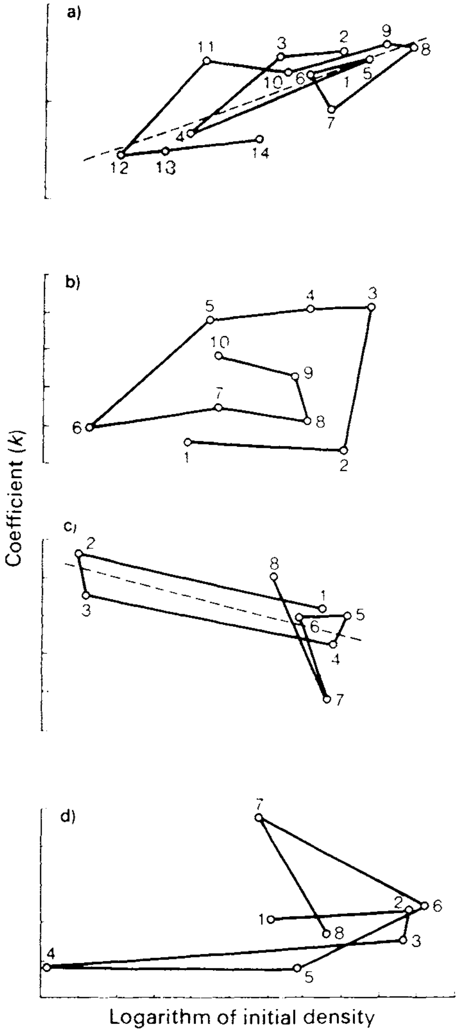


Fig. 4.17 Patterns produced by the dependencies of key factor effect on population density (after Dempster, 1975): a) density dependent factor, b) delayed density dependent, c) density inversely dependent, d) density independent, 1-14 — successive generations of insects, k — coefficient of mortality

straight line of regression of final density from the initial one ($\log N_{i+1}$ from $\log N_i$) have slopes distinctly varying from that of the straight line at $b = 1$ and both these lines are situated on the same side of line $b = 1$ (Fig. 4.18). The coefficient of correlation is the higher the closer are the lines of both regression dependences to each other.

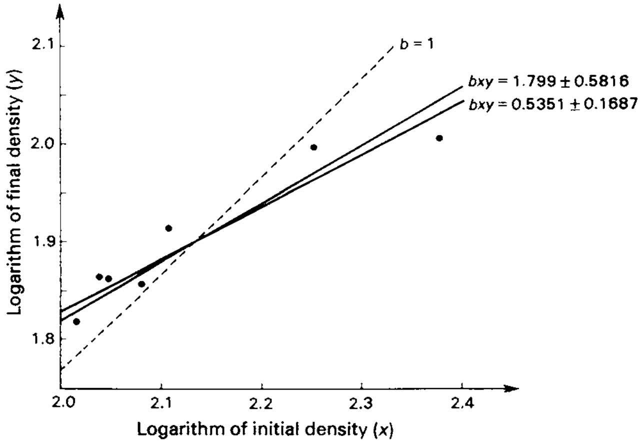


Fig. 4.18 Test of two-way regression (after Dempster, 1975)

The test of two-way regression may be readily criticized since the determination of log N_i by using log N_{i+1} is nonsensical. This is true, yet the determination of the dependences is not the aim of this test (Dempster, 1975). It seems that at present the test of two-way regression is the best method available of establishing the values depending on density, provided that the dependence is linear. Thus, it cannot be quite satisfactory, though the direction of the course of the straight line of regression describes the extent of activity of factors depending on density.

In the case of *Phytodecta olivacea* (Forster) none of the key factors exhibited a dependence on the density of the population. This was primarily due to the dominant role played by non-specific predators in the reduction of its abundance. Only the mortality of hibernating adults (k_3) exhibited a weak correlation with the logarithm of density of adults ($r = 0.8556$, $d, f = 3$, $P > 0.05$). On the other hand, the test of "two-way regression" of the initial and final density demonstrated that k_3 is independent of density, though one component of k_3, namely the activity of *Beauveria bassiana* exhibits such a correlation ($r = 0.9069$, $P < 0.05$). This is due to the fact that the character of the function of this species is masked by the parallel activity of *Perilitus dubius* (Wesmael), which is independent of density, and this influences the general evaluation of k_3. Though the analysis of key factors can only be applied to species producing one generation per year, it is the best method for the application of age life-tables in studies on the dynamics of the abundance of the population. Other techniques, such as the construction of survivorship curves or time life-tables, provide general data but do not determine the influence of individual ecological factors on the direction of quantitative changes in the population from generation to generation.

On the basis of similar materials Semevskii (1964) established that parasites, abiotic agents and diseases cannot separately determine the oscillation of abundance of the population during the period of the decrease in the abundance of *Lymantria dispar* (L.) (at periods between outbreaks). He established that even when mortality caused by parasites is null, the index of natality increases only 2.3 times in the course of the entire generation. Only mortality due to predators is a factor regulating the abundance under the conditions described and oscillations of this mortality can lead to outbreaks. In view of this, the author concluded that outbreaks result from decreases in mortality caused by predators and are frequently synchronized with decreased mortality due to abiotic factors and diseases. Such a situation may occur, particularly against the background of definite weather conditions.

Population dynamics

4.9 Level of abundance and its variation

There is a great deal of variation amongst insects as to the relative abundance of each species. On the whole, very few actual species may be regarded as being common with high numbers of individuals, the majority being classed as either rare or very rare, with low numbers and restricted geographical ranges. This is largely the result of each species' adaptations to its particular environmental conditions throughout its long evolutionary history – it has "come to terms" with its environment and its changing conditions and its life-cycle is adjusted accordingly.

However, changing environmental conditions can only be adapted to if they occur on a more or less regular basis, i.e. with a constant periodicity as in the 24-hour day-night cycle, the lunar monthly cycle and the annual seasonal cycle. Such "clocks" are set by the Earth's movements, both on its own axis and around the Sun, and by the Moon's rotation around the Earth. They are thus relatively stable and have no direct influence on the variation of an insect species' mean level of abundance. Slight climatic or seasonal changes, which occur gradually over a period of years due, for example, to the shifting of the Earth's axis may correspondingly alter mean levels of abundance. They do not, however, account for the short-term dramatic changes such as mass outbreaks or, at the other extreme, complete annihilation of populations or even species.

Short-term variations in abundance are the result of "casual" or unpredictable changes in an insect's environment. The environmental factors involved may be biotic or abiotic and include such phenomena as precipitation, winds, day-to-day (as opposed to seasonal) temperature variations, the activity of entomophages and pathogens and man's "interference". As already stated, these factors result in "casual" variations in abundance and do not affect an insect's mean level of abundance.

Biotic factors can also have significant effects on insect abundance at the ecosystem, biocenose or food-chain level. According to the "rules" governing such systems, organisms at the lower trophic levels should produce a definite excess of biomass (i.e. exceeding their own requirements), thus securing the survival of the organisms which form the subsequent links of the food chain at the higher trophic levels. Such "rules" of the functioning of biocenoses may have played an important role in determining the reproductive potential of individual species. Thus, phytophagous insects exhibit a higher fertility than predatory and parasitic species. The apparent exceptions to this rule are due to specific biological features of particular species, particularly oviposition habits and the probability of the successful development of the eggs. The high fertility of aphids is doubtless conditioned by the extraordinarily intensive activity of their natural enemies (Viktorov, 1967).

The maintenance of the mean level of abundance of a population of a particular species is also due to other mechanisms acquired during the evolutionary process, e.g. the divergence of ecological optima of phytophagous insects and their persecutors.

There have been many attempts to elucidate which biological properties of insects condition the different levels of their abundance. Initially it was believed that the fertility of a species is directly proportional to its occurrence in large numbers (or vice versa). It would appear, however, that this is not the case since there are numerous species with a high fertility which do not occur in large numbers. Thus, the species of the genera *Diprion* and *Pristiphora* appearing in masses do not differ in the fertility of females from other species of these genera which do not show any tendency to outbreak (Viktorov, 1967).

It is also interesting to note that *Neodiprion sertifer* (Geoffroy) and *Diprion pini* (L.) both tend to have high population densities and both lay eggs in deep incisions in pine needles. Due to the increased flow of resin, the eggs are subject to a higher mortality. On the other hand, rare species such as *Gilpinia frutetorum* (F.), lay eggs singly and only weakly damage needles and thus have a lower mortality caused by resin.

Similar relatively small differences were observed in the reproductive potential of a number of species of *Tortricidae*, otherwise differing widely as to their mean levels of abundance (e.g. *Dichelia histrionana* (Frölich), *Epiblema tedella* (Clerck) and *Tortrix viridana* (L.)).

According to some authors, the overlap of the geographical range of a phytophagous species with that of its host plant(s) is an important factor in determining the insect's level of abundance. The range of *Tortrix viridana* (L.) coincides completely with that of its host (European oak) and this thus forms a zone of optimum "noxiousness". This is not generally observed in insects characterized by a low level of abundance since their range only partly coincides with that of their hosts.

Differences in the complex systems of the natural enemies of a phytophage may constitute another important biocenotic agent determining the level of abundance of a species. Zwölfer (1963) compared the parasite complexes of a number of *Lepidoptera* of varying levels of abundance. He concluded that the abundance of a species is determined by the degree of adaptation of the natural enemy to the host, as well as by the lack of competition within the complex of parasites, and not by the total number of enemies.

Many species of *Hymenoptera* and *Diptera* of various degrees of specialization in the selection of their hosts, are parasitic on *Choristoneura murinana* (Hübner). None of these species is distinctly dominant and the effectiveness of each of them is considerably decreased by the intensive interspecific competition, as well as by their infection by secondary parasites. This leads to an outbreak of *C. murinana.* On the other hand, species of *Lepidoptera* with a low level of abundance and no tendency to occur in large numbers, are characterized by relatively poor parasitic faunae. The latter, however, exhibit dominance hierarchies and each species is well adapted to its host, and thus highly effective. Secondary parasites are scarce and no competition is observed amongst them.

Competition between insects has a significant effect on their levels of abundance, but data on this subject are scarce. The results of the selective struggles between some species indicate the presence of such competition since, after the abundance of one pest has been considerably limited, other species occupying analogous ecological niches appear in profusion.

The different effects of abiotic factors on species of varying levels of abundance has not been studied to any great extent and opinions as to their influence differ widely. Some authors consider that species occurring in large numbers are characterized by an ability to adapt rapidly to changing conditions, whereas others (e.g. Thalenhorst, 1953) claim that rare species such as *Diprion* are characterized by a wider tolerance to environmental factors than more abundant species.

It may thus be concluded that the differences in the level of abundance of individual species are independent on their reproductive potential. They do, however, appear to be due to: i. changes in physical conditions in the species' habitat; ii. changes in the biocenotic associations of the species in the biocenosis; iii. changes in the biological properties of the species (e.g. as a result of a change of host plant), particularly fertility and life processes.

On the other hand, these changes may be due to other causes of which the influence of man, at least in the forest environment, is very important.

Opinions regarding the factors which influence levels of abundance have gradually been modified as a result of the recognition of new facts and the appearance of new theoretical concepts.

4.10 Coefficient r and curves of population increase

Changes in the size of a population are ultimately the effect of reproductive potential and mortality. In the absence of limiting factors, the population exhibits an increase of abundance (Fig. 4.19) the rate of which is represented by the following formula:

$$\frac{dN}{dt} = rN$$

where N = the population size at the given moment, t = the time, r = the rate of increase at the given moment, i.e. the specific capacity for population increase.

The symbol r also represents the exponent of the increase of the population in the equation expressing the relationship between th nuem-

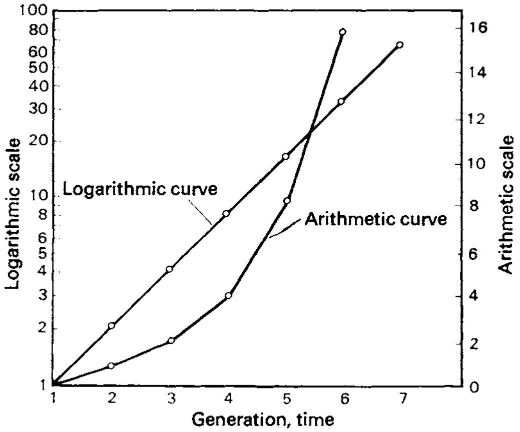


Fig. 4.19 Exponential growth of population (after MacArthur & Connell, 1966)

ber of individuals in the population and the rate of growth, with the assumption that the increase is not limited:

$$N_t = N_0 e^{rt}$$

where N_0 = the number of individuals at the beginning of the period (initial number), N_t = the number of individuals after time t, e = the base of the natural logarithm, r = the differences between the point value of the reproductive potential index (b) at the given moment and that of the mortality index (d), which can be expressed as $r = b - d$.

The precise calculation of the value r is difficult, and despite the application of various methods, it has been established for only a few species of insects. The following calculation comparing the rate of reproduction of laboratory populations with the absolute rate of reproduction (r_0), i.e. the ratio of the number of births of individuals of the same sex in two successive generations, is given in order to illustrate the value r.

Species	Absolute rate of reproduction r_0	Specific rate of reproduction per 1 day, r
Tribolium castaneum (Herbst)	275.0	0.101
Calandra oryzae (L.)	113.6	0.109
Pediculus humanus (L.)	30.9	0.111

This calculation indicates that, despite wide differences in their biology and in the value of r, insects may exhibit a similar rate of reproduction per 1 day. The knowledge of the coefficient r provides a possibility of an objective evaluation of the growth tendency of a population.

In the logarithmic form the formula $N_t = N_0 e^{rt}$ acquires the following form $\log_e N_t = \log_e N_0 + rt$, and this is the equation of the straight line with slope r when the size of the population in logarithimic form is represented as a graph (Fig. 4.19). Such an increase is called logarithmic or exponential and it determines the value and rate of increase of the population under constant conditions. On the other hand, such conditions do not exist in nature and thus such an unlimited increase of the population is purely theoretical. If the maximum value of r denotes the biotic potential of the species then the sum of all limiting factors and other environmental agents limiting the size of the population should be called the resistance of the environment. At the moment when the density of the population approaches the limit of the environment's capacity, its rate of increase begins to diminish considerably.

In view of this, more practicable than the exponential mode of the increase of the population is the increase expressed by the following equation:

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right),$$

where K = the constant value determining the capacity of the environment, i.e. the density of population which can be attained but not surpassed under the given ecological conditions.

After transformation of the differential equation:

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right) = rN - \frac{r}{K}N^2 = rN\left(1-\frac{N}{K}\right)$$

it can be presented in the form of the following integral equation:

$$N = \frac{K}{1+e^{(a+rt)}}$$

where $a = r/K$, and other notations are the same.

This formula represents an S-shaped logistic curve of which the upper asymptote is determined by the constant value K (Fig. 4.20).

The S-shaped curve is the result of the increasing intensity of the action of forces of the environment's resistance with the increase of the population density. This resistance evokes an increasingly greater reduction of the potential growth index as the size of the population approaches the efficiency of the environment (Odum, 1959). Such a growth is characteristic of populations of numerous phytophagous forest insects developing in rich or balanced forest biocenoses in which adaptation processes took place between them and their natural enemies (parasites, predators and diseases).

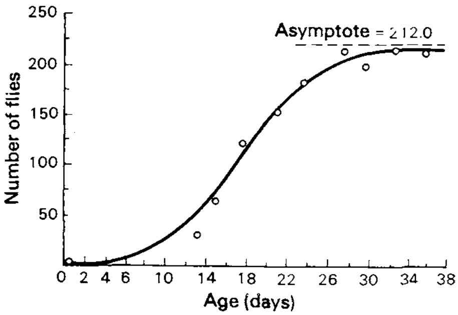


Fig. 4.20 Logistic curve illustrating the growth of abundance of flies in laboratory breeding (after Allee *et al.*, 1950)

Thus the logistic curve provides the possibility of the mathematical representation of the course of the changes in the size of the population, particularly of cyclic changes in which the upper (asymptote) and lower level can be distinctly determined, on the one hand, by the efficiency of the environment, and on the other, by the fact that "negative" populations cannot exist.

The logistic curve as "the law of population increase" has been frequently criticized, nevertheless it provides a satisfactory picture of the influence of negative factors on the population, which increases with the population density.

Most critics of the logistic curve claim that a simple analysis of the population increase, based on a logistic equation, does not indicate that the size of a population undergoes changes. In view of this the simplifications connected with the interpretation of this equation can lead to the following errors:

1) It is assumed that the unfavourable influence of the growing density of individuals immediately evokes a definite reaction of the population. In other words, if the expression $(K-N)/K$ decreases from 1 to 0 with rising density then the rate of growth of the population dN/dt falls correspondingly. This is completely wrong in cases when the reaction of

the population consists of a decrease in reproductive potential and also, perhaps, when it is manifested in the form of increased mortality.

In any system in which the geometrical growth is inhibited by a regulating factor dependent on increased density, there must be some rule of feedback: the size of the population increases, the intensity of the regulating factor increases, and in consequence the density of the population diminishes. This problem belongs to the realm of cybernetics and it will be discussed with respect to the dynamics of abundance of forest insects in a further chapter of this book. Here it needs only be mentioned that the occurrence of cyclic quantitative changes in the population is possible only when a certain time interval exists between the increase of the size of the population and the corresponding reaction of the regulating factor $(K-N)/K$. This may be proved mathematically. 2) The fact that the logistic equation considers neither the complicated age distribution of natural populations nor the dependence of reproductive potential and mortality on the age of individuals is an important shortcoming. Though variations of abundance corresponding to the logistic curve are observed in nature, it also occurs that the theoretical upper asymptote does not represent some absolute range which theoretically cannot be attained and that a number of species initially exhibit a tendency to achieve of a high density of population and then, after periodical changes, stabilize at a considerably lower level.

Despite the fact that a stable size of a population is actually observed in successive corresponding developmental stages of successive generations, this does not last long in nature. Deviations due to changes in reproductive potential and mortality cause changes in the abundance. These may be represented graphically in the form of curves of populations increase. No stable, uniform growth of the population size is observed, thus the curves of population increase may exhibit a varying though characteristic curve.

A knowledge of the dynamics of abundance and of the shape of curves of population growth is particularly important in the establishment and comprehension of the course of outbreaks of forest insects.

The following stages describing the various types of population increase are distinguished (Allee *et. al.*, 1950):

I, period of positive increase proceeding along the logistic curve,
II, balance (mean stable abundance),
III, oscillations and fluctuations (deviations from balance),
IV, period of negative growth (decrease or diminution),
V, extinction of the population,

VI, particular cases (striking, abrupt changes n the form of increase distinctly differing from the standards of I–V), i.e. "spurts" and "depressions" of the population.

The first five stages of growth are illustrated in Fig. 4.21.

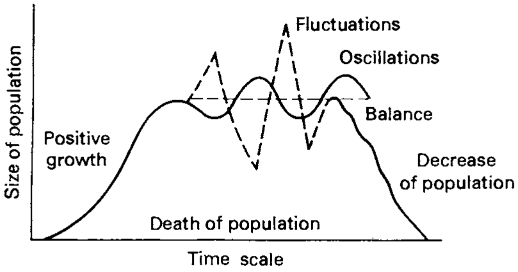


Fig. 4.21 Curves representing various schemes of forms of quantitative growth of population (after Allee *et al.*, 1950)

Two types of deviations from the inherent balance, i.e. oscillations and fluctuations, will be discussed here. Particularly strong fluctuations belonging to "particular cases" will be considered under the terms of outbreaks or "gradation".

4.10.1 Oscillations

Oscillations denote changes characterized by a distinct and stable periodicity. They depend mainly on internal factors of the population and include seasonal changes in abundance occurring every year (repeatedly), as well as those which take place in multi-year cycles.

The term "oscillation" has a number of meanings when employed in the ecological literature. Schwerdtfeger (1968) uses it to define the regular dynamics of abundance in the course of the year or of one generation, whereas most British authors apply it to cyclical changes over longer periods. Schwerdtfeger terms the latter "cycles" and the process of these changes "periodicity".

The present author assumes that the period of the amplitude of changes in abundance may vary in oscillations and agrees with Moran (1954) that oscillations have a common feature consisting of the fact that a deviation from the mean abundance in one direction is invariably followed by a deviation in the opposite one. Thus, when at a certain moment *t* the size *N* of a population is higher than its mean value, after a definite time the value *N* will tend towards a value smaller than the mean.

Most simple forms of oscillations are due to changes in the size of the population at various developmental stages of its individuals. The population is at its most numerous at the egg stage, its lowest numbers occurring at the adult stage (Fig. 4.22). This is due to the action of the forces of environmental resistance. In populations with two generations per year there are two peaks of abundance for each developmental stage. Where there is a one-year generation, one peak occurs, and where a generation takes four years to develop the peak accordingly occurs once in four years[1].

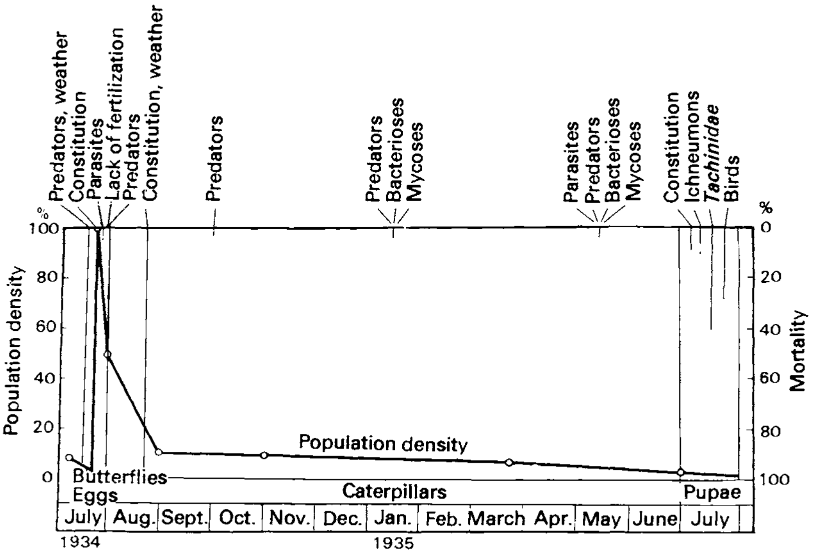


Fig. 4.22 Abundance of population of *Dendrolimus pini* (L.) in the course of one generation (after Schwerdtfeger, 1936)

If the individual developmental stages of a single generation or of several generations overlap, the oscillations exhibit a milder course than when they are distinctly limited in time (Fig. 4.23).

A significant number of the progeny of each parental pair must be destroyed if the density of the population of adult stage is to remain at a stable level over the course of a series of generations. For instance, a single parental pair should give rise to two surviving individuals in the next generation.

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[1] A population representing individuals of a single developmental stage is called a semaphorontic population of a given species.

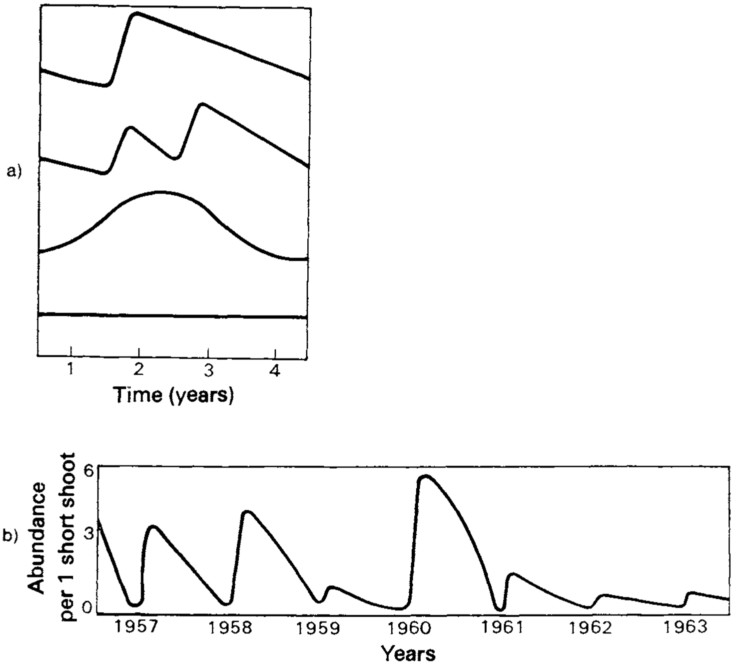


Fig. 4.23 Course of typical oscillations (a) and oscillations in *Coleophora laricella* (Hübner) (b) (after Schwerdtfeger, 1979)

This may be expressed as $\left(\frac{a-2}{a}\right)$ or $\left(\frac{(a-2)\,100}{a}\right)$, which represents the index of mortality of the progeny of a parental pair securing the maintainance of a population at an unchanged level (a = number of eggs laid).

Zwölfer (1930) developed this formula by considering the number of individuals contributing to reproduction with the assumption that this number may be expressed by the ratio of the sum of females and males to females, i.e. $(f+m)/f$.

Hence, the ideal case of stability between the resistance of the environment and the reproductive potential of the population (or, in other words, the resistance of the environment) may be expressed by the following formula:

$$W_0 = \frac{a-(m+f)/f}{a} \cdot 100 \, .$$

The value W_0 can also indicate the amplitude of changes in the abundance within a single generation.

It is known, however, that under natural conditions the true index of the mortality of the population in the course of a generation may acquire different values. This is also associated with the resistance of the environment, which differs from the ideal level in direct dependence on the density of the population. Such a true index of mortality may be expressed by the following formula:

$$W_x = \frac{P_0\, a - P_1\, (m+f)/f}{P_1\, a} \cdot 100 \quad \text{or} \quad \frac{100\,(P_0 - P_1) + W_0\, P_1}{P_1}$$

where P_0 = the density of the population at the beginning of the period, P_1 = the density of the population at the end of the period.

For example, for *Panolis flammea* (D. & S.) the value W_0 is $\left(120 - \left(\frac{2+1}{1}\right) \cdot 100\right) / 120 = 97.5$, but in the years of mass appearance 1924–1925) at $P_0 = 0.14$ and $P_1 = 0.92$, the percentage of mortality (actual resistance of the environment) was lower:

$$W_x = 100 \cdot \frac{(0.14 - 0.92) + 97.5 \cdot 0.92}{0.14} = 83.57$$

The Zwölfer's (1930) formula may be presented in the following form:

$$P_1 = P_0 \cdot a \cdot i \cdot L_1 \cdot L_2 \ldots L_n$$

where a = the number of eggs laid, i = the sex ratio, L_{1-n} = the contribution of surviving individuals in successive developmental stages.

When the symbol L is replaced by $1 - t/100$ (the index of mortality) then:

$$P_1 = P_0 \cdot a \cdot i \cdot (1 - t_1/100) \cdot (1 - t_2/100) \ldots (1 - t_n/100)\ .$$

This formula enables the prediction of the abundance of a pest at the end of the generation. It also indicates that the size of the population undergoes not only oscillations, but also otherwise unsuspected changes. These are referred to as fluctuations.

4.10.2 Fluctuations and outbreaks (gradations)

The term fluctuation denotes random changes in abundance, whose character and general tendency may or may not be determined mathematically. Fluctuations depend primarily on changes taking place from year to year in the physical environment of the population, i.e. on external agents. These are irregular and are correlated to a certain extent with changes in the principal physical limiting factors.

Intensive fluctuations characterized by a phasic increment of abundance are called outbreaks or gradations. The course of the fluctuations of *Bupalus piniarius* (L.) over several years is illustrated in Fig. 4.24

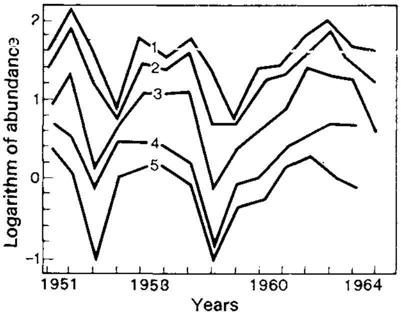


Fig. 4.24 Fluctuations of various developmental stages of *Bupalus piniarius* (L.) in the course of 15 years (after Klomp, 1966): 1–5 – developmental stages

Fluctuations are very frequent in nature and may be classified as follows:

1) latent,
2) temporal,
3) permanent.

In latent fluctuations the species constantly remains at a low quantitative level.

Temporal fluctuations are characterized by periods of low abundance with intervals of intensive increases of density. Such fluctuations are characteristic of many primary pine pests which appear in large numbers in certain regions of their range, e.g. *Dendrolimus pini* (L.) in the Kurpie Forest, *Panolis flammea* (D. & S.) in Western Pomerania and the Pisz Forest, etc.

Temporal fluctuations may be classified according to several criteria (Fig. 4.25).

1) In relation to the regularity of the successive occurrence of periods of outbreaks:

a. cyclic (resembling oscillations), e.g. outbreaks of *Zeiraphera griseana* (Hübner) in Switzerland;

b. acyclic, with long irregular intervals between periods of outbreaks.

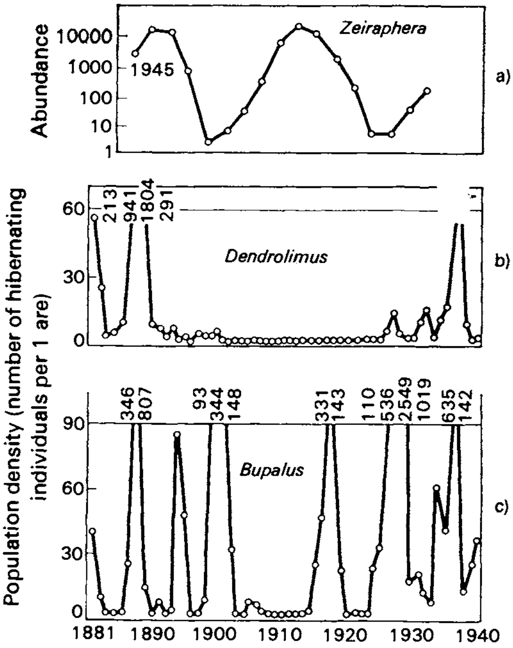


Fig. 4.25 Curves of the course of outbreaks (after Schwerdtfeger, 1979): a) cyclic (*Zeiraphera griseana* (Hübner) in Engadin), b) acyclic sporadic (*Dendrolimus pini* (L.) in Letzlingen), c) acyclic frequent (*Bupalus piniarius* (L.) in Letzlingen)

2) In relation to the frequency of outbreaks:

a. continuous, where one period of outbreak follows another and periods of latency are very short;

b. interrupted, where periods of outbreaks occur with long periods of latency in between.

3) In relation to the duration of the period of outbreaks:

a. counteractive, where the period of outbreaks is short, changes of the abundance are very intensive and short-lasting;

b. distractive, where the period of outbreaks is very long, lasting sometimes up to several dozen years (e.g. *Cephalcia abietis* (L.) in the Karkonosze Mts in Czechoslovakia).

Permanent fluctuations represent situations in which the insect exhibits a constantly high level of abundance (e.g. *Tortrix viridana* (L.) in many regions of Central Europe).

Areas where a definite type of fluctuation persists are called areas of latent, temporal or permanent outbreaks, respectively. The spatial dif-

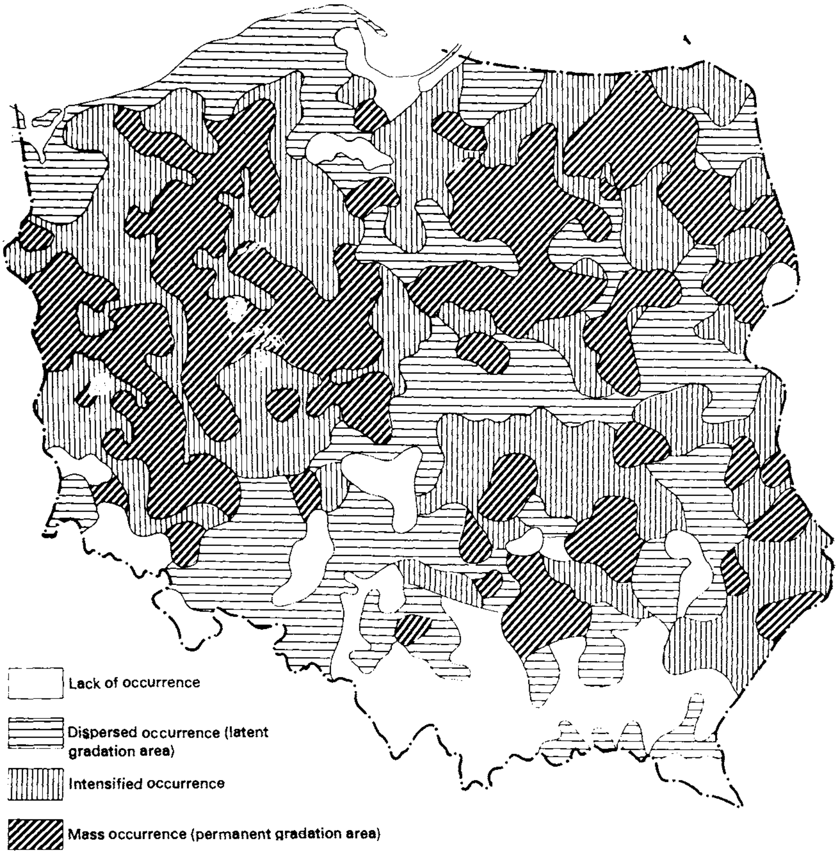


Fig. 4.26 Occurrence of *Amphimallon solstitialis* (L.) on areas assigned for afforestation in 1961–1965 (after Sierpiński, 1968)

ferentiation of the level of abundance is characteristic of insect populations and may be illustrated by the example of the occurrence of *Amphimallon solstitialis* (L.) in Poland over a 5-year period (Fig. 4.26).

4.11 Phasic character and spread of outbreaks (gradations)

Periods of outbreaks generally exhibit a phasic character, where a preliminary phase (or progradation) and a phase of decline (or retrogradation) may be distinguished. These phases represent an increase and decrease of abundance of the population, following the growth curves described above. The factors influencing the changes in abundance will be discussed in further chapters. Only the course of these changes will be described here, as exemplified by certain foliophagous insects.

At the phase of progradation the preliminary (incubation), premonitory (prodromal) and explosion stages may be distinguished.

In the period of transition from the normal (latent) condition to the preliminary stage the density of the population increases by two to fourfold in the course of a single generation of the insect, but this is not manifest in the form of damage to the trees. Frequently, but not always, the insects exhibit a somewhat increased fertility during this period.

At the prodromal stage, invariably including two generations of the pest, the abundance of the species increases to such a degree that damage is evident when the tree crowns are carefully inspected. The pest also spreads to new forest stands. The insects are resistant to diseases and parasites and frequently exhibit a high fertility and an increased proportion of females. From the morphological standpoint the eggs and pupae are characterized by a somewhat larger size, and the larvae have an increased body content of fat and proteins.

At the explosion stage, consisting of two or three generations, the abundance rises abruptly and leaf damage amounts to 50–70%. Consequently, this leads to the occurrence of unfavourable feeding conditions for the larvae which subsequently migrate to neighbouring trees (Fig. 4.27). Frequently the fertility of the females decreases and resistance to diseases and parasites of the insects becomes low. In species in which the males are distinctly smaller than the females, and therefore require less food, the proportion of males increases.

At the phase of retrogradation the population decreases abruptly as a result of unfavourable conditions. A quantitative predominance of males and a low fertility of females, a proportion of which lay non-fertilized eggs, is generally observed during this period. Also, the percentage of parasitization reaches 70%. The abundance of the pest falls to a minimum and after two to three years the outbreak passes through the post-crisis stage to latent period.

In the phase of retrogradation the forest stands are further endangered since, although they are already weakened, feeding still may be relatively intense. In any given forest stand the progradation and retrogradation (when not controlled) may last about seven years.

For *Bupalus piniarius* (L.) and *Dendrolimus pini* (L.) progradation includes four years and retrogradation three years; for *Panolis flammea* (D. & S.), three and three, and *Lymantria monacha* (L.) (in pine stands),

Fig. 4.27. Pine stand after outbreak of *Panolis flammea* (D. & S.) (photo by M. Nunberg)

two and two or two and one year, respectively, or (in spruce stands) up to seven years. The development of gradation in species exhibiting two generations per year is not so long, thus in *Diprion pini* (L.) both phases generally last four years. In the period between successive outbreaks, the abundance of the pest remains at a low but constantly oscillating level. This is known as the normal or, as it was called in the earlier literature, "iron" reserve of the pest.

Obviously, numerous deviations from this scheme are frequently observed in nature. The time of individual phases undergoes considerable disturbances and sometimes (most frequently under the influence of limiting abiotic or biotic factors) the outbreak may dissipate before reaching the explosion stage.

Outbreaks of insects generally cover thousands of hectares of forest stands but their development occurs in the most suitable sites called primeval outbreak foci.

Even-aged forest stands consisting of a single tree species and growing on poor soils most frequently constitute the outbreak foci (Fig. 4.28).

Fig. 4.28 Primeval outbreak focus of *Dendrolimus pini* (L.) in Biała Forest (photo by S. Kinelski)

These forest stands have generally been greatly affected by a number of anthropogenous factors such as the burning of clear felling areas, the sowing of seeds of unsuitable origin, the raking of the litter and cattle-grazing, etc.

The weakening of trees and the decrease in the effects of the complex of natural enemies of the pest lead to easy and frequent increments in its abundance, which generally occur in the outbreak foci about two years before the outbreak spreads to the neighbouring forest stands.

The high density of the pest's population in the primary outbreak foci leads to its dispersal to the neighbouring forest stands. This disper-

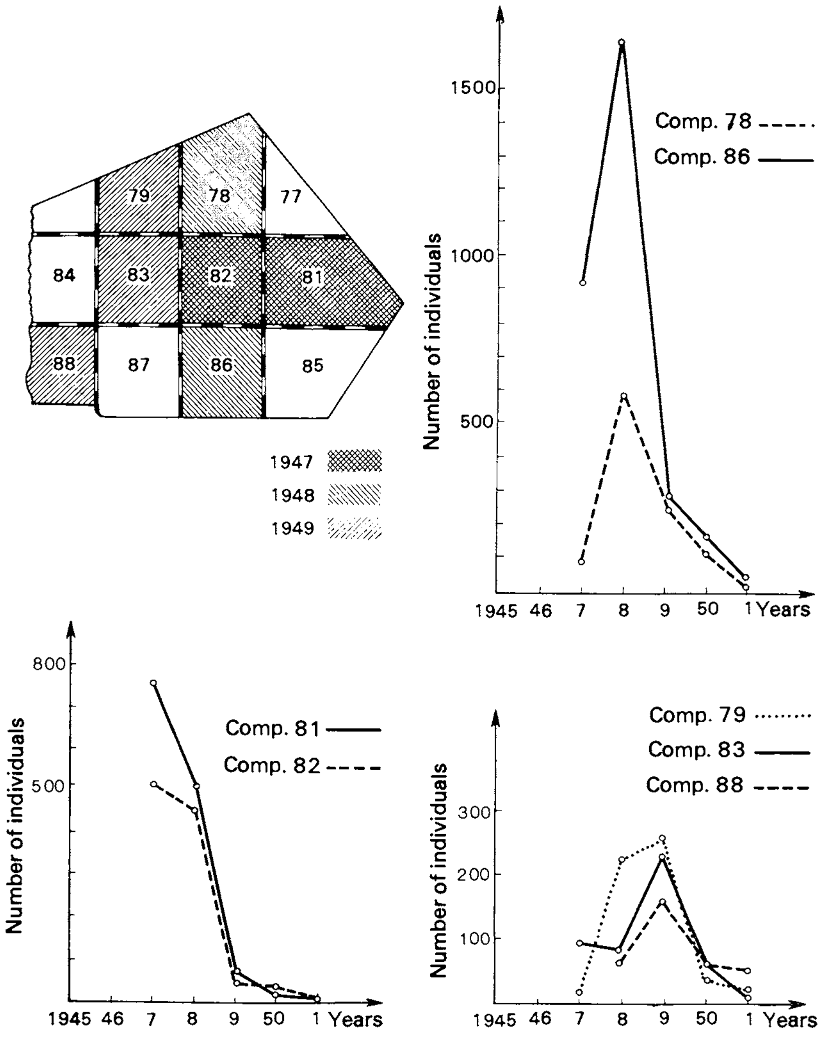


Fig. 4.29 Propagation of outbreaks of *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson) in the Pajęczno forest district (after Koehler, 1957)

sal mostly occurs towards the end of the prodromal and in the explosion stages.

Secondary outbreak foci develop in those forest stands less suitable for the reproduction of insects, i.e. with higher environmental resistance. The abundance of insects increases at a lower rate here owing to their lower fertility and higher number of natural enemies. The maximum number of damaged tree crowns occur here one or two years later than in primeval outbreak foci. In secondary gradation foci a keen competition for food between feeding larvae is rare and total defoliation exceptional.

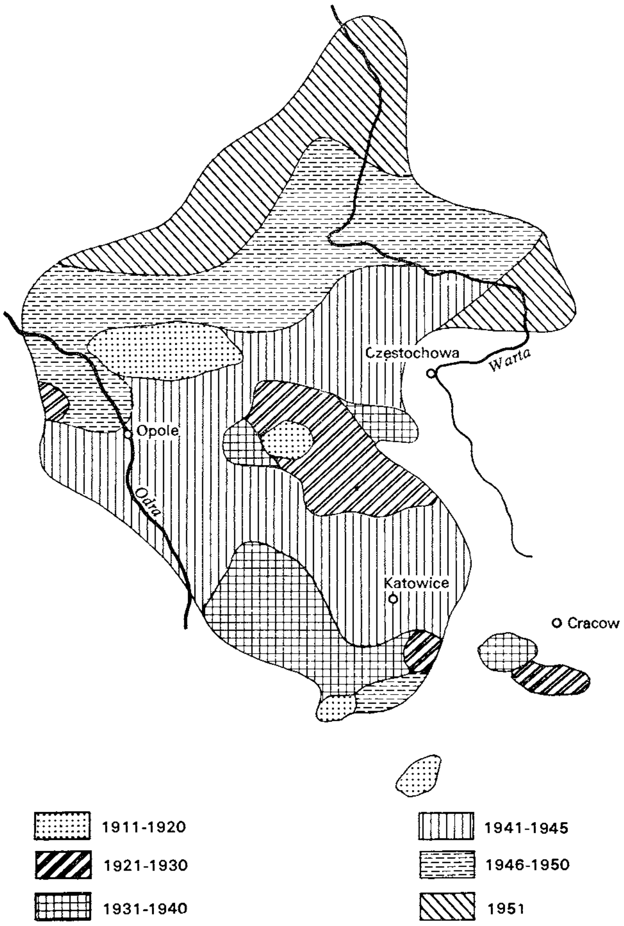


Fig. 4.30 Propagation of outbreaks of *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson on the eastern outbreak area (after Koehler, 1957)

Migrational foci develop in the neighbourhood of primary or secondary outbreak foci owing to the migration of insects from intensively damaged forest stands. Migration may take place at the flying adult stage as well as at the larval stage, when larvae are sometimes carried by the wind (young caterpillars of *Lymantria monacha* (L.)) or when they crawl over the neighbourhood. In exceptional cases migrational foci may develop at considerable distances from the outbreaks centres. This requires air currents and the occurrence of conditions favourable for the development of the pest on the invaded site.

Invariably, outbreaks spread from more favourable environments to those more difficult to invade.

The analysis of the spatial development of outbreak of pine pests over a longer period in a definite forest area allows the delimitation of certain outbreak centres against the background of which smaller but spatially compact outbreak zones develop at each stage of appearance (Figs. 4.29 and 4.30). These zones may differ spatially for various gradations of one pest species or several species, therefore they do not always correspond to analogous centres within the range of a single outbreak cycle. This may be distinctly observed in the spatial development of the outbreak of *Dendrolimus pini* (L.) (Luterek, 1965b).

5 Causes and course of changes in the abundance of insect populations

The dynamics of insect abundance constitute one of the most complex, controversial, difficult and unsatisfactorily solved problems. The opinions on the causes and course of changes in the abundance of populations have undergone many developments during the recent decades. Studies have gradually been extended to cover the ever-increasing numbers of new species and a knowledge of their geographical and ecological systems has been made possible by the refinement of modern techniques.

Basically there are two main schools of thought among ecologists. In the opinion of one, the factors depending on the density of the population are decisive for this density and thus determine the regulation of the abundance of the population. The other group does not ascribe such importance to these factors and, in some cases, does not even take them into consideration.

The regulation of insect numbers involves the natural reduction of abundance, this being the result of density-dependent processes, and it serves to keep the abundance of insects within the limits of the fluctuations observed during the course of a sufficiently long period.

Though the existence of mechanisms regulating the abundance of insect populations is, without doubt, accepted by most ecologists, the concept itself still remains a hypothesis, even though it has been confirmed repeatedly by observational evidence. Frequently we encounter opinions based on contrary assumptions, i.e. of the fortuitousness of changes in the abundance of populations, which also quote convincing arguments. Milne's concept, in which he attempted to combine the two antagonistic hypotheses, proved popular several years ago but met with severe criticism from parties on both sides of the argument. The problem has still not been satisfactorily resolved.

The recent achievements of cybernetics are of particular importance for the present formulation of opinions as to the causes of changes of abundance in animal populations. This science, concerned principally with self-regulating systems, has contributed to the methodical elucidation of the mechanisms of the phenomena of automatic regulation in population systems. The application of the concept of feedback (the indispensable element of self-regulated systems) to population ecology has been of particular importance here. The interest in cybernetics is mainly due to the fact that the results obtained with the use of cybernetic methods are of a general character and therefore may be universally applied.

Development of opinions on the causes of changes in abundance

5.1 Concepts not accepting the notion of automatic regulation of the abundance of populations

5.1.1 Concept of the decisive importance of one factor

Only some of the opinions on the factors of changes of abundance of insects will be discussed here. Although they are all based on actual recorded cases and have all contributed to the development of the knowledge of the causes of mass reproduction of insects, none of them can be generalized in its original form.

Concept of the decisive role of parasites. This concept is ascribed to Escherich (1914) although Ratzeburg, as early as the mid-19th century, pointed out the role of parasitic insects in limiting the abundance of forest insect pests. The principal natural regulators of those phytophages with a tendency to mass reproduction were considered to be parasites, particularly ichneumons and tachinid flies. It has been established that the percentage parasitization of populations of many pests amounts to 100%, and that the varying degree of specialization of different parasitic species lays the pest open to attack throughout its various developmental stages. The development and popularity of this concept in the first decades of this century was also due to the success achieved in the USA in the biological control of noxious phytophagous insects, mostly newcomers to the American continent.

According to this theory, the disturbance of the balance between the abundance of phytophagous insects and their parasites leads to the phenomenon of mass appearance, i.e. to an increase and decrease of the abundance of the pest. This was supported by the theoretical mathematical models of Volterra. Both this concept and works based on the theory of the regulating role of parasites in limiting the abundance of insects constitute a basis for the concept of automatic regulation of abundance. The theory that parasites played such a decisive role, however, was not satisfactorily developed. It appeared that entomophages, owing to their increasing abundance against the background of the developing gradation, were able to successfully decrease the abundance of the phytophage at the climax of the explosion stage (and later). However, the accretion of the pest's abundance at the preliminary stage of gradation could not be ascribed to anything but the inefficiency of its natural enemies.

The primitive host-parasite system had to be extended by including the chains of intermediate hosts and their host plants. This led to the creation of the biocenotic concept. Before we discuss this concept, however, we should first consider the opinions regarding the role of climatic factors in the determination of the abundance of phytophagous insects.

Concept of the decisive role of physical agents and particularly climate. The fundamental assumptions of these concepts are based on the works of Uvarov (1931) and Bodenheimer (1930). These concepts were largely formed as a result of laboratory studies and ascribed fluctuations of the abundance of insects to the direct influence of changes in abiotic, mainly climatic, agents over the period of several years. In order to provide evidence to support this concept, an enormous number of detailed experimental studies were carried out, the results of which elucidated the dependence of the fertility and the development of various stages of most economically important (noxious) forest insects on individual climatic elements, particularly temperature and air humidity. The dependence between the development of insects and climatic conditions of the compared localities or years was plotted graphically in the form of bioclimograms. The mortality curves based on the results of laboratory experiments demonstrated that the highest mortality (up to 90%) occurs at the early developmental stages which are only able to develop within very narrow temperature and humidity limits. In addition, the rule of the "sum of heat" was formulated.

According to the concept of the "sum of heat", and increase in an insect's numbers seems to occur as the result of the direct influence of increased temperature by the acceleration of the development and an increase in the fertility of the pest. On the other hand, any decrease in abundance was explained by the inhibition of development at a lower temperature and in humid conditions which favoured the spread of diseases. This view was confirmed by long-term observations on the synchronization of insect outbreaks with periods of drought and hot summers. As early as 1911, German investigators established that since the 15th century, in regions where the mean yearly precipitation amounts to 700–1000 mm, gradations of *Lymantria monacha* (L.) occurred in warm and dry periods of Brückner's cycle. Similar results were obtained in studies on the appearance of *Tortrix viridana* (L.). Also, other authors, e.g. Zwölfer, Ilinskii and Vorontsov, observed the stimulating influence of drought on the development of pests. They stressed that only extreme deviations from the standard, particularly at the period of feeding of third instar larvae, as well as their abnormal course over several years are important. On the other hand climatic agents can disturb the development of the pest by affecting the relationships between the synchronization of the host's life-cycle development and those of its natural enemies as well as its host plants.

It would thus appear that it is not just some general influence of the climate, but the action of definite meteorological conditions (either in definite periods of development of the pest or in periods of development of its natural enemies) that is significant here. For instance the studies carried out did not succeed in establishing a direct influence of climate on the development of *Panolis flammea* (D. & S.) in 1926–1933, but they did indicate a correlation between the amount of precipitation in June and July and the degree of mortality due to parasitism (Nunberg, 1937).

The outbreak of *Tortrix viridana* (L.) in the forest near Rogów was interrupted in 1962 due to abnormal temperatures in the spring. The warm March accelerated the hatching of larvae whilst the subsequent reccurrence of cold inhibited the development of oak buds and thus resulted in the starvation of the larvae. *Arhopalus* (= *Criocephalus*) *rusticus* (L.) and *Asemum striatum* (L.) (*Cerambycidae*) appear in large numbers when suitable weather occurs in June, whereas any rainfall during this month decreases the abundance of these species since water penetrates into the pupal cells (Dominik, 1968b).

The basis of the concept ascribing changes in the abundance of insects to climatic agents has gradually evolved over the years with the accumulation of meteorological data and with an understanding of the laws of geophysics. Its validity has also been consolidated by a better understanding of the interdependences between the physiological condition of plants and the physiology of the insects feeding on them. A number of significant findings were made in Canada by Wellington (1950–1957) as a result of his studies on *Choristoneura fumiferana* Clemens and *Malacosoma disstria* (Hübner). The former of these pests appeared in enormous numbers during periods when the weather was influenced by polar air-current circulation and characterized by a low air humidity. These gradations followed those of *M. disstria* which developed during periods of humid and cloudy weather resulting from south-western and western air-current circulation. Wellington's concept is based on the assumption that climate is the main agent limiting the abundance of insects which exhibit a tendency to gradation.

According to the supporters of the concept discussed, the lack of outbreaks in periods of normal weather conditions for any given locality or region, and the accretion of outbreaks due to deviations of atmospheric conditions from their mean values, confirm the limiting role of climate.

The elaboration of a technique for forecasting outbreaks is the crowning achievement of this concept. The forecast is based on the following: ecological studies establishing critical weather conditions favouring outbreaks, meteorological analyses establishing conditions of occurrence of such critical weather, the analyses of regional weather and the establishment of synoptic indices determining weather cycles dependent on the direction of circulation of air currents in the upper layers of the atmosphere.

Much information concerning the influence of synoptic factors and weather cycles on changes in the abundance of polyphages was obtained by Piatnitskii (1936) and Vorontsov (1962). Also Eidmann (1931, 1934, 1937) tentatively ascribed the cyclic character of outbreaks of forest insects to the occurrence of sun-spots (the intensity of sun-spot appearance influences the weather types). Soviet authors, like their Canadian counterparts, established that changes in the abundance of insects are associated with definite types of circulation in the upper layers of the atmosphere which determine long-term weather conditions. In their opinion the influence of climatic agents, particularly temperature and humidity, is not only direct (as the school of Uvarov and Bodenheimer endeavoured to prove), determining the rate of development, mortality and feeding of insects, but also indirect.

Indirect climatic agents influence the insect's food and its nutritional value, the abundance and activity of its entomophages and also its pathogens. The synchronization (favourable) or asynchronization (unfavourable) of the development of host plants and the insects which feed on them, or of the development of pests and their parasites and predators, is particularly important and is determined by changes in the direction of atmospheric circulation. According to the concept discussed, the type of atmospheric circulation may determine the beginning and end of gradations, the level of abundance of the pest at the period of gradation and also the change in the geographical range of gradations connected with abundance. Changes in atmospheric circulation may also influence the direction of dispersal of the outbreak (e.g. in Poland mainly from West to East). This explains the frequently observed irregularity of outbreaks within various parts of the total area of their occurrence, and their increasing dependence on local differences in the specific composition, age, density and history of the forest stand.

Many attempts have been made to compare the synchronization of climax periods in abundance of forest insect populations with, on the one hand, the development of various types (dry and humid) of long-term weather conditions, and with the time and intensity of the occurrence of sun-spots on the other (Fig. 5.1). In many cases a certain correlation of these phenomena was observed but several of the resultant

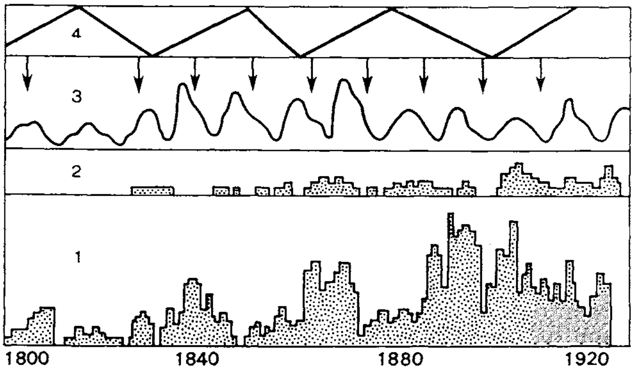


Fig. 5.1 Solar activity and intensification of outbreaks of noxious forest insects in Europe (after Schwerdtfeger, 1979): 1 – outbreaks of *Bupalus piniarius* (L.), *Panolis flammea* (D. & S.), *Lymantria monacha* (L.) and *Diprion pini* (L.), 2 – outbreak of *Tortrix viridana* (L.), 3 – intensity of sun-spot appearance, 4 – Brückner's cycles of weather course in 1800–1920 (arrows indicate exceptionally warm and dry years)

generalizations proposed are very dubious. For instance, Eidmann (1931) recorded the occurrence of five species of primary pine pests over the entire area of Central Europe against the background of cyclic Sun activity. This evoked a number of objections, the authors of which rightly claimed that it would be more correct to study this problem separately for each species and within a smaller, more definite area.

In Poland, Kiełczewski (1950) was also interested in this problem. He established that outbreaks of *Lymantria monacha* (L.) occur during periods of annual sun activity expressed by the "sum of the mean relative number of spots". The enormous outbreak of this species in 1948 occurred one year after the most intense sun activity since 1778.

The studies of Vorontsov (1962) exemplify the investigations of supporters of the synoptic trend. Vorontsov compared the course of the weather and the history of outbreaks of forest pests on the Russian plain within the past 100 years. The climatic conditions of the region discussed are not stable in any given area. Periods of dry or humid weather succeed one another due to the definite direction of atmospheric circulation. The air currents in this region run either parallel with latitude (eastern or western circulation) or meridionally (southern circulation).

In periods of western circulation (W) in temperate latitudes there are negative anomalies of air temperature and pressure, whereas in periods of eastern and southern circulations (E and S) positive anomalies are observed.

In successive periods from 1891 to 1958 the following types of circulation prevailed on the Russian plain:

1891–1899	S and W
1900–1928	W
1929–1939	E
1940–1948	S
1949–1958	E and S

One hundred years ago (since 1862) outbreaks of many xerophilous species prevailed, including *Lymantria dispar* (L.), *Dendrolimus pini* (L.), *Euproctis chrysorrhoea* (L.) and later also *Malacosoma neustria* (L.). The area occupied by these outbreaks reached its maximum in 1867–1896. In 1870–1871 the climax of an extraordinarily intense outbreak of *Bupalus piniarius* (L.) occurred. The climax of the second gigantic outbreak of *L. dispar* took place in 1879. In 1891 (the starting point of systematic meteorological observations) the outbreak centres of many insects shifted from the southern and north-eastern parts of the Russian plain to its centre where outbreaks of *L. dispar* prevailed. Outbreaks of *Lymantria monacha* (L.), *Panolis flammea* (D. & S.) and *Malacosoma neustria* (L.) were also observed. Their occurrence was associated with the period of dry weather resulting from the southern circulation.

At the beginning of the 20th century, the frequency of the occurrence of outbreaks distinctly decreased and corresponded in time to the setting-in of a western circulation and the lowered Sun activity. Throughout the entire period of western circulation, outbreaks rarely took place and only hygrophilous geometrid species exhibited strong outbreak tendencies. Only the onset of drought (as a result of the 11-year cycle of Sun activity) and short-lasting eastern circulation in 1906 evoked the reappearance of outbreaks of *L. dispar* (L.) and *E. chrysorrhoea.*

In the third decade of this century the western circulation gradually transformed into an eastern one, this being particularly distinct in 1923–1925, and evoked the occurrence of outbreaks of xerophilous species such as *Neodiprion sertifer* (Geoffroy) and *Tortrix viridana* (L.).

In 1929 outbreaks of *L. dispar* and *D. pini* occurred, as well as of *T. viridana* and *N. sertifer.* In 1937–1941 *E. chrysorrhoea, P. flammea* and *L. dispar* exhibited a mass appearance in the forest-steppe zone and many secondary pest species erupted in pine forests.

Subsequently the eastern changed to a southern circulation causing the onset of humid summers and warm winters. In 1945 the outbreaks of many species subsided, but after three years they started again with the change to an eastern and southern circulation. In 1958 the eastern and southern circulation influenced unprecedented strong and frequent oscillations of weather conditions. This created possibilities for population explosion of species which had hitherto never appeared in mass number (e.g. *Phalera bucephala* (L.), *Laothoe populi* (L.), *Acantholyda posticalis* Matsumura) and evoked atypical outbreaks of "traditional" pest species.

According to Vorontsov (1963), when only pandemic outbreaks (i.e. occurring over large areas) are taken into account and some local outbreaks evoked by the local effects of natural and economical conditions are left out, a distinct association is observed between the mass appearance of insects and climatic oscillations as well as cycles of sun activity.

Vorontsov quotes both the results of published geophysical studies distinguishing 11-year, 5–6-year and 80–90-year cycles of the sun's activity and establishing their influence on the weather, as well as his own and other authors' studies on the course of fluctuations in the appearance of forest insects.

The synoptic theory points distinctly to the fact that the dynamics of the abundance of forest insect populations are influenced, not by climatic conditions to which the insects have become adapted though natural evolutionary processes but by changes in these conditions, i.e. by deviations from the norm which cause the meteorological conditions to follow an abnormal course over a period of several years.

The most important shortcoming of the climatic concept is that it cannot prove that the climate acts as a stable limiting influence on the development of insects. Neither can it explain the focal nature of the development of outbreaks. It is obvious that the absence of outbreaks in "normal" years cannot be due to the limiting influence of the weather but is the result of the lack of other agents stimulating the outbreak.

In view of this, is should be noted that, despite the establishment of certain correlations between the type of weather and the development of outbreaks, the direct influence of the type of weather on insects has not been established and only indirect associations have been repeatedly observed. Studies carried out in Canada over a number of years established that dry weather is conducive to the development of outbreaks of *Choristoneura fumiferana* Clemens. This is because the balsam fir comes into flower more rapidly and in greater profusion under these conditions and therefore provides an abundance of food for the young larvae which feed on male inflorescences. The larvae thus grow more rapidly and this serves to protect them against the attack of certain parasites. Also, females develop within a shorter period and exhibit a higher fertility. The result is an outbreak of the pest (Morris, 1963).

Analogous phenomena were observed in the Soviet Union concerning the larvae of *Lymantria monacha* (L.) feeding on male pine inflorescences. The longer this pest feeds on inflorescences (this being dependent on weather condition and on the character of the forest stand) the lower is its mortality and the higher its fertility (Khanislamov *et al.*, 1962).

Thus, the coincidence (or its absence) of the development of insects and their host plants, as well as of the appearance of the given insect and its enemies, is the most important factor influenced by the course of weather. In view of this, the influence of the weather can be taken into account exclusively in the aspect of the biocenotic associations within a definite ecosystem.

Concept of the decisive role of trophic factors. It has been evident for a number of years now that any increase of a pest's abundance is possible only in the presence of sufficient amounts of food. A simple correlation between the amount of food consumed by larvae and the weight of pupae, as well as between the weight of pupae and the fertility of their emergent females, has been established many times in the laboratory. It has been also observed that the absence of food at the peak of the explosion stage of gradations leads to a high mortality of larvae due to starvation, lowers their resistance to pathogens and parasites and gives rise to underdeveloped adults. On the other hand, the presence of food alone cannot be regarded as the direct cause of the growth of the pest's abundance, even in the presence of a mean number of insects characterized by a normal level of fertility. Such a situation prevails in many forest stands over periods of several years but does not necessarily lead to outbreaks.

On the other hand, phytophagous species rarely suffer from a shortage of food in nature. Thus therefore cannot be the cause of a reduction in the pest's abundance during the course of outbreak. The development of outbreaks cannot therefore be ascribed to the amount of food available but must depend on some other agent which, according to many authors (e.g. Ilinski, Zwölfer, Rudnev and Grimalskii), is the variability of the quality of the food which in turn depends on the physiological condition of the host plants.

Investigations concerning this problem were initiated many years ago by Mokrzecki (1903) who studied the internal therapy of plants and by Stark (1926) who looked at the influence of the chemical properties of soil on the composition and number of poplar pests. It was Zwölfer (1953) who first considered the problem of the influence of soil conditions on the physiological condition of plants and its ultimate effect on the reproduction of phytophages feeding on their leaves. Hitherto such studies were almost exclusively confined to insects feeding under bark.

The effect to these investigations was to undermine the concept of the division of pests into "primary" and "secondary" ones.

The official authorship of the "trophic theory" of dynamics of insects is ascribed to Rudnev (1962), who recapitulated the studies of a number of German and Russian entomologists, particularly Khanislamov and

Grimalskii, and established the following factors influencing the development of outbreaks.

1) Food, both its amount and quality, is the main factor causing changes in the abundance of insects feeding on the assimilative apparatus (e.g. leaves) and under the tree bark.

2) The resistance of trees. This depends on the content of protective substances toxic to young larvae. Due to this the abundance of the pest cannot increase in healthy forest stands, despite the high production of eggs and the limited activity of parasites.

3) Gradations become possible when the physiology of host plants weakens, although both the degree and localization of this weakening may differ in individual cases.

4) Weather, soil and other ecological conditions exercise a considerable influence on changes in the abundance of insects. This influence is not direct but indirect, through the determination of the physiological condition of the host plants. In each particular case the factor being most distant from the optimum value appears to be decisive, determining the change in abundance of the insect.

In view of this, the oscillations of insect abundance are the result of changes in the food quality due to the physiological conditions of plants which may in turn be determined by weather, soil or anthropogenous factors.

The influence of food on the development of insects, and thus the mechanisms of the influence of the physiological condition of plants, has been discussed in one of the earlier chapters of this book.

The concept of the decisive role of nutritional agents (trophic concept) is supported by numerous examples indicating that the foci of outbreaks of pests feeding in the crowns of coniferous trees, as well as those of "secondary" pests, develop in forest stands weakened by changes in soil conditions and economic human activity and that they expand in years of a particular complex of meteorological conditions.

5.1.2 Concept of the complex influence of the components of the ecosystem

Hitherto concepts have been discussed which ascribe the changes in the abundance of insects to the influence of virtually a single decisive agent such as parasites, climate or food. At present we shall take into consideration several concepts, the authors of which assumed one common thesis claiming that the changes in the abundance of insects are determined by the complex influence of various (some or all) environmental agents.

Biocenotic concept. As compared with the somewhat primitive opinions of the supporters of the concept of the decisive role of parasites, the biocenotic concept put forward by scientists of the highests rank of the interwar period (e.g. Friederichs and Mokrzecki) takes into account not only the simple prey–predator and host–parasite association, etc., but their entire complex system existing in nature. The scientific notion of the biocenosis being a complex system of associations between various organisms overruled the conclusion that the disturbance of a certain point of the biocenosis can lead to quantitative and qualitative changes of the entire system. Thus the changes in insect abundance would be due to the interaction of an entire complex of biotic, reciprocally conditioned agents such as parasites, predators, parasites of a higher order, diseases, host plants of intermediate and substitutional hosts of the parasites, etc. Abiotic factors would also be included, but relegated to a secondary role.

According to the biocenotic concept, the disturbance of mutual relations in the biocenosis under the influence of human activity is one of the main factors causing mass appearances of insects. Indeed, badly managed human economic activity frequently leads to changes in the specific composition and distribution of the flora, causing it to take on a uniform character over vast areas (e.g. monocultures, pine plantations, etc.). The impoverishment of the flora and the destruction of various biotopes likewise ultimately impoverishes the fauna, particularly the complex of predators and parasites as well as those insects feeding on flower nectar and pollen as adults. Conditions are thus made favourable for the intensified occurrence of noxious insects.

This concept has been confirmed by frequent cases of outbreaks on sites of intensive exploitation and human economic activity, as well as in vast forest stands of single species of coniferous trees.

Although the antagonists of the biocenotic concept accumulated a number of facts contradictory to the evidence quoted above, the concept is constantly gaining new supporters. This is because it is constructed on a sound, natural basis on the impressive hypothesis that a biocenosis is a self-regulating system with its components remaining in a state of dynamic equilibrium.

One of the outcomes of a study of this concept, as applied to forest management, has been the advocation of the diversification of the species composition of forest stands, taking into account the suitability of the composition of their immediate environment and the possible effects of any new introductions.

Concept of gradocene. The biocenotic concept has given rise in turn to the concepts of "holocene" and "gradocene". The term holocene was introduced into the literature by Friederichs (1930) and denotes the total range of factors which act as a whole to influence and regulate the abundance of populations. According to Friederichs, the antagonistic action of individual environmental agents unites them into a homogeneous system, the effect of which leads to a balance in nature. The related concept of gradocene formulated by Schwerdtfeger (1941), denotes all the abiotic and biotic agents which condition the changes in abundance of a given species which exhibits a tendency to gradation.

Climatic conditions play the main role among these agents.

Their influence on the abundance of a species may be direct or indirect by affecting the host plants of the insect, its natural enemies (predators and parasites) and their intermediate hosts, etc. The insect itself constitutes the centre of the cenotic self-regulating system or gradocene (Fig. 5.2).

The loosening of biocenotic bonds, thus leading to outbreaks, may be the result of the influence of abiotic agents. The stronger the bonds are (i.e. the more numerous the biocenotic associations between the components of the biocenosis), the more difficult it is to break them down and thus cause an outbreak.

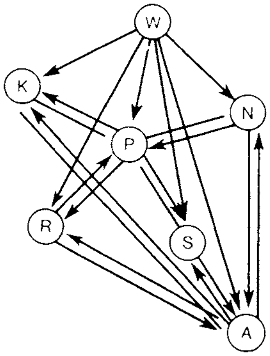


Fig. 5.2 Scheme of functioning of the gradocene (after Schwerdtfeger, 1979): P — insect population, W — weather, N — food, S — parasites, R — predators, K — diseases, A — another species being neither parasite nor predator

Studies on gradocenes (Schwerdtfeger (1941), Schwenke (1964), Thalenhorst (1951) and others) lead to the establishment of a science of outbreak processes in noxious forest insects called gradology, which established the complexity of the factors influencing their occurrence.

In the evaluation of both concepts discussed here it should be stressed that, in view of the considerable variation of forest biocenoses and their complicated structure, the complex of factors influencing the development of outbreaks may differ widely and virtually each outbreak is an unrepeatable, specific phenomenon. Many supporters and antagonists of the biocenotic concept forget about this difficulty, and, analysing the course of an outbreak, confine their studies to just those readily perceivable factors which evoke the outbreak, or to the absence of the more commonly acknowledged factors. Thus, by attempting to derive generalizations on this basis, such workers cause more harm than expedience to the sound concept.

In this respect, the opinion shared by Stolina (1959) and Viktorov (1960) seems particularly cogent. According to this opinion, the abundance of a given species in a definite biocenosis and a definite type of forest habitat be considered when the reproductive abilities of the species and the level of its abundance have been stabilized in the given ecosystem under the mutual influence of abiotic environmental agents, the basic food source and natural enemies.

Hence, the important conclusion can be advanced that disturbances in the biocenoses, such as the loss of certain components and the appearance of new elements, may lead to significant changes in the abundance of insects, particularly phytophages. Pertinent examples of this type of phenomena are quoted by Stolina in reference to the history of outbreaks of a number of species in the forests of Slovakia. In his opinion outbreaks of definite species invariably appear in the same types of forest stands in which the given tree species encounters unfavourable conditions but nevertheless occurs in excess due to human interference. He quotes an example where in the 19th century beech was replaced by fir in oak-beech or beech-oak forest stands. Subsequently the oaks were removed and pure fir forests remained on unsuitable habitats. After the drought of 1934 an intensive and long-lasting outbreak of *Choristoneura murinana* (Hübner) developed in this area, whereas in natural fir forests it did not occur in large numbers. This points to the fact that the relative stability of biocenotic systems consists not so much in the variation of its specific composition but mainly in the adaptation of this composition to the given conditions of the habitat.

The changes observed in recent decades as regards the outbreak significance of some species, particularly those of previous pest status, and the appearance of new ones seem to indicate the existence of adaptive changes in the structure and functioning of biocenoses which serve to protect against outbreak processes. They also indicate the lack of such adaptations in respect to pests hitherto exhibiting no tendency to mass appearance such as *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson).

Hence, a considerable number of investigators claim that favourable weather merely creates the conditions for the development of outbreaks whereas their realization depends on the mutual influence of all the components of the given biocenosis.

It would thus appear reasonable to accept the concepts of the biocenosis and the gradocene on the basis that they are both self-regulating systems, although this has not been proved experimentally and is still severely criticized by a number of ecologists.

Concept of biotic potential and environmental resistance. Chapman (1928) is the founder of this concept. He endeavoured to combine two previously independent lines of ecological study, namely the influence of various physical and chemical factors of the environment on organisms and the inter-relationships between these organisms. In order to do this, he formulated the concept of biotic potential and environmental resistance.

According to Chapman, the biotic potential denotes the "quantitative expression of the dynamic force of the species in its struggle for survival directed against the resistance of the environment in which it lives". In this both reproductive and survival potential may be distinguished. If the former is high the latter is low and vice versa.

For instance tachinid flies belonging to the genus *Sturmia* (Robineau-Desvoidy), which lay eggs on leaves of the food plants of their future hosts, exhibit a very high fertility because of the low probability of the successful development of the next generation. On the other hand, tachinids such as *Compsilura concinnata* (Meigen) and *Blondelia nigripes* (Fallén) which lay eggs directly into the host's body, produce few eggs since the probability of their successful development is very high. Many similar examples may be quoted.

According to Chapman the biotic potential is stable for each species. It is a definite and characteristic though abstract value because it represents the absolute optimum of reproduction under conditions where environmental resistance is nul. Such an optimum cannot possibly be calculated. In practice it is only possible to calculate the partial potential, i.e. the biotic potential of a given species under definite environmental conditions.

In view of the extreme variability of biotic and abiotic agents, the environmental resistance cannot be calculated either. It is determined on the basis of the higher or lower deviations of the biotic potential from its optimum (examples of such calculations have been quoted above). Consequently the quantitative occurrence of a given species is the index of the environmental resistance. If the biotic potential is higher than the environmental resistance the population quantitatively increases and vice versa.

The fact that the present-day fauna has survived for many thousands of years indicates that the biotic potential and the environmental resistance maintain a certain balance. Outbreaks take place when the resistance of the environment weakens and the biotic potential begins to prevail. Thus if the size of the population remains relatively stable at a low resistance of the physical environment then the biotic potential of the species is counterbalanced by the high biotic resistance of the environment (e.g. tropical forests and rich forests of the moderate zone). On the other hand, in areas exhibiting abrupt gradients of physical environmental conditions and in which a high resistance of the abiotic environment occurs, the size of the population is only moderately controlled by biotic agents (e.g. deserts, poor forests of the Far North and artificial monocultures of coniferous forests of the temperate zone).

If a new parasite is introduced into a new area for the purpose of the biological control of an insect pest, its choice is based on the assumption that the resistance of the abiotic environment is analogous to that in its native region, whereas the biotic resistance is lower. This can lead to significant increase in the numbers of the newly introduced and useful species, the biotic potential of which will not be inhibited in this area.

However, the course of the introduction of a foreign species into a new area is not always successful. Any increase in its abundance is accompanied by an increase of new natural enemies which reduce the abundance of the introduced species to a certain low level. On this basis, Koehler (1968) advanced the hypothesis of the "gradational aging of a species", according to which gradationally young species (i.e. those not previously exhibiting outbreak tendencies) are particularly persistent pests until various components of the biocenosis become adapted to its new mass-appearance habits and hence reduce its numbers once again.

Many authors (e.g. Friederichs, 1928 and Thompson, 1929) endeavoured to employ Chapman's concept in theoretical and practical works on outbreaks of pests but most attempts were unsuccessful.

It seems that Chapman's introduction of the very valuable and now commonly used concept of environmental resistance contributed significantly to the development of studies on the dynamics of insect populations. On the other hand, despite its basically correct assumptions, the concept applies over-simplified biological generalizations and therefore cannot provide perfectly satisfactory results.

Concept of specific requirements of a species. This concept arose and was developed (Thompson, 1929, 1939, 1956) as a contradiction to the concept of the quantitative self-regulation of the population as advanced by Nicholson (1933, 1954), who derived it from inductive methods of reasoning based on the opinion that the density of a population is the main factor of self-regulation.

Thompson assumed that each organism exhibits its own "specificity", differing from that of other organisms and manifested by specific requirements in respect to the environment. The environment responding to specific requirements of a species should be considered as optimal for it. However, optimal conditions ensuring an unlimited increase of abundance are rarely observed because of the great variability of interacting environmental factors. This indicates that regulation, i.e. the limitation of the size and any changes of that size for any population, is the "rule" whereas outbreaks are exceptional. Outbreaks of insect species occur when, at a certain moment, the conditions reach or approximate the ecological optimum. As these optimal conditions recede, the size of the population diminishes. Thus the changes of abundance are simply the result of the fact that organisms must live in an environment in which conditions continuously change from favourable to unfavourable and so on. According to Thompson, casual atmospheric factors (downpours, storms, strong winds and extreme temperatures) are the main cause of changes of the abundance.

Thompson does not envisage any possibility of creating a mathematical theory of population processes and claims that a biological theory for the elucidation of these processes should be deduced, although it will be more of an ascertainment of facts than a true theory.

Thompson disagrees with Nicholson's axioms and claims that a population cannot remain in a state of unstable balance with the environment since neither the lack of food (very rarely observed in nature) nor the activity of natural enemies (occurring at a low level of abundance when that of the pest is also low) can be considered as proof of this balance.

In view of this, the population neither constitutes nor can be considered as an independent system consisting of progress and control (regulation) since it is not the "organism" considered but only a notation. According to Thompson, the population is only an agreggation of individuals each living its own life as best it can, irrespective of the other individuals and the population as a whole.

Concept of factors determining the coefficient of increase of the population. Andrewartha & Birch (1954) considered the two main approaches to ecological studies, namely those of the biocenosis and population, and put forward a number of criticisms regarding the traditional studies of animal ecology which take the biocenosis as their basic starting-point. Such a traditional approach entails the enormous task of studying all of the ecological associations and interdependences which in practice invariably proves impossible. It also has a negatively effect on the knowledge of economically important species.

The distribution and abundance of a species cannot be elucidated by the study of the relationships between plants and animals in the biocenosis alone, since other components of the environment also require detailed ecological analysis. These include meteorological factors, other organisms, food and site of occurrence. The population is also a part of the environment for an individual and, therefore, the concept of the environment cannot be related to a population but only to a single individual. In the opinion of Andrewartha & Birch, the division of the environment into the density-dependent and density-independent factors of a population is incorrect. There are no factors which do not depend on density, thus no separate role should be ascribed to their influence.

Under favourable conditions the population size increases and under unfavourable ones it diminishes. In the opinion of Andrewartha & Birch this is due to the fact that variability is a universal law of nature, thus it is not necessary to refer to density-dependent factors in order to explain the mean abundance of a given population or the fluctuations which appear from time to time. They also claim that studies on agents of competition are of no use in elucidating the problem of abundance. It is doubtful whether a population exists in nature which would utilize or be able to utilize all the food stock available and, even if so, whether studies on competition would help to explain the observed density of the population. It is perhaps a striking fact that species of low abundance prevail due to the accessibility of excess food and that most predators and parasites exhibit a high degree of inefficiency even though many of them live among relatively dense populations of their prey.

Andrewartha & Birch also disregard the factors whose influence is either dependent or independent of the population density, particularly the role of competition and concepts such as the balance of the biocenosis and the regulation of abundance. They rely only on empirically obtained values which take into consideration changes in abundance and on the basis of the values they conclude that the size of a population increases when the fertility of the species exceeds its mortality, i.e. when the coefficient of population growth (determined by fertility, rate of development and length of life) is positive (see page 144). The value of this coefficient varies in time and obviously depends on individual environmental factors as well as their efficiency.

According to Andrewartha & Birch, the size of the population may be limited by:

1) a deficiency of the environment's material stock such as food, area of occurrence, etc.;

2) the inaccessibility of this stock which is conditioned by the animal's capacity for dispersal and locating such stock;

3) too short a period in which the rate of increase of the population size (r) is positive, the briefness of this period being due mainly to unfavourable atmospheric or climatic agents and further to the action of predators and other factors which can influence the population size.

As regards the third limitation, Andrewartha & Birch (1954) fully support Thompson's opinion concerning the briefness of periods favourable for the increase of the population size. They also claim that the factors listed first are probably the least important, whereas the last mentioned are most significant in nature.

Andrewartha & Birch admit that the higher the density of the population the higher is its decrease with constant intensity of the given agent.

5.2 Concepts based on the automatic regulation of population size

5.2.1 Concepts of self-regulation with respect to the decisive role of parasites and of overcrowding

Opinions of Howard and Fiske. On the basis of Darwin's theory of the struggle for survival, Howard & Fiske (1911) distinguished two groups of factors of the dynamics of the abundance of *Lymantria dispar* (L.) –

catastrophic and facultative. Catastrophic factors include unfavourable meteorological conditions, the influence of which is independent of the thus limited abundance of insects whilst parasitic and predatory specialized entomophages and pathogens comprise the facultative group. The influence of the latter is more effective in periods when other conditions favour the increase of the population size and secure its suitable level. In other words, the facultative agents destroy an ever higher percentage of the population as it increases.

Howard & Fiske also distinguished a third group of factors exhibiting an action opposite to that of facultative factors in that their influence diminishes with the increase of the population density. This group includes birds and other polyphagous predators, the abundance of which is independent of the density of the prey population. They therefore destroy a relatively stable number of individuals irrespective of the size of the population.

This had led to the concept that the population density is determined by the population itself, otherwise referred to as automatic regulation of abundance or self-regulation of the population.

The opinion of Eidmann. Eidmann's (1931) concept is also one of self-regulation, ascribing the role of regulator to the very species itself which exhibits mass occurrence. According to this concept: "owing to its intensively increasing reproduction the pest deteriorates its living conditions. This concerns both endogenous (decrease of fertility as well as percentage contribution of females and diminished resistance to diseases) and exogenous factors (food deficiency, mutual interference, facilitation of infection and development of epidemic diseases)".

5.2.2 Concept of the automatic regulation of abundance

The concept of Nicholson and Smith. Nicholson's (1933, 1954, 1958) works played a fundamental role in the development of the theory of the automatic regulation of the population size. He suggested that all animals exhibit a tendency to increased reproduction only if their life requirements are satisfied. Food, living space, the opportunity of meeting individuals of the opposite sex, suitable temperatures for securing development and humidity, etc. are all components of the basic requirements.

Since the existence of a species is determined by the fact that all of the basic requirements must be at levels exceeding those of the lowest possible for that existence, the population cannot reproduce without limits. This is because either the food stock or living space will be exhausted or the environment will deteriorate as a result of the limiting effect of some other agent or to an increase in the number of enemies.

The population thus remains in a state of unstable equilibrium with the environment and exhibits an internal quantitative regulation or "self-regulation" (automatic regulation of abundance).

Nicholson (1933) explicitly formulated the idea of the automatic regulation of the population, claiming that "the influence of the regulating agent should be directed by the density of the regulated population". In Nicholson's opinion various forms of competition in its widest sense, consisting of various forms of mutual influence between organisms including parasite/host and predator/prey systems, are the actual regulating factors. An important role in limiting the propagation of animals, as well as in the determination of the level of abundance at which the controlling agents regulate the population density, was ascribed by this author to climatic factors. Also, according to Nicholson, irregular changes in weather conditions are the cause of equally irregular changes in the density of populations.

Soon after, Smith (1935) distinguished those agents which are dependent and independent of the population density among the factors determining the dynamics of population size. Dependent agents, such as entomophages, diseases, lack of food and living space, augment their effect as the population density increases, whereas those independent of the density (e.g. physical properties of the environment, condition of host plants, etc.) destroy some part of the population irrespective of its density.

Nicholson (1954) subsequently divided the density-dependent agents into reactive and non-reactive categories. He remarked that the reactive factors considerably limit their influence at a low level of abundance of the population, and because of this the population rapidly restores its abundance and once again comes under the influence of the abiotic environment.

The classification of factors determining the dynamics of abundance is given in Fig. 5.3 (after Nicholson, 1954).

The non-reactive agents depend on changes in the density of the population but have no retrograde influence on the populations. Under certain conditions food may be classed as such a factor. For instance, the population only has a slight influence on the amount of food available in a given area during the latent phases of outbreaks of insect defoliators. On the other hand, the decrease of the amount of food cannot evoke a decrease of density of the population since food invariably occurs in excess. Reactive agents exhibit a different behaviour. When defoliation occurs at the explosion stage of an outbreak, the resultant food deficiency (i.e. caused by the increase in population density) influences the population itself.

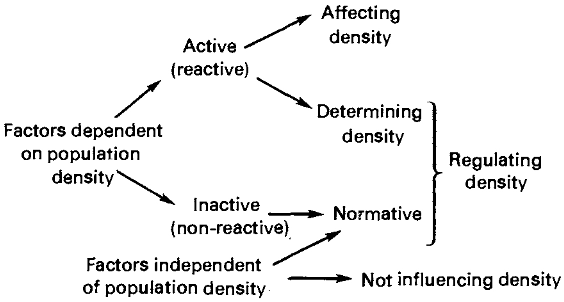


Fig. 5.3 Scheme of influence of factors in the dynamics of insect abundance (after Nicholson, 1954); explanations in text

Factors determined by the density of the population such as interspecific competition for food, susceptibility to persecutors, etc., are the main contributors to the diminution of the population size during the process of self-regulation. Normalizing agents dependent or independent of the density of the population play a lesser role in this respect, although they may lead to an increase in density to a level of unstable equilibrium determined by the properties of the environment and of the insects themselves.

The classification of dependent factors, which determine the density as well as non-reactive, normative factors and are not connected with the density as regulating agents aroused objections and led to the rejection of this classification by many ecologists and to the development of Smith's original concept.

Varley (1947, 1953) proposed the distinction of delayed factors, these being dependent on the density of the population and including such agents as entomophages, change in abundance of which is delayed in comparison with the change in the abundance of the host (Fig. 5.4). On the other hand, Solomon (1958) classed agents as either being directly or indirectly dependent on the population density, according to whether their influence increases or diminishes with the increment of density of the population, as well as distinguishing alternative agents

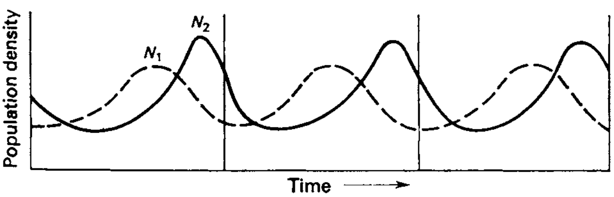


Fig. 5.4 Changes in population density of two species one of which is the predator of the other (after Volterra, quoted by Kot, 1970)

dependent on the population density and in which the delayed reaction to changes in abundance leads to a regular change of directly and inversely dependent phases.

Nicholson's theory encountered as many supporters (e.g. Varley, de Bach, Solomon, Voute and others) as opponents (e.g. Thompson, Milne and Schwerdtfeger). A basic dispute in this respect took place between Nicholson and Thompson. Those interested in this problem can follow the arguments as elaborated by Huffaker & Messenger in the collective work published under the editorship of P. de Bach (1964).

The mathematical models elaborated by Nicholson & Bailey (1935) are very important in the evaluation of Nicholson's concept. According to these models, under constant conditions the abundance of the host increases throughout the course of several generations and then decreases. The same occurs with a certain delay in the abundance of its parasite and the paths of each may be expressed mathematically. This phenomenon leads to cyclic, regular changes in both components of the system (Fig. 5.5). The model has been confirmed from data on several insect species in various parts of the world.

Regardless of whether Nicholson's opinions were either accepted or rejected by the majority of other ecologists, they constitute a very valuable contribution to the knowledge of the dynamics of insect abundance. The assumption that under conditions in which their life requirements are satisfied, animals may reproduce without limits and, due to limited space, food and the possibility of development of enemies, must decrease their abundance, is essentially valid and can be mathematically proved. However, it led Nicholson to the false, most frequently attacked conclusion that the population must remain in balance with its environment. According to many authors, there are no practical examples confirming this conclusion, in fact, on the contrary, experimental and practical studies demonstrate that considerable changes do occur in the size of populations.

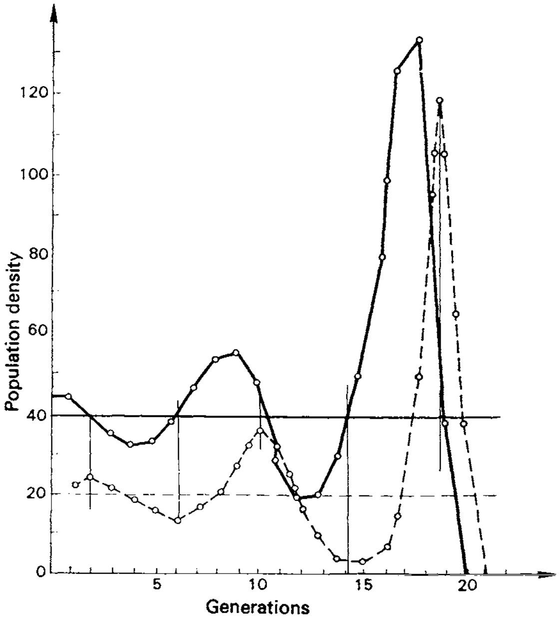


Fig. 5.5 Interaction of host (continuous line) and specific parasite (dashed line) under following conditions: fecundity of host $f = 2$, power of discovery of parasite $a = 0.035$, original arbitrary displacement of initial host density from 40–44 (after Nicholson and Bailey, 1935). Host curve shows initial host density, i.e. density of progeny at beginning of generation. Horizontal lines show steady density of host (continuous line) and parasite (dashed line). Abscissa and ordinate are calculated from formulas:

$$H_{n+1} = fH_n e^{-aP_n}, \quad P_{n+1} = fH_n - H_{n+1},$$

where H_n = host density at generation n, f = growth potential of the host population density, e = base of the Naperian logarithm (2.718), P_n = parasite population density at generation n

Nicholson derived the concept of self-regulation, i.e. of the adaptive capacity of the population to reduce of its abundance to a certain mean, from that of unstable equilibrium.

The problem of self-regulation (automatic regulation) of the population size is at present one of the central issues of population ecology.

5.2.3 Facts justifying the concept of the automatic regulation of abundance

According to Viktorov (1967), the existence of various mechanisms serving to regulate abundance is confirmed by evidence from the application of stochastic models, laboratory studies on insect populations and investigations on natural populations (particularly with the use of mathematical models for the establishment of the dependence of mortality, reproductive potential and rate of increase of the population on its density).

These sources of evidence will be discussed in turn.

Schwerdtfeger (1958) employed stochastic models in an attempt to prove the absence of any regulation of abundance. To do this he placed 20 white and 20 black balls in a box symbolizing the favourable and unfavourable influence of environmental factors causing a twofold increment or decrement of population size. The curve representing the course of abundance of a number of "generations" thus obtained changed at a rather low level. Occasionally, an extremely strong increment of abundance was observed. On this basis Schwerdtfeger concluded that the density of the population may be regulated for a long period by a completely casual influence of the environment, the longer the more agents influence the abundance. Relatively seldom does the increase of abundance attain a value which requires the activation of special regulating mechanisms.

On the other hand, later authors (Wilbert, 1963; Klomp, 1962) criticized the result of Schwerdtfeger's experiments, rightly remarking that the model described above did not ensure the independence of the influence of individual factors, since after the extraction of each successive ball the probability increased of extraction of a ball of the opposite colour. They employed other stochastic models, such as Pascal's triangle and coin-tossing, and reached contradictory conclusions. They found that the increase of the number of generations was accompanied by a constant increment of the probability of exceeding the given lower or upper limit of abundance, which indicates that the increment of casually acting agents does not favour stabilization. Similar results were also obtained when the model was complicated by the acceptance of several values of the coefficient of reproduction and by the selection of individual values in connection with favourable or unfavourable weather (in Holland). In this case also, the increment of the number of factors only increased the need for regulating mechanisms.

Analogously, it has been proved that the influence of weather on the density of insect populations is, in fact, accidental and cannot have any regulating influence.

The mathematical models of Lotka (1925) and Volterra (1931) as well as those of Nicholson & Bailey (1935) were tested in the laboratory because they had been criticized for their simplification of biological situations. The failure of these laboratory studies served as an argument for the rejection of the idea of automatic regulation of abundance.

Recently, the experiments of Utida (1950, 1955, 1957) have aroused particular interest. Utida reared a population of *Callosobruchus chinensis* (L.) and one of its parasites under stable temperature and humidity conditions. On the basis of over 100 successive generations he demonstrated the existence of mutually conditioned changes in the abundance of the host and that of the parasite (Fig. 5.6).

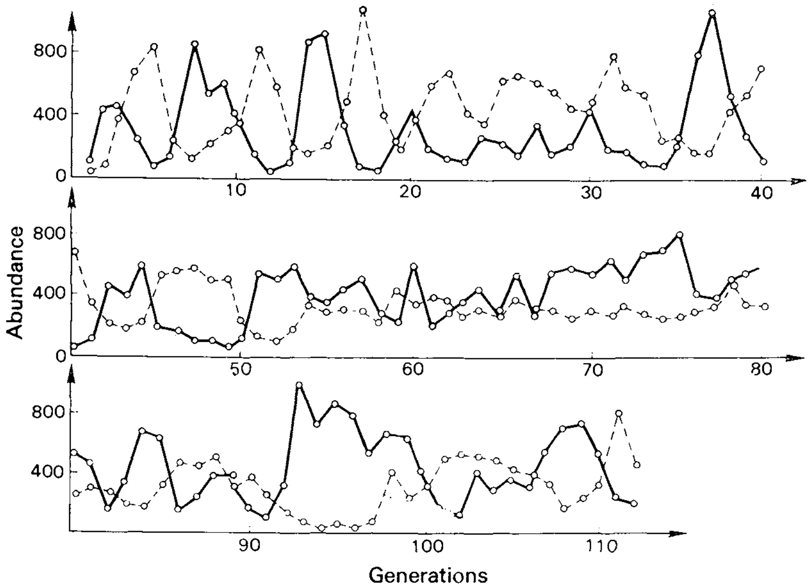


Fig. 5.6 Correlative oscillations in abundance of *Callosobruchus chinensis* (continuous line) and its parasite *Heterospilus proposidis* (dashed line) in experimental populations (after Utida, 1957)

Analogous results have since been obtained in experiments on numerous other host-parasite pairs mostly living in synanthropic environments.

It would appear that wide differences concerning the period and amplitude of oscillations occur between each pair of interacting organisms and that these differences correspond to the mathematical models of Nicholson & Bailey (1935).

The persistence of such regulating systems may depend on various agents, of which the most important is the avoidance of parasitism by at least some of the host's individuals (e.g. the thickness of the substrate in which the phytophage lives must be larger than the length of the parasite's ovipositor).

The differences in the scale of tolerance to environmental agents in phytophagous insects, as well as in their specialized parasites, are wide and common. The existence of such differences may thus be assumed to be the rule. Such an ecological divergence provides the host with the possibility of taking avoidance measures and, in consequence, the possibility for the survival not only of the host but also of its enemies.

Another important experimental observation which points to the existence of regulating mechanisms is that the level of abundance of the host was 2–3 times higher in the presence of either its parasite or predator than when the host was reared on its own. In addition to this, other interesting examples of compensatory reactions were obtained. These showed that the destruction of a part of the population of a given stage of the host provides a distinct increment of abundance in the next stage. For example, the destruction of 90% of a population of larvae of a species of *Lucilla* (*Diptera*) only caused its average abundance to decrease by two thirds in the next stage as compared with the control.

Since the results of experiments performed in laboratories under stable temperature and humidity conditions were frequently considered as inconclusive, the validity of mathematical models was also tested under natural conditions. Varley's (1947) work devoted to the dynamics of the abundance of the fly *Urophora jaceana* (Hering) in England is the most commonly known. His results comply with empirical data confirming the validity of the basic assumptions of the mathematical models of Nicholson & Bailey (1935). As a result of his studies on the changes in abundance of *Bupalus piniarius* (L.) over a 10 years period in pine forest stands in Holland, Klomp (1962) also concluded that the population density of this species in well regulated systems decreased after exceeding the mean level of abundance and increased when it fell below this level.

The nature of the dependence of mortality, reproductive potential and of the rate of increase of the population size on its density is an important criterion for the evaluation of the existence of automatic regulation.

According to Viktorov (1967), the mathematical evidence so far obtained is sufficient proof for the existence of such dependences, even under conditions of natural populations. Ullyett (1947) was the first to establish that the dependence between mortality and the density of the studied populations of cabbage moth could be represented by the func-

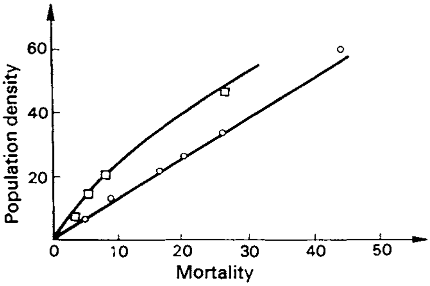


Fig. 5.7 Mortality of cabbage moth dependence on population density (after Ullyett, 1947)

tion $y = bx^n$ (Fig. 5.7). Finally, Morris (1963) elaborated objective methods of detecting regulating processes as a result of observations on populations of a number of noxious forest insects in Canada. These methods involve the use of regression analysis to determine the relationship between the density of the population in the previous (N_n) and subsequent generation (N_{n+1}). This dependence may be represented in linear form by converting the population density to logarithms (Fig. 5.8).

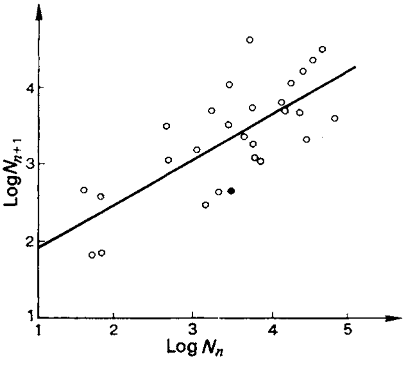


Fig. 5.8 Correlation of population density of *Choristoneura fumiferana* Clemens in two successive generations: N_n and N_{n+1} (after Morris, 1963)

In the absence of density-dependent factors, the coefficient of regression should be one, whereas deviations from this value indicate the degree of the contribution of factors which do exhibit a dependence on the population density.

Well known phenomena such as the absence of outbreaks of species normally showing this tendency, the absence being due to the action of natural enemies and diseases which reduce the population density to a normal level, also confirm the existence of regulating mechanisms. It has also long been known that the same species can have different intensities of population numbers at the climax of an outbreak in different types of forest stands (e.g. pure v. mixed). Engel (1942) found that during the course of synchronized changes in the abundance of *Bupalus piniarius* (L.) in pure forest stands, of both uniform and varying age, and in mixed stands, the amplitude of these changes was lowest in the mixed stands. Hence, in such stands the outbreak did not reach its peak. Similar examples have been quoted by authors for various other forest pests.

It is perhaps significant to note here that the role of parasites and predators should not merely be viewed as a mechanism serving to reduce the abundance of phytophages to low levels. It should also be borne in mind that their continued action maintains these low levels and thus also constitutes a regulating mechanism.

The definite existence of abundance-regulating mechanisms has been confirmed by arguments of a negative character, i.e. by the results of the influence of man's economic activities on these mechanisms as seen, for example, in the extensive use of insecticides. Such interference often has serious side effects, such as the rapid and intense propagation of the chemically controlled pest and prolonged periods of its occurrence, as well as the mass appearance of species hitherto having no harmful economic significance. The principle cause in such cases is the destruction of the natural enemies of the pest (and potential pests) which previously had a regulatory role. Analogous effects are the result of other human activities in the forest environment which suppress the system of existing biocenotic relationships.

The supposition that a definite organization exists within the biocenosis, as well as regulating mechanisms necessary for the preservation of the population and the biocenosis, is at present based on the results of a number of studies in various branches of biology which support the existence of the automatic regulation of abundance.

The possibility of employing cybernetic techniques to establish a general theory of management and to investigate any self-regulating systems that may exist, regardless of their physical nature, is particularly important in the understanding of the dynamics of abundance. Since the rule of feedback is an indispensable property of self-regulating systems, it is of particular importance in the problems discussed here. According to this rule, the regulator obtains information concerning the course of the regulated process and on the basis of this alters its regulating action. Since the regulation of abundance is known to exist in nature, the facts quoted above lead to the conclusion that regulators of abundance which act according to the rule of feedback must also exist.

It is obvious that only biotic agents can play the role of regulators since they are the only factors capable of reacting to changes in the abundance of other organisms. Viktorov (1967) was of the correct opinion that, in the case of mechanisms regulating the abundance we are obviously dealing with error-directed regulators, i.e. those which react not to the stimulating action itself, but to the changes in the population density evoked by this action. Obviously, regulators of this type cannot be decisive in that they are not capable of securing a definite population density. The abundance of a population invariably oscillates in parallel with the casual influence of external agents. The regulating influence is thus indicated by the decrease of the population density towards a definite mean value and by a moderation of amplitudes of the changes, as well as by compensatory reactions increasing the population density to the same definite mean.

These ideas are very important since the coincidence of changes of population abundance with changes in meteorological conditions frequently serves as an argument against the existence of regulating mechanisms and supports the theory of the complete dependence of the course of the population abundance on weather.

5.2.4 Milne's integrating concept

In view of the existence of essential divergences between the supporters of the idea of automatic regulation of abundance and their opponents, Milne (1957) advanced a new concept endeavouring to combine the contradictory opinions. According to Milne, his concept was the result of "impregnation of the theory of Thompson and that of Andrewartha & Birch with elements of Nicholson's theory".

This concept is based on the thesis that there is no balance between a population of any species and the surrounding environment. In spite of Nicholson's opinions, natural enemies cannot themselves decrease or regulate the host's abundance since their influence is imperfect, depending on the density of the population. This density simply increases when environmental conditions permit and decreases under a definite influence of these conditions. The continuous existence of a population is due to the wide variation of the stimulating and limiting influence of environmental agents within the geographical range of the given species. In Milne's opinion this assumption is founded on mathematical, physiological and ecological bases as well as on field observations.

Milne's reservations concerning the concepts of Thompson and Andrewartha & Birch are based on the fact that Thompson ascribed too little importance to density-dependent agents, whereas advanced a wrong (in Milne's opinion) conclusion concerning the spurious dependence of the intensity of the action of all environmental agents on the population density and consequently completely rejected the role of density-dependent agents as regulators of abundance. Milne claims that food and space cannot act in dependence on density whereas competition can.

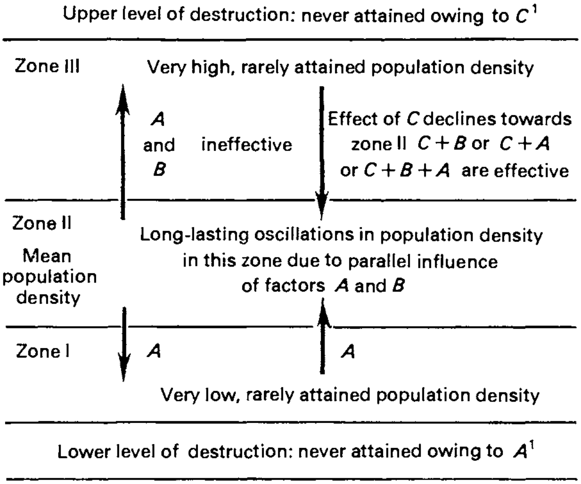


Fig. 5.9 Scheme of dynamics of insect abundance according to Milne (1958). The influence of factors may occur in the case when the range of the species is not too small and migration of the population is possible: A – general influence of factors independent of population density, B – general influence of factors not quite dependent on population density, C – only factor completely dependent on population density – intraspecific competition. Arrows indicate quantitative deviations from standard population density in zone II in the direction of its increase or decrease as well as its return to the zone. Factors evoking deviations are given beside arrows. Horizontal lines – limits of population zones considered to exhibit gradual transition from one zone to another. They depend strictly on the ecological requirements of the species as well as on factors A, B and C. Intraspecific competition depends primarily on the complex of environmental conditions and, under specific circumstances, may even appear at low population density. Destruction of small populations is not exceptional but the destruction of the entire population and species is doubtful against the background of ecological differentiation of the entire range of occurrence

Milne thus admits the existence of regulation but he confines it exclusively to the result of intraspecific competition which completely depends on the density of the population.

Milne classifies natural enemies (predators, parasites, pathogens and competitors) to the group of "limiting agents not completely dependent on population density". The tendency for changes of population density to decrease the maintenance of abundance at a more or less mean level and the consequent limitation of outbreaks to rare phenomena are ascribed by Milne to these agents.

On the other hand, the amplitude of the variations in abundance depends not only on the action of natural enemies (which, according to Milne, diminish the density of the population to the same degree and also inhibit this decrease) but also on a complex of factors independent of population density, particularly within the mean range of its value.

The system of dependences is illustrated by the scheme elaborated by Milne (Fig. 5.9).

The data quoted above indicate that Milne confines the complicated process of the dynamics of the population's size, as well as the complicated mechanism of the regulation of this process, simply to "overdensity", i.e. to the excessive density of the population. It is because of this overdensity that, what Milne regards as the only regulating mechanism, intraspecific competition comes into action.

Milne himself claims that instances where excessive density releases the regulating mechanism are very rare. Thus, on the one hand, he ascribes no possibility of self-regulation to the population and, on the other hand, he claims that the upper level of destruction of the population is not attained because of the, albeit rare, existence of the regulating mechanism of intraspecific competition.

This inconsistency prevents Milne's concept from being developed any further and has became the object of wide criticism.

5.2.5 Concept based on the influence of genetic mechanisms

According to the assumption accepted by Franz (1949, 1965), only the fittest individuals remain in a population during periods of low abundance resulting from a high percentage of mortality. In outbreak periods the effects of the factors which reduce the number of individuals are weakened and this leads to an increase of unfavourable, recessive features throughout the population. Also, in large colonies of individuals inbreeding develops. Consequently, a high proportion of the population dies despite the absence of external agents of mortality.

Chitty (1965) also claims that at various levels of population density different genotypes should attain a selective predominance thus providing the opportunity for the regulation of abundance by natural selection.

Pimental (1961) developed the concept of the regulation of insect abundance by the mechanism of genetic feedback. To illustrate this he employed an abstract model based on the following assumptions.

A plant exhibits a definite resistance to any given insect which feeds on it. Phytophages are uniformly distributed on plants and their reproduction (R) depends on the genotype of the plant on which they feed. The resistance of the plant is conditioned by a pair of alleles (A, a). When an insect feeds on a plant of genotype AA, the coefficient of reproduction (R) of the insect amounts to 2, with the heterozygotic genotype Aa this value is 1 and with the double recessive genotype aa it is 0.5. The density of the phytophage (N) of the initial period ($N_{t\,0}$) therefore either increases or decreases in the successive generations ($N_{t\,1}$), depending on the quantitative proportions of plants with the genotype AA, Aa and aa.

The mutual influence of such hypothetical populations of the phytophage and its host plant through 100 "generations" has been further studied with the use of a computer. The results obtained indicated that, at a definite genetic composition of the plant population, the abundance of the phytophage was stabilized within the course of approximately 72 generations.

According to Pimental, in the example studied the maximum density of the phytophage which would permit the survival of plants of the genotype AA should amount to 1075, that for Aa, 1500 and that for aa, 3000. This leads to the conclusion that the genotype destroyed by the lowest density of the phytophage is that on which the phytophage exhibits the highest rate of reproduction. It has also been calculated that, in this particular model, the proportions of plants exhibiting the individual genotypes AA, Aa, aa in a stable plant phytophage system amount to 0.172, 0.485 and 0.343 respectively, whereas the density of the phytophage is 795 individuals.

In a later work, Pimental (1963) remarked that the percentage of resistant plants may increase with the increment of the pest's abundance. This consequently leads to a decrease of this abundance and thus to a weakening of the influence of natural selection on all the plants. Under the conditions thus altered, a selective predominance of non-resistant genotypes may appear and their abundance will once more increase leading to a repeated increment of abundance of the phytophage and to a a further recurrence of this cycle.

Pimental extends this model of automatic regulation not only to plants and phytophages but also to other pairs of the "necessary and necessitous", i.e. to systems such as parasite–host, predator–prey, etc. The theoretical arguments were thus supplemented with the results of experimental studies on the dependences which exist betweeen the housefly and its parasite, *Nasonia vitripennis* (Walker). Two populations of the fly and the parasite were reared together over a period of 3 years (80 generations). In the experimental colony the progeny of the same individuals of flies was preserved whereas in the control they were not. In neither the experiment nor the control was the population of the parasite renewed. In the experimental population there was an abrupt decrease in the fertility and longevity of the adult parasites, whereas the oscillations of the abundance of the fly were considerably less intensive and occurred on a lower level than in the control. This points to the existence of regulating mechanisms based on the rule of genetic feedback. The scheme of this mechanism is illustrated in Fig. 5.10.

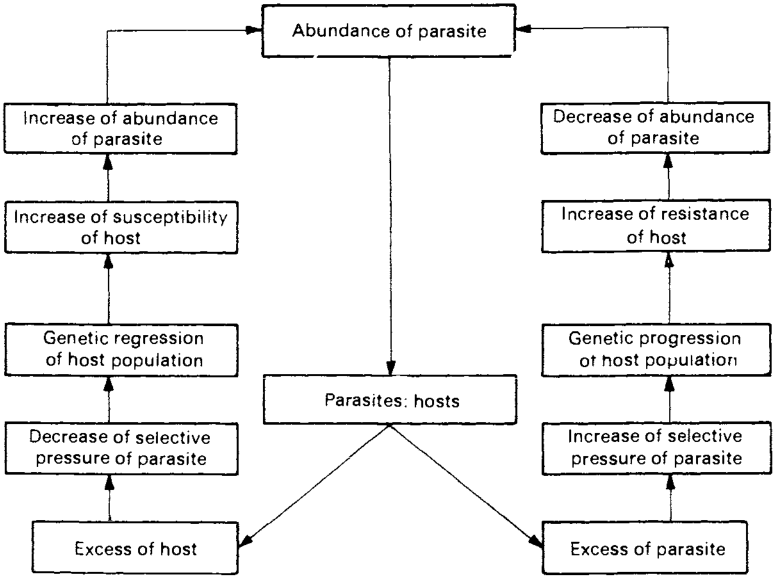


Fig. 5.10 Scheme of mechanism regulating abundance in the parasite–host system involving genetic feed-back (according to Pimental, quoted by Kiełczewski & Lipa, 1969)

5.2.6 Concept of modifying and regulating factors

Viktorov (1965, 1967) accepted the regulating nature of changes in abundance and endeavoured to eliminate the ambiguity of the terms "density-dependent and density-independent factors". Instead he proposed a new classification, distinguishing between factors which modify and those which regulate. Modifying factors evoke casual changes in abundance which subsequently stabilize at the mean level of abundance due to the feedback action of the regulating factors.

In view of the high consistency of Viktorov's concept it will be described in detail here, together with the author's discussion of the concepts given above.

Viktorov classifies meteorological conditions into those directly and indirectly influencing the insects through their biocenotic associations with the group of modifying factors. These factors cannot react to changes in the density of populations, i.e. they cannot act according to the rule of feedback.

Regulating factors include biotic factors which are represented by living organisms capable of reacting to changes in the density of their own population as well as that of other species with which they remain in mutual association. This does not mean, however, that all biotic agents act as regulating agents. For instance, polyphagous parasites which have different hosts in successive generations may act as modifying agents on some of these hosts, particularly when the abundance of any of these is high.

Modifying factors are important when discussing the problem of the causes of changes of abundance as well as in the prediction of outbreaks, whereas regulating factors are important when considering the possible ways to reduce the density and the intensity of changes of abundance. Their respective influences will be discussed below.

Viktorov suggests the acceptance of the scheme of the general rule of modification and regulation of the abundance of insects as presented in Fig. 5.11. The density of the population is expressed in this scheme by the ratio of processes increasing and those diminishing the number of individuals. All of the factors concerned with the dynamics of abundance affect these processes by altering the reproductive potential, mortality and migrations of individuals. The influence of modifying factors of the abiotic environment acts both directly and indirectly through food, natural enemies and pathogens, i.e. by means not related functionally to the population's density. This density is regulated by the existence

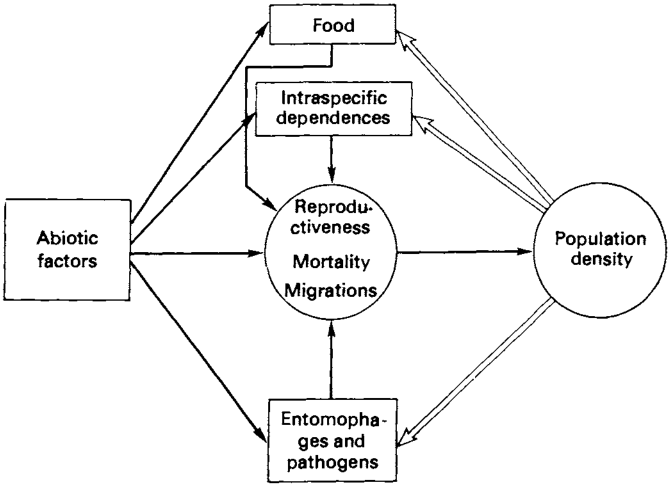


Fig. 5.11 General scheme of dynamics of insect abundance according to Viktorov (1967). Explanations in text

of feedback systems (denoted in the diagram by double arrows) expressing the influence of the population density on reproductive potential, mortality and migrations. This influence acts both directly and indirectly by means of intraspecific dependences, as well as changes in the activity of natural enemies, pathogens and food properties. Such feedback systems secure the occurrence of compensatory changes which supplement and reduce the population abundance and neutralize any accidental deviations from its mean density.

The diagram unequivocally indicates that the mechanisms regulating abundance belong to the type of regulators which are directed by chance, i.e. by deviations of the regulated population density value itself. According to the rules of cybernetics, such regulators cannot be decisive, i.e. they cannot secure an adequate stability of the regulated value. Moreover, the effect of their action is generally delayed and this concerns not only the abundance reaction of entomophages, but also the properties of intraspecific regulating mechanisms. The fact that the population density varies as a result of both external factors and autonomic changes conditioned by the delayed influence of regulating mechanisms (e.g. biocenotic regulators and intraspecific competition), is the result of the influence of regulating mechanisms described above.

Another specific feature of the mechanisms regulating the abundance of insects is their one-sided influence. In most cases the regulating processes only actively limit the increase of abundance, whereas the inhibition of the decrease of abundance takes place passively because of the weaker influence of regulating mechanisms.

Viktorov illustrates some properties of regulating mechanisms by means of a mathematical model in which the abundance of insects in a given generation is denoted by N_{t+1} and that in the proceeding generation by N_t. The value of N_{t+1} is then found using the following formula:

$$N_{t+1} = N_t P (1-M_1)(1-M_2),$$

where P = the mean fertility per individual, M_1 = the mortality due to modifying factors, M_2 = the compensatory mortality due to regulating factors.

If the abundance of the population in two successive generations were the same, then $N_{t+1} = N_t$ and $P(1-M_1)(1-M_2) = 1$. Thus the value of M_2 may be found, as given by:

$$M_2 = 1 - \frac{1}{P(1-M_1)}.$$

This is the equation of a rectangular hyperbola indicating that there should be an inversely proportional dependence between M_1 and M_2 in order to maintain a stable abundance of the population.

By accepting various values for P, a series of hyperbolas can be obtained as presented in Fig. 5.12. They express an ideal case of the regu-

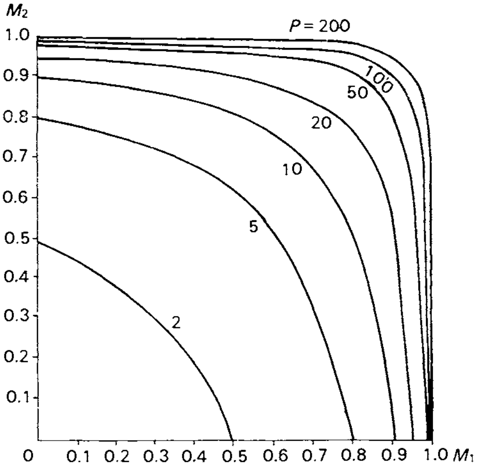


Fig. 5.12 Conditions of activity of regulating mechanisms at various values of mortality due to modifying factors (after Viktorov, 1967): M_1 – mortality due to accidental (modifying) factors, M_2 – compensative mortality due to regulating factors, P – fertility (mean per 1 individual)

lation of abundance in which the regulating action completely compensates for any oscillations in mortality due to accidental factors.

Such a scheme is never realized in nature but it can be useful for the elucidation of some basic problems of he dynamics of the size of populations.

It is apparent that there invariably exists a definite upper range of changes of M_1 which, if exceeded, cannot be compensated for by changes of M_2. The extent of this range diminishes progressively with the decrease of fertility. It is also important that at high values of M_1 any small increments (about several per cent) should be accompanied by large changes of M_2 amounting to several dozen per cent. This indicates that in the case of high mortality due to abiotic agents, the regulating mechanisms should exercise a particularly intensified or reduced influence on population density. The converse situation arises when mortality due to casual factors is low. In this case even very large changes of M_1 may be compensated for by small changes of M_2.

This regularity fully accords with the views of many ecologists concerning the fact that insect populations are characterized by a high instability on the periphery of their range of occurrence as well as in temperate regions. On the other hand, under the conditions found in natural humid tropical areas this stability is considerably higher. It also became obvious that changes of mortality (expressed as percentages) result in disproportional population effects depending on the level of mortality. For instance, changes of 1% at a mortality exceeding 90% have a stronger influence on the coefficient of reproduction than the same 1% at a low mortality level.

This model also indicates that a decrease of the reproductive potential is only possible when the resistance of organisms to abiotic and biotic mortality agents is increased. The influence of reproductive potential on the regulation of abundance is not so obvious. The more winding course of the curves when there is a decrease in fertility within the range of low mortality due to casual factors, indicates that in this case more rapidly acting regulators of abundance founded on intraspecific dependences are necessary for the preservation of a stable abundance.

Individual mechanisms which regulate the insect abundance exhibit their influence within various ranges of population density (Fig. 5.13).

Polyphagous entomophages are characterized by a low activity threshold, as well as a reduced level of activity in general. It was established that the percentage of larvae of some noxious forest *Lepidoptera* eaten by birds increases in proportion to the increase of density of the pest's population, but only at low values of this density and only up to a definite range, beyond which it decreases (Klomp, 1958). Thus the predaceous role of birds and many arthropods (e.g. spiders) is effective

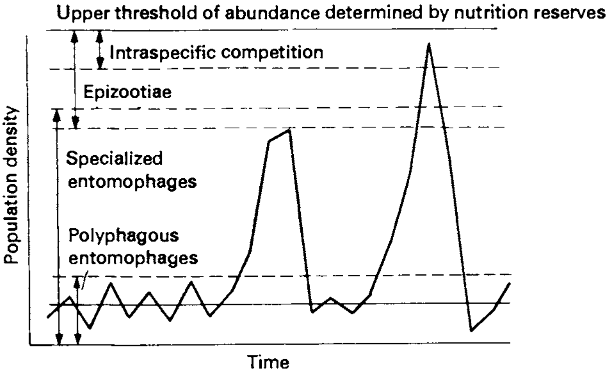


Fig. 5.13 Regulation of insect abundance in various ranges of population density (after Viktorov, 1967)

only at low levels of the pest's density. The limitation of the range of activity of polyphagous entomophages is due to their inability to react to the abundance of their prey.

It seems that specialized parasites and predators are both characterized by equally low activity thresholds. Their functional reactions occur at low population densities of the host or prey and these, of course, under such conditions also bring the abundance reaction into effect. This fact has been confirmed by the capacity of specialized entomophages to regulate the abundance of insects at low levels over long periods, as is well known in the practice of the biological control of pests. Flanders (1962) remarked that this property is possible in the case of *Hymenoptera*, for example, because they can complete their development in a single host individual, are capable of finding their hosts, are able to discern healthy host individuals from those already infected and can regulate the number and sex of eggs laid depending on the size of the host.

On the other hand, specialized parasites and predators, as compared with polyphagous species, may increase their abundance parallel to the increase of density of the host population. For this reason their regulating role encompasses a considerably wider range of values of the population densities of their hosts or prey. This is confirmed by many well known cases of the inhibition of outbreaks of phytophagous insects by specialized entomophages.

Pathogenic microorganisms are characterized by a high activity threshold. Frequently the epizootics evoked by these organisms develop at the period when the population of the pest approaches the moment of exhaustion of the food stock which affects the physiological condition of individuals.

The influence of intraspecific competition is initiated at the abundance level of the pest at which food becomes short and the individuals begin to starve and exercise pressure on one other. The increased frequency of contacts between individuals may become a signal evoking the appearance of definite regulating mechanisms. Such an adaptation, which naturally exhibits a considerably lower activity threshold, is able to prevent the increase of the population prior to the exhaustion of food.

The regulation of insect abundance takes place by means of an entire system of mechanisms successively brought into action in cases when the density of the regulated population exceeds the range of activity of the former regulator. In view of their higher stability such systems are termed ultrastable in cybernetic jargon.

Many facts point to the existence of such mechanisms. Outbreak of *Gilpinia hercyniae* (Hartig) in Canada has been inhibited by a virus disease. After being thus decreased the abundance is regulated at a low level by the parasites *Drino bohemica* Mesnil (*Tachinidae*) and *Exenterus vellicatus* Cushman (*Ichneumonidae*), which are particularly susceptible to even weak and short-lasting changes in the density of the host population. These parasites and the virus constitute an almost ideal system of abundance regulation.

In Switzerland it has also been observed that outbreaks of *Zeiraphera griseana* (Hübner) disappear under the influence of virus disease and starvation of the larvae followed by the action of parasites.

Viktorov disagrees with the opinion of various authors, particularly with that of Milne, concerning the inadequacy of parasites, predators and pathogenic organisms in the regulation of abundance of insects. He claims that the influence of these useful organisms depends to a large extent on weather conditions and that their requirements concerning these usually differ from those of their hosts and prey. These facts cannot serve as arguments for the conclusions that the regulating importance of entomophages is negligible. On the contrary, they indicate that the regulating role of these agents is limited by definite conditions, as is the role of intraspecific competition.

Finally, the defects in the influence of individual regulating mechanisms are compensated for by the successive action of each mechanism at various levels of the population density of noxious species. The weakened effect of parasites and predators attacking the insects during their early developmental stages may thus be compensated for by entomophages attacking the pest at a later stage in its life-cycle.

Viktorov is right in stressing that our present concept of the dynamics of insect abundance is based on the knowledge of this process in insects which exhibit outbreak tendencies, i.e. those disposing of the least effective mechanism regulating their abundance.

The elaboration of the course of the dynamics of insect abundance when maintained at low levels of abundance is indispensable for the knowledge of this problem. Fragmentary data in this respect indicate that their quantitative regulation is based not on a high number of enemies, but on several highly specialized ones securing a continuous and intensive infection of the host.

Factors determining the course of changes in abundance

5.3 Undirectionally acting (random) factors

Among those factors which may be described as having a random effect, meteorological conditions are the most important. Authors of various opinions regarding the dynamics of insect abundance are in agreement here. As stated above, temperature, precipitation and air humidity, etc. have a significant influence on the rate of development, fertility and longevity of insects, as well as on other parameters of life functions. The indirect influence of meteorological factors on food and on the variation of the activity of natural enemies, etc. also plays an important role in the dynamics of population abundance. From this standpoint Rubtsov (1937, 1938) rightly introduced the notion of a physiological and synecological development optimum. The latter represents the complex of conditions which leads to mass reproduction in a given species (such conditions not necessarily corresponding to those most favourable for that species) and which ensures the physiological optimum of reproduction.

The indirect influence of meteorological factors has been comprehensively presented in the gradocene scheme, in which none of the individual factors of the dynamics of abundance can be correctly evaluated if other factors and their mutual cooperation are not taken into account.

This leads to the conclusion that the consideration of the population and its quantitiative dynamics is possible only in terms of the biocenosis and not in isolated systems.

5.3.1 Direct influence of meteorological conditions

The direct influence of meteorological conditions may be realized either in a continuous, non-mechanical or an interrupted mechanical way. The former case concerns the influence on insects of factors such as temperature and air humidity. The synchronization of the mass appearance of insects with periods of drought and hot summers is a well known observation. Only extreme deviations from their usual occurrence and abnormal outbreaks lasting for many years are of significance. Analogously deviations unfavourable for insects may reduce their abundance.

A negative direct influence of meteorological conditions appears in the form of mechanical discontinuous action. Strong precipitation, winds and other similar phenomena may be classified here. Rains inundate the niches of xylophages and kill delicate insects which could not find shelter, whereas winds capture insects in flight and carry them to bodies of water, etc.

5.3.2 Indirect influence of meteorological conditions

Changes in the condition of host plants. The feeding conditions of phytophagous insects may undergo various, more or less essential changes due to the influence of the weather.

In the most simple case, weather can determine the degree of the correspondence between the phenology of the insect and its host plant. Phenomena of such coincidence have been considered by Thalenhorst (1951) and recently its consequences have been illustrated using the example of the course of population abundance in *Tortrix viridana* (L.). The coincidence of the spring hatching of caterpillars with the development of buds on oaks plays an important role in the dynamics of the abundance of this species. The degree of coincidence distinctly changes according to the course of the weather, which may be either the main cause of an outbreak or the reason for its breakdown. In 1962, in the Experimental Forests of the Agricultural University of Warsaw, for example, the particularly warm March caused the caterpillars to hatch early and they thus subsequently perished from cold and lack of developed oak buds.

An even more important role in the dynamics of the abundance of phytophagous insects is played by the physiological condition of their host plants. This dependence has been known for a long time in the case of secondary pests but it has now been extended to species feeding directly on the assimilative apparatus.

This phenomenon has been discussed above in Chapter 3 devoted to trophic relationships. Here we shall discuss the influence of the physiological condition of trees on the density of populations as elaborated by Schwenke (1963) (Fig. 5.14).

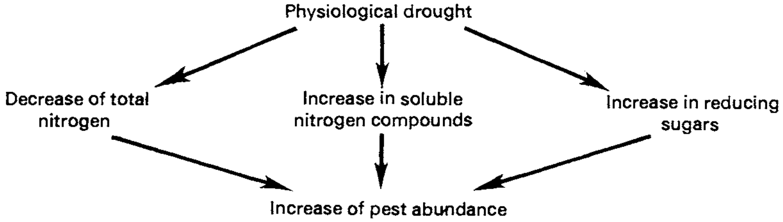


Fig. 5.14 Scheme of influence of nutrient factors (physiological condition of host plants) on the population density of foliophages (after Schwenke, 1963)

According to Schwenke, an inverse effect is obtained when soil water conditions and fertilization are improved, although, on the other hand, Merker (1961, 1963) points to the direct limiting influence of calcium and nitrogen introduced into the soil on insects feeding on leaves.

The influence of the physiological condition of trees on the factors which bring about increases in the numbers of insects is indisputable although it may be manifested in various ways according to the species of host plant and phytophage under consideration. The weakening of forest trees makes them more susceptible to insects which feed on their leaves and needles but, according to some authors, it causes a decrease in the abundance of aphids sucking the plant tissues. This problem requires further study.

It should be remembered that the influence of the host plant on insects may be masked by the action of other agents. For instance, the increased activity of predators due to the increase in the population density of *Lachnus* (Burmeister) (*Aphidoidea*) feeding on spruce, completely compensated for the stimulating effect of fertilization (Thalenhorst, 1964).

Changes in the activity of natural enemies. Differences which occur in the ranges of tolerance to abiotic factors of phytophagous insects and their natural enemies render the former susceptible to the indirect influence of weather conditions on their abundance. This has been confirmed by numerous laboratory and field observations. Thus a complex of meteorological conditions more favourable for the phytophage than for its parasites or predators may be the cause of occurrence of outbreak processes. The synchronization of definite development phases of the host and parasite determined by weather is also important.

Kadłubowski (1965) reported a lack of synchronization of the development cycles of *Trichogramma embryophagum* Hartig and its host, *Acantholyda posticalis* Matsumura = *nemoralis* Thomson). Owing to the development of mechanisms adapting it to its host, the adults of *T. embryophagum* usually appear during the periods of mating and oviposition of *A. posticalis.* Over a 4-year observations period, in only one year did the flight of *T. embryophagum* occur three days after the accomplishment of mating in its host and even the development of the eggs of the latter in the tree crowns was considerably advanced at this period. In this year (1962) temperatures remained below 12.5°C between the end of April and the beginning of June. This prevented the activity of *T. embryophagum* but did not impede oviposition in *A. posticalis* and thus only 15.5% of the host's eggs were infested. On the other hand, in 1964 *T. embryophagum* infested 89.3% of the host's eggs because the flight of this species and the oviposition of *A. posticalis* occurred exactly at the same time.

5.3.3 Cyclic character of culmination of outbreak phenomena

As mentioned above, the periodicity (usually every 11 years) of the culmination of outbreaks of many insects led to their being ascribed to changes in the activity of the sun, but in the light of both the earlier and recent literature the facts are not convincing. No such a dependence was observed in *Choristoneura murinana* (Hübner), the outbreaks of which occurred asynchronously in various parts of its geographical range (Franz, 1940, 1941), nor in *Panolis flammea* (D. & S.), *Bupalus piniarius* (L.) and *Dendrolimus pini* (L.) (Schwerdtfeger, 1941; Fig. 5.15). Even Vorontsov's (1962) work shows that over the last 100 years on the Russian Lowland there were ten outbreaks of *Lymantria dispar* (L.), eight of *B. piniarius,* seven of *Malacosoma neustria* (L.) and three of *Diprion* sp. and this indicates a lack of the dependence sought for.

This does not necessarily mean that this dependence cannot exist at all. It may occur, for example, particularly in gregarious, migrating locusts

Fig. 5.15 Caterpillars of *Dendrolimus pini* (L.) (photo by W. Strojny)

and also, perhaps, in *L. dispar* and *Barbitistes constrictus* Brunner von Wattenwyl. Further studies are, however, necessary in order to establish whether the 11-year cycles of peak abundance which sometimes occurs in certain species correspond to the 11-year cycle of solar activity and whether the regularity of the oscillations in abundance are determined, not by external agents, but by the mutual influence of organisms. Mathematical calculations based on the formula of Nicholson & Bailey (1935) indicate that intervals between peaks of abundance should fall to every 6–11th generation (Ohnesorge, 1963, 1964). In insects with a 1-year generation this would result in a value approximating to the 11-year cycle.

For these reasons the rhythm of the Sun's activity cannot at the moment be included among the factors which modify the abundance of insects, although the last word has in no way been said in this respect.

5.4 Factors acting (regulating) according to the rule of feedback

5.4.1 Types of mechanisms regulating abundance

Klomp (1964), who studied the population dynamics of *Bupalus piniarius* (L.), distinguished between the following mechanisms of regulation:

I. Regulation through interaction with organisms of another kind other than food.

II. Regulation through interaction with organisms on the same kind.

i. intraspecific competition for a limited requisite, e.g. food stock;

a. the degree of depletion of this requisite and not its quantity produced is influenced by its competitors,

b. both the degree of depletion and the quantity of the requisite are determined by the competing organisms;

ii. self-regulation or mutual interference: no requisite is in short supply, but mortality, reproduction or emigration are influenced by density-dependent mutual interference due to intolerance of crowding.

III. Regulation through modification of environment, e.g. the formation of cork cambium by the host plant as a protection against aphid feeding.

IV. Regulation through a genetic feedback mechanism.

In his discussion regarding this classification, Viktorov (1967) rightly claims that all of the various regulating mechanisms are essentially confined to the reaction of organisms to the density of their own population or to that of the populations of other organisms with which they remain in mutual association.

Two main groups of regulating mechanisms may thus be distinguished – intraspecific and biocenotic. The latter may also include the mechanism of genetic feedback, consisting of genetic changes in populations of organisms belonging to neighbouring trophic layers and having a direct influence upon one another.

As has already been shown, a necessary requirement of the regulation of abundance is the existence of both separate populations and the entire biocenosis of which they are a part.

5.4.2 Intraspecific regulating mechanisms

Direct influence of density of the population on its individuals. Excessive population density is always detrimental to individual organisms. An excessive increment of density leads to a decrease of the size and fertility of individuals, as well as to a higher mortality of larvae and pupae, to changes in the rate of development and to quantitative changes in the sex ratio.

On the other hand, however, changes in the sex ratio due to conditions of high population density do not occur in insects exhibiting a chromosomal or accidental sex determination and heterogametic males. Such insects include most *Diptera* and *Coleoptera* in which the increase of the population density does not influence the quantitative sex ratio. On the other hand, such a dependence does occur in insects in which the determination of sex is the result of the females being heterogametic, as in *Lepidoptera*, in which the percentage of females diminishes in linear dependence on the population density. An analogous situation is observed in parasitic *Hymenoptera* in which sex determination is not chromosomal but accidental.

The mechanism influencing the determination of the sex of the progeny in favour of males may have a physiological basis since, at high population densities, females do not lay all of their eggs due to various factors, such as the absence of a host. The non-laid eggs are resorbed by the female resulting in an abnormal functioning of the sex-determining mechanisms. The increased proportion of males may also be due to food deficiency which causes a higher percentage mortality of the future females since these require more food than larvae of males.

Cannibalism, migration and an increase in the number of individuals remaining in diapause are further intraspecific regulating mechanisms.

Cannibalism occurs only at high levels of population density, and has been observed in detail in insects living in the soil (grubs of *Melolontha* sp.) and in those living in stored products.

The migration of individuals of a given population is sometimes stimulated by the population density or by food deficiency. This has been observed during the formation of migratory gradation foci of primary pine pests and the migration of predaceous *Carabidae* to neighbouring

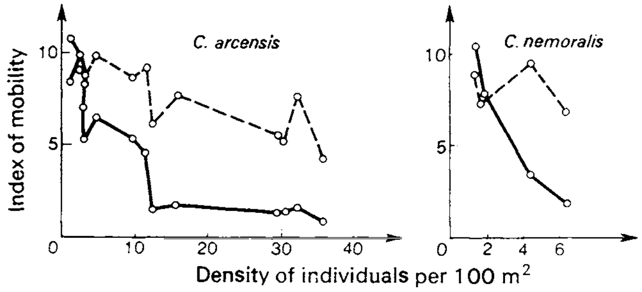


Fig. 5.16 Mobility of *Carabidae* against the background of the stock of food in forest environments and density of individuals (after Grüm, 1971): dashed line – hungry individuals, continuous line – satiated individuals

biotopes in their search for food (Fig. 5.16). *Carabidae* exhibit a higher mobility when hungry than when well-fed and this difference increases with rising population density. With this in mind, it is interesting to note that in aphids winged individuals capable of long-distance migration develop in overdensitied colonies.

An increase in the number of individuals in diapause under conditions of high population density has been observed in *Lepidoptera*, *Coleoptera* and *Hymenoptera*.

In cases when the density of the population is not limited by regulating mechanisms, the regulation is manifested in the form of an increased mortality of the progeny. Jamnicky (1962) quoted the following example on the influence of population density on the mortality of progeny in *Leperisinus fraxini* (Panzer).

Number of galleries per 2 dm^2 of ash-tree stem surface	8	15	20	25	29	36	45	55	60
Mortality of larvae, %	1.9	3.1	35.3	38.4	40.2	46.1	47.2	61.1	78.6

It was observed that when the number of maternal galleries of this borer exceeded 60 per 1 dm^2, the abundance of the subsequent generation was lower than that of the parental one due to the increased mortality of the larvae.

There is less data available regarding the role of intraspecific relationships in noxious insects feeding in forest tree crowns.

Indirect, reversible influence of density of the population on its individuals. Besides its direct influence on mortality and other developmental indices of insects, the population density may also exercise a reversible effect on the population. Thus insects react to the presence of other similar individuals in a way which leads to a decrease of the population density prior to the occurrence of food deficiency. This protects the population against acute intraspecific competition.

Such a case was observed in females of *Dahlbominus fuscipennis* (Zetterstedt), a species parasitic on *Diprion* sp. An increase in the population density of this chalcid leads to a decrease of the number of eggs laid by each female and of the number of infected hosts, thus the full egg potential is not fully realized.

It has been observed that in many parasites the adults of which feed on the body fluids of the host, any decrease in population density is accompanied by an increased percentage of adult host individuals utilized as food by the adult parasites and by a decrease of the proportion of those infected by the parasites' eggs. This inhibits the rate of reproduction of the parasites. The phenomenon described is not, however, the result of intraspecific competition but is the effect of the density of population on its individuals.

The role played by population density in the occurrence of phasic variability of *Locusta migratoria* L. is the most outstanding example of this phenomenon. It appears that the abundance of this locust does not depend on its phasic condition, but that the phasic condition is associated with the population density and constitutes a mechanism serving to regulate abundance.

The visual stimulation of individuals of the solitary phase (*phasis solitaria*) occurring at high levels of density leads to the gregarious phase of the locust which was once regarded as a separate species due to its completely different morphological appearance. *L. migratoria phasis gregaria* is characterized by a tendency to distant collective migrations as well as by a decreased fertility, increased mortality of young nymphs, higher rate of development and increased activity. These last mentioned characteristics can be safely regarded as mechanisms serving to regulate the abundance of this species.

Similar phenomena have been observed in some noctuid moth as well as in *Exaeretia ulmi* (D. & S.) which has four different types of larvae. One of them, corresponding to the gregarious phase of the locust and observed only in outbreak foci, is distinguished by a bright green colour with dark stripes and spots on the body. Two other larval forms are characteristic of less dense populations and their colour resembles that of tree leaves and bark. The fourth form is intermediate between those described above. In breeding experiments, the gregarious form was manifested under conditions of high population density. Hence Sharov (1953) advanced the theory that the transition to the gregarious stage is determined by the mutual influence of individuals and not by favourable weather conditions, i.e. the phasic changes are the result and not the cause of changes in abundance.

Novikova (1969) advanced an interesting concept regarding the phasic nature of the development of *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson). She established the occurrence of two forms of this species in the Buzułuk Coniferous Forest. Gradual changes in the proportions of each of these forms in outbreak foci exhibit a regular character and characterize the changes in the phases of development of the focus. The form characterized by later mating prevails in developing and active foci whereas the early form prevails in disappearing foci. This is because the late form exhibits a higher predisposition to rapid reproduction, due possibly to parthenogenetic development of the amphitoky type (i.e. either sex may be produced), with a predominance of females, whereas the early form prevails when there is competition for food between the forms. Since the population of the early form is more susceptible to the activity of natural enemies and abiotic environmental agents, it gradually decreases thus resulting in the disappearance of outbreak foci.

The appearance of the early form in growing outbreak foci under the geographical conditions considered may also be treated as an example of the internal quantitative regulation of the species.

It would also seem that Novikova had here extended the studies of Wellington (1957a, 1960) on *Malacosoma pluviale* Dyar. The latter author established that active colonies (consisting of active types of larvae and adults) prevail during the initial period of the development of outbreak foci, whereas the contribution of weak individuals (which also exhibit a weak spatial orientation) increases in subsequent years and persists until the abrupt decrease of the abundance of the population.

The two phenomena described here are associated with problems of genetic changes in the population, which act as a regulating mechanism and have became the basis of the concept of Franz and other authors.

The nature of these changes is distinctly different from that of the phasic changes in the population of the locust. The problem is, however, far from solved. It seems that the existence of regulating mechanisms founded on genetic changes in populations cannot occur on a wider scale because changes in abundance generally only involve few generations, whereas the regulating role of selection is only possible when selection pressure and population density are high and the process takes place over a sufficiently long period of time (Wilbert, 1963).

5.4.3 Biocenotic regulating mechanisms

Natural enemies. Natural enemies can react in three ways to changes in the population density of their prey. This response may be functional, numerical or aggregate. The functional, or individual, response consists of an increase in the number of individuals attacked by parasites or predators with the increase of the population density of the victim. The numerical, or intergeneration, response is the increase in the abundance of the natural enemy resulting from an increase in the abundance of the victim. This response is due to the enemy's higher reproductive capacity and to its increased chances of survival. The aggregate response consists of the immigration of the enemy into the outbreak zones or other sites of excessive prey or host density.

There are three principal types of functional response (Holling, 1959 quoted after Dempster, 1975). The first occurs when the number of individuals killed by a predator increases in direct proportion to the density of the prey population (curve 1 in Fig. 5.17). The second concerns cases in which the abundance of the attacked victims rises abruptly along with the initial increase in their population density, and then stabilizes

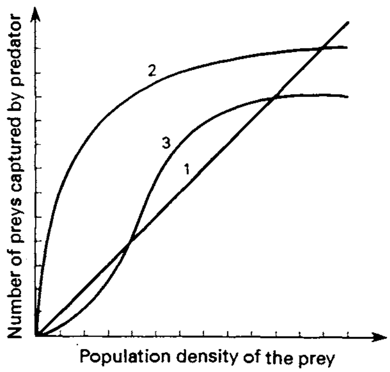


Fig. 5.17 Three kinds of functional response of predators to changes in the population density of their prey (according to Holling, 1959, quoted after Dempster, 1975); explanations in text

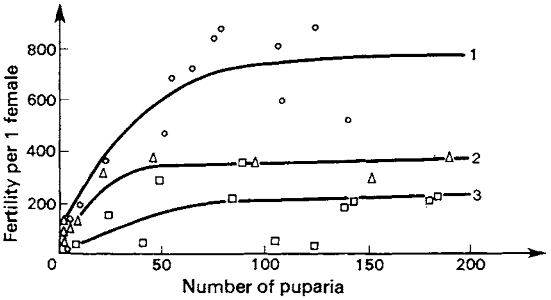


Fig. 5.18 Dependence of the number of progeny of one female of the parasitic chalcidoid *Nasonia vitripennis* (Walker) on the total number of fly puparia accessible to her (after Viktorov, 1967): 1 — *Calliphora vicina* (Robineau-Desvoidy), 2 — *Phormia terraenovae* (Robineau-Desvoidy), 3 — *Musca domestica* (L.)

at a certain level determined by the specificity of the predator/prey or parasite/host relationship (curve 2 in Fig. 5.17 and Fig. 5.18). The third type of functional response may be illustrated by the S-shaped curve representing the mutual relationship between the density of the prey or host population and the number of individuals attacked by predators or parasites in that population (curve 3 in Fig. 5.17). This type of functional response has been observed in small mammals feeding on the cocoons of *Neodiprion sertifer* (Geoffroy) found in litter (Fig. 5.19) as well as in some predators and parasites of *Operophtera* (= *Cheimatobia*) *brumata* (L.). However, the nature of this response has not yet been fully interpreted. In small mammals it may be associated with their habit of storing of the cocoons and feeding on them later.

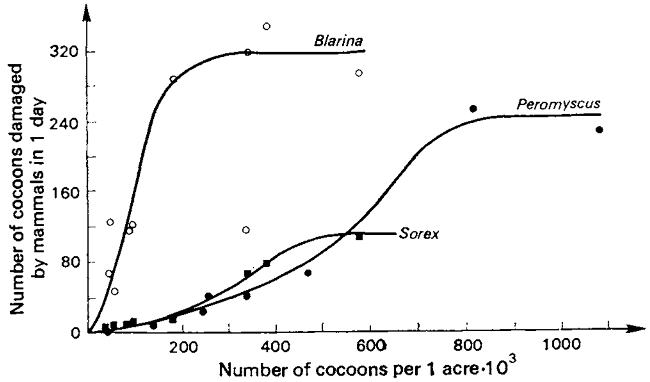


Fig. 5.19 The effect of host density on the number of *Neodiprion sertifer* (Geoffroy) cocoons taken by small mammals (according to Holling, 1959 quoted after Dempster, 1975)

The second type of functional response is the most frequently encountered and the best understood. It involves an increase in the number of eggs laid by one female and a decrease in their number per host individual, these two phenomena resulting in a distinct increase in the number of hosts attacked (Fig. 5.20). For example, during a field experiment, cocoons of *Neodiprion sertifer* (Geoffroy) were uniformly distributed over an area of 2.3 cm^2 into which 100 females of its parasite *Dahlbominus fuscipennis* (Zetterstedt) were introduced. The cocoons were collected after 18–20 hours and the number of eggs laid by the parasite counted. The experiment was repeated with varying numbers of cocoons. Table 5.1 shows that both the number of eggs produced per female parasite and the number of infested cocoons increased with the increase of the density of the host population.

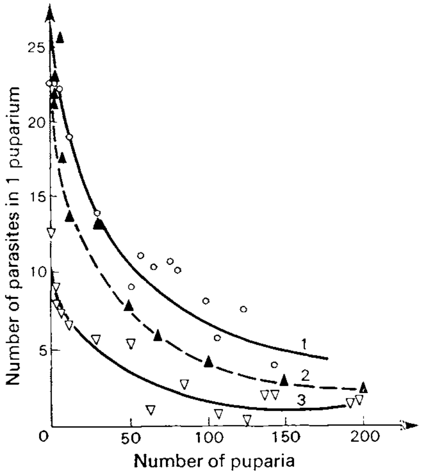


Fig. 5.20 Dependence of the number of individuals of the parasitic chalcidoid *Nasonia vitripennis* (Walker) in one puparium of the host on the total number of puparia accessible to one female of the parasite (after Viktorov, 1967): 1 – *Calliphora vicina* (Robineau-Desvoidy), 2 – *Phormia terraenovae* (Robineau-Desvoidy), 3 – *Musca domestica* L.

Further examples of similar functional responses in predators are quoted in the literature.

Functional responses play a significant role in the regulation of the dynamics of insect abundance since their intensity depends on the density of the victim. This peculiarity of the response is particularly distinct when a stable abundance of both the parasite and the host is maintained

Table 5.1 Influence of density of cocoons of *Neodiprion sertifer* (Geoffroy) on the intensity of reproduction of 100 females of its parasite — *Dahlbominus fuscipennis* (Zetterstedt) (according to Burnett, 1954, after Viktorov, 1967).

Number of host individuals per 2.3 m²	Mean number of infected host individuals at temperatures			Mean number of eggs laid by females of the parasite at temperatures		
	below 17.5°C	17.5–24.0°C	above 24°C	below 17.5°C	17.5–24.0°C	above 24°C
16	3.4	4.6	4.0	67.4	93.2	95.0
25	4.8	7.2	9.5	86.0	158.9	328.0
49	8.6	10.7	14.0	168.6	280.1	285.5
100	12.2	18.2	17.5	226.2	437.8	434.0
196	17.4	27.3	27.5	348.6	573.9	700.0
400	24.0	41.4	65.5	512.4	908.8	1933.0

in the experiment while the density of their populations is altered by reducing their area of occurrence. The higher the density of the host population, the more pronounced is the increase in the number of infected hosts. In all known cases of the second and third type of functional response, the increase in the number of individuals of the prey or host destroyed or infested by one individual of the entomophage decreased as the density of the victim population increased and then stabilized at a level characteristic of the species-pairs of host/parasite or prey/predator concerned. From this we can deduce that the regulating role of the reaction considered is confined to a small range of density changes at low population levels.

To facilitate the distinction of the three types of functional response, the dependence between the population density and the percentage of individuals killed by predators or parasites is illustrated for each case in Fig. 5.21. Curve 1 (first type of functional response) indicates a stable percentage of mortality at various levels of density of the population; curve 2 (second type of functional response) shows that the percentage of mortality decreases with the increase of population density, and curve 3 (third type of functional response) indicates that mortality is at first directly dependent on density but when the peak has been reached the dependence becomes inverse.

The functional response has a positive influence on the rate of reproduction of entomophages and therefore predisposes the entomophage's population to the numerical response.

The existence of the numerical (intergeneration) response has never

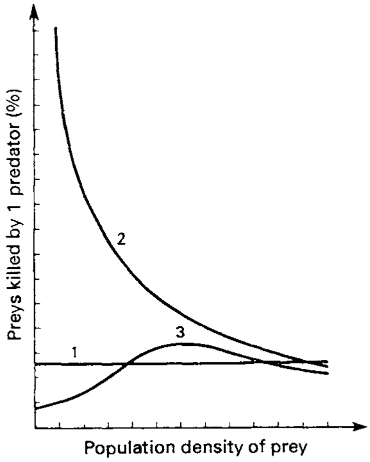


Fig. 5.21 Mortality of the prey due to predators acting according to the three kinds of functional response presented in Fig. 5.17 (according to Hassell, 1966, quoted after Dempster, 1975)

been doubted because it has been confirmed by numerous examples in which outbreaks of noxious insects have broken down due to the activity of entomophages as in, for example, the breakdown of the gradation of *Bupalus piniarius* (L.) in Poland in 1956 resulting from the mass reproduction of *Trichogramma* sp. Specialized entomophages which complete their life-cycle in a single host exhibit a particular predisposition to the numerical response.

Phenomena such as the mass migration of birds and other entomophages into outbreak areas should be classed as aggregate responses. Such a response limited the outbreak of *Panolis flammea* (D. & S.) in the Kampinos National Park in 1972 when the population of this moth was extensively exploited by immigrating starlings.

Diseases. Epizootics evoked by pathogenic microorganisms have, in many cases, led to the breakdown and extinction of outbreaks. The principal organisms involved are viruses and bacteria which usually attack caterpillars and other larvae feeding on foliage.

The development of epizootics is stimulated by the increasing density of the phytophage population and invariably it is most intense during the peak of an outbreak. Pathogenic effects are rarely observed at low levels of abundance.

Increased population density stimulates the development of epizootics by facilitating the transfer of the pathogenic agent and by weakening the host individuals thus rendering them more susceptible to infection.

Cryptotransfer of viruses is very common in insects. The virus remains in a benign form in the population, being transferred from one generation to the next through the eggs. The development of its virulent form is enhanced by the action of various unfavourable external factors which weaken the hosts and provide conditions conducive to the spread of the disease. Temperature, humidity and precipitation play an important role here, as may the unsuitability of the food plant. The latter may be particularly significant when conditions of high population density cause competition for food and the consequent transfer of the phytophage to an unsuitable alternative host plant.

Reaction of the host plant. An example of the regulating role of the host plant in the population dynamics of phytophages is seen in the reaction of the fir to intensive feeding by *Adelges* (*Dreyfusia*) *piceae* (Ratzeburg) on its bark. The protein and polysaccharide content of the bark parenchyma is decreased by the adelgids, subsequently leading to the complete degeneration of the cells of this layer. The cambium tissue also degenerates to form a non-cellular solid layer whilst a new cambium layer develops in the deeper strata of the parenchyma. All cells lying above this layer gradually die and render feeding by the adelgids impossible, thus preventing any potential outbreak on that site. It should be remembered, however, that this reaction only occurs under conditions of very high densities of the pest.

Schwenke (1963) observed analogous situations in insects feeding on pine needles, whereby the cell content of sugars essential for the development of the pest were depleted by the pest itself due to intensive damage to the needles. Thus an increased density of the phytophage population can lead to the deterioration of its own food source and therefore act as a regulating mechanism.

Leśniak (1973) gives an interesting account of the regulative influence of the host plant on the population of *Dendrolimus pini* (L.). The homeostatic mechanism of the system discussed depends on the preference shown by the larvae for the older needles. When this source of food is exhausted, the larvae are forced to feed on young needles which are nutritionally unsuitable. This reduces the numbers of larvae to a level at which the population of the pest may be controlled by natural enemies. This allows old needles to develop, which again may lead to an increased abundance of the phytophage. Leśniak thus supposed that the zones of resistance of pine forest stands in Poland also had a different cycle of exchange of needles in the given area which may also have been modified by the activity of *Lophodermium pinastri* and other fungi accelerating this exchange. Another cause of a higher resistance of forest stands to outbreaks of *D. pini* may be the more rapid exchange of the needles on pines growing on richer sites.

As has already been mentioned, the study of the influence of food in the abundance of insects requires much more attention in order to elucidate the nature of the mechanisms involved.

5.4.4 Mechanism of genetic feedback

The essence of the mechanism of genetic feedback has been described above in the discussion of Pimental's opinion on the dynamics of insect abundance.

Viktorov (1967) criticizes Pimental's conclusions concerning the regulatory nature of the genetic feedback mechanism and claims that the quoted changes in quantitative proportions between the pair of species studied exhibit properties of an evolutionary and not regulatory effect. Only short-lasting and reversible changes of the genetic structure of the population may be considered as a regulatory effect.

According to Viktorov, the results of Takahashi's (1963) studies on the moth *Ephestia cautella* (Walker) and its parasite *Nemeritis canescens* (Gravenhorst) are more indicative of the existence of a genetic feedback mechanism, although this is also only a hypothetical view. The changes in the abundance of these species were studied over a 2-year period, as a result of which Takahashi distinguished between three main types. The first change, occurring over a period more or less corresponding to a single generation, was conditioned by the influence of the host individuals; the second was evoked by the mutual influence of the host and parasite and lasted for 2–4 generations, whilst the third, lasting for 10 or more generations, was associated with variations in the ecological properties of the host due to the selective action of the parasite. Changes of this last type, which may last for 8–12 generations, involve the inhibition of the rate of development and a change of the host's feeding sites, as well as its concentration in the deeper layers of the food substrate. They are not stable and disappear when the host's population is reared in the absence of the parasite for 3 generations, thus meeting the requirements of a regulating mechanism and, apparently, confirming the existence of genetic feedback.

6 Insects in forest biocenoses

Entomocenoses, associations and communities of insects

The variety of species occurring in a biocenosis is the basis of its existence since it entails the species' coexistence even though this may be of an antagonistic nature. The persistence of a biocenosis in time is due to the various relationships which occur between the organisms in that biocenosis and which form a complex structure of trophic, paratrophic and competitive interspecific dependences. Each species finds food and shelter from its enemies and holds a definite position in the functional and spatial structure of the biocenosis.

The position of a species in the functional structure of a biocenosis, i.e. its trophic level and environmental requirements is called its ecological niche. The concept of a niche extends into the dimension of time in that it takes into consideration the duration of development and adult longevity, etc. The position of the species in the spatial structure of the biocenosis is called its site niche.

Various authors have different views regarding the scope of the concept of the ecological niche. According to Tarwid (1953), the niche includes all the environmental factors essential to the given species (food, site of reproduction, oxygen conditions, temperature, periods of life activity, etc.). Since only some of the factors are of significance to the given species at different stages of its life-cycle, these selected agents will constitute its specific ecological niche differentiating it from other species in time as well as space. On the other hand, the ecological niches of various species may partly overlap as, for instance, when they share certain life requirements (e.g. a common food source or site of occurrence, etc.). Such species are said to form an association. The concept of competition with respect to the ecological niche strictly conditions the relationships between the association-forming species.

Forest insects constitute a fragment of the biocenosis, referred to as the entomocenosis, and form very characteristic associations and communities within the latter.

According to Petrusewicz (1936) each group of animals selected from any ecological standpoint constitutes a community. An association (cenosis) is a grouping of which the components are linked by biocenotic dependences. It is a closed community in which there is competition for definite environmental factors.

Thus an association should be characterized by the following features:
I. partial concurrence of the ecological niches of the species composing the association;
II. quantitative regulation;
III. characteristic quantitative structure, i.e. occurrence of dominating, subdominant (influent) and accessory species.

The concept of the internal regulation of an association suggests the occurrence of mutual dependences between the individuals which form the association and, consequently, of definite quantitative and qualitative proportions of the components of that association. According to the Warsaw school of ecologists, competition between the species comprising the association, and the influence of predators and parasites on its components are the most important factors evoking quantitative regulation.

Due to the existence of regulating phenomena, the association assumes a characteristic quantitative structure regarding the numerical contribution of the individuals of the various component species. In general, an association contains at least one, and sometimes several, predominant (i.e. abundant) species (dominants), several species of moderate abundance (subdominant species) and more or less accessory species characterized by a small number of individuals (Fig. 6.1). These three categories of the association are strictly dependent on one another. The concurrence of ecological niches gives rise to interspecific competition which differentiates the quantitative proportions of the constituent species of the association.

On the basis of the criteria given above, Kaczmarek (1953) described an association of forest ants, referred to as "*Lasius niger*", occurring in the pine forests of the forest district Łobodno. He studied the nests of small forms near those of larger forms and concluded that the distinct size difference of the ants should exclude competition between them due to the different pathways of food circulation. The food waste not utilized (owing to the high degree of comminution) by the larger forms accumu-

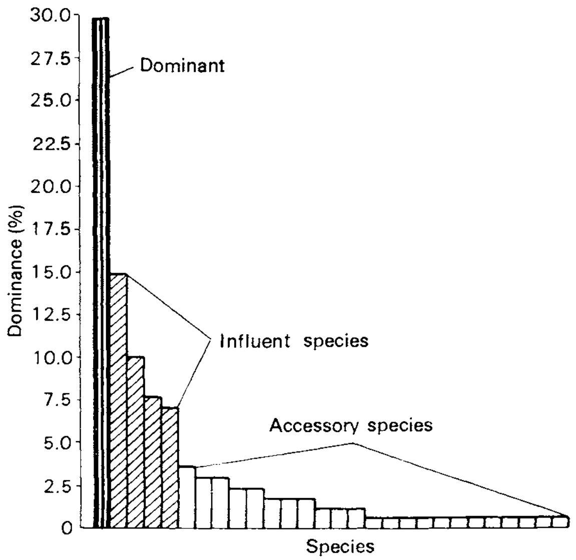


Fig. 6.1 Structure of dominance of an insect association or community

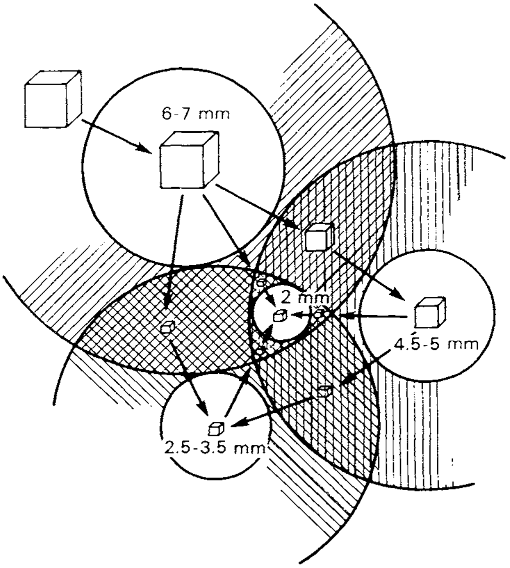


Fig. 6.2 Functional structure of the ant association "*Lasius niger*" (after Kaczmarek, 1953): The co-occurrence of ants is determined by the mode of food circulation. Food remains of species of larger body size are accumulated in their nest areas (shaded area) where they are utilized by smaller species which form an association competing for food

lates around their nests and is consumed by the smaller forms (Fig. 6.2). Kaczmarek thus claimed that the group of smaller species (*Stenamma westwoodi* Westwood, *Leptothorax acervorum* (F.), *L. muscorum* (Nylander), *L. nylanderi* (Forster) and *Tetramorium caespitum* (L.)) and the group of larger species (*Formica sanguinea* (Latreille and *F. rufa* L. does not form separate associations in the area studied. On the other hand, the species with moderate body size (*Lasius niger* (L.), *Myrmica rubra* (L.), *M. laevinodis* Nylander, *M. scabrinodis* Nylander, *M. sabuleti* Meinert, *M. lobicornis* Nylander, *M. schencki* Emery, *M. rugulosa* Nylander, *Formica fusca* L. and *Lasius fuliginosus* (Latreille) which compete with each other for food and space do form an association. In forest conditions this association is formed in April and disintegrates in October (Fig. 6.3). The degree of shading of the forest floor and the presence of *F. rufa* (L.) form the basis of the regulating processes within this association.

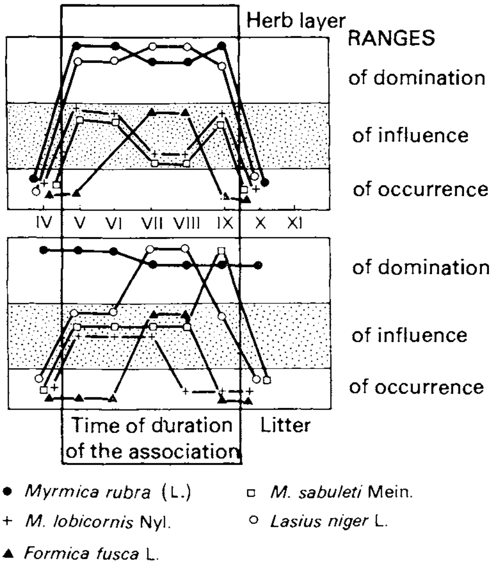


Fig. 6.3 Dynamics of the forest and association "*Lasius niger*" in the annual cycle (after Kaczmarek, 1953)

Studies on the forest entomofauna frequently demonstrate the existence of definite quantitative proportions between species inhabiting a given biotope (or a certain part of it), but merely describing the established structure of the dominant species is not sufficient for distinguishing an association. However, when the spatial relationships of the species studied within the biotope or the partial overlapping of their site niches are taken into consideration, it is possible to distinguish communities.

According to the definitions quoted above, it is evident that, in many cases, the associations of various insects which have been described in the literature are only communities. This is because the overlapping of the ecological niches of their species was not taken into account, and the animals belonging to other systematic categories which were competing with each other under the conditions of the given biocenosis and were actually influencing the quantitative proportions within the "association" were disregarded. This does not necessarily mean, however, that an association has no competitive connections with other associations of the biocenosis since this would contradict the very concept of the biocenosis as an indivisible whole.

In order to stress the narrow, often exclusively taxonomic sense of the concept of the association, Chodorowski (1960) proposed the introduction of a new cenotic unit, the taxocene. This may be defined as "a group of systematically related animals occurring in a definite environment and exhibiting a yearly recurring characteristic structure of dominance".

Synusiae are further examples of communities, i.e. of descriptive units of components of the biocenosis. According to Gams (1918), the author of this term, a synusia denotes a concrete local ecological community, the components of which depend on each other to a higher degree than on other components of the biocenosis. These groups of organisms (of various systematic categories) inhabit definite sections of a biotope. Depending on the quality and size of the section of the biotope occupied, synusiae have been assigned special terms of various rank such as stratocenosis, choriocenosis, connex, merocenosis and caryocenosis.

A stratocenosis is a grouping of species in a definite zone of the stratified structure of the biocenosis, choriocenosis denotes a definable small part of the biocenosis, whilst merocenoses are small groups of organisms inhabiting definite structures of living plants (e.g. flowers, fruits, leaves, etc.) and sharing by a common biocenotic regulatory influence.

Balogh (1958), on the other hand, preferred to use the term connex, which had already been introduced by Friederichs (1930). Connexes refer to organisms found in specialized or particularly defined habitats, such as pine stumps, fruiting bodies of fungi, vertebrate excrement, etc. Especially characteristic connexes receive special names, such as caryocenosis for the group of insects inhabiting decaying trees (Pawłowski, 1961).

Discussions concerning the concept of the synusia have indicated that it should not be applied to small groups of species which have developed as the result of direct historically established relationships between species. Such groups are called consortia and consist, for example, of flowers and their specific insect pollinators or hosts and their monophagous parasites. In general, a central organism with which other species are directly associated may be readily distinguished in a consortium. This central organism may be the host plant with respect to phytophages (and their parasites, predators, etc.) or the animal species in respect to its parasites. It is generally considered that in Central Europe most consortia developed in the Quaternary.

Insects constituting a part of the biocenosis may be denoted by the somewhat artificial term entomocenosis. Actually they may form communities of various categories, particularly those of the taxocene or connex.

6.1 Descriptive characteristics of associations and communities

6.1.1 Characteristics of quantitative proportions

Dominance. Dominance refers to the ratio of the number of individuals of the given species to the total number of individuals of all the species of the cenosis studied (entomocenosis, association or community) and is usually expressed as a percentage:

$$D = \frac{s}{S} 100,$$

where: D = dominance, s = number of individuals of the given species, S = number of individuals of all species of the cenotic unit studied.

Density of individuals. The density of individuals represents the mean number of individuals of a given species (systematic group) per surface unit of the area inhabited or per volume unit of the cenosis studied.

Density of mass. This is the mean total mass of individuals of a given species occurring per surface or volume unit of the habitat in the cenosis studied. The density of mass may also be determined by means of Haarlov's index, i.e. the mean product of the length and breadth of individuals of the given species multiplied by the number of individuals occurring per surface unit.

6.1.2 Characteristics of the structure of associations and communities

Frequency. Frequency is expressed as the percentage of the samples in which the given species occurred:

$$C = \frac{q}{Q}\,100$$

where: Q = number of samples studied, q = number of samples in which the species occurred.

Fidelity. Fidelity is an index of a synthetic character relating to domination and frequency and is the best expression of the degree of the association of individual species with the environment. It may be estimated or calculated.

The following classes of estimated fidelity are usually distinguished:

F_3 exclusive characteristic species, regularly occurring in the given environment, in others occurring casually as foreign elements;

F_2 selective characteristic species, most frequently observed in the given environment but also occurring in other communities;

F_1 associated species, occurring in the given community less frequently than in other environments or exhibiting no tendency to any community;

F_0 species foreign in the given environment (community).

The calculated fidelity is the ratio of the frequency of occurrence of the given species in the environment studied to the frequency of its occurrence in various environments (biotopes, patches of flora, habitat types of forest, etc.).

If, for instance, in biotope A the species X occurred 10 times, in B once, in C 0 times and in D 2 times then (for the same number of identical samples collected in each biotope) the fidelity of the species X in the biotope A is

$$F = \frac{A}{A+B+C+D} = \frac{10}{13} = 0.77 \quad \text{or} \quad 77\%.$$

Analogously, the fidelity of individuals of the given species (f) may be calculated. In this case the formula given above must be supplemented by the number of individuals. Thus, if in biotope A the species X was represented by 10×20 individuals, in B 1×2 individuals, in C 0, in D 2×2 individuals, then $f = \frac{200}{206} = 0.97$ or 97%.

Indices which allow the determination of differentiation of the community (association), on the basis of the distribution of individuals in the species and of the uniformity of this distribution, are important indices of the structure of community. These include the following:

I. *Index of diversity* (*of richness in species*) (Simpson, 1949)

$$d = \frac{S-1}{\log N}$$

where S = number of species in the community, N = total number of individuals in the community.

II. *Index of general specific diversity* (Shannon, 1948)

$$H' = -\sum_{i=1}^{S} p_1 \log_2 p_1$$

where p_1 denotes the fraction (n_i/N) of the ith species in the community, composed of S species, and n_i denotes the abundance of the ith species in the total number of individuals of the community (N).

III. *Index of evennessity* (Pielou, 1966)

$$J = \frac{H'}{\log_2 S}$$

expressing the "structure of dominance", where $\log_2 S$ denotes the maximum value attainable for the index H. This value is attained only when all the species in the community are represented by the same number of individuals.

6.2 Methods of comparison of cenoses and communities

Cenotic units may be compared by means of a number of mathematical formulae some of which will be discussed below. These are: Jaccard's number (similarity of species), Renkonen's number (similarity of dominance), Kulczyński's number (similarity of frequency) and some of the formulae extending the concepts of these indices.

The similarity of species of two cenoses is expressed by Jaccard's formula which can be expressed in the following two forms:

$$J = \frac{j}{a+b-j}\,100 \quad \text{and} \quad J = \frac{j}{a+b}\,100$$

where: J = coefficient of similarity, j = number of species common for both areas,

a and b are numbers of species on areas A and B respectively.

The first formula represents the number of species common for the areas (communities) A and B, expressed against the total number of species varying on these areas. Thus, the value of the coefficient is higher when a greater number of common species occur in both areas than when more species occur in only one area.

In the second formula, which represents the ratio of common species to the total number of species in both areas, the value of the percentage coefficient diminishes in dependence on the total abundance of the species found and this, of course, depends on the size of the samples.

The application of both formulae may lead to misunderstandings. When two samples are compared from within the range of one definite environment by means of the first formula, the value of the coefficient increases according to the increase of the size of the sample tending towards 1. On the other hand, when the entomofauna of two different environments is compared, the augmentation of the size of the sample above its optimum value should exercise no essential influence on the coefficient of community.

The coefficient of similarity (community) of species may also be expressed by the following formulae:

Kulczyński's (1928) formula

$$J = \frac{j}{2}\left(\frac{1}{a} + \frac{1}{b}\right) 100.$$

Sørensen's (1948) formula

$$J = \frac{2j}{a+b} 100.$$

They give very similar results and the value of the coefficient depends on the sample size. It rises with the increase of j and falls with the decrease of a and b.

In view of this, Williams (1947) and later Mountford (1962) elaborated a formula known as Williams–Mountford's formula. The coefficient of similarity of species calculated by means of this formula is practically independent of the size of the sample:

$$J = \frac{2j}{2ab-(a+b)j}.$$

The similarity of the frequency of two cenoses, i.e. Kulczyński's number "*Ku*", is obtained by calculating the frequency of species in each cenosis separately and then dividing the sum of values of identical stabilities of both cenoses by the sum of differences in frequency

$$Ku = \frac{\text{sum of values of identical frequencies in both cenoses}}{\text{sum of differences in frequencies in both cenoses}}$$

Example:

Frequency of species	in A	in B	Similarity $A+B$	Differences $A+B$
Frequency of species x	100	80	80	20
y	60	80	60	20
z	–	40	–	40

$$Ku = \frac{80+60}{20+20+40} = \frac{140}{80} = 1.75.$$

Kulczyński's formula may also be given as a percentage:

$$Ku = \frac{c/a+c/b}{2}\,100,$$

where a and b sum of coefficients of frequency of species in site A or B, c = sum of coefficients of frequencies common for both cenoses quantitatively compared, or

$$Ku = \frac{100}{2}\,\frac{\sum s_1+\sum s_2-\sum\sigma}{2\sum s_1} + \frac{\sum s_1+\sum s_2-\sum\sigma}{2\sum s_2},$$

where $\sum s_1$ = sum of degrees of frequency of all the species of community I, $\sum s_2$ = sum of degrees of frequency of all the species of community II, $\sum\sigma$ = sum of differences between the degrees of frequency of each species in both communities (I and II).

Example:

Species	Community I Degree of frequency s_1	Community II Degree of frequency s_2	Difference between s_1 and s_2
1	100	–	100
2	85	90	5
3	70	30	40
4	30	–	30
5	25	100	75
	$\Sigma s_1 = 310$	$\Sigma s_2 = 220$	$\Sigma\sigma = 250$

$$Ku = \frac{100}{2}\,\frac{310+220-250}{620} + \frac{310+220-250}{440} = 54.4.$$

The similarity of dominance of two cenoses A and B is obtained by adding identical values of dominance of species.

Hence: R = sum of identical values of dominance of all the species occurring in both entomocenoses.

Example:

Dominance of species	in A	in B	Similarity $A+B$
Dominance of species x	60	45	45
y	15	40	15
u	10	5	5
v	10	5	5
z	5	5	5
	100	100	75

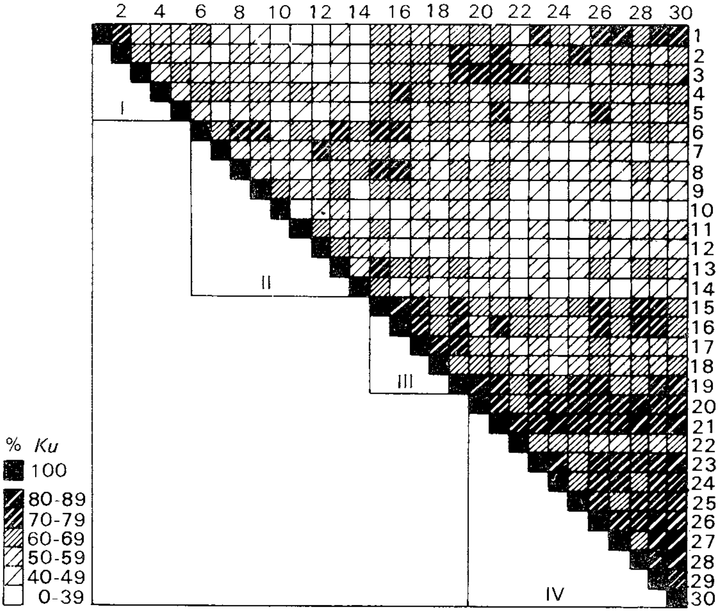


Fig. 6.4 Czekanowski's diagram representing the similarity of frequency (*Ku*) of *Staphylinidae* communities in pine forest stands of different age (after Szujecki, 1971): I – cutting areas and one-year plantations, II – plantations and 2–11 year-old thickets, III – 12–22 year-old thickets, IV – over 22 year-old forest stands

This indicates that 75% of individuals of five species exhibit a similarity of dominance in both cenoses compared.

Values of coefficients of community (similarity) are usually obtained in studies on entomocenoses for many pairs of associations or communitites of insects. In order to arrange the similarities of communities according to the coefficients, the results are either marked on Czekanowski's diagram or a dendrite or by other methods.

The coefficients are listed in a table (divided into plots resembling a chess-board). The numbers of samples are recorded in random order along the upper side of the table above each row of plots. The value of the coefficient of similarity is recorded in individual plots. The coefficients of similarity of each community (itself being 100%) are grouped on the diagonal of the "chess-board", thus a non-ordered diagram is obtained. The order of communities (samples) is then rearranged into a new table until an order is obtained in which the highest coefficients are grouped as close as possible to the diagonal on the smallest possible area. Where several distinct agglomerations are formed, the group of samples or communities observed in the diagram may be divided into a number of cenotic units corresponding to these agglomerations.

Figure 6.4 illustrates Czekanowski's diagram plotted using the results of the coefficient *Ku* (in percentages) for 30 litter habitats of *Staphylinidae* in pine forest stands of varying age. Analysis of this diagram by coupling those sites with similar compositions of staphylinid species (i.e. with the highest coefficient of similarity) showed that there were four distinct periods in the productive cycle of the forest stand. In these periods different quantitative ratios occurred between the insects studied.

Figure 6.5 illustrates the application of the dendrite method in analysing the relationship of taxocenes of *Coleoptera* of the massif of Babia Góra Mt. The principles of plotting the dendrite (Wrocław taxonomy) are given by Perkal (1953) and Romaniszyn (1960).

By application of the dendrite, Pawłowski (1967) established that the taxocene of *Coleoptera* of the Carpathian spruce forest (XIV) has more similarity with the taxocene of dwarf-pine thickets (XVII) than with that of the mixed coniferous forest of the lower mountain forest region (XIII). On the other hand, the taxocene of *Coleoptera* of the mixed coniferous forest exhibits a closer similarity with the corresponding taxocene of the Carpathian beech forest (XII) than with that of the Carpathian spruce forest.

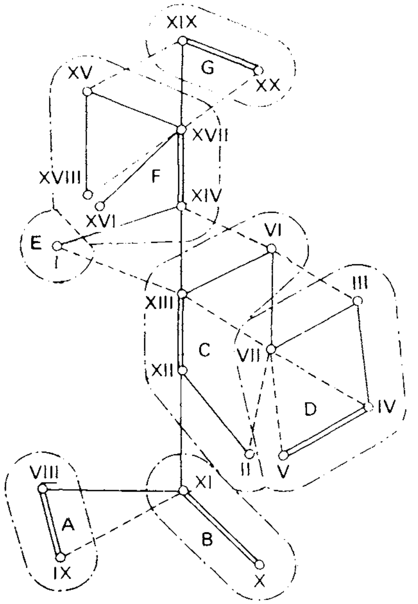


Fig. 6.5 Relationship of communities of *Coleoptera* of various environments of Babia Góra Mt represented by the dendrite method modified according to the "Wrocław taxonomy" (after Pawłowski, 1967): A – communities of aquatic environments, B – communities of gravel heaps and Carpathian alder forests, C – communities of the lower mountain zone, D – communities of the level of arable fields, E – communities of buildings, F – communities of upper mountain zone and dwarf pine, G – communities of rocky environments and alpine grass, double lines – primary bilateral similarities, single lines – primary unilateral similarities, dashed lines – secondary and tertiary similarities, dotted lines – borders between individual communities of *Coleoptera*, circles – environments studied; Roman numerals – biotopes

Insects in the spatial and time structure of forest biocenoses

6.3 Spatial differentiation

6.3.1 Insect communities in various forest habitat types

Each type of forest irrespective of the criterion of its distinction provides specific habitat conditions for insects. This is the result of the floristic composition, soil conditions, microclimate, stratification of the forest flora and the history of its formation. The influence of these factors on the occurrence of definite insect species and their abundance has been partly discussed in the preceding chapters. The full nature of this problem, however, is not sufficiently elucidated in the literature. It should be stressed that the autecological approach to the dependences between the flora and the composition of the entomofauna is one problem, whereas the synecological approach, which must also take into account the influence of interspecific relationships on the development of the specific system and the structure of dominance of insect communities in various forest associations, is another. It should be remembered that the strong pressure of competitors and enemies may severely, or even completely, limit the possibility of the occurrence of certain insects in definite forest associations although all other elements of the site and feeding conditions remain at an approximately optimum level (Fig. 1.9).

Considerable difficulties may also arise in the detection of correlations between the forest types and the insect species occurring in them when the intervals of the insects' tolerance to environmental factors are smaller than those to the same factors of the elements of the flora which distinguish the particular forest type or floristic association. The limits of occurrence of the insect species in such cases may not correspond with the limits of phytocenoses nor may they overlap with their internal units (e.g. vegetation stands). Analogous relationships may develop between communities of insects and plant associations, and the less uniform are the conditions within a stand of a definite forest type the wider may be the divergencies.

The influence of the flora on the distribution of insects may also be considered from two points of view, either as a trophic base for phytophages and saprophages or as a form of ground cover which directly influences the microclimate and indirectly influences the composition of entomocenoses. In the case of *Coleoptera* communities in mountain areas, the second aspect is more important. The influence of the flora as a source of food for phytophages is distinctly limited by the altitude as has been observed on Babia Góra Mt. This may be illustrated by the example of monophages and oligophages associated with grey alder, beech and fir. *Agelastica alni* (L.) and *Cryptorrhynchus lapathi* (L.) common on the grey alder at lower altitudes do not occur, or at least are very rare, at 600–700 m a.s.l. despite the occurrence of an abundant source of food in the *Alnetum incanae* association. A similar situation is observed in the occurrence of monophagous bark-beetless feeding on the beach on Babia Góra Mt such as *Ernopocerus fagi* (F.). and *Taphro-*

rhynchus bicolor (Herbst). The former species is extremely rare, whereas the latter was not found here at all. Pawłowski (1967) pointed out the characteristic lack of fir bark-beetles of the genus *Pityokteines* in the forest regions of Babia Góra Mt while at lower altitudes they are the most common fir pest. In effect the community of bark-beetles in these forest regions consists mainly of spruce and some pine species, all of which occur on the spruce as well as on the fir. It should be stressed that on Babia Góra Mt the beech range reaches the altitude of 1230 m a.s.l. and that of the fir extends to 1235 a.s.l.

In the example of Babia Góra Mt we thus observe the phenomenon of a lack of correspondence between the ranges of phytophagous monophages and oligophages and the range of the host plant. This phenomenon has been observed in bark-beetles by other authors. Nunberg (1929) did not find fir and beech bark-beetles at altitudes above 600 m a.s.l. in the western Carpathians and Pfeffer (1955) recorded the lack of alder, beech and fir bark-beetles in the 1000–1300 m a.s.l. zone in Czechoslovakia. Michalski (1957) found no bark-beetles feeding on beech and fir at an altitude above 750 m a.s.l. in the Śnieżnik Kłodzki massif, whereas, according to Bałazy & Michalski (1964b), species of *Pityokteines* as well as some beech-feeding scolytids are common in the Bieszczady Mts.

Despite these and other reservations which should be taken into account, sufficient evidence would appear to have been accumulated to support the existence of close associations between phyto- and entomocenoses.

Nevertheless, considerable difficulties arise in obtaining a synthetic picture of the development of insect communities in various forest types due to the frequently incomparable methods of sampling as well as of distinguishing and describing of communities and of classifying the typology of the flora.

Many works on forest entomology have distinguished the forest types most favourable for the outbreaks of certain insect species. Special studies have been also carried out to detect any connections between the occurrence of communities and a definite forest type and the development of quantitative proportions of individual species in various forest types, etc. Attempts have also been made to distinguish indicator insect species (characteristic and exclusive) for definite forest associations.

A relatively large number of studies of this type have been performed in the Białowieża Forest. In his work on the bark-beetles of this region, Karpiński (1933) established that only two species of bark-beetles, *Poly-*

graphus poligraphus (L.) and *Pityogenes chalcographus* (L.), occurred in all the forest types classified according to Romanov's system (dry pine forest, fresh pine forest, damp pine forest, swamp pine forest, fresh pine-spruce forest, damp pine-spruce forest, pine-oak forest, oak-linden-hornbeam forest proper, humid oak-linden-hornbeam forest, ash-alder carr, spruce-alder carr and alder carr). On the other hand, *Carphoborus cholodkovsky* Spessivtseff (swamp pine forest), *Scolytus carpini* Ratzeburg (oak-linden hornbeam forest) and *Hylesinus toranio* (Dhantoine) (humid oak-linden-hornbeam forest) occurred only in one forest type.

Twelve other species, each associated with a definite host plant or element of the habitat occurred in two or more forest types. Of these the following species are associated with a definite element of the habitat: *Pityogenes trepanatus* (Nördlinger), *Xylechinus pilosus* (Knoch) *Dendroctonus micans* (Kugelann), *Orthotomicus starki* Spessivtseff and *Ips duplicatus* C.R. Sahlberg. These species inhabit fresh and damp pine-spruce forests.

A second problem considered by Karpiński involved distinguishing bark-beetle communities which could be used to characterize definite forest types. It appeared that distinct communities of bark-beetles occur in four forest biotopes:

1) Swamp pine forest – the *Carphoborus* community with the exclusive characteristic species *Carphoborus cholodkovsky* Spessivtseff and 13 other species, such as *Tomicus piniperda* (L.), *Pityophthorus lichtensteini* (Ratzeburg) and *Scolytus ratzeburgi* Janson, the frequency of which on individual tree species exceeds 80%. *Ips sexdentatus* (Börner) was not observed here.

2) Mixed coniferous forest – the *Pityogenes* community, in which *Pityogenes quadridens* (Hartig) feeding on pine predominates. In addition, over 30 other species occur here such as *Scolytus ratzeburgi* Janson, *S. intricatus* (Ratzeburg), *Tomicus minor* (Hartig), *Pityogenes irkutensis* Eggers (= *monacensis* Fuchs), *P. chalcographus* (L.), *Trypophloeus granulatus* (Ratzeburg), *Polygraphus poligraphus* (L.), *Crypturgus cinereus* (Herbst) and *Orthotomicus proximus* (Eichhoff) exhibiting a frequency exceeding 80%.

3) Typical oak-linden-hornbeam forest – the *Ernoporus* community, with *Ernoporus tiliae* (Panzer) particularly abundant on the linden and 23 other species, among which the following exhibit a frequency exceeding 80%: *Scolytus intricatus*, *Polygraphus poligraphus*, *Pityophthorus traegårdthi* Spessivtseff and *Pityogenes chalcographus* (L.). A high

degree of fidelity is exhibited by *Scolytus carpini* Ratzeburg (characteristic and exclusive) as well as by *S. scolytus* (F.), *S. multistriatus* Marsham and *Triotemnus coryli* (Perris) (occurring exclusively in oak-linden-hornbeam forests).

4) Humid oak-linden-hornbeam forest – the *Trypophloeus* community in which *Trypophloeus granulatus* (Ratzeburg), occurring on the aspen, is very common. Among the other 31 species the following exhibit a high frequency of occurrence: *Scolytus ratzeburgi*, *S. intricatus*, *Ernoporus tiliae*, *Hylesinus crenatus* (F.), *Leperisinus fraxini* (Panzer), *Polygraphus poligraphus*, *Pityogenes chalcographus*, *Pityophthorus micrographus* (L.), *P. traegårdthi* and *Ips typographus* (L.). *Leperisinus orni* (Fuchs), occurring also in the ash-alder carr, is characterized by a high fidelity here.

Karpiński also distinguishes the following three communities of bark-beetles embracing two or three forest types: the *Blastophagus* (*Tomicus*) communtity, consisting of 24 species in dry, fresh and damp pine forests, the *Ips* community, consisting of 37 species in fresh and damp pine-spruce forests and the *Leperisinus* community, consisting of 26 species in ash, spruce and alder carrs.

As regards fidelity, the *Ips* community is characterized by: *Pityogenes trepanatus* (Nördlinger), *Xylechinus pilosus* (Knoch), *Dendroctonus micans* (Kugelann), *Orthotomicus starki* Spessivtseff and *Ips duplicatus* C.R. Sahlberg. In the *Blastophagus* community the species *Ips sexdentatus* (Börner) and *Hylurgus ligniperda* (F.) exhibit a stable occurrence.

The distinction of these seven communities, together with the characteristics of the habitats occupied by them and complemented by two types of biotopes in which bark-beetles do not occur (sedge areas and forest water bodies) provided a basis for Karpiński's new classification of the Białowieża forests into nine distinct biotopes. The biocenotic typology thus developed became the basis of scientific studies in the Białowieża National Park for a number of years. The biotopes proposed were as follows: (I) pine forest – *Pinetum typicum*, (II) coniferous forest – *Piceeto-Pinetum*, (III) mixed coniferous forest – *Querco-Piceeto-Pinetum*, (IV) high oak-linden-hornbeam forest – *Carpinetum typicum*, (V) low oak-linden-hornbeam forest – *Querco-Carpinetum*, (VI) alder carr – *Fraxino-Piceeto-Alnetum*, (VII) bog forest – *Pinetum turfosum*, (VIII) forest sedge area – *Caricetum*, (IX) forest water bodies – *Hylàquarium*.

Examples of elaborations of insect communities with respect to the typological classification of the Białowieża National Park will be quoted below.

Karpiński & Makólski (1954) described the *Carabidae* communities of the Białowieża National Park with particular emphasis on the faunistic aspect and the role of these beetles in the functioning of the biocenosis. Czekanowski's diagram (Fig. 6.6) indicates that carabid communities of coniferous forest biotopes (I–III) bear the most resemblance to each other. There is considerable similarity in the fauna of oak-linden-hornbeam forests (IV–V), although the carabid community of the low oak-linden-hornbeam forest (due to its specific composition) is more like the communities found in coniferous forests than those of the high oak-linden-hornbeam forest. Moreover, the communities of both types of oak-linden-hornbeam forests bear more resemblance to the mixed coniferous forest community than to each other. The carabid communities of the alder carr, bog forest and sedge area are related to each other whereas the community found on the banks of forest water bodies is

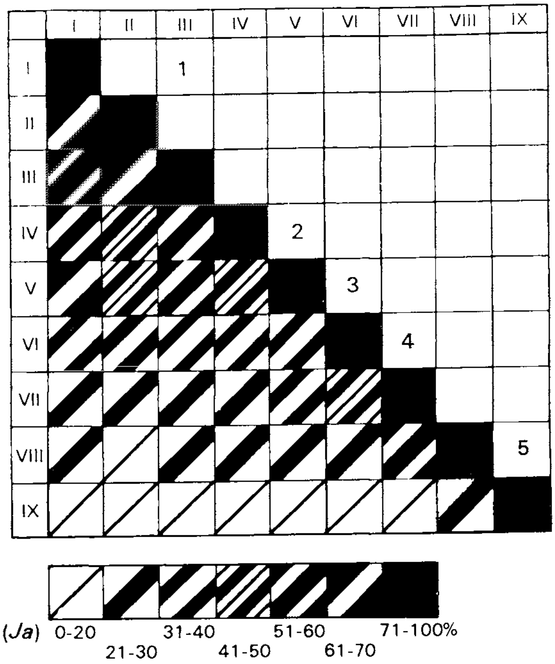


Fig. 6.6 Czekanowski's diagram representing the similarity of species (*Ja*) of *Carabidae* communities in the Białowieża National Park (original according to data of Karpiński & Makólski, 1954): Roman numerals — biotopes; 1 — coniferous forests, 2 — oak-hornbeam-linden forests, 3 — alder carrs, 4 — marsh forest and sedge patch, 5 — borders of forest water bodies

the most distinct, and bears no resemblance to any of the others. According to Karpiński & Makólski (1954), the quantitative proportions were as follows.

In the communities of coniferous forests, *Pterostichus oblongopunctatus* (F.) and several other species were dominant. Of the latter *Carabus violaceus* L. was the dominant species in pine forest and coniferous forest and a subdominant species in mixed coniferous forest. In oak-linden-hornbeam forests *Carabus nemoralis* Müller (and also *P. oblongopunctatus*) was dominant, whereas *C. violaceus* belonged to the group of accessory species. Both in coniferous and oak-linden-hornbeam forest *Carabus arcensis* Herbst belonged to the group of the most abundant species, whereas out of the other biotopes it was observed only in small numbers in swamp coniferous forest.

The number of *Carabidae* captured in the alder carr, swamp coniferous forest, sedge area and on the banks of forest water bodies was so low that Karpiński & Makólski were not able to distinguish dominant and accessory species. The absence of *P. oblongopunctatus* from these biotopes, with the exception of alder carr, as well as the lack of *Carabus* species on the border of forest water bodies, with the exception of species characteristic of this environment (*C. menetriesi* Hummel, *C. clatratus* L. and *C. granulatus* L. which is widely distributed but rare in the Białowieża Forest is characteristic.

Against the background of the distribution of *Carabidae* in the Białowieża biotopes and of the characteristics of their communities Karpiński & Makólski advanced conclusions concerning the biocenoses of definite biotopes. They call attention to the substitution of species playing a similar biocenotic role in successive biotopes and to the substitution of species in the course of time, i.e. at various seasons of the vegetation period in each biotope.

On the basis of Zlatnik's typology, Stolina (1959) studied the distribution of noxious forest insects and the course of their outbreaks in various forest associations of Slovakia. It appeared that outbreaks take place only in definite groups of forest types in which populations of individual insect species encounter optimal ecological conditions of development. Such conditions arise due to the incomplete adaptation of forest-forming species to the site occupied at that particular time. Fir forest stands occupying sites of *Fago-Quercetum* and *Querco-Fagetum* are particularly susceptible to outbreaks of *Choristoneura murinana* (Hübner). On the other hand, outbreaks of *Panolis flammea* (D. & S.) and *Bupalus piniarius* (L.) occur in Slovakia only in *Pino-Quercetum*. The nature of the course of the outbreaks also depends on the forest type. In *Querco-Fagetum Pityokteines spinidens* (Reitter) exhibits a short outbreak period with a high amplitude of population abundance, whereas in the association *Fagetum pauper*, the short course of the outbreak is accompanied by a low amplitude of abundance.

Data obtained in Stolina's studies are at present being used in the prediction of the occurrence of noxious forest insects in Slovakia.

6.3.2 Insects in the layers structure of the forest

The layered structure of the forest is one of the most characteristic features of forest biocenoses. It secures the existence and utilization of all kinds of habitat and environmental niches by plants, animals and microorganisms. Insects occur throughout the entire vertical profile of forest biocenoses from deep soil layers (grubs and many other pests of the root system) up to the tree tops (*Magdalis violacea* (L.), *Tortricidae* and other insects damaging the shoots or apical buds of trees) (Fig. 6.7).

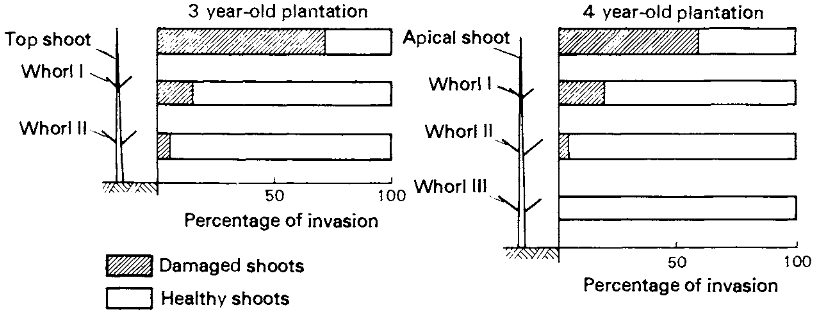


Fig. 6.7 Distribution of *Rhyacionia duplana* (Hübner) on the pine profile in 3 and 4 year-old plantations (after Śliwa, 1969)

Most insects inhabiting the soil environment occur in the litter, particularly in its fermentation and humification layers (Fig. 6.8). Only a few small insects of high abundance occur in the mineral soil. These are principally pests of the root system which occur around roots and migrate to the deeper soil levels in winter and periods of particular drought (not deeper than 1 m in Poland). The abundance of litter insects as compared with that of soil insects changes throughout the life of the forest stand. In the first forty years soil insects prevail whilst later those of the litter predominate. The holes remaining after the decomposition of the roots of dead plants play an important role in the translocation of insects in the soil, particularly in the penetration of deeper levels by superficial forms.

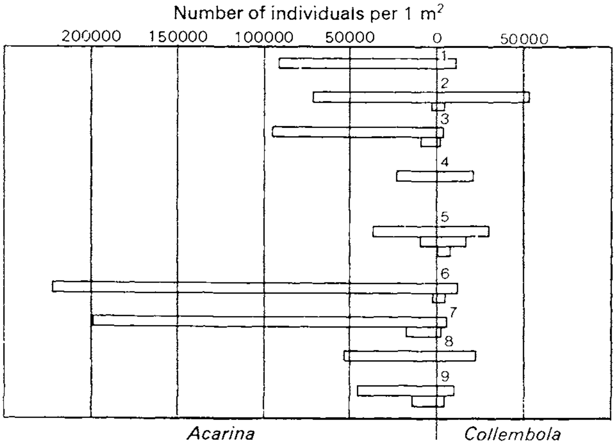


Fig. 6.8 Vertical distribution of *Acarina* and *Collembola* in soil forests of the Latvian Soviet Socialist Republic (after Eglitis, 1954): 1 and 2 – dry pine forests, 3 and 4 – fresh pine forests, 5 – pine-spruce forest, 6–9 – spruce forests (5 cm soil layers are indicated on the ordinate)

As *Collembola*, predatory *Coleoptera*, flies and ants prevail in the soil and litter, phytophagous *Lepidoptera* and *Coleoptera*, as well as bugs and *Diptera*, begin to predominate in the herb layer. There are also many *Hymenoptera* associated either with phytophagous insects (parasites) or with the occurrence of flowers (*Aculeata*). Karczewski (1962, 1967a) considered consortium connections between insects and the bilberry and heather. He recorded 132 species feeding on the bilberry and 73 species on heather (mainly *Lepidoptera*), as well as 69 and 302 species visiting flowers of the bilberry and heather respectively (e.g. *Diptera*, *Hymenoptera* and *Lepidoptera*). There were also many entomophages, such as ichneumonids, braconids, chalcids and tachinids whose hosts were on heather (120 species) and on the bilberry (249 species).

The zonal distribution of insects in the herb and shrub layers has hardly been investigated at all, although their occurrence on tree trunks is well known. This is due to the high economic interest in tree trunk feeding species, as well as the accessibility of the subject of such studies. The zonal distribution patterns of bark-beetles on various tree species in Białowieża Forest were analysed with respect to the biotope (Fig. 6.9). Analyses were also performed on the zonal distribution of insects feeding under the bark and in the wood of the beech (Fig. 6.10). It was found that this type of distribution in insects depends on the microclimatic conditions, the age of the trees and also the geographical conditions.

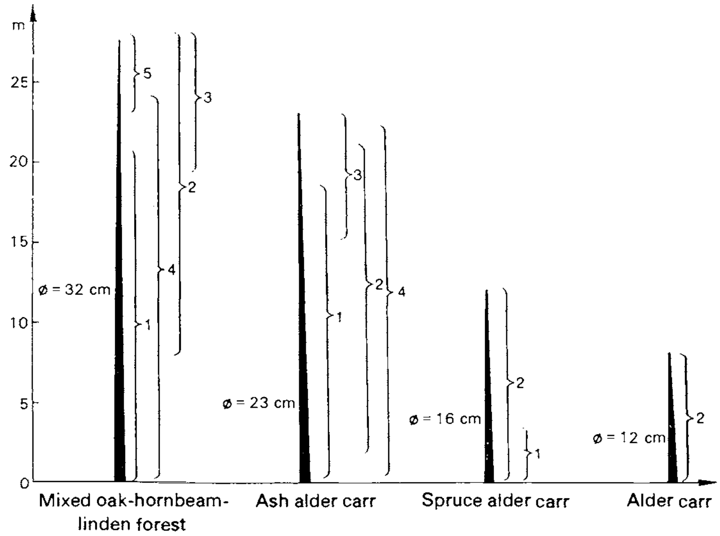


Fig. 6.9 Layered character of occurrence of *Scolytidae* on *Fraxinus excelsior* (L.) in various biotopes of the Białowieża National Park (after Karpiński, 1933): 1 – *Hylesinus crenatus* (F.), 2 – *Leperisinus fraxini* (Panzer), 3 – *Leperisinus orni* (Fuchs), 4 – *Trypodendron domesticum* (L.), 5 – *Hylesinus toranio* (Dhantoine)

The invasion of secondary pests on ten to twenty-year old pines damaged by red deer represents an interesting picture. It appears that the lower parts of the trunk near the root neck are invaded by larvae of *Rhagium inquisitor* (L.). This cerambycid, however, has not economic importance in this particular part of the tree, whereas *Pissodes notatus* (F.) occurring from the root neck to the height of about 2 m does have a significant effect on this part of the trunk. The distribution of *Tomicus* (= *Blastophagus*) *piniperda* (L.) is similar, but it is considerably less frequent nearer the root neck than the former species although its proportion distinctly rises from the height of 0.5 m upwards. Thus, the three species together dominate up to the height of 0.5 m and *T. piniperda* up to 1.1 m, i.e. up to the parts slashed by red deer. From this level upwards the number of galleries of *Pissodes piniphilus* (Herbst) rises,

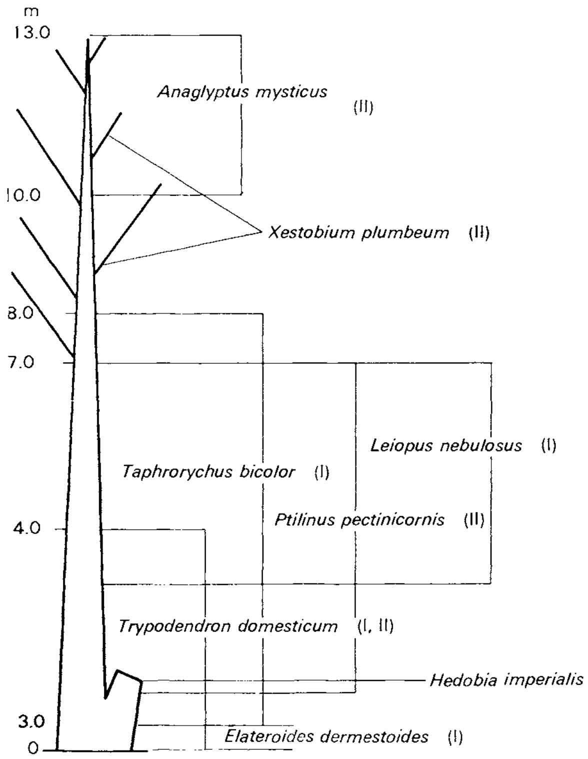


Fig. 6.10 Layered distribution of noxious *Coleoptera* on *Fagus silvatica* (L.) (after Capecki, 1969)

this species dominating up to the height of about 4.1 m beyond which *Magdalis violacea* (L.) begins to prevail (Fig. 6.11).

The following two communities of pests have been distinguished as based on the zonal distribution and relative proportions (and functions) of insects on the damaged trees. The first community occurs below the damaged bark with *P. notatus* and *T. piniperda* as dominants, while the second occurs above the damaged region and is dominated by *P. piniphilus*. The influence of these two communities as the slashed trees gradually die may not depend on each other. With heavy bark damage death occurs within the same year, the community responsible being that of *P. piniphilus*. Trees less heavily slashed and preserving their crowns are attacked several years later by the *P. notatus* community, along with parasitic fungi and other injurious organisms in the upper regions of the trunk.

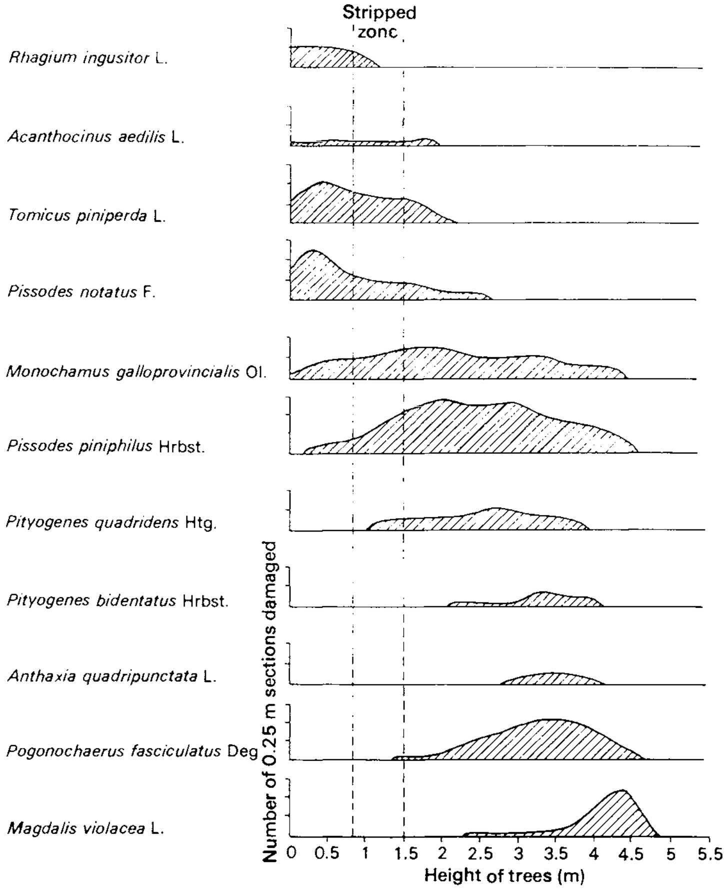


Fig. 6.11 Layered distribution of secondary pests on several year-old pines slashed by red deer (after Kinelski & Szujecki, 1963)

The distribution of bark-beetles occurring on spruce branches in three forest layers (upper-growth, second and first tree layers) is characterized by a varying abundance of individual species (Fig. 6.12) at different heights of the trees. Some of them, e.g. *Pityophthorus exsculptus* Ratzeburg and *Phthorophloeus spinulosus* Rey only invade lower tree branches. In addition, important differences were observed in the specific composition and abundance of bark-beetles in relation to the distance along the branch from the tree trunk (Fig. 6.13).

The vertical differences in the distribution of xylophages influence the distribution of their parasites. On the other hand, the mortality of

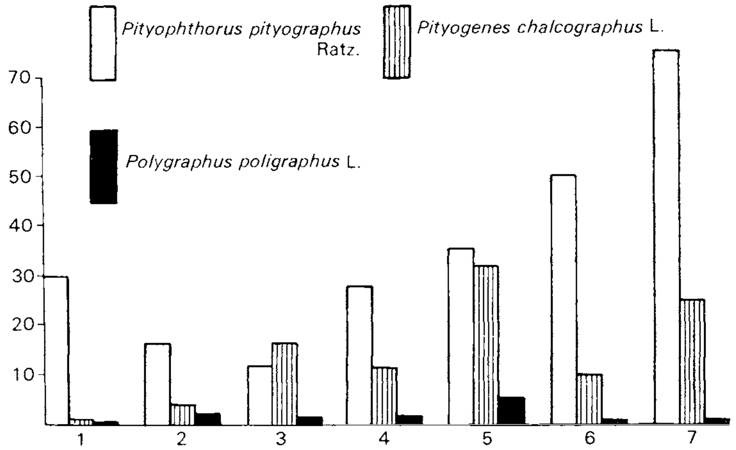


Fig. 6.12 Distribution of some *Scolytidae* species in the crowns of *Picea abies* (L.) Karsten (*Picea excelsa* (Lamarck) Link) in various forest layers; mean number of individuals per 1 cm^2 of branches on the cross-section of the crown (according to data of Seniczak, 1968): 1 – spruce undergrowth, 2, 4 and 6 – spruces of second tree layer, 3, 5 and 7 – spruces of first tree layer, 2 and 3 – lower tree parts, 4 and 5 – central tree parts, 6 and 7 – top tree parts

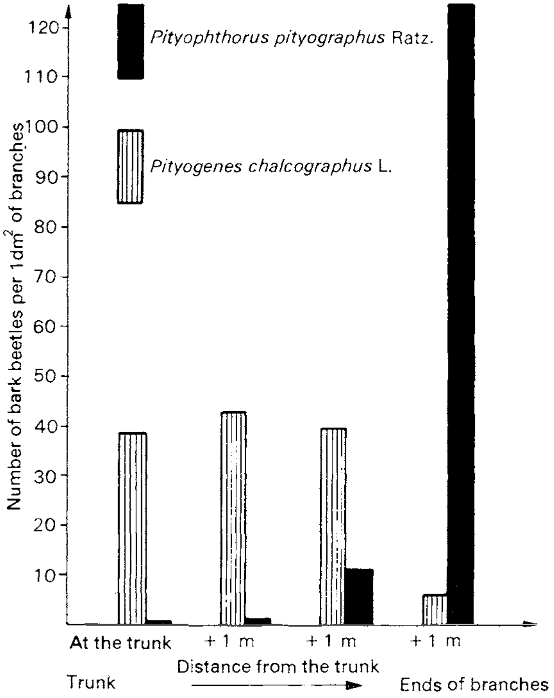


Fig. 6.13 Number of individuals of two *Scolytidae* species per 1 dm^2 of spruce branches in the central parts of crowns of dominant trees (in dependence on zonal distance from the trunk) (according to data of Seniczak, 1968)

larvae and pupae of *Ips typographus* (L.) due to parasitic *Hymenoptera* depends not only on the distance from the forest floor but also on geographical and habitat conditions and varies between exploited and natural forests (Fig. 6.14).

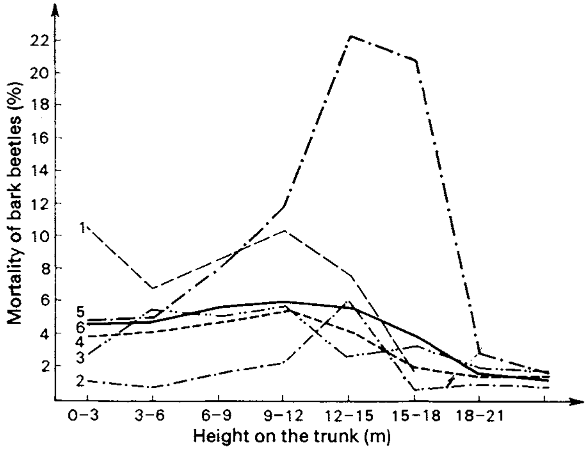


Fig. 6.14 Mortality of larvae and pupae of *Ips typographus* (L.) on spruce trunks caused by parasitic *Hymenoptera* in dependence on the height from the forest floor: 1 – in mountain forest stands, 2 – in lowland forest stands in the north-western range of the spruce in Poland, 3 – in lowland forest stands in the north-eastern range of the spruce in Poland, 4 – in general in managed forest stands, 5 – in forest stands of the Białowieża National Park, 6 – mean values for all forest stands studied in Poland (after Bałazy, 1968)

It is considerably more difficult to demonstrate the layered and zonal character of the distribution of insects feeding on the assimilative apparatus in the tree crowns and their natural enemies, and to present the qualitative and quantitative relations between them in the various forest layers (Fig. 6.15).

Studies on the entomofauna of pine crowns in Holland demonstrated that in summer it is relatively stable and consists of 130 species, these being mainly *Coleoptera* and *Heteroptera* (Klomp & Teerink, 1973).

There is a considerable amount of data available in Sawoniewicz (1979) concerning the vertical distribution of *Ichneumonidae* in the herb layer, upper-growth and tree crowns in relation to the habitat and specific composition of the forest stand. Unlike the case of the parasites of *Ips typographus* (L.), it was found that in Poland the layered character of the forest plays a higher role in the development of communities of these insects than geographical and habitat conditions and the specific composition of the forest stand.

The recognition of the vertical distribution of insects in the forest and their role in various stratocenoses, and the elucidation of mutual faunistic relations between individual forest plant layers are very important in forest management. This is because many natural enemies of insects which feed in the tree-crowns may find their indirect and substitute hosts in other forest layers, e.g. those of the herb and shrub. A significant amount of data has been accumulated to support the existence of such relationships. Such information assists in elucidating the dynamics of

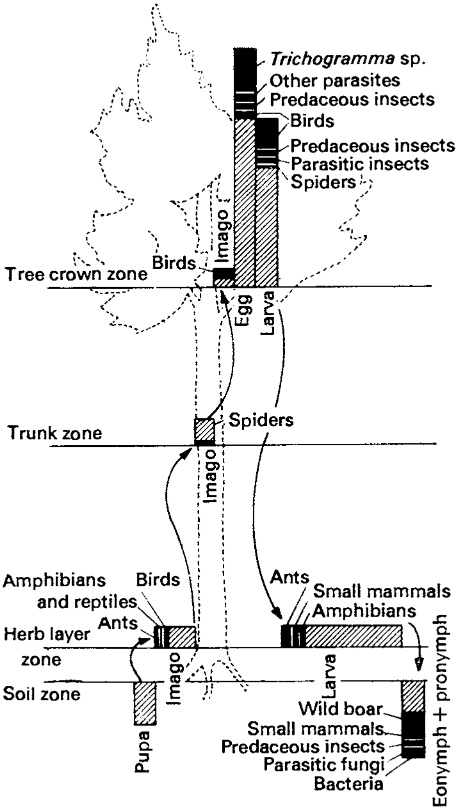


Fig. 6.15 Scheme of quantitative changes in the population of one generation of *Acantholyda posticalis* Matsumura occurring in various forest layers (after Koehler, 1957)

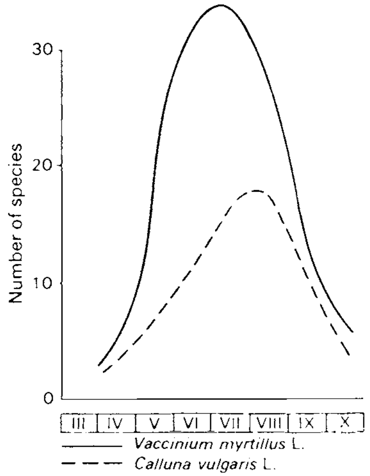


Fig. 6.16 Seasonal dynamics of appearance of various entomophages commonly parasitic on insects living in the herb layer on *Vaccinium myrtillus* (L.) or *Calluna vulgaris* (L.) and in crowns of the common pine (after Karczewski, 1967a); Roman numerals – months

these phenomena (Fig. 6.16) and should be taken into account in management projects which aim to provide the correct formation of biocenoses of managed forest stands.

6.4 Differentiation in time

6.4.1 Diurnal rhythm of activity

The different microclimatic conditions occurring throughout the 24 hours of the day evoke a differentiation of activity of the entomocenosis during this period. There are at least two forms of such activity – that of the day and that of the night. Under the successively changing light conditions in the course of 24 hours, the maxima and minima of the diurnal curve of definite functions of the insects appear repeatedly in the successive days of the definite vegetation period at the same time of the day. The differences in the time of appearance of individual insect species in the course of 24 hours may be also due to competitive dependences occurring between these species as well as to the tendency of avoiding non-specialized enemies.

Due to the separation of diurnal activity periods, species having similar requirements may live parallelly in the same biocenosis, thus not eliminating each other in the struggle for the utilization of the environment. This is illustrated in Fig. 6.17 in which changes in 24-hours activity of two groups of insects (ants and gnats) and large spiders are presented.

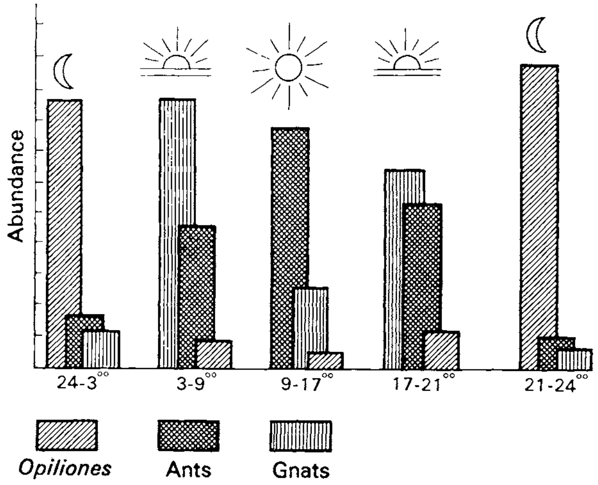


Fig. 6.17 Changes in 24-hour activity of three groups of *Arthropoda* in the forest (after Łuczak & Prot, 1967)

Various life processes contribute to the diurnal rhythm of insects. These are – individual development and transformation stages (e.g. emergence of *Lepidoptera* from pupae), nuptial flight and egg-laying, micromigrations within the biotope and feeding, etc. The locomotor activity of large insects is one of the most frequently studied symptoms of diurnal activity, which also include egg-laying, respiration and susceptibility to insecticides.

It is obvious that each species contributing to the composition of the biocenosis also has its definite place in time. Thus its diurnal rhythm of activity is as characteristic as any other of its specific biological properties. This feature may therefore also undergo modifications due to the influence of environmental factors. For instance, the carabid *Pterostichus madidus* (F.), which occurs in various biotopes, is diurnal in habits in meadows whereas in forests it is nocturnal. Caterpillars of many species of *Agrotis* which normally feed at night on the leaves of seedlings, also feed during the day when the weather is cloudy. The seasons of the year may also significantly alter the activity rhythms of certain species of insect.

The 24-hour activity rhythm of the cerambycid *Gaurotes virginea* (L.) is very characteristic. Its larvae live under the bark of the common spruce, whereas the adults are found abundantly on flowers in mountainous regions. The period of activity of the adults from morning to evening depends on the hours of sunrise and sunset, i.e. on the season of the year. The activity pattern of this species under normal illumination conditions exhibits three distinct peaks (Fig. 6.18): the morning (between 7 and 9 a.m.), noon (between 12 and 1 p.m.) and evening (between 6 and 7 p.m.). Thus the activity of *G. virginea* may be regarded as being of the intermittent diurnal type in which the greatest mobility occurs in the morning, noon and evening (Fig. 6.19.1). Under laboratory conditions, the application of continuous artificial illumination or constant darkness throughout the 24-hour period, upset the rhythm of activity, transforming it to a multi-phase type. When the 24-hour period is reversed (reversed illumination conditions) a new type of activity develops with two peaks in the period of artificial day, (Fig. 6.19.2,3).

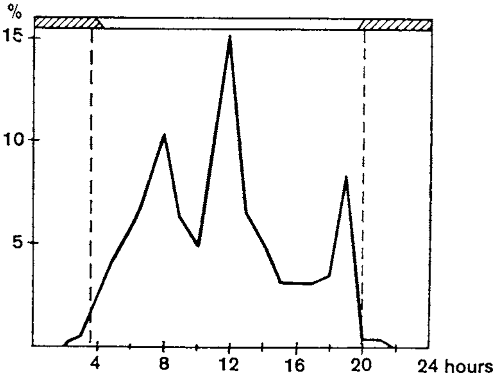


Fig. 6.18 Rhythm of 24-hour activity of adults of *Gaurotes virginea* (L.) under natural conditions (after Starzyk, 1968)

The main role in regulating the 24-hour activity of the adults of *G. virginea* is played by exogenous (environmental) factors, principally light but also to a lesser degree by air humidity and temperature. On the other hand, endogenous factors determine the pattern of the rhythm. It appears that the 24-hour activity of *G. virginea* is highly plastic, readily undergoing changes under the influence of the environment.

6.4.2 Seasonal rhythm of activity

Insect communities occurring in forest biotopes or their various parts frequently exhibit both a quantitative and qualitative variability which are repeated every year in definite seasons. As well as greatly complicating the understanding of entomocenoses, this phenomenon may sometimes obscure the observation of short-term microsuccessions within the range of biocenoses and thus deserves closer attention.

The seasonal rhythm of insects may be due to various factors such as the direct influence of definite agents of the abiotic environment (e.g. day length), the indirect influence of these agents through other elements of the ecosystem (e.g. host plants or hosts) and finally endogenous agents inherent in the populations themselves of species constituting the communities. The existence of a seasonal rhythm is manifested by the increase or decrease of activity of the insects as regards their development and basic life functions such as feeding, egg-laying and copulation, etc. Migrations of insects at definite seasons of the year are particularly characteristic of rhythmical seasonal phenomena. These migrations are associated with seeking or abandoning hibernation sites, changes of feeding sites or reproduction. Studies on the times of occurrence of characteristic periodical phenomena in life-cycles of organisms under natural conditions are the subject of phenology.

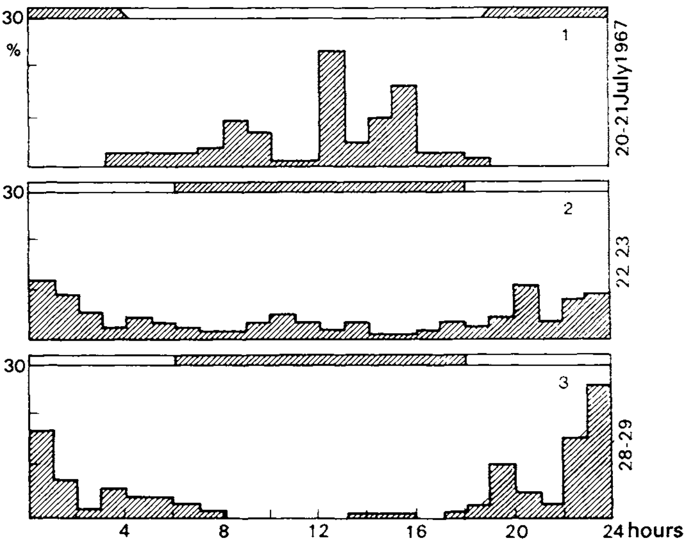


Fig. 6.19 Rhythm of 24-hour activity of adults of *Gaurotes virginea* (L.) under experimental conditions (after Starzyk, 1968)

The particular periods of development of *Trypodendron lineatus* (Olivier) in Poland fall into the following phenological seasons:

mating and attacks of trees – early spring, spring
egg-laying and development of eggs – end of early spring, spring
feeding of larvae – spring, early summer
pupal period – early summer
hatching and feeding of young beetles – early summer
abandoning of trees by young beetles (culmination) – summer, early autumn (summer)
hibernation – summer, early autumn, autumn, winter, early spring

The phenology of the life processes of *Hylesinus crenatus* (F.) is presented in Table 6.1. The flight of *Trichogramma* sp. in spring is also strictly correlated with particular phenological phenomena (Fig. 6.20).

Table 6.1 Phenology of *Hylesinus crenatus* (F.) (after Okołów, 1970a).

Phenomena in development of *Hylesinus crenatus* (F.)	Phenomena in development of plants characteristic of ash alder carr and low oak-hornbeam linden forest
First beetles abandon hibernation sites and establish maternal galleries	beginning of florescence of: *Oxalis acetosella* L. end of florescence of: *Corydalis solida* (L.) Shmit
First eggs appear in egg niches	beginning of florescence of: *Dentaria bulbifera* L., *Galeobdeon luteum* Huds., *Glechoma hederacea* (L.)
Hatching of first instar larvae	full florescence of: *Allium ursinum* L. *Geum urbanum* L., *Cardamine amara* L., *Orchis maculatus* L.
First pupae	end of florescence of: *Dentaria bulbifera* L. full florescence of: *Geranium robertianum* L.
First uncoloured beetles	full florescence of: *Impatiens noli-tangere* L., *Filipendula ulmaria* (L.), Maximowicz *Lysimachia vulgaris* L. beginning of florescence of: *Stachys silvaticus* L.
Flight of first young beetles hatched – first traces of supsupplementary feeding	full florescence of: *Angelica silvestris* L. beginning of florescence of: *Cirsium oleraceum* L. Scopoli

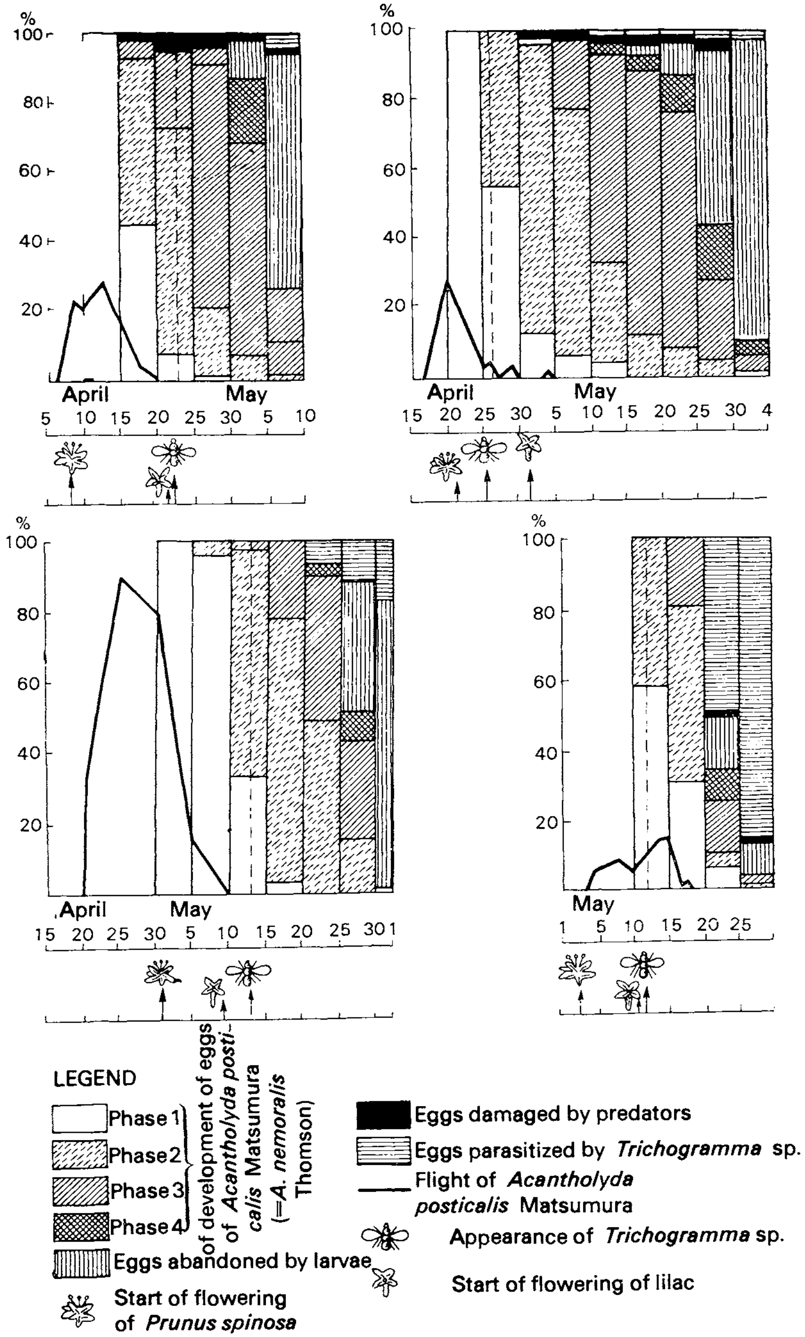


Fig. 6.20 Phenology of *Trichogramma* sp. (after Kadłubowski, 1965)

The accomplishment of developmental and general biological functions during the life of an individual insect also exhibits peaks of activity which occur at definite times in the annual cycle according to geographical conditions and the course of the weather in the given year. The culmination of the penetration of *Tomicus piniperda* (L.) under the bark of pines in the environs of Zielona Góra occurs at the end of March and beginning of April. In the environs of Vilnius, however, it does not take place until the last ten days of April, the traps being set at 5 dates (April 5, 15 and 25, May 6, and 15) and the first penetrations being observed after April 15 (Fig. 6.21).

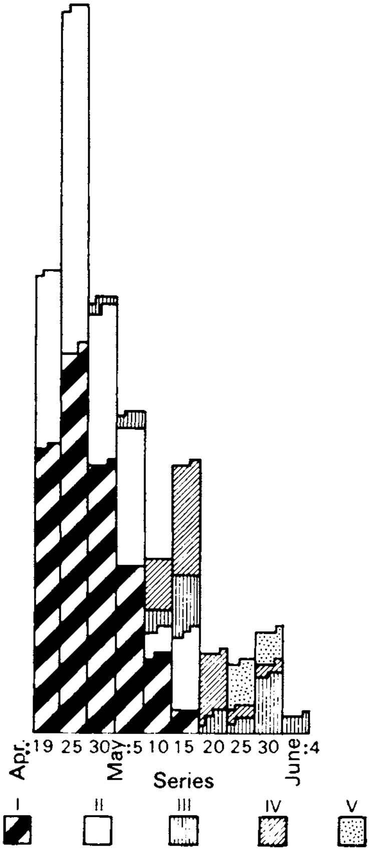


Fig. 6.21 Increase of number of inlets of *Tomicus piniperda* (L.) in individual periods between April 19 and June 4 in five series of traps set in the environs of Vilnius on the following dates: I – April 1, II – April 15, III – April 25, IV – May 6, V – May 15 (after Prüffer, 1948)

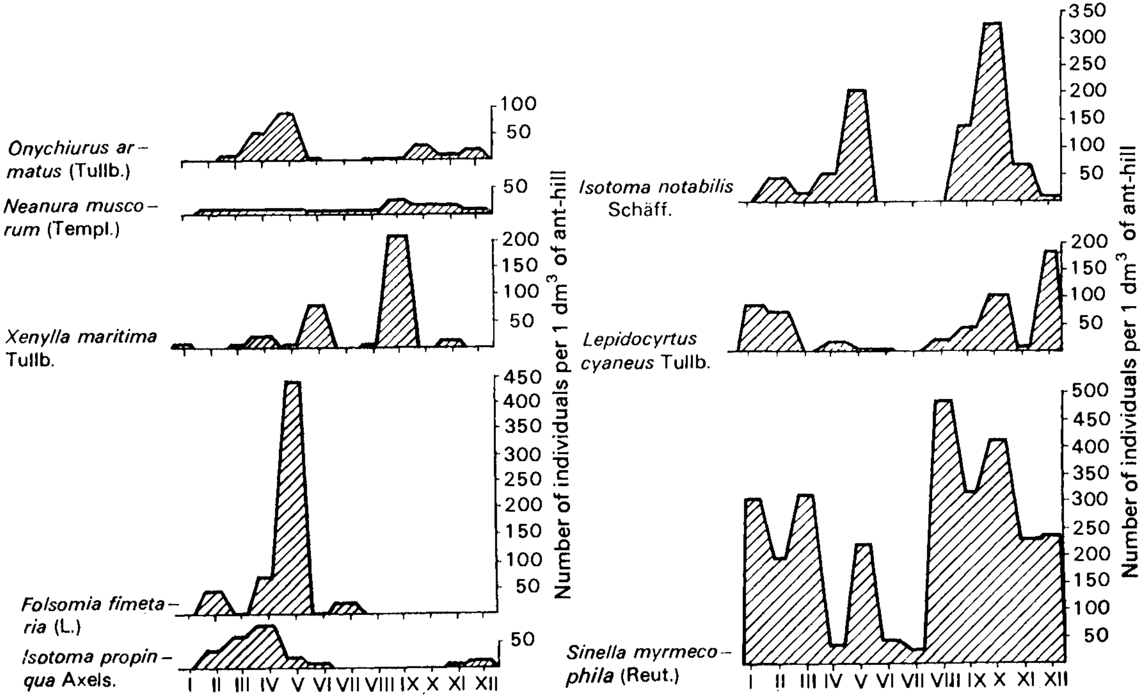


Fig. 6.22 Seasonal rhythm of activity of *Collembola* in ant-hills of *Formica polyctena* (Forster) (after Wiśniewski, 1967); Roman numerals – months

The fact that elements of the seasonal rhythm of species which are closely related or which have similar roles in the ecosystem do not overlap is a very important characteristic with regard to the functioning of biocenoses (Fig. 6.22). Because of this each functional group of entomocenoses is adequately represented at any time of the vegetation season. The seasonal changes of various trophic groups of forest insects thus take place against the background of the rhythm of the entire biocenosis as a whole. There has been ample evidence accumulated concerning the seasonal activity of insects, particularly for *Coleoptera* and especially the *Carabidae* (Fig. 6.23).

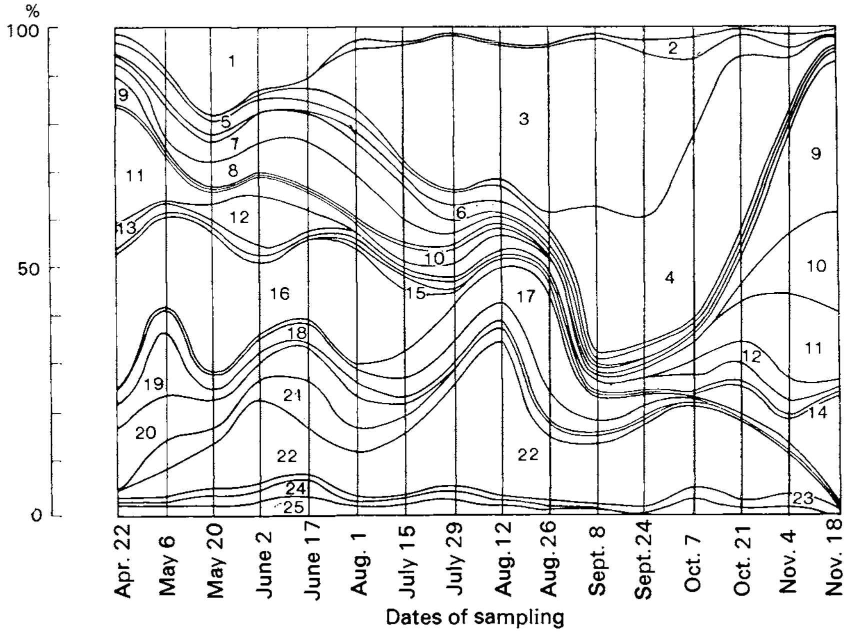


Fig. 6.23 Seasonal rhythm of dominance ratios in the community of epigeic *Coleoptera* in the association *Ulmeto-Fraxinetum* (after Obrtel, 1971): 1–15 predators of invertebrates – *Carabus* spp., 2 – *Leistus* spp., 3 – *Epaphius secalis* (Paykull), 4 – *Patrobus atrorufus* (Stroem), 5 – other *Carabidae*, 6 – *Staphylinus* and *Ocypus* spp., 7 – *Philonthus* spp., 8 – *Quedius* spp., 9 – *Ocalea badia* Erichson, 10 – *Xantholinus–Othius* spp., 11 – *Aleocharinae*, 12 – *Omaliinae*, 13 – other *Staphylinidae*, 14 – *Pselaphidae*, 15 – *Phosphaenus hemipterus* (Goeze), 16–21 – predators of eggs and necrophages of invertebrates: 16 – *Bembidion* spp., 17 – *Pterostichus niger* (Schaller), 18 – *Pterostichus vulgaris* (L), (= *melanarius* (Illiger)), 19 – *Pterostichus anthracinus* (Illiger), 20 – other *Pterostichus* spp., 21 – *Abax parallelepipedus* (Piller & Mitterpacher), 22 – necrophages of vertebrates, 23 – saprophages, 24 – myrmecophils, 25 – phytophages

Species of carabids feeding on fresh dead bodies of invertebrates and on eggs of other soil insects (e.g. *Bembidion* spp., *Pterostichus* spp., *P. anthracinus* (Illiger), *Abax parallelepipedus* (Piller & Mitterpacher)) predominate in the association *Ulmeto-Fraxinetum* in the spring aspect of the community of epigeic beetles. Predatory beetles such as *Carabus ullrichi* Germar, *Aleocharinae*, *Quedius* spp., *Philonthus* spp. and necrophagous *Silphidae* (burying beetles) are less frequent. In this period ephemerals come into flower in the herb layer and the trees are without leaves. During late spring and summer, when there is an abundant development of the herb layer and tree foliage, the contribution of predators (e.g. *Epaphius secalis* (Paykull), *Philothus* spp., *Quedius* spp., *Staphylinus* spp., *Ocypus* spp., *Xantholinus* spp., *Othius* spp. and *Phosphaenus hemipterus* (Goeze)) to the community increases, whereas the dominance of species feeding on invertebrate and vertebrate corpses decreases. In late summer and early autumn, when fruits of the herb layer ripen, predators (e.g. *E. secalis* and *Patrobus atrorufus* (Stroem) and necrophages (e.g. *Ptomaphagus sericatus* Chaudoir) are distinctly predominant over other trophic groups of the *Coleoptera* community. In the autumn aspect characterized by the die-back of plant foliage and the loss of leaves by deciduous trees, the dominance of predators persists but the abundance of necrophages rises and saprophages attain their peak of abundance (Obrtel, 1971).

In carabids the climax of the period of activity is invariably also the time when the young adults begin to appear and mating and oviposition occur. In Białowieża Forest among *Carabidae* the following species exhibit the earliest activity (end of February, March): *Carabus hortensis* L., *Pterostichus diligens* (Sturm) and *P. aethiops* (Panzer). In November the following species were active: *Cychrus caraboides rostratus* (L.), *Carabus coriaceus* L., *C. arcensis* Herbst, *C. nemoralis* Müller, *C. hortensis* L., *Nebria brevicollis* (F.), *Harpalus latus* (L.), as well as a number of species of *Pterostichus*. In the period of studies performed by Karpiński & Makólski (1954) at the beginning of December the following species were active: *N. brevicollis*, *Pterostichus anthracinus* (Illiger) and *P. aethiops* (Panzer). Many species exhibit activity from April to October. Other works, however, indicate that the periods of activity of these species vary in time.

Carabids may hibernate either as larvae or as adults. The species hibernating as adults are active in early spring and early summer whereas their larvae develop during the summer. These species survive the cool period of the year as young adults with underdeveloped reproductive organs whereas in spring they undertake supplementary feeding, acquire sexual maturity and start to reproduce. Some of these species lay eggs at the end of April and beginning of May, others in June, and they are particularly active during these periods. Species which hibernate as larvae and complete their development in spring generally reproduce and are most active in August and September. The development of the larvae of the second generation therefore cannot be completed before the beginning of winter.

The fact that species of northern origin generally accomplish their mating very early whereas those of southern origin mate in summer is an interesting feature of the seasonal activity of various species.

A number of eurychronous species, i.e. species exhibiting no variability in seasonal activity, is also known.

Table 6.2 summarizes the phenological periods of flights of some secondary pests of the beech in Poland.

The seasonal activity associated with migrations may evoke vertical or horizontal translocations of enormous numbers of insects in forest biocenoses. The most intense migrations are observed in autumn and spring when large numbers of insects fly to their hibernation sites and then return to their feeding grounds. Among noxious forest insects such migrations within individual layers of the biotope are well illustrated by the example of the caterpillars of *Dendrolimus pini* (L.) which feed in the tree crowns and hibernate in the forest litter. Interesting insect aggregations hibernate in fissures of the outer tree bark (Szozda, 1972). The most favourable conditions for the occurrence of insects in this habitat are found in cracked bark. For this reason the larch, pine, alder, spruce, oak, birch, hornbeam, beech and aspen are the most abundantly invaded trees. Most beetles inhabit tree trunks up to the height of 0.5 m and their abundance decreases with height such that at 1–1.5 m it is only 10% of that in the butt (Fig. 6.24).

The hibernation of about 60 species of *Coleoptera* belonging to 20 families was observed under these conditions. Among the hibernating individuals, 78% belonged to the family *Chrysomelidae*, whereas among other families *Coccinellidae*, *Scolytidae*, *Carabidae* and *Curculionidae* were most numerous. Under the conditions observed the following species were dominants of the aggregation: *Phyllotreta nemorum* (L.) (*Chrysomelidae*), individuals of which probably fly to the forest from field biotopes, as well as *Myrrha octodecimguttata* (L.) and *Harmonia quadripunctata* (Pontoppidan) (*Coccinellidae*), living in the vegetation season in pine crowns where they feed on the aphids *Pineus pini* (Gmelin)

Table 6.2 Phenological seasons of flight of some secondary beech pests in Poland (after Capecki, 1969)

Species	Phenological season of the year according to Szafer (1922)					
	very early spring	early spring	spring	early summer	summer	early autumn
1	2	3	4	5	6	7
Trypodendron domesticum (L.)	—	—	—	—		
Trypodendron signatum (F.)	—	—	—	—		
Xyleborus dispar (F.)	—	—	—	—	—	
Xyleborus saxeseni (Ratzeburg)	—	—	—	—	—	
Ernopocerus fagi (F.)	—	—	—	—	—	—
Taphrorychus bicolor (Herbst)		—	—	—	—	—
Hylecoetus dermestoides (L.)		—	—	—		
Ptinomorphus imperialis (L.)		—	—	—	—	
Rhagium mordax (De Geer)		—	—	—	—	
Xestobium plumbeum (Illiger)			—	—	—	
Melasis buprestoides (L.)			—	—	—	
Melandrya caraboides (L.)				—	—	
Pyrochroa coccinea (L.)				—	—	
Sinodendron cylindricum (L.)				—	—	—
Ptilinus pectinicornis (L.)				—	—	
Lichenophanes varius (Illiger)				—	—	—
Tomoxia biguttata (Gyllenhal)				—	—	—
Leptura scutellata (F.)				—	—	—
Clytus arietis (L.)				—	—	—
Plagionotus arcuatus (L.)				—	—	
Anaglyptus mysticus (L.)				—	—	
Leiopus nebulosus (L.)				—	—	—
Saperda scalaris (L.)				—	—	
Platystomus albinus (L.)				—	—	—
Scolytus intricatus Ratzeburg					—	
Dorcus parallelopipedus (L.)					—	—
Dicerca berolinensis (Herbst)					—	—
Chrysobothris affinis (F.)					—	
Agrilus viridis (L.)					—	—
Strangalia quadrifasciata (L.)					—	
Necydalis major (L.)					—	
Cerambyx scopolii Fuessly					—	
Rosalia alpina (L.)					—	
Xylotrechus antilope (Schönherr)					—	

The period of flight observed in each species is denoted by a horizontal line.

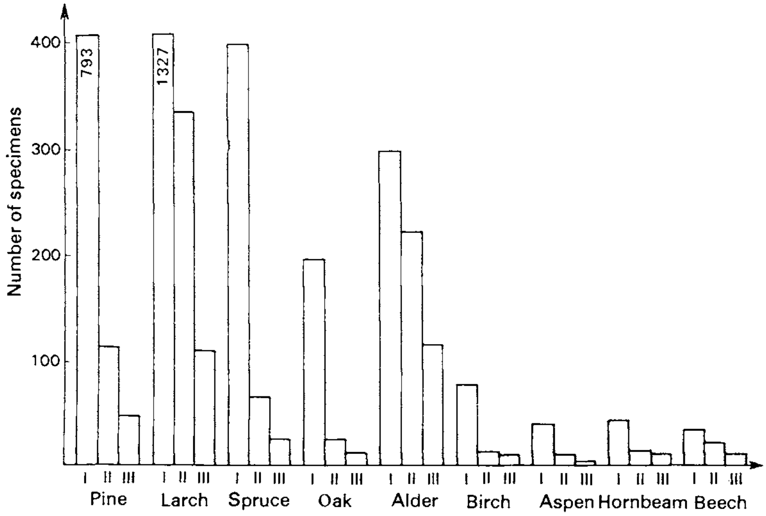


Fig. 6.24 Distribution of hibernating insects on tree trunks (after Szozda, 1972): I – 0–0.5 m above ground, II – 0.5–1 m above ground, III – 1–1.5 m above ground

and *Cinara* (= *Lachnus*) *pinicola* (Kaltenbach) (*Harmonia*) and on the mycelium occurring on tree needles and bark (*Myrrha*). The following species are characteristic of the bark environment considered: *Carabidae – Dromius schneideri* Crotch, *D. quadrimaculatus* (L.), *D. quadraticollis* Morawitz, *D.* and *D. agilis* (F.) the adults of which live in tree crowns while their larvae inhabit galleries of xylophages; *Coccinellidae–Rhyzobius chrysomeloides* (Herbst), *Scymnus suturalis* Thunberg, *Chilocorus bipustulatus* (L.), *Adalia conglomerata* (L.), *A. decempunctata* (L.) and *Anaspis melanostoma* Costa, which belong to the fauna of tree crowns. Other *Coleoptera* occurring in this habitat, such as *Salpingus* (*Sphaeriestes*) *castaneus* (Panzer), *Rhinosimus planirostris* (F.), *R. ruficollis* (L.), *Orchesia fasciata* (Illiger), *O. minor* Walker and *Calambus bipustulatus* (L.), represent communities of sub-bark insects and are also species characteristic of decomposed wood and bark.

Litter species hibernating under the bark greatly contribute to the aggregation described. Very many hygrophilous beetles, particularly staphylinids, abandon the damp biotopes in which their development takes place and migrate in autumn to drier forests in search of hibernating sites. *Staphylinidae* characteristic of damp forest meadows and alder forests, such as *Gabrius pennatus* Sharp and *Philonthus micans* (Gravenhorst), fly as far as several kilometres and from the end of September onwards are found in agglomerations consisting of numerous individuals in the litter of dry pine forests. The tendency to lose a proportion of their body water to facilitate survival in low temperatures is probably the main reason for their migration from a damp environment to a dry one. Moreover individuals probably originating from the same parents undergo considerable regrouping, thus possibly preventing inbreeding in the next vegetation season.

Migrations sometimes take place during the course of the vegetation season and may then exhibit a cyclic character. In aphids this phenomenon is sometimes associated with a change of host plant and alternation of generations, i.e. heterogony.

Migrations associated with food deficiency and excessive population density in the environment are particularly important in the functioning of biocenoses and productivity of ecosystems. As a phenomenon of quantitative regulation it has been described in earlier parts of this book.

6.4.3 Changes in insect communities occurring with the growth of forest stands

Most forest stands in Poland are even-aged and are formed as the result of artificial or sometimes natural regeneration of clear fellings. Such forest stands pass through the following life stages: plantation, thicket, old thicket, pole-sized stand, forest maturing and mature forest. The forest is then felled and reafforested. Each stage is characterized by definite microclimatic conditions which also depend on other environmental factors and the specific composition of the forest stand. These stages are also characterized by definite properties of timber production, the effect of tree increment and the process of self thinning.

The process of the growth of forest stands is accompanied by regular changes in the specific composition and structure of insect communities as a result of the influence of variable factors of the abiotic and biotic environment. Changes are observed in the entomofauna inhabiting all the existing forest layers from the soil and litter, through the herb layer, shrubs, tree trunks and up to the tree crowns.

Such changes have been studied in detail in litter *Staphylinidae* and have been found to be cyclic and conditioned by the existence of successive generations of even-aged forest stands. They do not lead to any essential exchange of species, but involve considerable variations in the abundance of individual species within the community in successive stages of the development of the forest stand. The cyclic course of the changes in the composition of staphylinid groups occurring during the lifetime of a pine forest stand in a young coniferous forest is described below.

In timber forest stands, *Sipalia circellaris* (Gravenhorst) is the dominant species with *Othius myrmecophilus* Kiesenwetter and *Mycetoporus splendidus* (Gravenhorst) (Fig. 6.25) subdominant. The composition of the community corresponds to the habitat since *G. circellaris* and *O. myrmecophilus* are forest species adapted to living in the superficial layer of the forest soil. Clear felling and the preparation of the soil plantation lead to a degeneration of the community, resulting in the elimination of specialized soil *Staphylinidae* in favour of eurytopic species and in a decrease in their density from 16 to 8 individuals per 1 m^2. In young plantations the staphylinid community passes through a particularly critical period, during which its quantitative and specific composition appears isolated from the rest of the forest entomofauna.

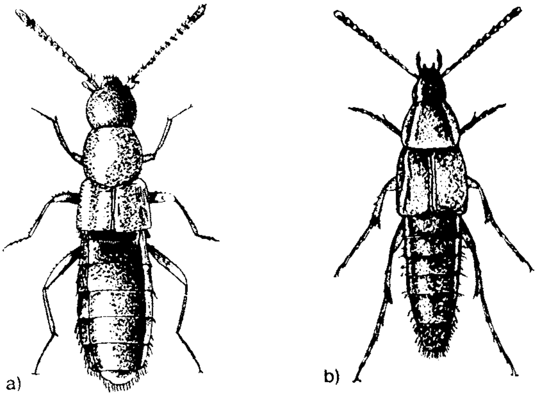


Fig. 6.25 Most important species of litter *Staphylinidae* occurring in pine forests: a) *Sipalia circellaris* (Gravenhorst), b) *Mycetoporus splendidus* (Gravenhorst)

The eurytopic *Tachyporus chrysomelinus* (L.) dominates here and the density of the community decreases to 4–5 individuals per 1 m^2, whereas the distribution of the beetles acquires an aggregation character. Two or three years after the stand reaches full compactness, the community starts to regenerate as the result of microclimatic changes and the accumulation of litter. The dominance of eurytopic species wanes, whereas *M. splendidus* and *Stenus geniculatus* Gravenhorst prevail quantitatively. The proportion of *S. circellaris* and *O. myrmecophilus* rises and the density of the community increases to 10–11 per 1 m². The regeneration phase of the community occurs over a 10 year period, during which a final exchange of dominants takes place. Between the 20th and 30th year of the forest stands life *Sipalia* and *Othius* again begin to dominate and the density returns to the level of 16 individuals per 1 m².

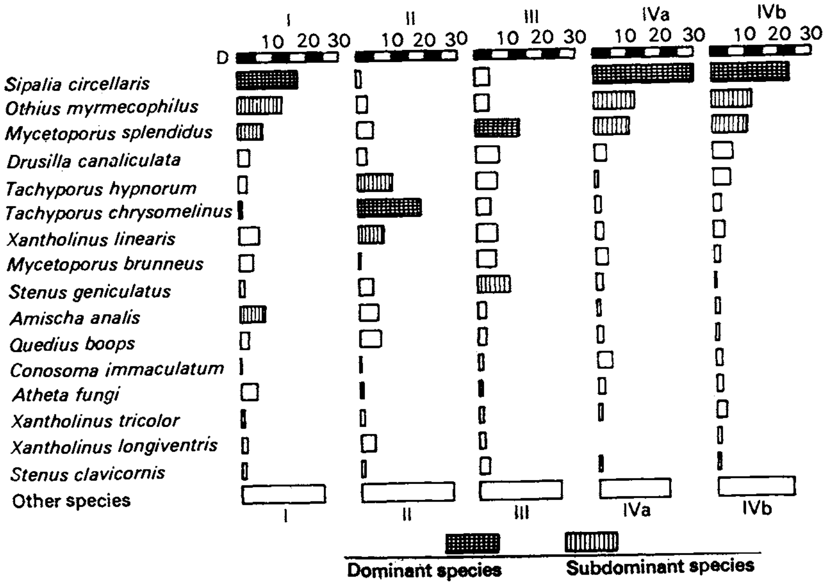


Fig. 6.26 Structure of the community of litter *Staphylinidae* in various period of the productive cycle of pine forest stands I–IVb (after Szujecki, 1966c): D – dominance percentage

Figure 6.26 represents the structure of the staphylinid community in various periods of the productive cycle of forest stands (I – fellings and 1-year plantations, II = plantations, III – thickets, IV – middle-aged and older forest stands).

Obviously such changes proceed somewhat differently in insect communities of the other layers of the forest biotope and in other forest habitat types.

A study of the specific and quantitative composition of *Chalcidoidea* in two 3–2 year-old pine plantations and a 14 year-old thicket in a habitat of mixed forest in the Experimental Forests of the Agricultural University in Warsaw, indicates that there is a gradual exchange of species associated with the herb layer to species indirectly associated with the pine. The abundance of individuals of the family *Pteromalidae* distinctly increased with the age of the plantations, whereas the abundance of *Eulophidae*, which are mostly parasitic on leaf-mining larvae, abruptly decreases in the thicket. In 7 year-old plantations, the high numbers of *Eulophidae* was almost entirely due to the abundance of the parasites of *Thecodiplosis brachyntera* (Schwägrichen) which was destroying the pine needles (*Tetrastichus charoba* (Walker) and *T. gaus* (Walker)).

The ageing of the plantations and the thicket was accompanied by characteristic changes in the distribution of individuals in the herb layer and in the tree crowns. These changes are indicative of the complex influence of environmental factors (microclimate, competition of plants for light, presence of hosts) on the composition of the parasitic *Hymenoptera*. It appeared that in the 3 year-old plantation, 67.8% of these insects occurred in the herb layer and 32.2% in the crowns, whereas in the thicket there were 36.5% in the herb layer and 63.5% in the crowns (Szczepański, 1968).

The differences in the competition between phytophages feeding on trees of varying age are particularly well known. Many manuals of forest entomology stress such differences, using them as a basis for classifying insects into pests of plantations, thickets, middle aged and old forest stands respectively. The distribution of closely related species in various age classes of forest stands shows that there is a tendency for them to

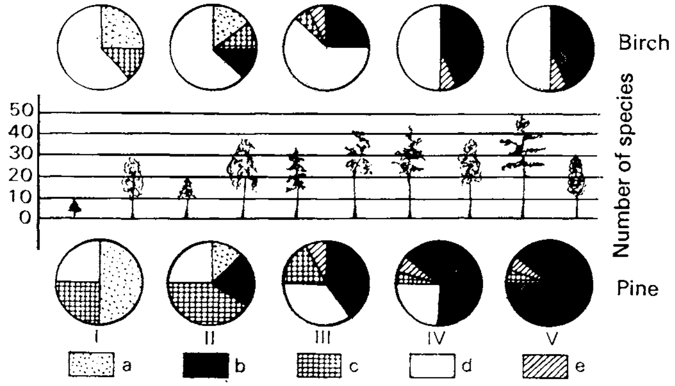


Fig. 6.27 Change in the biological groups of pine and birch pests during the course of the growth of the forest stand (after Vorontsov, 1963): I – plantation, II – old thicket, III – average-aged forest stand, IV – mature forest stand, V – superannuated stand: a – pests of roots, b – pests of trunks and branches, c – pests of shoots and buds, d – pests of leaves, e – pests of generative organs

occupy different ecological niches, thus reducing the competition between such species.

Of the few species belonging to the genus *Acantholyda* which feed on the pine in Poland, one feeds in plantations (*A. hieroglyphica* (Christ)) one in thickets (*A. erythrocephala* (L.)) and one in middle-aged and old forest stands (*A. posticalis* Matsumura (= *nemoralis*) Thomson).

The contribution of pests which attack definite parts of trees also undergoes important changes in the individual developmental stages of the forest stand (Fig. 6.27).

Insects classified as secondary pests may play an important role in the process of self-thinning and natural pruning during the development and growth of forest stands. This useful role of insects otherwise regarded as pests, has so far been poorly understood and evaluated.

Insects in the functioning of forest biocenoses

6.5 Biotic associations of forest insects

Besides the process of photosynthesis and plants mineral consumption mutual relationships between living organisms and their contribution to the consumption of dead organisms also play a decisive role in the functioning of biocenoses. These dependences both serve to determine the turnover of matter and the flow of energy through the ecosystem. Thus, the ecological specialization of the components of the biocenosis determines its trophic, competitive and paratrophic structure (Trojan, 1975).

Trophic structure of biocenoses. The trophic structure consists of systems of "exploitation" relationships which link individual elements of the biocenosis from plants, through phytophages and parasites to coprophages and necrophages.

There are chains and networks which consist of several links, but usually not more than five to seven. The trophic structure may be very sparse and consist of small populations in each or some links of the alimentary chain. In such cases this structure is particularly susceptible to external stimuli and this is manifested by a low quantitative stability of their components.

Green plants assimilating energy from the sun are the first link of the alimentary chain. The second consists of the phytophages, while the third is composed of their parasites and predators. The natural enemies of the named group constitute the next link. Such elementary trophic structures are somewhat unstable, but if habitat conditions are favourable they tend towards expansion. In such cases a number of parallel alimentary chains may be connected by common links and thus form an alimentary network. Figure 6.28 represents a section of such a network (the pine being its first link) illustrating the host–parasite system of *Rhyacionia buoliana* (D. & S.).

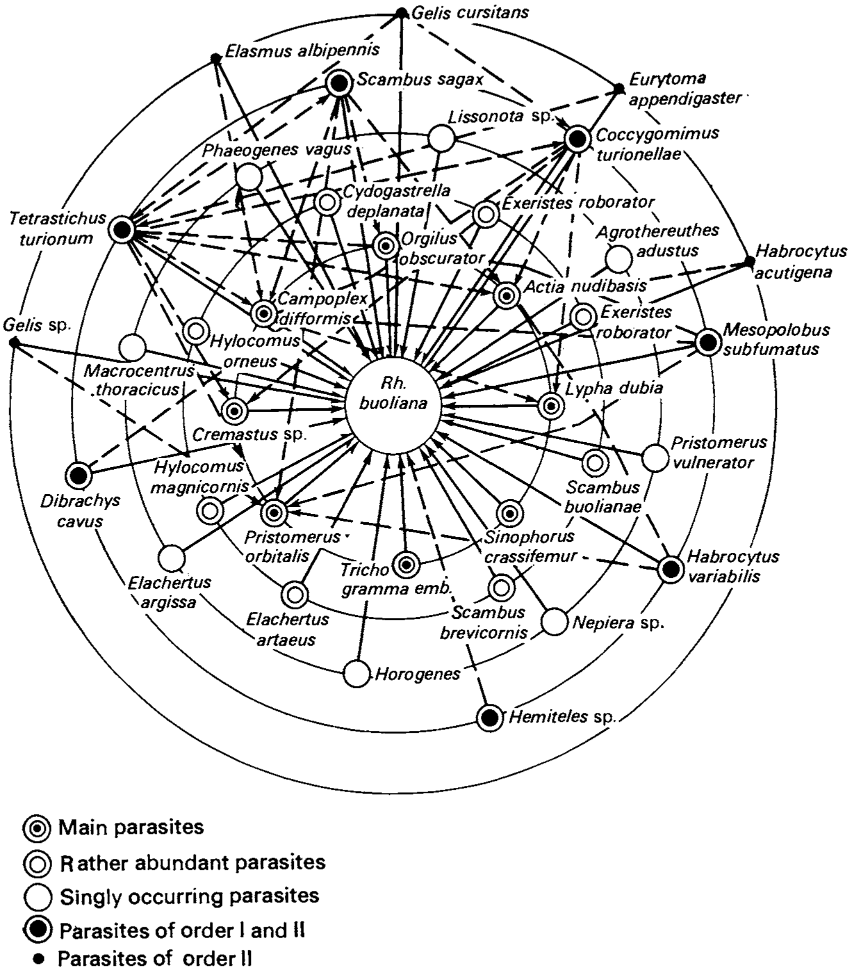


Fig. 6.28 Systems of host–parasite relationships of *Rhyacionia buoliana* (D. & S.) (after Koehler, 1967)

The number of chains forming the networks of trophic relationships increases with the diversity of the specific composition of the biocenosis especially with regard to the polyphagous species which participate in it.

In such cases there is, invariably, the possibility that one species may be substituted by another in each link. This ensures the stability of the trophic structure of the biocenosis, although it does not prevent the quantitative proportions of species contributing to its composition from changing. On the other hand, however, deformations of the network are inversely proportional to the number of its links. Thus, the extension of the specific composition of the forest stand tends to increase the homeostatic capacities of forest biocenoses. Thus the number of insect species in muti-species forest stands is distinctly higher than that in monocultures.

Changes in the links of alimentary chains are normal occurrences. They are due to a number of factors, including different alimentary requirements of species at their various developmental stages, the selectivity of alimentary requirements of polyphages and seasonal phenomena. Figure 6.29 represents the possible changes in the links of the alimentary chain of insects associated with the bilberry depending on the season of the year. The ichneumonid parasite *Scambus brevicornis* (Gravenhorst) begins to attack the caterpillars of *Chloroclystis debiliata* (Hübner) feeding on bilberry leaves in April. The development of this parasite takes 15–20 days and thus two generations may develop on the host. In the beginning of June the second generation of the ichneumon lays eggs in the caterpillars of another geometrid, *Angerona prunaria* (L.), whereas in summer it may parasitise other species of *Lepidoptera*, such as *Rheumaptera hastata* (L.) and *R. undulata* (L.). Finally, in early autumn

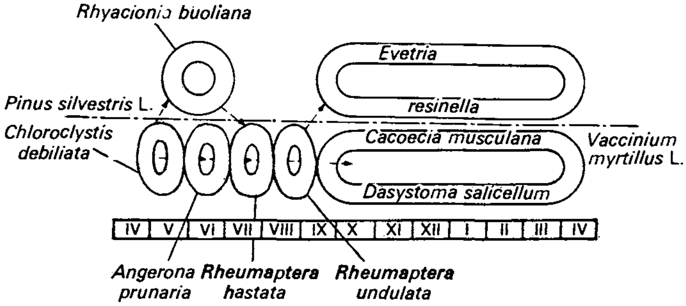


Fig. 6.29 Changes in the links of the alimentary chain of the ichneumon *Scambus brevicornis* (Gravenhorst) (after Karczewski, 1962): Roman numerals – months

it attacks the caterpillars of *Cheimophila* (= *Dasystoma*) *salicella* (Hübner) and *Syndemis* (= *Cacoecia*) *musculana* (Hübner) in which it hibernates. Thus *S. brevicornis*, which is also an important parasite of the pine pests *Rhyacionia buoliana* (D. & S.) and *Petrova resinella* (L.), can find substitute hosts in various seasons of the year in the form of insects which feed in the herb layer (Karczewski, 1962). This is very important from the standpoint of forest protection.

The alimentary chains may be particularly complex when the same species happens to be both a primary and secondary parasite. For instance, *Paranastatus egregius* (Foerster), the primary parasite of *Euproctis similis* (Fuessly) may also be a parasite of the second or even third order attacking its parasites and secondary parasites.

Many interesting works have been published on the subject of alimentary chains. They are of particular value when the authors have succeeded in combining studies on the biology of feeding with observations of changes in the structure of alimentary chains within a determined period. A good example of this is Robinson's (1953) study on the association of organisms dwelling in the brown sap secreted from wounded elms which appears to exhibit a peculiar rhythm. The animals appear and disappear depending on the season of the year. Various forms replace one another, each new form taking over the ecological functions of the former as soon as the latter ceases its activity. The states of activity, rest and migration of all these forms constantly alternate, thus securing both the preservation of mutual relationships within the association and the normal course of life processes of the contributing forms (Fig. 6.30) within the year.

The number of links in the alimentary chains of any biocenosis is limited by the rule of the pyramid of numbers which was formulated by Elton in 1927. The pyramid of numbers, or more precisely the pyramid of masses, determines the loss of biomass of every successive link in an alimentary chain. This loss is due to the fact that not all the food is utilized for the growth of individuals, a considerable part being used to compensate for the energy losses of the organism (respiration, functioning of muscles, etc.). Thus each successive link dispenses with a lesser and lesser amount of biomass.

Competitive structure of biocenoses. Competition is the interaction of two or more organisms contesting for the same resource, such as food, life space and light, etc., and it exercises an unfavourable influence on the increase and survival of populations. In cases where the ecological niches of competitive species partly overlap, competition plays an important role in the development of insect associations, whereas in cases where these niches overlap completely such species cannot occur together. Thus, competition exercises a negative influence on both species taking part in this interaction.

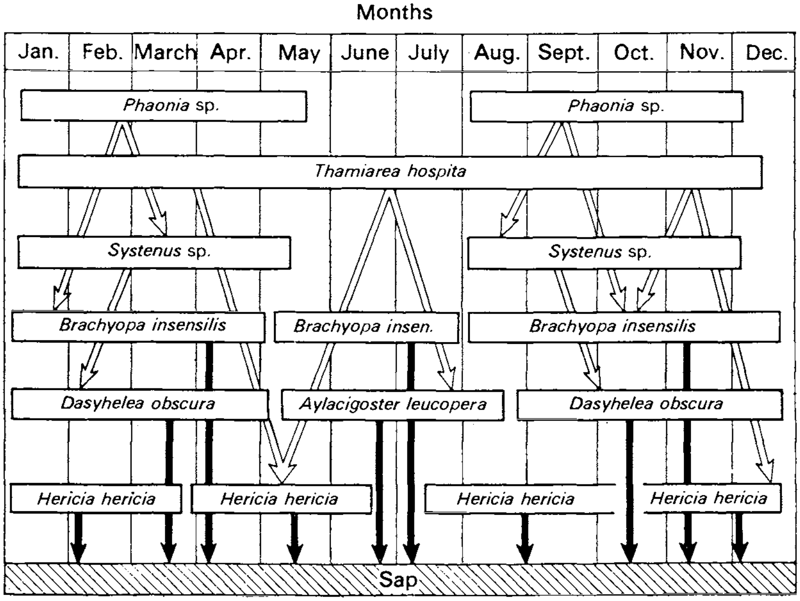


Fig. 6.30 Alimentary chains of organisms living on the elm in brown sap flowing from trunks (after Robinson, according to Macfadyen, 1963): black arrows indicate alimentary dependences of animals feeding on sap, light arrows indicate the influence of their parasites and predators

Examples of competition for space and food can be seen in insects which occur under bark. The simultaneous occurrence of two bark beetles such as *Ips amitinus* (Eichhoff) and *Polygraphus poligraphus* (L.) on a limited surface, restricts the abundance of both species. The effects of competition are considerably less severe for one species than for the other. In cases when *Acanthocinus aedilis* (L.) and *Tomicus piniperda* (L.) feed simultaneously under the bark, their competition limits the larvae of the bark-beetles more than those of the cerambycid.

The competition for food which occurs between the larvae of *Tortrix viridana* (L.) and the adults of *Melolontha* sp. feeding on oak also limits the abundance of the tortricid more than that of the melolonthine. Migration of the latter to other trees is possible and only a mass appearance of *T. viridana* may considerably limit the food stock leading to a decrease of fertility of females of these beetles.

The competitive structure of a biocenosis is manifested by the quantitative variability of its components and by the occurrence of a dominance hierarchy of the species in the associations. Dominant species play the most important role in the biocenosis since the largest amount of energy flows through their level. Changes in environmental conditions, evoked by various causes, change the dominance structure of individual elements of the biocenosis. Under new ecological conditions other species usurp the position of the dominants. This secures the functioning of associations and is an expression of the homeostatic capacities of the biocenosis.

Paratrophic structure of biocenoses. The paratrophic structure of a biocenosis also includes trophic relationships between its components which play a very important stimulating role in the life processes of organisms but do not involve any form of exploitation. Thus, the paratrophic association is favourable for at least one of the components and has no negative effect on the other. Such relationships include mutualism, symbiosis, protocooperation and commensalism.

Mutualism is a positive interaction with advantages for both partners and indispensable for at least one of them.

Among forest insects the phenomenon of mutualism is rare and really only the coexistence of "true" ant-hill guests (i.e. adult symphils with ants) can be cited as an example here. The adult symphils are nursed, protected and fed by ants. In some cases this careful protection extends to other developmental stages of symphils. On the other hand, the symphils secrete a substance produced in the allotrophic glands which is readily licked by the ants. *Lomechusa paradoxa* Gravenhorst and *Lomechusoides strumosa* (F.) are examples of symphils which coexist with ant species of the genus *Formica* (Fig. 6.31).

Further examples where mutualism is obligatory for both partners are observed in various species which live in wood and in fungi. In Polish forests, *Hylecoetus dermestoides* (L.), *Trypodendron* spp., *Xyleborus* spp., *Platypus cylindrus* (F.) and most *Siricidae* belong to this group. *H. dermestoides* has pockets containing spores at the base of the ovipositor. The spores pass onto the eggs, and when the larvae hatch they eat them along with the chorion. The spores are excreted onto the walls of the galleries formed in the wood and their resultant mycelia become the food of the larvae. From the population standpoint, the advantage of

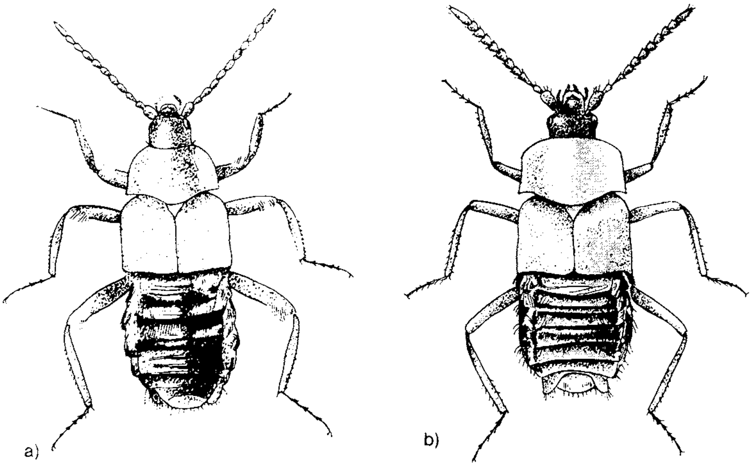


Fig. 6.31 Symphiles living in ant nests: a – *Lomechusoides strumosa* (F.), b – *Lomechusa paradoxa* Gravenhorst

such a coexistence is obvious when it is realized that the propagation of the fungus *Endomyces hylecoeti* is possible only with the contribution of *H. dermestoides.*

The obligatory mutualism which occurs between *Xyleborus* spp. and *Trypodendron* spp., on the one hand, and fungi (of which *Monilia candida* associated with *Trypodendron lineatum* (Olivier) is the best known example) on the other, is of a similar nature to that observed in the case of *H. dermestoides.* The transfer of spores by the bark-beetles, however, is mainly associated with the structure of the prothorax on which special spore containers (detected by Nunberg (1951a) in *T. lineatus*) occur in the form of glands (Fig. 6.32). In other bark-beetles they resemble pockets and hollows and sometimes occur between the mesothorax and metathorax (*Xylosandrus germanus* (Blandford), introduced into Germany in timber from the tropics), at the base of the elytra (*Xyleborus saxeseni* (Ratzeburg), between the elytra (*Tomicus minor* (Hartig)), behind the base of mandibles (*Xyleborus eurygraphus* (Ratzeburg)) or on other parts of the body (Fig. 6.33).

Symbiosis in which two organisms are in mutual contact is a particular form of mutualism. Such relationships have been observed in and between wood-dwelling insects (e.g. *Anobiidae*) and microorganisms (e.g. *Saccharomycetes*) which occur in their alimentary canal. The *Saccharomycetes* serve to provide the anobiid larvae with proteins which are absent from the hardwood on which these beetles feed. The benefit

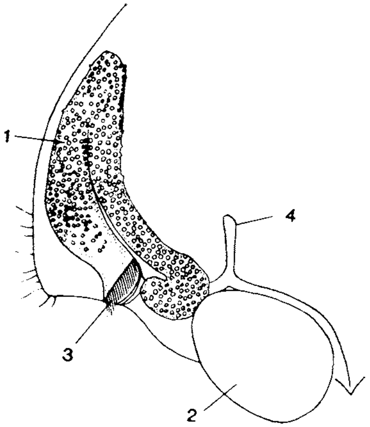


Fig. 6.32 Left prothoracic gland of the female of *Trypodendron lineatum* (Olivier) (after Francke-Grossman, 1959): 1 – gland, 2 – coxa, 3 – gland inlet, 4 – parts of the skeleton of the coxal acetabulum

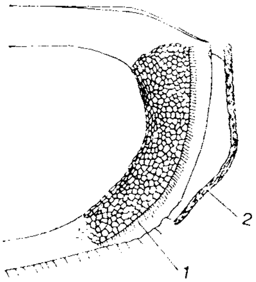


Fig. 6.33 Right integument of *Scolytus scolytus* (F.) (internal view) in which spores of *Graphium ulmi* are carried (after Francke-Grossman, 1959): 1 – setae securing spores carried beneath integument, 2 – extracted membrane of secretion with spores

gained by the *Saccharomycetes*, on the other hand, is that they feed on the undigested cellulose in the alimentary canal of the larvae.

Protocooperation occurs when the two species involved both benefit from the association (as in symbiosis), but in this case the association is not obligatory for either partner. The phenomenon of trophobiosis, i.e. the feeding of ants on honey-dew exuded by aphids, is an example of protocooperation. The advantage is mutual since the ants obtain food, whereas the presence of ants protects the aphids from their enemies.

Ants feed on proteins and sugars. The proteins are obtained in the form of insects and other invertebrates as well as seeds and other plant products rich in nitrogen compounds which are accumulated in the ant-hills. Honey-dew is the main source of essential sugars and is produced by various *Homoptera* such as aphids, coccids and psyllids. The relationships between individual ant species and producers of honey-dew vary and may either be very loose or very close. Trophobiosis has been observed in those ant species in which the mutual provision of food takes place. The ant demanding food from the aphid behaves as if it were demanding food from another ant. The aphid raises its third pair of legs to a horizontal position and thus resembles an ant offering food (Fig. 6.34), and when irritated by the ant's antennae it excretes drops of honey-dew which is consumed by the ant.

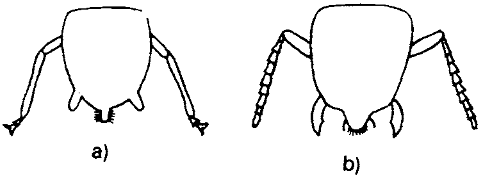


Fig. 6.34 Outline of abdomen of an aphid (a) and of ant head (b) (after Haragsim, 1966)

Ants which do not force honey-dew from aphids but collect the secreted droplets from plant surfaces do not protect the aphids from their enemies.

Ants taking part in trophobiosis not only protect the aphids, but also transfer their eggs and even adult females, prepare sites suitable for the settlement of their colonies, etc.

Relationships which occur between insects feeding on nectar and pollen on the one hand, and flowering plants on the other, may also be regarded as instances of protocooperation. In extreme cases, particularly where entomophilous plants are concerned, these associations are obligatory and are of a mutual nature, supported by morphological adaptations of both partners.

Diptera belonging to the families *Tachinidae* (particularly *Exoristinae* and *Echinomyiinae*) and *Calliphoridae* are most readily attracted by flowers which have easy access to the nectar such as *Umbelliferae*, *Euphorbiaceae*, *Rhamnaceae* and *Ericaceae*, etc. Flowers with less readily accessible nectar such as *Compositae* or *Labiateae* are visited by species of the subfamilies *Dexiinae* and *Phasiinae*. These have a relatively long oral apparatus and narrow oral plate, thus enabling their penetration to the base of the style where the nectar is available (Tables 6.3 and 6.4).

Table 6.3 Number of *Tachinidae* species in flowers with readily accessible nectar (after Karczewski, 1967b).

Item	Name of plant	Subfamilies			
		Exoristinae	*Echinomyiinae*	*Dexiinae*	*Phasiinae*
1	*Euphorbia cyparissias* L.	21	9	3	6
	Euphorbia esula L.	13	7	3	5
	Frangula alnus Miller	29	7	6	2
	Pimpinella saxifraga L.	9	3	7	8
	Heracleum sibiricum L.	17	12	1	3
	Peucedanum oreoselinum (L.) Moench	14	9	4	6
	Peucedanum palustre (L.) Moench	23	10	2	6
	Pastinaca sativa L.	26	10	5	7
	Daucus carota L.	7	6	4	5
2	Mean number of *Tachinidae* species per 1 plant species	17.4	8.1	3.8	5.3
3	Number of *Tachinidae* species on flowers	68	36	20	25
4	Ratio 2:3, %	25.6	22.5	19	21.2

In pine forests, nectariferous plants do not flower simultaneously and thus provide a continuous source of food for ichneumons, tachinids and other insects. Flowers are most important for mellitophages at the beginning and end of the vegetation season when there is no honey-dew available in the forest environment (Karczewski, 1967b). *Peucedanum oreoselinum* (L.) Moench (*Umbelliferae*; Fig. 6.35) is the most important nectariferous plant in pine forests and occurs mostly on dry and sandy soils, in forest plantations as well as on compartment lines. *Peucedanum palustre* (L.) Moench has a similar biocenotic role in forest associations on moist soils. Flowers of each of these plants are visited by over 50 species of tachinid flies, including *Tachina magnicornis* (Zetterstedt), *T. grossa* (L.), *Staurochaeta albocingulata* (Fallén), *Senotainia conica* (Fallén), *S. albifrons* (Rondani), *Actia tibialis* (Robineau-Desvoidy) and *Pollenia rudis* (F.) (Fig. 6.36). Sawoniewicz's (1973) studies demonstrated that flowers of *P. oreoselinum* in pine plantations in the Podlasie region are visited by 205 ichneumonid species, among which *Scambus brevicornis* (Gravenhorst), a parasite of *Tortricidae*, and *Exoteleia dodecella* (L.) as well as *Lissonota paralella* Gravenhorst, a parasite of phytophages feeding on the herb layer, dominate. About 5% of the individuals of this community are parasites of *Agrotis vestigialis* (Hufnagel) and *A. segetum* (D. & S.) and include *Ichneumon sarcitorius* (L.), *Banchus falcatorius* (F.) and *Amblyteles pulchellus* (Christ).

Table 6.4 Number of *Tachinidae* species on flowers with hardly accessible nectar (after Karczewski, 1967b).

Item	Name of plant	Subfamily			
		Exoristinae	*Echinomyiinae*	*Dexiinae*	*Phasiinae*
1	*Solidago virga-aurea* L.	1	4	3	1
	Bellis perennis L.	5	0	4	4
	Anthemis arvensis L.	0	1	1	5
	Achillea millefolium L.	7	11	7	18
	Tripleurospermum inodorum Schultz – Bipontium	2	0	5	6
	Matricaria chamomilla L.	2	1	2	2
	Senetio vernalis Waldstein & Kitaibel	4	1	2	3
	Cirisium arvense (L.) Scopoli	2	4	3	3
2	Mean number of *Tachinidae* species per 1 plant species	2.8	2.7	3.3	5.2
3	Total number of *Tachinidae* species on flowers	68	36	20	25
4	Ratio 2:3, %	4.1	7.5	16.5	20.8

In older forest stands the number of individuals is smaller than in plantations by a factor of 30, many species being absent due to the shading of the forest floor. *Diplazon laetatorius* (F.), a parasite of predaceous syrphid larvae, dominates in this community, whereas among other species *Campoletis agilis* (Holmgren) and *Lissonota cylindrator* (F.), which are probably parasites of phytophages of the herb layer, are subdominant species. Parasites of noxious forest insects do not occur on flowers here. The flowers of *P. oreoselinum* are visited by numerous

Fig. 6.35. Flowers of *Peucedanum oreoselinum* (L.) Moench on an anti-fire shelterbelt n pine forest stands (photo by S. Kinelski)

Fig. 6.36 Tachina grossa (L.) (photo by T. Bojasiński)

species of *Coleoptera* (*Staphylinidae*, *Cerambycidae*, *Cleridae* and *Nitidulidae*), *Hymenoptera* (*Tenthredinidae*, *Formicidae*, *Vespidae*, *Apidae* and *Sphecidae*), *Diptera* (*Muscidae*, *Bombylidae*, *Syrphidae*, *Conopidae* and *Anthomyiidae*) and pentatomid bugs (Karczewski, 1961c). The entomofauna visiting heather flowers is also very rich. Heather blooms in the second half of summer and during this period it is the only source of nectar and pollen for many species of insects. A total of 301 species of insects belonging to 55 families of 5 orders has been observed on heather flowers (Karczewski, 1967a).

Commensalism is an interaction advantageous to one partner only and most frequently involves the utilization of the food remnants of one partner by the other. Numerous species of *Coleoptera* called synoeketes are indifferently tolerated guests of ants and live permanently in ant-hills. They feed on food remains, dead ants and faeces with advantage only to themselves.

Honey-dew feeding in situations where the producers gain no advantage should more properly be classified as peculiar cases of commensalism rather than as coprophagism.

Honey-dew is a very good source of food for the adults of many parasitic forest insects. In poor pine forests the honey-dew of various species of aphids and coccids living in the tree layer, undergrowth and herb layer is the main source of food for many parasitic insects such as tachinids. The following tachinids feed on honey-dew: *Bessa selecta* (Meigen), *Medina* (= *Degeeria*) *luctuosa* (Meigen), *Carcelia lucorum* (Meigen), *C. excisa* (Fallén) and *Thelaira nigripes* (F.), There are also some tachinids which feed casually on honey-dew (Karczewski, 1967b). It is essential for the correct functioning of the paratrophic structure that the sources of food obtained from non-exploitative associations be ensured in the course of the entire vegetation period. This is made possible by the large number of producers of honey-dew, each of which is active in different seasons of the year. *Phyllostroma myrtilli* Kaltenbach, living on the bilberry, supplies honey-dew to many parasites, particularly those flying early when aphids living on the pine are not yet active and produce only small amounts.

The feeding of adult parasitic insects on nectar or honey-dew is particularly important for the functioning of biocenotic regulating mechanisms in forest ecosystems. The paratrophic structure of the biocenosis may thus either enhance or limit (when not sufficiently extended) the occurrence of definite species in the biocenosis and therefore determine its homeostatic properties.

6.6 Contribution of insects to the flow of energy in the ecosystem

6.6.1 Energy budget of insects

As in other animals, the energy budget of insects is based on the energy assimilated by plants (Fig. 6.37). Insects may be phytophages, predators and parasites of successive orders or saprophages and thus take part in the transfer of energy throughout the whole ecosystems. Within the range of secondary production they may form a part of the biomass of any heterotrophic layer of the biocenosis. The feeding process of heterotrophic organisms consists of the assimilation of organic substances of plant or animal origin and their transformation into body tissues and organs. Assimilation consists of digestion, absorption, dissimilation (converting stored compounds and body tissues into available energy) and excretion of organic waste. Fat bodies, containing fats, glycogen and proteins, are the basic source of material for dissimilation. Being storage bodies they are particularly important during metamorphosis and the formation of the gametes and other products of the reproductive system, as well as during diapause and hibernation. The energy utilized in metabolic processes is obtained from the oxidation of carbohydrates:

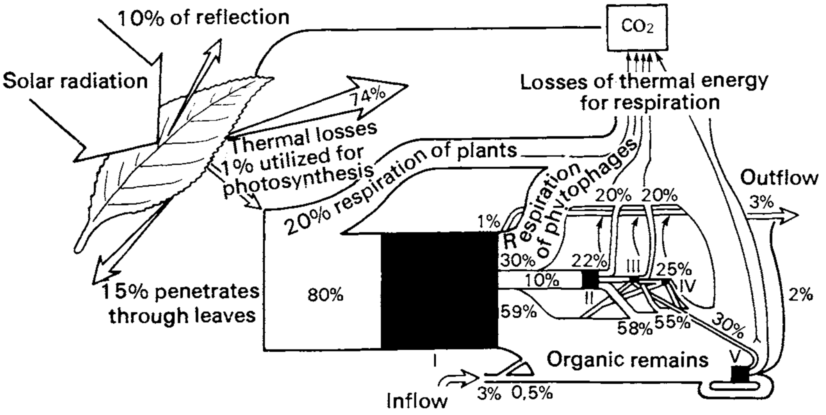
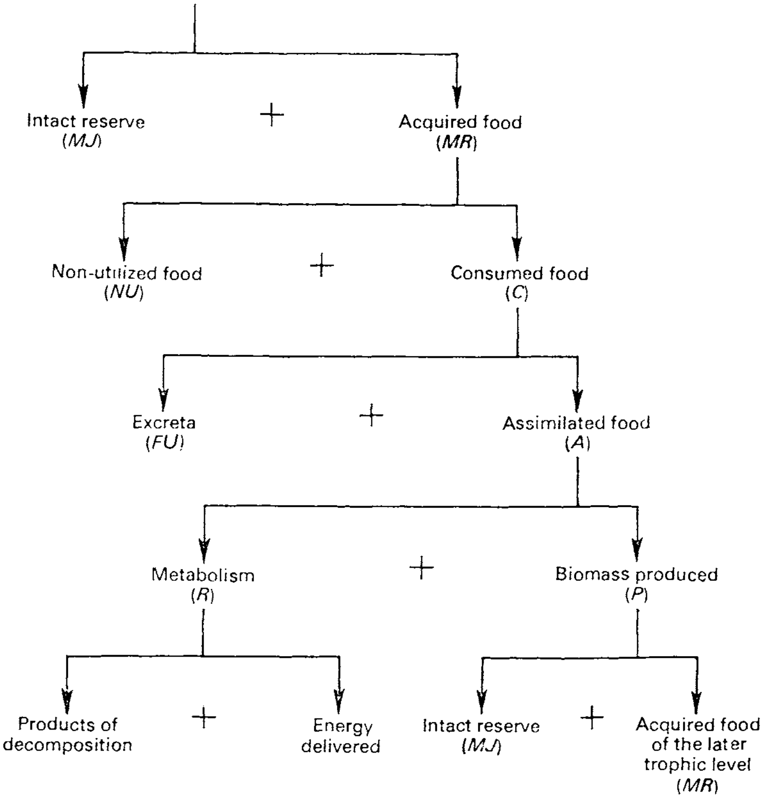


Fig. 6.37 Energy flow through the forest ecosystem (after Rafes, 1968): I – biomass of plants, II – phytophages, III – zoophages of first order, IV – zoophages of second order, V – saprophages. Black rectangles indicate the total amount of energy received by each trophic level

$$C_6H_{12} + 6\,O_2 \rightarrow 6\,CO_2 + 6\,H_2O + \text{energy}.$$

This takes place in several stages, each catalysed by special enzymes or other specific substances. The flow of energy through the given trophic level of heterotrophic organisms is expressed by the following diagram:



Only a part of the food available to the consumer (MA) is acquired and eliminated from the reserve (MR). A smaller or larger proportion of the alimentary base remains as an intact reserve (MJ). This reserve has a decisive role in the production of biomass at the trophic level of autotrophic organisms and biophages. The participation of the given species in the utilization of the food reserve of the lower trophic level is expressed by the exploitation coefficient:

$$E_e = \frac{MR}{MA}$$

The quantity of the assimilative apparatus of trees (e.g. leaves) exploited by foliophages is very important in the production of forest stands (Varley, 1967) since the increment of trees depends directly on the surface of this apparatus. Rafes *et al.* (1972) proved that losses in wood production take place when the daily consumption of leaves by phytophages exceeds 0.3% of the assimilative apparatus. When it is lower than this value, however, compensative chloroplast reactions maintain the increment at a normal level.

The food preferences of insects determine what part of the food acquired is consumed (C) and what part remains in the form of waste matter (NU).

The ratio of food consumed to food acquired is called the coefficient of material utilization:

$$E_c = \frac{C}{MR}$$

Four ecological groups of heterotrophic organisms, characterized by different degrees of utilization of the food acquired, have been distinguished by Trojan (1975).

The first group includes those predators which entirely consume their prey ($E_c = 1$).

The second group is composed of those species which do not entirely utilize the food source ($E_c = 0.75$), such as predaceous insects which suck their prey (*Asilidae*, *Pentatomidae*, etc.) and phytophages which reject a part of the leaves bitten. Rejection of parts of leaves results from the fact that the larvae feeding on the assimilative apparatus damage more leaves or needles than they are able to consume. The amount of "scrap", i.e. damaged and drying leaves or needles, constitutes a considerable percentage of the food of phytophages, particularly older larvae and species which tend to feed "wastefully", such as caterpillars of *Lymantria monacha* (L.). The gnawing of needle margins or skeletonizing of leaves invariably leads to their drying and premature shedding, etc. This mode of feeding also exploits the preceding trophic level to an extent exceeding the requirements of the next level. The non-consumed part of the leaves, which is chemically almost identical with those remaining on the tree, drops to the ground prematurely, before the seasonal fall of leaves, and it thus subjected to the action of the soil fauna. This is very important in the cycle of the flow of energy and biomass through the ecosystem.

The third group includes species which consume only small parts of the material selected ($E_c = 0.25$) and reject the rest, such as *Barbitistes constrictus* Brunner von Wattenwyl which gnaws whole needles but consumes only their basal parts.

The fourth group is composed of those species which consume even less of the material selected. These are mainly phytophages, including insects feeding on cambium (e.g. bark-beetles) and buds (*Exoteleia dodecella* (L.), *Archips oporana* (L.)). The effects of their activity in the ecosystem are considerable since even the slightest amount of food consumed excludes considerable amounts of the biomass from further production (Fig. 6.38). The ingested food or consumption (C) determines the amount of energy flow (energy budget of organisms) in the subsequent trophic level according to the formula:

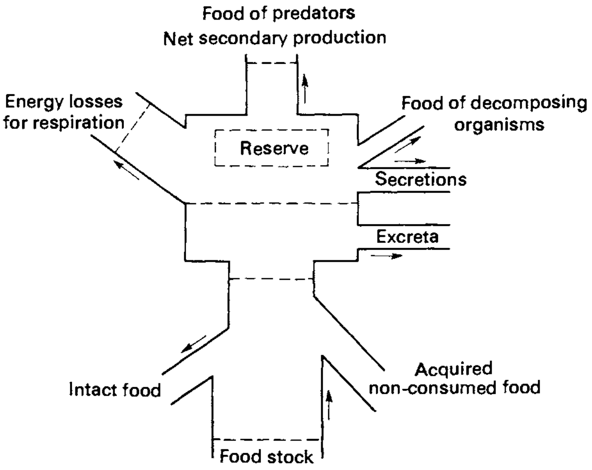


Fig. 6.38 Diagram of flow of energy and matter at the phytophage level (according to Macfadyen, after Rafes, 1968)

$$C = P + R + FU$$

where C = consumption or food requirements, P = production (accretion of energy or biomass in the trophic level), R = respiration or respiration losses (energy of the cost of living), FU = faecal or excretion losses (faeces + urine).

Two values of the energy budget, i.e. production and respiration include the energy assimilated or assimilation (A). Therefore:

$$A_1 = P + R \quad \text{or} \quad A_2 = C - FU$$

Data for these equations are obtained from laboratory measurements which may be extrapolated to the entire population and environmental conditions. It then appears, however, that $A_1 \neq A_2$. This was observed by Winter (1971) who studied assimilation in *Diurnea fagella* (D. & S.) and Smith (1972) who studied some *Geometridae.*

The secondary production, i.e. the difference between the amounts of biomass in the given time interval may be calculated in terms of weight or energy.

Phillipson (1971) proposed the following formula for calculating secondary production:

$$P = P_g = P_r + P_e$$

where P = production, P_g = body growth, P_r = accretion due to reproduction, P_e = excretion and shedding of the cuticle.

There are two methods of calculating production, based either on elimination or circulation. These methods are described by Trojan (1975).

In *Leucoma* (= *Stilpnotia*) *salicis* (L.) the production due to growth (P_g) exhibits two peaks. This is due to the fact that the body weight of the larvae increases in two successive generations. In spring the value P_g is several times higher (due to the development of larvae L_3-L_7) than in autumn, when the accretion of weight of the youngest larval stages is very low. Thus, the total annual production (P_g) was mostly determined by the two last larval stages which produced 93.5% of the biomass of the entire generation (Table 6.5). The production of eggs

Table 6.5 Production (Pg) of a population of *Leucoma salicis* (L.) per 1 m^2 in two environments (*A* and *B*) (after Migula, 1975).

Development stage	1971				1972			
	A		*B*		*A*		*B*	
	mg	J	mg	J	mg	J	mg	J
l_1	0.230	4 454.3	0.280	532.9	0.134	2 616.3	0.009	178.3
l_2	0.156	3 213.7	0.019	391.4	0.148	3 001.5	0.007	150.7
l_3	0.131	2 551.0	0.022	426.2	0.231	4 530.1	0.018	356.7
l_4	0.234	4 835.7	0.044	1 053.3	0.337	6 939.6	0.031	635.1
l_5	0.282	6 250.4	0.070	1 542.8	0.692	15 291.8	0.066	1 471.2
l_6	1.527	34 775.5	0.339	7 717.5	2.650	60 331.3	0.350	7 959.5
l_7	5.198	129 435.3	1.055	26 264.6	4.440	109 499.8	0.546	13 626.7
Total	7.758	185 515.9	1.577	37 928.7	8.632	202 210.4	1.027	24 378.2

of *L. salicis* is low and amounts to only 0.6–2.3% of P_g, thus the entire net production depends mainly on the value P_g (Migula, 1975). The value P_r is also low in populations of insects exhibiting an annual cycle of development, particularly in cases when the biomass also increases during the imaginal stage, as for instance in *Orthoptera* (Gyllenberg, 1969). The calculation of P_e is complicated by the fact that the products of excretion are often difficult to determine quantitatively. The technique of determining P_e is given by Wiegert (1964). The amount of production connected with excretion is very low.

Respiration is the main factor in the energy budget which limits production. Respiration, i.e. the "cost of living" of individuals, is difficult to calculate under natural conditions. The application of respirometric data obtained under laboratory conditions to natural conditions is risky because of the considerable dependence of metabolic processes on external conditions (particularly temperature) exhibiting a high variability in mosaic biotopes as well as in 24-hour and seasonal cycles. Energy expenses in metabolic processes are determined by the respiration quotient (RQ) of animals:

$$RQ = \frac{CO_2}{O_2}.$$

RQ depends on the nature of the substance oxidized. For carbohydrates it is about 1.0, for fats about 0.71 and for proteins about 0.83. When the value RQ is known the caloric value of respiration can be determined and tables can be constructed from which the caloric value can be read using measurements of oxygen consumption during the course of respiration (or CO_2 excretion). The utilization of oxygen by individuals increases with the increase of their body size as the function of the body weight to surface ratio. The increase of the body weight of an individual of a given species decreases the amount of metabolism per unit of weight, due to the higher ratio of body surface to volume. The dependence of oxygen utilization (y) on body weight is expressed by the following equation:

$$y = a \cdot x^b,$$

where a and b are constants.

The results of the studies of Edwards (1953), Migula (1975) and Persson (1975) indicate that the coefficient of regression b between holometabolic respiration and the weight of insects oscillates around a value of 1 (Table 6.6). Respiration is also significantly affected by temperature.

Table 6.6 Dependence between the weight of live insects (x) and oxygen consumption (y) according to the equation $y = ax^b$ where x in grams, y in mm^3, O_2 per individual per 1 hour, a and b const (Byzova, 1972, after Persson, 1975).

Taxon	a	b	°C
Collembola	62	0.74	18
Protura	62	0.74	18
Thysanoptera	5200	1.00	20
Formicidae (im.)	350	1.00	20
Staphylinidae (im.)	132.7	0.772	13
Staphylinidae (l.)	729.5	0.830	20
Cantharidae (l.)	729.5	0.830	20
Elateridae (l.)	14.41	0.299	15
Chrysomelidae (l.)	231.0	1.0	10
Strophosomus sp. (im.)	123.3	1.0	8
Amphimallon solstitialis (L.) (l.)	213.0	0.82	20
Cetonia aurata (L.) (l.)	128.0	0.55	20
Melolontha hippocastani F. (l.)	171.0	1.01	20
Tipula peliostigma (Schummel) (l.)	115.0	0.52	20

im. – imago, l. – larva.

An increase of temperature by 10°C evokes a 2–3-fold increase of intensity of respiration (Reichle, 1968, 1971; Huhta & Kaskenniemi, 1975).

The dependence of respiration on temperature is expressed by the following equation:

$$\log y = a+bx,$$

where y = oxygen uptake, x = temperature in degrees centigrade, a and b are constants. (The value b may be obtained from the equation $\log Q_{10} = 10b$ where Q_{10} is the coefficient determining the increase of respiration with a 10°C increase of temperature).

The equation $C = R+P+FU$ indicates that heterotrophic organisms, including insects, do not utilize all of the potential energy contained in food.

Appropriate coefficients are used to evaluate the degree of utilization of food consumption by the organism. The coefficient of efficiency of gross production determines the degree of utilization of the food adsorbed (i.e. the increment of biomass, the value of which is given in terms of weight or energy):

$$J_1 = \frac{P}{C} \cdot 100.$$

According to Phillipson (1966), the coefficient of efficiency of production (J_1) may vary within the range of 5–30% and in most phytophages it is generally 10–15% (Slobodkin, 1968). In *Leucoma salicis* (L.) the changes in J_1 were distinct in spring when the development of the caterpillars caused a gradual decrease of this coefficient. On the other hand, the population density exercised no influence on the P/C ratio, the mean annual value of which amounted to about 0.172 (Migula, 1975). For caterpillars of *Hyphantria cunea* (Drury), bred in the laboratory on leaves of *Acer negundo* (L.), the coefficient J_1 was calculated as 16.5% using the following data. The caterpillar assimilates 376.2 mg of completely dry food having an energy value of 6895.6 J (C) of which it utilizes 1141.7 J for production P (Gere, 1956, 1957; Rafes, 1968). Thus, $J_1 = \frac{P}{C} = \frac{1141.7}{6895.6} \cdot 100 = 16.5\%$.

The index of efficiency of assimilation (α) for this species, where $R = 865.4$ J was calculated using the following formula:

$$\alpha = \frac{A}{C} = \frac{R+P}{C}$$

and was found to be:

$$\alpha = \frac{865.4+1141.7}{6895.6} \cdot 100 = 29\% .$$

This indicates that 29% of the energy contained in the food assimilated was utilized for respiration and production ($FU = 4891.0$ J). Wiegert & Evans (1967) established that phytophagous insects generally assimilate 25–35% of the energy contained in the food utilized. Later studies indicated, however, that assimilation may be considerably higher ($\alpha > 80\%$). In *L. salicis* the efficiency of assimilation is dependent on the larval stage and oscillates within the limits of 35.2–54.9% (Migula, 1975).

The coefficient of the contribution of cost of maintenance $(R/C) \cdot 100$ and that of faeces $(FU/C) \cdot 100$ are additional indices which characterize the efficiency of the energy budget. Moreover, in order to establish the distribution of the energy assimilated by the organism we can calculate the value of production and respiration against assimilation: $(P/A) \cdot 100$ or $(R/A) \cdot 100$. The utilization of the energy contained in its food by *L. salicis* calculated using these coefficients is given in Table 6.7.

The fact that the utilization of energy contained in food is somewhat higher than that of its mass, indicates that the reserve of energy per unit of dry body weight of individuals is variable. In the caterpillars of *H. cunea*, which utilize 23% of the mass and 29% of the caloric value of food,

Table 6.7 Utilization of energy contained in food by larvae of *Leucoma salicis* (L.) in successive developmental stages under laboratory conditions (after Migula, 1975)

Larval stage	$\frac{A}{C}\cdot 100$	$\frac{P}{A}\cdot 100$	$\frac{P}{C}\cdot 100$	$\frac{P}{F}\cdot 100$	$\frac{F}{C}\cdot 100$
I	35.2	42.9	15.1	23.3	64.8
II	41.5	20.0	8.3	14.2	58.6
III	33.4	43.1	14.4	21.6	66.6
IV	44.6	43.9	19.6	35.4	55.4
V	59.9	34.5	19.5	43.1	45.1
VI	39.6	43.8	17.3	28.6	60.4
VII	36.8	38.7	14.2	28.5	63.2
Mean	40.7	35.9	14.5	23.6	59.3

the energy reserve as compared with the caloric content of the food is 25% higher in the first larval stage, 20% higher in the sixth stage and 51% higher in the pupa. On the other hand, the caloric value of the excreta is lower than the energy reserve in the food, amounting to 8% in young caterpillars, 4–6% in the second to sixth stages, and 10–11% at the end of larval life. This is attributable to the accumulation of body reserves towards the end of the larval stage (Gere, 1956). In *L. salicis* the energy values are also distinctly higher in later instars, as a result of their accumulation of considerable amounts of lipids in the body tissues (Migula, 1975). The caloric values of the bodies of adult *Lepidoptera* generally oscillate between 18 840–27 214 J per 1 g of dry mass. For example, in males of *L. salicis* it is 24 283 and in females 26 795 J per 1 g.

Starving insects make greater use of their food and retain it for a longer period in the alimentary canal. Thus if $(F/C)\cdot 100$ usually amounts to 60–75%, this value may, under certain circumstances (e.g. in the presence of excessive food), increase to 90%.

The efficiency of food utilization oscillates widely between different species and between the various developmental stages. It may also change according to the nature of the food source. The amount of energy actually assimilated (D) as opposed to assimilation (α) is calculated according to the following formula:

$$D = P+R+U = C-F.$$

The degree of food utilization for the purposes of growth and the value of parameters such as food requirements, assimilation, respiration and production depend to a large extent on the life conditions of the insect, temperature, quantity and quality of food, etc., as well as on the size of the individual. Hence it should be noted that data concerning food requirements of insects and the degree of food utilization under laboratory conditions may be somewhat different from natural ones. In the latter the energy requirements must be higher due to the greater locomotory activity which consequently enhances respiration and caloric losses. Furthermore, species which have a high number of individuals of large body size may play a smaller role in the functioning of ecosystems than less abundant or smaller species characterized by a high reproductive activity. This is due to their relatively slow metabolic rates. In order for ecosystems to function smoothly, it is very important that the activity of the primary consumers (phytophages) stimulates the production of the producers (green plants), thus causing them to replace the biomass lost. This activity should also accelerate the circulation of matter in the conversion of large amounts of plant material to animal tissues. In this way energy is transferred to higher trophic levels and made available to zoophages and saprophages. Phytophagous insects may thus be regarded as constituting the "key industry" of the ecosystem (Elton, 1927).

6.6.2 The role of phytophagous insects in the productivity of forest ecosystems

In forest stands consisting of a single tree species and characterized by a high output of wood mass, outbreak phenomena would be justifiable in the normal functioning of the forest association if it were not for human interference, whereby a part of the primary production is transferred to other ecosystems.

Rafes (1964) attempted to calculate the production of *Lymantria dispar* (L.) over the course of its 7-year outbreak cycle. It was found that during this period the caterpillars consumed 17.9033 t of leaves and 4.4826 t of uneaten leaf matter fell to the ground per 1 ha. The caterpillars thus destroyed 22.4133 t of leaves out of the total weight of 23 t, i.e. 97.4% of the mass of oak leaves which have developed in spring. The secondary production of the primary consumers I (*Lymantria*) amounted to 1.9944 t, of which 0.0145 t was accounted for by the weight of eggs, 1.9161 t by the weight of individuals which perished during the course of development due to various causes and 0.0638 t by the weight of adults. The secondary production thus constitutes about 9.4% of the weight of leaves destroyed and 11% of that of the leaves consumed. The full data are summarized in Table 6.8.

Table 6.8 Utilization of foliage from 1 ha of oak forest stand by *Lymantria dispar* (L.) in the course of a 7-year outbreak cycle (after Rafes, 1964).

Out-break stage	Successive years of outbreak	Number of caterpillars hatched	Individuals which perished		Individuals which accomplished development		Eggs		Stock of spring leaves, tons[a]		Foliage losses tons[a]		
			number	weight tons[a]	number	weight tons[a]	number	weight tons[a]	oak	all dicidous species	consumed	fallen scrap	total
I	1	840	770	0.002	70	0.0000	17 500	0.0000	4.0	9.3	0.0018	0.0004	0.0022
II	2	16 625	15 225	0.0061	1 400	0.0011	525 000	0.0004	4.0	9.3	0.0670	0.0169	0.0844
	3	472 500	466 550	0.4665	5 950	0.0110	3 718 750	0.0026	4.0	9.3	4.3300	1.0827	5.4135
III	4	2 940 000	2 866 500	0.5733	73 500	0.0316	11 025 000	0.0077	3.5	8.5	5.5000	1.3738	6.8692
	5	6 615 000	6 561 100	0.6561	53 900	0.0199	5 390 000	0.0038	3.0	7.8	6.1000	1.5251	7.6354
IV	6	2 135 000	2 134 461	0.2134	539	0.0002	26 950	0.0000	2.5	7.0	1.9000	0.4806	2.4030
	7	5 250	5 196	0.0005	54	0.0000	135	0.0000	2.0	7.0	0.0045	0.0011	0.0056

[a] Weight values are rounded as follows: $\geqslant 50$ g = 0.0001, < 50 g = 0.0000.

Outbreaks of *L. dispar* cause significant changes in the flow of matter and energy in the oak forest stand:

1) The amount and quality of leaves shed in the course of a year decreases. This amount is made up of a small proportion of intact leaves and also of leaf debris and new leaves which have developed during the regeneration process. The biochemical composition of the new leaves is obviously somewhat different from that of normal leaves. They account for about 75% of the mass of the leaves which develop in the spring in the initial outbreak years (1st to 4th year) and 50% towards the end of gradation (6th and 7th year). The total amount of leaves which fell over the 7-year period was 54.566 t.

2) The amount of matter of animal origin transferred to the soil increases. It consists of the excreta of the caterpillars, the bodies of caterpillars, pupae and adults, the excreta of birds and other vertebrates feeding on *L. dispar* (50% of the population of the moth is destroyed by birds), and the bodies of parasites and predators attacking this insect. The total mass of animal matter transferred to the soil during the course of the outbreak amounted to 7.9308 t per 1 ha. The full data are summarized in Table 6.9 and illustrated in Fig. 6.39.

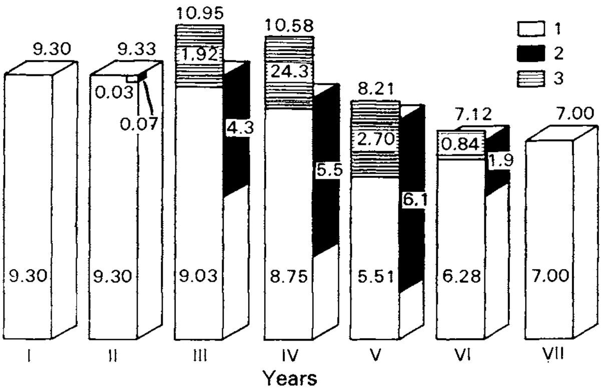


Fig. 6.39 Changes in the quantitative and qualitative composition of the precipitation of organic remains on the soil during the course of the 7-year outbreak cycle of *Lymantria dispar* (L.) in an oak forest stand (after Rafes, 1964): 1 — general biomass of leaves, 2 — part of biomass utilized by caterpillars, 3 — substances of animal origin (tons per 1 ha)

The data given in this table indicate that the mass of organic matter transferred to the soil in the 3rd and 4th year of outbreak is 17–24% greater than in the years between outbreaks, this increase taking place

Table 6.9 Amount of organic matter transferred to the soil in the course of a 7-year outbreak cycle of *Lymantria dispar* (L.) (after Rafes, 1964)

	Precipitation of plant matter, tons per 1 ha				Substances of animal origin, tons per 1 ha				Amount of organic matter transferred to the soil			
Successive years of outbreak	intact leaves	scrap from feeding of caterpillars	regenerated leaves	total	excreta of caterpillars	dead individuals of the pest	excreta of birds and other vertebrates	total	total tons per 1 ha	of this, %		Total as percentage of amount of first year
										plant	animal	
1	9.2978	0.0004	0.0015	9.2997	0.0007	0.0002	0.0000	0.0009	9.3006	100.0	0.0	100
2	9.2156	0.0169	0.0632	9.2957	0.0248	0.0036	0.0006	0.0290	9.3247	99.7	0.3	100
3	3.8865	1.0827	6.0600	9.0292	1.6330	0.2387	0.0466	1.9183	10.9975	82.5	17.5	117
4	1.6308	1.3738	5.1500	8.1546	2.0735	0.3024	0.0573	2.4332	10.5878	77.1	22.9	114
5	0.1646	1.5271	3.8177	5.5094	2.2997	0.3380	0.0656	2.7033	8.2127	67.1	32.9	88
6	4.5970	0.4806	1.2015	5.2791	0.7160	0.1068	0.0213	0.8441	7.1232	88.2	11.8	78
7	6.9944	0.0011	0.0028	6.9983	0.0017	0.0003	0.0000	0.0020	7.0003	100.0	0.0	75

at the expense of matter of animal origin which constitutes 17.5–22.9% of the biomass transferred to the soil. In the 5th year of the outbreak the contribution of animal matter increases to as much as 32.9%, although its absolute mass decreases.

The silkworm assimilates only 62.3% of the total nitrogen content of leaves, the rest being excreted. Thus, if nitrogen constitutes 3.32% of the weight of leaves, it amounts to 23.1% in the faeces and 9.6% in the bodies of the larvae. Despite the lack of data we may assume that these proportions are similar in *L. dispar*. Although the percentage of nitrogen in the faeces of caterpillars is the highest in absolute content, its actual amount is less here than in the leaves. On the other hand, the faeces are more rapidly decomposed and this, along with the numerous bodies of dead caterpillars, improves the C:N ratio in the soil and thus exercises a favourable influence on the quality of humus.

Moreover, the faeces of phytophages constitute a perfect substrate for the development of microorganisms particularly when they accumulate in large amounts on the surface of the forest soil. During outbreaks of *Tortrix viridana* (L.), about 0.5 t of air-dry faeces falls onto the litter of oak forests per 1 ha. When they fall they contain 70 times less microorganisms than the litter. After 24 hours, however, the number of microorganisms (mainly representants of *Bacillus*) in the litter supplemented with the faeces of *T. viridana* is 40 times higher than in the litter itself (Kurcheva, 1971).

Thus from the standpoint of the metabolic processes of the ecosystem, the main effect of an outbreak is a distinct increase of the activity of soil microorganisms. There is also an acceleration of the mineralization process of organic remains in the soil. As will be described further below, this exercises a favourable influence on the process of accretion of wood mass in the ensuing years.

Many authors have noted the decrease of tree increment due to the effects of pests feeding on the tree leaves or needles (Fig. 6.40).

The regeneration of the assimilative apparatus of trees destroyed by foliophages is a specific feature of the individual tree species. The degree of regeneration depends, however, on the extent of damage as well as on the general situation as regards the particular features of the environment, particularly weather. The possibility of the tree regaining its normal physiological condition is also particularly important. In the case of damage or destruction when buds, shoots or leaves are damaged or destroyed, the hormonal action of the tree activates the dormant buds. This is very significant in coniferous trees and forest stands which only change their assimilative apparatus once in a number of years and are thus not able to supplement it immediately after being damaged. The mode of regeneration of needles in the pine may vary depending on the season and intensity of feeding. If the scales of the needles are not destroyed, they may survive but develop into twisted, thick "stub needles"

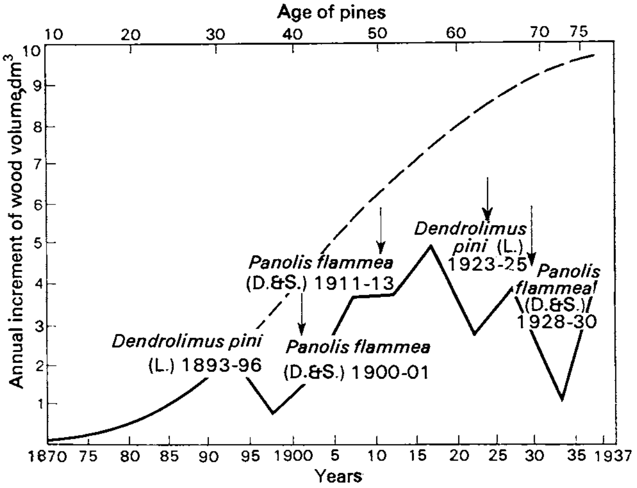


Fig. 6.40 Influence of the feeding activity of *Panolis flammea* (D. & S.) and *Dendrolimus pini* (L.) in the period between 1870 and 1931 on the annual increment of volume of the pine (after Vorontsov, 1963): dashed line – expected increment, continuous line – actual increment

which thus sometimes allow the tree to survive through summer. When insects consume the May shoots, secondary shoots with few pairs of needles may develop from dormant buds. Secondary shoots may also develop from the primordia of stimulated whorl buds. Scale shoots develop from dormant buds between the pairs of needles on shortened shoots. When food reserves are absent the pine sometimes produces rosette shoots with flat pseudo-needles developed from the scales. These shoots cannot ensure regeneration of the tree. Transitory scale shoots developing from dormant buds invariably indicate the regeneration of the tree. Pine forest stands which have been intensively damaged regenerate their needles in 85–90% of trees. Trees with well developed crowns regenerate the most successfully. The regeneration of pine needles takes up to 4 years and tends to follow a logistic curve (Fig. 6.41). The death of trees due to feeding by *Dendrolimus pini* (L.) only occurs when at

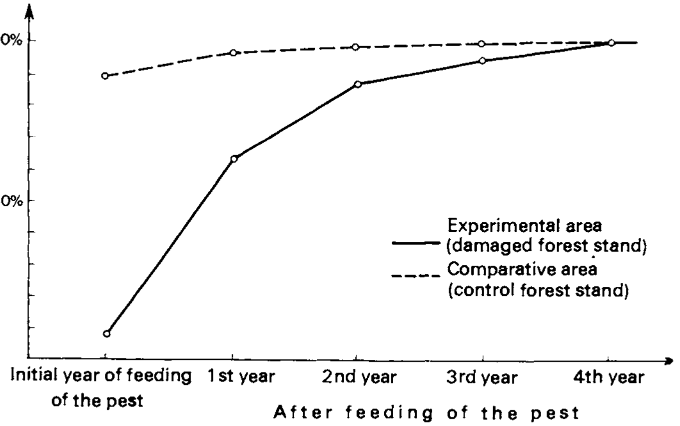


Fig. 6.41 Course of regeneration of needles in the common pine after the feeding of *Dendrolimus pini* (L.) (after Śliwa & Cichowski, 1975)

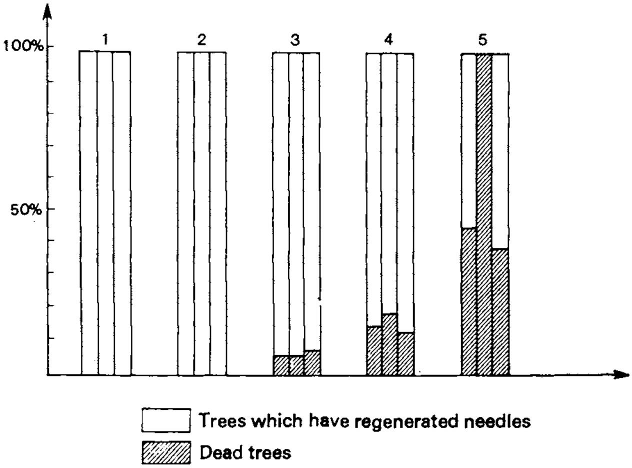


Fig. 6.42 Death of the common pine in dependence on the degree of damage of needles by foliophages (after Śliwa & Cichowski, 1975), 1 – unnoticeable, 2 – weak, 3 – moderate, 4 – intensive, 5 – full damage of needles in the tree crown

least 30% of the needles are damaged (Fig. 6.42). Totally defoliated and thin, stifled trees with small crowns are the first to perish. Death may take up to 3–4 years and is most intense in the first and second year after the loss of the needles (Fig. 6.43). The feeding of *D. pini* has the greatest effect on reducing the increment of the tree height (65%) and to a lesser extent that of the wood mass (30%). Heavy defoliation, however, reduces the increment of the mass by about 50% and about 44% per 1 ha, i.e. 13 m^3 during a 5-year period (Śliwa & Cichowski, 1975). The supplementary and regenerative feeding of *Tomicus* spp. in the terminal shoots of tree crowns may also play an important role in the increment of the pine volume (Fig. 6.44). In the vicinity of sawmills the annual loss of volume increment in a 20 year-old pine forest stand caused by such damage amounted to 30.2% and that of height to 27.5% as compared with the increment of a non-attacked forest stand (Michalski & Witkowski, 1959). The spruce is more susceptible to damage of the assimilative apparatus since it cannot fully adapt to the changed water balance and is thus severely affected by the long period needed for needle regeneration. The feeding of foliophages on old and young shoots before the setting of new buds is extremely dangerous. Under favourable weather conditions in summer and autumn, however, the spruce is able to regenerate the damage inflicted after the development of shoots and the setting of new buds from which "St John's (June) shoots" may develop.

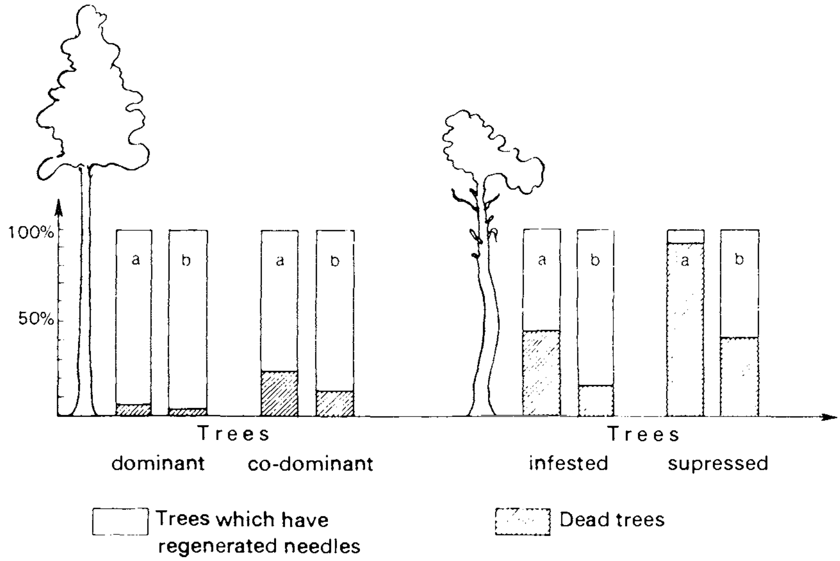


Fig. 6.43 Dying of trees after the feeding activity of foliophages in dependence on the biosociological position of the pine in the forest stand (after Śliwa & Cichowski, 1975): a – damaged forest stands, b – healthy forest stands

The death of deciduous trees due to the feeding of foliophages does not occur as frrequently as that of conifers. On the other hand, the new shoots of the former are often not able to lignify before early frosts and therefore perish. Repeated feeding also leads to dying back of branches and tree tops. The death of entire trees is attributable to insects attacking the phloem. Nevertheless, the direct losses of increment due to the deprivation of leaves are significant and exhibit an inverse correlation with the extent of damage (Fig. 6.45).

Fig. 6.44 Pine forest stand after the feeding activity of adults of *Tomicus* spp., (photo by S. Kinelski)

In phase III of the outbreak of *Lymantria dispar* (L.), the increment of the diameter of the oak at a height of about 4 ft (breast-high) decreases by 40% or more as compared with that of intact forest stands. The increment accumulating in summer is most diminished here. In middle-aged oak forest stands the loss of the assimilative apparatus due to the feeding of the pest leads to a loss of increment (of breast-high and stand volume) by 15–52%. Heavy defoliation in oak thickets (in spring) decreases the increment of diameter by 75.4%, whereas feeding in the top part of the crown decreases it by 37.7%. The increment of height diminishes by 66.2 and 41.3% respectively.

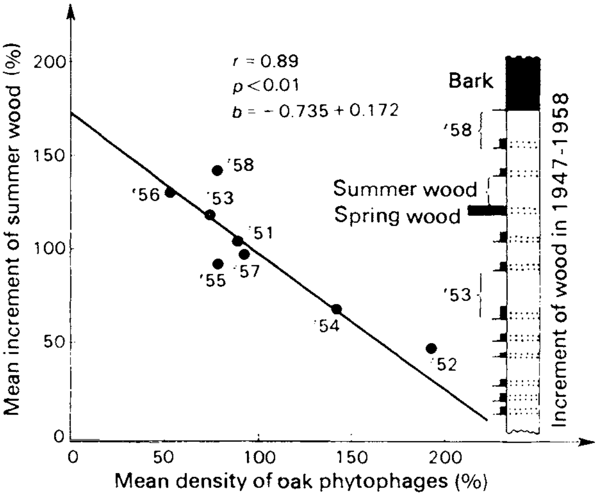


Fig. 6.45 Regressive dependence between the increment of summer wood of the oak and the density of caterpillars of *Operophtera brumata* (L.) and *Tortrix viridana* (L.) (after Varley, 1967)

The reductions in diameter in oak forest stands due to the feeding of *Tortrix viridana* (L.) and accompanying species is summarized in Table 6.10. This table indicates that the increment losses in the first two years of the outbreak oscillate within the range of 10.1–51.4%.

Table 6.10 Losses in chest-high diameter increment of the oak in outbreak foci of *Tortricidae* (after Vorontsov, Erusalimov & Mozolevskaya, 1967).

Age of forest stand	Number of experimental plots	Losses in increment, %		Losses in increment %, in 1964 at crown damage of:		
		1962	1963	50%	80%	100%
25	1	0	0	52.0	–	–
35	1	0	0	0	–	43.1
40–42	2	0	0	–	30.9	39.3
50–57	8	29.6–51.4	25.4–44.4	–	–	31.4–50.2
60–65	3	37.6–41.1	12.9–41.6	31.5	–	47.6–60.0
70–75	2	0	0	–	36.4	35.7
85	1	15.1	15.1	–	37.8	–
90	1	25.4	10.1	–	–	37.8
100	1	0	0	–	–	25.1

Partial damage of the crown (about 50%) brings distinctly smaller losses to the increment than total defoliation and this decrease of losses is higher in younger than in older forest stands. On the other hand, differences between the losses due to damage amounting to 80 and 100% are slight.

An interesting compensatory reaction was observed in forest stands consisting of many tree species in which the oak was damaged by *Tortrix* spp., while the increment of thickness of the oak diminished by 14% the increments of the ash, linden, maple and elm increased by 30–70% and the total increment of these species increased by 34%. At the same time the increment of the surface of the cross-section of the entire forest stand increased by 13%, thus remaining at the mean level occurring in years between outbreaks (Vorontsov *et al.*, 1967). This type of compensatory reaction in forest stands consisting of numerous tree species was not observed when the causative species were polyphagous phytophages.

Studies performed by the Department of Dendrometry, Agricultural University of Warsaw, demonstrated an interesting regeneration course in trees after an outbreak of *Lymantria monacha* (L.) in Silesia. During the feeding period of this insect, there was no, or very little, increment of the height and thickness of the trees. Seven to eight years after the critical stage of the outbreak, the increment regained its standard level and in some biosocial classes of trees (e.g. I) it even exceeded it.

It also appeared that the forest stand, the current increment of height of which culminates in its 20th year, exhibited an abnormal "second culmination" in the 40th–42nd year as a result of the outbreak, and this may be considered as a compensatory tendency (Figs. 6.46, 6.47 and 6.48).

Outbreaks of insects feeding on the assimilative apparatus of trees not only affect the productiveness of forest ecosystems by accelarating the decomposition of organic remains and by changing the increment of wood biomass, but also influence the production of the herb layer by changing the light, thermal and humidity conditions.

As a result of the feeding activity of the larvae of *Notodonta anceps* Goeze in oak forest stands over a two-year period, the herb layer increased from 14 to 70% and after three years it amounted to 85%. Although the dominant species of the herb layer remained unchanged, the contribution of grasses occurring throughout the summer increased, whereas that of the plants of the spring aspect diminished, this being

Fig. 6.46 Mean values of current annual increment of height in individual biosocial classes of trees and in all the trees of a pine forest stand subjected to an outbreak of *Lymantria monacha* (L.) around 1950 (after Pawlik, 1970)

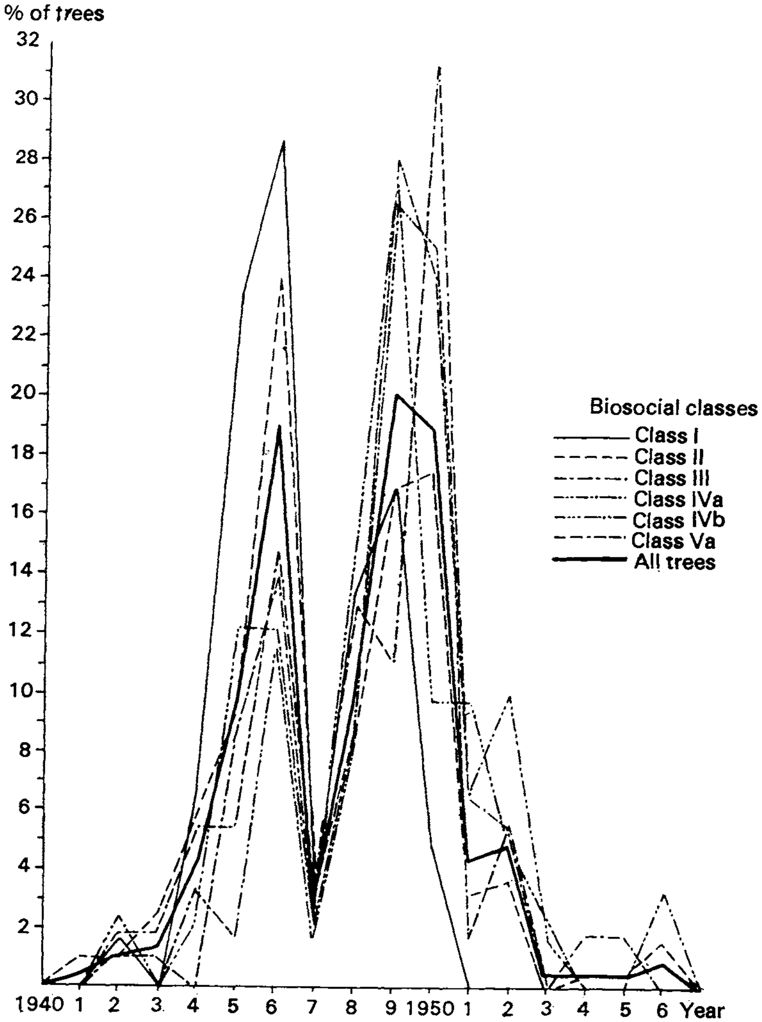


Fig. 6.47 Distribution of occurrence of the second culmination of the current increment of height in successive years in a pine forest stand damaged by an outbreak of *Lymantria monacha* (L.) around 1950 (after Pawlik, 1970)

associated with the feeding season of the notodontid. Weeds introduced by animals also began to appear. During the two year period after the abatement of the outbreak, the grass cover of the forest floor decreased by 31 %, but the weeds remained, whereas five to six years after the outbreak the herb layer returned to its normal state (Table 6.11).

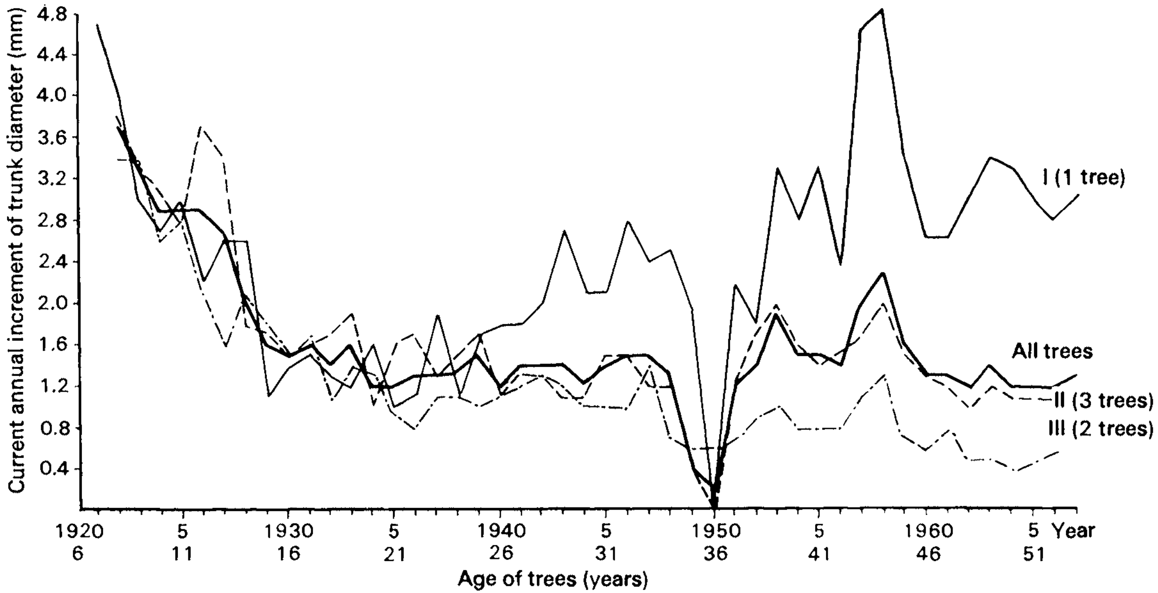


Fig. 6.48 Mean values of annual increment of diameter breast high (DBH) in a forest stand damaged during the course of an outbreak of *Lymantria monacha* (L.) around 1950 (after Pawlik, 1970)

Table 6.11 Changes in the herb layer and small undergrowth in forest stands damaged by feeding of *Notodonta anceps* Goeze (after Vorontsov, Erusalimov & Mozelevskaya, 1967).

Ecological plant groups	Cover, %			
	lack of feeding	total and heavy defoliation		
		1963–4	1962–4	1960–1
Dominants of grass cover	12	51	65	20
Plants of clearings and glades	1	2	3	3
Weeds and nitrophilous species	–	1	2	–
General cover of grasses	13	54	70	24
Small undergrowth	1	16	15	7
General vegetal cover of forest floor	14	70	85	31
Mean surface of leaves of an individual tree of low undergrowth (dm^2)	0.21	1.95	1.89	1.28

6.6.3 *The role of saprophagous soil insects*

The quantitative proportions of soil organisms are decisive in their role in the metabolic processes of ecosystems as well as in soil-forming processes. Soil invertebrates constitute 25–30% of the total biomass of soil organisms, bacteria, fungi and other organisms accounting for the rest. The biomass of living invertebrates may amount to 3.5 t per 1 ha (Edwards, 1966) but in forest ecosystems on poor, sandy and dry soils it is much less. For instance, the biomass of the soil macrofauna in pine forest stands in the fresh coniferous forest habitat in the western part of the Bory Tucholskie Forest is about 0.03 t per 1 ha (Szujecki *et al.*, 1975). The biomass of the macrofauna of the litter in the Kampinos Forest is lowest in fresh coniferous forest (*Pino-Vaccinietum myrtilli*) and in mixed forest (*Pino-Quercetum*) (10.1 kg per 1 ha), and highest in alder forests (23.7 kg per 1 ha). *Tilio-Carpinetum* occupies an intermediate position (12.3 kg per 1 ha) in this respect (Stachurski & Zimka, 1976). On the other hand, the quantitative proportions expressed as the number of individuals or body weight per unit of surface or soil weight are not equatable with the role of these organisms in the process of matter and energy circulation. Invariably the food requirements of an insect is inversely proportional to its body weight. *Acarina* and *Collembola* weighing 1.1 g but occurring in large numbers (200 000 individuals per 1 m^2) utilize 40 times more litter than larger animals weighing 6 g but exhibiting a low abundance.

It is known that the abundance and composition of the soil fauna depend to a large extent on the type of litter. The coarse and only partly decomposed litter of the robhumus type contains a considerable number of small individuals, particularly *Acarina* and *Collembola*, whereas in the fine and readily decomposing litter of the mull type, earth-worms, *Diptera* larvae and other large invertebrates prevail. In the litter of certain beech forest stands the quantitative ratio of animals belonging to the macrofauna to those of the mesofauna (including insects) was 3:1, whereas that of their biomass was 1:4. On the other hand, their oxygen consumption, being indicative of the metabolic processes taking place (i.e. their role in the flow of energy and decomposition of organic remains) exhibited a ratio of 2:3 (Bornebusch, 1930).

The role of insects in the soil-forming process is less significant than that of other invertebrates (e.g. *Acarina*, earth-worms enchytreids and myriapods), although there are situations in which their role is decisive in this respect. This role involves the decomposition or acceleration of decomposition of plant remains into humus compounds, the decomposition of animal remains, the transfer of organic matter, the alteration of the physical and chemical soil properties, the transformation of certain food substances into more assimilable compounds, the accumulation of organomineral compounds in the insect's bodies, the enrichment of the soil microorganimsms, the propagation of soil organisms, the regulation of the abundance of other animals contributing to the soil-forming processes as well as in the intensification and complication of the circulation of matter and the flow of energy within the ecosystem.

The litter is the main source of organic compounds in the forest soil. The amount of litter of tree origin accumulated on the forest floor may oscillate within the limits of 1 to 28 tons of dry weight per 1 ha depending on the specific composition of the forest stand and on the climatic zone. Due to the progressive fall of leaves and the decomposition of the litter by living organisms, its amount on the forest floor changes during the course of the year and also varies in successive years (Fig. 6.49). This is the result of the activity of the fauna and microorganisms which in turn depends on weather conditions, particularly on the amount of precipitation the profusion of which stimulates the feeding of animals and increases in their abundance.

The amount of fallen leaves lying on the forest floor is inversely proportional to their annual fall. The increased rate of leaf decomposition is accompanied by an increased metabolic activity of macrosaprophages, as well as a larger amount of leaf fall from the trees and vice versa. The

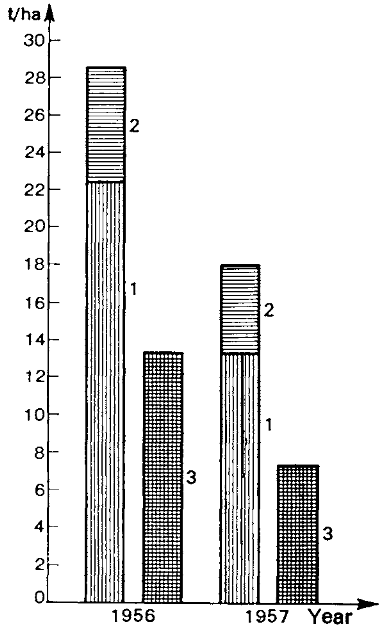


Fig. 6.49 Changes in the litter stock in an oak forest (tons per 1 ha) (after Kurcheva, 1971): 1 — litter remaining from the end of the preceding year, 2 — leaf fall in the current year, 3 — litter stock at the end of the year

slower the decomposition of the litter the earlier the deciduous trees shed their leaves. Thus the higher the rate of leaf decomposition the higher is the production of foliage. This regularity is due to the higher rate of release of elements under conditions of a more rapid litter decomposition leading to a higher trophic abundance of the environment (Stachurski & Zimka, 1975).

The action of insects and other soil animals is closely associated with the action of microorganisms. The latter are the first to induce the preliminary decomposition of litter, which then undergoes comminution by higher organisms, thus increasing its surface and facilitating its further microbiological decomposition (Fig. 6.50).

In the alder carr saprophages decompose 73.5% of the litter, particularly in spring and summer, whereas microorganisms decompose 26.5% of this litter particularly after the autumn fall of leaves (Stachurski & Zimka, 1976). Contrary to common opinion, however, the amount of consumption by saprophages is not the result of the influence of microorganisms.

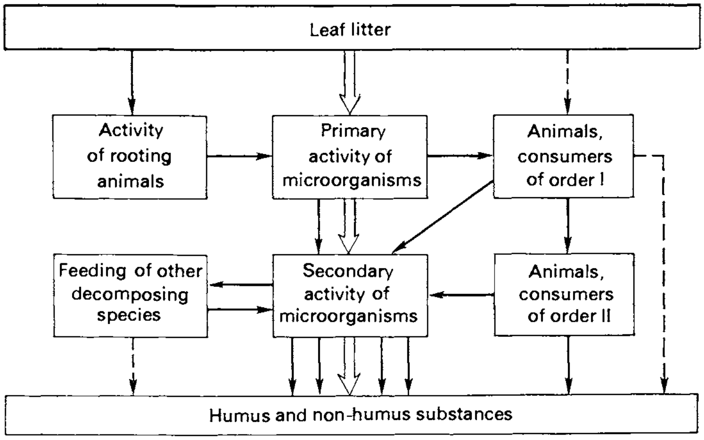


Fig. 6.50 Cooperation of microorganisms and soil fauna in the process of litter decomposition (after Dunger, 1964)

The larvae of *Tipula scripta* Meigen consume 10–15 mg of dry weight of oak litter per 24 hours, thus amounting to several grams during the course of their life. Since several hundred individuals of this species occur per 1 m^2 of deciduous forest stands, in one year they can decompose 0.5–1.0 kg of litter.

A similar role is played by other *Diptera*, such as *Bibionidae*, in coniferous forest stands. Chemical analysis of their faeces demonstrated an increase in nitrogen content and a decrease in the C:N ratio. *Bibionidae* are even more abundant in deciduous forests. The abundance of the obligatory saprophage *Bibio marci* (L.) sometimes reaches 3.500 individuals per 1 m^2. Thus, the enrichment of soils by the faeces of bibionids leads to an intensification of humification processes, this being particularly important in the degraded soils of pine forest stands.

Borowski (1960) established that decomposing litter is the basic food source of *Geotrupes stercorosus* (Scriba). The adults of this beetle prepare food reserves from the litter (conglomerates) for their larvae which develop in the soil environment. The conglomerates weigh about 10.5 g and are placed 15–30 cm deep in the soil where they are completely decomposed and mineralized.

Borowski also calculated that in the Białowieża National Park an average of 2.4 fresh conglomerates were found per 1 m^2 with the exception of the alder carr and the marsh coniferous forest habitats where *G. stercorosus* is almost absent. This indicates that in one year these beetles can bury up to 252 kg of litter per 1 ha. Since the process of the complete mineralization of the conglomerates takes 3 years, the weight of litter transferred to the soil by these insects at any given moment amounts to about 1000 kg per 1 ha. It may be supposed that because of the continuous supply of conglomerates below the humus level, the accumulative soil level of fresh and mixed coniferous forests of the Białowieża Forest undergoes regeneration and increase. In this case *G. stercorosus* successfully supplements the earth-worms which are relative few in the habitats concerned.

Moreover, the useful role of these beetles is manifested by the fact that even the subsuperficial roots of older trees develop numerous young roots around the conglomerates since they encounter particularly favourable mineral conditions here.

The role of *Collembola*, some of the smallest but most numerous insects in forest soils, in the decomposition of the litter has not yet been fully elucidated. The majority of authors, however, consider them to be extremely important and also point to the fact that in some mountain soils the humus layer almost exclusively consists of faeces of these animals. *Collembola* feed on decomposing plant remains, fungal hyphae and spores, humus, chitin debris and the faeces of other invertebrates. Moreover, it has been established that *Collembola* may also feed on fresh leaves, although leaves attacked by microorganisms are more easily consumed.

The transfer of various organic substances, as well as those which undergo little decomposition (e.g. chitin), through the alimentary canal has a favourable influence on soil-forming processes and enhances the propagation of soil fungi. The production of faeces also improves the properties of the forest soil. Some populations of *Collembola* consisting of 100 000 individuals per 1 m^2 in the mountain habitats of the Pyrenees produce 183 cm^3 of faeces annually. These faeces form a layer 0.2 mm deep. Although the contribution of *Collembola* in Polish forests is considerably smaller (their abundance amounts to several dozen thousands per 1 m^2) the comminution of plant remains, as well as the activity of such a relatively large number of organisms in raw humus, under certain conditions may have a significant influence on the fertility of the soil.

Kurcheva (1960) established that the exclusion of the soil fauna from decomposition processes decreases their rate considerably. In experiments described by Kurcheva, 55% of oak litter originating from the spring fall of leaves was decomposed during the course of one vegeta-

Table 6.12 Influence of invertebrates on the rate of decomposition of litter from spring fall of oak leaves (after Kurcheva, 1971).

Years	Experimental variant	Initial amount of precipitation	Remaining after 140 days	Decomposition in course of 140 days (May 21–Oct. 8)		Decomposition in course of 225 days (Oct. 8–May 21)		Remaining after a year	Annual decomposition (May 21–May 21)	
		dry weight grams			%	dry weight grams	%	dry weight grams		%
1958–1959	Without contribution of invertebrates	373	339	34±7	9.1	49	13.1	290	83±10	22.2
	Control	373	167	206±18	55.2	76	20.4	91	282±6	75.6
1959–1960	Without contribution of invertebrates	373	335	38±3	10.1	25	6.8	310	63±4	16.9
	Control	373	236	137±8	36.7	33	6.9	203	170±16	45.6
1960	Without contribution of invertebrates	373	336	27±2	9.9					
	Control	373	236	139±9	36.7					

Note: In control litter decomposition took place with contribution of invertebrates.

tion season in the presence of the fauna. On the other hand, in areas from which the fauna was artificially eliminated only 9% of the litter was decomposed. Over the next two years only 10% of litter was decomposed in areas deprived of fauna compared with 37% in areas with fauna (Table 6.12). Similar results were obtained by Kurcheva in her studies on the role of fauna in the decomposition of oak leaves from the autumn fall (Table 6.13).

The intensification of the local soil fauna by the introduction of saprophages also increases the rate of litter decomposition. The effectiveness of this operation is considerably higher when it is accompanied by sprinkling of the forest floor with artificial rain (Fig. 6.51).

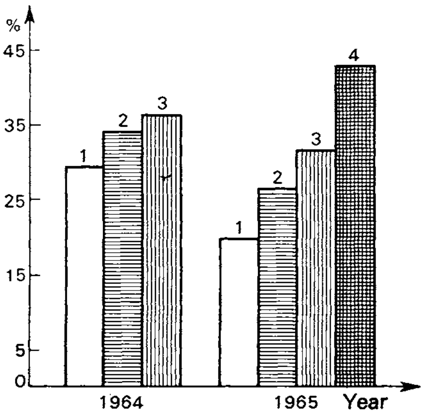


Fig. 6.51 Decomposition of oak litter in dependence on zoomelioration and irrigation of the forest floor (after Kurcheva, 1971): 1 — natural distribution, 2 — distribution under conditions of artificially increased density of saprophages, 3 — distribution under conditions of shower of the forest floor, 4 — distribution under conditions of artificially increased density of saprophages and shower

The mineralization of organic remains without the contribution of insects and other representatives of the fauna is very unfavourable since the mineral compounds not assimilated by plants are washed away and penetrate into the inaccessible deeper soil layers. Thus, a part of the organic matter is stored in the form of humus and may be utilized by plants as it undergoes further gradual mineralization by the simultaneous action of fungi, bacteria and soil fauna. Successful litter decomposition is favoured by the simultaneous occurrence of the invertebrates which consume the litter which has been untouched by other organisms, and invertebrates exhibiting secondary alimentary dependences which utilize

Table 6.13 Influence of invertebrates on the rate of decomposition of litter from autumn fall of oak leaves (after Kurcheva, 1971).

Years	Experimental variant	Initial amount of pre-cipita-tion	Re-main-ing	Decomposition in cool period		Decomposition in warm period		Re-main-ing	Decomposition in course of the year	
		dry weight grams			%	dry weight grams	%	dry weight grams		%
		Oct. 12–June 9				June 9–Oct. 11		Oct. 12–Oct. 11		
1958–1959	Without contribution of inverte-brates	373	321	52±2	13.9	27	7.2	294	78±4	21.1
	Control	373	275	98±7	26.2	100	26.8	175	198±2	53.0
		Oct. 27, 1959–May 20, 1960				May 20–Oct. 22, 1960		Oct. 27, 1959–Oct. 22, 1960		
1959–1960	Without contribution of inverte-brates	373	344	29±1	7.8	28	7.5	316	57±5	15.3
	Control	373	329	44±2	11.8	74	19.8	255	118±1	31.6

Note: In control litter decomposition took place with contribution of invertebrates.

litter primarily comminuted by representatives of the first group. Most insects, with the exception of the larvae of *Tipulidae*, *Bibionidae*, *Lycoridae* and a few *Collembola*, belong to secondary litter consumers utilizing the plant remains which have passed through the alimentary canal of primary consumers (Dunger, 1958, 1963).

As mentioned above, the role of soil insects in soil-forming processes is their favourable influence on the soil structure. Forest ants transfer great amounts of mineral soil to the surface and enrich the soil with organic remains, particularly faeces and remains of invertebrates with a high nitrogen content and neutral pH (Fig. 6.52). The food of *Formica rufa* (L.) consists of the excreta of aphids (about 40% of food), insects (40%), sap flowing from trees (10%), seeds and fruits (5%), fungi and other substances (5%). In outbreak periods of noxious forest insects their contribution to the ant's food rises to 90%. Despite a number of divergences in this respect, we can suppose that the ants of an average nest devour about 2 million insects per year. It was observed, for instance, that during the course of an outbreak of *Acantholyda posticalis* (Matsumura) (= *nemoralis* Thomson), the ant-hills were covered by a yellow layer of these sawflies carried in by the ants. This may suggest that a large amount of nitrogen is transferred by forest ants to the soil. Moreover, it is possible that ant faeces play an important role in the neutralization of the soil pH in the vicinity of ant-hills. This is particularly valuable in poor and acidic soils, since the high activity of the ants as they penetrate the area improves the structure and aeration of the soil. The role of individual species of forest ants in these processes varies.

The mixing of soil with organic remains in the alimentary canal of insects (e.g. larvae of *Lycoridae* and *Bibionidae*), influences the formation of aggregates and of a granular soil structure while the form and size of clods depend on the composition of the fauna. Since the faeces of insects are not very soluble in water and the quality of the soil structure depends on the resistance of clods to dissolution, the activity of insects is distinctly favourable.

Thus, insects and other invertebrates increase the fertility of forest soils as well as actively contribute to the circulation of matter and flow of energy through the ecosystem. They also have a favourable indirect influence on the productivity of biocenoses through the improvement of the physiological condition of trees which, since they are growing on soils undergoing successful soil-forming processes, are provided with readily assimilable nitrogen compounds.

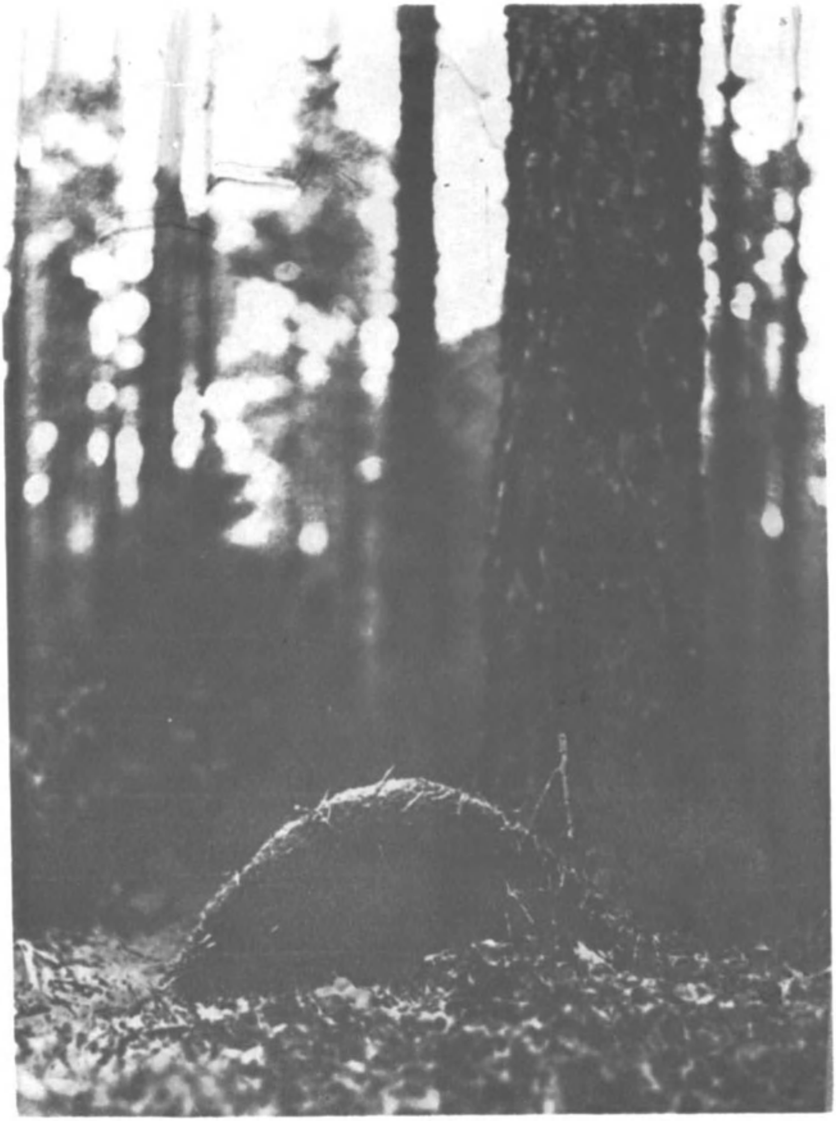


Fig. 6.52 Earth mound overgrown with haircap-moss formed by *Lasius* sp. in a pine forest stand (photo by S. Kinelski)

6.7 *Succession of insect associations and communities*

Ecological succession is still poorly understood and its undoubted existence has been, and often still is, variously nterpreted. It is assumed here that an ecological succession is an ordered progressive or regressive succession of associations or communities of organisms superceding each other at a given point on a given area or in another ecological, environmental or geographical unit. This succession is directional, it may be described and the rate of its changes, as well as its final effect, can generally be anticipated.

The agents evoking the succession may either be internal with respect to the association (primarily the reactions of organisms to changes evoked by the environment) or external, caused mainly by variations in the influence of abiotic (changes in climate, ground water level, etc.) or biotic agents (activity of foreign organisms, including the influence of anthropogenous factors).

Forest insects may undergo successive changes which occur within the entire forest association (macrosuccession), or which take place on a less extensive scale such as in the decomposition of wood, fungi, animal faeces and corpses, etc. (microsuccessions).

The influence of external factors such as climatic changes, variations in ground water level and the filling of lake basins with sediment may lead to a phenomenon called physiographic succession.

The ageing process of eutrophic and dystrophic lakes, as can be observed in many parts of Poland, is the motive force behind the succession of plant associations caused by edaphic agents such as the decrease of soil humidity and alteration of other soil properties on areas surrounding lakes when the water level is reduced. These floral successions are accompanied by successions of insects.

The physiographic succession of staphylinid soil beetles was studied under such conditions in the Pisz Forest around lakes, the littoral zone of which is progressively overgrown by vegetation. Six zones of varying humidity and other soil characteristics have been distinguished. They include the following plant associations: *Caricetum elatae* (pioneer association progressively overgrowing the littoral zone of the lake), *Alnetum glutinosae*, *Pino-Quercetum* and *Pino-Vaccinietum myrtilli* around Lake Jaśkowo as well as *Caricetum elatae*, *Sphagnetum fusci* and *Pino-Vaccinietum myrtilli* around Lake Mauzy. Erosion processes were observed on the border of marshy and podsol-sandy soils, and entailed the shifting of sandy soils onto peat soils and the covering of parts of the former lake bottom with sand.

Thus, the successive process described is a standing process taking place over a number of years and accompanied by the local climatic changes. Studies on the distribution of *Staphylinidae* contributed to the establishment of an existing, parallel and analogous succession of communities and species associated with the changes in the soil humidity. This succession was, as one may expect, more differentiated than that of the plant associations. In the six zones of the more fertile soils on the borders of Lake Jaśkowo, communities contained the following dominants: *Lathrobium gracile* Hampe, *Ochthephilum* (= *Cryptobium*) *fracticorne* (Paykull), *Sipalia circellaris* (Gravenhorst), *Atheta sylvicola* (Kraatz) and *Othius myrmecophilus* Kiesenwetter, whereas on the borders of Lake Mauzy the following species were dominant: *Erichsonius cinerascens* (Gravenhorst), *Gabrius sphagnicola* (Sjöberg), *Ochthephilum fracticorne* (Paykull), *Stenus atratulus* Erichson and *Sipalia circellaris* (Gravenhorst) (Fig. 6.53).

The successions of edaphic communities of *Staphylinidae* given above indicates that they are somewhat similar on the borders of the two lakes investigated. The communities change along with the decreasing soil humidity. Just as in the plant associations, the succession of staphylinids passes from the borders of forest water bodies towards the coniferous forest habitats where the communities are dominated by the Euro-Siberian species *Sipalia circellaris.* These communities are well suited to the area of the Pisz Forest and its present climatic conditions which favour the occurrence of the association *Pino-Vaccinietum myrtilli* under the existing edaphic conditions (Fig. 6.54).

On sites where the bed of the former lake is not covered with dry sandy soils by erosion, the succession may be concluded by a community dominated by another species such as *Ochthephilum fracticorne* (Paykull).

The succession of *Staphylinidae* communities described above is called a primary succession. It starts from a zero stage when the bank emerges as a result of the lowering of the lake water level. This stage is formed by pioneer plant species and their remains which are in turn invaded by pioneer insect species adapted to both aquatic and terrestrial modes of life.

Secondary successions occur for example when a felling or burnt area becomes overgrown and the original insect community, temporarily

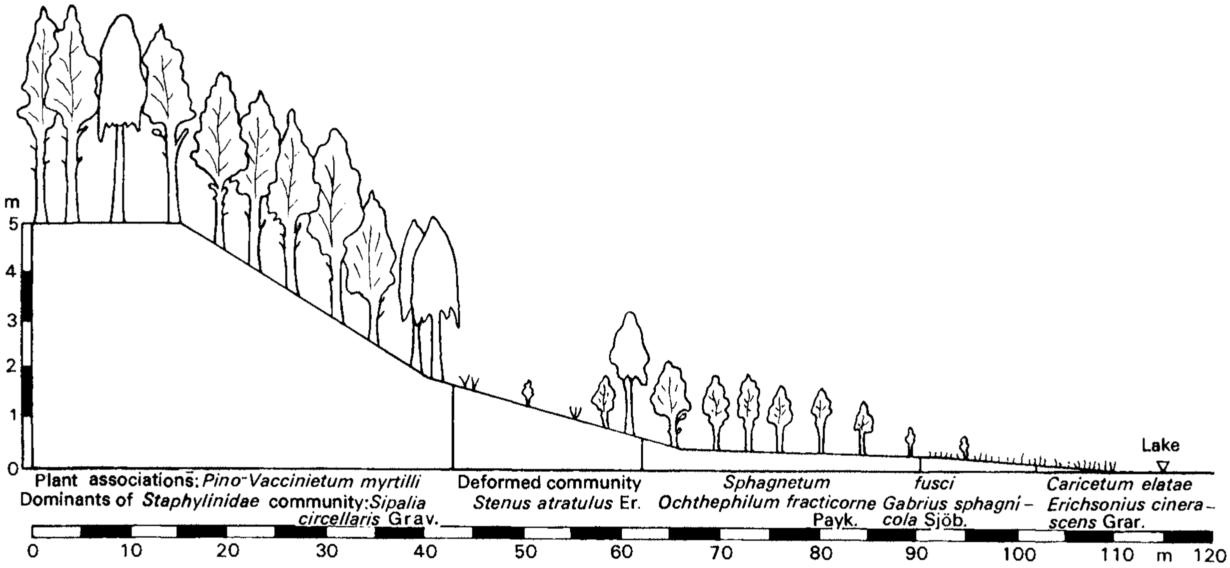


Fig. 6.53 Succession of *Staphylinidae* communities on the borders of a small overgrown mid-forest lake (after Szujecki, 1963)

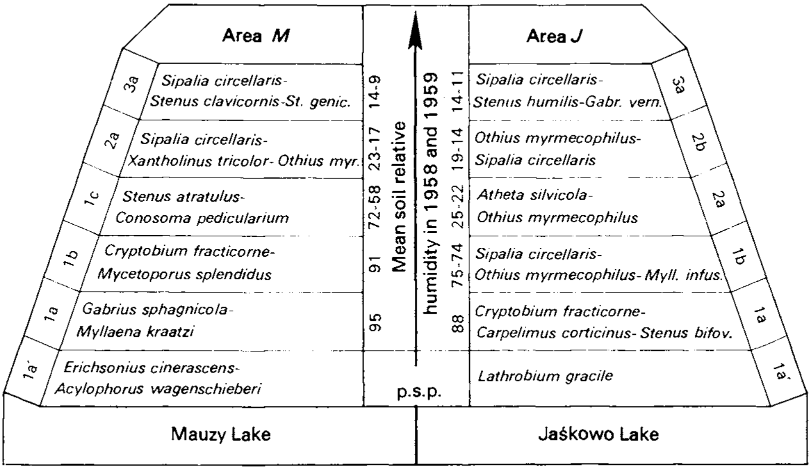


Fig. 6.54 Diagram of distribution of *Staphylinidae* communities and the direction of their succession in relation to decreasing soil humidity (after Szujecki, 1966b)

destroyed by felling or by the fire, resettles. Secondary successions generally occur at a faster rate than primary ones.

The succession of *Staphylinidae* on fellings in pine forests includes successive stages of regeneration of the fauna typical of this habitat and extends to the 25th year of the life of forest stands. The succession of dominant species is as follows: *Tachyporus chrysomelinus* (L.), *Mycetoporus splendidus* (Gravenhorst) and finally *Sipalia circellaris* (Gravenhorst).

Primary and secondary successions of insects which take place over the course of many years are not very well known due to the time factor involved. Short-term successions occurring within limited areas in the range of biocenoses in definite connexes and synusiae are, of course, better documented.

The mechanism and existence of such microsuccessions generally involves the alteration of conditions by one group of organisms which subsequently leads to the immigration of new species and communities and the disappearance of the original communities.

The absence of a climax stage in the series of successively occurring communities is the essential difference between microsuccessions and successions of associations in the classical ecological sense. The environment within which the phenomena of microsuccessions take place becomes completely transformed and finally disappears (along with its final ecological association) as a result of the exploitation by the organisms concerned. Such a course of microsuccession of associations of organisms is observed in dead wood, in the faeces of forest animals, in fungal fruiting bodies, under the bark of trees attacked by bark-beetles and other insects, in seasonal water bodies, in tree hollows, in ground depressions, etc. Microsuccessions thus involve the sequential action of associations of organisms, which serves to accelerate the break down and mineralization of material, ultimately restoring it to the biocenotic circulation. Such a phenomenon has been termed parasuccession or apparent succession (Trojan, 1975) and its course does not significantly differ from that of successions exhibiting a climax stage. Even though the time scale involved may be relatively short in terms of, for example, human life or of man's history on Earth, microsuccessions may still be regarded as successions of ecological communities following a definite order in space and time.

We shall first consider the microsuccessions which occur in pine stumps, in decomposing wood of deciduous trees and in beech trees attacked by secondary pests in the galleries of the bark-beetle *Tomicus piniperda* (L.).

The wood of freshly felled pine stumps contains the richest source of nutritional compounds. It has the highest percentage of cellulose and large amounts of starch, proteins, fats and sugars, as well as having the lowest content of those substances which cannot be digested by insects. Almost as soon as the wood has been felled it is invaded by various microorganisms, particularly *Ascomycetes* of the genus *Ophiostoma* which cause the wood to change colour. Due to the action of enzymes secreted by fungi and from the guts of insect larvae, cellulose and also partly hemicellulose are broken down to form sugars which constitute the food of these larvae (Fig. 6.55). Over the course of 10 years, the con-

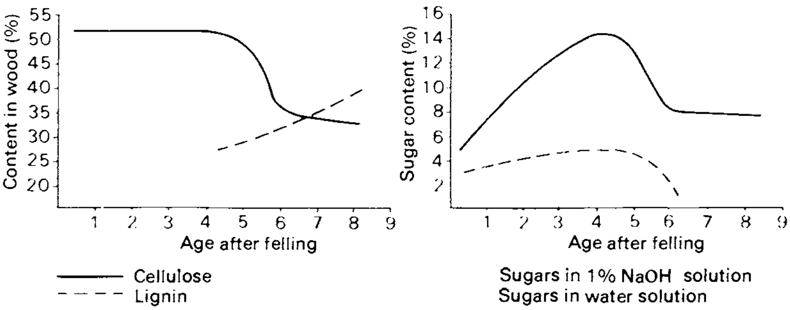


Fig. 6.55 Changes of cellulose, lignin and sugar content in the sapwood of pine stumps in dependence on their age (after Wiąckowski, 1957)

tent of cellulose in the sapwood of pine stumps is reduced by about 20%. The decomposition of cellulose is effected by the weakening of its long molecular chain and its break down into shorter chains which in turn are broken down to simple sugars.

The quantitative composition of sugars in wood and its variation in time are particularly important for the organisms which occur in pine stumps because they are indicative of the available food reserves at any given time. Due to fungal activity, the amount of sugar in the wood of stumps increases up to the fifth year after felling. This is of particular importance for those insects which are only capable of digesting readily soluble sugars and it also helps us to understand the nature of the successive changes which occur in the entomofauna. Furthermore, as well as the quality and quantity of food, the microclimate (temperature and humidity) in the wood of stumps also varies with age. Humidity changes are particularly important for insects since they not only affect the microclimate but also the physiology of feeding (Fig. 6.56).

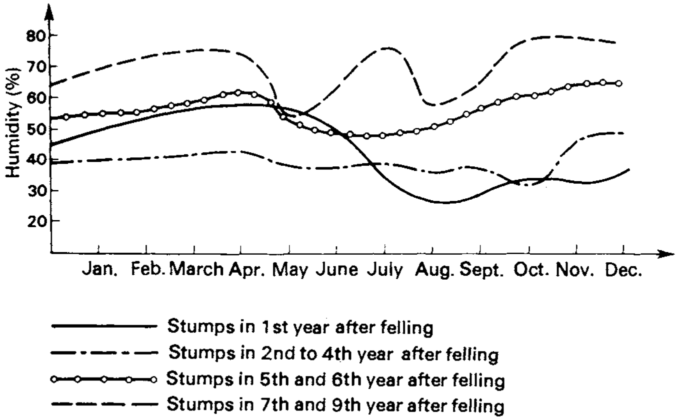


Fig. 6.56 Changes in relative humidity of sapwood of pine stumps in dependence on their age (after Wiąckowski, 1957)

Wiąckowski (1957) distinguished five different types of pine stump environments according to the degree of decomposition of the wood and corresponding to the five successive stages of insect associations occurring in them (Fig. 6.57).

The first stage consists of *Scolytidae*, *Curculionidae*, *Cerambycidae* and *Lymexylonidae*, the larvae of which feed under the bark. The cambium on which they feed has a high nutritional value, being rich in proteins and short-chained carbohydrates, and thus precludes the need

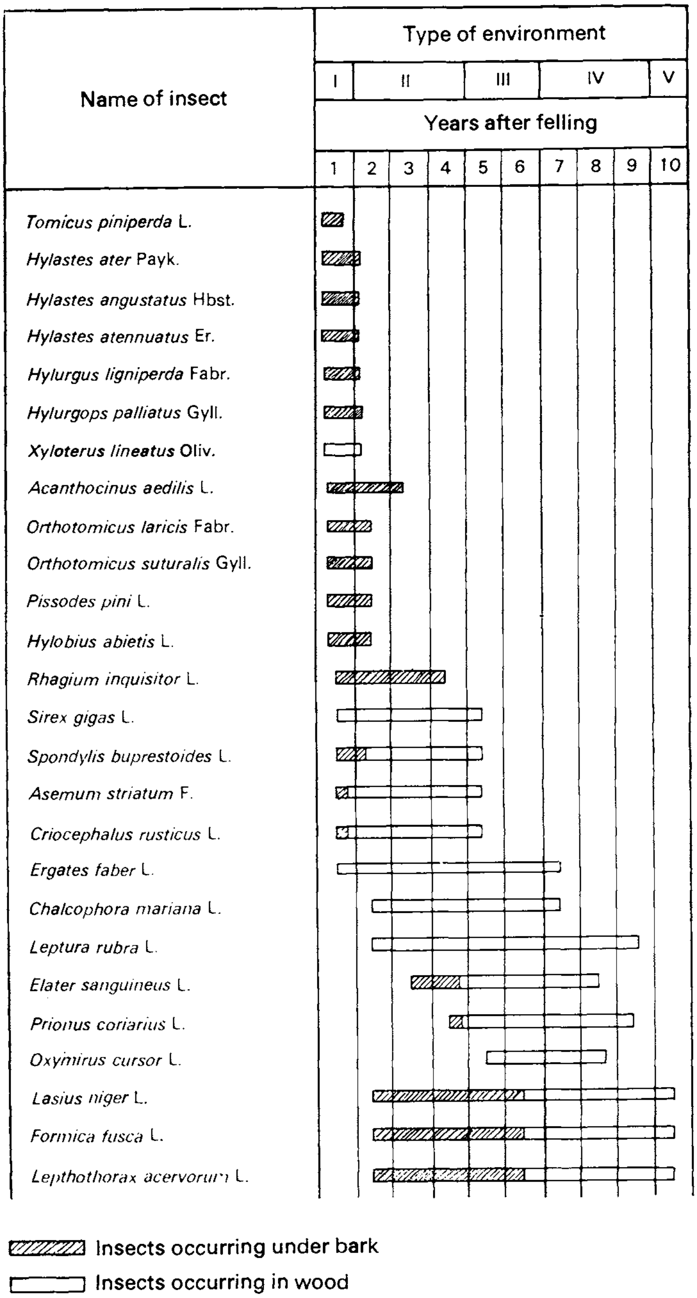


Fig. 6.57 Microsuccession of insects in pine stumps (after Wiąckowski, 1957)

for any close symbiotic relationships with wood-decomposing microorganisms. Only some insects which attack the bark rather than the wood (e.g. *Acanthocinus aedilis* (L.) and *Rhagium* sp.) contain symbiotic saccharomycetes in their digestive tracts. *Rhagium inquisitor* (L.), *A. aedilis*, *Hylobius abietis* (L.), *Pissodes pini* (L.) and a few others are the dominant species beneath the bark. During this period, which only lasts for one year and is characterized by insects feeding under the bark, only *Trypodendron lineatum* (Olivier) and *Hylecoetus dermestoides* (L.) actually invade the wood.

The second stage includes insects which occur in the stumps from the second half of the first to the fourth year after felling. During this period the bark becomes loose and the cambium gradually dies, while the chemical composition of the wood is almost identical to what it was in the first stage. The entomofauna of the second stage is characterized by an increase in the number of species feeding on the wood, the digestion of which is facilitated by the presence of special enzymes or symbionts in the digestive tracts of the insects. The dominant species in the wood during this period are *Chalcophora mariana* (L.), *Ergates faber* (L.), *Leptura rubra* (L.), *Spondylis buprestoides* (L.), *Asemum striatum* (L.), *Arhopalus* (= *Criocephalus*) *rusticus* (L.) and *Urocerus gigas* (L.). Also present under the bark at certain stages in their life-cycles are *Rhagium inquisitor*, *Spondylis buprestoides*, *Asemum striatum* and *Arhopalus rusticus*. There is an increase in the number of species associated with those which feed on cambium and wood, particularly staphylinids, histerids, rhizophagids and colydiids, as well as ants and *Diptera* larvae, for example, which occupy the abandoned cerambycid and scolytid galleries.

The third stage in the succession includes those insects which occur in partly decayed wood in the fifth and sixth year after felling, the wood already having undergone considerable changes as a result of the action of fungi and insects in the two previous stages.

Almost all the gallery-forming larvae feed on wood, only the earlier instars of *Prionus coriarius* L. being found under the bark of roots. Such insects also generally exhibit a well developed intracellular symbiotic relationship with saccharomycetes (e.g. *Leptura rubra* L. and *Oxymirus cursor* (L.)). Larvae of *L. rubra* dominate at this stage while ants, particularly *Lasius niger* (L.) prevail under the bark. At the end of the sixth year after felling, there is also a distinct invasion of the wood by ants which is possibly associated with the high concentration of sugars in the wood. In addition, the extensive structural decay of the wood makes it an ideal site for the hibernation of carabids.

The third stage is generally distinguished by the predominance of insects feeding or living in the wood as opposed to those under the bark.

In the intermediate period betweeen the third and fourth stage the wood undergoes essential chemical transformations due to the action of fungi and insects, resulting in the utilization of about 16% of cellulose and a large amount of accumulated sugars. Fungal action is particularly enhanced by the high humidity of the wood and, as a result of this, in the seventh to ninth year after felling the stumps exhibit an advanced state of sapwood decomposition but still retain their shape.

The fourth stage is characterized by the presence of almost the entire entomofauna in the wood, *Leptura rubra* L. being particularly predominant. Ants, elaterids and tenebrionids (*Uloma rufa* (Piller & Mitterpacher)), as well as larvae of asilids and tipulids, are also typical representatives of this stage. The accompanying entomofauna is also very abundant, consisting mainly of staphylinids (e.g. *Conosoma*, *Atrecus* and *Gabrius splendidulus* (Gravenhorst) and hibernating carabids. Hibernating insects are most abundant in the seventh year after felling, whereas they are totally absent from stumps from the ninth year onwards. The highest number of fungivorous and adventitious species are observed during this period.

In the fifth stage in the succession only the heartwood of the stumps remains. This part of the wood retains its shape whereas the sapwood has decomposed to an amorphous mass of mould, such a condition occurring in stumps over ten years of age. However, the wood may still contain 30% of cellulose and its humidity may amount to up to 300%.

The fauna of this stage loses the character of the wood habitat and the contribution of insects decreases. Earth-worms and myriapods predominate, whereas insects are represented by *Collembola*, *Forficula* sp., *Blattodea* and some *Coleoptera* such as *Carabidae*, *Staphylinidae* and *Elateridae*.

The following four stages of invertebrate succession, including insects, have been distinguished in the decomposing wood of oak logs (Mamaev & Sokolov, 1960). I, cerambycoidal; II, lucanoidal; III, formicoidal, and IV, lumbrocoidal. In central Russia in the environs of Tuła, *Leptura sexguttata* F. and the melandryid *Hypulus quercinus* (Quensel) dominate in the wood in stage I and decompose 13.5% of the sapwood. In stage II *Ceruchus chrysomelinus* (Hochenwarth), *Diptera* larvae (*Lycoriidae*) and *Elateridae* (*Melanotus* spp. and *Elater* spp.) predominate. During this period *Ceruchus chrysomelinus* processes 50% of the oak wood (a single larva consuming 0.45 cm^3 of wood per 24 hours) and 13–15% of the resulting wood dust is made up of the faecal waste of this species. The following ants occur in stage III: *Lasius niger* (L.), *L. fuliginosus* (Latreille), *Myrmica rubra* (L.) and various other species. Finally, in stage IV the oak wood undergoes decomposition and humification due mainly to the activity of diplopods and earth-worms, the contribution of insects being negligible.

There is a somewhat different succession of species taking part in the decomposition of wood in the Telerman Forest but the general character of process is similar. *Xestobium rufovillosum* (De Geer) is the main agent of decomposition here and destroys 50% of the sapwood, while the heartwood is attacked by *Cerambycidae* of the genus *Strangalia*. In stage II, 40% of wood in stumps and logs is decomposed by lucanid larvae of the genera *Lucanus*, *Dorcus* and *Sinodendron*, half of the wood mass being utilized as food by these insects along with the alleculid *Prionychus ater* (F,), *Lasius niger* (L.) and *L. nylanderi* (Forster), predominate in stage III and earth-worms in stage IV.

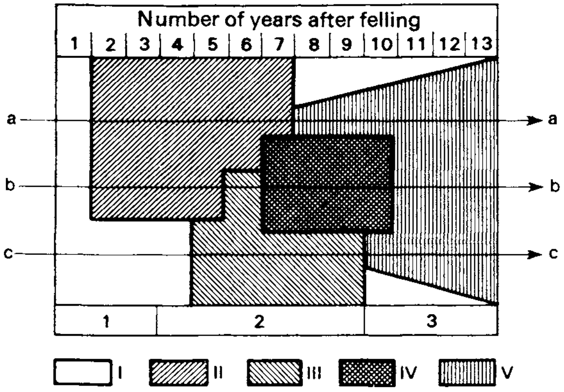


Fig. 6.58 Diagram of microsuccession of wood-decomposing invertebrates (after Mamaev, 1960): arrows – direction of microsuccession, bb – full microsuccession, aa, cc – abridged microssuccession, I – fungal-bacterial decomposition, II – cerambycoidal stage, III – lucanoidal stage, IV – formicoidal stage, V – lumbricoidal stage; 1 – stage of wood-staining fungi, 2 – phase of wood-decomposing fungi, 3 – stage of pileate *Basidiomycetes*

The diagram given in Fig. 6.58 represents the course of the succession of invertebrates in wood and their role, along with that of fungi in its decomposition.

Studies performed in the uplands of central Poland have shown that

the course of the invasion of oak stumps by insects proceeds as follows.
I. Scolytoidal (first year after felling): *Xyleborus saxeseni* Ratzeburg, *X. dispar* (F.), *Agrilus biguttatus* (F.), *Rhagium mordax* (De Geer) and *Synanthedon vespiformis* (L.) play a decisive role in decomposition.
II. Cerambycoidal – pyrochroidal (second and third year after felling): *R. mordax*, *Prionus coriarius* (L.), *Strangalia quadrifasciata* (L.), *Schizotus pectinicornis* (L.) and *Xylocoris cursitans* (Fallén) occur here.
III. Formicoidal (4th–6th year after felling): the ants *Lasius niger* (L.) and *Formica sanguinea* Latreille or larvae of *Elateridae* such as *Melanotus erythropus* (Gmelin) (= *rufipes* (Herbst)) and *Ampedus* (= *Elater*) *pomorum* (Herbst) dominate here.
IV. Myrmicoidal (7th year after felling onwards): *Myrmica laevinodis* Nylander and *M. rubra* (L.) are abundant at this time

In addition, larvae of *Platycerus* (= *Systenocerus*) *caprea* (De Geer) (*Scarabaeidae*) are sometimes present during stages II–IV (Zajączkowski, 1968).

The data given above demonstrate that the scheme of succession is similar even under different geographical conditions and in the wood of various tree species. It is initiated by the action of scolytid and cerambycid larvae and passes through the subsequent stage in the presence of either lucanids (oak) or cerambycids which do not require cambium for their development (e.g. *Leptura rubra* (L.) in pine stumps). Stage III is dominated by ants and stage IV, which sees the culmination of the decomposition process, is characterized by the presence of earth-worms, myriapods and other invertebrates.

Thus, the duration and result of succession may be foreseen since the replacement of species is the functional effect of the existence and action of the components of each stage of the succession.

It would, however, be erroneous to claim that the process of microsuccession in dying trees and their fragments is always identical. Its course is somewhat different in standing trees as compared with fallen logs or even tree stumps. It also varies in different sections of the standing tree and in stumps of different dimensions and in their various parts. Moreover, the successive series even in the same tree species are usually formed by different but functionally similar insect species.

According to Capecki (1969) the microsuccession of insects in beech is characterized by the following four variants of occurrence: 1) in standing trees of full vitality, 2) in standing but weakened or dead trees, 3) in fallen trees, 4) in snags and stumps.

Within the range of each variant, the series of microsuccession may be further differentiated by varying environmental conditions.

For instance in variant I1, insects occurring in the crowns may be distinguished from those in damaged parts of the trunks. It appeared that *Agrilus viridis* (L.) and *Ernopocerus fagi* (F.) dominated in the crowns as well as in fresh boughs and branches in the initial phases of the decomposition of the bark and wood. *Xestobium plumbeum* (Illiger), however, prevailed in drying and dry boughs and branches in phase II of bark decomposition and in phases II and III of wood decomposition. Moreover, different species occurred in boughs and branches undergoing decomposition in the tree crowns (phases III and IV of wood decomposition) as compared with those lying on the ground (e.g. *Sinodendron*).

Chrysobothris affinis (F.) and *Agrilus viridis* occurred in damaged parts of the trunk covered with bark in phase I of its decomposition, whereas *Rhagium mordax* (De Geer) dominated in the trunks when both the wood and bark were in phases I and II of decomposition. Parts deprived of bark where the dried wood was in phases I and II of decomposition were invaded by *Ptilinus pectinicornis* (L.), whereas those, where the wood was in phases II and III of decomposition were attacked mainly by *Leptura scutellata* F. and *Anaglyptus mysticus* (L.). Finally, larvae of *Sinodendron* were predominant when both the wood and bark of the damaged sections of the trunk were in phases III and IV of decomposition.

Capecki (1969) further divided the microsuccessions of insects on weakened and dead standing trees into those taking place in younger forest stands and those characteristic of timber forests and superannuated stands. He also took into consideration the phases of decomposition of the wood and bark. In general, the trees of younger forest stands are initially invaded by *Ernopocerus fagi* (F.), *Leiopus nebulosus* (L.) and concurrent species, to be followed by the anobiids *Ptinomorphus* (= *Hedobia*) *imperialis* (L.) and *Ptilinus pectinicornis* (L.) as well as the cerambycine *Anaglypticus mysticus* (L.). Finally, in phases III and IV of decomposition, *Sinodendron cylindricum* (L.) predominates. Older forest stands exhibited a richer faunistic composition. Initially they are attacked by *Buprestidae* (*Agrilus viridis* and *Chrystobothris affinis*), *Cerambycidae* (*Saperda scalaris* (L.), *Rhagium mordax* and *Leiopus nebulosus* (L.)), *Scolytidae* (*Taphrorychus bicolor* (Herbst) and *Trypodendron domesticum* (L.)) and other insects such as *Hylecoetus dermestoides* (L.). Later, in phases II and III of decomposition, they are invaded by *Anobiidae* (mainly *Ptilinus pectinicornis* and *Xestobium plumbeum*), *Platystomus*

(= *Anthribus*) *albinus* (L.) and *Anaglyptus mysticus*, and finally, in phases III and IV, the trees are mainly inhabited by larvae of *Sinodendron* as in younger forest stands.

The insect microsuccessions in fallen trees depend to a large extent on the humidity of such trees. They consist mainly of species which de-

Fig. 6.59 Rhagium mordax (De Geer) (photo by W. Strojny)

velop under the bark and in fresh wood, such as *Taphrorychus bicolor*, *Rhagium mordax* (Fig. 6.59), *Trypodendron domesticum*, *T. signatum* (F.), *Xyleborus saxeseni* (Ratzeburg), *X. dispar* (F.) and *Hylecoetus dermestoides*, in phases I and II, and *Rhagium mordax* and *Pyrochroa coccinea* (L.) in phases II and III of decomposition. Finally, *Tomoxia biguttata* (Gyllenhal), *Sinodendron cylindricum* (L.) and tipulid larvae contribute to the last stage of the microsuccession studied by Capecki (1969).

The microsuccession of insects occurring on snags and stumps exhibits intermediate characteristics between those of standing and fallen trees. Only the tips of snags have a characteristic association consisting of *Leiopus nebulosus* and *Ptinomorphus imperialis* as well as *Clytus arietis* (L.) in lowland forest stands.

Thus, in general, the course of microsuccession of insects in beech exhibits the following stages: I, bupresto-scolytoidal stage; II, anobiidoidal stage; III, lucanoidal stage; IV, formicoidal stage, and V, lumbricoidal stage. This resembles the courses observed in oak wood and pine stumps.

The occurrence of the anobiidoidal stage is a specific feature of insect microsuccession in standing beeches, as compared with that occurring in the wood of oak logs or in oak and pine stumps. This is associated with the specific microclimate of standing trees which favours the invasion of the dead bark by anobiids. The course of succession of individual species in beech wood and under its bark is illustrated in Fig. 6.60.

Insects which cause the decomposition of wood and which contribute to the composition of successive stages of the entomofauna of dying trees, fallen trees, stumps and snags play an important role in the circulation of matter in forest ecosystems. Lamellicorn larvae, which invariably occur in stage II or III of decomposition, are particularly important in this respect, and are principally lucanids and trichiine and cetoniine scarabaeids, e.g. *Osmoderma eremita* (Scopoli), *Liocola lugubris* (Herbst), *Trichius fasciatus* (L.).

Microorganisms in the alimentary canal of lamellicorns partly break down cellulose and proteins are broken down here by the action of enzymes (Table 6.14). Despite the fact that the food mass can remain in the alimentary canal for as long as three weeks, the processing of mould and faecal production is considerable (Fig. 6.61). The larva of *Liocola lugubris*, when fed with horse-chestnut wood, produces 342 g of air-dry faecal waste in its three-year developmental period and 349 g when this period extends to four years. On the other hand, when these larvae are reared on willow (*Salix* sp.) wood, they produce an average amount

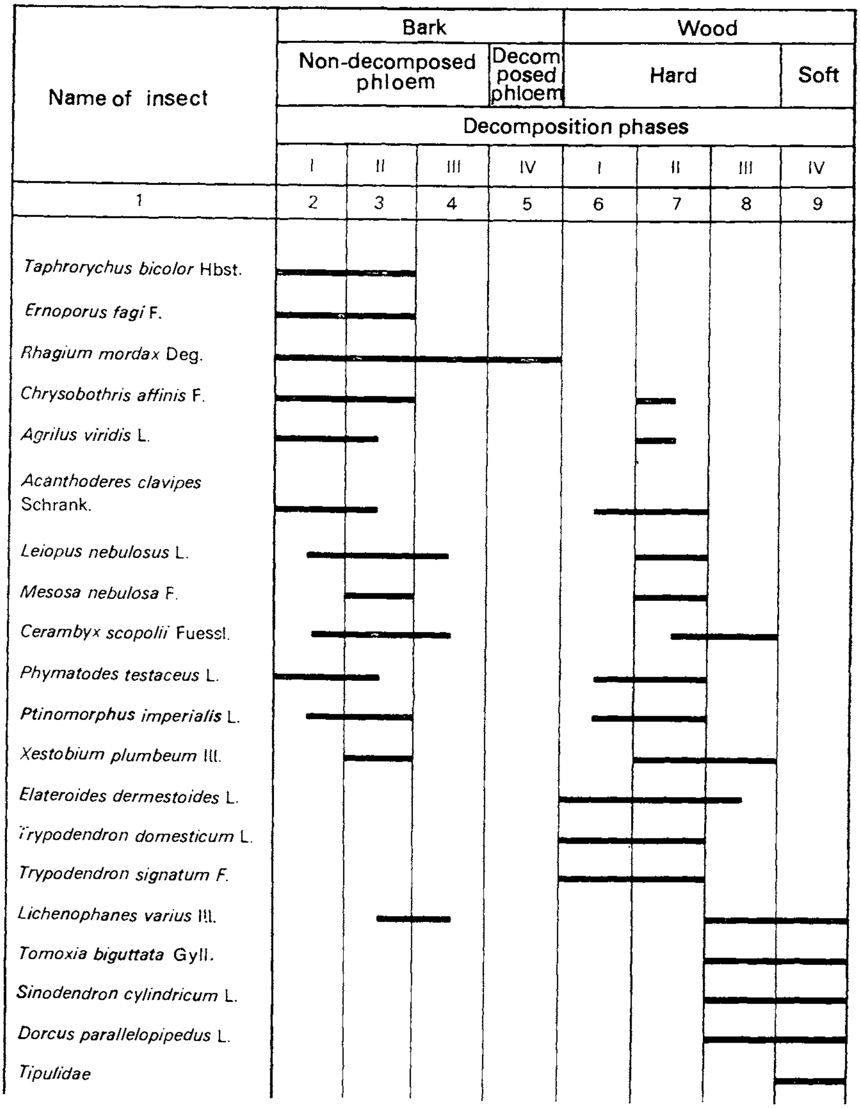


Fig. 6.60 Succession of some secondary pests in wood and under the bark of *Fagus silvatica* (L.) (after Capecki, 1969)

of 373 g of faecal waste during the 3-year generation period which indicates that there is a difference in the nutritional value of the decomposing wood of these two trees. It may therefore be calculated that, when the developmental period lasts four years, ten larvae of *L. lugubris* feed-

Table 6.14 Comparison of raw cellulose content in mould and excrements of larvae of *Lamellicornia* (after Pawłowski, 1961).

Tree species	Percentual contribution of cellulose in mould	*Lamellicornia* species	Percentual contribution of cellulose excrements
Fagus silvatica L.	27.5	*Sinodendron cylindricum* (L.)	25.1
Fagus silvatica L.	18.6	*Osmoderma eremita* (Scopoli)	2.5
Carpinus betulus L.	31.8	*Sinodendron cylindricum* (L.)	29.5
Salix sp.	23.4	*Liocola lugubris* (Herbst)	8.7
Aesculus hippocastanum L.	13.8	*Liocola lugubris* (Herbst)	4.3
Aesculus hippocastanum L.	13.9	*Osmoderma eremita* (Scopoli)	7.7
Picea excelsa Link	30.1	*Ceruchus chrysomelinus* (Hochenwarth)	28.1

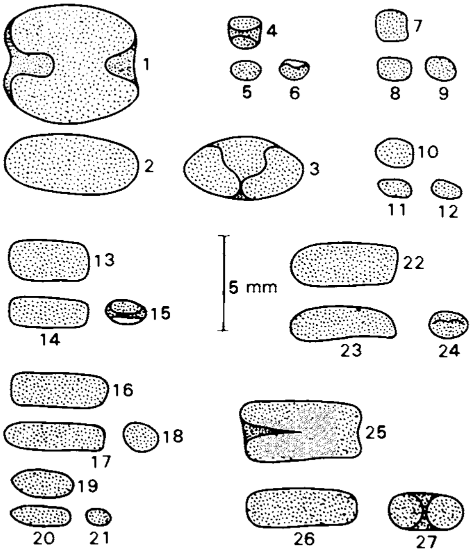


Fig. 6.61 Shape and size of larval excrements of some *Lamellicornia* species (after Pawłowski, 1961): 1–3 – *Lucanus cervus* (L.), 4–6 – *Platycerus caprea* (De Geer), 7–9 – *Sinodendron cylindricum* (L.), 10–12 – *Ceruchus chrysomelinus* (Hochenwarth), 13–15 – *Cetonia aurata* (L.), 16–18 – *Cetonia* (= *Potosia*) *cuprea* (F.), 19–21 – *Trichius fasciatus* (L.), 22–24 – *Liocola lugubris* (Herbst), 25–27 – *Osmoderma eremita* (Scopoli)

ing on the horse-chestnut process 3.5 kg of air-dry weight of mould per year.

The faecal waste of lamellicorn larvae collects in galleries or hollows of the moulding tree (Fig. 6.62). The volume of this waste accumulating

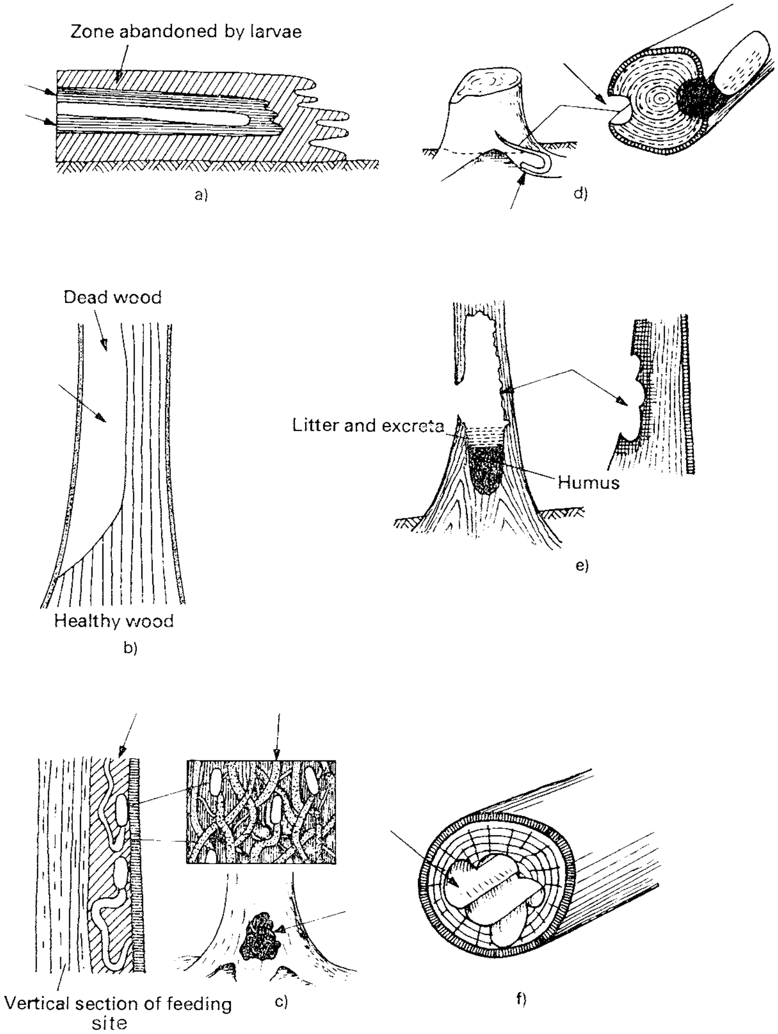


Fig. 6.62 Various types of feeding sites in mould (after Pawłowski, 1961): a — feeding site of *Ceruchus chrysomelinus* (Hochenwarth) in fallen spruce trunk, b — feeding site of *Sinodendron cylindricum* (L.) in external mould on hornbeam, c — gallery feeding site of *Valgus hemipterus* (L.), d — open gallery feeding site of *Lucanus cervus* (L.) in an oak stump, e — feeding site of *Osmoderma eremita* (Scopoli) in a hollow, f — feeding site of *Trichius fasciatus* (L.) in a fallen birch branch

in old hollows over a number of years can amount to several hundred litres, particularly when larvae of *Osmoderma eremita* (Scopoli) are involved. Needless to say, the mass of excreta is processed by other organisms but their precise association is still unknown, although many authors have suggested a number of insects, such as the larvae of *Ampedus* (= *Elater*) *cardinalis* (Schiödte) and some tipulids which occur exclusively in this environment. Sooner of later (but usually not before several or even a dozen or so years have elapsed) the faeces eventually pass into the soil, due to the disintegration of logs and the collapse of the trees. Generally they exhibit no characteristic shape but are cloddish and therefore improve the structure of the soil.

At first, the waste material is not utilized by plants, but it increases the crop of plants growing on poor podsol soils by 100%, probably as a result of the improvement of the physical properties of the soil (Pawłowski, 1961). Lamellicorns therefore play an important role in the circulation of organic matter in the forest ecosystems (Fig. 6.63).

The invasion of the galleries of *Scolytidae* by predacious and saprophagous *Coleoptera* and other insects is characterized by a high specificity. Depending on the stage in the development of the galleries, they are constantly invaded by new communities of these insects. On the other hand, in the majority of the more common species of *Scolytidae*, the communities are the same and their composition in galleries of the same

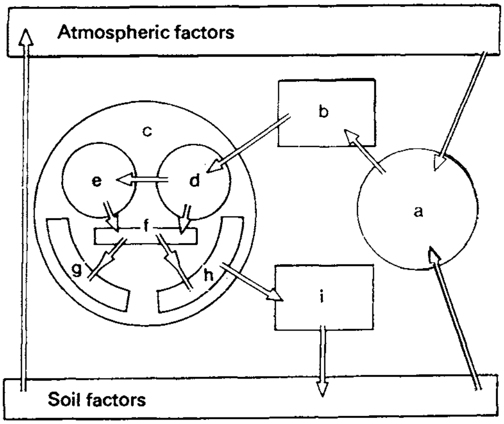


Fig. 6.63 Diagram of contribution of *Lamellicornia* larvae in the circulation of organic matter in the forest biocenosis (after Pawłowski, 1961): a – green plants, b – parts of dead plants, c – larvae, d – bacteria, e – *Flagellata*, f – protease, g – assimilable compounds, h – unassimilable compounds, i – excrements of *Lamellicornia* larvae

species does not vary with differing site conditions or species composition of forest stands. Thus, for example, almost all *Coleoptera* inhabiting the galleries of *Tomicus piniperda* (L.) also occur under the bark of various coniferous and even deciduous trees, and are components of communities of the concurrent fauna of various *Scolytidae* and other cambiophages. This suggests that the specialization of *Coleoptera* which occur under bark has not evolved in the direction of the selection of hosts or tree species, but towards the specific conditions of the habitat beneath the bark (Mazur, 1974). The ranges of penetration of these *Coleoptera* are invariably small and are frequently confined to a single scolytid gallery. Such beetles also exhibit a high susceptibility to changes of temperature and humidity. Thus the succession of species is indirectly dependent on the development of the gallery of cambiophages and directly dependent on the consequent changes in the quality of the alimenatary base and humidity of the substrate. Two stages represented by different communities of *Coleoptera* may be distinguished in the development of this particular microsuccession. The first consists of a few specialized stenotypic predators which invade the gallery during the egg and larval developmental stages of *T. piniperda.* The second develops towards the end of feeding period of these larvae and during the pupal stage in abandoned galleries. It consists mainly of eurytopic non-carnivorous *Coleoptera* represented by a large number of species and individuals exhibiting a progressively looser association with the sub-bark environment (Figs. 6.64 and 6.65). This community disappears with the decay of the cambium and phloem, and the microsuccession finally ends when the bark falls from the tree trunk.

The microsuccessions of the sub-bark entomofauna therefore constitute a fragment of whole range of similar phenomena which occur at the onset of the death of trees and which precede microsuccessions associated with the decomposition of wood.

The invasion of fruiting bodies of forest pileate fungi by insects also proceeds through a course of definite successive stages.

In stage I, *Collembola* and *Staphylinidae* invade the fruiting bodies and numerous mycetoxenes (to which various species of *Coleoptera* and flies of the family *Chloropidae* belong) appear near the fungi. The decomposition of the fruiting body begins from the moment when the fungus ripens and sheds its spores.

Collembola, staphylinids, elaterid larvae and dipterous larvae and pupae of the family *Fungivoridae* then appear in the early stages of decomposition in stage II of the microsuccession.

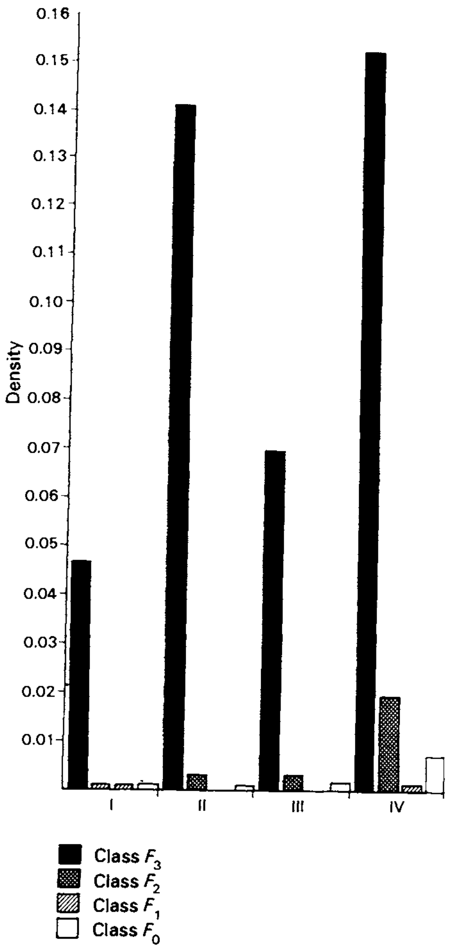


Fig. 6.64 Contribution of predacious and saprophagous *Coleoptera* of various fidelity classes ($F_3 - F_0$) in the sub-bark environment in successive developmental stages of feeding sites (galleries) of *Tomicus piniperda* (L.) (after Mazur, 1974): density = number of individuals in one feeding site:; I — phase of boring of maternal gallery and oviposition, II — phase of feeding of larvae, III — phase of development of pupae and young beetles, IV — phase of abandoned galleries

Necro-, sapro- and coprophagous larvae of *Diptera* belonging to the families *Drosophilidae*, *Muscidae* and *Anthomyiidae* are most numerous in the next phase of decomposition (stage III).

In the last phase of decomposition (stage IV), *Collembola* as well as fungivorous *Staphylinidae* and *Elateridae* withdraw, whereas necro- and

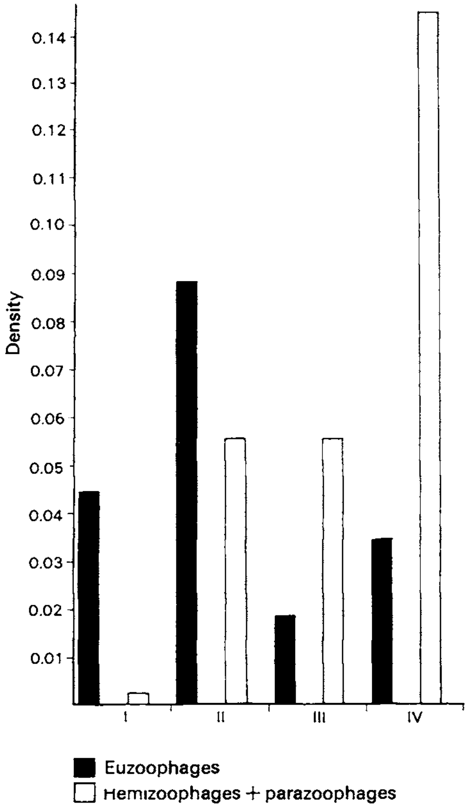


Fig. 6.65 Contribution of predacious *Coleoptera* of various degrees of alimentary specialization in individual developmental stages of galleries of *Tomicus piniperda* (L.) (after Mazur, 1974): legend as in Fig. 6.64

saprophages of the families *Silphidae*, *Scarabaeidae*, *Muscidae* and *Sphaeroceridae* (= *Borboridae*) appear. Predacious *Coleoptera* and parasitic *Hymenoptera* are also abundant during this period (Luterek, D., 1969).

Thus, complex, mutually interdependent, serial phenomena are continuously taking place in forest ecosystems. They secure ecological niches for many species of insect and provide the biocenoses with a constant flux of matter and energy, transferring it to progressively higher trophic levels. They are therefore particularly important in determining the stability of forest ecosystems.

7 Characteristics of the forest entomofauna of Poland

7.1 *History of the forest entomofauna of Poland*

The present entomocenoses of Polish forests originated mainly in the Quaternary period, when the ice sheets of the Last Glaciation retreated. Only some mountain species in the Sudeten and Carpathian region were able to survive all of the Pleistocene glacial periods and are thus of a more ancient origin. Representatives of the *Trechinae*, for example, belong to such relict preglacial groups. In the fauna of Poland they date from the Palaeocene (*Trechus amplicollis* Fairmaire and *Pseudanaphthalmus* Jeannel, the Miocene (*T. striatulus* Putzeys and *T. splendens* Gemminger & Harold) and the Pliocene (*T. pulchellus* Putzeys and *T. latus* Putzeys). The theories regarding the dispersal of Preglacial relicts and Pleistocene species of the genus *Trechus* in Poland has been comprehensively presented by Pawłowski (1975) (Fig. 7.1).

The withdrawal of the ice sheets from Poland took place in a series of successive stages. The deglaciation of the areas delimited by parallel 50°N began about 400 thousand years ago. That of the areas south of parallel 51°N began 220 thousand and from parallel 52°N, 190 thousand years ago. Only the areas lying north of parallel 53°N have a decidedly shorter Postglacial history since the glacier ice sheets did not begin to retreat until about 15 thousand years ago (Różycki, 1972).

It may be supposed that in the early Postglacial period, as based on the history of the flora of Poland, the insect communities consisted of species of the cold arctic climate which receded along with the glaciers and tundra towards the present Arctic Circle. Nevertheless, some of them remained in Central Europe occurring in specific environments, such as the soil environment of marsh coniferous forests, for example, as relict species of the glacial age.

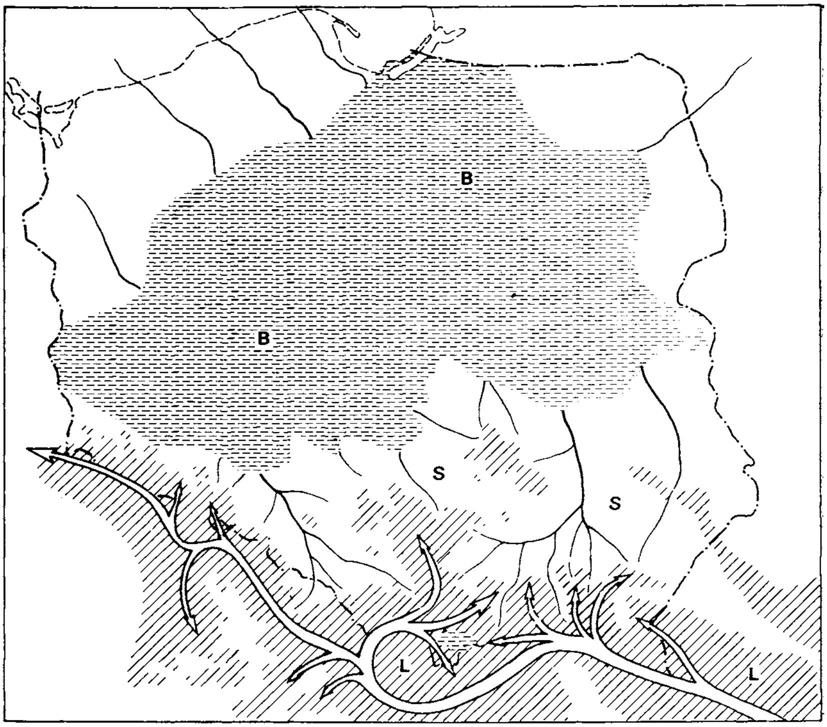


Fig. 7.1 Probable route of migration of *Trechus pulchellus* Putzeys in the Sudeten-Carpathian region against the palaeogeographical reconstruction of the Pliocene (after Pawłowski, 1975): S — steppe areas, L — forest areas, B — bog areas

Species of *Trechinae* such as *Perileptus areolatus* (Creutzer), *Epaphius rivularis* (Gyllenhal), *Epaphius secalis* (Paykull) and *Trechus quadristriatus* (Schrank) proceded northward with the thawing of the continental glacier, their alate forms being prevalent (Pawłowski, 1975).

Along with the development of birch (preboreal Yoldia period) and pine (8000–7000 B.C.), forest insect species of the coniferous forest zone, which at present occur in Europe and Siberia and sometimes even the Holarctic Region, colonized Poland from adjacent areas and from Siberia. Many representatives of the Siberian element in Poland's fauna may have arrived later, along with the appearance of the spruce during the Subboreal period (2500–500 B.C.). *Pytho kolwensis* C.R. Sahlberg (Fig. 7.2) belongs to this group and it still occurs in the Białowieża Forest in the ash-alder alluvial forest under spruce bark. Burakowski (1962) looked at the possible origins of this species in the Białowieża Forest from the standpoint of the direction of its migration from the Far East and the distribution of its host tree, the common spruce. In the past this species may have been more widely distributed throughout the northeastern range of the spruce but is has probably now died out in managed forests.

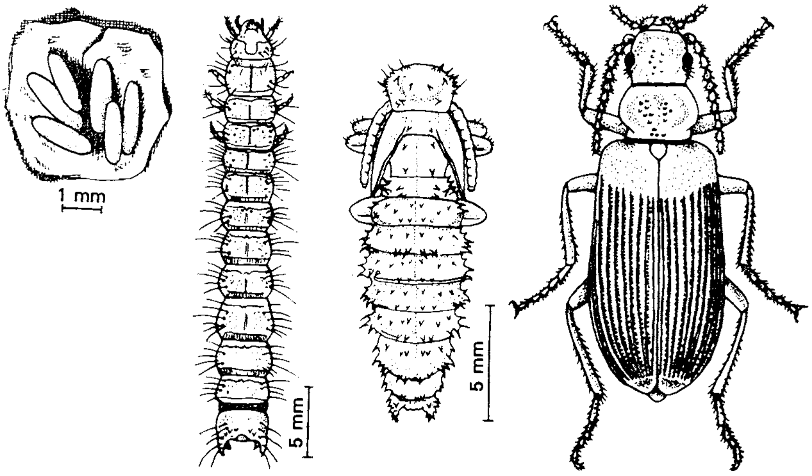


Fig. 7.2 Pytho kolwensis (C. R. Sahlberg), a species which immigrated to Poland with the spruce *Picea excelsa* (Link) (after Burakowski, 1962): egg batch, larva, pupa and adult

Other species typical of coniferous forests and which occur throughout a considerable part of the ranges of pine and spruce, at present constitute a characteristic element of Polish coniferous forests. *Panolis flammea* (D. & S.) and the litter-inhabiting staphylinids, *Sipalia circellaris* (Gravenhorst) and *Mycetoporus splendidus* (Gravenhorst) are representative of such species.

Insects of deciduous forests and open areas, many of which at present occur throughout Europe and the Caucasus, appeared in Poland as the climate continued to ameliorate (Fig. 7.3). The culmination of the occurrence of the alder took place during the Atlantic period and evoked an expansion of species connected with this forest association, such as *Trechus obtusus* Erichson. The onset of the return of the beech to southern Poland from its refuges lying to the south of the main Sudeten-Carpathian border may be dated back to the Atlantic period. The development of the entomocenoses of beech forests as characterized by

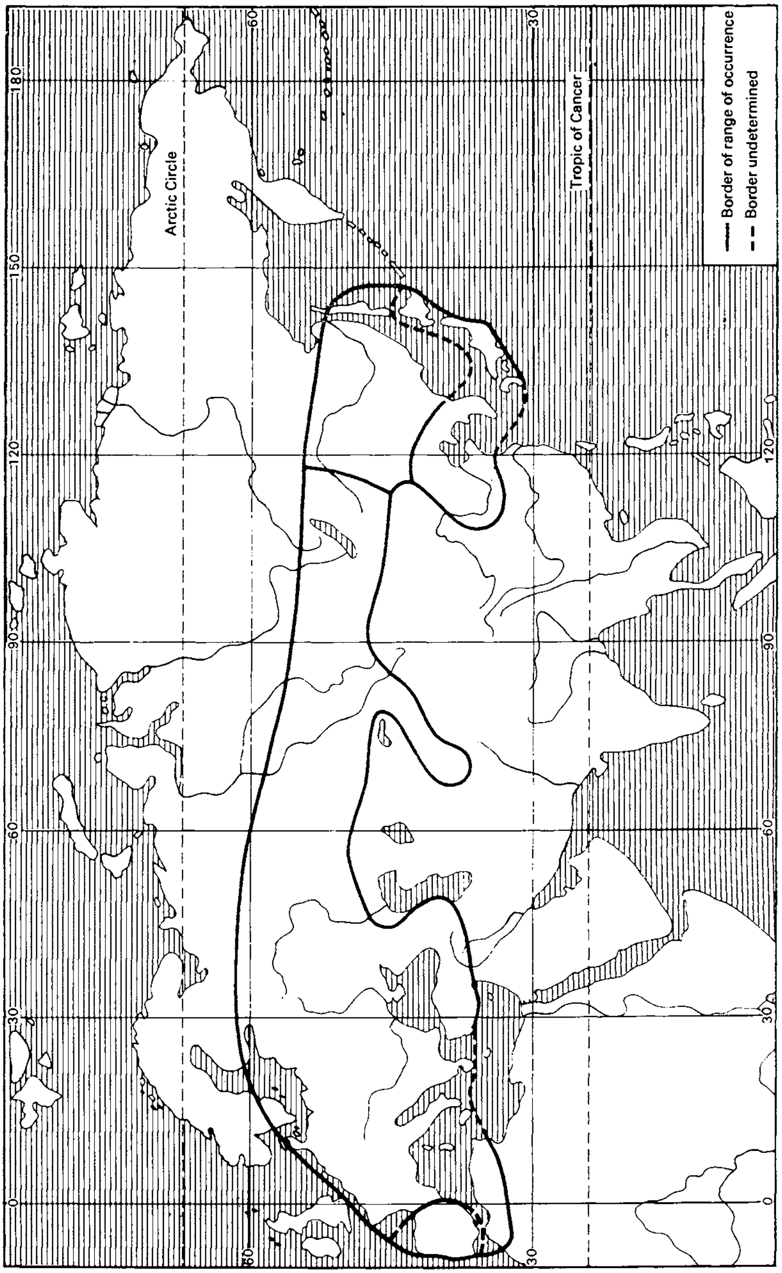


Fig. 7.3 Range of *Lymantria dispar* (L.)

the presence of *Trechus cardioderus pilisensis* Csiki is also associated with this period (Fig. 7.4).

Further long-lasting climatic changes and the progress of civilization resulted in an influx of a large number of insect species to the forests of Poland. These species represent geographical elements of various origin and to a certain degree have supplemented the entomocenoses studied by the present author at various periods throughout the forests' history. Examples of these are certain species of *Melolontha* which are of Asiatic origin (Fig. 7.5).

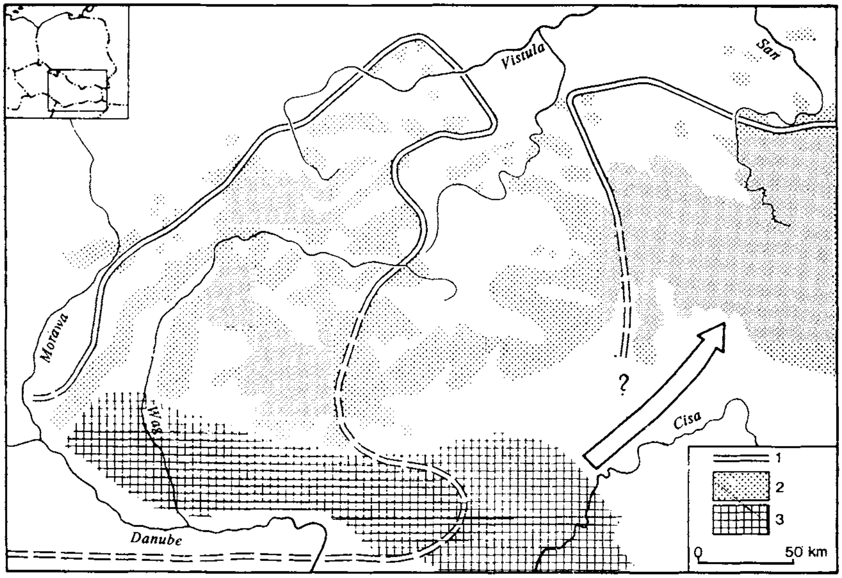


Fig. 7.4 Disjunction of the range of *Trechus cardioderus pilisensis* Csiki (1) in the north Carpathians compared with the present distribution of beech forests (2) and the situation of the beech refugium (3) (modified after Pawłowski, 1975)

The geographical origin of insects as well as the evolutionary history of each species have determined their ecological requirements, particularly their attitude to abiotic environmental factors, inter-specific dependences, their position in the spatial and temporal structure (phenology) of forest biocenoses and their ecological role. Unfortunately, there have been very few studies on the evolutionary history of particular species and their contemporary ecological requirements from the standpoint of their economic importance. However, of those that have been per-

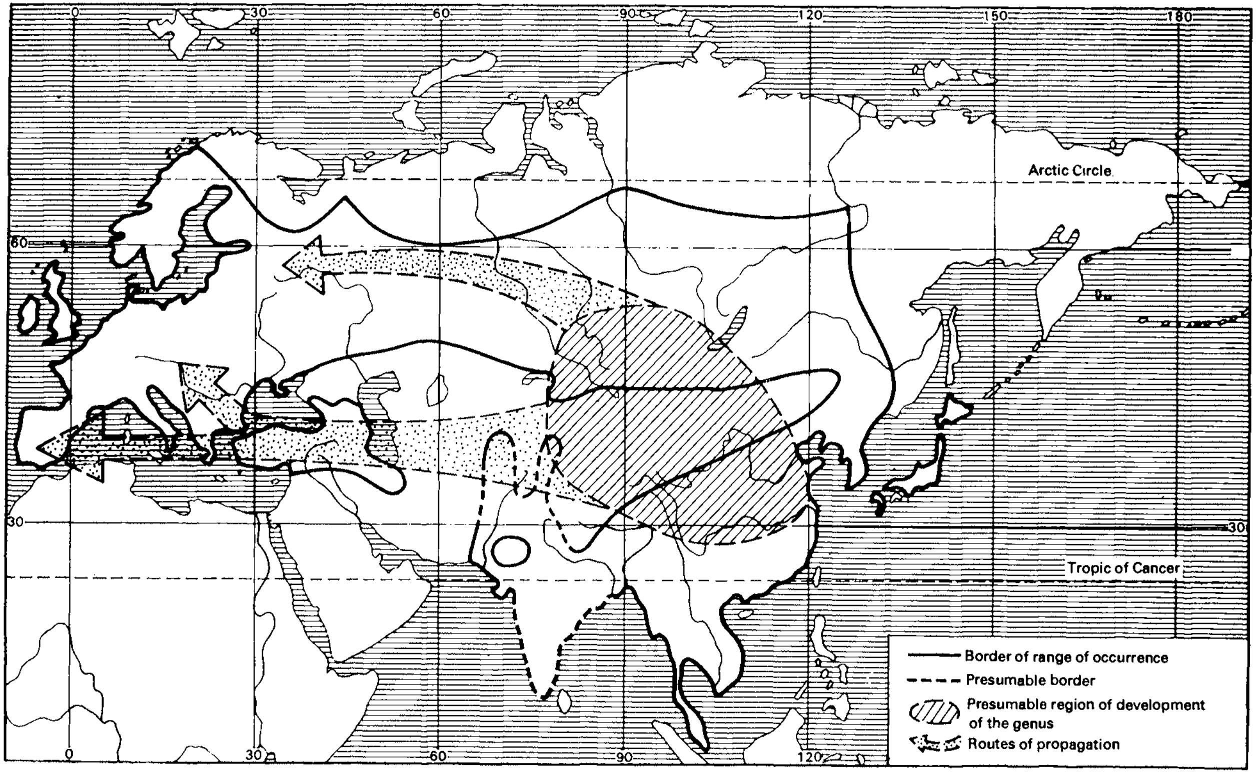


Fig. 7.5 Diagram of dispersal of the genus *Melolontha* with its genetic centre in East Asia (after Kryzhanovskii, 1965) formed, the analysis of phylogenetic relationships and geographical distribution of the Palearctic representatives of the genus *Dendrolimus* is particularly noteworthy. This genus evolved in the Pliocene and during the Pleistocene it underwent considerable speciation, these species being further differentiated in the Holocene in conjunction with the dispersal of various coniferous trees, particularly the pine (Rozhkov, 1963).

There have been a relatively larger number of studies performed on the occurrence of representatives of various zoogeographical regions in certain groups of insects, distinguished on the basis of the present geographical ranges of insects.

It appears that the contribution of various zoogeographical elements to different insect communities is extremely variable, although species of Euro-Siberian origin generally prevail in Poland (Fig. 7.6). The picture of such a zoogeographical spectrum is closely linked with the history of the formation of plant associations, against the background of which the insect communities studied have developed.

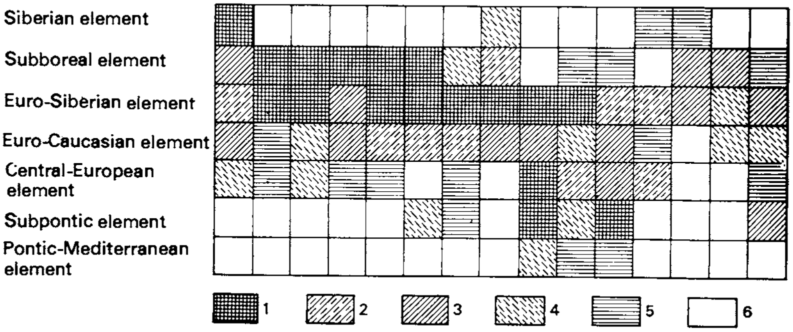


Fig. 7.6 Mean abundance of representatives of individual zoogeographical elements in the *Lepidoptera* community of the forest association *Piceeto-Alnetum* (first vertical column) as compared with communities inhabiting meadow environments of the Supraśl reservation. The high contribution of representatives of the Siberian element in the forest environment is noteworthy (after Kostrowicki, 1963): 1 – over 10 individuals per species, 2 – 7.6 to 10 individuals per species, 3 – 5.1 to 7.5 individuals per species, 4 – 2.6 to 5 individuals per species, 5 – below 2.6 individuals per species, 6 – lack of representatives of the given zoogeographical element

Thus, the spatial differentiation of entomocenoses is the result of the history of their component species, their geographical distribution and ecological requirements which have developed in the process of their evolution.

7.2 Problems of regionalization

Studies on regionalization serve to aid the understanding of the differentiation of entomocenoses of the various continents and geographical regions. Genetic, ecologic and utilitarian regionalizations may be distinguished (Kostrowicki, 1965).

The aim of studies on genetic regionalization is to gain an insight into the differentiation of the entomofauna (and the fauna and flora in general) of various areas of the Earth's surface as well as into their interrelationships, history and evolutionary trends. The zoogeographical regionalization of the Palaearctic using the example of the *Macrolepidoptera* is such a study (Kostrowicki, 1965). It has shown that, from the zoogeographical standpoint, Poland belongs to the European-West Siberian Province of the European-Siberian region.

Similar studies may concern smaller areas in which even smaller zoogeographical units may be further distinguished. However, there has as yet been no satisfactory zoogeographical subdivision of Poland from the entomological standpoint (i.e. as based on distribution of various systematic insect groups).

A working division adopted during the course of the production of the Catalogue of the Polish Fauna, including insects is given here (Fig. 7.7).

Ecological regionalization is sometimes identified with genetic regionalization. According to Kostrowicki (1965) this is erroneous since these two concepts serve different purposes. Ecological regionalization aims to group together those areas with similar ecological characters, similar systems of the utilization of the productive forces of the environment and similar life-styles of the organisms which occur in them and which frequently belong to widely differing systematic units. Not species but biocenoses or groupings of organisms are the object of such studies. Geobotany, for example, is a study of this type which concerns plants. The geobotanical division of Poland has recently been performed by Szafer & Pawłowski (1972).

There have been several works concerned with the division of Poland into natural-forest regions and zones, but that adopted by Mroczkiewicz (1952) and amended in 1969 according to the breeding regulations in force in State Forest Management is perhaps the best known (Szczuka, 1969). This division is based on the ecological-utilitarian regionalization approach. The development of ecological regionalization in zoology

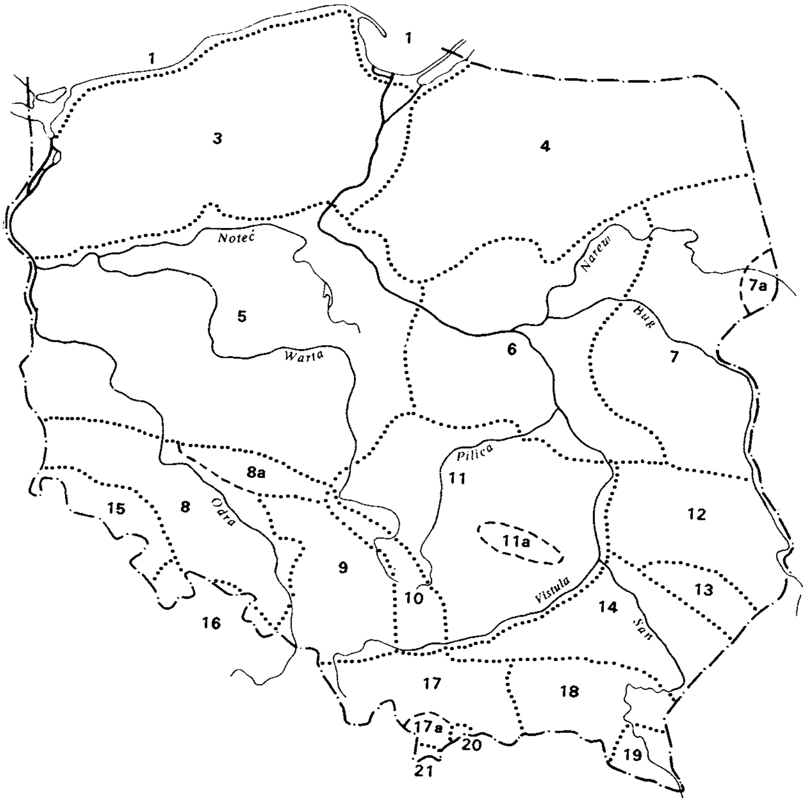


Fig. 7.7 Faunistic regionalization of Poland – working classification according to the Catalogue of Polish Fauna

encounters considerable difficulties due to the extensive systematic and ecological differentiation of the fauna.

The attempt to divide Poland into zones on the basis of the occurrence of lamellicorns (Fig. 7.8) is an example of a regionalization exercise of an ecological-genetic character. The following five zones have been distinguished (Pawłowski, 1961).

I. The spruce-hornbeam zone. This includes the Podlasie and Suwałki regions as well as the Masurian Lakeland. It is characterized by *Sinodendron cylindricum* (L.) on hornbeam and *Ceruchus chrysomelinus* (Hohenwarth) on spruce, as well as *Trichius fasciatus* (L.) and *Potosia cuprea* (F.).

II. The beech zone. This includes Pomerania and the northern part of Wielkopolska. It is characterized by *S. cylindricum* and *Dorcus paralle-*

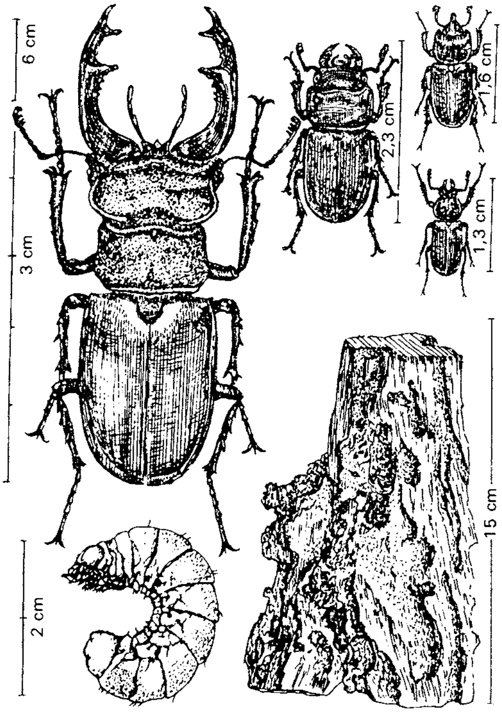


Fig. 7.8 Representatives of *Lamellicornia*

lopipedus (L.) occurring mainly on beech and to a lesser extent by *Platycerus caprea* (De Geer), *Lucanus cervus* (L.) and *Gnorimus variabilis* (L.).

III. The oak zone. This includes Mazovia, the southern part of Kujawy, Upper and Lower Silesia, a part of Małopolska and the Lublin province (the Roztocze highland). This is faunistically the richest area as regards *Lamellicornia* since all the Polish species, with the exception of *C. chrysomelinus*, occur here. *Aesalus scarabaeoides* (Panzer) and *Platycerus caraboides* (L.) (= *cribratus* (Mulsant et Rey)) are the characteristic exclusive species, *L. cervus* and *D. parallelopipedus* are characteristic selective species, whereas *Osmoderma eremita* (Scopoli) and *Oryctes nasicornis* (L.) are characteristic accessory species here.

IV. The beech-fir zone. This includes the Świętokrzyskie Mts, the sub-Sudety and sub-Carpathian belts as well as parts of the Cracow–Wieluń and Roztocze highlands. *S. cylindricum* occurring on beech and *C. chrysomelinus* on fir are characteristic here. *T. fasciatus* and *Gnorimus nobilis* (L.) are of secondary importance, while *L. cervus* and *O. eremita*, which are characteristic of the third zone, appear sporadically here.

V. The spruce zone. This includes the upper part of the mountain forest zone as well as the coniferous forests of the Sudety, Beskidy, Tatra and Bieszczady (mountain pastures) upper forest zone. The specific composition of *Lamellicornia* of this zone corresponds to that of the taiga. Only *C. chrysomelinus* and *T. fasciatus* occur here but even these species are rare (Fig. 7.9).

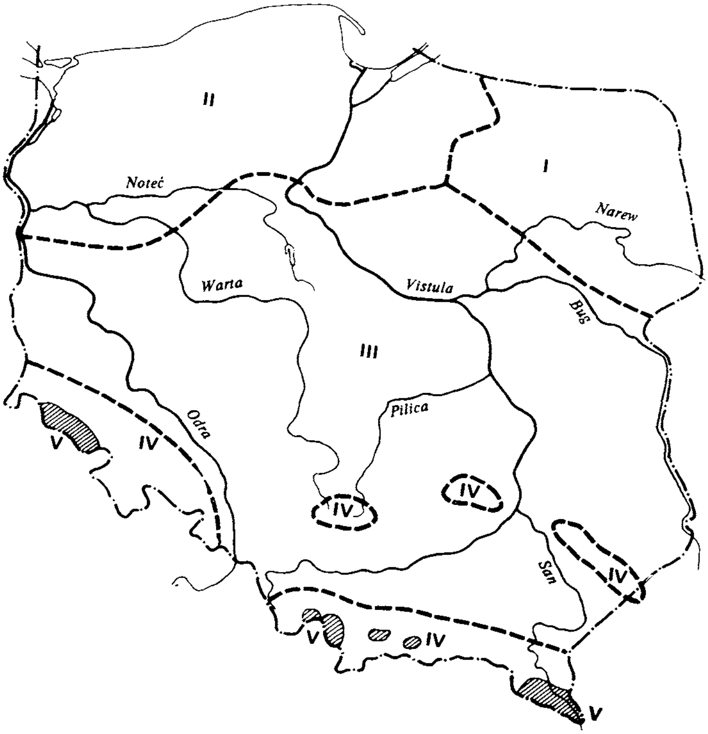


Fig. 7.9 Genetic-ecological regionalization of Poland as based on the distribution of *Lamellicornia* (after Pawłowski, 1961); explanations in text

Utilitarian regionalization deals with the spatial differentiation of the function of groups of living organisms or other objects playing or potentially capable of playing a role in human economy. This includes studies on the regionalization of noxious forest insects, taking into account both the distribution of the areas in which the noxious species occur (Fig. 7.10) and the intensity of their noxiousness from the historical point of view.

The first study of the regionalization of noxious insects in Poland was made by Nunberg (1951a). He divided the forests of Poland into

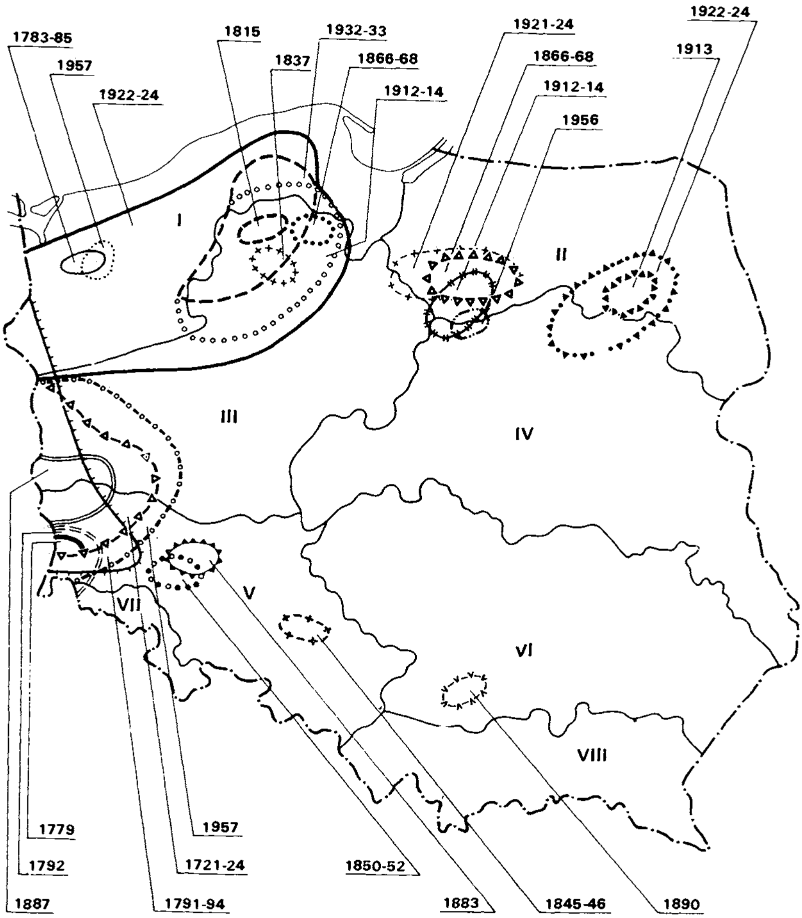


Fig. 7.10 Historical outbreak areas of *Panolis flammea* (D. & S.) in Poland compared with the division of the country into natural-forest regions (Śliwa, after Koehler, 1971)

three zones according to their sanitary condition as based on the frequency of outbreaks and the distribution of the forest stands involved. He also took into account those anthropogenic factors serving to facilitate the development of these outbreaks (Fig. 7.11).

Zone I included the western part of Poland in which the poorest and most destroyed of the Central Europe pine forests occur. In this region outbreaks of pests acquired a periodical character and recurred every 10–12 years, due primarily to the contribution of *Panolis flammea* (D. & S.) and *Dendrolimus pini* (L.) and, to a lesser extent, that of *Ly-*

mantria monacha (L.), *Bupalus piniarius* (L.), *Diprion* spp., *Acantholyda erythrocephala* (L.), *Rhyacionia buoliana* (D. & S.) and other species. The impoverished condition of the biocenoses of these forest stands weakened their environmental resistance and thus led to the need for constant action against the insects. This zone was called the zone of periodical impendence.

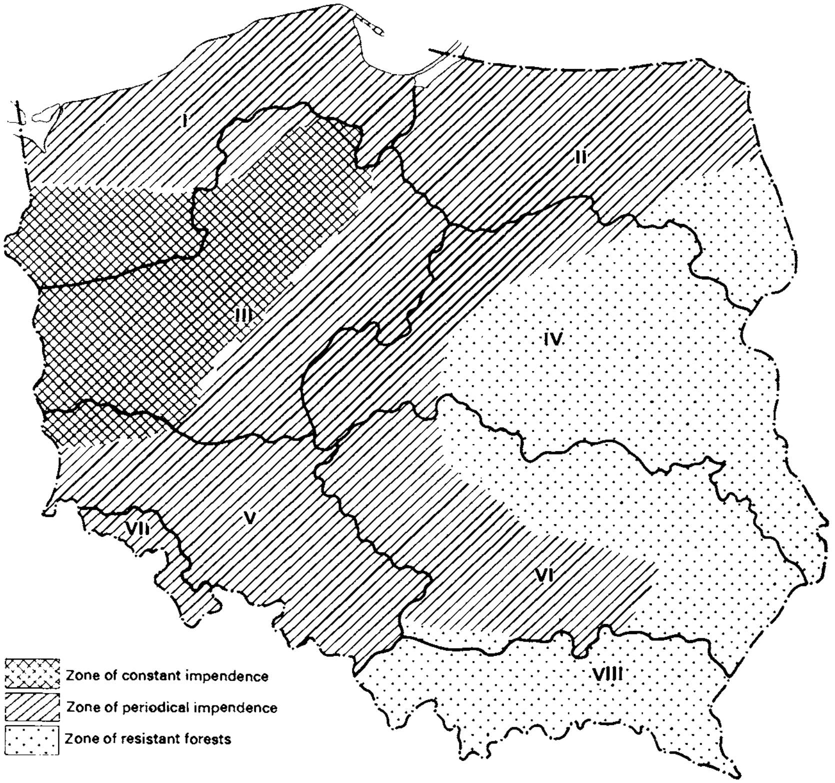


Fig. 7.11 Sanitary zones of forests in Poland (after Nunberg, 1951a) compared with natural-forest regions

Zone II adjoined the former one to the north, east and south, extending through the Masurian Lakeland to the eastern frontier and south through the Cracow Province to Sandomierz and Rzeszów. The same pests as observed in zone I all occurred here with the addition of *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson), outbreaks of which persisted for many years in the Częstochowa–Katowice–Opole triangle and in the Niepołomice Forest. On the other hand, outbreaks of other species were less frequent here than in zone I and occurred over smaller areas. This zone was called the zone of periodical impendence.

Zone III extended to the extreme east and south of Poland, including a part of the former Białystok, Warsaw and Lublin Provinces as well as the sub-Carpathian region and the Carpathian Mts. This zone was characterized by the highest resistance of the forest stands. Despite the presence of all the pests observed in zones I and II, outbreaks did not occur here. *Diprion* spp. were most frequently encountered, whereas *Melolontha* spp., *Ips typographus* (L.) and *Hylobius* sp. were economically significant. Weak gradations of *Lymantria monacha* were also observed. This zone was called the zone of resistant forest due to the slight deformation of the forest stand which consequently endowed the area with considerable environmental resistance.

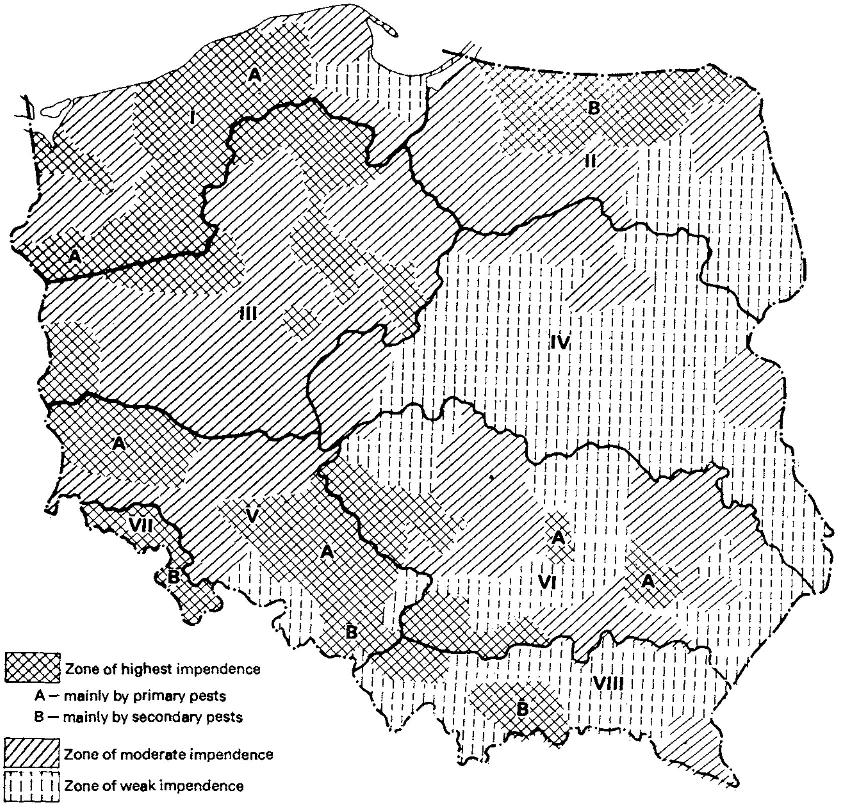


Fig. 7.12 Zones of impendence of pathogenic factors and pests compared with the natural-forest regions of Poland (after Koehler, 1971)

Twenty years later the distribution pattern of noxious insects in Poland underwent considerable transformations. Due to changes in the structure and functioning of the forest biocenoses, the outbreak areas of many insect pests moved eastwards. Changes in the economic roles of many pests in various regions of Poland were also favoured by the recent changes in meteorological conditions, as well as by anthropogenic influences such as the drainage of certain areas and the influences of industry on the forest stands. The division of Poland into zones of impendence of forests as elaborated by the Forest Research Institute in Warsaw presented a very different picture in this respect. Zones of high, moderate and continuous impendence were distinguished, corresponding, from the economic standpoint, to the respective zones established by Nunberg (1951a) (Fig. 7.12).

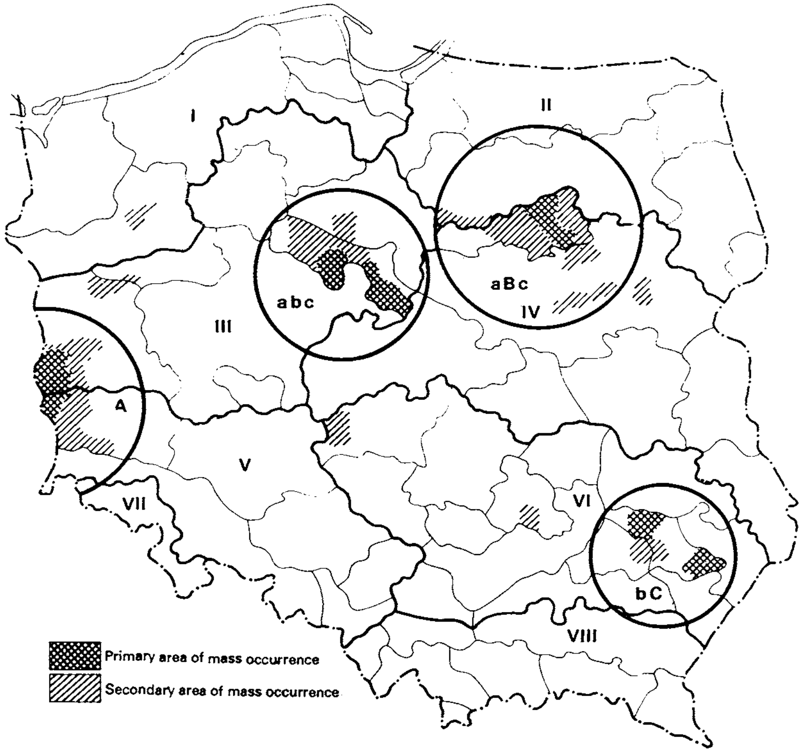


Fig. 7.13 Main foci of the outbreak area of *Dendrolimus pini* (L.) in 1946–1966 (after Koehler, 1971): A – heavy outbreak (1948–1951), a – moderate outbreak (1949–1951), B – heavy outbreak (1948–1951), b – moderate outbreak (1956–1957), C – heavy outbreak (1964–1966), c – moderate outbreak (1964–1966)

The zone of the highest impendence extended northward and southward and shifted eastward. The zone of low impendence was confined to the Mazovia–Podlasie region. The economic role of individual pests in various sanitary zones, as well as the frequency of outbreaks, also changed. According to Koehler (1968), adaptation processes within biocenoses took place in the pure pine forests of the western part of the country (zone of continuous impendence, after Nunberg), for example in the Bory Tucholskie Forest, the Noteć Forest and the pine forests of the Zielona Góra Province. These processes led to an increase of the regulative processes which served to hinder the violent and intense propagation of pests in these biocenoses. Pests such as *Panolis flammea* and *Dendrolimus pini* underwent "gradational ageing" here, whereas "gradationally young" species such as *Acantholyda posticalis* showed a strong outbreak tendency (Figs. 7.13 and 7.14). The interesting hypothesis of Koehler derived from the observed disease processes in Polish

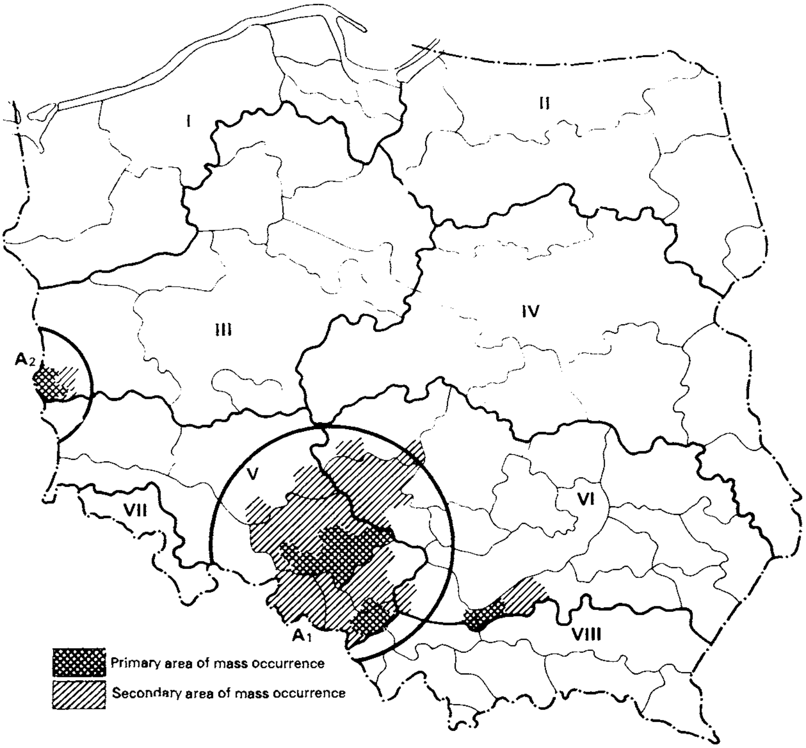


Fig. 7.14 Outbreak areas of *Acantholyda posticalis* Matsumura (= *nemoralis* Thomson)

forests, and supported by the well known fact of the quantitative "absorption" by the biocenosis of its components several years after the pests' mass appearances (e.g. the crab *Eriocheir sinensis* on the western coast of the Baltic, the musk-rat on the borders of water bodies in Poland, etc.) requires further confirmation.

Details concerning the current regionalization of Polish forests as regards their sanitary condition, with particular reference to the impendence of outbreaks of noxious insects are given by Koehler (1971).

7.3 Characteristics of the entomofauna of Polish forests

Studies on the entomofauna of Poland are particularly well documented although, for a number of years, authors did not realize the need for an ecological approach to the analysis of the regional entomofauna. However, before World War II, there were a few exceptions of which the most notable perhaps are the works of entomologists such as Koźmiński (1925), Kuntze & Noskiewicz (1938), Karpiński (1933) and Nunberg (1929). Such authors based their zoogeographical analysis of the fauna on a knowledge of the ecological nature of the occurrence of the insects studied and their communities. The situation became so alarming that at the general assembly of the Polish Union of Entomologists held in Cieplice in 1953, two lectures (Tarwid, 1958; Kostrowicki, 1956) were devoted to the problem of the "ecologization" of entomological studies. Furthermore, the next assembly of this Union held in Poznań in 1955 advanced the proposition of the need to make "faunistic-ecological records in order to provide bases for studies on the transformations occurring in the fauna" (Jaczewski, 1957). Indeed, the progress of anthropization of the entomofauna of Poland, as well as the ever increasing tasks concerning the protection of plants against insects with particular emphasis on prophylactic and integrated methods, made indispensable the knowledge of the occurrence of individuals of various species, and of their populations and communities, indispensable. Due to the extreme variability of the environments in which insects live, as well as that of the topography of Poland, the description of the entomofauna of this country is still in its initial stages and lags far behind the knowledge of plant associations, in spite of the efforts of both entomologists and ecologists alike. Analytical difficulties in the evaluation of quantitative ratios of entomocenoses, the large amount of time and labour involved in such studies and the shortage of taxonomists and systematists with specialist knowledge of the numerous groups of insects occurring in Poland are the main reasons for this discrepancy. Thus, since the taxocenes of both natural and synanthropic environments have not yet been characterized, there exist no bases for the comparison of geographical differentiation of these taxocenes on a country-wide scale.

This also concerns taxocenes and entire entomocenoses of Polish forests. Thus their characteristics as given in this chapter merely constitute a preliminary attempt at their definition. The present author has, in the first place, utilized data defining the character of the forest environment of the insect species studied and their quantitative dependences on other components of the local entomofauna. The entomocenoses

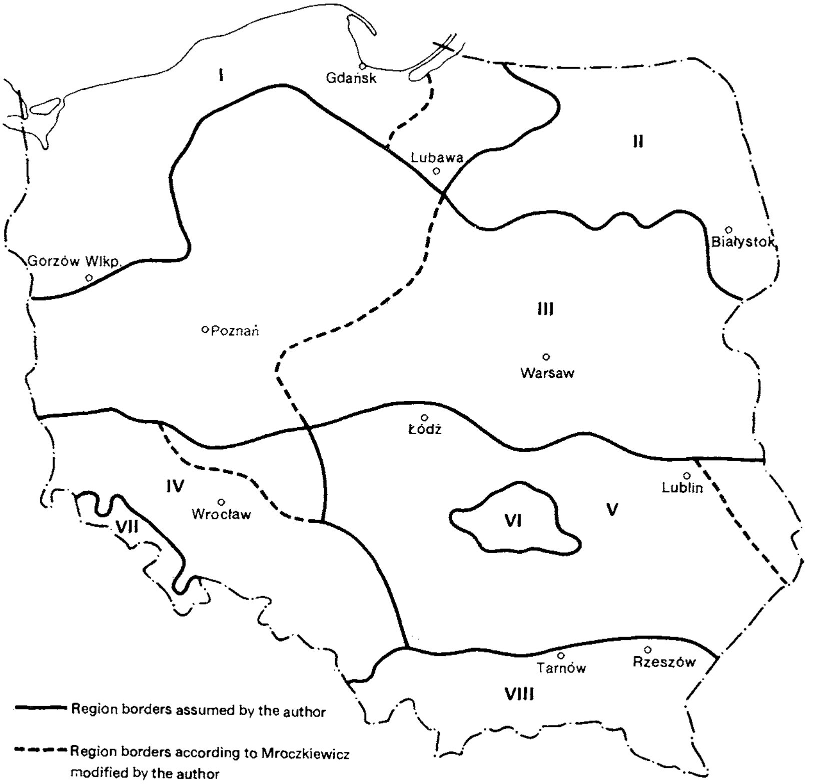


Fig. 7.15 Division of Poland into natural-forest regions (after Mroczkiewicz, 1952, modified by the author): I – Baltic Region, II – Masurian-Podlasie Region, III – Range of Central Polish Lowlands, IV – Silesian Region, V – Region of Central Polish Uplands, VI – Region of Świętokrzyskie Mts, VII – Sudeten Region, VIII – Carpathian Region

have been described with reference to the division of Poland into natural-forest regions and zones according to Mroczkiewicz (1952), as given in the "Silviculture Regulations" in force in state forest management (Szczuka, 1969) with the following amendments resulting from the quoted works on geobotany and entomofaunistic regionalization.

The Elbląg–Warmia zone (Mroczkiewicz, 1952) is included in the Baltic Region along the eastern border of the beech range. The Chełm zone is included in the region of Central Polish Uplands areas, whereas the Mazovia–Podlasie and Wielkopolska–Pomerania regions are treated jointly as the Great European Lowland Region. The zone of the Świętokrzyskie Mts is described separately within the scope of the region of Central Polish Uplands (Fig. 7.15). The characteristics of forest communities of noxious insects is based on Koehler (1971) and has been supplemented with later publications of various authors and the present author's own observations. The principal aims, however, concerned the definition of the communities of forest insects, including parasites, predators and saprophages, as well as phytophages of the forest herb layer, since these species are most susceptible to anthropogenic pressure and their populations are likely to undergo further transformations. The nature of these transformations will be the subject of the next chapter of this book. Studies on the population dynamics of economically significant phytophages and their complex interrelationships with other groups of insects are very important. Thus, a knowledge of the present forest entomofauna is the leading research and management problem as regards the ecology of forest insects.

I. Baltic Region

The Baltic Region lies within the range of the Last Glaciation in the area of the terminal and ground moraines, in the Baltic and lakeland climate. The beech is the predominant species in the forests of this region. It occurs in pure forest stands as well as in mixed stands along with pine, oak, linden, maple, sycamore and the artificially introduced spruce and larch.

Entomofauna of the forest tree layer. The beech forest stands are attacked by a moderate number of phytophages, among which the weevil *Rhynchaenus fagi* (L.) is particularly common in this region. Its massive outbreak in 1969 occurred in all the forests of the eastern part of the Pomeranian Lakeland and those of the Coastal Belt. *Operophthera* *brumata* (L.), *Erannis defoliaria* (Clerck) and *Dasychira pudibunda* (L.) are also characterized by dynamic outbreaks, while *Lymantria monacha* (L.) frequently appears in large numbers in the beech forests of Pomerania. The aphid *Phyllaphis fagi* (L.), individuals of which occur on the under-side of beech leaves, belongs to the group of economically less important but characteristic phytophages in the Baltic Region.

Cryptococcus fagi (Bärensprung), which is particularly common in the western part of the Coastal Belt, sucks the bark tissues and plays an important role in the propagation of diseases and of "mucorrhoea of the beech".

The following insects occur most frequently in the wood or under the bark of beeches: *Hylecoetus dermestoides* (L.), *Ptilinus pectinicornis* (L.), *Agrilus viridis* (L.), *Rhagium mordax* (De Geer) and *Leiopus nebulosus* (L.). The following species are characteristic of the environment discussed in the Baltic Region: *Ptinomorphus imperialis* (L.), *Tomoxia biguttata* (Gyllenhal), *Leptura scutellata* F., *Cerambyx scopolii* Fuessly, *Clytus arietis* (L.), *Ernopocerus fagi* (F.) and *Taphrorychus bicolor* (Herbst) (Capecki, 1969).

The wide differentiation of forest habitats in the region under discussion makes it possible for pine phytophages to occur in certain habitat conditions. These include pine forest stands on postglacial sands and gravels, as well as those on soils of the ground moraine where the ground water level may undergo considerable changes. *Panolis flammea* (D. & S.) and *Bupalus piniarius* (L.) are of particular economic importance here, while outbreaks of *Lymantria monacha* are of a more local nature. *Thaumetopoea pinivora* (L.) is one of the pests of the pine forests of the Coastal Belt. *Philopedon plagiatus* (Schaller) and *Strophosomus* spp. occur in large numbers in plantations, particularly on vast areas of afforested arable soils, whereas *Rhyacionia buoliana* (D. & S.) occurs in older plantations and thickets. Insects developing under the bark or in the wood, among which *Tomicus minor* (Hartig), *T. piniperda* (L.), *Monochamus galloprovincialis* (Olivier) and *Phaenops cyanea* (F.) are the most important, and abundant in pine forest stands weakened by the activities of phytophages.

The course of the microsuccession of beetles in galleries of *Tomicus piniperda* on felled pines in fresh coniferous forests was studied in the Elbląg–Warmia zone (Mazur, 1974). *Rhizophagus depressus* (F.) dominates in phases I and II of the microsuccession (oviposition and larval development), whereas *Phloeonomus pusillus* (Gravenhorst) prevails in phases III (pupal development) and IV by the scolytids in abandoned

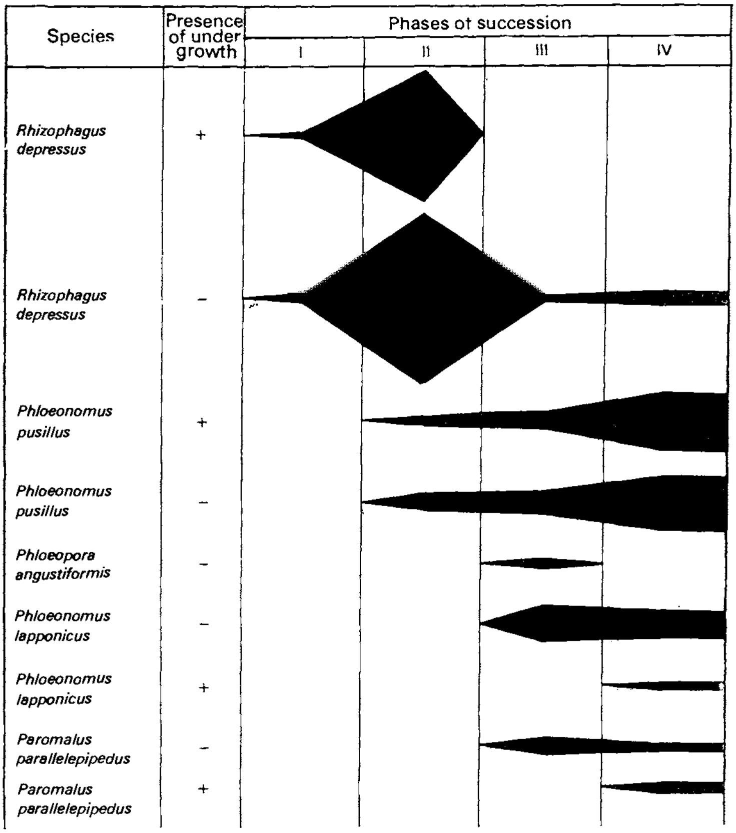


Fig. 7.16 Microsuccession of most important *Coleoptera* species in galleries of *Tomicus piniperda* (L.) in the Smolniki forest district (after Mazur, 1974)

galleries (Fig. 7.16). The course of the microsuccession in the mixed fresh coniferous forest habitat is similar.

A total of 50 species of *Coleoptera* were observed under the bark. As well as *Rhizophagus depressus*, *Phloeonomus pusillus* and the other species represented in Fig. 7.16, the following species were also frequently encountered: *Plegaderus vulneratus* (Panzer), *Phloeopora angustiformis* Baudi, *Placusa atrata* (C.R. Sahlberg), *P. depressa* Mäklin, *Thanasimus formicarius* (L.), *Paromalus parallelepipedus* (Herbst) and *Gabrius splendidulus* (Gravenhorst).

Diadegma eucerophaga Horstmann, the parasite of *Exoteleia dodecella* (L.) dominates in the community of parasitic insects of the family *Ichneumonidae*, whereas *Scambus sagax* Hartig is one of the subdominant species of this community in the tree crowns of pine forest stands of various site types in the Elbląg-Warmia zone. About 30% of the ichneumon populations in the crowns of pole-sized pine stands are parasites of the caterpillars of *Microlepidoptera* feeding on the pine. However, the parasites of pine-feeding *Macrolepidoptera* are relatively scarce and include *Banchus hastator* (F.) (= *femoralis* Thomson), *Stenichneumon pictus* Gmelin, *Enicospilus ramidulus* (L.) and *Barichneumon bilunulatus* (Gravenhorst). *Idiogramma* sp., the parasite of *Symphyta* of the genus *Xylea*, the larvae of which occur in pine cones, is frequent under the conditions described.

The presence of oak undergrowth in the habitat of fresh coniferous forest has no significant effect on the ichneumon community in the pine crowns. On the other hand, *Ichneumonidae* whose hosts occur on the oak such as *Cratichneumon lanius* (Gravenhorst) (the contribution of which to the community is 10.7%), *Campoplex difformis* (Gmelin) (D = 6%) and *Agrypon flaveolatum* (Gravenhorst) (D = 4.7%) prevail in the pine crowns in fresh mixed coniferous forest habitats in stands with oak undergrowth.

Species indirectly associated with the pine, such as *Trichosis legator* Thunberg and *Macrus parvulus* (Gravenhorst) are less common.

Entomofauna of the forest undergrowth and herb layers. Data concerning the entomofauna of the undergrowth and herb layer of the region discussed, including *Ichneumonidae*, *Aphidodea*, *Orthoptera* and insects of various systematic groups (mainly *Diptera*) mining leaves of herbaceous plants, are scarce. As many as 201 species of *Ichneumonidae* were observed in the layer of oak undercrop in the fresh mixed coniferous forest habitat in the Elbląg–Warmia zone. *Eusterinx* sp. predominates, while *Cratichneumon varipes* (Gravenhorst), *C. nigritarius* (Gravenhorst), *C. lanius* (Gravenhorst), *Ichneumon subquadratus* Thomson and *Proclitus grandis* (Foerster) are among the most frequently encountered species here. The predominant species of the genera *Eusterinx* and *Proclitus* are parasites of *Diptera* living in fungi, whereas *Cratichneumon* spp. and *Netelia* sp. are parasites of phytophagous *Macrolepidoptera* feeding on deciduous or coniferous trees.

Representatives of the genus *Eusterinx* predominate but *Cratichneumon nigritarius*, *C. varipes*, *Pleolophus basizonus* (Gravenhorst), *Proclitus grandis*, and *Macrus parvulus* are also frequent in pine forest stands in the fresh coniferous forest habitat in the layer of beech undergrowth, as well as on the forest floor with or without undergrowth. About 25%

of the total number of *Ichneumonidae* occurring here belong to the subfamily *Microleptinae* parasitic on larvae of *Diptera* feeding on pileate fungi.

Insects mining plant tissues have been recorded from the Wolin National Park (Nowakowski, 1954) and *Orthoptera* from the reservation of *Quercus pubescens* in Bielinek on the Odra River. The occurrence of many insect species characteristic of south-eastern European forest-steppes was observed in the association *Querceto-Lithospermetum* in Bielinek.

The xerothermophilous subpontic species, *Leptophyes albovittata* (Koll.) dominates along with *Chorthipus mollis* Charpentier (common all over Poland) in the *Orthoptera* community of thermophilous oak forest. These species are accompanied by *Metrioptera roeseli* (Hagenbach), *Chorthippus vagans* (von Eversman) and *C. brunneus* (Thunberg) (Liana, 1973).

Detailed studies on aphids on the Vistula Spit revealed the presence of 137 species of these phytophages against 650 species recorded from the whole of Poland (Szelęgiewicz, 1974). Some of these (64 species) inhabit the coastal coniferous forest (*Empetro-nigri-Pinetum*) and are mostly associated with the pine forest environment, e.g. *Pineus pini* (Gmelin), *Cinara* spp., *Aphis mirifica* (Börner), *Aulacorthum pirolacearum* Szelęgiewicz (hitherto known only on the Vistula Spit where it lives on *Pirola* spp.). Some aphid species constitute an element which has penetrated from the belt of coastal dunes, e.g. *Laingia psammae* Theobald, *Schizaphis jaroslavi* (Mordvilko) *Aphis hieracii* Schrank, and *Dactynotus* (= *Uroleucon*) *obscurus* (Koch), while others are synanthropic species which occur on the outskirts of coniferous forest and have penetrated into the forest along roads and paths invading open areas such as clearings. The latter include *Forda formicaria* von Heyden, *Pterocomma konoi* Hori, *Aphis frangulae* Kaltenbach and *Brachycaudus linariae* Stroyan.

Entomofauna of the forest litter layer. The specific composition and frequency of communities of litter *Staphylinidae* in the Coastal Belt of the cliff Baltic coast is very rich. This may be associated with air humidity conditions favouring the occurrence of these hygrophilous beetles under the orographic conditions discussed. *Xantholinus tricolor* (F.) dominates and myrmecophilous species (no ably *Zyras laticollis* (Märkel)) inhabiting numerous ant nests of the genus *Lasius* are particularly abundant on the poorer sandy soils of cliffs overgrown with pine and *Hippo-*

phaë rhamnoides. *Quedius fuliginosus* (Gravenhorst) is the dominant species of the staphylinid community in beech forests growing in fertile situations. Moreover, species of the genus *Staphylinus* (= *Ocypus*) are also present among which *S. ophthalmicus* Scopoli seems to be characteristic of the environment discussed. This species is associated with soils of high calcium content and occurs on insolated sites such as the borders of the beech forest, clearings, etc. *Mycetoporus splendidus* (Gravenhorst) exhibits a high frequency, along with *Othius myrmecophilus* Kiesenwetter in pine forests of low compactness occurring on the coastal dunes. *Phylan gibbus* (F.) (*Tenebrionidae*), damaging young pine plantations, belongs to species characteristic of open dunes of the Coastal Belt.

Carabus arcensis Herbst, *C. violaceus* L., *C. hortensis* L., *Pterostichus oblongopunctatus* (F.) and *P. niger* (Schaller) are the most important species of the carabid community of the mixed forest habitat in the Elbląg–Warmia zone.

The contribution of each of these species varies in communities depending on the habitat conditions and the specific composition of the forest stand. The total number of species in the community, the density of individuals, the contribution of species of spring and autumn developmental types, as well as the contribution of species of different feeding forms also vary (Table 7.1).

Serica brunnea (L.) dominates, whereas *Dalopius marginatus* (L.), *Maladera holosericea* (Scopoli) and *Brachyderes incanus* (L.) are less frequent in the community of larvae of soil *Coleoptera* of the peripheral parts of deciduous forest stands of the *Fageto-Quercetum* association (adjacent to meadow associations) in the Baltic Region. On the other hand, *Dalopius marginatus* dominates whereas *Athous subfuscus* (Müller) *Ectinus aterrimus* (L.), *Brachyderes incanus* and *Tanymecus palliatus* (F.) are less frequent in a similar ecotonic system on the periphery of pine forest stands on the habitat *Pino-Vaccinietum myrtilli* (Cykowski, 1975).

II. Masurian-Podlasie Region

The Masurian-Podlasie Region includes the area of ground and terminal moraines within the range of the Last Glaciation. Spruce is the main forest-forming species here. It occurs in the forests along with pine or various deciduous tree species. Vast spruce forests in which the spruce occurs on more humid sites extend to the sandr sands of this Region.

Table 7.1 Ecological characteristics of litter *Carabidae* in various site forest types in the Elbląg-Warmia district (tabulated according to Szyszko, 1972).

Species	Site forest type					
	Mixed forest/ Fresh mixed coniferous forest		Fresh mixed coniferous forest		Fresh coniferous forest	
	Presence of forest undergrowth					
	−	+	−	+	−	+
Carabus arcensis Herbst	D	S	S	S	S	S
Pterostichus niger (Schaller)	S	D	S	D		D
Pterostichus oblongopunctatus (F.)	S	S	D	S	D	S
Carabus violaceus L.	S	S	S	S	S	S
Carabus hortensis L.	S	S	S			
Number of attendant species	13	12	16	15	26	16
Contribution of individuals of spring species	60	36	51.5	37.6	79.6	40.4
Contribution of individuals of autumn species	40	64	48.5	62.4	21.1	59.6
Density per 1 m^2	3.3	1.5	3.0	1.8	1.3	1.2
Individuals of large zoophages, %	69.9	69.0	67.9	73.6	48.5	71.9
Individuals of small zoophages, %	22.4	29.5	30.5	18.7	46.1	25.1
Individuals of hemizoophages, %	7.7	0.7	1.6	7.6	5.5	3.0

D – dominant, S – subdominant species of *Carabidae* community.

Entomofauna of the forest tree layer. Insects of pest status are well known in this region due to their frequent outbreaks (Burzyński, 1961; Klarowski, 1957; Schnaider, 1952; Schnaider & Sierpiński, 1954; Wolski, 1966).

Outbreaks of noxious insects occur here in two extremely different ecological situations. On the one hand, outbreaks of *Lymantria monacha* (L.) and the disastrous occurrence of secondary pests take place in spruce forest stands on very fertile soils (but with spatially and phenologically changed hydrologic conditions) and, on the other hand, outbreaks of *Panolis flammea* (D. & S.) appear to be associated with pure pine forests growing on outwash sands. Due to the formation of pure spruce stands in the rich habitats of the Masurian Lakeland zone, these stands developed a particular susceptibility to chain diseases, the last link of which consists of a community of secondary pests in which *Ips typographus* (L.) dominates and *I. duplicatus* C. R. Sahlberg is specific for this Region (Fig. 7.17). *Polygraphus poligraphus* (L.) occurs

Fig. 7.17 Spruce windfall in the Borecka Forest invaded by bark beetles (photo by W. Strojny)

here in large numbers in younger spruce forests, whereas *Pityogenes chalcographus* (L.) and *I. amitinus* (Eichhoff) prevail on thinner trees. This community is particularly active in periods of drought (Table 7.2).

Hylurgops palliatus (Gyllenhal), *Dryocetes autographus* (Ratzeburg) and *Orthotomicus proximus* (Eichhoff) which occur in large numbers are of less economic importance since they invade dying tress. The occurrence of *Pityophthorus micrographus* (L.) on the spruce is characteristic of this region.

The vast outbreaks of spruce bark-beetles leads to an abundance of insects inhabiting their galleries. The community of beetles living under the bark of the spruce in the Borecka Forest consists mainly of species invading the galleries of bark-beetles both in coniferous and deciduous trees (*Thanasimus formicarius* (L.), *Nudobius lentus* (Gravenhorst), *Phloeonomus pusillus* (Gravenhorst), *P. punctipennis* Thomson, *P. planus* (Paykull), *P. lapponicus* (Zetterstedt), *Bolitochara obliqua* Erichson, *Rhizophagus depressus* (F.), *R. dispar* (Paykull), *R. bipustulatus* (F.), *R. nitidulus* (F.), *R. politus* (Herbst), *Bitoma crenata* (F.), *Cerylon histeroides* (F.) and others). Species characteristic of galleries of various bark-beetles on coniferous trees (*Cylister angustatus* (Hoffmann). *C. linearis* (Erichson), *Paromalus flavicornis* (Herbst), *P. parallelepipedus*

Table 7.2 Invasion of the spruce by secondary pests in Olsztyn Province in 1955–1964 (according to dead spruce logging) as compared with changes in water level in the main lake system of the Masurian Lakeland (Śniardwy, Mamry, Niegocin, Bełdan and other lakes) (according to data of Wolski, 1966).

Year	Difference between current minimum and minimum water level in 1955	Period of maintainance of water level lower than the minimum of 1955 (months)	Logging of spruce wood invaded by secondary pests (m^3)
1955	6	–	100 808
1956	13	–	129 546
1957	46	–	88 276
1958	19	–	45 896
1959	– 14	3.0	37 108
1960	– 13	3.5	40 028
1961	– 14	2.5	37 293
1962	– 6	about 2.0	38 268
1963	– 63	10.0	46 981
1964	– 64	4.0	195 518

Note: The large amount of dead wood logged in 1955 and 1956 resulted from damages due to hurricanes. Data for the years 1960–1964 are calculated for the periods: Oct. 1 of the former year to Sept 30.

(Herbst), *Plegaderus* spp., *Crypturgus* spp., *Corticeus fraxini* (Kugelann) and others) as well as species characteristic of galleries of bark-beetles occurring only on the spruce (*Laemophloeus corticinus* Erichson and *Corticeus linearis* (F.)) are less frequent. Most of these species invade the butt of the trunk during the period when the fully-grown larvae or pupae of the bark-beetles are present in the galleries. The boreal-mountain species *Quedius plagiatus* (Mannerheim) (= *laevigatus* Gyllenhal), appears as the galleries are abandoned and the bark disintegrates. A total of 38 species inhabiting the galleries of bark-beetles in spruce have been observed in the Borecka Forest (Okołów, 1963). Further information regarding the species of this ecological group is to be found in Bałazy & Michalski (1960) and Szujecki (1967), whereas data on the parasites of bark-beetles in the Borecka Forest are included in Szczepański (1960); (Table 7.3).

In the southern part of the Masurian Plain zone, in the Pisz Forest and less frequently in the Suwałki–Augustów zone, rather intensive outbreaks of *Panolis flammea* (D. & S.) and other pine foliophages occasionally take place. Outbreaks of *Acantholyda erythrocephala* Christ are local in nature here.

Table 7.3 Chalcidoidea parasitizing on bark-beetles in the Borecka Forest (after Szczepański, 1960).

Host	Parasite	Notes
Hylurgops palliatus (Gyllenhal)	*Eurytoma rufipes* Walker	Captured in galleries
Polygraphus poligraphus (L.)	*Pachycerus xylophagorum* Ratzeburg	,,
Polygraphus punctifrons Thomson	*Macromesus amphiretus* Walker	,,
Tomicus piniperda (L.)	*Rhopalicus tutela* Walker	,,
Tomicus minor (Hartig)	*Metacolus unifasciatus* Thomson	,,
	Rhopalicus brevicornis Thomson	,,
	Dinotiscus calcaratus Thomson	,,
Hylesinus crenatus (F.)	*Dinotiscus bidentulus* Thomson	bred
	Pediobius planiventris Thomson	captured in galleries
Leperisinus orni (Fuchs)	*Torymus bohemani* Thomson	bred
	Eurytoma flavovaria Ratzeburg	,,
	Eurytoma morio Boheman	,,
	Cerocephala trichotus (Ratzeburg)	captured in galleries
	Rhaphitelus maculatus Walker	bred
	Cheiropachus colon (L.)	,,
	Dinotiscus bidentulus Thomson	,,
	Tetrastichus ulmi Erdös	,,
Trypodendron lineatum (Olivier)	*Ipideurytoma spessivtsevi* Bouček & Novicki	captured near galleries
Pityophtorus micrographus (L.)	*Macromesus amphiretus* Walker	bred
Scolytus ratzeburgi Janson	*Entodon leucogramma* Ratzeburg	presumable host

In the years following the Second World War these areas became foci of outbreaks of *Phaenops cyanea* (F.), *Tomicus piniperda* (L.), *Ips acuminatus* (Gyllenhal) and other secondary pine pests. Specific communities of dendrophilous, xylophagous insects also developed here, due to the weakening of the pines by bark damage caused by red deer (Kinelski & Szujecki, 1963).

A community of arboreal *Staphylinidae* consisting of 66 species was observed in the Pisz Forest. Communities of *Staphylinidae* occurring under the bark, in hollows and in rotting wood, as well as in arboreal fungi have also been distinguished. Representatives of the genera *Phloeonomus*, *Placusa*, *Phloeopora* and *Anomognathus* are very numerous under the bark of pines and spruces. *Gabrius splendidulus* (Gravenhorst), *Leptusa pulchella* (Mannerheim), *Dinaraea aequata* (Erichson), *D. linearis* (Gravenhorst), *Phloeopora testacea* (Mannerheim) and *P. angustiformis* Baudi occur under the bark of deciduous trees.

Quedius brevicornis Thomson, *Heterothops dissimilis* (Gravenhorst), *Haploglossa pulla* (Gyllenhal) and *H. picipennis* (Gyllenhal), i.e. nidicolous species which may be regarded as relicts of primeval forests, as well as cariophilous species such as *Quedius scitus* (Gravenhorst), *Sepedophilus* (= *Conosoma*) *bipunctatus* (Gravenhorst), *S. testaceus* (F.), *S. littoreus* (L.), *Phloeocharis subtilissima* Mannerheim and *Atrecus affinis* (Paykull) are characteristic of communities inhabiting oak and aspen hollows. The occurrence of the latter group of insects is becoming increasingly more restricted in the forests due to the application of clear cuttings, formation of pure forest stands consisting of a single tree species and to the reduced production cycle of forest stands (Szujecki, 1967, 1973).

Primary pine pests are of no major importance in the Podlasie Forest zone. On the other hand, intensive outbreaks of secondary pests of the spruce and of foliophages of deciduous trees, particularly the oak, occur here. They principally involve *Theria* spp. and *Erannis* spp. and, to a lesser extent, *Lymantria dispar* (L.). The occurrence of a large number of dendrophilous species in forest biocenoses, which are dependent on the rich resources of the local forest stands frequently approximating natural ones, is characteristic of this zone and of the entire Masurian-Podlasie Region. Representatives of the boreal and Siberian zoogeographical element also occur more frequently here than in other parts of Poland.

Studies performed by Nunberg (1929) and Karpiński (1933) revealed as many as 78 scolytid species within the limits of the Białowieża Forest. These include the following rare species characteristic of this area: *Carphoborus cholodkovskyi* Spessivtsev, *Pityogenes trepanatus* (Nördlinger), *P. saalasi* Eggers and *Orthotomicus longicollis* (Gyllenhal). Parasites of *Scolytidae*, particularly those of *Ips typographus* (L.) such as *Coeloides bostrychorum* Pic, *Dendrosoter protuberans* (Nees) (= *middendorffii*) (Ratzeburg)), *Tomicobia seitneri* (Ruschka) and *Rhoptrocerus xylophagorum* (Ratzeburg) are common here. The association of parasites and predators of *Hylesinus crenatus* (F.) in the Białowieża Forest is represented in Fig. 7.18. A total of 91 species of the family *Ceramby-*

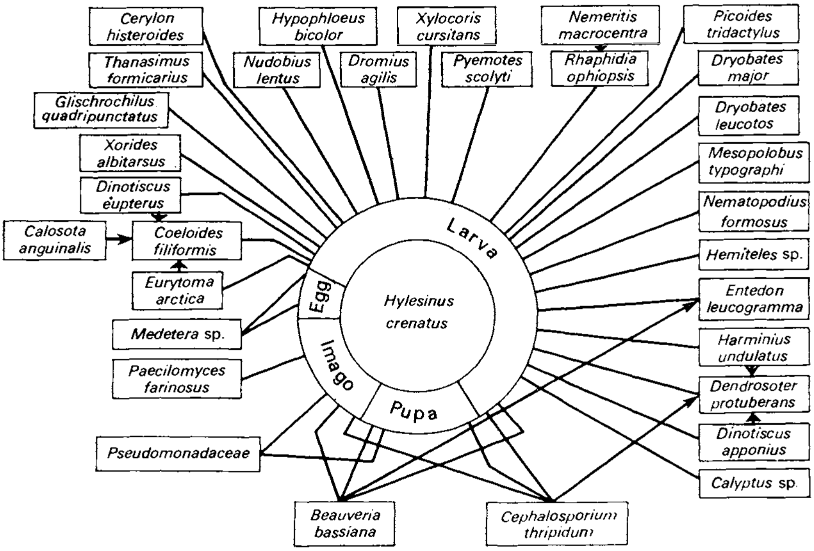


Fig. 7.18 Organisms influencing the abundance of *Hylesinus crenatus* (F.) in the Białowieża Forest (after Okołów, 1970a)

cidae has been recorded in the Białowieża Forest (Karpiński, 1949a). The distribution of the dominant species of these insects in individual biotopes is illustrated in Fig. 7.19. *Evodinus borealis* (Gyllenhal) and *Strangalia thoracica* (F.) are boreal species which are very rare in Central Europe, the Białowieża Forest being their locality in Poland. *Monochamus urussovi* (Fischer) is a Siberian species. Among other *Cerambycidae* characteristic of this Forest, *Leptura variicornis* Dalman, *Strangalia nigripes* (De Geer) and *Semanotus undatus* (L.) should be mentioned here.

Urocerus gigas (L.), *Sinodendron cylindricum* (L.) and *Ceruchus chrysomelinus* (Hochenwarth) are species characteristic of the Białowieża Forest belonging to other systematic groups. *Bius thoracicus* (F.) is a relict of primeval forests (Fig. 7.20).

Entomofauna of the forest undergrowth and herb layers. As well as *Operophthera* and *Erannis* spp., other *Lepidoptera* such as *Ptilophora plumigera* Schiffner, *Aglia tau* L., *Ptilodon capucina* (L.) and *Gonepteryx rhamni* (L.) are frequent in the undergrowth. Butterflies of the superfamilies *Papilionoidea* and *Hesperioidea* are represented here by 107 species, among which the following are noteworthy in view of their relict

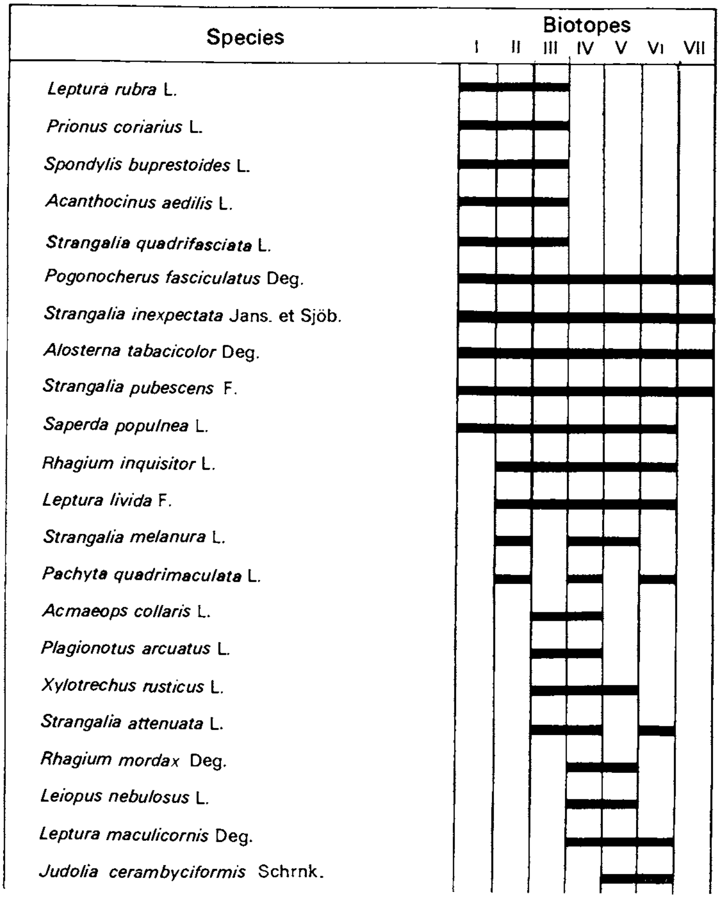


Fig. 7.19 Dominant species of *Cerambycidae* in biotopes of the Białowieża National Park (original according to data of Karpiński, 1949a)

character: *Colias palaeno* (L.), *Proclassiana eunomia* (Esper), *Boleria althea* (Hemming) and *Coenonympha oedippus* (F.).

The taxocenes of *Heteroptera* are rich in species in the Białowieża Forest. Of the 234 species listed from this region most occur in meadows in the vicinity of the forest (136 species) and in mixed coniferous forest (83 species). They generally occur in the undergrowth and herb layers but some of them inhabit the tree crowns. *Phytocoris tiliae* (F.), *Piezodorus lituratus* (F.), *Pentatoma rufipes* (L.) and *Elasmostethus interstinctus* (L.) are the most characteristic species of the mixed coniferous forest *Querceto-Betuletum*.

Fig. 7.20 Mixed forest in Białowieża (photo by W. Dudziński)

In the *Querceto-Carpinetum* association, 45 species have been recorded including *Phytocoris longipennis* (Flor), *Monalocoris filicis* (L.) and *Bryocoris pteridis* (Fallén). In *Carpinetum typicum* 41 species occur, among which *Metatropis rufescens* (Herrich–Schäffer) is exclusively characteristic of this biotope, while *Phytocoris tiliae*, *P. dimidiatus* Kirschbaum and *Calocoris ochromelas* (Gmelin) are characteristic of the *Querceto-Piceeto-Pinetum* association. The following species are found in coniferous forests: *Gastroides abietum* Bergroth, *Elasmucha ferrugata* (F.), *Capsus mariopterum* Scopoli, *Eremocoris plebejus* (Fallén). and *Cyrtorhinus caricis* (Fallén) (in bog coniferous forest). *Dicyphus stachydis* Reuter and *Mecomma ambulans* (Fallén) are characteristic species of alder carrs.

Entomofauna of the forest litter and soil layers. The occurrence of 22 ant species (mostly belonging to the epigeic fauna) has been established in the Białowieża National Park. *Myrmica rubra* (L.) and *M. laevinodis* Nylander are the most commonly encountered species and occur in all forest types. *Lasius niger* (L.) and *Formica transkaukasica* Nassonov are absent only from the *Tilio-Carpinetum Stachyetosum* association, while *F. fusca* L. is also absent here as well as from the *Tilio-Carpinetum Typicum.*

Of the 135 species of *Carabidae* observed in the Białowieża Forest the following are included amongst the rarer Polish species: *Carabus menetriesi* Hummel, *Leistus piceus* Froelich, *Agonum quadripunctatum* (De Geer), *A. hypocrita* (Apfelbeck), *A. krynickii* (Sperk) and *Dromius quadraticollis* Morawitz. The characteristics of carabid communities are given above.

Further essential data concerning the entomocenoses of the Białowieża Forest is to be found in the works of Adamczewski (1950), Gieysztor (1938), Karpiński & Makólski (1954), Koźmiński (1925), Krzywicki (1967), Okołów (1970a,b), Strawiński (1956) and other authors.

The dependence of the occurrence of *Carabidae* on the age of the forest stand has been studied by Leśniak (1963) in the North Masovian zone (Tabórz forest district). *Carabus hortensis* L. and *Pterostichus niger* (Schaller) occur most frequently in pine forest stands in the habitat of fresh coniferous forests (association *Pino-Vaccinietum myrtilli* passing to *Pino-Quercetum*) whereas *Epaphius secalis* (Paykull), *Pterostichus niger* and *Carabus glabratus* Paykull are most common in beech forests in the habitat of deciduous forest (association *Querco-Carpinetum Typicum*).

Staphylinids belonging to the soil environment have been studied in the North Masovian zone in the forest associations of the Pisz Forest (Szujecki, 1966b) where the communities of these insects consists of 250 species.

Sipalia circellaris (Gravenhorst) dominates whereas *Othius myrmecophilus* Kiesenwetter, *Xantholinus tricolor* (F.), *Stenus clavicornis* (Scopoli), *S. geniculatus* Gravenhorst, *Mycetoporus clavicornis* (Stephens), *M. splendidus* (Gravenhorst), *M. lepidus* (Gravenhorst) and *Sepedophilus immaculatus* (Stephens) are subdominant and accessory species of communities of litter *Staphylinidae* in fresh pine forests (association *Pino-Vaccinietum myrtilli*) (Fig. 7.21). The predominant species are derived mainly from the European (about 30%), Holarctic (23%) and Eurosiberian (19%) zoogeographical faunae. *Quedius boops* (Gravenhorst) and *Philonthus lepidus* (Gravenhorst) are species characteristic od dune crests where the conditions are more xeric and the pine forest exhibits features of the dry forest habitat. The eurytopic species, *Xantholinus linearis* (Olivier) also occurs commonly here along with *Sipalia circellaris.*

Fig. 7.21 Pine forest stand in the Pisz Forest; environment of the *Staphylinidae* community with *Sipalia circellaris* (Gravenhorst), *Othius myrmecophilus* Kiesenwetter and others (photo by S. Kinelski)

Othius myrmecophilus and *Sipalia circellaris* are the dominant species in the mixed coniferous forest *Pino-Quercetum*. Sometimes, particularly on sites of lower soil humidity, *S. circellaris* dominates, with *O. myrmecophilus* as a subdominant member of the community and

Stenus humilis (Erichson), *S. clavicornis* (Scopoli), *Rugilus rufipes* (Germar), *Gabrius vernalis* (Gravenhorst) and *Mycetoporus splendidus* as accessory species. Eurosiberian (25%), European (15%), Subboreal and Holarctic species prevail. Considerable numbers of *Othius punctulatus* (Goeze), *Stenus humilis* and *Quedius fuliginosus* (Gravenhorst) characterize the habitat intermediate to the mixed forest.

The typical hygrophil, *Ochthephilum fracticorne* (Paykull), dominates in bog coniferous forests (association *Sphagnetum fusci*), with *Mycetoporus splendidus*, *Stenus geniculatus*, *S. lustrator* (Erichson) and *Acidota crenata* (F.) as the subdominant species. *Gabrius sphagnicola* (Sjöberg), known in Poland only from the Pisz Forest and representative of the Boreal element, and *Myllaena kraatzi* (Sharp) occur as characteristic exclusive species in the *sphagnum* association discussed above, in which patches of *Caricetum limosae* appear along bodies of water. Subboreal and Boreal (25%), as well as Holarctic (25%) species prevail here.

The same species as those occurring in mixed coniferous forests (*Sipalia circellaris* and *Othius myrmecophilus*) dominate in alder associations (*Alnetum glutinosae auct. pol.*) growing on the border of eutrophic lakes, along with the following accessory species: *Myllaena infuscata* (Kraatz), *Stenus lustrator*, *S. bifoveolatus* (Gyllenhal), *Anthobium* (= *Lathrimaeum*) *atrocephalum* (Gyllenhal), *Lathrobium longulum* (Gravenhorst) and *Gabrius trossulus* (von Nordmann). Subboreal (27%) and European (20%) elements prevail here.

Numerous staphylinid species, 65% of which are representative of the Palaearctic, Holarctic or Cosmopolitan faunae, occur in the decomposing litter of the forest floor. These are eurytopic, strongly flying species which penetrate into the forest association along roads and compartment lines. They include *Anotylus* (= *Oxytelus*) *rugosus* (F.), *A. laqueatus* (Marsham), *Gyrohypnus angustatus* (Stephens), *Philonthus splendens* (F.), *P. chalceus* (Stephens), *Ontholestes tessellatus* (Fourcroy), *Tachinus rufipes* (L.), *Aleochara lanuginosa* (Gravenhorst) and others.

Only *Deliphrum tectum* (Paykull) and *Tachinus laticollis* (Gravenhorst) may be considered as forest species associated with the zone of Eurosiberian coniferous forests.

The entomofauna of the ant-hills of *Formica rufa* (L.) consists of typical myrmecophilous species which are widely distributed throughout Poland (*Leptacinus formicetorum* (Märkel), *Gyrohypnus atratus* (Heer), *Quedius brevis* (Erichson), *Lyprocorrhe* (= *Notothecta*) *anceps* (Erichson), *Thiasophila angulata* (Erichson), *Oxypoda haemorrhoa* (Mannerheim), etc.) as well as litter species (e.g. *Gabrius vernalis* (Gravenhorst). Other myrmecophilous species such as *Lamprinodes saginatus* (Gravenhorst. *Zyras collaris* (Paykull), *Z. funestus* (Gravenhorst), *Z. humeralis* (Gravenhorst) and *Z. limbatus* (Paykull) occur in the nests of *Myrmica* or *Lasius* and sometimes in the litter (Szujecki, 1967).

III. Region of the Great European Plain

This region lies within the central Polish glaciation in the zone of the Great European Plain. It also comprises a part of the sandr areas of the Baltic glaciation. From the standpoint of the physiography it is poorly differentiated. The rather dry climate with its continental features increasing towards the East and the rather poor soil conditions favour the development of pine forest in this region. The considerable contribution of the oak to mixed coniferous forests is worthy of note, while pure deciduous forests (oak and oak-hornbeam-linden forests) are rare here. This region is divided into the Wielkopolska–Pomerania and the Masovia subregions.

Entomofauna of the forest tree layer. The north-western part of the Great European Plain Region, including the Bory Tucholskie and Noteć Forests lies within the zone exhibiting the highest potential danger to coniferous forests from foliophages. This is associated with the extent of pure pine forest stands which are of the same age and occur on poor, washed, sandy soils of glacial origin where the ground water level is frequently very low. Massive outbreaks of *Panolis flammea* (D. & S.), *Bupalus piniarius* (L.), *Lymantria monacha* (L.) and *Diprion* spp. occur in these forests. Pests of plantations were abundant here, including *Hylobius abietis* (L.), *Philopedon plagiatus* (Schaller), *Strophomus* spp., while pests of thickets also occurred frequently (e.g. *Rhyacionia buoliana* (D. & S.), *Barbitistes constrictus* Brunner von Wattenwyl, *Neodiprion sertifer* (Geoffroy), *Pissodes notatus* (F.) and *Aradus cinnamomeus* (Panzer) (Figs. 7.22 and 7.23).

The outbreaks of foliophages and the frequent occurrence of fires favour the propagation and intensity of occurrence of pine xylophages. At present the Noteć Forest is subjected to more outbreaks of secondary pests than the Bory Tucholskie Forest while the forests of the eastern part of the Wielkopolska-Kujawy Plain lie in the zone of the highest

Fig. 7.22 Panolis flammea (D. & S.) on a pine trunk (photo by S. Kinelski)

impendence. This is due to the continuous influence of the dry climate which exhibits the lowest precipitation in Poland and which, along with the poor sandy soils, leads to a dearth of biocenoses. In this region *Dendrolimus pini* (L.) (Fig. 7.24) and *Diprion pini* (L.) repeatedly develop strong outbreak tendencies, whereas the appearance of *Panolis flammea, Bupalus piniarius* and *Lymantria monacha* poses less of a threat

Fig. 7.23 Barbitistes constrictus Brunner von Wattenwyl (photo by S. Kinelski)

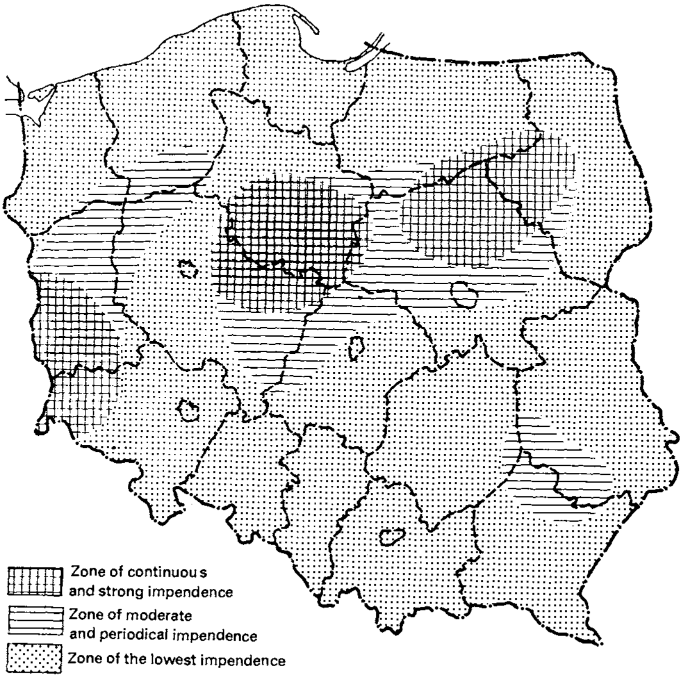


Fig. 7.24 Outbreak area of *Dendrolimus pini* (L.) in Poland (after Śliwa & Cichowski, 1975)

here. *Exoteleia dodecella* (L.) and *Aradus cinnamomeus* are persistent pests of pine plantations and thickets in the vicinity of industrial centres in this region and there are also frequent outbreaks of *Rhyacionia buoliana* (D.&S.) *Blastesthia turionella* (L.) and *Petrova resinella* (L.). A high degree of pest impendence is also characteristic of the Lubusz Lakeland where *Dendrolimus pini*, *Panolis flammea* and *Lymantria monacha* belong to primary pine pests with high turnovers of outbreak processes. The late form of *Acantholyda posticalis* Matsumura is a foliophage specifically occurring in this area. Xylophages such as *Monochamus galloprovincialis* (Olivier) have been numerous here, particularly since the end of World War II. The pine forests of the Masovia-Podlasie subregion are more resistant to outbreaks of phytophages, although the Kurpie Plain and the northern part of the Masovia-Podlasie Plain belong to areas susceptible to the mass appearance of *Dendrolimus pini*. This species repeatedly developed outbreaks in the Zielona (Green) Forest and Biała (White) Forest. A short-lasting but astonishingly strong outbreak of *Panolis flammea* took place in the Kampinos Forest in the early 1970's. Among secondary pine pests, *Ips acuminatus* (Gyllenhal) (frequently accompanied by the otherwise rare species *Carphoborus minimus* (F.)) is characterized by a high reproductive potential. In the eastern part of the region discussed, deciduous forests are attacked over considerable intervals of time by *Euproctis chrysorrhoea* (L.) and *Lymantria dispar* (L.), i.e. species characteristic of the continental climate of eastern Europe. *Aporia crataegi* (L.), another species of eastern origin, is also more abundant in this region where *Tortrix viridana* (L.) and *Leucoma salicis* (L.) also make frequent appearances. A local outbreak of the polyphagous, although rather typical beech forest species, *Dasychira pudibunda* (L.) appeared in the pine forests growing on the rich soils of the Bug River valley.

The large number of small complexes of afforestation on arable soils contributes to the damages produced by *Exoteleia dodecella*, various *Tortricidae* and *Brahyderes incanus* (L.),

The continentalization of the climate towards the eastern part of the region and the considerable proportion of oak in mixed forests favour the occurrence of xylophages associated with this tree. The small Bielany Forest in Warsaw and the forests which once occurred near the city have been noted in this respect for almost two centuries. Many *Cerambycidae* which are usually extremely rare in this part of Europe appeared here in the nineteenth century (Hildt, 1917; Stobiecki, 1939). Even more recently, outbreaks of *Cerambyx cerdo* L., *Plagionotus detritus* (L.)

(Fig. 7.25), *P. arcuatus* (L.), *Phymatodes testaceus* (L.), *Xylotrechus antilope* (Schoenherr) and *Mesosa curculionides* (L.), as well as the occurrence of *Phymatodes alni* (L.) and *Rhopalopus femoratus* (L.) have been recorded from this area.

Fig. 7.25 Plagionotus detritus (L.) on an oak trunk (photo by W. Strojny)

The cerambycids *Notorrhina punctata* (F.), which lives in old pines, and *Chlorophorus varius* (Müller) are typical representatives of the continental climate of eastern Europe and Asia and are also characteristic elements of the dendrophilous fauna of the Masovia–Podlasie Region (Kinelski and Szujecki, 1959).

Among other dendrophilous species associated with the deciduous wood habitat, the following deserve mention here: *Tropideres albirostris* (Herbst), *Tropiderinus undulatus* (Panzer), *Agrilus elongatus* (Herbst), *A. biguttatus* (F.), *Rhamnusium virgo* (Voet), *Necydalis major* L., *Hypulus bifasciatus* (F.), *Ptilinus fuscus* (Fourcroy) and *Calopus serraticornis* (L.). The occurrence of the xylophages mentioned above leads to the presence of predators which invade their galleries and rotten trees. Such species include *Pelecotoma fennica* (Paykull) and *Teretrius fabricii* Mazur (in galleries of *Ptilinus*), *Aulonium trisulcum* (Fourcroy) (a predator of *Scolytus* spp. in elm) and *Corticeus fasciatus* (F.) (in galleries of *Lymexylon navale* (L.) and *Cerambyx cerdo* L.) (Kinelski & Szujecki, 1959).

Staphylinidae living in the mould of old deciduous trees are only observed here on rare occasions. These are *Xantholinus glaber* (von Nordmann), *Quedius microps* (Gravenhorst), *Q. brevicornis* Thomson, *Euryusa sinuata* Erichson and *Tachyusida gracilis* (Erichson). There has been no substantial evidence concerning the recent occurrence of these species, or of those species which visit the sap of wounded trees such as *Philonthus rotundicollis* (Ménétriés), *Velleius dilatatus* (Paykull), *Silusa rubiginosa* Erichson and *Thamiaraea cinnamomea* (Gravenhorst). Thse species are threatened with complete extinction before long due to the absence of suitable environments (Szujecki, 1968; 1973).

Insects inhabiting the nests of forest birds constitute members of the arboreal component of the entomocenoses. Communities of *Coleoptera* of these specific environments were studied in coniferous and mixed forests of the Masovia Plain (Gotzman & Szujecki, 1968). Species found to be dominant in this community included *Haploglossa pulla* (Gyllenhal), *Sciodrepoides watsoni* (Spence), *Atheta nigricornis* (Thomson), *Gnathoncus* spp. and *Hister merdarius* Hoffmann. They inhabit nests of the starling, *Ficedula hypoleuca* (Pallas), *Parus caeruleus* L., and *Passer montanus* (L.) nesting boxes, as well as the open, above-ground nests of the thrush and blackbird in which the humidity is relatively high. The *Coleoptera* mentioned above are usually predatory in these nests, feeding on the eggs or larvae of nidicolous *Diptera*, although sometimes they may be saprophagous.

Communities of flying parasitic insects are partly arboreal. *Diadegma eucerophaga* Horstmann, the parasite of *Exoteleia dodecella* (L.), dominates in pine crowns in the ichneumonid community of fresh coniferous forests. *Scambus sagax* Hartig, *Phaeogenes vagus* Berthoumieu, *Glypta resinana* Hartig, *Gelis areator* (Panzer) (parasite of *Ocnerostoma piniarella* Zeller, *Campoplex rufinator* Aubert and other species parasitic on the caterpillars of *Microlepidoptera* feeding on pine, are also frequent in this environment.

The community of *Coccinellidae* feeding in the tree crowns in pine thickets and pole-sized stands consists of eight species. *Coccinella septempunctata* L. dominates, particularly in thickets (D = 49.6%), whereas *Anatis ocellata* (L.) (D = 40%) usually invades pole-sized stands *Halyzia sedecimguttata* (L.) (D = 4.7%) is an accessory species of this community. The other species are *Adalia bipunctata* (L.), *Coccinella quinquepunctata* L., *Calvia quattuordecimpunctata* (L.) and *Myzia oblongoguttata* L. (Gumoś & Wiśniewski, 1960).

Entomofauna of the undergrowth and herb layer of pine forests. A total of 69 species of *Ichneumonidae* was observed in the oak undergrowth and herb layer of the fresh coniferous forest in the Kampinos Forest. *Barychnemis anurus* (Thomson) (D = 8.4%) and *Proclitus praetor* (Haliday) dominated, whereas *Campoplex rothii* (Holmgren), *Lissonota variabilis* Holmgren, *Oronotus* sp., *Cratichneumon culex* (Müller) and *Spinolachus laevifrons* Holmgren are accessory species of this community. The dominant species of this community are parasites of *Diptera* which live in fungal fruiting bodies. The frequency and dominance of parasites of the foliophages *Cratichneumon viator* (Scopoli), *C. varipes* (Gravenhorst) and *Lissonota variabilis* are similar both in pure pine forest stands and in stands with an oak undergrowth. Only the abundance of *Cratichneumon rothii* Holmgren is higher in forest stands with an undergrowth layer since this ichneumon is a parasite of *Lepidoptera* which feed on deciduous shrubs. However, the abundance of *Pimpla* (= *Coccygominus*) *contemplator* (Müller) and *Cratichneumon culex* is higher in forest stands lacking an undergrowth layer but in which birch occurs, this being the foodplant of the host of these parasites (Sawoniewicz, 1979).

The occurrence of oak undergrowth in pine forest stands in fresh coniferous or degraded mixed coniferous forests is common in the regions under discussion. Under these conditions *Rhynchaenus quercus* (L.)

frequently invades the undergrowth in large numbers, although these are often drastically reduced by the action of parasites, among which *Triaspis caudatus* (Nees) and many species of *Chalcidoidea* are most abundant (Szujecki, 1961). The intensive deformation of oak leaves in the undergrowth caused by *R. quercus* renders them unsuitable as food for other foliophages which would otherwise serve as supplementary hosts for the parasites of pine pests. It would also appear that the birch, being a natural component of pine forest stands of poor habitats, may play a more important biocenotic role than may at first have been thought, since many phytophagous species serving as hosts of useful parasites are associated with this tree (Głowacki, 1951). Furthermore, many otherwise rare insects such as *Otiorrhynchus repletus* Bohemann, *Lasiorrhynchites coeruleocephalus* (Schaller) and *Cryptocephalus coerulescens* C. R. Sahlberg are associated with birch, particularly with its saplings growing on compartment lines in the forest of Masovia–Podlasie zone (Szujecki, 1961; 1966a).

The juniper, which occurs abundantly on the Masovian Plain and is the direct or indirect host of a number of insect species, may play a certain biocenotic role in pine forests (Kapuściński, 1949; Szczepański, 1973). Six species of *Chalcidoidea*, for example, are parasitic on *Phloeosinus thuyae* Perris and among these *Metacolus unifasciatus* Forster, the parasite of *Tomicus piniperda* (L.), *T. minor* (Hartig), *Ips accuminatus* (Gyllenhal) and *Pissodes notatus* (F.) is the most abundant.

The goat willow (*Salix caprea* (L.)) and the aspen occur on sites of somewhat richer soil conditions in pine forests. Unfortunately their biocenotic role has been hitherto unknown, although it is suspected that it should be quite considerable in view of the large number of phytophages connected with both of these species. It would appear, however, that on relatively poor sites the chrysomelids *Lochmaea caprea* (L.) and *Plagiodera versicolora* (Laicharting) are the main consumers of the goat willow leaves, while the pteromalid *Schizonotus latus* (Walker) is a specific parasite of *P. versicolora* (Szujecki, 1966a).

Fresh pine forests are characterized by the occurrence of communities of thermophilous insects in the herb layer. These communities are particularly rich on the borders of forests, reforested cutting areas and compartment lines. In the curculionid community, which consists of several dozen species, the following occur in considerable numbers: *Apion corniculatum* Germar (feeding on *Genista tinctoria* L. and *Cytisu* spp.). *Sitona lineatus* (L.), *S. griseus* (F.) and *Tychius venustus* (F.) (on *Papilionaceae*), *Cionus olivieri* Rosenschloed and *C. thapsus*

(F.) (on *Verbascum* sp.) and *Lixus cylindricus* (L.) (on *Peucedanum oreosolinum* (L.)) (Szujecki, 1961). Larvae of the latter species feed in the stems whereas the adults feed on inflorescences of *P. oreosolinum*. The ichneumon *Ephialtes roborator* (F.), which is noted for its role in regulating the abundance of various noxious insects, is also a parasite of these larvae (Szujecki, 1956/1957). The following curculionids are also associated with the herb layer: *Coniocleonus glaucus* var. *turbatus* (F.), *Otiorrhynchus ovatus* (L.), *Trachyphloeus scabriculus* (L.), *T. bifoveolatus* (Beck), *Neliocerus faber* Herbst and *Lepyrus capucinus* (Schaller) feeding on *Rubus* sp. Thermophilous *Chrysomelidae* also occur in the herb layer of dry pine forests (Fig. 7.26). Among them *Chrysolina gypsophilae* (Küster) which feeds on *Gypsophila fastigiata*, and *Hispa atra* L. are characteristic of the Masovian Plain.

More or less xerothermophilous species also determine the character of the community of *Chrysomelidae* in light pine forests of the Wielkopolska-Pomerania subregion. These are *Hispa atra*, *Cryptocephalus fulvus* Goeze and *Psylliodes cucullata* (Illiger). On reforested cutting areas *Mantura chrysanthemi* (Koch), *Batophila rubi* (Paykull) (on raspberry bushes) and *Lochmaea suturalis* (Thomson) (on heather) are particularly abundant (Stypa-Mirek, 1963).

Under similar conditions of fresh coniferous forest the following thermophilous *Aculeata* also occur: *Bombus pratorum* (L.), *B. agrorum* (L.), *B. terrestris* (L.), *B. lucorum* (L.), *Psithyrus bohemicus* (Seidlitz) and *Anthidiullum strigatum* (Panzer) as well as (particularly on dry and insolated sites on heather) *Colletes succinctus* (L.) and *Andrena fuscipes* (Kirby) (Banaszak, 1974a).

The fauna of *Orthoptera* and *Dermaptera* associated to a large extent with pine forests and open areas in the Masovia-Podlasie subzone is well known due to the works of Bazyluk (1949) and Liana (1962; 1966). Of the total number of 81 species of *Orthoptera* occurring in Poland, 51 have been observed on the Masovian Plain. *Tettigonia viridissima* L. occurs abundantly in all forest and other biotopes here. *Tetrix bipunctata* (L.) prevails in the *Orthoptera* community in coniferous forest environments of *Pino-Callunetum* and *Pino-Quercetum*. *Myrmeleotettix maculatus* (Thunberg), a species typical of pioneer stages in the succession of dune associations, is one of the few representatives of this order in the driest associations of the *Pino-Cladonietum* type in these environments. Most of the other species of *Orthoptera* prefer unforested areas, dunes or forest borders. *Oediopoda coerulescens* (L.) is the most abundant while the following species also occur here: *Platycleis denticulata* (Pan-

Fig. 7.26 Pine forest in the Wielkopolski National Park; environment of *Hispa atra* (L.) (photo by W. Strojny)

zer), *Metrioptera brachyptera* (L.), *Decticus verrucivorus* (L.) (particularly on clayey soils), *Stenobothrus lineatus* (Panzer) (abundant on the Masovian Plain in the association *Pino-Quercetum* and *Pino-Callunetum*), *S. stigmaticus* (Rambur), *Omocestus haemorrhoidalis* (Charpentier), *Chorthippus apricarius* (L.) (in *Pino-Quercetum*), *C. brunneus* (Thunberg), *C. biguttulus* (L.) and *Psophus striulus* L.

Chorthippus mollis (Charpentier), *Tetrix bipunctata*, *T. undulata* (Sowerby) and *Stenobothrus stigmaticus* are characteristic species of open areas, compartment lines and fellings in pine forests in the Łuków–Siedlce zone. Most *Orthoptera* are xerophilous and have extended their ranges in the region discussed within the last 200 years when the areas of compact forests were restricted. The subpontic species *Ephippiger ephippiger* (Fiebig), the distribution of which in Poland corresponds to the occurrence of steppe flora, also occurs on some sites in south-eastern Masovia and in Podlasie in the coniferous associations *Pino-Callunetum* and *Pino-Vaccinietum myrtilli* (Fig. 7.27). *Calliptamus italicus* (L.) is also of steppe origin and becomes increasingly more characteristic of

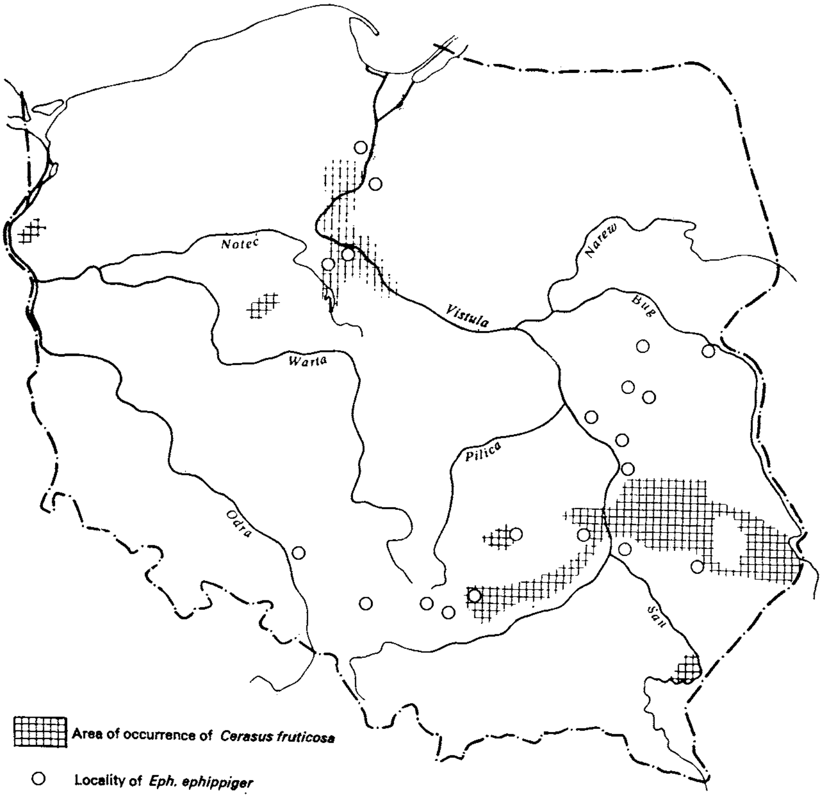


Fig. 7.27 Distribution of *Ephippiger ephippiger* (Fiebig) in Poland (after Liana, 1966)

clear felling areas in pine forests accompanying mainly grassy associations of the *Corynophoretum* type.

Pholidoptera griseoaptera (De Geer), *Meconema thalassinum* (De Geer) and *Brabitistes constrictus* Brunner von Wattenwyl have been observed in mixed and deciduous forests. Interesting communities of *Orthoptera* occur on the Masovian Plain in marshes and peatbogs which lie between dunes and exhibit a specific climate. Many such sites occur in the Kampinos Forest and are characterized by the presence of *Tetrix jarockii* Bazyluk. *Omocestus rufipes* (Zetterstedt) occurs in the *Pino-Vaccinietum uliginosi* association.

Entomofauna of the undergrowth and herb layer of alder forests. Alder forests, *Alnetum glutinosae typicum* occurring on sodden soils mostly along water courses, are characteristic in the region discussed, as are various types of pine forests. The community of curculionids is very specific here. It consists of hygrophilous species which feed mostly on herbs and shrubs, including *Apoderus erythropterus* (Gmelin) (on *Comarum palustre* (L.)). *Phytobius comari* (Herbst), *P. waltoni* Bohemann, *P. canaliculatus* Fahreus, *Cidnorhinus quadrimaculatus* (L.), *Coeliastes lamii* (F.), *Orobitis cyaneus* (L.), *Nanophyes marmoratus* (Goeze), *Gymnetron beccabungae* (L.) and *Cionus scrophulariae* (L.). Moreover, many species of the community discussed occur on moist meadows and other sodden open areas (Szujecki, 1961).

The community of *Chrysomelidae* is represented in alder forests by numerous species among which the following exhibit the highest degree of fidelity with the floral association: *Chrysolina menthastri* (Suffrian), *C. polita* (L.), *Galerucella lineola* (F.), *Agelastica alni* (L.) (dominant of the community), *Linaeidea aenea* (L.) (occurring on the border of alder forests on drier sites), *Aphtona nonstriata* (Goeze) (occurring on inundated sites) and *Longitarsus pratensis* (Panzer) (Stypa-Mirek, 1963).

The entomofauna of leaf-mining insects is very rich in this type of forest habitat (Beiger, 1955; Kubska, 1961; Michalska & Nowak, 1965) and amounts to 90–130 species. Depending on the local character of the environment the following species are dominant in this community: *Phytomyza lycopi* Nowakowski, (monophagous on *Lycopus europaeus* L.), *Agromyza flaviceps* Fallén (monophagous on *Humulus lupulus* L.), *A. reptans* (Fallén) (on *Urtica dioica* L.) and *Metallus gei* Brischke (on *Geum urbanum* L.). The following species are characteristic of the forest association under discussion: *Phytomyza lycopi*, *Agromyza flaviceps* and *A. igniceps* Hendel. Most of the mining insects

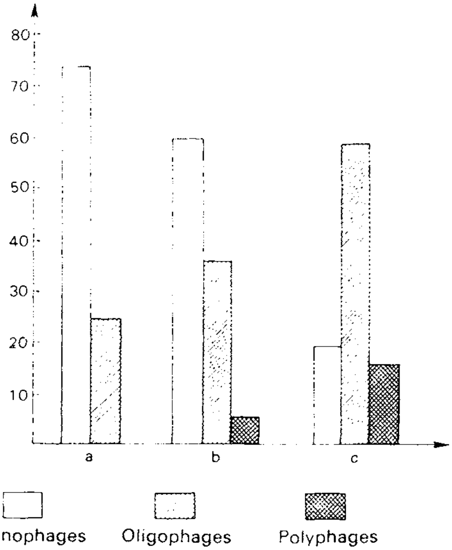


Fig. 7.28 Trophic spectrum of mining insects in *Alnetum glutinosae* (after Michalska & Nowak, 1965): a — characteristic species, b — accessory species, c — accompanying species

which occur in alder forests are *Diptera* (70%), the remainder being *Lepidoptera*, *Hymenoptera* and *Coleoptera*. About 45–46% of the species are monophagous, 48% oligophagous and about 6% polyphagous (Fig. 7.28).

Entomofauna of the undergrowth and herb layer of deciduous and mixed forests. The leaf-mining insects of light oak forests have recently been studied by Michna (1975). This xerothermic forest association occurs in the Wielkopolski National Park on the ground and terminal moraine area, particularly on south-facing slopes. Due to the high differentiation of the flora, the specific composition of leaf-miners is very rich here. There are at least 90 species in this association, among which 45 are *Lepidoptera*, 35 *Diptera*, 4 *Hymenoptera* and 2 *Coleoptera*. The predominance of *Lepidoptera* over *Diptera* (as opposed to the situation in alder forests) is due to the fact that *Lepidoptera* are photophilous, whereas leaf-mining *Diptera* generally exhibit higher requirements in respect to humidity and shading. Both *Diptera* and *Lepidoptera* dominate in this community, representative species being *Ophiomyia maura* (Meigen), *Phytomyza brunnipes* Brischke, *P. agromyzina* Meigen, *Tischeria ekebladella* (Bjerkander), *Phyllonorycter nicelli* (Stainton), *P. lautella*

(Zeller), *Kaliofenusa ulmi* (Sundewall) and *Stigmella oxyacanthella* (Stainton).

The highest number of leaf-miners occur on oak (nine species), followed by hazel, hawthorn and elm (each with six species). The following species occur on the oak: *Stigmella basiguttella* (Heinemann), *Nepticula heringi* Toll, *Tischeria ekebladella, Rhynchaenus quercus* (L.), *Coleophora cerrucipennella* Zeller, *Phyllonorycter lautella* (Zeller), *P. heegeriella* (Zeller), *Bucculatrix ulmella* Zeller and *Ectoedemia subbimaculella* (Haworth). Among the plants characteristic of the association *Querceto potentilletum albae* only *Lathyrus niger* L. is attacked by insects, of which *Agromyza lathyri* Hendel and *Acrocercops hofmanniella* (Schleich) are indicators of the community described.

The community of leaf-mining insects of the beech forest *Fageto-europaeum* is very poor and consists of just seven species. Most of these are associated with the main forest-forming species, i.e. the beech, on which the following three species of insect occur: *Phyllonorycter maestingella* (Müller), *Nepticula tityrella* Stainton and *Stigmella hemargyrella* (Kollar). These are also the dominant species of this particular community.

The relatively small number of leaf-mining species in beech forests is due to the lack of host plants, the number of which is limited by the high compactness of the tree crowns and the rather unfavourable humidity conditions which occur here. These beech forests are of an acidophilous type and occur on poor and rather dry soils. Forty-two species of leaf-miners have been recorded from beech forests with a more diverse herb layer as occur, for example, in the Lubusz zone (Mazur, 1970).

Over 40 species of leaf-miners, 90.5% of which are *Diptera,* occur in the hornbeam forest *Querceto-Carpinetum.* There are no characteristic species here, but among the accessory species the following deserve mention: *Agromyza orobi* Hendel, *Phytomyza glechomae* Kaltenbach and *P. aegopodii* Hendel.

Among the 34 species observed in the mixed forest *Periclymeno-Quercetum* none was found to be characteristic. The contribution of *Diptera* here amounts to 76.5%. *Agromyza pulla* Meigen and *Nepticula dulcella* Heinemann are noteworthy among the accessory species (Beiger, 1955).

Light conditions on the forest floor, as well as the presence of the herb layer, determine the differences between the communities of *Orthoptera, Dermaptera* and *Blattodea* in thermophilous oak forests (Wołyńska, 1975). Nine species have been recorded from oak forests, *Meconema thalassinum* (De Geer) and *Tettigonia viridissima* L., were the most abundant, whereas *Mecostethus grossus* Thunberg (= *Stethophyma grossum* (L.)) and *Chortippus brunneus* Thunberg were relatively rare. Five species have been observed in beech forests, including *Meconema thalassinum*, *Chelidurella acanthopygia* Géné and *Apterygida media* Hagenbach, whereas only three species occur in the oak-hornbeam-linden forest.

Communities of *Chrysomelidae* were studied under similar ecogeographical conditions (Stypa-Mirek, 1963). The community of these beetles in the oak-hornbeam forest is characterized by *Lilioceris lilii* (Scopoli), *Aphtona euphorbiae* (Schrank) and *Longitarsus parvulus* (Paykull) which live in the herb layer, as well as *Clytra quadripunctata* (L.), *Altica brevicollis* (Foudras) and *Gonioctena quinquepunctata* (F.) which inhabit the shrub layer.

Lilioceris merdigera (L.) in pine-oak forest stands and *Altica quercetorum* (Foudras) in poorer faciae are characteristic *Chrysomelidae* (Stypa-Mirek, 1963).

The entomofauna of the fruiting bodies of pileate fungi of the families *Cantharellaceae*, *Boletacede*, *Pauxillaceae*, *Agaricaceae* and *Russulaceae* in various forest habitat types of the Wielkopolska–Pomerania subzone consists of 108 insect species. These are represented by *Collembola*, *Dermaptera*, *Coleoptera*, *Diptera* and *Hymenoptera* (Fig. 7.29). The abundance of insects on the surface of fruiting bodies (*Collembola*, *Coleoptera*, *Dermaptera*) or inside them (mainly larvae of *Diptera*) differs widely depending on the habitat, season of appearance of the fruiting bodies, weather and developmental stage and size of the fungus. The following insects are most abundant here. *Collembola*: *Hypogastrura denticulata* (Bagnall) (on *Lactarius deliciosus* Fr., *Lepidocyrtus lignorum* (F,) (on various fungal species), *Tomocerus* (= *Pogonognathellus*) *longicornis* (Müller) and *T. flavescens* (Tullberg) (mostly on *Russula* spp.); *Staphylinidae*: *Lordithon thoracicus* (F.), *L. exoletus* (Erichson) and numerous species of the genus *Gyrophaena*, including *G. williamsi* Strand.

The larvae of *Diptera* inhabiting the interior of fungal fruiting bodies belong to the following families: *Trichoceridae*, *Anisopodidae*, *Limoniidae*, *Psychodidae*, *Scatopsidae*, *Fungivoridae* (including those species occurring abundantly on fungi, among which *Mycetophila alea* (Laffoon) (= *guttata* Dziedzicki) is characteristic on *Russula* and *Lactarius*), *Sciaridae*, *Ceratopogonidae*, *Phoridae*, *Heleomyzidae*, *Sphaeroceridae*, *Chloropidae*, *Drosophilidae*, *Anthomyiidae* and *Muscidae*.

Fig. 7.29 Diptera on fruiting bodies of the stinkhorn (photo by W. Strojny)

Ichneumonidae, *Braconidae* and *Proctotrupidae* are parasites of *Diptera* larvae.

Entomofauna of the litter and soil of pine forests. The communities of insects of the soil environment of fresh pine forests are rather well known in the region under discussion as a result of numerous studies carried out in Masovia and in the Krajna-Pomerania zone (Szujecki, 1966c, 1971, 1977; Szyszko, 1975; Szujecki, Szyszko, Mazur & Perliński, 1975; Perliński, 1975; Szujecki & Perliński, 1975; M. Kaczmarek, 1975).

The community of ants in fresh pine forest in the Krajna-Pomerania zone consists of 26 species, almost all of which are typical of light dry soils and require considerable insolation. Only *Lasius niger* (L.) and *Formica fusca* L. occur in all types of environment, whereas *Formica pressilabris* Nylander and *Lasius flavus* (F.) may occur either in dry or completely humid environments. *Myrmica* rubra (L.) *M. sabuleti* Meinert, *M. lobicornis* Nylander, *Lasius flavus* and *Formica sanguinea* Latreille are forest ants which build their nests within light forest stands. Other species are elements of the fauna of open areas, whereas *Formica pratensis* Retzius is a typical ecotonous species inhabiting forest borders. Most species (46.1%) belong to the European faunistic element. The Holarctic element is represented by 26.9% of the species and the Eurosiberian one by 11.5%. Only *Formica pressilabris* may be regarded as a typical Eastern Pomerania species. *Anergetes atratulus* (Schenck) is rarely observed in Poland.

Almost all of the ants occurring here utilize honey-dew as food. *Tetramorium caespitum* (L.), *Lasius niger* (Fig. 7.30) and species of the genus *Formica* absorb honey-dew casually, whereas *Lasius flavus* feeds almost exclusively on excretions of aphids which have been purposely

Fig. 7.30 Lasius niger abandoning its nest during the nuptial flight period (photo by T. Bojasiński)

cultured on the above ground parts of plants. Honey-dew also prevails in the diet of species belonging to the genera *Myrmica* and *Leptothorax*, which also, however, feed on aphids, other small insects and occasionally grass seeds. Finally, *Anargetes atratulus* and *Strongylognathus testaceus* (Schenck) are social parasites of ants.

The course of the changes in the ant community which occur along with the growth of the forest stand proceeds as follows: *Tetramorium caespitum* dominates with *Lasius niger* as the subdominant in plantations – this is a xerothermophilous community. During the period from thicket to old thicket, a complete exchange of dominants takes place,

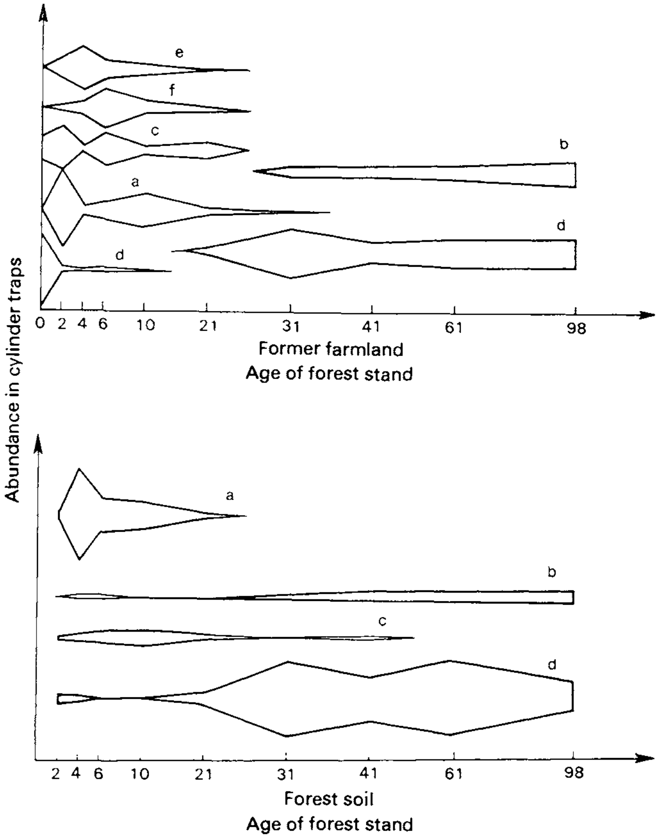


Fig. 7.31 Course of changes in abundance of *Formicidae* along with the growth of pine forest stands in the fresh coniferous forest habitat in the Człuchów Forest (after Szujecki *et al.*, 1977): a – *Tetramorium caespitum* (L.), b – *Myrmica lobicornis* Nylander, c – *Lasius niger* (L.), d – *Myrmica rubra* (L.), e – *Formica cunicularia* (Latreille), f – *Lasius alienus* (Forster)

resulting in *Myrmica rubra* (L.) and *M. lobicornis* dominating in pole-sized forest stands. The course of changes in the density of ant-hills, together with the growth of forest stands is illustrated in Fig. 7.31.

The insects inhabiting nests of *Formica polyctena* Forster in pine forests of the Wielkopolska–Kujawy zone have been studied in detail (Wiśniewski, 1967). The occurrence of 221 species of either obligatory or facultative myrmecophils has been observed here. The family *Entomobryidae* was most abundantly represented among the *Collembola*, accounting for 40% of the representative species of this order and with a density amounting to 261 per 1 dm^3 of the nest material. On the other hand, *Isotomidae* dominated as regards the actual number of species (Fig. 7.32). Most *Collembola* inhabit the outer layer of the ant-hill

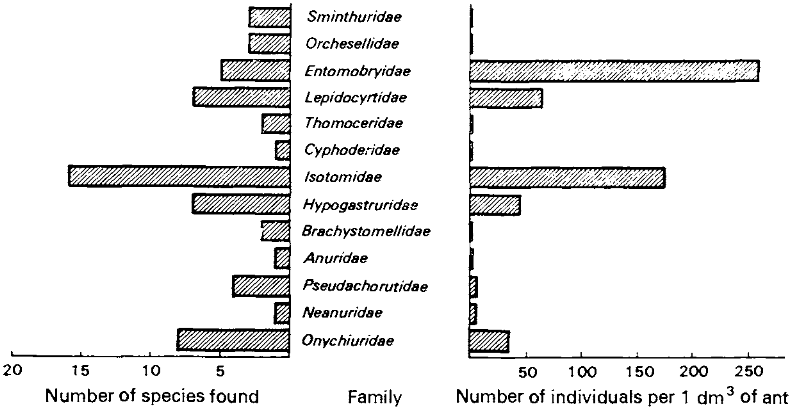


Fig. 7.32 Quantitative proportions of *Collembola* in ant-hills of *Formica polyctena* Forster in pine forests (after Wiśniewski, 1967)

Coleoptera ranked third as regards abundance after *Collembola* and *Psocoptera*. Their density per 1 dm^3 of the nest material amounted to 28 individuals. The following species were most frequent: *Ptenidium formicetorum* Kraatz (= *myrmecophilum* (Motschulsky)), *Acrotrichis atomaria* (De Geer), *Leptacinus formicetorum* Maerkel and *Dendrophilus pygmaeus* (L.). *Psocoptera* such as *Liposcelis subfuscus* Broadhead and *L. terricolis* Badannel exhibited a high density (121 per 1 dm^3) in the ant-hills.

The contribution of *Hymenoptera* to the total number of insects occurring in ant-hills does not exceed 1%, *Formicoxenus nitidulus* (Nylander) being a dominant representative.

Diptera constitute the predominant element of the entomofauna on the surface of ant-hills and also directly above them during the vegetation period. Within the ant-hill the density of these insects amounts to 11 individuals per 1 dm^3, with *Psychoda* and *Scatops* being the most frequently represented genera.

Thysanoptera are represented by 14 species in the ant-hills, their density amounting to 10 per 1 dm^3. *Xylocoris formicetorum* (Bohemann) predominates among the few *Heteroptera* and *Homoptera* which sometimes occur here. The quantitative ratios of various orders of insects inhabiting ant-hills are illustrated in Fig. 7.33.

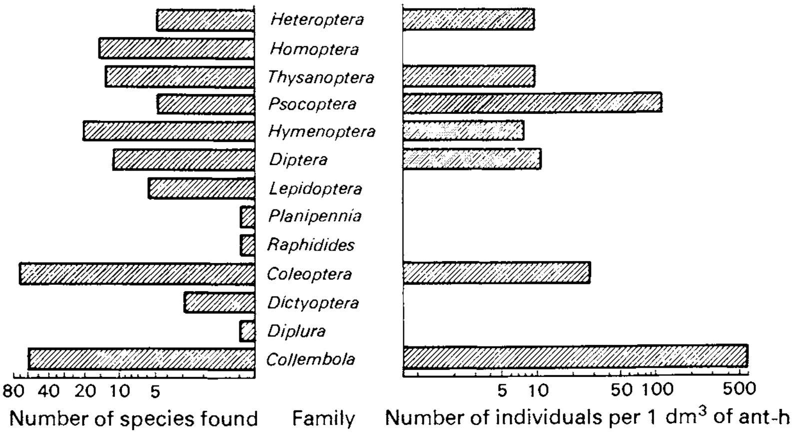


Fig. 7.33 Quantitative proportions of various insect orders in ant-hills of *Formica polyctena* (Forster) in pine forests (after Wiśniewski, 1967)

The specific composition of myrmecophils and their abundance depend on the season of the year and the layer of the ant-hill. The climax of the number of species, as well as that of density, occurs in May and again in September and October. Older ant-hills (two-years or more) exhibit a richer specific composition of myrmecophils, whereas one-year old nests are poorer in this respect.

Notiophilus biguttatus (F.) and *Calathus micropterus* (Duftschmid) predominate, whereas *Carabus arcensis* Herbst and *Pterostichus oblongopunctatus* (F.) are subdominants in the carabid community of the litter of fresh pine forests (*Pino-Vaccinietum myrtilli*) in the Kampinos Forest and the neighbouring forests of Masovia. A total of about 20–30 other *Carabidae* species occur here, representatives of the genus *Carabus* being the most important epigeic species. Among them *Càra-*

bus nemoralis Müller dominates in the fresh mixed coniferous forest habitat, whereas *C. arcensis* dominates in two extremely varying habitat conditions, namely those of the mixed forest and fresh coniferous forest.

The course of the changes in the dominant species of the carabid community with the growth of pine forest stands in the Wielkopolska–Pomerania subregion is as follows: *Bradycellus caucasicus* Chaudoir (= *collaris* (Paykull)) and *Amara quenseli* (Schönherr) dominate in older plantations, *Calathus erratus* (Sahlberg) in thickets, *Calathus micropterus* in old thickets to timber forest and *Notiophilus biguttatus* in timber forest.

Among other studies on insect communities of the region under discussion, the work of Leśniak (1972) and Szyszko (1972) regarding the *Carabidae* of the Noteć Forest are worthy of note. *Leistus ferrugineus* (L.), as well as *Calathus micropterus, C. erratus, Pterostichus oblongopunctatus, Carabus violaceus* L. and *Notiophilus biguttatus* were the most abundant species occurring in the habitat of fresh coniferous forest in its poorer facies (*Pino-Cladonietosum*). Here the ground water level is very low and the forest stands were subjected from time to time to outbreaks of foliophages. The characteristics of the occurrence of carabids in various habitats in relation to the presence of oak undergrowth is summarized in Tables 7.4 and 7.5.

The staphylinid community, which consists of over 100 species, is the most numerous community of litter-soil insects in the fresh coniferous forest as regards the number of species. They reach the peak of their abundance in 23–35 year-old pole-sized stands, whereas their lowest numbers occur in 8–9 year-old stands. The development of this community within the productive cycle of the forest stand is characterized by an increase in the density and domination of *Othius myrmecophilus* Kiesenwetter and also, in the eastern part of the region, of *Sipalia circellaris* (Gravenhorst). Of the other 31 species, the following exhibit a high abundance: *Mycetoporus clavicornis* (Stephens), *Stenus geniculatus* Gravenhorst, *Xantholinus linearis* (Olivier) and also, on the Masovian Plain, *Mycetoporus splendidus* (Gravenhorst).

Mycetoporus lepidus (Gravenhorst) (= *brunneus* (Marsham)), *Aleochara bipustulata* (L.), *Deliphrum tectum* (Paykull) and *Xantholinus linearis*, as well as species of the genus *Tachyporus*, exhibit a high mobility on reforested felling areas, whereas *Quedius boops* (Gravenhorst), *Sipalia circellaris, Amischa analis* (Gravenhorst) and *Mycetoporus lepidus* dominate in older plantations. Either *Stenus geniculatus* or *Que-*

Table 7.4 Ecological characteristics of litter *Carabidae* in various habitat forest types in the Noteć Forest (tabulated according to Szyszko, 1972).

Species	Habitat forest type		
	Fresh mixed coniferous forest		Fresh coniferous forest
	Presence of deciduous undergrowth		
	–	+	–
Pterostichus oblongopunctatus (F.)	D	S	S
Pterostichus niger (Schaller)	S	S	S
Carabus hortensis L.	S	D	
Carabus cariaceus L.			D
Carabus violaceus L.			S
Abax parallelepipedus (Piller & Mitterpacher) = *ater* (Villers))	S	S	
Carabus nemoralis Müller		S	
Carabus arcensis Herbst			S
Carabus convexus F.		S	
Number of attendant species	15	9	8
Contribution of individuals of spring species	52.1	31.3	56.7
Contribution of individuals of autumn species	47.9	68.7	43.3
Individuals of large zoophages, %	63.7	84.2	69.9
Individuals of small zoophages, %	32.9	14.5	29.6
Individuals of hemizoophages, %	3.9	1.4	0.5

D – dominant, S – subdominant species of *Carabidae* community.

dius boops dominate in thickets where the contribution of *Othius myrmecophilus* also increases. Individuals of *Xantholinus linearis* are most mobile, particularly in autumn.

The community with *Othius myrmecophilus* (D = 40.9%) as the dominant species, the density of which amounts to 7.1 individuals per 1 m^2, stabilizes in old thickets. A full regeneration of the community destroyed by clear fellings takes place in 32–42 year-old forest stands. The overall density of *Staphylinidae* during this period exceeds 40 individuals per 1 m^2. The absence of *Sipalia circellaris*, the dominant species of fresh pine forests in central and north-eastern Poland, is the negative feature of forest stands over 23 year-old in the Krajna–Pomerania region. *Quedius nigriceps* Kraatz is one of the particularly characteristic species of the poorest and driest parts of the forest.

Table 7.5 Ecological characteristics of litter *Carabidae* in various habitat forest types on the Masovian Lowland (tabulated according to Szyszko, 1972).

Species	Habitat forest type			
	Mixed forest	Fresh mixed coniferous forest		Fresh coniferous forest
	Presence of deciduous undergrowth			
	+	−	+	−
Carabus nemoralis Müller	S	D	D	S
Carabus arcensis Herbst	D	S	S	D
Pterostichus oblongopunctatus (F.)	S	S		S
Amara brunnea (Gyllenhal)		S		
Pterostichus niger (Schaller)		S		S
Leistus ferrugineus (L.)				S
Harpalus latus (L.)		S	S	
Number of attendant species	25	26	17	22
Contribution of individuals of spring species	74.7	72.1	74.7	57.6
Contribution of individuals of autumn species	25.3	27.9	25.3	42.4
Individuals of large zoophages, %	70.9	53.5	61.0	68.8
Individuals of small zoophages, %	22.3	31.0	11.2	30.1
Individuals of hemizoophages, %	6.8	15.5	27.8	1.1

D – dominant, S – subdominant species of *Carabidae* community.

Mycetoporus mulsanti Ganglbauer is associatated with the dune areas of the Kampinos Forest.

Othius myrmecophilus is the dominant species with *Othius punctulatus* (Goeze) and *Sipalia circellaris* as characteristic subdominants of the deciduous forest litter in the mixed coniferous forest on the Masovian Plain.

The characteristics of communities of other families of *Coleoptera* and the changes which they undergo during the productive cycle of pine forest stands are as follows.

Byrrhidae are typical representatives of the soil macrofauna of pine plantations in which the density of their larvae amounts to 12.5 individuals per 1 m^2. *Byrrhus fasciatus* (Forster) and *B. pustulatus* (Forster), *Morychus aeneus* (F.) and *Simplocaria semistriata* (F.) occur most frequently here. In older age classes of forest stands the abundance of *Byrrhidae* is very low.

Larvae of *Cantharidae* occur in the soil under pine forest stands of various age groups but particularly in pole-sized and older stands where their average density amounts to 25 individuals per 1 m^2. They mostly belong to the genus *Malthodes*.

Curculionidae are particularly abundant in pine forests. Species which larvae develop in the soil mostly belong to the genera *Brachyderes*, *Strophosomus* and *Trachyphloeus*. *Brachyderes incanus* (L.) causes considerable damage in older plantations and thickets. *Strophosomus flavicornis* (De Geer) is specific for the Krajna–Pomerania zone along with the widely distributed Polish species *S. capitatus* (De Geer) (= *rufipes* (Stephens)). Representatives of the genus *Trachyphloeus* (among which *T. scabriculus* (L.) and *T. bifoveolatus* (Beck) are the most common) belong to xerothermophilous species, the occurrence of which in pine forests is associated with the stage of the plantation. The density of *Curculionidae* larvae in the soil reaches its maximum between the 20th and 35th year of the forest stand and amounts to 29 individuals per 1 m^2. The dendrophilous species *Hylobius abietis* (L.) and *Pissodes pini* (L.) are amongst the other curculionids which occur most abundantly. Furthermore, *Coniocleonus hollbergi* (Fahraeus) exhibits a high abundance whereas representatives of genera associated with the forest herb layer, such as *Apion* and *Hypera* for example, are few.

The saprophagous species *Geotrupes stercorosus* (Scriba) and *G. vernalis* (L.) dominate in the geotrupid community of the fresh pine forest. *G. stercorosus* in 60 year-old forest stands and *G. vernalis* in thickets exhibit the highest mobility. *Typhoeus typhoeus* (L.), the range of which in Poland approximates to that of the wild rabbit, is a specific species of the western part of the region under discussion and does not occur to the east of the Vistula.

Larvae of *Elateridae* comprise the major groups of soil insects in the fresh pine forest environment. The facultative saprophages *Athous subfuscus* (Müller) and *Dalopius marginatus* (L.) are most typical of the litter and soil. The obligatory predators *Ampedus balteatus* (L.), *Cardiophorus ruficollis* (L.) (during the plantations stage) and *Prosternon tessellatum* (L.) also exhibit a high density. The phytophages *Selatosomus aeneus* (L.), *S. impressus* (F.) and *Sericus brunneus* (L.) which feed on the subterranean parts of mosses, are most abundant in younger forest stands. The relative quantitative ratios of elaterid communities in the soil, which consist of a dozen or so species in pine forests, are as follows: *Athous subfuscus*, 50%; *Dalopius marginatus*, 25%; *Prosternon tessellatum*, 9.0%, and *Sericus brunneus*, 6.4%. The average density of elaterid larvae in timber stands in the vegetation season amounts to 130 individuals per 1 m^2. The course of the quantitative changes in the community of *Elateridae* in the productive cycle of forest stands is illustrated in Fig. 7.34.

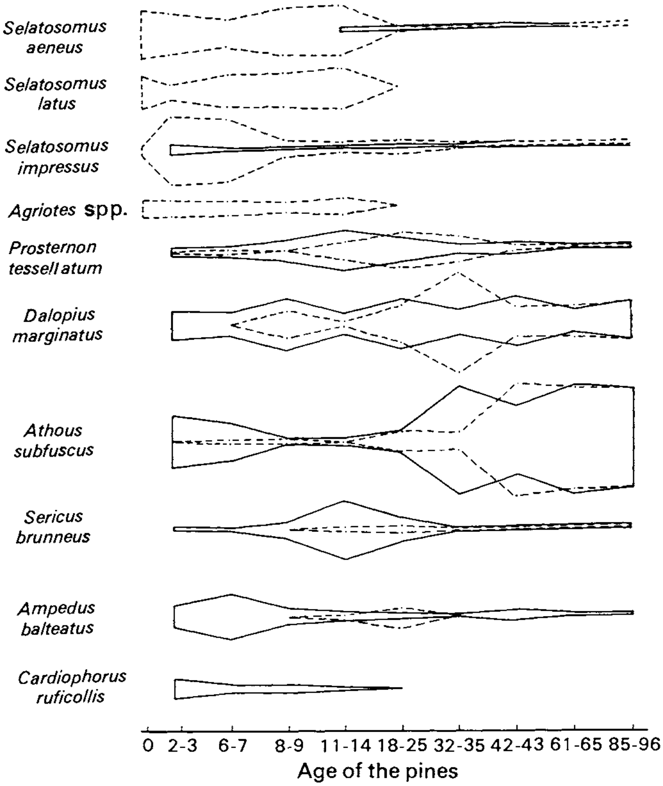


Fig. 7.34 Course of changes in relative dominance of *Elateridae* larvae along with the growth of pine forest stands in the fresh coniferous forest habitat in the Człuchów Forest (after Szujecki *et al.*, 1977): continuous line – forest soil, dashed line – afforested old arable land

Trixagus dermestoides (L.) (the larvae of which feed on the roots of trees, bushes and shrubs with an ectotrophic mycorrhiza, and occur most abundantly near the roots of birches, oaks, pines, broom and blueberry), *Meligethes aeneus* (F.) (feeding on the blueberry), *Calvia quattuordecimpunctata* (L.) (also occurring on the blueberry) and *Strophosomus capitatus* (De Geer) belong to species representing various *Coleoptera* families which dominate in the litter of fresh pine forests of the Kampinos Forest. The last three species mentioned are essentially elements of the forest herb layer or tree crowns, although *Strophosomus* and *Meligethes* also penetrate the litter for oviposition and larval development.

Agathidium laevigatum Erichson (*Leiodidae*), *Stenichnus scutellaris* (Müller & Kunze) (*Scydmaenidae*) and *Trimium brevicorne* (Reichenbach) (*Pselaphidae*) also occur abundantly in these habitats, pselaphids being predators of soil *Acarina*. Some tenebrionid larvae occupy similar ecological niches to those of elaterids and are most frequently encountered in older plantations where their density reaches 16.5 individuals per 1 m^2 (*Crypticus quisquilius* (L.) and *Opatrum sabulosum* (L.) dominate).

Litter and soil *Diptera* are represented by a dozen of families, usually as larvae although the average density of adult sciarids and empidids in the litter of 61–83 year-old forest stands can sometimes exceed 50 individuals per 1 m^2. *Diptera* larvae exhibit a wide variety of feeding habits. Obligatory and facultative saprophages, which play an important role in soil-forming processes, prevail quantitatively and include species of *Chironomidae* (subfamily *Orthocladiinae*), *Sciaridae*, *Sciophilidae*, *Petauristidae*, *Bibionidae*, *Tipulidae* (particularly *Tipula meigeni* Mannheims), *Limoniidae*, *Heleidae*, *Fungivoridae* and many species of *Cedidomyiidae* (particularly subfamily *Lestremiinae*). Predaceous larvae are represented by *Rhagionidae* (*Rhagio* sp.), *Dolichopodidae* (*Dolichopus* sp., *Neurogona* sp., *Systemus* sp.), *Empididae* (*Empis sp.*, *Hilara* sp., *Ocydromia* sp.), *Therevidae* (*Thereva* sp.) and *Asilidae* (*Asilus* sp., *Dysmachus* sp., *Dioctria hyalipennis* (F.)). In addition, some *Cecidomyiidae* larvae which pupate in the soil are phytophagous.

The relative densities of the larvae of various *Diptera* families change with the growth of the forest stand. *Bibionidae* dominate in plantations and thickets, *Cecidomyiidae*, *Sciaridae* and *Dolichopodidae* in thickets and pole-sized stands, *Tipulidae* in older pole-sized stands and, finally, *Empididae*, *Chironomidae* and *Sciaridae* in maturing and timber forest stands. The highest density of *Diptera* larvae was observed in 11–14 year-old thickets where it amounted to 85 individuals per 1 m^2. Relatively high densities were also recorded from 42–43 year-old pole-sized forest stands (76 individuals per 1 m^2) and from 6–7 year-old plantations where there is an abundant organic layer between rows (73 individuals per 1 m^2). The wide variations in the abundance of *Diptera* larvae between neighbouring age classes of the forest stand are due to the rapid succession of dominant representatives of different families.

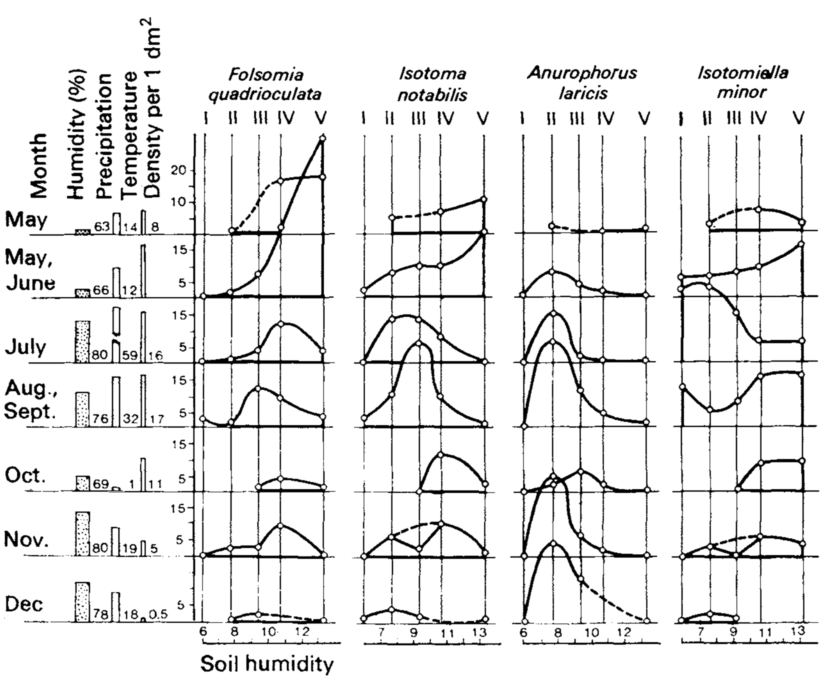


Fig. 7.35 Density and dominance of most frequent *Collembola* species in depend ence on the soil humidity in the pine forest (after M. Kaczmarek, 1975)

In the *Collembola* community of pine forests, 90% of the individuals belong to the nine most abundant species, the density and dominance of which changes with variations in the soil humidity in different parts of the biotope (Fig. 7.35). The mean density of *Collembola* is less dependent on the soil humidity than is that of polyvalent and oligovalent species which exhibit inverse changes in their density in the middle values of the humidity gradient (Fig. 7.36).

The *Heteroptera* of the litter of mixed coniferous forest passing into mixed *Pino-Quercetum* (*Querceto-Carpinetum-medioeuropaeum*), a forest type which occurs among fields, were studied in the border areas of the Eastern Podlasie and Łuków–Podlasie zones. *Lygaeidae* predominate as regards both the number of species and the density of individuals. *Nabis ferus* L. (D = 20.6%) is the dominant species of the entire community with *Cymus claviculus* (Fallén), *Saldula saltatoria* (L.), *Rhyparochromus pini* (L.) and 6 others as the subdominant species. A total of 56 additional species were also observed. Many of the species of the community, including *Nabis ferus*, are most abundant from late autumn to

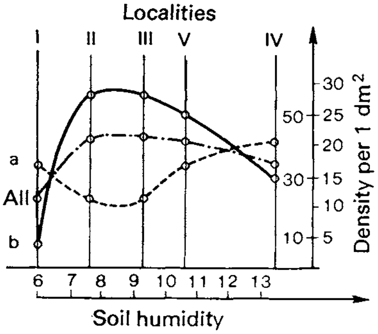


Fig. 7.36 Influence of soil humidity on the density of *Collembola* belonging to various ecological types: a – oligovalent species, b – polyvalent species (after M. Kaczmarek, 1975)

spring and mainly consist of individuals immigrating from neighbouring open areas. In general it would appear that the *Heteroptera* community of litter occurring here is essentially xerophilous in character (Fedorko, 1957).

IV. Region of the Central Polish Uplands

The region of the Central Polish Uplands includes a highly differentiated area as regards physiography, climate and geobotany. The altitude a.s.l., the character of watershed and the delimitation of the region by the borders of the ranges of the beech, fir, spruce and also in part of the larch, are all common features of this area.

Various types of forest flora and their associated communities of insects occur here. The beech is the typical forest-forming species on the Cracow–Wieluń Upland. Oak-pine forest stands, with a considrable contribution of beech, hornbeam and fir, occur on the Lublin Upland. The entomofauna is also very diverse. The frequent contact of elements derived from the montane or submontane fauna with thermophilous elements of the fauna specific for regions of southern and south-eastern Europe, plus the differentiation of the orography and vegetal cover are characteristic features of this area. The following seven zones may be distinguished here: the Cracow–Wieluń Upland, the Łódź–Radom Eminences, the Nida Syncline, the Lublin Upland, Roztocze, the Sandomierz Lowland and the Sandomierz Upland.

The entomocenoses of the tree crowns, undergrowth and herb layers of the region of the Central Polish Uplands are the best known in Poland due mainly to studies performed by Karczewski (1957, 1961a, 1961b, 1962, 1967a, 1967b) and Sawoniewicz (1979).

Relatively few works, however, concern the forest litter and soil insects of this region (Karczewski, 1961a; Nunberg, 1949; Pętal, 1961; Szyszko, 1972).

Entomofauna of the forest tree layer. Outbreaks of *Diprion pini* (L.) concentrate in the southern part of the Piotrków–Opoczno Upland and in the Nida Syncline. The pine plantations of this area are attacked by *Thecodiplosis brachyntera* (Schwägrichen) (*Cecidomyiidae*) which favours the propagation of the parasitic fungus *Cenangium ferrugosum* Duby resulting in the premature shedding of needles. In older forest stands this hinders the regeneration of the assimilation apparatus after the feeding of *Diprion* spp. The economic importance of *Lymantria monacha* (L.) and *Panolis flammea* (D. & S). has increased here in the recent decade, the former species exhibiting a higher outbreak tendency on the Western Lublin Upland, Sandomierz Lowland and Biłgoraj Plain. The edaphic conditions and poor biocenoses in the Solec Forest favour the mass appearance of *Dendrolimus pini* (L.), whereas the Niepołomice Forest was once subjected to an intensive outbreak of *Acantholyda posticalis* Matsumura.

Fir pests play some role in the state of health of the forests of the Biłgoraj Plain and Roztocze.

The absence of *Diadegma eucerophaga* Horstmann, the parasite of *Exoteleia dodecella* (L.) which dominates in central and northern Poland, is the negative feature of the community of ichneumons of pine crowns on the Lublin Upland as compared with the Masovia, Podlasie and Masury–Podlasie regions. The following parasitic species are most abundant here: *Ichneumon subquadratus* Thomson, *Scambus sagax* Hartig, *Trychosis legator* (Thunberg), *Macrus parvulus* (Gravenhorst), *Gelis areator* (Panzer), *Lissonota variabilis* Holmgren, *Phaeogenes vagus* Berthoumieu, *Glypta resinana* Hartig and several others. They are mostly parasites of the caterpillars of *Microlepidoptera*. *Olesicampe macellator* Thunberg, the parasite of *Diprion* spp., and *Aptesis abdominator* (Gravenhorst), the parasite of *Dendrolimus pini* (particularly in the presence of oak undergrowth) are also abundant in coniferous forests here.

Besides the communities typical of the pine forests of central Poland, rich communities of insects also occur in the entomofauna of the Łódź–Radom Eminences in deciduous and mixed forest stands generally forming small complexes on fertile sites. The diversity and high differentiation of species of phytophage communities here is proportional to the differentiation of the forest flora – trees, shrubs and herbs and the frequently preserved structure of forest stands consisting of trees of various ages. The deciduous forest stands are frequently subjected to intensive outbreaks of *Tortrix viridana* (L.), *Operophtera brumata* (L.) *O. fagata* (Scharfenberg), *Erannis defoliaria* (Clerck) and *Agriopis aurantiaria* (Hübner) in the presence of other less abundant species (Fig. 7.37)

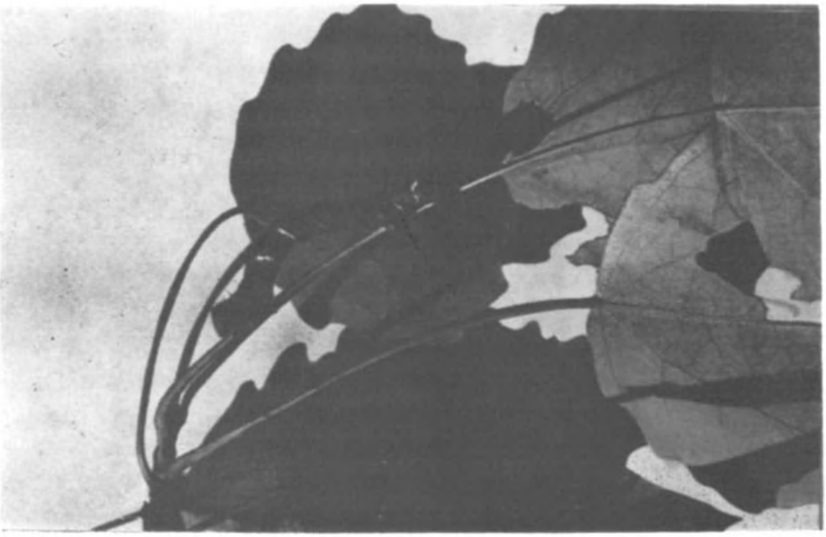


Fig. 7.37 Geometrid larva on the aspen (photo by S. Kinelski)

The abundance of specialized predators such as *Calosoma inquisitor* (L.) and *Dendroxena quadrimaculata* (Scopoli), as well as that of numerous parasitic species, increases against the background of outbreaks of the foliophages mentioned above. The occurrence of many phytophagous *Coleoptera* is characteristic – *Cryptocephalus cordiger* (L.) and *C. octopunctatus* (Scopoli) on the oak and the goat willow, curculionids of the genera *Phyllobius* and *Polydrosus*, among which *Polydrosus picus* (F.) as well as *Attelabus nitens* (Scopoli) are particularly abundant on the oak. Among species of the tribe *Rhynchitini* the following occur: *Caenorhinus nanus* (Paykull), *C. tomentosus* (Gyllenhal) (on willows), *C. aeneovirens* (Marsham) (on the oak), *C. aequatus* (L.) (on *Rosaceae*) and the most interesting, although rarely observed in Poland, *Lasiorhynchites cavifrons* (Gyllenhal), the larvae of which feed on dying oak shoots.

The goat willow exhibits the following dominants. *Chrysomelidae*: *Lochmaea caprea* (L.), *Labidostomis tridentata* (L.), *Smaragdina aurita* (L.), *Cryptocephalus frenatus* Laicharting, *Plagiodera versicolora* (Laicharting), *Phytodecta viminalis* (L.) and *Chrysomela lapponica* (L.) (mostly represented by the coloured variety *C. lapponica* ab. *bulgharensis* (F.), *Curculionidae*: *Rhynchaenus salicis* (L.) and *R. stigma* (Germar). Many other *Coleoptera* and *Lepidoptera* also occur on this species. On the aspen, *Chrysomelidae* are particularly abundant, including *Phytodecta decemnotata* (Marsham), *Zeugophora subspinosa* (F.) (the larvae of which mine leaves), representatives of the genera *Phyllodecta* and *Chrysomela*, as well as *Anacampsis populella* (Clerck) (the caterpillars of which roll leaves into cornet-like forms). *Clytra quadripunctata* (L.), which develops in ant-hills, belongs to the spring aspect of the entomofauna. Its adults sometimes appear abundantly on leaves of willows and oaks. *Phyllobius arborator* (Herbst), *P. pyri* (L.), *P. argentatus* (L.), *P. maculicornis* Germar, *Polydrosus pallidus* (Gyllenhal), *P. cervinus* (L.), *P. pilosus* Gredler, *P. undatus* (F.) and *Oxystoma pomonae* (F.) feed on various deciduous trees and shrubs.

Seventeen species of *Chalcidoidea* are parasites of *Lepidoptera* which mine oak leaves on the Łódź–Radom Eminences and on the Sandomierz Lowland, and belong to the genus *Phyllonorycter* (*P. heegeriella* (Zeller), *P. lautella* (Zeller), *P. quercifoliella* (Zeller), *P. roboris* (Zeller), *P. harisella* (L.)), as well as to the genus *Tischeria* (*T. ekebladella* (Bjerkander), *T. dodonaea* Stainton). *Sympiesis sericeicornis* (Nees), *S. gordius* (Walker), and *Pnigalio pectinicornis* (L.) are amongst the most abundant species in this respect. Many *Chalcidoidea* also parasitize insects which produce oak galls. These are *Torymus cingulatus* Nees (on *Cynips longiventris* Hartig and *C. disticha* (Hartig), *Mesopolobus fasciventris* (Westwood) (on *Andricus ostreus* Hartig and *Cynips longiventris*), *Eurytoma rosae* Nees (on *Cynips disticha*, *C. longiventris* and *Andricus ostreus* (Nunberg & Szczepański, 1965).

Besides the economically important species such as *Pissodes harcyniae* (Herbst), *Ips typographus* (L.) and *Polygraphus poligraphus* (L.), the occurrence of *Ips duplicatus* C. R. Sahlberg, *Pityophthorus traegardhi* Spessivtsev and *Phleotribus spinulosus* (Rey) which are rare in central Poland, was observed on the common spruce on this area. A mass appearance of *Dendroctonus micans* (Kugelann), accompanied by its specific predator *Rhizophagus grandis* Gyllenhal was noted on the introduced Sitka spruce.

The community of *Coleoptera* living under-bark and inhabiting the galleries of *Tomicus piniperda* (L.) on the Lublin Upland differs from those described in the Masury–Podlasie Region in that there is a lower contribution of *Rhizophagus depressus* (F.) in the habitat of fresh coniferous forest and a rather abundant occurrence of the thermophilous *Phloeopora angustiformis* Baudi. Furthermore, *Siagonium quadricorne* Kirby is also present.

Further data concerning the forest entomofauna of the region of the Central Polish Uplands, and particularly that of the Łódź Upland, can be found in the works of Dominik (1966a), Szujecki & Zaborowski (1968), Wiąckowski (1957) and other authors.

The occurrence of many insect species which constitute a permanent component of entomocenoses of mountains, highlands and sometimes also the Masury–Podlasie Region is a specific feature of the zone of Łódź–Radom Eminences and distinguishes it from the neighbouring region of the Central Polish Uplands. The following species are found here: *Zilora sericea* (Sturm), *Serropalpus barbatus* (Schaller), *Pachyta quadrimaculata* (L.) and *Ips duplicatus* C. R. Sahlberg. Species of a warmer climate associated with deciduous trees also occur here. *Xylonites retusus* Olivier lives in dry oak branches (Kinelski & Szujecki, 1959) and *Gastrallus immarginatus* (Müller) in the oak bark (Dominik, 1966a). Both species belong to representatives of the Mediterranean fauna known in Central Europe only from a few localities.

Typical lowland species characteristic of pine forests, as well as of vast areas of sandy inland dunes and sandr of terminal moraine foreland, are absent or few here. For instance, *Ergates faber* (L.) was not observed whereas *Chalcophora mariana* (L.) was only rarely encountered.

Entomofauna of the undergrowth and herb layer of pine forests. The undergrowth and herb layer of the habitat of fresh coniferous forest on the Lublin Upland revealed the presence of 187 ichneumon species, among which *Lissonota variabilis* Holmgren dominated (D = 33.6%), whereas *Ichneumon subquadratus* Thomson, *Proclitus autumnalis* Foerster, *Exochus pictus* Holmgren, *Cratichneumon viator* (Scopoli) and *Cymodusa antennator* Holmgren were accessory species. Many species of this community parasitize larvae of *Fungivoridae* (*Diptera*) or phytophages of the herb layer. *Lissonota variabilis* and *Ichneumon subquadratus* are parasitic on caterpillars feeding on lichens and mosses. Parasites of phytophages of deciduous trees may also belong to this group. Their abundance is higher in pure pine forest stands (Sawoniewicz, 1979).

In fresh pine forests in the association *Pino-Vaccinietum myrtilli* the layer of blueberry is accompanied by a community of its phytophages, parasites and predators as well as a community of insects which visit the flowers of this plant.

The community of insects feeding on the blueberry in the Nida Syncline consists of 138 species belonging to 28 families and 6 orders (Karczewski, 1962). The following species dominate: *Elasmucha ferrugata* (F.) (*Acanthosomatidae*), *Strictopleurus crassicornis* (L.) (*Rhopalidae*), *Lygus pratensis* (L.), *Capsus meriopterum* (Scopoli) (*Miridae*), *Aphis vaccinii* (Börner) (*Aphidae*), *Phyllostroma myrtilli* Kaltenbach, *Mytilococcus ulmi* (L.) (*Coccidae*), *Nepticula myrtilella* Stainton (*Nepticulidae*), *Coleophora vacciniella* (Herrich-Schäffer), *Cheimophila salicella* (Hübner) (*Coleophoridae*), *Acleris maccana* (Treitschke), *Semasia vacciniana* (Zetterstedt) (*Tortricidae*), *Arctia caja* (L.) (*Arctiidae*), *Ectropis bistortata* (Goeze), *Ematurga atomaria* (L.), *Todis putata* (L.), *Chloroclystis debiliata* (Hübner) (*Geometridae*), *Eurois occulta* (L.), *Lithomoia solidaginis* (Hübner) (*Noctuidae*), *Orgyia gonostigma* (F.) (*Lymantriidae*), *Lasiocampa quercus* (L.) (*Lasiocampidae*), *Saturnia pavonia* (L.) (*Saturniidae*), *Callophrys rubi* (L.) (*Lycaenidae*), *Pristiphora quercus* (Hartig) (*Tenthredinidae*) and *Dasineura vaccinii* (Rübsaamen) (*Cecidomyiidae*).

A total of 233 species (among them 110 *Ichneumonidae*) are parasitic on the phytophages of the blueberry, 16 of which are predatory. These are *Picromerus bidens* (L.), *Troilus luridus* (F.) (*Pentatomidae*), *Nabis ferus* (L.) (*Nabidae*), *Hyperaspis campestris* (Herbst) (*Coccinellidae*), *Itoplectis alternans* (Gravenhorst), *Hemiteles areator* (Panzer), *Theronia atalantae* (Poda), *Scambus brevicornis* (Gravenhorst) (*Ichneumonidae*), *Aleiodes geniculator* (Nees), *Apanteles congestus* (Nees), *Microplitis mediana* (Ruthe), *Meteorus gyrator* (Thunberg) (*Braconidae*), *Trichomasthus albimanus* Thomson (*Encyrtidae*), *Aphelinus subflavescens* (Westwood) (*Aphelinidae*), *Pteromalus* (*Habrocytus*) *dispar* (Curtis) (*Pteromalidae*), *Elasmus westwoodi* (Girault) (*Elasmidae*), *Euplectrus bicolor* (Swederus), *Eulophus abdominalis* Nees, *Colpoclypeus florus* (Walker) (*Eulophidae*), *Telenomus tetratomus* (Thomson) (*Scelionidae*), *Actia tibialis* Robineau-Desvoidy, *A. pilipennis* (Fallén) and *Compsilura concinnata* (Meigen) (*Tachinidae*).

The parasites and predators obligatorily or facultatively associated with the blueberry may be divided into the following two groups: (i) species whose cenotic associations are confined to the herb layer and (ii) species which also have hosts in the layer of tree crowns. The latter constitute 40% of all the species observed by Karczewski (1962). A particularly large proportion of tachinid species (70%) have parallel hosts on the blueberry and in the pine crowns and about 50 species are important parasites of noxious pine foliophages. *Chalcidae* exhibit the lowest number of species which are common to both the forest layers under discussion. Oligophages which only have a few hosts constitute the most abundant group of parasites associated with the blueberry layer and include *Casinaria ischnogaster* Thomson and *Winthemia amoena* Meigen. On the other hand, *Aleiodes nunbergi* (Noskiewicz) and *Dusona confusa* (Forster) are among the monophagous species of this layer. Besides parasites of the first order, secondary parasites also occur here of which there are 37 species, i.e. 15% of the total number of parasites in the blueberry layer. Most of them belong to the genera *Hemiteles*, *Gelis*, *Mesochorus* and *Trichomalus*.

Insects which visit the flowers of the blueberry are very abundant, totalling 67 species belonging to the following families: *Apidae* (16 species, *Noctuidae* (9 species), *Syrphidae* (14 species) and others.

Vaccinium uliginosum L. plays an analogous biocenotic role to the blueberry in the humid coniferous forest habitat. Many phytophages and their parasites, as well as melitophages are associated with this plant.

The entomofauna of the heather *Calluna vulgaris* L. was studied under the same geographical conditions but in poorer facies of the fresh pine forest. A total number of 68 species of insect, representing 23 families of 4 orders, feed on this plant and include *Orthotylus ericetorum* (Fallén) (*Miridae*), *Stygnocoris pedestris* (Fallén), *Macroparius helveticus* Herrich-Schäffer, *Scoloposthetus decoratus* (Hahn) (*Lygaeidae*), *Dolycoris baccarum* (L.) (*Pentatomidae*), *Ulopa reticulata* (F.) (*Cicadellidae*), *Stophingia ericea* Curtis (*Aphalaridae*), *Spinococcus calluneti* (Lindiger) (*Pseudococcidae*), *Acanthococcus* sp. (*Eriococcidae*), *Diaspidiotus bavaricus* (Lindiger) (*Diaspididae*), *Lochmaea suturalis* (Thomson), (*Chrysomelidae*), *Micrelus ericae* (Gyllenhal) (*Curculionidae*), *Rhagades pruni* (D. & S.) (*Zygaenidae*), *Coleophora juncicolella* Stainton (Fig. 7.38) *Coleophoridae*), *Aristotelia ericinella* (Zeller) (*Gelechiidae*), *Ematurga atomaria* (L.), *Eupithecia absintihiata* (Clearck) (*Geometridae*), *Anarta myrtilli* (L.), *Lycophotia porphyrea* (D. & S.) (*Noctuidae*), *Coscinia cribraria* (L.) (*Arctiidae*), *Macrothylacia rubi* (L.) (*Lasciocampidae*), *Saturnia pavonia* (L.) (*Saturniidae*) and *Celastrina argiolus* (L.) (*Lycaenidae*).

The phytophages which live on heather are the hosts or prey of 118 species of parasites and predators belonging to 19 families of 3 orders. They include *Nabis ericetorum* Scholtz (*Nabidae*), *Coranus subapterus*

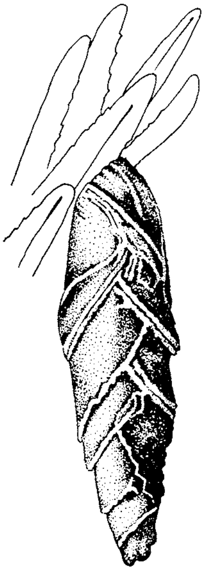


Fig. 7.38 Larval basket of *Coleophora juncicolella* Stainton on heather (after Karczewski, 1967a)

(De Geer) (*Reduviidae*), *Deraeocoris scutellaris* (F.) (*Miridae*), *Rhacognathus punctatus* (L.) (*Pentatomidae*), *Mellinus arvensis* (L.) (*Sphecidae*), *Formica fusca* L. (*Formicidae*), *Barylypa insidiator* (Forster), *Campoletis erythropus* (Thomson) (Fig. 7.39), *Banchus volutatorius* (L.) (*Ichneumonidae*), *Microplitis ruricola* Lyle (Fig. 7.40), *Aleiodes testaceus*

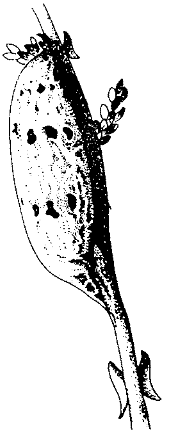


Fig. 7.39 Cocoon of *Campoletis erythropus* (Thomson) (after Karczewski, 1967a)

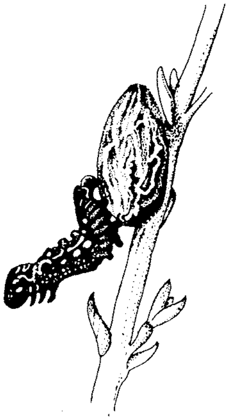


Fig. 7.40 Cocoon of *Microplitis ruricola* (Lyle) beside dead caterpillar of *Anarta myrtilli* (L.) (after Karczewski, 1967a)

(Spinola), *Microchelonus basalis* (Curtis), *Apanteles geryonis* Marshall, *Oncophanes minutus* (Nees) (Fig. 7.41) (*Braconidae*), *Aphycus callunae* Ashmaed (*Encyrtidae*), *Elasmus westwoodi* Girault (*Elasmidae*), *Euplectrus bicolor* (Swederus) (Fig. 7.42), *Pediobius claviger* (Thomson) (*Eulophidae*), *Telenomus tetratomus* (Thomson) (*Scelionidae*), *Dioctria hyalipennis* (F.) (*Asilidae*), *Spoggosia fasciata* (Egger), *Campylochaeta*

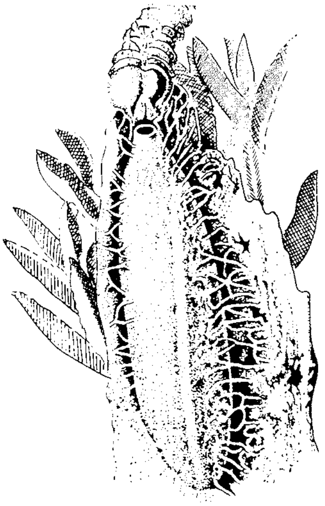


Fig. 7.41 Cocoon of *Oncophanes minutus* (Nees) (after Karczewski, 1967a)

inepta (Meigen), *Athrycia impressa* Wulp (*Tachinidae*) and *Hilarella hilarella* (Zetterstedt) (*Calliphoridae*).

Hymenoptera (including 22 species of *Pteromalidae*), *Lepidoptera* (including 33 species of *Noctuidae*) and *Diptera* (including 30 species of *Syrphidae* and 30 of *Tachinidae*) are the most abundant orders. Many of them fly to heather flowers from other, sometimes distant biotopes. Amongst these are *Athalia rosae* (L.) *A. glabricollis* Thomson (*Tenthredinidae*), *Colletes succinctus* (L.) (*Colletidae*), *Andrena fuscipes* Kirby (*Andrenidae*), *Halictus calceatum* (Scopoli), *Sphecodes ephippius* (L.) (*Halictidae*), *Nomada rufipes* F., (*Anthophoridae*), *Bombus* spp. (*Apidae*), *Mellinus arvensis* (L.) (*Sphecidae*), *Psammochares proximus* (Dahlbom), *Pompilus viaticus* (L.) (*Pompilidae*), *Eumenes coarctatus* (L.) (*Eumenidae*), *Myrmica rubra* (L.), *Lasius niger* (L.), *Formica fusca* L. (*Formicidae*), *Trechnites flavipes* Mercet (*Encyrtidae*), *Catolaccus ater* (Ratzeburg) (*Pteromalidae*), *Euplectrus bicolor* (Swederus) (*Eulophidae*), *Telenomus tetratomus* (Thomson), (*Scelionidae*), *Agriphila selasella* (Hübner), *Semiothisa liturata* (Clerck), *Chloroclysta truncata* (Hufnagel, *Cyclophora punctaria* (L.) (*Geometridae*), *Autographa gamma* (L.) (*Noctuidae*), *Thymelicus acteon* (Rottemburg) (*Hesperiidae*), *Lycaeides argyrognomon* Bergsträsser, *Lycaena titytrus* (Poda), *L. al-*

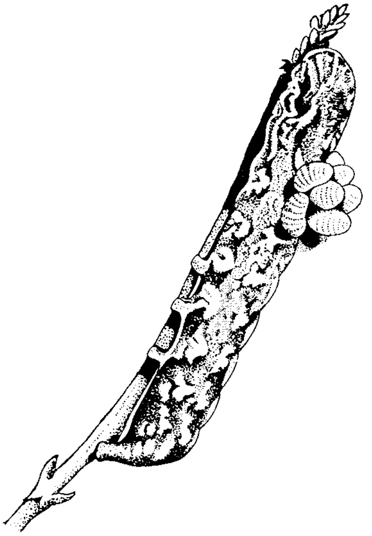


Fig. 7.42 Caterpillar of *Anarta myrtilli* (L.) with larvae of *Euplectrus bicolor* (Swederus) on its back (after Karczewski, 1967a)

ciphron (Rottemburg), *L. phlaeas* (L.) (*Lycaenidae*), *Mellicta athalia* (Rottemburg), *Melitaea didyma* (Esper) (*Nymphalidae*), *Coenonympha pamphilus* (L.) (*Satyridae*), *Dilophus febrilis* (L.) (*Bibioniae*), *Syrphus* spp., *Sphaerophoria* spp., *Eristalis* spp. (*Syrphidae*), *Sepsis cynipsea* (L.) (*Sepsidae*), *Pherbella brunnipes* Meigen (*Sciomyzidae*), *Ensina sonchi* (L.) (*Tephritidae*), *Chlorops pumilionis* (Bjerkander) (*Chloropidae*), *Trimerina madizans* (Fallén), *Hyadina guttana* (Fallén), *H. scutellata* Haliday (*Ephydridae*), *Scaptomyza pallida* (Zetterstedt) (*Drosophilidae*), *Myopa fasciata* Meigen, *Conops quadrifasciata* De Geer, *Sicus ferrugineus* (L.) (*Conopidae*), *Helina duplicata* (Meigen), *Musca autumnalis* De Geer (*Muscidae*), *Drino inconspicua* (Meigen), *Tachina magnicornis* (Zetterstedt), *Lydina aenea* (Meigen), *Aphria longirostris* (Meigen), *Gymnosoma rotundatum* (L.) (*Tachinidae*), *Sarcophaga vicina* (Villeneuve), *S. carnaria* (L.) (*Sarcophagidae*), *Pollenia* spp., *Lucilia* spp., *Melinda* spp. (*Calliphoridae*).

Within the group of insects which occur on the heather, parasitic and predatory species may be distinguished whose entire developmental cycle is accomplished on this plant (e.g. *Platylabus pactor* Wesmael, *Casinaria morionella* Holmgren, *Barylypa insidiator* (Foerster), *Apanteles geryonis* Marshall and *Spoggosa fasciata* (Egger). A total of 23 species, i.e. 20% of all entomophages, also have hosts in the pine crown layer (e.g. *Banchus falcatorius* (F.), *Meteorus versicolor* (Wesmael), *Trichogramma embryophagum Hartig*, *Telenomus tetratomus* (Thomson) and *Exorista larvarum* (L.)). The third group consists of species inhabiting various biotopes and various forest layers (e.g. *Hyposoter didymator* (Thunberg), *Trichiosoma nigripes* Gussakovskii, *Euplectrus bicolor* (Swederus), *Strobliomyia tibialis* (Robineau-Desvoidy)).

Ematurga atomaria and *Anarta myrtilli* are the most important phytophages which feed on heather and are either the hosts or prey of 34% of the predators and parasites observed in the heather layer.

As compared with the entomocenose of the blueberry, heather does not provide suitable conditions for the development of *Tortricidae*, which in the blueberry layer are the host of 25% of the total number of parasitic species and also include the parasites of *Archips oporana* (L.) and *Exoteleia dodecella* (L.).

Furthermore, *Coccidae* which occur on heather only produce small amounts of honey-dew whereas *Phyllostroma myrtilli*, which lives on the blueberry provides sufficient amounts of this substance for the adults of many parasites, particularly those exhibiting early flights when aphids occurring on the pine are not fully active and only produce small amounts of honey dew. In this respect heather is less useful than the blueberry and plays a less important role in the development of entomocenoses of pine forests. On the other hand, heather provides nectar and pollen for many forest insects.

Entomofauna of the undergrowth and herb layer of deciduous and mixed forest. On the Lublin Upland in the fresh forest habitat in pine forest stands with an oak-hornbeam undergrowth, as well as in forest stands without undergrowth, 276 species of ichneumons were observed in the undergrowth and herb layer. *Cratichneumon culex* (Müller) predominates (D = 8%), *Pleolophus basizonus* (Gravenhorst), *Cratichnumon fabricator* (F.) and *Encrateola laevigata* (Ratzeburg) are subdominant species, and the most abundant accessory species include *Phobocampe bicingulata* (Gravenhorst), *Pimpla aquilonia* Gresson, *Sussaba cognata* (Holmgren), *Phygadeuon exiguus* Gravenhorst, *Phaeogenes infimus* Wesmael, *Cratichneumon varipes* (Gravenhorst), *Mesoleptus filicornis* (Thomson), *Apechthis quadridentatus* (Thomson), *Dichrogaster liostylus* (Thomson), and *Charitopes chrysopae* (Brischke). This community is thus particularly diverse as regards species. Parasites of *Lepidoptera* which occur on deciduous trees, as well as *Bupalus piniarius* (L.) and *Lymantria monacha* (L.), are represented by the highest number of individuals. *Pleolophus basizonus* is an important regulator of the abundance of *Diprion* spp. *Cratichneumon culex*, the parasite of *Cheimatobia brumata* (L.), occurs most abundantly in forest stands with a deciduous undergrowth. Due to the low abundance of pine phytophages in the fresh forest habitat, the abundance of their parasites (e.g. *Cratichneumon viator* (Scopoli) and *Lamachus* sp.) is also low.

In fresh mixed forest in pine stands with and without deciduous undergrowth, 201 species of *Ichneumonidae* have been recorded from the undergrowth and herb layer. *Eusterinx* sp. (D = 18%) is the dominant species, whereas the following are subdominants: *Cratichneumon varipes* (Gravenhorst), *C. viator*, *Crypteffigies lanius* (Gravenhorst), *Ichneumon subquadratus* Thomson, *Cratichneumon culex*, *Proclitus grandis* Foerster, *Cratichneumon fabricator*, *Ichneumon gracilentus* Wesmael, *Acrolyta distincta* (Bridgman) and *Netelia latungulus* (Thomson).

The species belonging to the genera *Cratichneumon* and *Netelia* are parasitic on the caterpillars of larger *Lepidoptera* which live mainly on deciduous trees, whereas the dominating species of the genera *Eusterinx* and *Proclitus* are parasites of *Diptera* feeding on pileate and bracket fungi. *Cratichneumon nigritarius* is known to parasitize *Bupalus pinia-*

rius (L.) and *Panolis flammea* (D. & S.), whereas *Acrolyta distincta* is a parasite of spider oothecae.

The abundance of parasites of phytophages of deciduous trees is higher in forest stands which have an oak undergrowth than in pure pine stands, whereas the abundance of the main parasites of pine phytophages is higher in pure pine forests. Thus, the abundance of regulators is determined by the abundance of their hosts and therefore also depends on the specific composition of the forest stand.

Entomofaunistic studies on the Cracow–Wieluń Upland were concentrated in the environs of Ojców. The results of studies on leaf-mining insects are particularly valuable for an understanding of the communities of forest insects (Beiger, 1960).

In all the forest associations and neighbouring non-forest biotopes a total of 163 species have been observed, 78.3% of which belong to *Diptera*, 14.2% to *Lepidoptera*, 4.9% to *Coleoptera* and 2.4% to *Hymenoptera*. Most species belong to the European element (129 species) and a dozen or so to the montane fauna.

In the beech forest, *Fagetum carpaticum* Klika, 39 species have been recorded, 88% of which belong to *Diptera*. *Phytomyza brunnipes* Brischke (on *Sanicula europaea* L.) and *P. actaeae* Hendel (an oligophage feeding on *Actaea spicata* (L.) here) are characteristic species. *Phytobia morio* Brischke, *P. lamii* Kaltenbach, *Phytomyza milii* Kaltenbach and *P. senecionis* Kaltenbach are also common in this habitat.

Only *Scaptomyza flaveola* Meigen which mines the leaves of *Dentaria glandulosa* Waldstein & Kitaibel occurs abundantly in the sycamore forest *Acereto-Fraxinetum*. *Phytomyza scolipendri* Goureau, the oligophage on *Polypodiaceae*, is a characteristic species and exhibits a high frequency of occurrence, as do *P. actaeae* and *Scaptomyza flaveola*. A total number of 17 species were observed here.

The community of leaf-mining insects of the oak-hornbeam forest, *Querceto-Carpinetum medioeuropaeum*, consists of the largest number of species which amounts to 77, including 7 species of *Lepidoptera*, 4 of *Hymenoptera* and 2 of *Coleoptera*. The remaining species are all *Diptera*. *Pegomya holosteae* Hering, *Coleophora solitariella* Zeller and *Phytomyza primulae* Goureau (montane species) are characteristic. A high frequency is exhibited by 11 species including *Pegomya holosteae* which lives on *Stellaria holostea* L.

The insect community under discussion is also very rich in the mixed forest *Pino-Quercetum* and amounts to 75 species, 61 of which belong to *Diptera*. *Agromyza pulla* Meigen (on *Genista tinctoria* L.), *Pego-*

mya nigrisquama (Stein) and *Leucoptera laburnella* (Stainton) are characteristic here.

From the zoogeographical standpoint in particular, interesting insect communities occur in the deciduous (oak and hornbeam) forest stands on gypsum eminences in the Nida Syncline where numerous xerothermic species have been observed in the herb layer, in clearings and particularly in Karst craters. The *Lepidoptera* community of oak forest stands consists of 70 species which may be supplemented by a further 262 species which occur in neighbouring biotopes. The following species are exclusive to this region: *Depressaria furvella* (Treitschke), *Cepphis advenaria* (Hübner), *Pararge aegeria tircis* (Butler) and *Eupithecia gratiosata* Herrich-Schäffer (Fig. 7.43). Furthermore, *Noctua fimbriata* (Schreber), *Xanthia gilvago* (D. & S.), *Agrochola circellaris* (Hufnagel) and *Ladoga camilla* (L.) are characteristic selective species, as is *Agrochola macilenta* (Hübner) in the hornbeam forest stand.

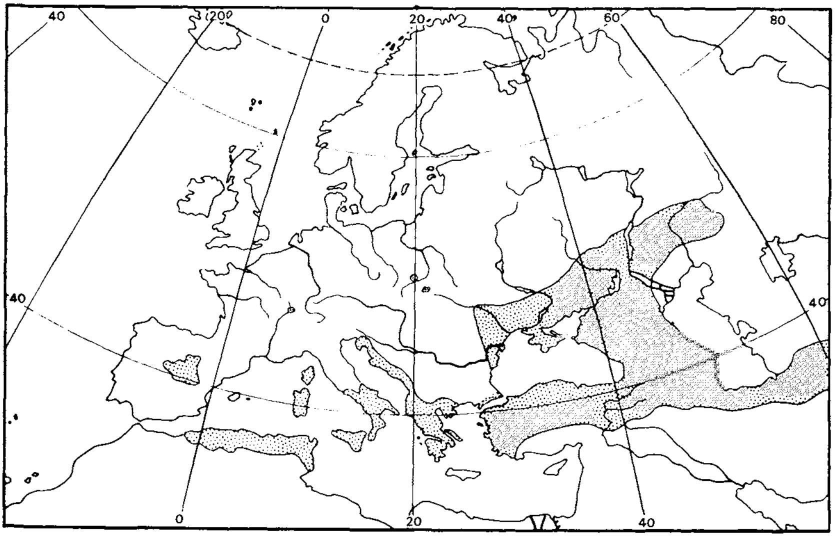


Fig. 7.43 Geographical distribution of *Eupithecia gratiosata* Herrich-Schäffer (after Kostrowicki, 1953)

Many species of *Lepidoptera* of southern origin occur on the borders of forest stands when the latter adjoin associations of steppe flora situated on slopes with a southern exposure. An example is *Depressaria furvella* which is a monophage of the shrub *Dictamus fraxinella* (Persoon), the habitat of which in the Grabowiec reservation near Pińczów exhibits a similar disjunctive character in respect to the forest-steppes of southern Europe to that of its phytophages. Representatives of the Euro-Caucasus faunistic area dominate here, constituting 64.8% of species. The relatively high contribution (for the conditions of central Europe, that is) of the ponto-Mediterranean element (3.6% of species occurring in oak and hornbeam forest stands) is particularly characteristic of the community of forest *Lepidoptera* under discussion. *Eupithecia gratiosata* is representative of this element (Fig. 7.43).

The majority of the 96 species of *Curculionidae* recorded on the Łódź Upland in the mixed forest and mixed coniferous forest sites occur in the rich herb layer, particularly in felling areas, compartment lines and on borders of the forest stands. The representatives of the genus *Apion* are most abundant (particularly *Apion dichroum* Bedel, as well as *A. viciae* (Paykull), *A. aethiops* (Herbst), *A. carduorum* Kirby, *A. laevigatum* (Paykull), *A. vicinum* Kirby, *A. haematodes* Kirby, *A. curtirostre* Germar, *A. trifolii* (L.), *A. virens* Herbst and *A. apricans* Herbst). Amongst the other genera of *Curculionidae* the following species have been observed: *Apion cerdo* Gerstaecker, *Rhinoncus castor* (F.), *Miarus campanulae* (L.), *Sibinia potentillae* Germar, *Sitona griseus* (F.), *S. hispidulus* (F.), *S. lepidus* Gyllenhal, *S. sulcifrons* (Thunberg), *S. lineatus* L., *S. suturalis* Stephens, *S. macularius* (Marsham), *Hypera postica* (Gyllenhal), *H. nigrirostris* (F.), *H. meles* (F.), *H. arator* (L.) and *Tychius venustus* (F.). Many of these curculionids live on *Papilionaceae* and occur on the broom. They are most abundant on intensively insolated sites. *Apion fuscirostre* (F.), *Sitona striatellus* Gyllenhal and *Polydrosus confluens* Stephens are characteristic of this plant.

Many other phytophages and their parasites are associated with the forest herb layer of the habitat under discussion. For instance parasites of *Cecidomyiidae* feeding on herbaceous plants and, less frequently, on the pine are amongst the most abundant chalcids. These include *Tetrastichus charoba* (Walker) and *T. pausiris* (Walker) from the family *Eulophidae*.

With the growth of plantations and the limitation of the herb layer, the contribution of *Eulophidae* to the community of chalcids, as well as the abundance of the individuals of these insects, diminishes in the herb layer in favour of the entomofauna of tree crowns in which *Pteromalidae* prevail (Szczepański, 1968).

Entomofauna of the forest litter and soil. A community of ants occurs in the association *Pino-Vaccinietum myrtilli* of the reservation Bukowa

Góra in the Roztocze Upland. *Lasius niger* (L.) dominates here on intensively illuminated sites. The density of the nests of this species occurring in deeper layers of the litter and in decomposed stumps exceeds 1 per 1 m^2. *Myrmica sabuleti* Meinert, *M. schencki* Emery, *M. scabrinodis* Nylander, *Leptothorax acervorum* (F.), *L. corticalis* (Schenck) and *Lasius alienus* (Forster) occur abundantly. The abundance of nests of *Formica sanguinea* Latreille is higher on shaded sites.

Myrmica laevinodis Nylander is most abundant in the association *Abietetum polonicum* where the forest floor is shaded. It builds nests in the litter under decaying pieces of wood and in decaying stumps, as well as in piles of sand and humus in tufts of *Polytrichum*. The density of these nests amounts to 3–4 per 1 m^2. *Lasius flavus* (F.), *L. fuliginosus* (Latreille), *L. brunneus* (Latreille), and *M. rubra* (L.) are less abundant here.

Lasius umbratus (Nylander), *Myrmica laevinodis* Nylander, *M. rubra* other species occur in the association *Fagetum carpaticum* where the forest grows on calcareous rubble. Among the 29 species of ants observed in this reservation, particularly on its borders, there are also thermophilous species of southern origin such as *Leptothorax corticalis*, *Camponotus fallax* (Nylander) and *Lasius affinis* (Schenck), which give the local myrmecofauna a rather specific character (Pętal, 1961).

Epigeic insects were also studied in the Nida Syncline. *Pterostichus oblongopunctatus* (F.) and *Harpalus latus* (L.) predominate, whereas *Carabus arcensis* Herbst, *C. nemoralis* Müller, *C. linnei* Panzer, *Abax ovalis* (Duftschmid), *Pterostichus burmeisteri* Heer and *Harpalus laevicollis* (Duftschmid) are subdominant species in the community of *Carabidae* in habitats of mixed forest (Nunberg, 1949). The occurrence of *Carabus linnei* is a characteristic feature of the region under discussion in which it inhabits eminences overgrown with deciduous and mixed forest, particularly in the vicinity of water courses. *Notiophilus aquaticus* (L.), *Amara aenea* (De Geer) and *Calathus erratus* (Sahlberg) dominate among the 69 species of the ecotonic community of *Carabidae* of pine forests on the borders of older forest stands and 1 year-old plantations (Karczewski, 1961a).

Philonthus laevicollis (Lacordaire) is an abundantly occurring characteristic species of the staphylinid community of deciduous forest litter in the Nida Syncline.

The high contribution of *Pterostichus aethiops* (Panzer), *Abax carinatus* (Duftschmid) and *Carabus linnei* is characteristic of the carabid community of the southern part of the Lublin Upland (Table 7.6).

Carabus auronitens F., *Pterostichus oblongopunctatus*, *Othius myrmecophilus* Kiesenwetter and *Philonthus cognatus* Stephens are among the most abundant epigeic insects in the litter of forest habitats of the Łódź Upland.

Table 7.6 Ecological characteristics of litter *Carabidae* in various habitat forest types on the Lublin Highland (tabulated according to Szyszko, 1972).

Species	Habitat forest type				
	Fresh forest		Fresh mixed coniferous forest /Fresh coniferous forest		Fresh coniferous forest
	Presence of deciduous undergrowth				
	−	+	+	−	+
Pterostichus niger (Schaller)	D	D			
Pterostichus aethiops (Panzer)			S	D	D
Pterostichus oblongopunctatus (F.)	S	S	D		
Abax carinatus (Duftschmid)	S				
Agonum assimile (Paykull)		S			
Pterostichus vulgaris L.		S			
Carabus violaceus L.			S		
Carabus linnei Panzer	S	S			
Carabus hortensis L.			S		
Number of attendant species	29	25	13	19	16
Contribution of individuals of spring species	28.8	36.9	63.8	94.1	94.3
Contribution of individuals of autumn species	72.3	63.1	36.2	5.9	5.3
Individuals of large zoophages, %	61.1	57.7	39.3	6.9	4.2
Individuals of small zoophages, %	32.8	38.8	60.0	93.0	95.7
Individuals of hemizoophages, %	6.1	3.5	0.7	0.1	0.1

D – dominant, S – subdominant species of *Carabidae* community.

Carabus problematicus Herbst, *C. convexus* F. and *Abax carinatus*, which are characteristic of this region, are also found here, as is the montane species, *Tachinus elongatus* Gyllenhal. The communities of soil insects requires further studies.

V. Region of Świętokrzyskie Mountains

The region of the Świętokrzyskie Mountains includes the oldest and highest part of the Świętokrzyski Region. The forests of the main range of the Świętokrzyskie Mountains stretch from Łysica Mt (611 m a.s.l.) in the north-west to Święty Krzyż Mt (598 m a.s.l.) in the south-east. These forests are typical of the lower mountain region with fir and beech dominating and with characteristic areas of barren land (fields of quartzite boulders). Pine forests, mixed oak forests and larch forest stands occur in the valleys and on the lower slopes. The two-layer, mountain forest character of the flora of the Świętokrzyskie Mountains very distinctly differentiates this area from the neighbouring regions, this also being reflected in the composition of the forest entomofauna which includes numerous montane and boreo montane species which mostly occur in the main mountain range. Fir forest stands (*Abietum polonicum*) as well as fir-beech forest stands (a poor variation of *Fagetum carpaticum*) occur here. The fir grows here at the borders of its range and therefore is characterized by a high susceptibility. It develops against the background of the meteorological anomaly, particularly the high summer and very low winter temperatures.

Entomofauna of the forest tree layer. The fir forest stands, particularly those growing at lower altitudes, have been subjected to outbreaks of *Choristoneura murinana* (Hübner), *Zeiraphera rufimitrana* (Herrich–Schäffer), *Pityokteines* spp. and *Pissodes piceae* (Illiger) for at least a century. Old fir dying due to secondary invasion by the association of xylophages consisting of *Pityokteines curvidens* (Germar), *P. spinidens* (Reitter), *P. vorontzovi* (Jacobson), *Cryphalus piceae* (Ratzeburg), *Pissodes piceae*, *Serropalpus barbatus* (Schaller), *Hylecoetus dermestoides* (L.), *Urocerus augur* (Klug) and *U. fantoma* (F.), as well as by the species specific for this region – *Acanthocinus reticulatus* (Razoumowsky), are subsequently inhabited by communities of predators and sub-bark saprophages. *Phloeonomus pusillus* (Gravenhorst) dominates among them, its individuals constituting 75% of the entire community of *Coleoptera. Rhizophagus dispar* (Paykull), *Leptusa fumida* (Erichson), *Paromalus parellelepipedus* (Herbst) and *Zeteotomus brevicornis* (Erichson) are subdominant species of this community. The boreo-montane species *Phloeonomus monilicornis* (Gyllenhal), as well as primeval-forest elements such as *Pachygluta ruficollis* (Erichson), *Acrulia inflata* (Gyllenhal) and *Cyphaea curtula* (Erichson) should be distinguished among the

30 additional species of this community (Kołkowski, 1973). The subpontic species *Zeteotomus brevicornis*, the predator of *Pityokteines curvidens*, is particularly noteworthy since in Poland it is known only from this region and virtually only from fir and mixed forest stands at lower altitudes in the Świętokrzyski National Park. In central Europe this species is dying out (Szujecki, 1973).

Communities of insects on dead trees both standing and lying are equally rich in species and are very interesting from the faunistic standpoint. Otherwise rare *Coleoptera* such as *Thymalus limbatus* (F.), *Colydium elongatum* (F.), *Rhinosimus ruficollis* (L.), *Triphyllus bicolor* (F.) are observed under the detached bark of old broken trees overgrown with the fruiting bodies of *Polypores*. Fruiting bodies of these fungi on beaches and sycamores support such species as *Bolitochara lucida* (Gravenhorst), *Ostoma ferrugineum* (L.), *Peltis grossa* (L.), *Endomychus coccineus* (L.), *Diaperis boleti* (L.), *Bolitophagus reticulatus* (L.), *Mycetina cruciata* (Schaller) and numerous species of the genus *Cis*.

Rosalia alpina (L.) (one of the most rarely observed insects here) as well as *Hedobia imperialis* (L., (*Ptilinus pectinicornis* (L.) and *Sinodendron cylindricum* (L.) (Fig. 7.44) live in the wood of dead beeches.

Larvae of *Ceruchus chrysomelinus* (Hochenwarth) occur in large numbers in fallen fir logs infected by brown rot. *Atrecus affinis* (Paykull),

Fig. 7.44 Sinodendron cylindricum (L.), female and male (photo by S. Kinelski

the boreo-montane *A. longiceps* (Fauvel), *A. pilicornis* (Paykull), *Ampedus erythrogonus* (Müller) and other *Coleoptera* with a wider range such as *Quedius maurus* (Sahlberg), *Q. xanthopus* Erichson, *Sepedophilis testaceus* (F.), *S. bipustulatus* (Gravenhorst) and *Dryophthorus corticalis* (Paykull) belong to characteristic elements of the entomofauna of the Świętokrzyskie Mountains, occurring in humid stumps and fallen trunks of firs during the initial stages of the development of xylophylous fungi (Szujecki, 1958).

Various insect species which are predatory during the vegetation season in fir crowns hibernate under the detached bark on fir buts, particularly on the borders of forest stands. They include such species as the ladybirds *Myrrha octodecimguttata* (L.) and *Aphidecta obliterata* (L.), as well as the carabid *Dromius fenestratus* (F.).

Forests growing on slopes in the lower parts of the Świętokrzyskie Mountains and in valleys include a considerable proportion of oak and pines. Oak and oak-hornbeam-linden forests also occur here but their entomofauna is very poorly known. *Lucanus cervus* (L.) and *Xylopsoeus* (= *Bostrychus*) *capucinus* (F.) occur here in the wood of old oaks, whereas the rare curculionid *Gasterocerus depressirostris* F. is observed between the wood and bark and in the surface layer of wood. The boreo-montane beetle *Boros schneideri* (Panzer), known from only a few localities in Poland, and the predatory *Tillus elogatus* (L.) were also observed under the bark. Relatively large numbers of the larvae of *Osmoderma eremita* (Scopoli) develop in oak mould, and *Nosodendron fasciculare* (Olivier) also occurs on this tree in the sap flowing from wounded trunks.

A total of 87 insect species has been recorded as being associated with the larch in the Świętokrzyskie Mountains, some of them are known only from this region (Karpiński, 1963, 1967).

Entomofauna of the forest undergrowth and herb layer. *Chrysomelidae* and *Curculionidae* are particularly abundant on the flora of mid-forest meadows and on shrubs. The following chrysomelids are distinguished by their high abundance: *Cryptocephalus vittatus* (F.), *C. moraei* (L.), *Chrysolina polita* (L.) as well as *Gonioctena viminalis* (L.), *Cryptocephalus decemmaculatus* (L.) and *Gynandrophthalma cyanea* (F.) living on willows. A total of 163 *Curculionidae* species was recorded in the Świętokrzyski National Park (Gotwald, 1968). *Judolia cerambyciformis* (Schrank), *Anoplodera maculicornis* (De Geer), *A. sanguinolenta* (L.) and *Strangalia attenuata* (L.) among the *Cerambycidae*, as well as *Ctenicera* *pectinicornis* (L.) among the *Elateridae* are most frequently observed on the flowers of *Umbelliferae* in forest meadows. *Anthaxia morio* (F.) occurs frequently on flowers of plants belonging to the *Compositae* family (Szujecki, 1958).

Entomofauna of the forest litter and soil. The litter and soil insects have not been studied in the Świętokrzyskie Mountains from the standpoint of the relative quantitative proportions of species. It is known, however, that many *Coleoptera* of this environment belong to the montane and boreo-montane elements (*Leistus piceus* Frölich, *Amara erratica* (Duftschmid), *Pterostichus burmeisteri* Heer, *Timarcha metallica* (Laicharting), *Plinthus tischeri* Germar). *Carabus linnei* Panzer, *C. auronitens* F. and *C. intricatus* F. are most abundant here.

VI. Silesia Region

The Silesia Region lies within the climate range of submontane lowlands and valleys. All of the principal forest tree species occur here and depending on the local conditions, they may develop in various types of forest. Pure beech forests or beech forests with an admixture of oak and fir grow on fertile soils. At higher altitudes in the southern part of the region, the forest-forming role of the spruce increases and the larch becomes more abundant. The pine prevails in the coniferous forests of Lower Silesia. Forest stands consisting of many tree species, as well as lowland forests, occur in river valleys on fertile alluvial and silt-peat soils.

The wide habitat variability of the Silesia Region, together with the very significant influence of anthropogenous factors and oscillations in the ground water levels, favours the development of the susceptibility of forest stands to noxious forest insects. The Lower Silesia Coniferous Forests as well as the Bolesławiec Forest which are subjected to intensive outbreaks of *Dendrolimus pini* (L.), *Panolis flammea* (D. & S.), *Bupalus piniarius* (L.) and *Lymantria monacha* (L.) are particularly impended. *Acantholyda posticalis* Matsumura has occurred in large numbers under various site conditions for several decades in the Opole Valley. *Lymantria monacha* also appears here.

Under the conditions discussed the feeding of phytophages invariably renders the area marshy and brings about the occurrence of secondary pests, among which *Phaenops cyanea* (F.) causes the greatest damage. *Acantholyda posticalis* and *Lymantria monacha* occur in large numbers in the Upper Silesia Industrial District where pests of pine plantations and thickets also become dangerous due to the air pollution from industrial plants.

The composition of the entomofauna of the Silesia Region is very well known and is perhaps the best known in Europe. On the other hand, information on the communities of forest insects here is very scanty.

Fig. 7.45 Platystomus albinus (L.) (photo by W. Strojny)

Just as in the Baltic Region the xylophages *Hylecoetus dermestoides* (L.) and *Ptilinus pectinicornis* (L.) are most abundant in beech forest stands here. The following species are also abundant: *Xestobium plumbeum* (Illiger), *Ernopocerus fagi* (F.), *Taphrorychus bicolor* (Herbst), *Leiopus nebulosus* (L.) and *Rhagium mordax* (De Geer). *Cerambyx scopolii* Fuessly, *Platystomus albinus* (L.) (Fig. 7.45) and *Tomoxia biguttata* Gyllenhal also occur locally. The cerambycid *Callimellus angustatum* (Schrank) has its only site of occurrence in the forest district Henryków. *Rosalia alpina* (L.) also used to be found in the Silesia Region before 1900 (Fig. 7.46).

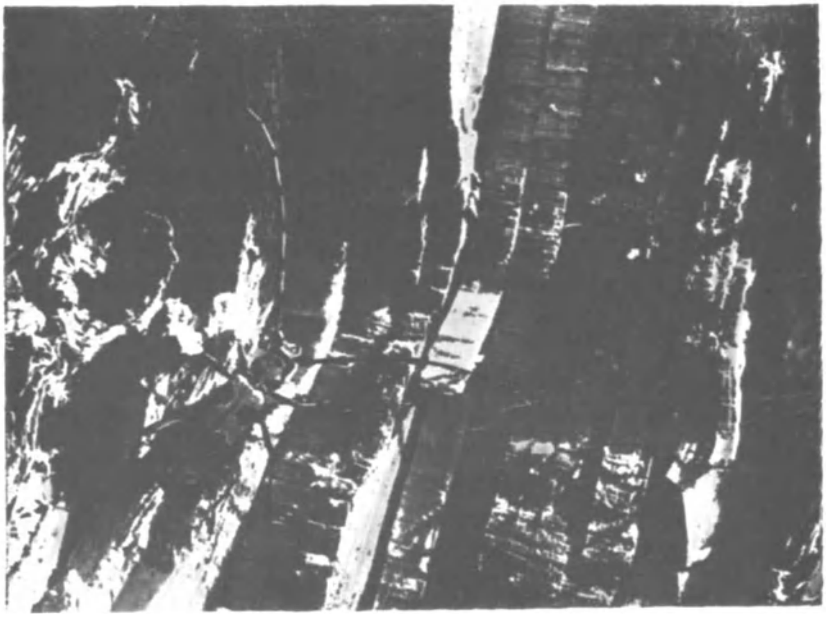


Fig. 7.46 Rosalia alpina (L.) (photo by W. Strojny)

Ichneumons belonging to the subfamilies *Ichneumoninae*, *Banchinae*, *Ophioninae*, *Anomalinae* and *Ephialtinae* occur within beech forest stands while *Tryphoninae* and *Gelinae* are concentrated on the borders. *Poemia collaris* (Haupt), *Ichneumon sulphuratus* Kriechbaumer, *Agrothereutes aterrimus* (Gravenhorst) and *Trychosis legator* (Thunberg) are ichneumons rarely observed in Poland but which have been recorded in the beech forest of the reservation Muszkowice Beech Forest (Fig. 7.47) (Kościelska, 1971). The occurrence of 55 species of *Chrysomelidae* was also established here. They belong to three ecological groups.

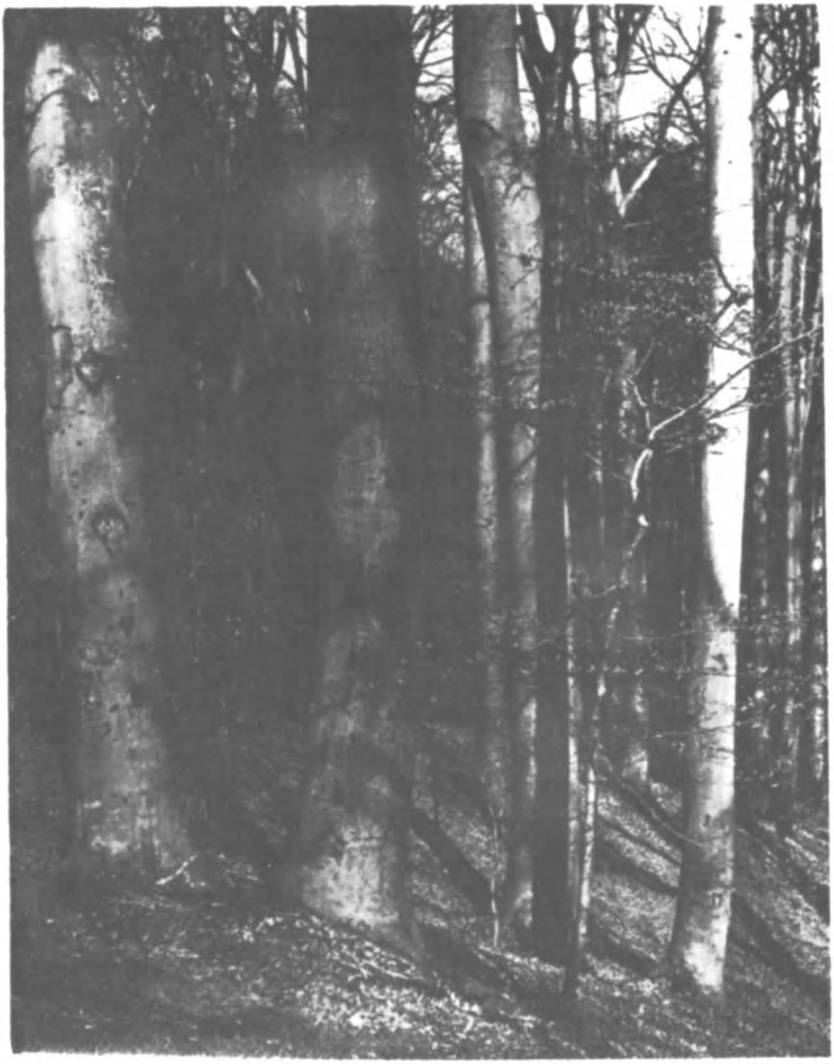


Fig. 7.47 Reservation "Muszkowice Beech Forest" (photo by W. Strojny)

The first group includes species associated with the flora of humid meadows and the borders of water bodies entering into the peripheral zones of beech forests along water courses. The second group consists of species characteristic of anthropogenous environments. The third group consists of forest species associated with thermophilous plants. These include the exclusive forest species *Oomorphus concolor* (Sturm), *Chrysolina oricalcia* (Müller) and *Hermaeophaga mercurialis* (F.), and also selective forest species such as *Lilioceris merdigera* (L.), *Galerucella lineola* (F.), *Longitarsus kutscherae* (Rye), *Haltica brevicollis* (Foudras), *Batophila rubi* (Paykull) and *Psylliodes dulcamarae* (Koch) (Warchałowski, 1974). The great amount of shade in the beech forests limits the occurrence of *Orthoptera* although they invade the intensively insolated neighbouring areas in large numbers (Bednarz, 1971).

Detailed studies have been performed on the nests of *Formica rufa* L. in the Niemodlin Coniferous Forests (Wiśniewski, 1969a, b) where it was found that this ant invades seven of the eleven types of forest habitats occurring here. This species is most abundant in humid mixed coniferous forest, as well as in fresh coniferous forest in spruce forest stands where there is one ant-hill about every 18 ha. Its abundance is somewhat lower in pine forests (1 ant-hill per 23 ha). Deciduous forest stands, particularly those with a high contribution of the birch, are also less abundantly inhabited by these ants. Furthermore it has been established that *Formica polyctena* Forster occurs more frequently in the interior of forest stands than does *F. rufa.*

VII. Sudeten Region

The Sudeten Region consists of a number of mountain ranges of extremely diverse geological structure and montane climate which differentiate the layer system of plant associations and entomocenoses.

Alpine spruce forests prevail in the upper zone whereas the spruce, beech, and fir dominate in the lower zone. *Cephalcia abietis* (L.) is a specific foliophage of the spruce here. The oak is one of the characteristic trees of the foot-hills (below 400 m a.s.l.).

The forests of the Sudeten Region differ widely as regards their specific composition from their primeval natural character and this negatively influences their health condition, especially since the present forest stands have been grown from seeds of unknown origin.

The spruce forests are susceptible to winds, storms and snow accumulation on the branches which leads to the occurrence of outbreaks of secondary pests, particularly those of *Ips typographus* (L.) and *Ips amitinus* (Eichhoff) (Fig. 7.48). Forest stands growing at lower altitudes and subjected to industrial air pollution are invaded by large numbers of *Pissodes harcyniae* (Herbst).

Fig. 7.48 Focus of *Ips typographus* (L.) in the Sudeten spruce forest (from the collection of the Institute of Forest and Wood Protection, Agricultural University of Warsaw)

The distribution of bark-beetles in this region is closely linked with the layered structure of the vegetation (Fig. 7.49).

The occurrence of 40 species of ants has been recorded, among which 21 were observed in the upper zone and 12 in the lower zone. These are almost exclusively boreo-montane and north-palaearctic species. The altitude limit for *Formica pratensis* Retzius, *F. rufa* L., *F. polyctena* Forster is confined to the lower zone. The richest ant communities occur in the Sudeten plateau and consist of 32 species occurring in both forest and non-forest environments. Dendrophilous species (Fig. 7.50) such as *Camponotus fallax* (Nylander), *Lasius fuliginosus* (Latreille) and *L. umbratus* (Nylander) occur here (Banert & Pisarski, 1972). About 90 accessory insect species occur in the ant-hills of *Camponotus herculeanus* (L.) and *C. lingiperda* (Latreille). Otherwise than in ant-hills of other ant genera no typical myrmecophils were observed here. *Collembola*, the species of which constitute 45% of all the insects, occur most fre-

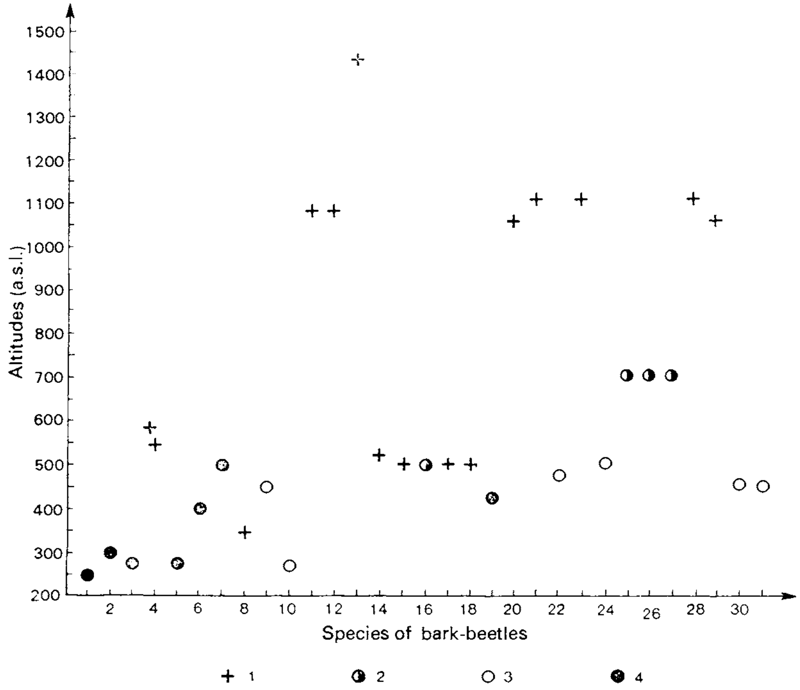


Fig. 7.49 Vertical distribution of bark-beetles in the Sudeten Mts (after Michalski, 1957): 1 – spruce bark-beetles, 2 – fir bark-beetles, 3 – pine bark-beetles, 4 – bark-bettles of deciduous trees

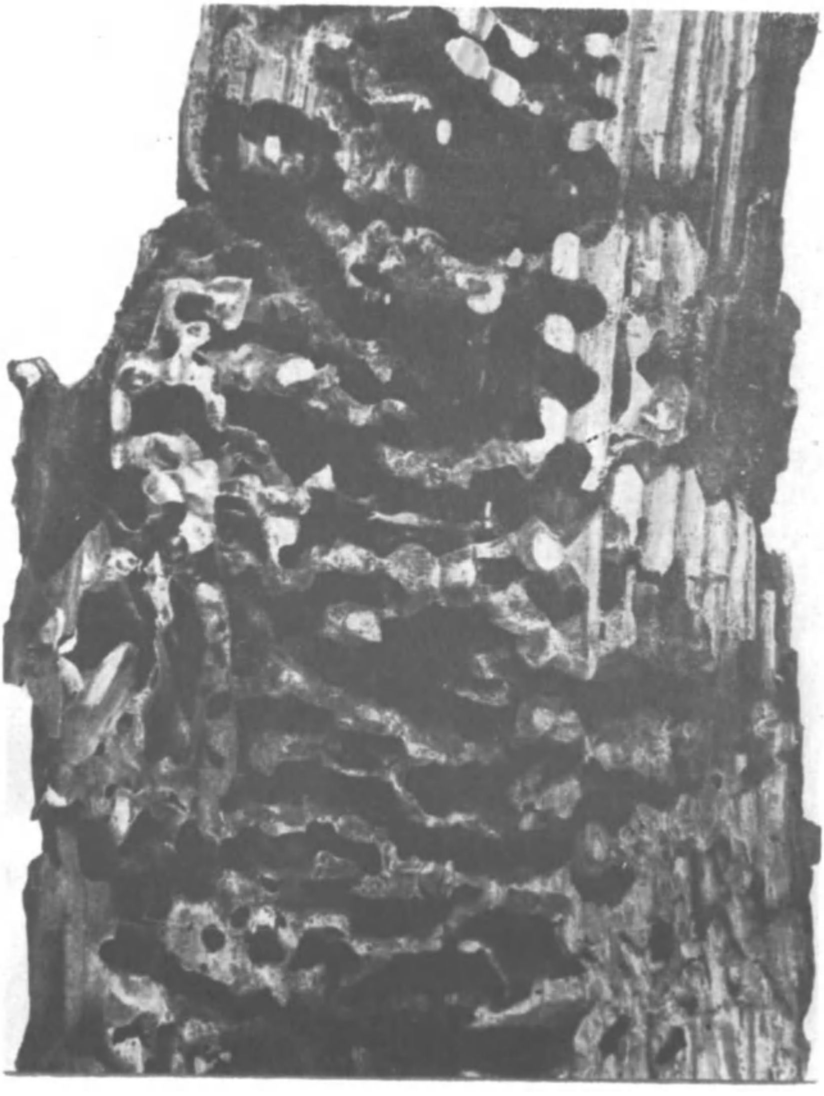


Fig. 7.50 Cross-section through a nest of *Camponotus herculeanus* (L.) (photo by W. Strojny)

quently in the nests of *Camponotus* spp. The most abundant species are: *Tomocerus minutus* (Tullberg), *Heteromurus nitidus* (Templeton, *Entomobrya myrmecophila* Reuter, *E. corticalis* (Nicolet) and *E. multifasciata* (Tullberg). *Coleoptera* constitute 28% of all species, of which *Ptenidium* spp., *Ptinella aptera* (Guérin-Méneville) and *Euplectus karsteni* (Reichenbach) are particularly abundant. The relative abundance of *Diptera* belonging to the family *Phoridae* is also worthy of note (Nawrot & Wiśniewski, 1970).

The abundance of montane species of the genus *Trechus* is a distinctive feature in the taxocenosis of litter *Coleoptera*. *Trechus pulchellus* Putzeys, which generally occurs in beech and sycamore litter, is a characteristic species of the lower zone as well as part of the upper zone (up to 1000 m a.s.l.). Locally it is accompanied by *T. pilisensis sudeticus* Pawłowski. *T. striatulus* Putzeys predominates in the Karkonosze Mts in the higher spruce forests, in the dwarf mountain pine range and in the alpine zone. *T. pulchellus* and *T. pilisensis sudeticus* are abundant in the beech forests of the lower zone, as well as in clusters of sycamores or other deciduous trees in spruce forest stands of the upper zone of the Śnieżnik Kłodzki massif where the forests are less deformed by human management. The Sudeten plateau is distinguished by the presence of *T. amplicollis* Fairmaire (Pawłowski, 1975).

VIII. Carpathian Region

The Carpathian Region includes the Carpathians and the Subcarpathians and is widely differentiated from the physiographic point of view. The following five zones are distinguished here: the zone of the Carpathian plateau (with forest stands consisting of pines and oaks as well as beeches and firs); the zone of the Silesian and High Beskid (with beech forests or fir-beech forests in the lower zone and spruce forests in the upper zone); the zone of the Island and Low Beskid, including the Bieszczady Mts (with beech forests with an admixture of spruces, firs and sycamores in the lower zone and spruce forest stands at higher altitudes); the zone of Podhale foot-hills (with spruce or pine forests), and the zone of the Tatra Mts with distinct mountain forest zones.

Ips typographus (L.) and its attendant species play the most important role in the health condition of spruce forests of the region under discussion. In the Beskidy and Gorce Mts this bark-beetle is particularly abundant in spruce forests artificially introduced into the lower zone and attacked by *Armillariella mellea* (Vahl ex Fries) P. Karsten and windbreaks. The same factors also stimulate intensive outbreaks of this beetle in the Tatra and Bieszczady Mts. Secondary pests of the fir also play an important role throughout the entire region.

Knowledge relating to individual insect communities of the Carpathian Region varies widely. Ecological data obtained from the Tatra Mts are particularly deficient although the general list of insects occurring here is somewhat more detailed as a result of numerous faunistic studies. This is also true for the zone of the Carpathian plateau, particularly its eastern part. However, there have been no studies performed on the insect communities of the forests of the Podhale foothills.

The characteristics of forest insect communities of the Carpathian Region will therefore be discussed with respect to the Babia Góra Mt and Bieszczady Mts. The works of Pawłowski (1967, 1975) concerning the *Coleoptera* of the Babia Góra Mt are particularly noteworthy in this respect.

Cantharis pallida Goeze and *Anoplus roboris* Suffrian are characteristic species of the tree crown layer, whereas *Mantura rustica* (L.) and *Scleropterus serratus* (Germar) are characteristic of the herb layer in the association *Alnetum incanae.* The community of litter beetles is characterized by *Anthobium atrocephalum* (Gyllenhal) and *Tachinus corticinus* Gravenhorst. In general, the beetle community of *Alnetum incanae* is relatively poor and consists of only 62 species. Representatives of the zoogeographical European (23%), Eurosiberian (21%) and Palaearctic (19%) elements dominate here.

Polydrosus tereticollis (De Geer), *Cychramus variegatus* (Herbst), *C. luteus* (F.), *Platycerus caprea* (De Geer), *Hylecoetus dermestoides* (L.), *Absidia schoenherii* (Dejean), *Rhizophagus dispar* (Paykull) and *Trypodendron lineatum* (Olivier) are characteristic species of the community of *Coleoptera* of tree crowns (layer of trees and shrubs) in *Fagetum carpaticum.* A total of 98 species was recorded here, i.e. more than all those found in *Alnetum incanae.*

Among the 105 species occurring in the herb layer 18 characteristic ones were distinguished, among the most important of which are *Meligethes atratus* (Olivier), *Anaspis rufilabris* (Gyllenhal), *Molorchus minor* (L.), *Anoplodera sangvinolenta* (L.), *Hypera oxalidis ovalis* (Bohemann), *Liparus glabrirostris* Küster and *Judolia cerambyciformis* (Schrank).

Pterostichus foveolatus (Duftschmid), *P. burmeisteri* Heer, *P. oblongopunctatus* (F.), *Trechus pulchellus* Putzeys, *Tachinus laticollis* Gravenhorst), *Quedius paradisianus* Heer and *Philonthus decorus* (Gravenhorst) dominate in the litter environment among the 146 species of the forest floor layer.

Cis jacquemarti Mellié and *Agathidium badium* Erichson are characteristic species invading decomposing logs and stumps.

Representative of the zoogeographical Eurosiberian element (20%)

prevail in this beech forest, while montane species constitute 17%, Palaearctic species 16% and European species 15%.

In the mixed coniferous forest of the lower mountain zone (*Abieto-Piceetum montanum*) the characteristic species of the layer of trees and shrubs are *Pissodes piceae* Illiger, *Pityophthorus pityographus* (Ratzeburg), *Pityogenes chalcographus* (L.) and *Crypturgus pusillus* (Gyllenhal). A total of 66 other species was observed here.

The herb layer is characterized by staphylinids which live in the fruiting bodies of fungi such as *Oxypoda alternans* (Gravenhorst), *Lordithion lunulatus* (L.), *L. trinotatus* (Erichson) and 47 other species occur here.

Only one species – *Phlectophloeus fischeri* (Aubé) has been distinguished in the forest floor layer as characteristic, although 77 other species were also observed here.

The *Coleoptera* community of mixed coniferous forest consists of only 50% of the number of species found in *Fagetum carpaticum* of the lower mountain zone. Eurosiberian elements constitute 23% of the entomofauna, montane species 19%, Holarctic species 15%, Palaearctic species 14% and European species 11%.

The layer of trees and shrubs of the Carpathian spruce forest, *Piceetum excelsae carpaticum*, is characterized by *Dryocoetes hectographus* Reitter amongst the 39 species observed here. Only a single species, *Rhytidosoma fallax* (Otto) characterizes the herb layer and occurs with 35 other species. No species characteristic of the forest floor were distinguished, although *Catops picipes* (F.), *Hapalaraea linearis* (Zetterstedt), *Bryoporus rufus* (Erichson) and *Notaris aterrimus* Hampe are rare but exclusive here. A further 44 other species were recorded.

Pterostichus unctulatus (Duftschmid), *Carabus linnei* Panzer, *Quedius cincticollis* Kraatz, *Calathus metallicus* Dejean and *Trechus striatulus* Putzeys dominate on the forest floor. *Trechus cardioderus* Putzeys as well as representatives of the genus *Philonthus* are absent here. A total of 44 species was observed in the forest floor layer.

Species representing the montane element in the *Coleoptera* community constitute 29% and those of the Palaearctic, European and boreomontane element 12%.

Thus, it appears that in the successive zones of the forest flora – beech forest, mixed coniferous forest of the lower mountain zone, spruce forest of the upper mountain zone – the *Coleoptera* community consists of progressively fewer species. The ratio of the number of species in the individual three mountain environments (assuming the number of species in the beech forest to be 100) is 100:67:40 in the layer of trees and shrubs, 100:44:34 in the herb layer and 100:48:28 in the forest floor layer. This indicates that the fauna of the forest floor is the most deplete. Analogously, the number of *Coleoptera* species (Fig. 7.51), particularly that of non-forest species, decreases with increasing altitude (Table 7.7).

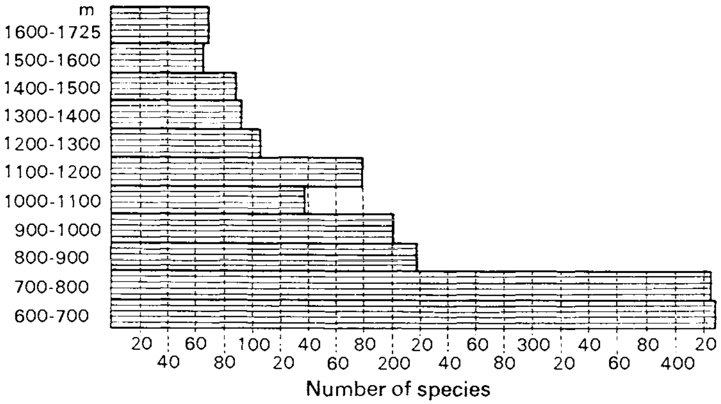


Fig. 7.51 Number of *Coleoptera* species observed on Babia Góra Mt in successive altitude zones (original after Pawłowski, 1967)

Thickets of the dwarf mountain pine, *Mughetum carpaticum* support 92 species of *Coleoptera. Pityogenes alpinus* Eggers is characteristic of the tree crown layer, *Luperus viridipennis* Germar of the herb layer and *Quedius obscuripennis* Bernhauer of the forest floor layer. The montane and boreo-montane elements constitute 41 and 13% respectively.

Table 7.7 Species of non-forest *Coleoptera* in forest zones of the northern slope of Babia Góra Mt (after Pawłowski, 1967).

Altitude (m a.s.l.)	Number of forest and eurytopic species	Number of non-forest species
1200–1300	92	14
1100–1200	143	36
1000–1100	109	29
900–1000	183	18
800–900	187	30
700–800	249	176
600–700	244	184

The *Coleoptera* community of the dwarf mountain pine more closely resembles that of the Carpathian spruce forest than that of alpine environments, i.e. of rubble and ledges as well as alpine grassland.

The communities of aphids of the Babia Góra Mt, like those of other northern Carpathian slopes, are particularly poor. Only 145 species of these insects have been recorded in forest and non-forest environments here and their number decreases with increasing altitude. Lowland and boreal-montane species prevail in the richest zone of the plateau. Relatively more species also occur in the lower mountain zone where, along with lowland and boreo-montane species, typical montane aphids also occur, such as *Cinara confinis* Koch, *C. stoyani* Pasek (dominating species of the genus *Cinara* living on the spruce), *Macrosiphum prenanthidis* Börner, *M. oredonenses* Remaudière (on *Lonicera nigra*), *M. funestum* (Macchiati) (on bramble), *Sitobion dryopteridis* (Holman) (on *Dryopteris austriaca*) and *Amphorophora ampullata* Buckton (on *Athyrium felix femina* and *Dryopteris austriaca*). *Adelges* (*Sacciphantes*) *viridis* (Ratzeburg), the two-host species migrating from the spruce to the larch, is rare while *Mindarus abietinus* Koch which is associated with the fir is abundant.

The number of tree aphid species distinctly decreases in the upper mountain zone. Lower-zone elements prevail here and, near the upper border of this zone in the Carpathian spruce forest, alpine species dominate which penetrate to lower altitudes but only along streams. *Adelges tardus* Dreyfuss, a species spreading in the lower mountain zone and on the plateau, is associated with the spruce here. Alpine species such as *Eulachnus alticola* Börner (on the dwarf mountain pine), *Aphis veratri* (Walker) and *Delphiniobium junackianum* (Karsch) characterize the dwarf mountain pine zone. *Dysaphis sorbi* (Kaltenbach) which causes a deformation of the mountain ash is particularly abundant in both mountain zones and on the plateau (Szelęgiewicz, 1972).

The entomocenoses of the Western Bieszczady Mts are the best known in the zone of the Island Beskid and High Beskid Mts as a result of the intensive faunistic studies carried out in the recent 20 years (Bałazy & Michalski, 1964a, b; Szujecki, 1970; Śliwiński & Lessaer, 1970; Bańkowska, 1971a, b, c; Bazyluk, 1971; Bielawski, 1971; Burakowski, 1971; Draber-Mońko, 1971; Kieych, 1971; Klimaszewski, 1971; Mikołajczyk, 1971; Parapura & Pisarski, 1971; Pisarski, 1971; Bielewicz, 1973; Pawłowski, 1975).

The insect community in the Bieszczady Mts exhibits a differentiation of the specific composition and abundance in the system of alpine zones and the associated floristic systems typical for mountains. The plateau zone may be distinguished here and includes mixed forests, oak-hornbeam-linden forests and grey alder brush. The lower mountain zone with beech or beech-fir forest stands is also worthy of note. The upper mountain forest zone is absent in the Bieszczady Mts, mountain pastures with patches of green alder brush extending above the belt of beech forests. Spruce forest stands occur here in the lower mountain zone. They are mostly of an artificial nature, although spruce stands also grow in natural sites at 800 m a.s.l.

The mixed forests of the plateau of the Bieszczady Mts exhibit the highest number of species of *Lepidoptera* which mainly occur on forest borders, in felling areas and in plantations. The dendrophilous forms of *Erannis defoliaria* (Clerck), *Biston betularia* (L.), *Pheosia tremula* (Clerck), *Gastropacha populifolia* (Esper), *Apatura ilia* (D. & S.), *Limenitis populi* (L.), *Lamellocossus terebra* (D. & S.) and *Synanthedon cephiformis* (Oschenheimer) are species typical of this environment. They are mainly species associated with the pioneer stages in the succession of the forest in which the aspen and willows prevail. Species typical of the herb layer such as *Deilephila elpenor* (L.) also occur here. Dendrophilous forms also prevail amongst ladybirds. *Scymnus nigrinus* Kugelann is the species characteristic of the pine, *Aphidecta obliterata* (L.) that of the spruce and *Calvia decemguttata* (L.) that of hazel. Typical lowland soil forms such as *Athous subfuscus* (Müller) and *Dalopius marginatus* (L.), as well as the piedmont species *Denticollis linearis* (L.), are distinguishable in the community of *Elateridae.*

Photophilous ants, *Orthoptera* and *Diptera* of the family *Syrphidae* are virtually absent here.

The following *Lepidoptera* associated with the oak occur in the fragments of oak-linden-hornbeam forest in the northern part of this zone. They are *Dichonia aprilina* (L.), *Moma alpium* (Osbeck), *Catocala sponsa* (L.), *C. promissa* (D. & S.) and *Catephia alchymista* (D. & S.). The number of species of ladybirds is relatively low but includes *Calvia quattourdecimpunctata* (L.) and *C. quattuordecimguttata* (L.). The high compactness of tree crowns causes intensive shading of the forest floor and in consequence confines the entomofauna of this environment to typical shade-seeking forest species. On the other hand, *Diptera* of the family *Mycetophilidae* are numerous. *Boletina basalis* (Meigen) is a specific representative here. An East-Carpathian beetle of the family *Tenebrionidae*, *Laena reitteri* Weise lives in the thick hornbeam-beech and hazel litter abundantly interwined with mycelia.

At present grey alder brushwood occupies vast areas of the Bieszczady Mts both along river or torrent valleys and on dry slopes where it overgrows old farmland. *Synanthedon spheciformis* (D. & S.), *Tetheella fluctuosa* (Hübner), *Ochropacha duplaris* (L.) and *Acronicta alni* (L.) may be assumed to be characteristic species of the relatively poor community of *Lepidoptera* here. Communities of ladybirds on *Prunus padus* on which aphids of the species *Rhopalosiphum padi* (L.) feed are the most abundant in spring (Fig. 7.52). The dominant species here are *Coccinella septempunctata* L., the individuals of which constitute 40% of the community, *Adalia bipunctata* (L.) (20%), *Calvia quattuordecimguttata* (L.) (20%), *C. quattuordecimpunctata* (L.), *Adalia decempunctata* (L.) and *Hippodamia tredecimpunctata* (L.). In other seasons *Adalia bipunctata* and *Calvia quattuordecimguttata* are most abundant. Communities of other families of phytophagous insects studied are very poor here. Only few individuals of several species such as *Pholidoptera griseoaptera* (De Geer) (*Orthoptera*) and *Liposthenes glechomae* (L.) (*Cynipidae*) were observed deep in the brushwood. Xylophages associated with the alder such as *Cryptorhynchus lapathi* (L.), *Trypodendron* spp. and *Xyleborus*

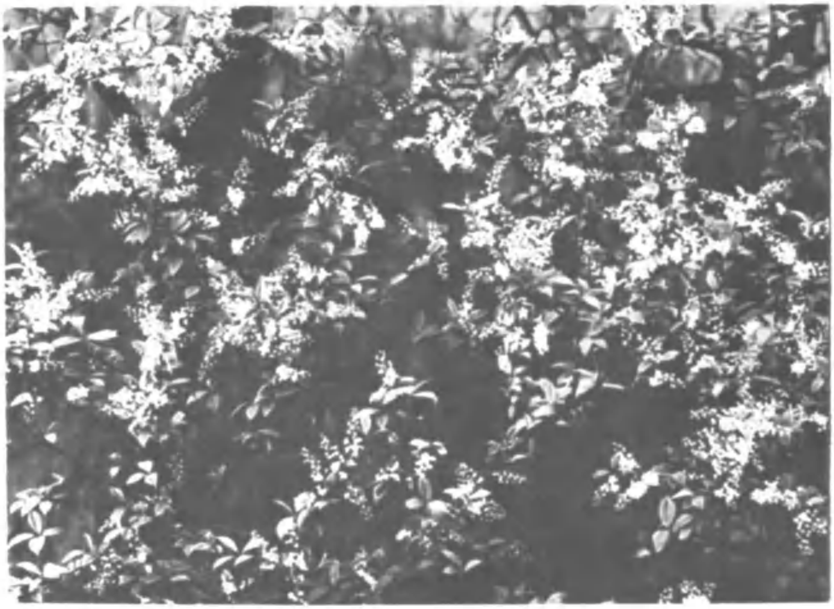


Fig. 7.52 Flowering bird cherry. Environment of *Coccinellidae* agglomerated around colonies of *Rhopalosiphum padi* (L.) (photo by W. Strojny)

spp., as well as numerous species of litter and soil staphylinids and carabids occur abundantly here.

Two basic environments may be distinguished in the lower mountain zone. These are the beech forests of *Fagetum carpaticum* type with locally varying soil humidity and acidity conditions and forest clearings (meadows). Besides the beech forest stands, fir-beech and spruce stands may also occur in the beech forest habitat.

The scolytid community of beech forest stands consists of *Ernoporus fagi* (F.), *Taphrorychus bicolor* (Herbst) and *Trypodendron domesticum* (L.) and, in forest stands with a high contribution of firs, species of the genus *Pityokteines* (*curvidens* (Germar), *vorontzovi* (Jacobson) and *spinidens* (Reitter)), *Pityophtorus pityographus* (Ratzeburg), *Trypodendron lineatum* (Olivier), *Dryocoetes autographus* (Ratzeburg), *Crypturgus hispidulus* Thomson and *Hylurgops palliatus* (Gyllenhal). The same species of *Scolytidae* comprise the community in fir-beech forest stands, although *Ernoporus* fagi is absent here, whereas *Pityophthorus exculptus* (Ratzeburg) occurs on the fir. All of the bark-beetles accompanying *Ips typographus* (L.) in various parts of Poland occur on the spruce here, with *Pityogenes chalcographus* (L.) which inhabits the branches of tree crowns being the most abundant species.

No parasitic *Hymenoptera* were observed on the bark-beetles feeding on the beech. In the Bieszczady Mts only a few of them are associated with bark-beetles of the fir, and almost exclusively with *Cryphalus piceae* (Ratzeburg). These are *Roptrocerus xylophagorum* (Ratzeburg), *Ecphylus silesiacus* (Ratzeburg) and *Dinotiscus capitatus* (Forster). Most species are parasitic on bark-beetles of the spruce, of which *Coeloides bostrichorum* Giraud and *Dendrosoter protruberans* (Nees) are commonest on the trunks. In the branch layer these species are replaced by *Ecphylus silesiacus* and *Rhopalicus tutela* (Walker) by *Dinotiscus capitatus*. The quantitative ratios in the community of *Hymenoptera* parasitic on bark-beetles in the Bieszczady Mts resemble those observed in the Sącz Beskid and Sudeten Mts.

The *Lepidoptera* community in the Carpathian beech forest consists of just a few shade-seeking species. Notable species are *Operophtera brumata* (L.), *Epirrita dilutata* (D. & S.), *Campaea margaritata* (L.), *Agriopis* (= *Erannis*) *aurantiaria* (Hübner), *Bena prasinana* (L.), *Pseidoips fagana* (F.), *Dasychira pudibunda* (L.), *Aglia tau* L., *Pararge aegeria tircis* (Bufler) and *Lasiommata maera* (L.). The community of ladybirds is also relatively poor here. They mostly occur on blackberry and raspberry bushes on the forest borders. *Chilocorus renipustulatus*

(Scriba) and *Adalia decempunctata* (L.) (on forest borders) are most abundant here. Many species of mycetophilid flies occur here, *Bolitophila dubia* Siebke, *Mycomya fusca* (Meigen) and *Phronia forcipata* Winnertz being characteristic of the environment under discussion. *Elateridae* are also numerous including, 25 species occurring in the lower mountain zone of the beech forests, i.e. 50% of all elaterid species recorded from the Bieszczady Mts. Dendrophilous species prevail, 16 such species having been observed. The boreo-montane species *Ampedus tristis* (L.), associated here with the spruce or the fir, and the montane species *A. aethiops* (Lacordaire) are relicts of primeval forests. *Denticollis linearis* (L.), *Harminius undulatus* (De Geer) and *Ampedus pomorum* (Herbst) are characteristic species of beech forests. *Anostirus castaneus* (L.) which inhabits fir windfalls is an interesting species. Its young larvae feed on rotten roots whereas the older ones move into the soil where they pupate.

The East-Carpathian carabids *Trechus pulchellus* Putzeys and *T. pulpani* Reska which occur in various biotopes in the Bieszczady Mts are noteworthy among the species of the soil environment. *T. latus* Putzeys is a characteristic species of humid ravines in beech forests where it occurs abundantly in the thick litter layer, particularly on sites with flowing water, together with *Nebria fuscipes* Fuss. *Patrobus quadricollis* Miller, *Deltomerus carpathicus* (Miller) and *Duvalius subterraneus* (Miller). This community is of a typical East-Carpathian character and does not occur in other natural forest regions of Poland. Of the species mentioned here, only *Trechus pulchellus*, *T. pulpani* and *T. latus* also occur in the Niski (Low) Beskid as far as Jaworzyna Krynicka. The other species are confined to the Western Bieszczady Mts. The vertical distribution of *Trechinae* in the Bieszczady Mts is illustrated in Fig. 7.53.

Although meadows in beech forests lie in the lower mountain zone, their entomofauna exhibits a considerably closer similarity to that of Bieszczady Mts grasslands (Mountain pastures – "połoniny") than that of beech forests and they are very rich in species. The butterflies *Parnassius mnemosyne* (L.), *Pieris bryonia* (Hübner), *Erebia medusa* (D. & S.) and many others occurring here are all pasture species.

The specific composition of ladybirds is also very diverse here. *Coccinella septempunctata* L. predominates (80% of individuals), *Calvia quattuordecimpunctata* (L.) (12%) and *Hippodamia variegata* (Goeze) (6%) are also rather abundant. The other five species only constitute 2% of the community. The pasture species *Adaliopsis alpina* (Villa) is found in some meadows. Of the 44 species of *Cynipidae* occurring in the Biesz-

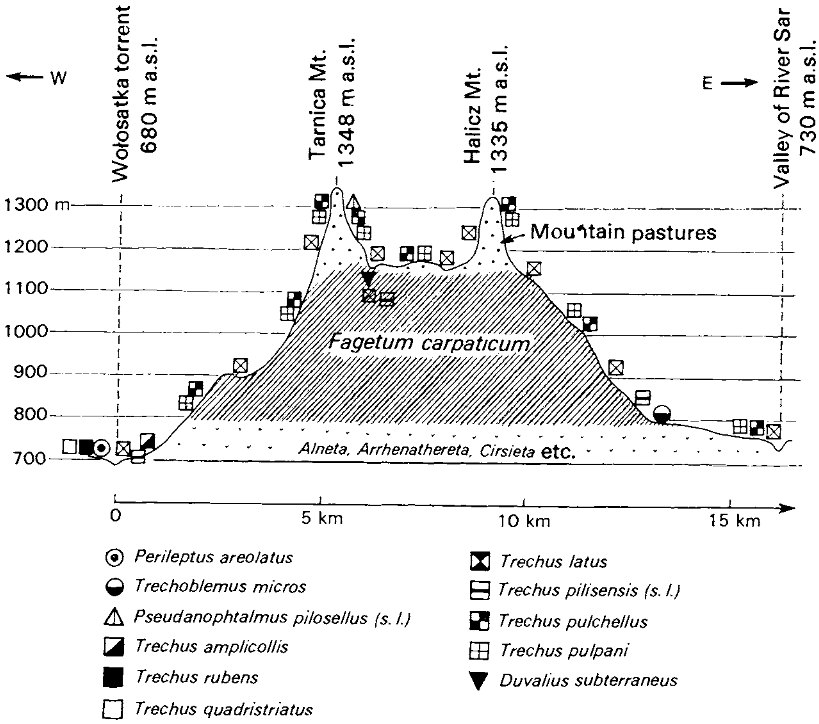


Fig. 7.53 Vertical distribution of *Trechinae* in the region of Tarnica Mt in the Western Bieszczady Mts (after Pawłowski, 1975)

czady Mts on 38 host plants, the following are characteristic of the meadows of the lower mountain zone: *Xestophanes brevitarsis* (Thomson) (living on *Potentilla erecta*), *Diplolepis rosae* (L.) (on the rose) and *Aulacidea pilosellae* (Kieffer) (on hawkweed). Among the 115 syrphid species, *Cheilosia canicularis* (Panzer) (the larvae of which mine the stems of *Petasites*) and *Syrphus torvus* Osten-Sacken, predominate. *Syrphus ribesii* (L.), *S. vitripennis* (Meigen), *Sphaerophoria scripta* (L.), *Scaeva pyrastri* (L.), *Eristalis nemorum* (L.) and *E. pertinax* (Scopoli) are subdominant species here. Predatory larvae prevail in the family discussed (61 %), whereas larvae of phytophages constitute 22%, those of aquatic saprophages 13.5% and those of forest saprophages 3.5%. The zoogeographical composition of the *Syrphidae* of the Bieszczady Mts and their phenology are summarized in Table 7.8 and illustrated in Fig. 7.54.

Of the calyptrate *Diptera*, the most abundant species are saprophage *Sarcophaga subvicina* Rohdendorf and snails parasite *Bellardia biseta* (Kramer). *Meigenia mutabilis* Fallén, the parasite of chrysomelid lar-

Table 7.8 Zoogeographical characteristics of *Syrphidae* in Western Bieszczady Mts as compared with other regions of the Carpathians (after Bańkowska, 1971b).

Zoogeographical elements	Percentual contribution of *Syrphidae* fauna		
	Polish Tatra Mts	Western Bieszczady Mts	Ukrainian Carpathians
Holarctic	13.9	19.3	18.5
Palearctic	4.8	14.3	17.8
European	46.4	33.5	27.4
Eurosiberian	13.2	24.2	22.6
Alpine and boreoalpine	21.5	6.0	4.2
Mediterranean	–	2.7	9.5
Total number of species observed	144	183	168

vae, which occurs abundantly in forest meadows is a characteristic species here. Soil *Elateridae* occur in these meadows, of the 18 species of which *Prosternon tessellatum* (L.), *Cidnopius aeruginosus* (Olivier), amongst others are typical forest forms. Over 30 species of *Orthoptera* occur here, including the East-Carpathian species *Isophya brevipennis* Brunner von Wattenwyl. Other species characteristic of this environment are *Isophya modestior stysi* Čejchan, *I. camptoxipha* (Fieber) (= *I. pyrenea* (Serville, [1838])), *I. posthumoidalis* Bazyluk and *Pholidoptera aptera* F. The group *Psylloidea* is represented in these meadows by *Aphalara exilis* (Weber & Mohr), *Trioza cerastii* (L.), *T. galli* Forster and *T. rumicis* Löw.

The flowers of meadows of the lower mountain zone are visited by many *Cerambycidae*, the larval development of which takes place in the forest environment. *Anoplodera scutellata* (F.), which visits the flowers of *Angelica silvestris* L., as well as *Judolia cerambyciformis* (Schrank), *Acmaeops collaris* (L.) and many others are particularly abundant. The pontic species *Leptura tesserula* Charpentier, which most frequently visits the flowers of *Astrantia maior* (L.), *Filipendula ulmaria* L. and other plants, is one of the characteristic cerambycids of the Bieszczady Mts.

Very few ant species occur on the borders of beech forests of the lower mountain zone. They include *Manica rubida* (Latreille), *Myrmica rubra* (L.), *Leptothorax acervorum* (F.), *Lasius flavus* (F.) and *Formica pratensis* Retzius. As a rule ants do not occur within the forest stands

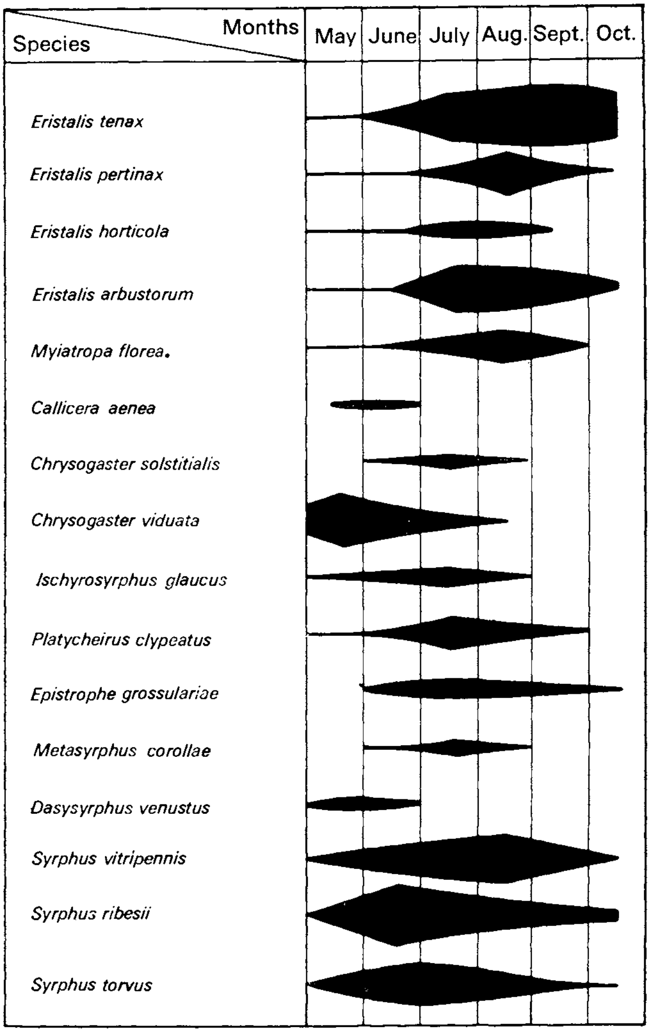


Fig. 7.54 Phenology of most abundant *Syrphidae* species in the Western Bieszczady Mts (after Bańkowska, 1971b)

(grey alder brushwood, oak-hornbeam-linden forests, beech forests). The communities of ants here differ from the analogous ones in the Western Carpathians by the presence of *Camponotus vagus* (Scopoli) and the absence of *Myrmica sulcinodis* Nylander.

The communities of litter *Staphylinidae* occurring on mountain pastures in green alder brushwood are extremely interesting. *Sipalia koczii*

Bernhauer is the dominant species here, whereas *Quedius cincticollis* Kraatz, *Leptusa carpathica* Weise, *Stenus obscuripes* Ganglbauer and *Othius transsilvanicus* (Ganglbauer) are subdominants. These belong principally to the East-Carpathian element inhabiting areas above the upper forest range. *Stenus carpathicus* Ganglbauer and *Othius crassus* Motschulsky, on the other hand, are rarely observed here and belong to forest species. Larvae of *Amphichroum canaliculatum* (F.), the adults of which appear in large numbers in spring on the green alder inflorescences, also live in the litter. The density of ants in the pastures is relatively high amounting to 0.44 nests per 1 m^2. *Myrmica rubra* (L.) is the dominant species, whereas *Formica lemani* Bondroit is characteristic of this habitat. They also occur on the borders of green alder brushwood.

8 Human influence on forest entomocenoses

General regularities of the processes of anthropization of the forest entomofauna

Anthropization of the flora and fauna, the forest entomofauna included, is part of the directional changes which occur on the globe as a result of human influence. It consists of the replacement of specific (i.e. endemic) components by nonspecific, cosmopolitan ones as well as the replacement of native or autochthonous components by foreign or allochtonous elements and the substitution of stenotopic components by eurytopic ones. Consequently it consists of the replacement of primeval systems conditioned by the mutual activity of endogenous and exogenous factors by secondary systems conditioned mainly by exogenous factors (Faliński, 1972).

The anthropization of forest environments may be due to factors which are not associated with forest management but which exhibit a wide range of influence (changes in soil water conditions, destruction of the forest herb layer and litter, forest fires, air pollution, mining) or to direct influence of forest management on the forest and the organisms inhabiting it (various forms of cultivation of forest soils, their fertilization, establishment of a specific composition of forest stands, felling, side-effects of biocides, etc.). At present the exogenous factor of industrial air pollution and paraendogenous factors (i.e. due to human activity in the forest), such as clear felling and the mechanical and intensive soil cultivation of felling areas, play the most important role in the process of anthropization of forest entomocenoses. A specific role in the process of anthropization is played by the ever-increasing recreational and tourist activities. These may be regarded as exogenous factors with respect to the forest, but in the economic sense they become increasingly more distinct components of nonproductive forest functions. Unfortunately we lack even the least, methodically correct, observations on these activities as regards their scale of influence on forest entomocenoses phenomena. A general analysis of this problem is given by Okołów (1976).

Industrial air pollution (Fig. 8.1) not only affects an enormous part of Poland, including considerable forest areas, but the range of its influence also systematically increases. Clear felling is carried out in various habitats and comprises one of the basic economic measures employed in forest management affecting about one per cent of the total forest area per year in Poland. This operation is associated with logging which enhances the mechanization of this process as well as the mechanical cultivation of the soil which prepares the felling area for replantation. As described below, the biological consequences of clear felling in the entomocenoses extend to a quarter to a third of the productive cycle of forest stands, such that the range of influence of this operation on the forest covers an even larger area than that subjected to the influences of industry and urbanization.

Fig. 8.1 Industrial air pollution around chemical plants (photo by S. Kinelski)

The range of the changes which occur in the composition and structure of the forest entomofauna under the influence of anthropogenous factors varies widely. On the one hand, it depends on the nature of the factors involved and the intensity of their action and, on the other hand, on the regeneration capacity of the composition and structure of entomocenoses. This capacity varies in different forest environments and depends on the frequency and timing of the activities determining the process of anthropization.

In order to determine the intensity of the anthropization process, the concept of the "coefficient of ecological resistance" was introduced in phytosociology. This coefficient defines the difference between the ecological conditions existing on a definite site and the ideal model which optimally fulfils the requirements of individual groups of species. Thus, this coefficient of ecological resistance (O_e) is the reciprocal of ecological efficiency:

$$O_e = 100 - S,$$

where $S = \dfrac{\text{number of characteristic species on the given site}}{\text{total number of species characteristic of the given taxonomic or ecological unit}} \cdot 100 \cdot$

This formula may also be applied to the quantitative proportions of the cenoses studied, presenting them in the form of the product of the number of species and their density. In this case the product of species characteristic of the given group and the maximal possible covering of the area, calculated either theoretically or empirically, is accepted as the ideal model (Kostrowicki, 1972). The ecological resistance expressed by the coefficient O_e invariably consists of the natural resistance (O_n) due to the current state of abiotic and biotic conditions and of the introduced resistance (O_w) due to the anthropogenous factor. These components may be discerned by comparing the condition of the best preserved cenosis belonging to the same association and occurring under identical site conditions with the condition of the degraded cenosis. This comparison is performed according to the formula given above in which the numerator represents the conditions of the cenosis studied (number of characteristic species) and the denominator represents those of the best preserved cenosis (Kostrowicki, 1972). The higher the intensity of the process of anthropization the higher is the coefficient of introduced resistance (O_w).

In practice, this formula has not been applied to insect communities undergoing anthropization. This is because entomocenoses are relatively poorly known as compared with plant associations which makes it difficult to select a suitable basis for their study.

The calculation of the coefficient of introduced resistance for *Staphylinidae* on 6 plant patches in fresh pine forest of the Kampinos Forest (characteristic forest species F_3-F_2: *Sipalia circellaris* (Gravenhorst), *Xantholinus tricolor* (F.), *Mycetoporus lepidus* (Gravenhorst), *M. splendidus* (Gravenhorst), *Acidota crenata* (F.), *Stenus geniculatus* Gravenhorst, *Othius myrmecophilus* Kiesenwetter, *O. punctulatus* (Goeze), *Sepedophilus immaculatus* (Stephens), *Mycetoporus rufescens* (Stephens), *Quedius obliteratus* Erichson, *Atheta castanoptera* (Mannerheim), *Atheta* sp., *Lordithon thoracicus* (F.), *Stenus impressus* Germar, *Staphylinus erythropterus* L., *Mycetoporus clavicornis* (Stephens), *Quedius fuliginosus* (Gravenhorst), *Lordithon exoletus* (Erichson); other data also (after Szujecki & Perliński, 1975) gave the results summarized in Table 8.1.

Table 8.1 Distribution of species in vegetal patches of fresh pine forest studied and calculation of introduced resistance O_w (after Szujecki & Perliński, 1975).

Fidelity class	Number of species in vegetal patches					
	poorer facies			richer facies		
	blueberry	litter	moss	blueberry	litter	moss
F_3	3	3	4	5	3	4
F_2	5	6	2	9	4	3
F_3 and F_2	8	9	6	14	7	7
F_1	19	13	14	15	6	9
F_0	7	7	12	7	5	3
F_1 and F_0	26	20	26	22	11	12
Total number of species	34	29	32	36	18	19
S	42	47	31	74	37	37
O_e	58	53	69	26	63	63
O_n	15	16	11	26	13	13
O_w	43	37	58	0	50	50

The results showed that the highest introduced resistance was recorded in uniform moss patches of both facies. The lowest resistance was in the environment of the most deformed herb layer, i.e. in patches of blueberry in the rich facies of the coniferous forest where this plant occupied 88% of the covered surface, as well as under oak clusters in the pine forests strongly degraded by anthropogenous influence and on soil of low humidity where patches of blueberry occupied only 1% of the area. Due to the degradation of the environment, the clusters of pedunculate oak played a protective role for the primeval forest entomofauna of fresh pine forests.

It is thus possible to evaluate the anthropogenous influences as well as the course of anthropization on entomocenoses. The utilization of information concerning only the characteristic species (exclusive and selective) for this purpose is justified since the number of nonforest species (accessory and foreign), not taken into account in the calculation of introduced resistance, varies in the course of the year due to their dynamic seasonal immigration from the neighbouring biotopes (Szujecki & Perliński, 1975).

Influence of anthropogenous factors not associated with forest management on the entomocenosis.

8.1 Changes in soil water conditions

Oscillations in the soil water level due to human activity outside of the forest are the result of drainage, water intake construction, mining (particularly in quarries), building, river regulation, drawing underground water for communal and industrial purposes, etc. These phenomena acquire an increasingly wider range as a result of improved technology which leads to a rapid decrease of the ground water level. Instances where this level is increased are rare and are essentially confined to the close environs of large artificial water reservoirs. Oscillations of the ground water level of anthropogenous origin, being either exogenous or endogenous as regards the forest environment, influence the forest stands and their associated insects in the same way as do the natural changes in the ground water level which have been frequently observed in recent years. The differences in the ground water level due to changes in the amount and distribution of precipitation and transpiration during the year amount to an average of 0.5 m and occasionally even to 3 m. The highest oscillations in the ground water level occur in 60–80 year-old forest stands and the lowest in thickets, whereas from the standpoint of specific composition they are highest in oak stands and lowest in beech forests (Kiełczewski & Wiśniewski, 1973).

Forest stands growing in river valleys and on lake borders where the tree root system is adapted to a stable water level in the water body are the most susceptible to a decrease in the ground water level. This decrease is particularly harmful to forest stands on sandy soils. Spruce forest stands, due to their flat root system are particularly susceptible to both a decrease of the ground water level and inundation.

Oscillations in the ground water level constitute one of the most important causes of deficiency of forest stands and of an increased abundance of dendrophilous insects infesting weakened trees in the Koszalin and Elbląg–Warmia zones, as well as in the Masurian Lakeland, Masovian Plain, Bielsk–Białystok Upland, Białowieża Forest, Noteć Forest, Lublin Lakeland, Upper Silesian and Cracow Industrial Regions.

The reaction of pine forest stands to a decrease in the ground water level is manifested in the disappearance of small tree roots and a tendency for the needles to become red and fall prematurely. This provides an opportunity for diseases to attack the root system and for insects to invade the phloem, cambium or wood. *Phaenops cyanea* (F.), *Tomicus piniperda* (L.) and *T. minor* (Hartig) play a particularly significant role under such conditions. In spruce forest stands the population of *Ips typographus* (L.) and accessory species undergoes particularly dynamic changes in abundance. In oak forest stands the decrease of the ground water level causes the occurrence of dry-topped trees infested by large numbers of individuals of species belonging to the genera *Plagionotus*, *Mesosa*, *Agrilus* and *Scolytus* which leads to the death of entire trees or to accelerated felling of forest stands.

An abrupt decrease of the ground water level causes such a rapid drying of trees that secondary pests with low levels of abundance are not capable of infesting them. On the other hand, however, in the subsequent years the progressive influence of unfavourable water conditions on the forest stand causes the abundance of xylophages to increase so drastically that they even infest relatively healthy trees.

Permanent changes in the ground water level determine the soil humidity and consequently bring about changes in the soil entomofauna. These are indicated by differences in the specific and quantitative composition of insects occurring in forest environments of similar soils and occupied by the same plant associations but with differing ground water levels.

Areas with different ground water levels were distinguished in pine forests of the Kampinos Forest. In compartment No. 161 the ground water level was high and periodically rose to a depth of almost 1 m, whereas in compartment No. 84 this level oscillated within the limits of 214 to 247 cm. As a result of these differences, the soil humidity of the two areas under comparison also varied to the same extent and their herb layers differed as regards relative composition. In compartment No. 84 the blueberry occupied 1% and mosses 89% of the surface, whereas in compartment No. 161 the blueberry occupied 88% and mosses only 11% of the area (Górny, 1975b). This consequently affected the occurrence of *Coleoptera* in the litter.

Athous subfuscus (Müller) was the dominant species and *Dalopius marginatus* (L.) the subdominant in the community of elaterid larvae in both areas. In the facies with the higher ground water level (161) *Othius myrmecophilus* Kiesenwetter was dominant and *Sipalia circellaris* (Gravenhorst) subdominant in the staphylinid community, whereas the quantitative proportions between these species in the poorer facies were reversed.

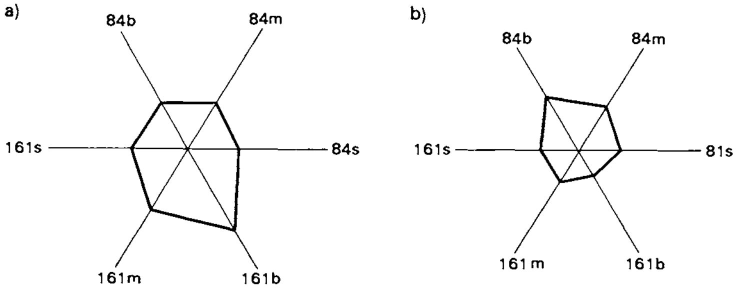
Other insect species studied exhibited a higher or lower preference for the conditions of one or the other area.

Three factors determining the distribution of litter *Coleoptera* have been distinguished. They act according to the following hierarchy: (i) site (as well as ground water level); (ii) contribution of compact floral patches to the total cover of the forest floor (blueberry, oaks, mosses), and (iii) species or group of species forming the given patch.

It has been found that the ground water level determines the general density level of individual taxonomic groups of *Coleoptera* (imagines or larvae) and their dominance proportions (Perliński, 1975). It also appears that larvae (particularly those inhabiting the mineral soil as well as the litter) exhibit higher requirements as regards humidity conditions than the litter and surface dwelling adult stages (Table 8.2). The "environmental roses" plotted for species, the distribution of which was determined by the ground water level, are given in Fig. 8.2. On the other hand, Fig. 8.3 illustrates the preference for other environmental factors (dominating floral patches, species forming the given patch) of insects.

Table 8.2 Density of some *Coleoptera* in 0.25 m^2 litter samples proportional to the contribution of vegetal patches in the pine forest of the Kampinos Forest.

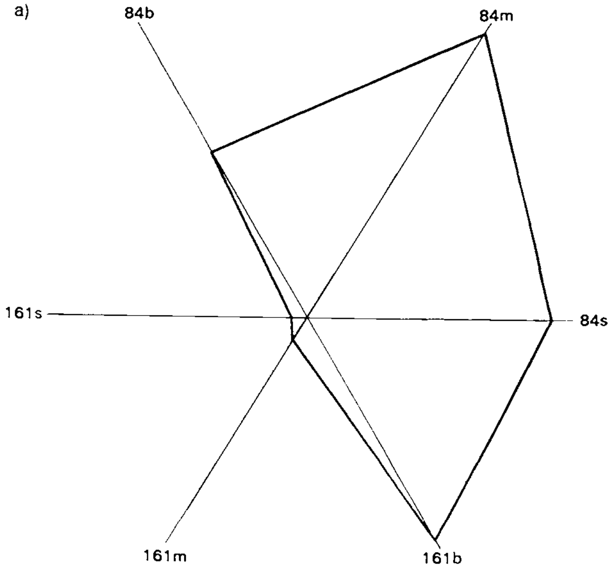
Taxon	Forest compartment	
	84	161
Staphylinidae (imagines)	10.8	8.1
Staphylinidae and *Carabidae* (larvae)	2.2	5.5
Elateridae (larvae)	10.3	21.2



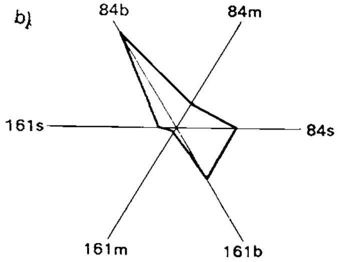
Larvae of *Dalopius marginatus* L.

Xantholinus linearis Ol.

Fig. 8.2 Preference of soils of high (a) and low (b) ground water level by litter *Coleoptera* in the pine forest of the Kampinos Forest (after Perliński, 1975): b -- blueberry, m — mosses, s — oak litter



Sipalia circellaris Grav.



Propylaea quattuordecimpunctata L.

Fig. 8.3 Preference of the size of the plant patch (a) or plant species forming the patch (b) by insects (after Perliński, 1975)

8.2 Destruction of the forest herb layer and litter

The destruction of the forest herb layer and litter is due to various anthropogenous factors. The process of destruction may either affect both the litter and the herb layer or only the latter. The destruction of both elements of the forest floor is primarily due to villagers raking the litter in regions where straw is deficient and the forest litter is used as bedding for cattle. Although this habit has now died out, the consequences of its occurrence in the past will influence forest entomocenoses and the productiveness of forest stands for several years to come. The amount of litter remaining after being raked in forest stands of varying specific and age composition depends on the frequency of raking. However, even when raking is only repeated every 6 years, this still does not prevent a decrease in the amount of litter (Table 8.3).

Table 8.3 Influence of frequency of litter raking on its supply (100 kg/ha) (after Kiełczewski & Wiśniewski, 1973).

Tree species	Bonitation class	Age class	Stand with raked litter				Unraked stand
			every year	every 2 years	every 4 years	every 6 years	
Beech	II–III	21–40	35	59	63	70	81
		61–80	46	77	82	92	107
	IV–V	41–60	35	59	63	70	81
		61–80	37	62	66	74	86
Pine	II–III	21–40	33	54	80	102	145
		61–80	32	53	78	99	140
	IV–V	41–60	23	38	56	71	101
		61–80	22	36	53	68	96
Spruce	II–III	21–40	30	66		89	125
		61–80	43	94		128	179
	IV–V	41–60	30	65		90	124
		61–80	27	80		109	152

The removal of the litter affects the entomofauna directly by the destruction and limitation of its natural environment as well as indirectly by changing the structure, humidity and chemical properties of the soil and the physiological reaction of plant hosts of phytophages. Soils deprived of litter are characterized by wide temperature amplitudes which evoke a limiting effect on insects. Furthermore, changes occur in the entomofauna of the forest herb layer which is destroyed during raking and the mobility of epigeic insects also changes since under these conditions they migrate further in search of food.

Raking beech litter causes changes in the structure of the associations of the soil meso- and macrofauna and their abundance which last for more than 100 years (Ronde, 1951, 1953). Larvae of soil insects are amongst the most susceptible animals and are completely absent in beech forest stands in which the litter has been freshly raked (Fig. 8.4). The survival of *Calosoma sycophanta* (L.) in winter depends on the thickness of the litter and the depth to which the soil freezes. The absence of litter causes an increase in the mortality of these predators (Vorontsov, 1957). The negative effects of the destruction of litter in pine forest stands also influence the growth and health conditions of the next forest generation. Pine plantations established on sites on which the litter has been raked over a period of several years exhibit poor growth and are subjected to mass infestations by *Exoteleia dodecella* (L.), *Rhyacionia buoliana* (D. & S.) and *Aradus cinnamomeus* (Panzer). The feeding activity of these pests inhibits the growth of trees and causes their deformation as well as morphological changes in the wood (Fig. 8.5).

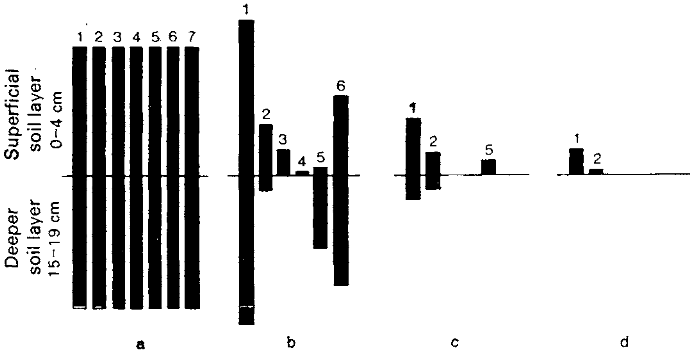


Fig. 8.4 Influence of litter raking on the abundance of soil fauna (after Dunger, 1964): a — forest stand with litter not raked for 300 years, b — not raked for 100 years, c — not raked for 50 years, d — currently raked: 1 — *Collembola*, 2 — *Acarina*, 3 — *Myriapoda*, 4 — *Nematoda*, 5 — *Insecta* (larvae), 6 — *Lumbricidae*, 7 — *Isopoda*

Devastation of the forest herb layer and litter is mainly due to cattle grazing, the collection of fungi and berries, the systematic gathering of dry branches and intensified tourism. For these reasons, forest stands at the borders of villages or towns are generally characterized by poor growth and are devoid of a herb layer which is replaced by a trampled and impoverished layer of litter. The porous and cloddish structure of the superficial soil layer is also disturbed. Such forest stands generally

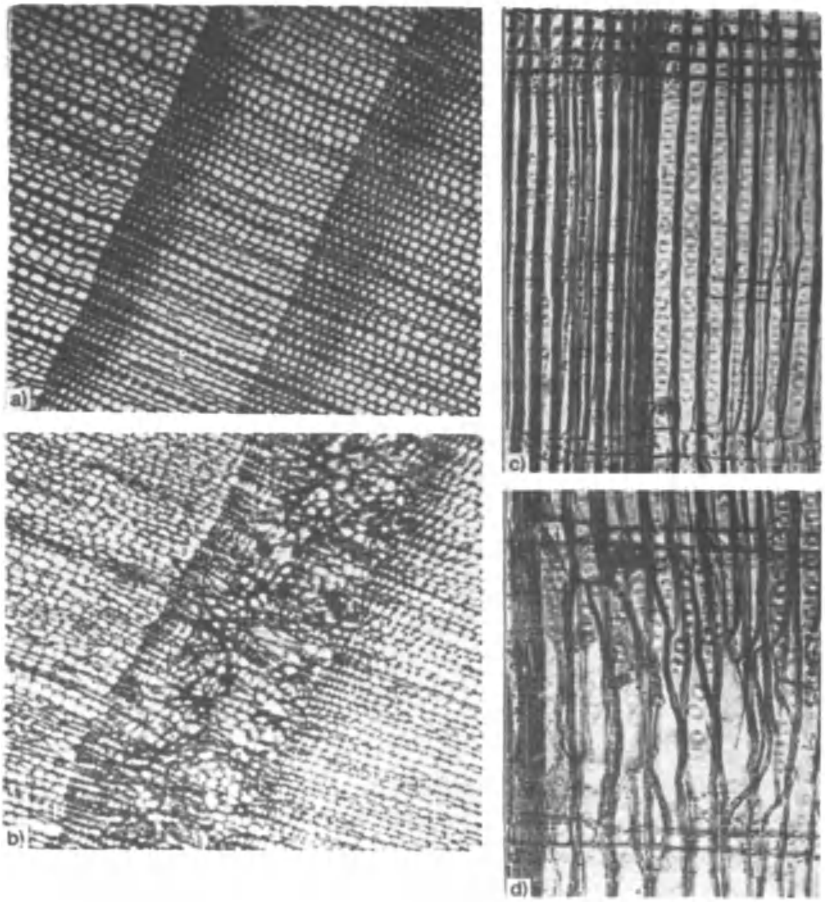


Fig. 8.5 Morphological changes in the wood of the common pine under the influence of feeding of *Aradus cinnamomeus* (Panzer) (after Brammanis, 1975): a, b — cross section of wood, c, d — radial section, a, c — healthy wood, b, d — wood of trees damaged by feeding of *Aradus cinnamomeus* (Panzer)

become the primary gradation foci of numerous pine foliophages such as *Panolis flammea* (D. & S.), *Dendrolimus pini* (L.), *Diprion pini* (L.), *Lymantria monacha* (L.) and *Acantholyda posticalis* Matsumura and, in the larch forest stands of Siberia, *Dendrolimus sibirica* Tschetverikov (Grimalskii, 1964).

Four stages of anthropogenous changes caused by trampling, litter raking and grazing in the vicinity of villages have been distinguished in the oak forests of the Ukraine (Karpisonova, 1962).

In the first natural stage, oak forests exhibit a compact upper layer, a second layer with the linden and maple and an undergrowth consisting of hazel, buckthorn and other shrubs. In the first phase of anthropogenous destruction the oak and the undergrowth remain whereas the contribution of ephemeral species decreases in the herb layer. In stage II the undergrowth becomes less compact under human pressure, whereas meadow plants appear in the herb layer and species resistant to strong illumination predominate. In stage III the undergrowth covers only one fifth of the surface area, meadow plants predominate in the herb layer, whereas forest species remain only under the tree and undergrowth canopy. In stage IV the undergrowth disappears completely, whereas the herb layer lacks plants specific for oak forests. Dry-topped trees appear in the dying forest stand after 100–120 years, and the capacity for natural regeneration is lost. Thus, even without felling, the plant associations and microclimatic conditions of the forest change and this has a decisive effect on the composition of the entomofauna. This leads to an outbreak of *Lymantria dispar* (L.) (Grimalskii, 1964) as well as a significant increase in xylophages which feed on the oak, especially *Cerambyx cerdo* L. The composition of the entomofauna of the forest floor also changes.

The devastation of the forest floor under the influence of human mobility is usually greatest within the range of urbanization and its progress is of a continuous nature as illustrated by the history of the Bielany Wood in Warsaw. The following three facts affected the natural environment of this wood: 1) changes in water conditions resulting from the direction of flow of the Bielany Torrent into the main Warsaw collector constructed in 1886–1906, as well as the connection in 1925 of the flood dam with the high bank rendering the inundation of the lower terrace of the forest by the Vistula impossible; 2) destruction of the natural insulation of the forest by the construction of the Bielany Fort at the end of the 19th century and the destruction of the neighbouring afforested areas around 1914; 3) uncontrolled utilization of the forest, breaking of branches, removal of the litter, trampling of the vegetation, destruction of the undergrowth and herb layer taking place over several dozen years mainly as a result of recreational activities.

The anthropogenous factors mentioned above determined the rate of disappearance of the oak forest stand which was unique in this part of Europe. In 1907, when the Bielany Forest was turned over to the Warsaw military authorities and tree-felling was forbidden, the forest covered about 147 ha on which 30 479 old oaks were recorded. Recreational activities, however, were not restricted until 1934, by which time over one half of the trees had already been destroyed. Many of these trees were removed in sanitation cuttings by 1939. In the same period, however, many drainage ditches were dug which resulted in a further deterioration of the water conditions in this area. Severe damage to old trees was caused by military operations during World War II. As a result of the situation described above and under favourable meteorological conditions, *Cerambyx cerdo* and many other accessory xylophages appeared in large numbers here in the middle of this century. Thus by 1960, several hundred more trees which were either drying or infested by *Cerambyx cerdo* had to be felled.

In the ensuing years, due to the construction of an enclosure around a considerable area of the forest, the recreational activities have been restricted which has led to a regeneration of the undergrowth, undercrop and herb layer, as well as to a decrease in the abundance of *Cerambyx cerdo*. Nevertheless, in 1968–1969 only about 2700 old oaks (Fig. 8.6), i.e. 9% of the number recorded in 1907, remained here (Wiśniewski, 1969). Trees between 200–350 years of age and growing singly are most intensively infested (about 100%) by *Cerambyx cerdo* and accessory xylophages. The number of trees damaged by insects in 150 year-old forest stands is a third of that in 220–350 year-old ones. Nonwithstanding the age, the highest percentage of infestation is exhibited by windbreaks as well as by standing dead and dying trees. The lowest frequency of xylophages is recorded on living trees of between 120–150 years of age (15.5%). Dying trees are primarily infested by species such as *Xestobium rufovillosum* (De Geer) and *Ptilinus pectinicornis* (L.) (*Anobiidae*), *Lymexylon navale* (L.) (*Lymexylidae*), *Eremotes ater* (L.) (*Curculionidae*) and *Xyleborus monographus* (F.), *X. saxeseni* (Ratzeburg) and *X. dispar* (F.) (*Scolytidae*). Trees with living cambium are infested by *Cerambyx cerdo* (Fig. 8.7), *Plagionotus arcuatus* (L.) and *P. detritus* (L.). The characteristic species *Synanthedon vespiformis* (L.) var. *rufimarginata* Spuler and *S. conopiformis* (Esper) occur abundantly in and under the bark as well as in tree wounds and cankers. *Agrilus elongatus* (Herbst) is particularly abundant in branches. The abundance of these insects is proportional to the anthropogenous destruction of the forest environment (Wiśniewski, 1969c).

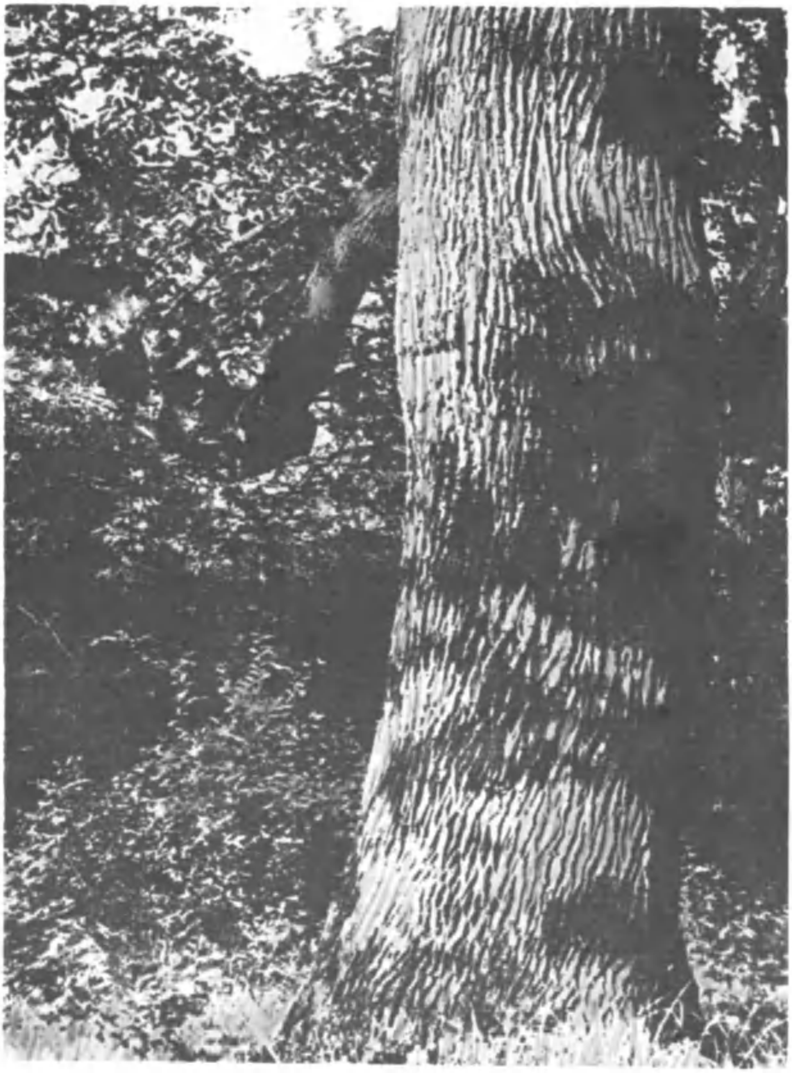


Fig. 8.6 Oak in the Bielany Forest (photo by T. Bojasiński)

The most decisive influence effecting changes in the forest herb layer, as well as in the amount of litter on a country-wide scale and the consequent changes in the entomocenoses, however, is not due to the action of tourists but to forest management. This involves, for example, clear felling, the cultivation of the soil and plantations, and the skidding and haulage of felled trees. Further parts of this discussion will be devoted

Fig. 8.7 Feeding ground of *Cerambyx cerdo* L. larvae around a hollow (photo by W. Strojny)

to these problems as well as to the consequences of the destruction of the undergrowth, litter and soil on forest entomocenoses. The impoverishment of the forest litter leads primarily to an increase in the introduced resistance (see page 111) and consequently to an intensification of the process of anthropization of the forest environment. Studies performed in the Kampinos Forest showed that the anthropization of litter *Coleoptera* in fresh pine forests is determined by the reduction of the occurrence of the blueberry in favour of photophilous mosses which are able to tolerate drying of the soil (Szujecki & Perliński, 1975).

8.3 Forest fires

Primeval coniferous forests in the northern part of the Holarctic Region formed ecosystems which were primarily dependent on fires as the key environmental factor initiating succession processes and controlling the specific composition and age structure of forest stands. Fires also influenced the production of the herb layer on which the composition and abundance of many insects and other forest animals depends. Most forest fires in North America during the period between 1600–1920 occurred at 5–50 year (less frequently at 200–300 year) intervals such that 80–90% of the primeval forests occurring there at present are of post-fire origin (Figs. 8.8 and 8.9).

Fires, as the main agents of the destruction of the oldest forest stands, have maintained a considerable part of the forests in the regeneration and thicket classes. It is known that young forest stands are less susceptible to pests, diseases and windfall. Thus, under primeval forest conditions, fires have played a sanitary role in eliminating forest stands with a disposition to disease, as well as a selective role in removing superannuated or pest-infested forest stands. It would appear that in eastern Canada outbreaks of the most dangerous pest there, *Choristoneura fumiferana* Clemens, are most intensive in fir and spruce timber forests. It may thus be supposed that these outbreaks had a smaller chance of development in primeval forests than at present since fires regularly limited the expansion of this climax, shade-seeking species (Heinselman, 1970a, b).

Primeval forest fires in the northern Holarctic Region took place in various areas. The largest ones, like that of the Siberian taiga in 1915 for example, covered over a dozen or so million hectares.

In Poland 90% of forest fires are at present caused by human activity, due mainly to increased human penetration of the forest environment and the direction of atmospheric disturbances (these being the main cause of fires in primeval forests) to buildings and technical con-

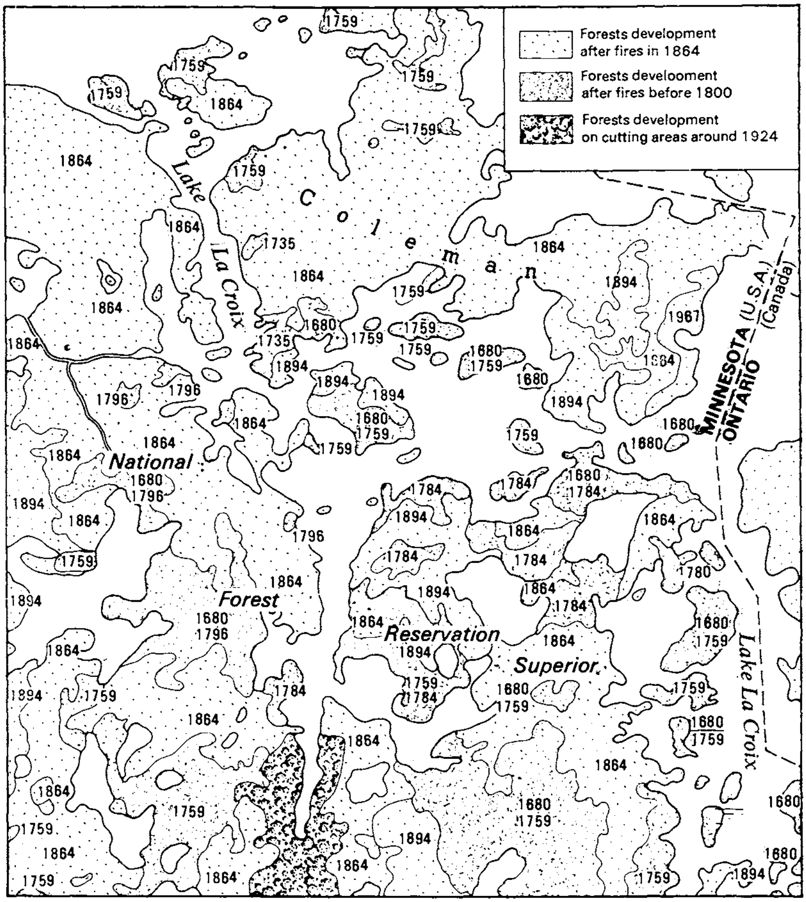


Fig. 8.8 Contribution of forests of post-fire origin in the region of Great Lakes of North America (after Heinselman, 1969)

structions beyond the forests. The absence of trees of outstanding height may essentially account for the avoidance of forests by storms.

Fires now also constitute one of the principal "disaster" factors which influence the forest stands and biocenosis in managed forests.

The degree of the negative effects of fires depends primarily on the nature and intensity of the fire and the rate of its expansion, as well as on the specific composition of forest stands, their age, configuration of the area and other environmental factors.

The weakening of a tree due to fire is the result of changes in the water content of the phloem as well as changes in the course of exosmotic processes, respiration, content of carbohydrates and nitrogen compounds.

Fig. 8.9 Forest stand destroyed by a crown fire (after Heinselman, 1970a)

In the case of crown fires (Fig. 8.9) when root swellings, trunks and tree crowns are damaged, the phloem humidity initially increases whereas the amount of bound water decreases and exosmosis, intensity of respiration and the contribution of soluble compounds rise. At the onset of the infestation of the trees by secondary pests the phloem humidity and the amount of bound water decrease and the supply of starch and sugars is exhausted. These processes are most pronounced in the middle and top parts of the trees, whereas in the butt up to 1–1.3 m the death of the formative tissue is a slow process.

In the case of surface fires (Fig. 8.10) only root swellings and parts of the trunk (and sometimes also fragments of the crown) of individual

Fig 8 10 Pine forest stand damaged by a ground fire (photo by S. Kinelski) trees are damaged (Fig. 8.11). Assimilation is thus preserved and determines the furthe course of metabolism in the phloem. The gradual weakening of the trees is a slow process and lasts longer than in the case of crown fires. The final fate of trees depends on the activity of secondary pests. The resistance of trees to their attack is distinctly lower in the lower part of trunks damaged by fire which are, in the first place, infested by insects. The progress and intensity of debilitation of trees as a result of this further favours the infestation of the entire trunk by insects up to the crown.

Fig. 8.11 Changes in annual increments of trees damaged by fire (after Heinselman, 1969)

The process of infestation of trees damaged by surface fires generally lasts two years. The weakening of trees in the case of surface fire is manifested by changes in the water balance of exosmotic processes as well as in respiration and synthesis of carbohydrates and nitrogen compounds. Over a period of two years the humidity of phloem of the Siberian larch is higher under these conditions than that of healthy trees. The exosmosis of soluble compounds in the first year is lower than in healthy trees but in the subsequent stages of the tree's death it increases in its middle and top parts. The accumulation of assimilated substances in the phloem leads to an increment of the amount of bound water and to drying up of the phloem in the upper sections of the trunk. In the first year respiration increases, whereas in the second acidification processes prevail. Starch synthesis is inhibited only in the initial months after the fire and is later intensified in the upper part of the trunk and lasts until the tree eventually dies. In the first year after surface fire the amount of total nitrogen and protein nitrogen increases, whereas the further course of changes in the nitrogen content in the phloem depends on the course of the death of the tree during the second year.

Due to the different courses of physiological and biochemical processes in trees damaged by crown and surface fires, the infestation of trees by secondary pests also follows different courses. This phenomenon has been studied in detail in the Siberian larch in relation to the associated insects occurring beneath the bark and occasionally in wood.

Trees damaged by crown fire may die even without the contributary action of secondary pests. However, in the presence of such organisms the death of the tree proceeds much more rapidly and the scolitid, *Ips subelongatus* Motschulsky plays a decisive role here (Figs. 8.12 and 8.13).

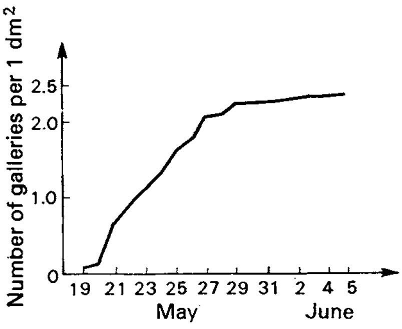


Fig. 8.12 Dynamics of invasion of the Siberian larch by *Ips subelongatus* Motschulsky after crown fire (after Isaev & Girs, 1975)

On the other hand, trees damaged by surface fire are still capable of exhibiting considerable protective reactions and can embed the bark-beetles in resin. Because of this the course of infestation of such trees by secondary pests is slower than that of trees damaged by crown fire. *Phaenops guttulata* (Gebler) and *Tetropium gracilicorne* Reitter play a decisive role here. These species are more resistant to resin secretions and are capable of remaining in the larch bark until the resin secretion is reduced (Figs. 8.14 and 8.15). *Ips subelongatus* is only successful in infesting weakened trees during the second year after the occurrence of the surface fire (Isaev & Girs, 1975).

Trees with a thinner bark than that of the larch and which regenerate their assimilation apparatus over a longer period than one year may react to damages due to surface fire in a different manner. The rate of the death of trees is proportional to the part of the circumference of the trunk on which the cambium was destroyed. Pines damaged on one side generally regenerate but during the regeneration period they become the object of infestation by various xylophagous species. Characteristic

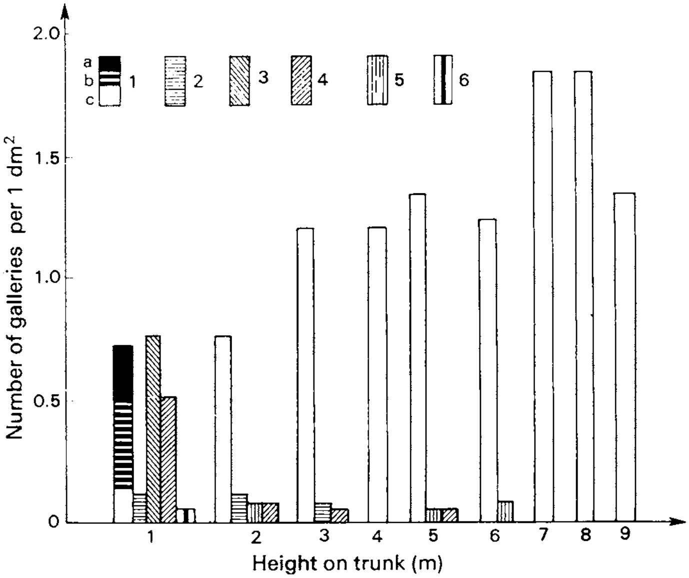


Fig. 8.13 Density of secondary pests and effectiveness of invasion on the Siberian larch after crown fire (after Isaev & Girs, 1975): 1–6 – various pest species, 1 – *Ips subelongatus* Motschulsky; a – galleries filled with resin, b – supplementary feeding, c – developed feeding sites

insects which infest pine forest stands damaged by fires are *Monochamus galloprovincialis* (Olivier), *Arhopalus rusticus* (L.) and *Spondylis buprestoides* (L.), (*Cerambycidae*), *Melanophila acuminata* (De Geer) (*Buprestidae*) and certain *Siricidae* (Schnaider, 1954). Bark-beetles also find the conditions favourable for development, including *Tomicus piniperda* (L.), *T. minor* (Hartig), *Ips sexdentatus* (Börner), *I. acuminatus* (Gyllenhal), *Trypodendron lineatum* (Olivier), *Pissodes piniphilus* (Herbst) as well as the cerambycids *Phaenops cyanea* (F.), *Acanthocinus aedilis* (L.), *Ergates faber* (L.) and *Asemum striatum* (L.). Species such as *Arhopalus rusticus* and *Asemum stratum* not only infest dying trees but also butt parts of living trees in places where the cambium is destroyed (Dominik, 1977).

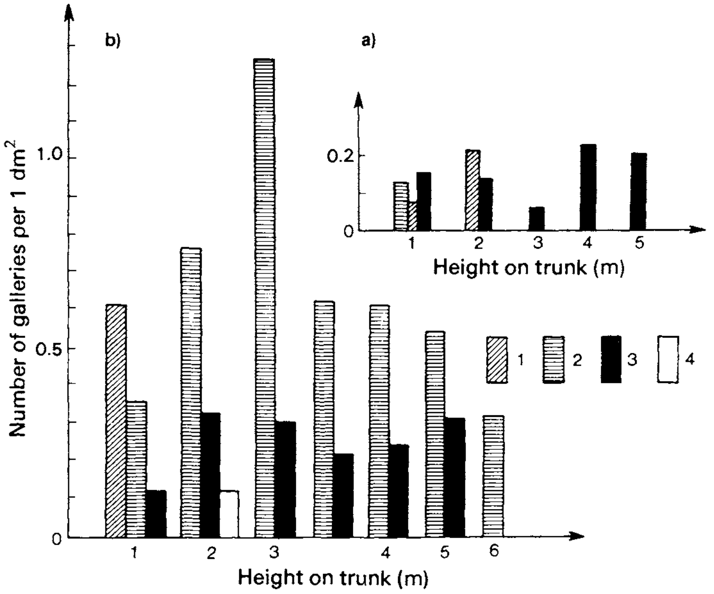


Fig. 8.14 Density of secondary pests and effectiveness of invasion of the Siberian larch after surface fire; 2-year cycle of invasion (after Isaev & Girs, 1975): a — with intact crown, b — with damaged crown; 1 — *Acanthocinus carinulatus* (Gebler), larval galleries, 2 — *Phaenops guttulata* (Gebler), larval galleries, 3 — *Ips subelongatus* Motschulsky, maternal galleries of bark-beetles filled with resin, 4 — *Ips subelongatus* Motschulsky, completed maternal galleries of bark-beetles

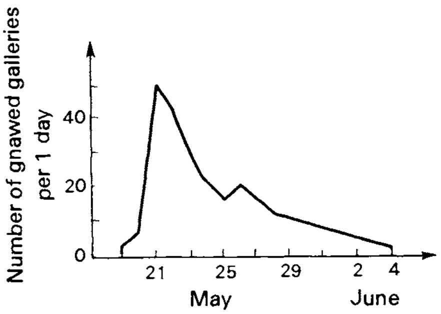


Fig. 8.15 Dynamics of invasion of the Siberian larch by *Ips subelongatus* Motschulsky after surface fire (after Isaev & Girs, 1975)

The course of invasion of burnt forest stands by insects depends on the site conditions and on the habitat type of the forest as well as on the season, the intensity and range of the fire and the age of forest stands. The original abundance of the insect population in the environs of the burnt area, as well as the sanitary condition of the forest and weather conditions play an important role in the propagation of pests. In general the composition of the entomofauna invading trees weakened by fire is more stable in spruce forest stands than in pine stands. *Monochamus* spp., *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) predominate in such spruce forests.

Depending on the season of the occurrence of the fire, spring (April–May), summer (June–July) and autumn (August) burnt sites may be distinguished. Spring burnt sites are invaded by insects in the same year and are potentially most dangerous for forest stands due to the rate and intensity of the development of xylophages. *Polygraphus poligraphus* (L.) and *Tetropium castaneum* (L.) are most abundant in spruce forests in such situations. Autumn burnt sites are less dangerous since they are not infested by pests during the same year.

The invasion of burnt forest stands of an area up to 5 ha occurs mainly in the first and second years after the fire. In larger areas, however, this occurs in the third or fourth year since insect populations have a limited capacity for the immediate invasion of large areas of debilitated forest stands. *Tomicus piniperda* and *Pityogenes chalcographus* remain for the longest period in such forest stands and are even observed in the sixth and seventh year after damage due to fire. *Phaenops cyanea* and *Polygraphus poligraphus* remain for the shortest period in burnt forest stands. *Ips typographus* and *Tomicus minor* occupy an intermediate place in this respect and their abundance distinctly decreases in the third year (Vorontsov, 1963). The dynamics of the invasion of burnt forest stands by secondary pests is determined by the food requirements of these insects. The species remaining in burnt stands for the shortest period generally infest the most severely damaged trees. The intensity of the invasion of burnt forest stands by insects depends, moreover, on the age and compactness of the stands. This is due to the fact that the abundance of xylophages is invariably higher in old forest stands with low compactness.

The influence of fires on the occurrence of phytophages may even extend to the second forest generation. This is manifested, for instance, by an increase in the occurrence of *Agrotis* sp., *Philopedon plagiatus* (Schaller) and *Strophosomus* sp. in pine plantations established on burnt sites.

Fires also have an important influence on the soil fauna. The essential significance of fires in the formation of soil insect communities consists of the destruction of the litter and the decrease of the acidity of the organic soil layer due to the accumulation of ashes containing mineral substance from the litter. The direct influence of temperature is of lesser importance since fire is a short-lasting phenomenon and the soil entomofauna may find shelter in soil crevices and other refuges. Moreover high temperatures only occur in the litter (75°C) whereas at the junction between thin litter and mineral soil it is only 37°C (Huhta *et al.*, 1967). Under such conditions the litter was only 40°C and the surface of mineral soil 28°C an hour after the fire. The consequences of fire are lasting and the regeneration of communities of some soil invertebrates may take up to about 30 years (Karppinen, 1957).

Three groups of litter invertebrates may be distinguished according to their different reactions, namely changes in abundance, due to fires evoked on clear felling sites in pine and spruce forests. The first group includes various *Coleoptera*, the abundance of which remains low for many years after the fire. Although adults survive the fire in hiding-places, the reduction of the food stock on these sites limits their subsequent occurrence with the result that the abundance of the larvae of hese insects also decreases (Fig. 8.16).

The second group consists of species whose abundance exhibits wide oscillations on fire sites, as seen in certain species of *Collembola*, for example.

The third group includes insects such as *Diptera* larvae, the abundance of which distinctly decreases after a fire and then, after a period of several years, rises to a level exceeding that in forest stands not damaged by fire (Huhta *et al.*, 1967; 1969).

It has not been established when stabilization of the communities of soil insects takes place on sites involved in surface or crown fires, but this process usually lasts at least ten years.

On burnt sites, particularly in the vicinity of scorched parts of trees, insects may appear which under other circumstances are very rare or even completely absent. Such insects include the carabid *Agonum quadripunctatum* (De Geer) (Burakowski, unpublished work). It is possible that in the past these species were associated with natural fire sites and at present constitute a very peculiar relict element of primeval forests.

Thus, surface and crown fires have an important influence on the arboreal and soil insect communities in that they significantly alter their structure and functions. The premature death of trees and the acceleration of the mineralization of organic remains due to the process of burning leads to an intensification of the circulation of matter in forest ecosystems. This, together with the advanced leaching of mineral com-

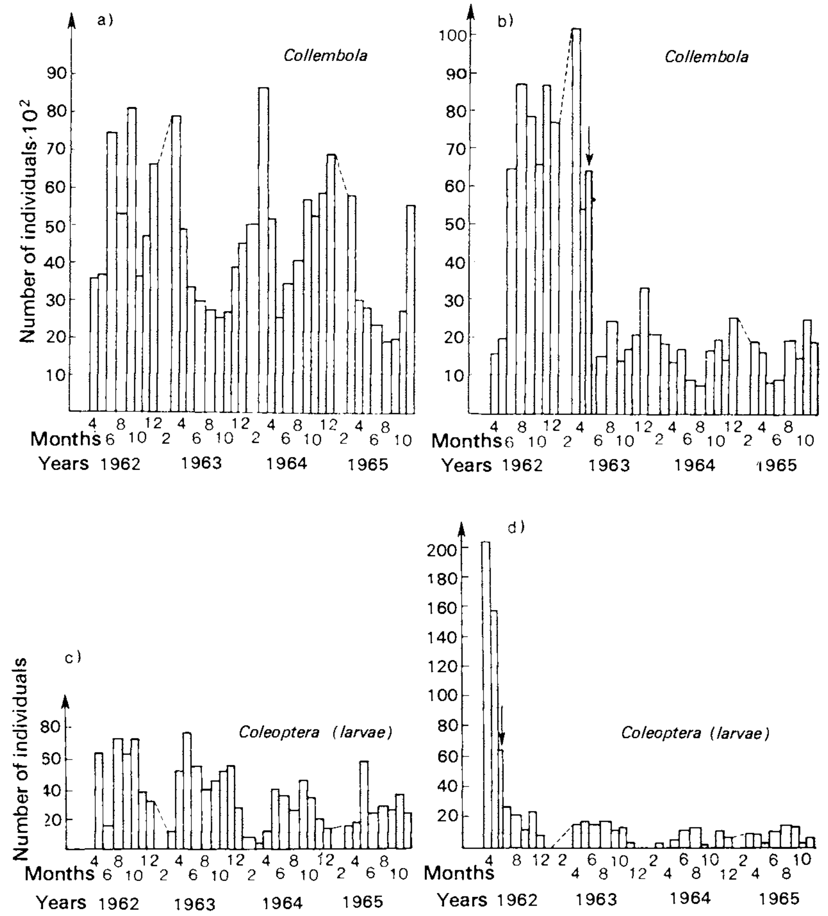


Fig. 8.16 Changes in soil entomofauna of *Vaccinium* forest under the influence of fire (after Huhta *et al.*, 1969): a, c — forest stands undamaged by fire, b, d — burnt clear cuttings; arrows indicate dates of fire

pounds and the inhibition of the formation of zoogenous humus exerts a negative influence on the productivity of forest stands which have been exploited for many years. The influence of fires on the forest environment could only be favourable if the matter produced and energy accumulated here were not transferred to other ecosystems.

The course and consequences of ground fires differ widely from those described above. Ground fires arise in peat soils or in shallow lignite deposits and may last for several dozen years, proceeding slowly and radially from the site of origin. Trees and the herb layer perish and the ocnfiguration of the area and water conditions change as a result oj ground fires. The temperature of the superficial soil layer over the zone of the fire may rise to 75–80°C. There is no data available at present concerning the changes in the entomofauna on areas of ground fires, although studies on other invertebrates (*Oribatei*) have demonstrated a zonal (with respect to the source of the fire) variability of communities. These communities did not regenerate their specific composition and abundance in a period of 45 years following the fire (Fig. 8.17).

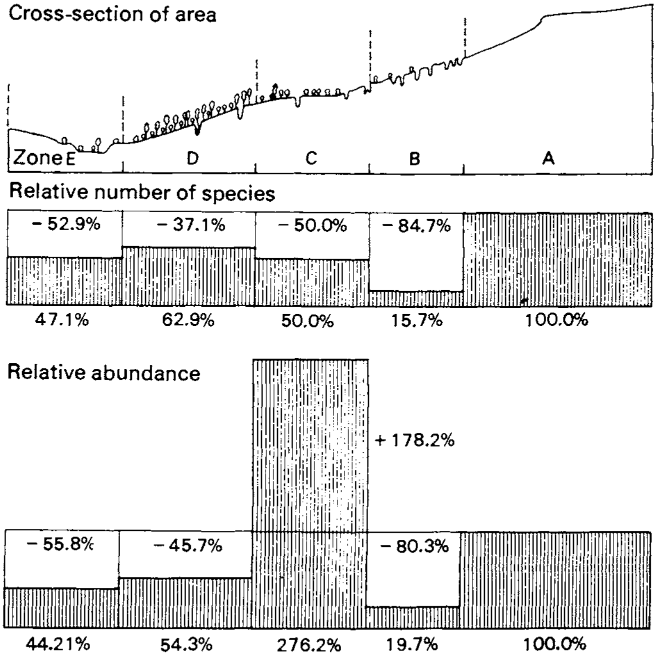


Fig. 8.17 Changes in the community of *Oribatei* under the influence of ground fire of lignits seams (after Vaněk, 1975)

8.4 Industrial air pollution and its accumulation in the soil

Industrial centres and large chemical plants are the main sources of air pollution (Fig. 8.18). Gases, vapours, smokes and dusts of various chemical composition contribute to this pollution. A list of sources of air pollution is given in Table 8.4.

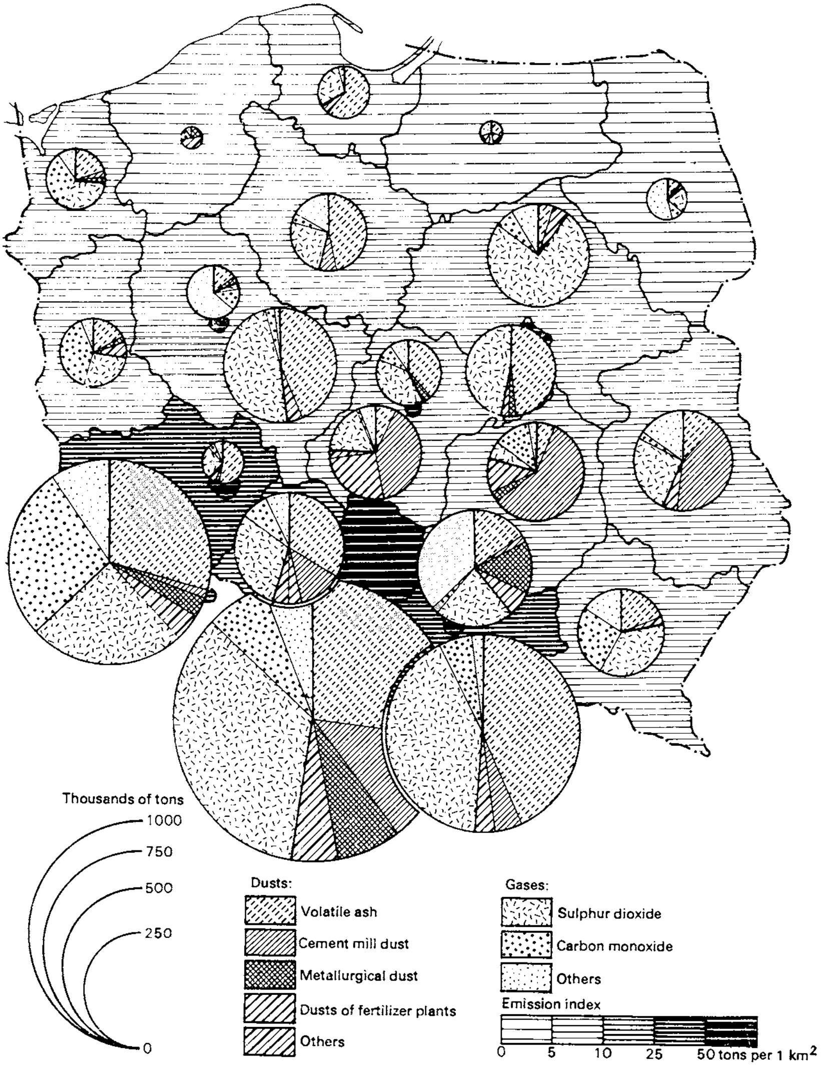


Fig. 8.18 Distribution of industrial air pollution in Poland (after Chief Census Bureau, 1971)

The range of the influence of industry on the forest continues steadily to increase. In 1957 the first listing of the range of the influence of industrial air pollution on forests demonstrated that 35 000 ha of forest stands are endangered in the Katowice and 590 ha in the Cracow State Forest District. In 1965 as much as about 250 000 ha of forests were

Table 8.4 List of sources of pollution of atmospheric air (after Bartkowski, 1975).

Group of sources	Aerosol	Gases and vapours	Amount of losses
Combustion processes	dust, smoke	NO_2, SO_2, CO_2, organic substances, acids	0.05–1.5% of fuel weight
Run of motorcar engines	smoke	NO_2, CO_2, acids, organic substances	4–7% of fuel weight
Oil processing	dust, fogg	SO_2, H_2S, NH_3, CO, carbohydrates, mercaptans	0.25–1.5% of weight of material processed
Chemical processes	dust, smoke fogg, spray	dependent on the process (SO_2, CO, NH_3, acids, organic substances, fragrant substances, solvents, sulphides)	0.5–2.0% of weight of material processed
Piro-and electro-metallurgic processes	dust, smoke	SO_2, CO, fluorine compounds, organic substances	1.0–3.0% of weight of material processed
Material processing	dust, smoke	dependent on the process (SO_2, CO, fluorine compounds, organic substances)	1.0–3.0% of weight of material processed
Fodder and food production	dust, fogg	fragrant substances	0.25–1.0% of weight of material processed

under the influence of industrial emissions and 20% of them were dying as a result of this process. In 1971 the surface of forest stands endangered by the influence of industrial dusts and gases amounted to 239 147 ha, 45 703 ha of which were dying forest stands. In 1978 the area of forests influenced by industrial emissions increased to 379 000 ha. In 1985 the forest area morphologically damaged by industry air pollution rised up to 650 000 ha. If this rising tendency is not inhibited, about 1 million hectares will be under the influence of industrial pollution between 1985 and 1990.

The industrial pollution of atmospheric air mainly influences insects indirectly through the physiological condition of their host plants, as well as directly through changes in the chemical condition of their environment, particularly that of the soil. The noxious influence of pollutants on plants depends on the degree of the atmospheric pollution, the period and duration of their activity, the amount of dust precipitation and the degree of its comminution or nature of the constituent chemical compounds. In Poland, oxides of sulphur play the most important role among the gaseous air pollutants. They cause intensive perturbations in the life processes of trees and acidify the soil. Moreover, nitrogen oxides exhibit a toxic influence on plant and animal organisms and fluorine compounds negatively influence the enzymatic system of trees (Dominik, 1977). The acidification of forest soils by sulphur compounds takes place even at considerable distances from the source of emission and exercises a significant influence on the forest environment and entomocenoses (Braekke, 1976).

The fir, spruce and pine are tree species most susceptible to various air pollutants. The weakening of trees due to air pollution causes an increase in the abundance of primary and secondary insect pests. Pine plantations and thickets under such conditions exhibit an increased abundance of *Exoteleia dodecella* (L.), *Rhyacionia buoliana* (D. & S.), *Retinia resinella* (L.), *Blastethia turionella* (L.), *Phycis mutadella* (Fuchs), *Brachyderes incanus* (L.), *Thecodiplosis brachyntera* (Schwägrichen), *Brachonyx pineti* (Paykull), *Aradus cinnamomeus* (Panzer) (Sierpiński, 1966) and many species of plant lice, particularly those belonging to the genera *Cinara* and *Schizolachnus* (Wiąckowski, 1977). Contrary to situations in forest stands growing beyond the polluted zone, many phytophagous species such as *Exoteleia dodecella* and *Aradus cinnamomeus* are more tolerant to factors such as the age of the trees and the nature of habitat. They thus occur in large numbers in forest stands of all age classes and on various soils, whereas their occurrence is generally associated with pine thickets growing on sandy soils which are relatively poor as regards their plant nutrient content.

The following species invade the pine trunks of trees weakened by industrial air pollution in large numbers: *Tomicus piniperda* (L.), *Pissodes piniphilus* (Herbst), *Phaenops cyanea* (F.), *Anthaxia qaudripunctata* (L.), *Trypodendron lineatum* (Olivier), *Monochamus galloprovincialis* (Olivier), *Arhopalus* (= *Criocephalus*) *rusticus* (L.), *Asemum striatum* (L.), *Ips sexdentatus* (Börner), *Hylurgops palliatus* (Gyllenhal) and *Urocerus gigas* (L.) (Schnaider & Sierpiński, 1967). The following species occur on the spruce under analogous conditions: *Pissodes harcyniae* (Herbst), *P. scabricollis* (Miller), *Hylurgops palliatus*, *Trypodendron lineatum*, *Ips typographus* (L.) and *Siricidae*. The following species are observed on the fir: *Pissodes piceae* (Illiger), *Pityokteines curvidens* (Germar), *P. spinidens* (Reitter), *P. vorontzovi* (Jacobson), *Cryphalus piceae* (Ratzeburg), *Hylecoetus dermestoides* (L.), *Trypodendron lineatum* (Olivier) and *Siricidae*.

Due to the pollution this group of insects also exhibits changed ecological optima and an extended range of tolerance to environmental factors, particularly food. This may lead to changes in the succession of the invasion of weakened trees by insects. In the Upper Silesian Industrial Centre *Pissodes piniphilus*, and *Arhopalus rusticus* invade the pine before *Tomicus piniperda*, i.e. contrary to the succession in non-polluted forest stands. *Siricidae* also infest the trunks of pines while the crowns are still green, whereas elsewhere such trees are never attractive to these insects and do not provide the sites of their oviposition (Schnaider & Sierpiński, 1967). *Matsucoccus pini* Green, a species which, until recently, was only very seldom observed in Central Europe, occurs in large numbers in pine bark in industrial areas (Siewniak, 1972).

Although deciduous trees are less susceptible to pollution than conifers, the xylophages of these trees also find conditions conducive to their development conditions in the zone of activity of industrial emissions. *Aegeria sphaeciformis* Germar, *Xiphydria camelus* (L.) and *Tremex fuscicornis* (F.) occur on the birch. The alder is invaded by large numbers of *Cryptorrhynchus lapathi* (L.), *Cossus cossus* L. and *Aegeria sphaeciformis*. The aspen and the poplar are likewise invaded by *Saperda populnea* (L.) and *Paranthrene tabaniformis* (Rottemburg).

Besides the chronic debilitation of trees, the low compactness of forest stands due to the intensified dying off of trees is the main cause of the mass appearance of secondary pests. The invasion of trees by insects around the sources of emission is doubtless of zonal character (Fig. 8.19), although the data accumulated on this subject are insufficient for an evaluation of the regularity of this phenomenon.

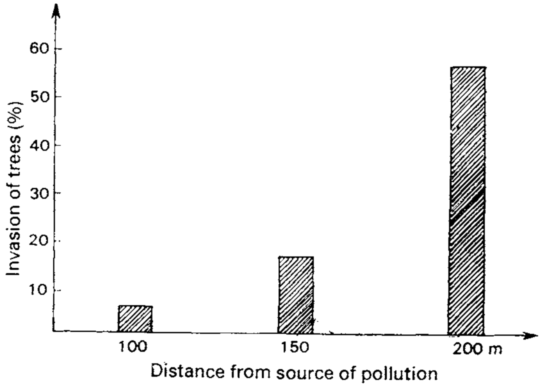


Fig. 8.19 Zonal character of occurrence of noxious insects on birch around sources of emission of Czarna Huta (ironworks) (after Schnaider & Sierpiński, 1967)

A relatively low abundance of foliophagous insects is observed in forest stands growing within the range of the noxious influences of industry. This may be due to the fact that the assimilation apparatus of trees is covered with dust containing substances which are harmful to such insects. Only *Pristophora abietum* (Christ) on the spruce and *Acantholyda posticalis* Matsumura on the pine exhibit a tendency to mass appearance in industrial areas.

Industrial air pollution in the form of dust, suspensions or in solution may accumulate in the soil. Considerable amounts of these substances reach the soil along with the fallen leaves on and in which they were originally accumulated. Notwithstanding the chemical changes in the soil, they cause the disapearance or limitation of the flora of the forest floor, disturb the water conditions of the soil and deteriorate the soil structure thus leading to essential changes in the edaphon. Solid particles of pollutants such as urea or ammonium nitrate accumulating in the superficial soil layer exert a direct influence on soil organisms. Gases such as ammonia or sulphur dioxide mainly act indirectly through their influence on plants, the condition of which is decisive for the gustatory attraction and nutrient value of the litter. As a result of changes in the vegetal cover pollution also indirectly influences the soil microclimate, which in turn determines the occurrence of soil insects and other animals (Górny, 1974). The range of influence of industrial air pollution on various organisms may be considerable and encompass up to several dozen kilometres. The area affected by such pollution exhibits characteristic changes in the communities of organisms which may be indicated, for example, by changes in the number of species, which occur there, changes in the index of diversity of the community, etc. Analysis of these changes indicates that their course invariably exhibits a typical decline towards the centres of pollution.

This regularity affects various organisms and demonstrates that the highest pressure of pollution on living organisms occurs at a certain distance from its source (Fig. 8.20). Furthermore, pollution may evoke various changes in population and bioenergetic phenomena, as well as changes in the behaviour and morphology of insects, etc.

During the course of a seven year study in the region of Puławy, three phases in the reactions of communities of soil invertebrates have been distinguished (Górny, 1974).

The first phase, which lasted 2–3 years from the onset of production by Nitrogen Fertilizer Works, was primarily characterized by quantitative changes in the communities of the entomofauna. In the first

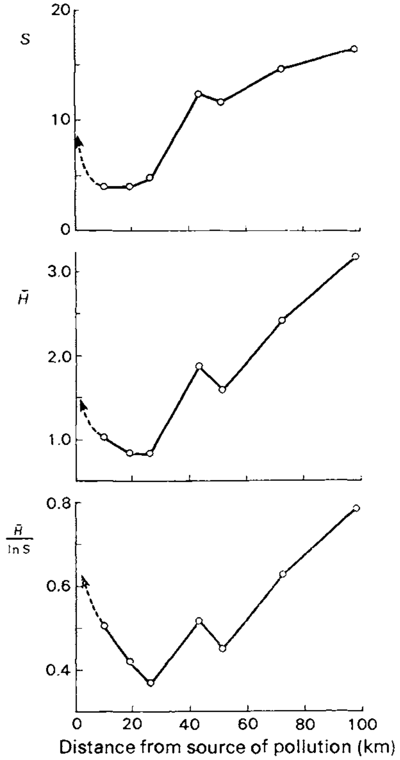


Fig. 8.20 Value of some ecological indices of invertebrate communities in dependence on the distance from the source of pollution (after Jacobs, 1975): S – number of species, $\bar{H}$ – index of general species diversity, $\bar{H}/\ln S$ – index of evenness (J) evenness

year the specific composition of *Collembola* remained intact but the number of individuals increased. In the second and third years this phenomenon was intensified, with *Schoettella ununguiculata* (Tullberg) and *Folsomia quadrioculata* (Tullberg) exhibiting the highest increase of abundance. The increase in the number of *Collembola* by 156% as compared with the control area could be associated with the parallel reduction of the abundance of predators. As early as after just one year, the population density of predacious carabid beetles decreased to 25% of the original number. On the other hand, the mobility of *Carabidae* increased in the vicinity of the sources of emission which may have been due to the reduction of the food stock of these insects as well as to the absence of a herb layer in the zone concerned (Leśniak, 1971). The dominance structure of this community was also affected.

The second phase of changes was characterized by a reduction in the number of species and individuals due to the increase of concentration of the emitted substances in the soil. A further dissociation of the structure of communities was also observed. A considerable reduction in the number of species and individuals of *Collembola* occurred in the fourth year. In the fifth year the abundance of *Collembola* in the most polluted zone, in which the dead forest stand was felled and the yearly precipitation per 1 ha of forest amounted to 3800 t of ammonium nitrate, 19 t of ammonia, 4100 t of nitrogen oxide and a certain amount of SO_2 and CO_2, fell to 5–10% of the number in non-polluted forest stands. Considerable changes also occurred during this period in the specific composition of *Carabidae*. Structural curves of the frequency of species of this family illustrating the situation in the fourth to sixth year after the onset of production in the factory indicate that, with the accumulation of pollution, the number of species of a higher degree of stability increased whereas that of rare species decreased. This is shown by the higher symmetry of the curves discussed (Fig. 8.21). The coefficient of Odum "Od" is the quotient of the number of rare species to the number of species of high frequency and may be regarded as an index of pollution. In this particular case for the years 1972, 1973 and 1974 it was calculated as 1.60, 1.85 and 1.71 respectively. The lower the value of this index the stronger was the action of pollution during the period under consideration (Leśniak, 1975).

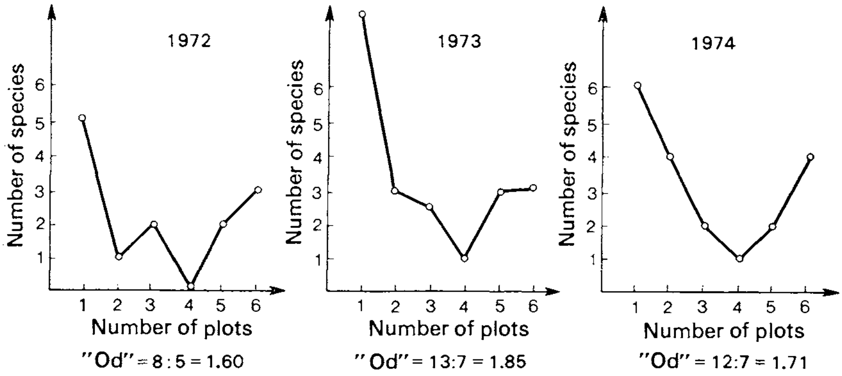


Fig. 8.21 Distorted structures of frequency of *Carabidae* in successive years after the start of production in the Nitrogen Fertilizer Works in Puławy (after Leśniak, 1975); left to right: more rare species to species of high degree of stability

The third phase exhibited disturbances of the systems of mutual dependence between various groups of organisms. These were indicated by changes in the ecological niches of species constituting these communities, and were the results of selective adaptations to new environmental conditions. It has been proved experimentally (Górny, 1975a) that the intoxication of the third zone by nitrogen compounds during this period was so intensive that when soil organisms were transferred with their environment (soil blocks) to this zone from zone 0 (forest stands with no symptoms of intoxication), they perished after one or two months. This indicates that the intoxication of the soil environment proceeded rapidly and that the accumulation of substances emitted by the Nitrogen Fertilizer Works steadily intensified the process of intoxication. For this reason, soil blocks transferred from zone 3 to zone 0, even during the course of one year, were not inhabited by the local soil fauna to any degree which would differentiate it from the fauna of zone 3. This points to difficulties in the zoological recultivation of forest areas polluted by industrial emissions.

During the phase of intensive environmental pollution, ants behaved differently to other soil animals. *Formica polyctena* Foerster exhibited peculiar reactions of adaptation to the new ecological systems produced in the environs of Puławy. Reactions resulting from the group mode of life and based on the resistance of this species made it possible for it to consolidate its population on areas where the soil was intensively polluted with nitrogen compounds. The probable stimulation of development of nitrophilous microflora within the range of the ant nests was the basic adaptation reaction. Studies demonstrated that nitrophilous microflora was most abundant and diversified in the above ground parts of the ant-hills. Cellulolytic bacteria and actinomycetes dominated and saccharomycetes were also abundant here. Górny (1974, 1976) supposes that the abundant occurrence of nitrogen-binding microorganisms reduces the nitrogen excess in the nests, thus securing the efficient functioning of the ants. Furthermore, the establishment of new nests of *F. polyctena* in the third zone of pollution seems to indicate the existence of a rich source of food for this species here. Indeed the toxic influence of air pollution affected many groups of strongly flying or rapidly moving groups of arthropods (*Hymenoptera*, *Diptera*, *Raphidioptera*, *Locustidae*, *Araneidae*, *Chilopoda*) which congregate on the forest floor and become an additional food stock for *F. polyctena*. The latter observation has not yet been confirmed and thus cannot be generalized, but the increased activity of the microflora in ant-hills has been thoroughly studied in investigations on other ant species such as *Lasius niger* (L.) and *Myrmica rubra* (L.) in the environs of Puławy. These species occurred here in the zone of the highest destruction on completely degraded sites covered with tufts of grass of the genera *Calamagrostis* and *Agrostis*, as well as *Senecio silvaticus* L. Of the two ant populations, that of *L. niger* was more resistant and its abundance was higher than that of *M. rubra*. The higher adaptibility of *L. niger* is also manifested by the modification of the activity of the microflora and the content of pollutants in its nests. The abundance of microorganisms in the nests of *M. rubra* is lower than that in the soil environment, whereas it is higher in the nests of *L. niger*. The microorganisms here are mainly those which utilize mineral nitrogen and aminifying bacteria, as well as the resting forms of bacteria. A fundamental discovery of these studies is the establishment of the fact that the numbers of microorganisms utilizing mineral nitrogen as well as those of aminifying bacteria are inversely correlated with the pollution of the environement. *L. niger* occurs when the numbers of these microorganisms are at their lowest (i.e. highest pollution) and the activity of individuals in the ant-hill varies according to an inverse dependence. *M. rubra* prefers to build its nests on sites where the numbers of aminifying bacteria and organisms utilizing mineral nitrogen are higher. This consequently reduces the ants' activity in the nest in dependence on the en-

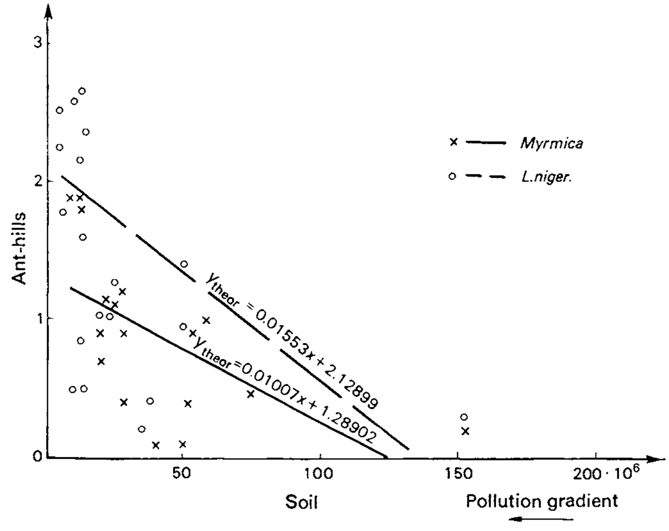


Fig. 8.22 Dependence between the number of microorganisms utilizing mineral nitrogen in the polluted environment and in ant-hills (after Pętal *et al.*, 1975)

vironmental gradient (Figs. 8.22 and 8.23). Nitrification in the ant-hill is inversely proportional to that in the environment. It is higher for *M. rubra* and lower for *L. niger*.

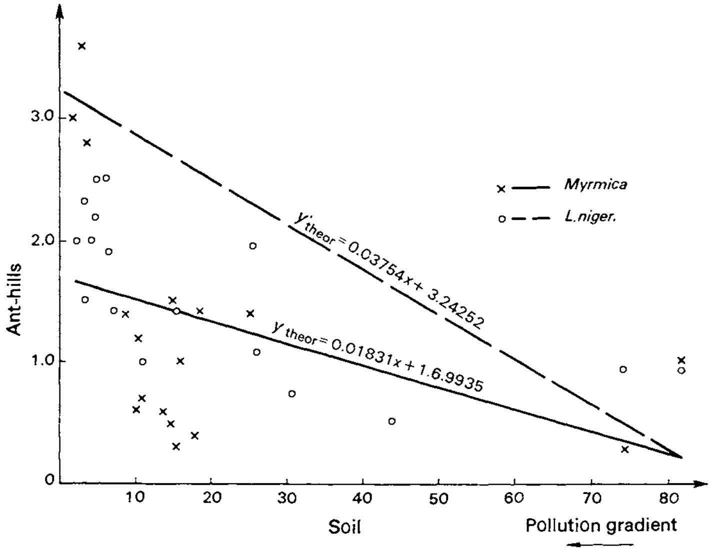


Fig. 8.23 Dependence between the number of aminifying bacteria in the environment and in the ant-hills (after Pętal *et al.*, 1975)

It would thus appear that microbiological processes undergo compensation in ants' nests and the more intensive they are in the environment the less intensive is their course in the ant-hill and vice versa. This leads to a reduction of pollution undergoing buffer effects in the ant-hills. Although the populations of ants mentioned above are many times less abundant on the areas affected by pollution than in other environments, e.g. meadows, the index of growth of their immature generation is higher here. This may be the result of biological adaptation due to the restriction of the developmental period to the occurrence of the maximum stock of available food. In the polluted zone development is completed by the end of June, whereas under other conditions it takes distinctly longer. The mortality of *M. rubra* adults also seems lower in the most heavily poisoned zone due to the decelerated circulation of the biomass (Pętal *et al.*, 1975).

It is thus evident from the examples given above that the reactions of different organisms to industrial air and soil pollution may vary widely and the changes in the environmental systems cause peculiar adaptations in insects which exhibit the highest degree of social life.

It is noteworthy that the selective pressure exerted by predators on non-melanistic *Lepidoptera* in industrial centres in England (and other countries) led to the occurrence of a phenomenon known as industrial melanism, i.e. the consolidation of dark-coloured forms adapted to the colour of the substrate on which they usually rest. The melanistic forms of *Biston betularia* (L.), *Odontoptera bidentata* (Clerck), *Lymantria monacha* (L.), *Polia nebulosa* (Hufnagel) and other species are particularly well known. Many of them have now spread beyond the industrial centres (Ford, 1964). In Silesia in Poland 26.2% of *Lepidoptera* species (296 out of 1111) exhibit melanistic varieties, their number being by 38% higher in Upper than in Lower Silesia (Drozda, 1970).

8.5 Mining

Industrial waste land occupies an increasingly larger area in many countries. In Poland it already accounts for 300 000 ha. Mine spoils, as well as areas with deformed surfaces covered by depressions, hollows, craters, ditches, crevices, sills, etc. due to mining activity are particularly prominent here (Figs. 8.24 and 8.25).

On forest areas these deformations result in the destruction of the root systems of trees or change the hydrography of the area. This affects the physiological condition of the trees and indirectly changes the

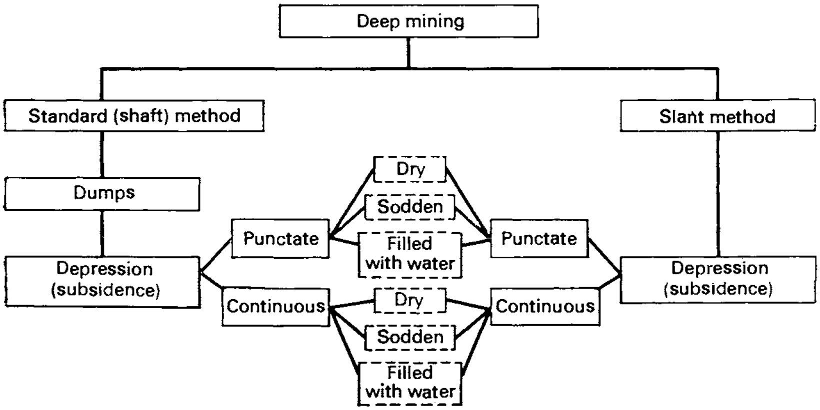


Fig. 8.24 Scheme of transformations of surfaces in deep mining (after Greszta, 1976)

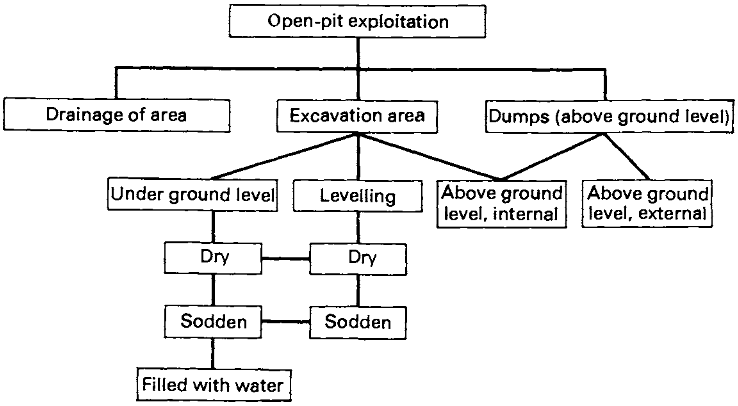


Fig. 8.25 Scheme of transformations of surfaces in open pit exploitation (after Greszta, 1976)

course of dynamic-population processes in phytophages, particularly *Scolytidae*, *Cerambycidae*, *Curculionidae* and *Buprestidae* which invade weakened forest stands. It may also have a direct influence on the abiotic conditions of occurrence of the soil entomofauna. Physiographic deformation of the environment of industrial centres influences the insects in parallel with the advancing chemical and mechanical air pollution and this increases the reaction of the entomofauna.

The diversification of physical and chemical properties of various industrial waste, as well as the different ways in which it is stored, result in the fact that the course of changes which generally occur in succession processes may potentially acquire any form in the ecological systems new for the entomofauna. Unfortunately the processes of the invasion of mine spoils and areas remaining after aggregate exploitation by insects are still poorly understood. Several noteworthy works dealing with this problem published in recent decades, including the fundamental dissertation of Dunger (1968) devoted to the succession of soil fauna on waste-heaps and dumping grounds produced in the course of open-pit exploitation of lignite in the German Democratic Republic, concern the ecological situation of non-controlled recultivation activities, including the processes of afforestation. The results of these studies will thus be presented in a subsequent section of this work.

The industrial deformations of areas, if they do not lead to the occurrence of toxic rubble, are subject to a natural process of colonization by plants, shrubs and trees as well as the parallel immigration of insects from neighbouring areas. Specific systems of abiotic environmental factors may arise in successive stages. They may make possible a mass occurrence of stenotopic forms observed in nature in quite different ecological situations or even of species rarely observed in the given geographical region. Under such conditions on dumps of Tertiary rubble of a lignite quarry near Leipzig, *Labidura riparia* (Pallas) spread in large numbers in the summer of 1960. This species is characteristic of humid sandy sea shores and some river banks, as well as of inland dunes exhibiting specific water conditions. In the German Democratic Republic it had not been observed inland (with the exception of the quarry areas) for about 100 years (Dunger, 1968).

The process of invasion of waste-heaps and dumping grounds by insects follows a definite pattern. Forest *Carabidae* invade afforested waste-heaps, heading for them along the dark outline of the eminence (Neumann, 1971). A suitable microclimate and adequate soil humidity are the decisive factors for successful immigration. Because of this, specific possibilities of invasion arise on sites of exploitation of aggregates of Quaternary origin. Enormous excavations left after the exploitation of clay create conditions under which many otherwise rare species of *Carabidae* and *Staphylinidae*, noteworthy from the zoogeographical standpoint, may occur.

Influence of forest management on the entomofauna

The forest environment provides many examples of the influence of economic activities on biocenotic relationships and on the occurrence of plants and animals. This is because the managed forest, which has a long-term cycle of production, has retained many of its natural features whereas forest organisms readily react to any human interference in their environment. The problems of anthropogenous influences on forest entomocenoses in relation to the economic utilization of the forest and to the occurrence of noxious insects, as regards forest protection, come within the scope of forest sanitation and are well known because of their importance in the productivity of forest stands (Schimitschek, 1969).

The influence of forest management on the occurrence of insects which regulate the abundance of noxious species, as well as on the soil entomofauna which plays an important role in soil-forming processes is much less well known.

Since the influences of forest management on the entomofauna result in a multitude of diverse biological situations, the discussion in this chapter will be confined to those which are the direct result of willful human activities rather than to those due to the methods used in controlling noxious forest insects.

The consequences of such forest management which will be discussed here have a long history and a wide scope of influence on entomocenoses. These include the specific composition of forest stands, sanitation and exploitation felling, cultivation and fertilization of forest soils, and the mechanical and chemical cultivation practices on plantations.

8.6 Species composition of the forest stand

Each type of forest, regardless of the criterion of its distinction (i.e. with respect to site or economy), provides specific possibilities for its invasion by insects. These possibilities are largely determined by the species composition of the forest stand, as well by the soil conditions, floristic composition of the herb layer, microclimate and history of the site. Human economic activity influences the entomofauna by the purposeful selection of the species composition of the forest stand and by the methods of forest management adapted to the biological requirements of the chosen tree species (Szujecki, 1976).

There are two main trends of thought influencing the selection of the composite species of forest stands which are suited to the local natural conditions. These are (i) those aiming at the establishment of a species composition which does not conform with the local geobotanical conditions but from which more favourable economic or natural results may be obtained than from the native species, and (ii) those aiming, consciously or unconsciously, at the establishment of a species composition of the forest stand which does not conform with the site conditions but which is based on native species.

Apart from financial reasons, such as obtaining the variety of wood demanded by trade in a short time, organizational reasons such as the ready availability of planting material or the use of simple cultivation measures in coniferous monocultures may also be the motive of such actions.

The first category mentioned above includes examples of the formation of forest stands or plantations of tree species introduced from other geobotanical regions or of species which, although occurring within the given geographical region, do not usually grow in the area under consideration. Instances of the latter include the occurrence of the pine in the western part of Central Europe and forest stands of the European larch in a considerable part of Central Europe. The formation of such forest stands leads to a high impendence of various phytophages (Schimitschek, 1969).

The introduction and acclimatization of species foreign to the local flora, from the entomological standpoint, may lead to one of two consequences. The first is the unconscious introduction of phytophages indigenous for the tree which frequently leads to their acclimatization and subsequent dynamic population processes in the new locality. This has been studied in detail for parthenogenetic populations of the aphid *Gilletteella cooleyi* (Gillette) feeding on Douglas spruce. The second is the adaptation of local phytophages to the introduced tree species which leads to new (initially xenophagous) nutrient systems which extend the range of the host plants of the given insect species.

Thus, in some regions of Europe the larch monophage *Coleophora laricella* (Hübner) became adapted to feeding on the North-American Douglas spruce, which resulted in a considerable increase in its abundance. In another instance, some populations of the largest European bark-beetle, *Dendroctonus micans* (Kugelann) invaded the introduced Sitka spruce and developed certain new morphological features which distinguished them as separate ecological races (Francke-Grosman, 1950). The range of xenophagous phenomena associated with introduced tree and shrub species is very wide. Over 60 species of local phytophages feeding on trees and shrubs of foreign, mainly North-American, origin have been observed in the experimental forests of the Warsaw Agricultural University in Rogów on the Łódź Upland and this number is steadily increasing (Dominik, 1966, a, b; 1968a; 1972). In Poland the introduced poplars in particular became infested with numerous species of insects, of which *Saperda carcharias* (L.) predominated, This was due to the planting of these trees on a large scale, which resulted in a bitter economic disappointment. With no exaggeration it may be said that, besides fungal diseases, this pest was the major cause rendering the use of any of the planned mass of poplar wood impossible.

Although many more such examples may be quoted, their economic significance and biological consequences can in no way be compared with those caused by the disregard of the rules of the cultivation of forest stands, which must conform to the local site conditions with respect to their specific composition and methods of management, as well as by the disregard of the origin of the seeds used for regeneration.

Three kinds of activity may be distinguished here (Schimitschek, 1969):
1) the formation of monocultures on areas of mixed forests where the preferred tree species is native but does not occur in the form of pure forest stands;
2) the formation of pure coniferous forest stands within deciduous forests; and
3) the formation of monocultures which do not conform in general with the site.

The new site-forest stand systems lead to changes in the dynamic-population processes of numerous phytophages as well as their parasites and predators. The mechanism of these changes is based both on the new microclimatic conditions of pure forest stands and on the altered physiological reactions of the trees which are now growing under different soil and often also unfavourable water conditions.

The mass appearance of phytophages feeding on introduced coniferous trees in the form of pure forest stands in habitats of mixed forest, became particularly evident in Central Europe. *Choristoneura murinana* (Hübner) occurs under such conditions in fir forest stands where it encounters particularly favourable conditions during the period when the second instar caterpillars are feeding on the fir buds in April and May. Such conditions arise on the borders of older, pure fir forest stands characterized by a warm and dry microclimate where extreme temperatures are even wider than on felling areas and consequently lead to physiological disturbances in the trees. Since the physiological age limit of the fir is attained earlier on the borders of its natural range and in unsuitable sites than under conditions appriopriate for its growth, outbreaks of secondary pests also arise. These are mainly of *Pityokteines* spp. and *Pissodes piceae* (Illiger), and are of an intensity never observed in forest stands which consist of a number of different species or under conditions optimal for fir growth. The most intensive outbreaks of primary and secondary pests of the spruce also occurred beyond the natural range of this species and in pure forest stands introduced into habitats of mixed forest. These were due to the accelerated ageing of the spruce under unsuitable conditions and the parallel progressive decline of physiological processes in this tree. The outbreaks of *Ips typographus* (L.) in spruce forests introduced in the place of fir-beech forests in the lower mountain zones are particularly notorious.

Pine phytophages are most prevalent in vast, pure forest stands consisting of trees of uniform age, especially under unfavourable soil water conditions, as well as in pure forest stands of unsuitable sites which previously consisted of pine and various deciduous species.

Numerous manuals and publications concerning forest entomology and forest protection are devoted to the problems of susceptibility of forest stands to diseases and pests in the systems of "chain forest diseases" (Szujecki, 1977).

The influence of changes in the composition of forest stands on phytophages, however, does not only act directly through changes in microclimatic conditions or indirectly through changes in the physiological condition of nutrient plants. There are also indirect effects caused by changes in the abundance and activity of insects and other organisms which have regulatory roles in definite forest biocenoses.

The low regulative ability of pure pine forests is due to the fact that human economic interference with floristic relations of forest biocenoses exerts a stronger influence on the simplification and impoverishment of parasite and predator associations here than in natural coniferous forest habitats (Szujecki, 1976). In the cases discussed the impoverishment of the specific composition of forest stands due to the reduction of diversification unsettles the stability of forest ecosystems and in consequence limits the previously existing regulative ability. This has been clearly shown by Engel (1942) and Klomp (1962) for *Bupalus piniarius* (L.), as well as by Stolina (1959) who studied the occurrence of pests in the forests of Slovakia. Furthermore, changes in the species composition of forest stands evoke changes in the soil entomofauna which play a definite and useful role in the development of the biological efficiency of forest soils. This also, therefore, has a distinct effect on the functioning of the entire forest ecosystem.

Purposefully directed team studies devoted to the influence of the species composition of forest stands have been carried out by the Institute of Forest and Wood Protection, Agricultural University of Warsaw. Such studies were performed on the common pine under various site conditions and included observations on predacious insects occurring in litter (*Carabidae*, *Staphylinidae*) or the sub-bark environment (*Coleoptera*), as well as parasitic insects (*Ichneumonidae*) penetrating the herb layer, undergrowth and tree crowns as adults (Mazur, 1973, 1974, 1979; Sawoniewicz, 1979; Szujecki, 1975, 1977; Szujecki & Perliński, 1975; Szyszko, 1974). The abundance of some pine phytophages (foliophages and xylophages) in relation to the forest stand and environmental conditions was also studied at the same time.

It was found that the soil conditions, which influence the species composition and structure of insect communities, constitute the most important element in the hierarchy of environmental factors determining the occurrence and abundance of insects which act as regulators. The second most important factor is the layered structure of the forest, whereas the differentiation of entomocenoses by the species composition of forest stands occupies only the third place in this respect. Predacious *Coleoptera* which occur under bark are exceptional here. Their occurrence is not influenced by the factors mentioned above, and their species composition and abundance are principally determined by the developmental phase of their prey. The species composition of ichneumons occurring in the tree crowns was also found to be less dependent on the site conditions and presence or lack of undergrowth than that of members of the same family occurring in the undergrowth or herb layers.

It has not been established in potential outbreak areas that the abundance of pine foliophages hibernating in the litter (*Bupalus piniarius* (L.), *Panolis flammea* (D. & S.), *Hyloicus pinastri* (L.), *Diprion* spp., *Dendrolimus pini* (L.), *Semiothisa liturata* Clerck is significantly dependent on the presence of deciduous species in pine forest stands. Nevertheless the number of those phytophages was the lowest in deciduous forest habitats (Fig. 8.26). As regards xylophages, it appeared that the lower abundance of *Tomicus piniperda* (L.) in the fresh forest habitat was correlated with the presence of undergrowth and with the lack of undergrowth in the humid mixed coniferous forest habitat. In fresh mixed coniferous forest and fresh coniferous forest habitats, the presence of undergrowth exercised no influence on the occurrence of this bark-beetle.

The abundance of oligophagous and monophagous ichneumonids developed in dependence on the density of foliophages, whereas the density of the galleries of xylophages exercised no influence on the density predators and saprophages.

The influence of the species composition of forest stands, particularly that of the undergrowth, differed for the various groups of the invertebrates studied. These will be discussed in turn below.

Carabidae. In pine forest stands in coniferous forest habitats the introduced deciduous (oak and beech) undergrowth limited the specific composition and abundance of *Carabidae*. The pressure of undergrowth was higher as its compactness increased, such that its influence on the microclimatic conditions of the forest floor was more effective. On the other hand, *Carabidae* exhibited a greater mobility in the presence of

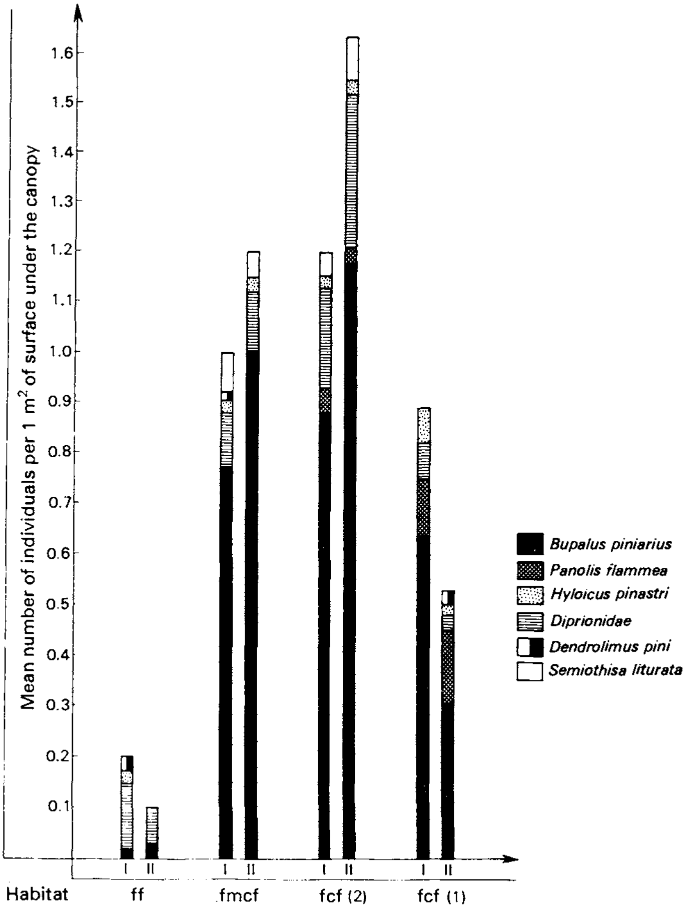


Fig. 8.26 Density of pine foliophages under various habitat conditions (after Sawoniewicz, 1979): ff — fresh forest, fmcf — fresh mixed coniferous forest, fcf — fresh coniferous forest; I — forest stands with deciduous undergrowth, II — pine forest stands without undergrowth, (1), (2) — various localities in Poland

undergrowth. The situation was reversed in the case of deciduous undergrowth and undercrop in pine forest stands in deciduous forest habitats. The abundance of *Carabidae* was higher when the composition of the forest stand and undergrowth showed most similarity to that of the natural one. Carabid species of the autumn developmental type, as well as large predators in coniferous forest habitats, were characterized in the presence of deciduous undergrowth by a higher dominance as compared with the community of these beetles in pure pine forest stands. This was due to the limiting influence of undergrowth on species of the spring developmental type, as well as on the small zoophages and hemizoophages.

Staphylinidae. Oak undergrowth introduced into pine forest stands on poor sites alters the existing environmental conditions which are important to the insects which occur in litter, including *Staphylinidae*. It increases the shading of the forest floor, inhibits the penetration of precipitation into the litter and diminishes its humidity, diminishes the acidity of the superficial litter layer, slightly differentiates the carbon content in soil organic compounds and generally improves the course of litter decomposition, which is indicated by lower C:N value under the undergrowth canopy. Even 30 years after the introduction of undergrowth, there is no significant increase in the density of litter *Staphylinidae* nor is there any change in the dominance structure of their community. On the other hand, the undergrowth, particularly when growing in clusters, differentiates the distribution of various ecological groups of these insects within the range of the forest stand. Forest species concentrate under the undergrowth whereas the non-forest ones (including many species which immigrate here in the autumn from marshes and fields) occur beyond the range of oak crowns (Figs. 8.27 and 8.28). Moreover, the presence of the undergrowth makes it possible for a few species typical of deciduous and mixed forests to occur here, which are otherwise not observed or rare in pure pine forests. The conditions of litter decomposition, as expressed by the content of organic carbon in layer A_L and the C:N ratio, are decisive as regards the density of *Staphylinidae* in various parts of pine forest stands with undergrowth and in pure pine stands (the density of *Staphylinidae* being inversely proportional to these indices). The thickness of the litter is of less significance here (the density of *Staphylinidae* being directly proportional to the thickness of litter).

Predacious and saprophagous sub-bark Coleoptera. The site and forest stand conditions did not play a decisive role in the development of communities of sub-bark beetles in the successive phases of the development of *Tomicus piniperda* (L.) in galleries on fallen trap trees. The first community (seral stage) appearing in the egg and larval developmental phases of *T. piniperda*, with *Rhizophagus depressus* (F.) as the dominant species, consists of specialized, stenotopic predators. The second community which develops at the end of the larval development of *T. pini-*

Fig. 8.27 Single oak undergrowth in pine forest (photo by the author)

perda and persists until the abandonment of its one-year old galleries, consists mainly of eurytopic non-carnivorous species among which *Phloeonomus pusillus* (Gravenhorst) predominates. The deciduous undergrowth in both coniferous and deciduous forest habitats does not affect the rules of the system described above. In rich sites (fresh forest, fresh mixed coniferous forest) the absence of undergrowth leads to an intensive development of the herb layer which shades the traps and therefore

Fig. 8.28 Clumped oak undergrowth (photo by S. Kinelski)

causes their moistening and eliminates the sub-bark species. The introduction of undergrowth into coniferous habitats evokes no directional changes since even the shading of 20–40% of the surface of the forest floor by the undergrowth in the relatively dry environment cannot change the microclimate to a degree which would limit the occurrence of sub-bark beetles.

Ichneumonidae. The layered forest structure is the most important factor in the determination of the composition and structure of the ichneumonids community. Regardless of the site and the composition of the undergrowth, the same community occurred in the tree crowns on all the sites examined. Habitat conditions, along with the associated plants of the herb layer, were decisive in determining the ichneumonids community of the forest floor. Thus different communities of characteristic species composition and dominance structure occurred in each habitat type. The deciduous undergrowth and undercrop in pine forests only constitute the third most important factor which serves to modify the quantitative ratios of some ichneumons. In the first place in all the habitats studied, the ratio of the number of polyphagous *Ichneumonidae* species (parasites of pine foliophages) to that of oligophages was more favourable in the presence of undergrowth (Fig. 8.29). Pine forest stands

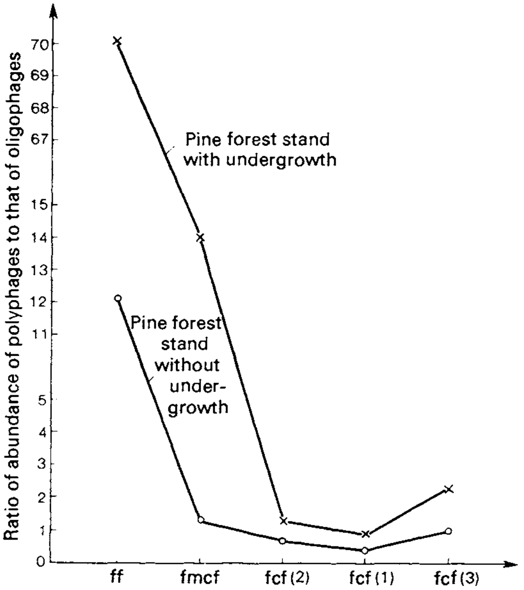


Fig. 8.29 Ratio of the number of polyphagous individuals of *Ichneumonidae* to that of oligophagous individuals in dependence on the presence of deciduous undergrowth in pine forest stands (after Sawoniewicz, 1979)

with an oak undergrowth in habitats of fresh forest and fresh coniferous forest were characterized by a higher total number of species and a higher abundance of ichneumonids parasitic on dendrophilous *Lepidoptera* as compared with forest stands lacking undergrowth. Nevertheless, polyphages associated with *Lepidoptera* living on deciduous trees or on herb plants predominate here. On the other hand, under conditions of richer habitats the undergrowth exercised no influence on the general abundance of ichneumonids. In poorer sites of fresh coniferous forest the presence of deciduous undergrowth, particularly of beech, exercised no influence on the number of species and abundance of ichneumons, this being due mainly to the distinct limitation of the herb layer in which many hosts of the parasites under discussion occur. A situation favourable for the occurrence of nchneumonids arose in the fresh coniferous forest habitat where the introduced oak undergrowth encountered favourable growth conditions, due to the high ground water level. This high level, which determines the physiological condition of the oak, favours the feeding of foliophages the abundance of which is higher here than on sites where the water supply of deciduous trees is insufficient (Ruppert & Langer, 1957). Because of this phenomenon, ichneumonids which find their hosts on oak are more abundant in such forest stands than in those without undergrowth or with undergrowth but under drier conditions. In general, however, in the fresh coniferous forest habitat the forest stands with deciduous undergrowth exhibit a lower abundance and generally a smaller number of species of ichneumonids than forest stands without undergrowth (Fig. 8.30). This may suggest that some other factors are limiting the occurrence of phytophages, including pine pests, and this directly influences the abundance of their parasites in forest stands with an undergrowth layer.

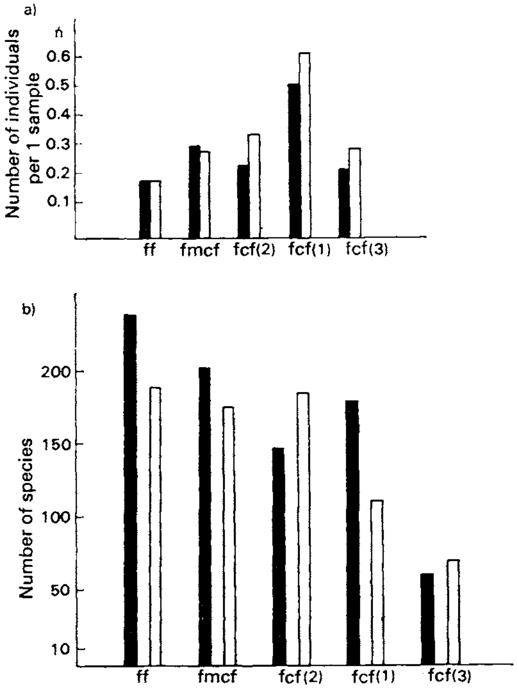


Fig. 8.30 Abundance of individuals (a) and number of species (b) of *Ichneumonidae* in dependence on the habitat and deciduous undergrowth in pine forest stands (after Sawoniewicz, 1979): black bars – pine forest stand with undergrowth, white bars – pine forest stand without undergrowth

The data given above indicate that human economic interference with the floristic relations of forest biocenoses exercises a stronger influence on the deformation of the composition of entomocenoses in richer sites (fresh forest, fresh mixed coniferous forest) than in poor ones. This concerns cases of both the impoverishment of the specific composition of forest stands and (probably) the restoration of the specific composition of entomocenoses by means of a reconstruction of the forest stand tending to an adaptation of its specific composition to habitat conditions. For instance, in the deciduous forest habitat the abundance and mobility of *Carabidae* is several dozen per cent lower in pure pine forest stands than in stands with a specific composition typical of the habitat (Nunberg, 1949; Szyszko, 1974). Such wide differences between pure forest stands and those with deciduous undergrowth were not observed in analogous systems in the mixed coniferous forest habitat (Fig. 8.31). The introduction of deciduous undergrowth into pine forests in poor sites of coniferous forest is a management measure equally disregardant of the rule of the adaptation of the composition of the forest stand to site conditions as of the establishment of pure-coniferous forest stands in habitats of mixed forest or mixed coniferous forest. This unnatural likening of pure pine forests growing in the poorest sites to more stable mixed coniferous forests of more fertile sites by means of the introduction of a foreign undergrowth layer, was to realize the rule expressed as "the higher the diversity of phytocenosis, the higher the diversity of zoocenosis and the higher the stability of the system".

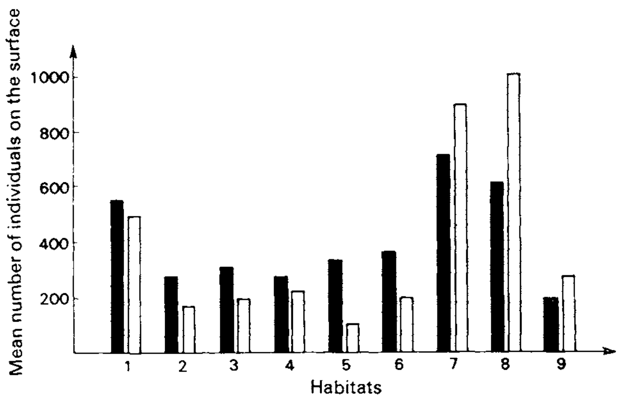


Fig. 8.31 Abundance of *Carabidae* in dependence on the habitat and presence of deciduous undergrowth in pine forest stands, (after Szyszko, 1974): 1–6 and 9 – coniferous forest habitats, 7, 8 – deciduous forest habitats; black bars – pine forest stands, white bars – forest stands with contribution of deciduous species

It appears, however, that under such conditions the undergrowth only increases the indices of diversity of entomocenoses to a limited degree. This is true in the case of forest stands consisting of many species and growing in more fertile sites. The role of deciduous undergrowth in fresh pine forests mainly consists in its influence on the differentiation of the spatial distribution of insects such as *Staphylinidae* and *Ichneumonidae*. This is the result of the differentiation of the light and humidity conditions of the forest floor, as well as of the herb and shrub layer, by the undergrowth and this determines the distribution and behaviour of insects such as *Carabidae*. With the occurrence of undergrowth a spatial separation of ecologically varying insect groups is observed. These

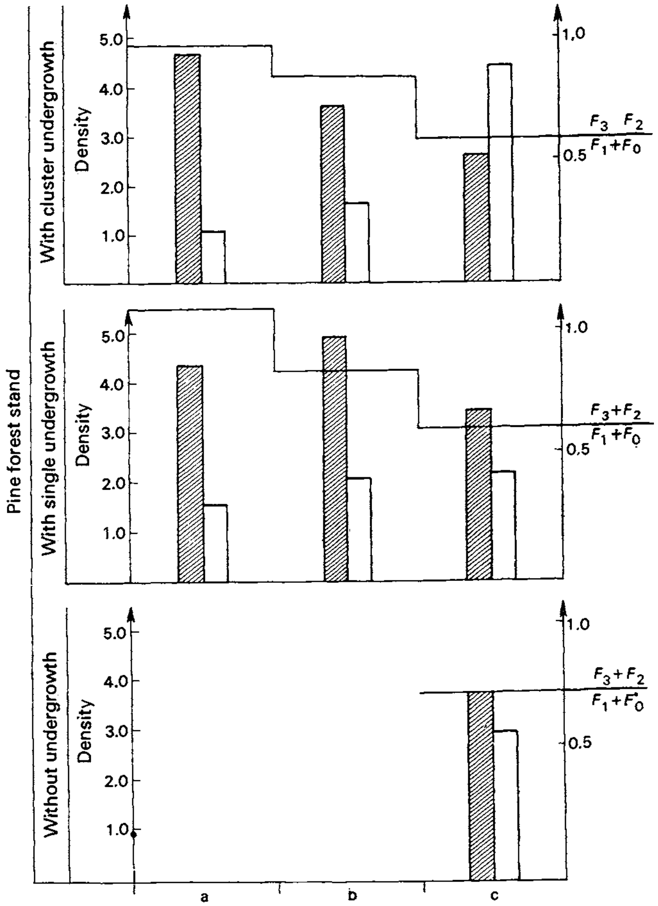


Fig. 8.32 Distribution of various ecological groups of *Staphylinidae* in pine forest stands in dependence on occurrence of oak undergrowth (after Szujecki, 1971): density: individuals per 0.25 m^2, dark bars — (F_2+F_3) forest species, white bars — (F_1+F_0) non-forest species

groups occupy the parts of phytomeliorated forest stands which are most favourable for them (Fig. 8.32). A limitation is observed of photophilous species which include many insects generally "favoured" by human activity such as non-forest species of *Staphylinidae* and certain of the spring developing *Carabidae*. The role of deciduous admixtures as the nutrient source of intermediate and supplementary hosts of insect parasites has only been partly confirmed in the fresh coniferous forest habitat with respect to polyphagous ichneumonids, and has not been confirmed at all for oligophages. This is also due to the fact that nutrient chains include intermediate hosts of many economically important parasites living on plants in the herb layer (Karczewski, 1962; 1967a), which are sometimes limited by the undergrowth. It appeared also in this case that the influence of the undergrowth layer is of higher significance in richer sites (Fig. 8.33).

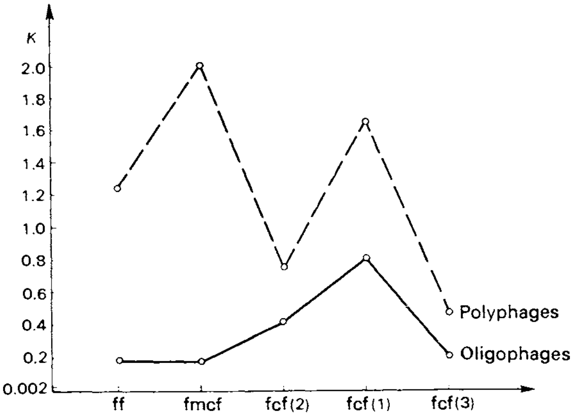


Fig. 8.33 Influence of deciduous undergrowths on the occurrence of polyphages and oligophages of the family *Ichneumonidae* (after Sawoniewicz, 1979): *K* – ratio of number of individuals in forest stands with deciduous undergrowth to number of individuals in forest stands without undergrowth

Thus, the purposeful or accidental human influence on entomocenoses through changes in the specific composition of forest stands is an extremely complex phenomenon. There are no data confirming the thesis that it occurs only or primarily through exerting pressure on organisms which regulate the abundance of phytophages and consisting mainly of the disturbance of the biocenotic trophic net in the tree and shrub layers. The reduction of the regulative capacities of entire forest ecosystems is due to changes of the abiotic environment of sites and to the deterioration of the physiological conditions of arborescent plants, which is the effect of the formation of vast areas of forest stands consisting of a single tree species (frequently in unsuitable sites or based on unsuitable seeding material) with a simplified circulation of matter and deformed herb layer. The rule of adaptation of the species composition of forest stands to site conditions should be strictly observed in forest and mixed coniferous forest sites. This is the most appropriate form of the indirect development of local zoocenoses in situations in which rich sites are endangered by degradation due to the protection of monocultures. The presence of deciduous species significantly increases the regulative potential of these biocenoses.

In poor sites of fresh coniferous and dry coniferous forests, the deciduous undergrowth admixtures play a different role, which has relatively little significance regarding the homeostatic capacity of zoocenoses but is very important for the favourable development of soil-forming processes and for the turnover of biogenes and the consequent acceleration of succession processes. This is also the result of the stimulating influence of undergrowth on the occurrence of animal species which favour humification more than mineralization processes (e.g. *Diptera* and *Elateridae* larvae) or which are characterized by lower living expenses (large *Carabidae* and *Carabidae* of the autumn developmental type). The efficiency of undergrowth (whether deciduous or coniferous) in soil-forming processes and as an element of the homeostatic potential of biocenoses depends directly on the associations of the species which form the undergrowth layer with local geographical and site conditions.

The forest herb layer is thus an important element of phytocenoses, influencing the composition of zoocenoses in poor site conditions. This layer should therefore be the object of hylotechnical measures.

In exceptionally poor sites in which the natural composition of forest stands consists exclusively of pine with a birch admixture, the introduction of oak and especially beech undergrowth is a measure too modest as regards its influence and cannot give rise to any significant increase in the regulative capacity of the biocenose. Nevertheless, the increased differentiation of the phytomeliorated forest environment may, under certain circumstances, secure the realization of the divergence of exploited and exploiting populations which provides the possibility for the stabilization of the system. This thesis seems to be confirmed by the results of studies performed by Nunberg (1937). This author established that the infestation of eggs of *Panolis flammea* (D. & S.) by parasites amounted to 47% of their total number in a pine forest stand with juniper undergrowth, while in a pure pine forest stand only about 12% of the eggs were parasitized. Zinoveva (1955) also showed that pine-spruce or pine forest stands with spruce undergrowth were characterized by a richer soil fauna than that observed in pure forest stands. Thus studies on the role of both deciduous and coniferous undergrowths seem to indicate that the conformity of the specific composition of the forest stand and undergrowth layer with the site is decisive for the achievement of the specific composition of the entomofauna.

The lack of stability of intensively exploited forest ecosystems is due primarily to the methods of management of forest stands, including simplified methods of felling and regeneration. Changes in the specific composition of the forest stand, undergrowth and herb layer are the effects of such measures. They are decisive in the selection of the tree species cultivated and secure the most efficient exploitation of accumulated supplies under the conditions of a poorly differentiated ecosystem. This is confirmed by the hypothesis of Odum (1975) that the optimal diversity of forest ecosystem is the function of the quality and quantity of the flow of energy, whereas the positive correlation between diversity and stability is a secondary dependence.

8.7 Cutting systems and improvement fellings

The different methods used in logging and uncovering the forest surface for regeneration, as well as forest cultivation measures consisting of the removal of parts of trees from the forest stand, i.e. pruning, thinning and prelogging, are amongst the basic economic activities in forestry which have the most radical effects on the forest biological ecosystem.

The method of clear cutting is most frequently employed in pine and mixed forest stands in Poland (Fig. 8.34). It initially leads to the exposure of areas usually covering several hectares and subsequently to the formation of vast forest stands of a poorly differentiated age and species composition. Young trees growing in open spaces differ as regards their chemical properties from trees from regenerations performed under the forest canopy (Nunberg, 1969) and exhibit morphological and physiological features favouring the occurrence of many phytophages. The method of regeneration of felling areas is also important here. Tree planting, as opposed to seeding, favours the occurrence of phytophages, the activity of which is sometimes facilitated by the weakening of the root system of plant seedlings. The uniform age of plantations and

Fig. 8.34 Clear cutting area in pine forest after ploughing (photo by the author)

forest stands developed from the regeneration of clear cut areas facilitates the concentration and favours the increase of abundance of insects associated with definite developmental phases of trees. The mass appearance of *Hylobius abietis* (L.) in pine plantations, as well as the chronic mass occurrence of the pine bud pest *Exoteleia dodecella* (L.) in older pine plantations and thickets with an impoverished and degraded herb layer (due to the method of felling applied) or extensive outbreaks of *Dendrolimus pini* (L.), *Panolis flammea* (D. & S.) and other pests feeding on needles of pine forest stands of mean or older age deprived of herb layer and shrubs are classic examples of this phenomenon.

The exploitation of pine forest stands by the method of clear felling in general provides the best economic and organizational effects and thus would appear to be irreplaceable in poor sites. The attempts made by the Germans during the inter-war period to carry out forest management procedures without clear felling were ineffective. The cutting system thus requires more detailed studies from the standpoint of its biological consequences, particularly the biology of forest soils. Moreover, the reconsideration of the opinion regarding the continuity of forest management by means of the clear cutting system based on Hundeshagen's theory of 1827 becomes particularly topical. It should be verified not by the historical approach as an environmental circumstance of extensive outbreak of noxious phytophages, but from a new standpoint.

This concerns the steady impoverishment of forest soils which necessitates the use of various fertilization methods hitherto employed only in agriculture as an extreme measure to improve the productivity of forest stands because of the exhaustion of the content of plant nutrient compounds in forest soils. Although the exposure of soil on a clear cut area initially stimulates mineralization processes in the accumulated organic remains, as well as humidity, aeration and soil reactions several years later, the absence of trees inhibits the supply of organic matter. Moreover, the amount of precipitation, which is higher than under the forest canopy, washes away plant nutrient substances from the superficial layers of the felling area, particularly under montane conditions (Likens & Borman, 1974) and destroys the cloddy structure of the soil. The sudden removal of forest stands at repeated intervals of about 100 years also has significant effects on soil organisms.

The density of soil animals in spruce forests in Finland underwent intensive changes during a four year period after felling and then started to regenerate towards the condition typical of older forest stands but failed to attain it even after ten years. Of the insects and arachnids involved in decomposition processes, the abundance of *Collembola* increased, whereas that of *Oribatei* and other *Acarina* diminished on the felling area (Huhta *et al.*, 1967; 1969). The increased abundance of *Collembola* was due to favourable soil humidity conditions and the absence of competition from *Acarina*, the abundance of which was limited by conditions which were unfavourable for the development of fungi which decompose spruce needles rendering them suitable as food for *Acarina* (Huhta, *op. cit.*). The increased abundance of *Collembola* on felling areas cannot be regarded as a general rule. In Alpine spruce forests, for example, their abundance decreased by half after felling and three years later a further reduction in their numbers was observed (Schimitschek, 1938). The abundance of invertebrates in oak forests in rich sites also falls to a minimum level during the second year after felling. The decrease in the abundance of large saprophages is particularly noticeable under such conditions (Kudryashova, 1970).

Later studies performed by Huhta (1976) in Finland further indicated that the exposure of the large amount of organic matter left on the clear cut area to decomposition leads to a parallel increase of biomass and respiration of the entire soil fauna. This is due, however, to the intensive development of *Lumbricus* sp., and *Enchytraeidae*, whereas the density and respiration of arthropods is lower on felling areas which are several years old than in forest stands.

Studies performed by the present author indicate that the application of the clear felling system in pine forest stands in the fresh coniferous forest habitat either completely or considerably eliminates the typical forest *Staphylinidae* (F_3+F_2) for about one quarter of the average productive cycle of forest stands (Fig. 8.35). The course of such changes has been described in an earlier chapter. The anthropization. process resulting from the practice of felling is manifested by the elimination of the forest fauna and the increased role of eurytopic species (Szujecki, 1966c; 1971; 1972b). It is also supposed that the predominance of non-specialized species exhibiting a wide tolerance to environmental factors, as observed on clear cut areas as well as in plantations and partly also in thickets, may lead to further simplifications of biocenotic associations in forest environments. This is because, as has been established by W. Kaczmarek (1961; 1963), in poor ecosystems such species play a decisive role in the regulation of the abundance of specialized species. The increased abundance of hemizoophagous *Staphylinidae* due to the application of the clear cutting system is symptomatic in this respect. The results of studies justify the supposition that the increased abundance

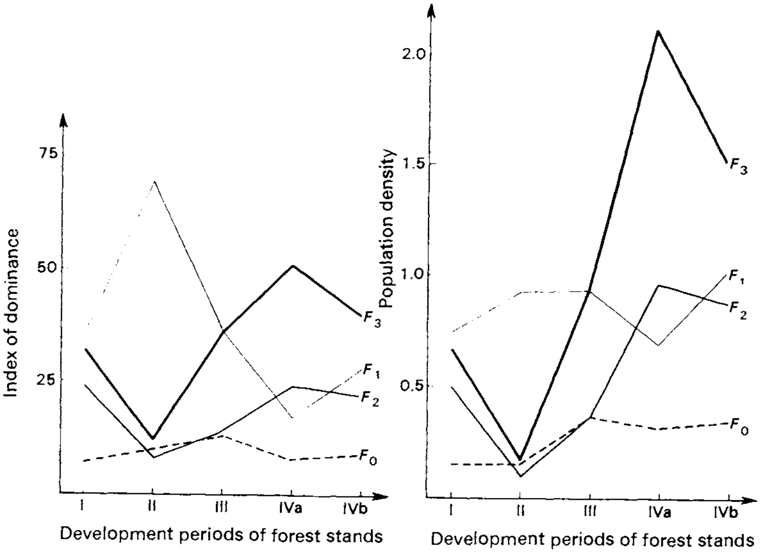


Fig. 8.35 Influence of clear cutting in pine forest on forest *Staphylinidae* species (after Szujecki, 1971): I – cutting areas and 1-year plantations, II – older plantations, III – thickets, IVa – old thickets and pole-sized forest stands, IVb – maturing and timber forest stands

of eurytopic species has only occurred recently and is now becoming progressively more intensive, resulting in the elimination of primeval forms of the given biocenosis. This may evoke a chain reaction which destroys the previously existing homeostatic mechanisms of forest biocenoses and leads to an extreme simplification of associations between soil organisms. This would be detrimental to the course of soil-forming processes, the regularity of which (particularly the formation of humus, this being the reservoir of nutrient compounds for woody plants) depends on the activity of the entire complex of soil organisms. Such conclusions have also been justified by the results of studies on the microbiological and faunistic consequences of the clear felling system on the one hand, and on the role of microorganisms and animals in the soil-forming process on the other (Braune, 1954; Broen, 1965; Dunger, 1956, 1969; Gretschy, 1952, Musierowicz, 1960; Nef, 1957; Ronde, 1951; Zonn, 1964; Zrazhevskii, 1954). Particularly symptomatic results have been obtained in zoological studies on the brown soils of southern France where the felling of oak forests irrevocably eliminated endemic species of *Leptotyphlinae* which played an important role in the biology of these soils (Coiffait, 1956; Herve, 1959). Strip selection cutting, alternate strip felling, strip and group clear cutting and particularly shelter-wood felling have a less negative influence as compared with clear cutting. Nevertheless, these felling systems cannot be universally applied in all habitats and in cultures of certain tree species. Under montane conditions, clear cutting on vast areas has disastrous ecological effects, due mainly to erosion and the greatly accelerated leaching of plant nutrient substances and various mineral compounds from the soil. Thus other felling systems are applied in mountains, the influence of which on biogeochemical cycles and leaching processes is less drastic (Fig. 8.36).

Insects classified as secondary pests exhibit a distinct reaction to the microclimatic conditions caused by felling (clear cutting, strip selection cutting, alternate strip felling). In montane forest stands under identical local conditions the number of generations of *Scolytidae* on the edges of clear felling areas may be as much as double that on the edge of strip selection felling areas, the width of which is considerably smaller than that of clear felling areas. Alternate strip felling areas in montane spruce forest stands employed in the past also provided microclimatic conditions which were considerably more favourable for the development of *Ips typographus* (L.) than those under the forest canopy. When cuttings were repeated every three to four years, 50% of the spruces died on the

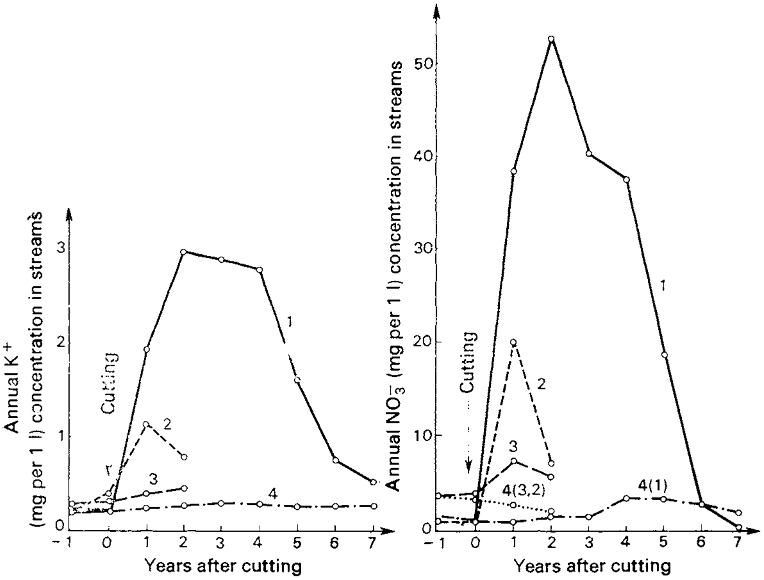


Fig. 8.36 Influence of cutting methods on washing of some chemical elements and compounds from forest soils 1 – deforested area, 2 – clear felling, 3 – shelter-wood felling, 4 – non-felled forest stands

edges of cutting areas with a southern exposure and 25–27% on those with a northern exposure, whereas in conditions in which the forest had not been exposed by felling 8–9 and 2–3% of the trees respectively perished due to infestation by *Ips typographus* (Vasyechko, 1967 quoted after Girits, 1975). The unappropriate application of shelter-wood felling in fir forest stands may evoke a high abundance of *Dreyfusia nuesslini* (Börner), the aphid which exploits young firs weakened by being exposed too early to the direct action of the Sun's rays. Thinning should be performed at short intervals but it involves too small a number of trees to make it possible for the undercrop to adapt to new microclimatic conditions.

The compactness of forest stands may also have a considerable effect on the occurrence of insects. It is modified by forest management practices not only through planting trees densely where appropriate but primarily by improvement fellings which are decisive for the access of light and precipitation to the forest floor. Wide oscillations in soil and cambium temperatures occur in intensively thinned forest stands. These lead to physiological disturbances which weaken the trees and stimulate changes in the abundance of cambio- and xylophages such as *Agrilus* sp. on the alder and beech as well as *Monochamus* spp., *Tetropium* spp., *Scolytidae* and *Siricidae* on coniferous trees. Schematic thinning performed using mechanical equipment exercises a particularly distinct effect here. Only selective thinning applied in moderation does not evoke an increase in the abundance of wood-borers and, in fact, even limits such an increase.

Changes in the forest microclimate caused by thinning have various effects on the abundance of different soil invertebrates as well as of insects which penetrate the forest floor. Various insect groups reacted to thinning by either increasing or decreasing their abundance in different geographical and ecological conditions.

Contrary to the situation observed in cutting areas, it has been established that in the fourth year after thinning practices involving the removal of spruces from the spruce-pine forest stand, the density of *Collembola* and *Diptera* larvae increased while the density of the larvae and imagines of many *Coleoptera* decreased (Huhta *et al.*, 1967; Table 8.5).

Table 8.5 Influence of thinning of a spruce-pine forest on the density of soil insects (per 1 m^2) in the first and fourth year after thinning (after Huhta *et al.*, 1967).

Taxon	First year after thinning		%	Fourth year after thinning		%
	Forest stand			Forest stand		
	control	thinned		control	thinned	
Collembola	18 500.0	51 200.0	278	20 200.0	32 600.0	162
Diptera (larvae)	21.8	28.3	130	8.3	20.0	241
Coleoptera (imagines)	40.7	77.4	190	23.0	15.0	65
Coleoptera (larvae)	51.3	58.3	114	28.8	9.3	32

On the other hand, in pine and spruce forest stands of the second age class the population density of *Collembola*, *Diptera* larvae and *Coleoptera* decreased after thinning (Górny & Dunikowski, 1968). In the tree rows of a spruce forest stand the density of these insects was found to be higher than that between the rows. It was also observed that more intensive thinning brought about a greater decrease in the abundance of soil insects and various other arthropods. The unidirectional decrease in the abundance of all invertebrates caused by thinning is not compensated for by species immigrating from open areas as is partly observed on cutting areas. However, thinning does not bring about violent changes of abundance (as on cutting areas) due to the fact that the litter and soil remain intact and there is still some shade left.

The significant role of thinning in the determination of the condition of entomocenoses consists of the fact that the resultant changes in the forest microclimate favour the development of the forest herb layer which was previously limited during the course of felling and with which many parasitic insects are associated, either indirectly through their hosts or directly through paratrophic relations. Furthermore, the penetration of light to the forest floor stimulates the activity of parasites as has been shown by Sawoniewicz (1973) who studied the *Ichneumonidae* visiting the flowers of *Umbelliferae* in pine forest stands of variable compactness.

Both the clear cutting system and improvement fellings lead to a simplification of the species composition and age structure of forest stands and almost completely eliminate superannuated rotting trees. This creates very difficult life conditions for the complex of dendrophilous, frequently stenotopic insects associated with the final stages in the succession of wood decomposition, particularly of deciduous trees, or with nests of animals inhabiting tree hollows. This group of insects is the closest to extinction and forest reservations and old parks are its only refuge (Szujecki, 1973).

On the other hand, the manipulation of wood logged on cutting areas and in the course of thinning, as well as its storage in the forest, provide conditions for the intensive propagation of insects invading living, but weakened, tree tissues and particularly the phloem, cambium and wood. This process is favoured by the increasingly common practice of felling trees in summer when certain insects are very active invading the substrate on which eggs are laid.

Stumps which remain after trees have been cut favour the development of many borers, particularly bark-beetles such as *Hylastes* spp., *Hylobius sp.* and their accessory entomofauna (Wiąckowski, 1957). Moreover, the butts of trees are damaged during the removal of wood from shelter-wood fellings and during thinning, such damage increasing with the growth of forest stands thus further weakening the trees and hence favouring their invasion by some xylophages, particularly by *Siricidae* and *Scolytidae.*

8.8 Mechanical soil cultivation

Under forest conditions it is hard to differentiate the influence of soil cultivation on the soil entomofauna from that of periodical deforestation due to clear cutting. No studies have been devoted to the differentiation of the influence on entomocenoses of various systems of soil cultivation on cutting areas, either in forest nurseries or under forest stands. Agricultural experiments indicate that ploughing of open areas evokes profound changes in the composition of the soil entomofauna. In the forest zone these changes are more marked than in the steppe zone because the cultivation of podsol soils destroys the thin humus (turf) layer with which most insects of non-cultivated soils are associated. The type of plough and other cultivation equipment on which the depth of ploughing and the degree of soil crumbling depend is also important. For example, rotary ploughs and rotary cultivators destroy larvae of insects which have a developmental cycle lasting several years, whereas mouldboard ploughs cause smaller losses in the edaphon (after Tischler, 1965). Finally, changes in the entomofauna due to soil cultivation are modified by the nature and humidity of the soil. Gilarov (1965) divided such changes into the following three classes:

1) the impoverishment of the specific composition and decrease of the number of morphoecological groups of soil invertebrates;
2) the general reduction of the abundance of invertebrates, often with a parallel increase in the abundance of individual species;
3) the increase of the relative abundance of saprophages in associations of saprophages and phytophages.

Thus, amongst the soil phytophages, soil cultivation (Fig. 8.37) favours those polyphagous species which have a short developmental cycle

Fig. 8.37 Soil cultivation on cutting area regenerated with seeded pine (photo by the author)

and are capable of periodical adaptation to saprophagism. The populations of such species generally exhibit a lower stability than those of species with long developmental cycle. The advancing degradation of forest soils and the developing possibilities of using heavy mechanical equipment encourage foresters to disregard the natural layer structure of forest soils and to apply soil cultivation and fertilization methods previously employed in agriculture. Deep ploughing to the depth of 60 cm alters for hundreds of years the natural layer structure of forest soils and the characteristic communities of soil insects associated with it. Such effects may persist for hundreds of years and are arousing particular anxiety from the standpoint of soil zoology. The biological consequences of these measures are unpredictable, but doubtless the possibility of the restoration of edaphic conditions with which our forests have been associated from time immemorial becomes more and more problematic.

8.9 Fertilization and lupin manuring of forest soils

The fertilization of forest soils has become necessary over the past 20 years due to the abrupt reduction of the productivity of forest sites. This has resulted from the centuries-old transferring of considerable amounts of substances, nitrogen, calcium, potassium, phosphorus and microelements compounds to other, mainly agricultural, ecosystems, together with the wood material (particularly thin stems), litter and components of the herb layer. This process has been and still is particularly intensive in the vicinity of densely populated areas on poor soils. These areas also exhibit the highest frequency of outbreak foci of pine foliophages which encounter favourable development conditions on undernourished trees generally suffering from water deficiency. Possibilities of indirectly influencing populations of phytophages through the limitation of the deficiencies mentioned above were sought in fertilization measures.

Initial attempts to purposefully influence the feeding conditions of phytophages were begun as far back as the beginning of this century when Mokrzecki started to apply an internal therapy to trees by means of injecting certain chemical compounds into the trunks of fruit-trees in order to reduce the abundance of feeding *Coccidae* (Fig. 8.38). It was also observed by Hoffman that the complete fertilization of garden plantations diminished the abundance of *Scolytus* spp. feeding on plum-trees.

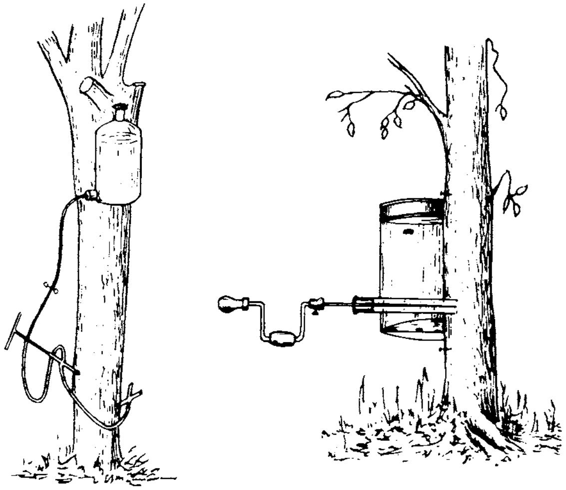


Fig. 8.38 Equipment used by Mokrzecki in early years of our century in experiments on internal tree therapy and extra-root alimentation (after Czyżewski, 1937)

Methodical studies on the role and possibilities of the fertilization of the forest were initiated in the 1950's, especially in the Federal Republic of Germany (Büttner, 1956, 1961; Oldiges, 1959; Merker, 1961, 1963). Fertilizers containing phosphorus (100–150 kg per 1 ha), potassium (80–200 kg per 1 ha), nitrogen (40–200 kg per 1 ha) and calcium (25–2000 kg per 1 ha) were employed for the fertilization of forest soils. The dosage depended on the age of the forest stand and the existing content of nutrient compounds in the soil. It has been established that these measures should be repeated eight to eleven times in the course of 100 years and that effects generally appear after several years.

The results of these experiments varied, but most authors agree that the mortality of insects fed on needles of trees from forest stands fertilized with various chemical fertilizers is higher than that of the same insect species at the same stages of development on material derived from non-fertilized forest stands.

For example, in 1951 in a certain forest stand in the Federal Republic of Germany lime was applied to the soil and in the subsequent year lupins were seeded here. As a result of this the number of pupae of *Bupalus piniarius* (L.) in the winter of 1953/1954 fell to 37.6% as compared with the control areas.

In another case, sandy soil was limed in the spring with a dosage of 1000 kg per 1 ha. Superphosphate (500 kg 1 ha) and nitrogen fertilizers (100 kg per 1 ha) were also applied and resulted in a decrease of the number of pupae of *Bupalus piniarius* from 5.7 to 2.6 per 1 m^2, i.e. by 54%, in the next winter. The same measures parallelly employed on clayey, wet soils gave no effect in this respect.

It should be stressed that the role of calcium consists in this case of the neutralization of the soil acidity which sometimes favours the active development of that part of the soil fauna which is directly involved in humification processes and indirectly in the mineralization of plant remains leading to the liberation of nitrogen compounds in a form available for woody plants.

The subsequent continuation of similar experiments in various countries and under various natural conditions frequently led to discordant results. These divergences mainly concern the influence of fertilization on the quantitative sex proportion and developmental rate of phytophages.

Burzyński and Luterek used mineral fertilizers against several pest species obtaining negative results.

Burzyński (1966) employed fertilizers against *Rhyacionia buoliana* (D. & S.), *Exoteleia dodecella* (L.) and *Thecodiplosis brachyntera* (Schwägrichen). The use of chemical fertilizers improved the growth conditions of the pine and altered its physiology towards the optimal requirements of the insects studied. This led to a quantitative increase of *Rhyacionia buoliana* and *Exoteleia dodecella* which had not previously encountered favourable conditions for their development on poorly growing young trees with underdeveloped buds. No distinct influence of fertilization on the occurrence of *Thecodiplosis brachyntera* feeding on pine needles was observed (Fig. 8.39).

Luterek (1969) employed fertilizers in laboratory cultures and in field experiments in order to control the larvae of *Dendrolimus pini* (L.), *Bupalus piniarius* (L.), *Gilpinia pallida* (Klug) and *Hyloicus pinastri* (L.). These studies were performed in pine forest stands growing in the fresh coniferous forest habitat using the following fertilizers: ammonium sulphate, superphosphate, potassium salt, calcium carbonate and the NPK fertilizing mixture "Mikro" containing a number of microelements (B, Mn, Mg, Cu, Zn). No significant influence of the application of these fertilizers on the mortality and body weight of insects was observed in field experiments.

On the other hand, however, a surprising increase in the mortality of *Dendrolimus pini, Gilpinia pallida* and *Bupalus piniarius* was noted

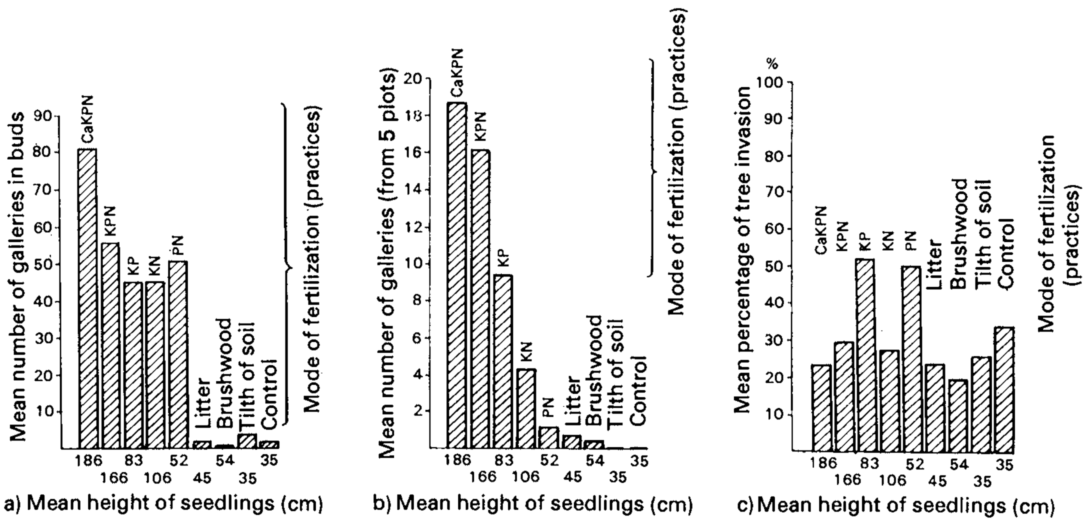


Fig. 8.39 Abundance of plantation pests in dependence on fertilization (after Burzyński, 1966): a – *Rhyacionia buoliana* (D. & S.), b – *Exoteleia dodecella* (L.), c — *Thecodiplosis brachyntera* (Schwägrichen)

in pot experiments in the variant treated with potassium and phosphorus, whereas the application of nitrogen fertilizers gave no positive results. The author also noted no influence of fertilization on the content of essential oils and sugar in pine needles.

These results contradict those of studies carried out by many other scientists. This points to the existence of unknown factors capable of exercising a sinificant influence on the effect of fertilization. Soil properties, specific food requirements of various insect species and properties of natural populations of the pest (artificially intensified populations were studied in the experiments of Luterek) probably belong to these factors.

It has been commonly observed that nitrogen fertilizers are the most effective, particularly on poor soils of coniferous forests. This has been also established by Grimalskii (1964) who endeavoured to improve the growth conditions of the pine in 10–23 year-old forest stands growing on abandoned farm land. He employed ammonium nitrate, superphosphate and potassium salt, introducing the phosphorus and potassium fertilizers in early spring and the nitrogen in April and May over a period of two years and using a yearly dose of 50–150 kg. Phosphorus fertilization gave positive results in richer soils while no positive effect of potassium was observed. Büttner (1956; 1961) also noted that potassium fertilizers favour the development of pests. A twofold decrease of the number of feeding caterpillars as compared with the control area resulted from the application of nitrogen fertilizers.

It is commonly stressed that nitrogen fertilization does not influence insects feeding on deciduous trees or on coniferous trees growing on soils with a high content of nutrient compounds. On the other hand, the increase of the nitrogen content of the soil stimulates the noxious effect of insects assimilating fluid food such as aphids sucking sap from the leaves.

Büttner (1956; 1961) investigated the influence of fertilization on the mortality of *Lymantria monacha* (L.) and *Pristiphora abietina* (Christ) and observed varying results of this economic measure. Oldiges (1959) observed the highest mortality of *Lymantria monacha* and *Bupalus piniarius* (L.) in the first larval instar and in forest stands fertilized with nitrogen. On the other hand, however, Oldiges noted no significant quantitative differences in the sex proportions of these insects and recorded only slight differences in the weight of individuals and egg production as compared with insects feeding in non-fertilized forest stands.

The influence of fertilization on the content and secretion of essential oils remained unknown for many years (Otto & Geyer, 1970). The composition and amount of essential oils contained in the needles, phloem and wood of the common pine depend on the plant genotype as well as on many variable non-genetic factors associated with the environment and development of plants (Zavarin *et al.*, 1971). Tobolski (1968) indicated that a number of pine monoterpenes seem to be under a simple genetic control, such that their content is very variable in the tree population and also varies (with the exception of γ-terpinene) in different tissues. According to Tobolski, the composition of monoterpenes is only slightly dependent on environmental conditions. Otto & Geyer (1970) found no distinct differences in the content of oils in the resin and needles of fertilized (N, P, K, Ca, Mg, and their compositions) and non-fertilized pines. Only the recent studies of Hiltunen, Schantz & Löyttyniemi (1975) threw more light on this problem, although many aspects still remain obscure. These authors investigated terpenes in the needles, phloem and buds of the common pine. It appears that the general concentration of essential oils depends on nitrogen fertilization (Table 8.6). The influence of fertilization was particularly important in the resting periods of the trees, whereas in the vegetation period it was not distinct in view of the high individual changeability of trees and the varying rate of processes of biosynthesis. Nevertheless, the concentration of 3-carene, sabinene and terpinolene increased during this period. This indicates that fertilization stimulates biochemical reactions evoking the formation of compounds of the 3-carene group.

Besides changes in the intensity of resin secretion and its content of toxic components of essential oils, which seem to be an important regulator of the mortality of insects feeding on tree needles, the fertilizers may also evoke other changes in the host plants. These include the chemical changes as described above and changes in the physical properties of the assimilation apparatus as, for instance, the hardening of needles. Ohnesorge (1957) established that fertilization of the soil with calcium at a dosage of 500 kg per 1 ha caused an accelerated lignification of spruce shoots. This consequently reduced the abundance of the population of *Pristiphora abietina* by 75% since, in the initial feeding period, larvae of this species feed only on young, soft needles. In experiments, the mortality of these insects on young shoots 2–8 cm long increased in proportion to the length (and hardening) of shoots.

Bupalus piniarius also exhibited a more rapid larval development when the catterpillars were fed on pine needles from mixed forest stands than on those from pure pine forests and this was closely associated with

Table 8.6 Concentration of essential oils in needles, phloem and buds of the common pine in dependence on fertilization (after Hiltunen, Schantz and Löyttyniemi, 1975).

		$\bar{X}$	*S.d.*	*F*	*R*
Needles – 72	C	1048	323	5.03	0.03
	F	1284	344		
Phloem – I	C	76	41	1.16	0,29
	F	101	95		
Buds – 72	C	1670	344	4.40	0.04
	F	1881	291		
Phloem – II	C	43	33	1.08	0.31
	F	82	113		
Phloem – IS	C	59	38	0.01	0.94
	F	60	53		
Buds – 73	C	2015	243	0.33	0.53
	F	1934	375		

Phloem – I – phloem taken from butt part of trees felled in January, 1973.
Phloem – IS – phloem taken from butt part of the trees felled in January, 1973 which lay till spring 1973 and were attacked by the first bark-beetles.
Phloem – II – phloem taken from butt part of trees felled in June, 1973.
Needles and buds – 72 – collected from top branches in January, 1973.
Buds – 73 – collected from top branches in June, 1973.
C – control.
F – fertilization in May, 1971 (150 kg of nitrogen per 1 ha).
$\bar{X}$ – mean amount of essential oils per 100 g of fresh material (microlitres).
R – risk for rejection the null hypothesis, when true.
S.d. – standard deviation.
F – test.

the softness and small thickness of needles from trees growing under conditions of higher air humidity.

Izhevskii (1967) performed interesting studies on the influence of lupin manuring on the feeding conditions and abundance of *Dendrolimus pini* (L.) in Byelorussia. It appeared that the introduction of lupin under endangered forest stands produces an increase in the nitrogen content and humidity of the soil. This further influences the humidity of needles and their biochemical composition. The correlation between the content of nitrogen in the soil and that in needles was sufficiently high ($r = +0.76$) and faithful. The increase of the humidity of needles and the accumulation of mineral salts in them favour the decrease of the relative content of soluble carbohydrates and their transformation into starch. The total amount of sugars in one-year-old needles during the summer–autumn period differed in various forest types. Under the worst growth conditions of trees this amount was proportionally higher than in richer sites. An important discovery resulting from this is that the differences in carbohydrate content between the control material and that derived from lupin-enriched forest stands were more distinct than between analogous values for different forest types. The content of carbohydrates in needles diminished on lupin-fertilized areas. The content of essential oils increased in parallel with the increases of humidity of needles and the decrease of the contribution of soluble carbohydrates.

Furthermore, lupin manuring influenced the mechanical properties of needles, that is their weight, size and hardness increased. Such features play a significant role in the feeding of young caterpillars of *Dendrolimus pini.*

As has been seen, the influence of lupin evokes physiological and biochemical changes in needles which affect the feeding of caterpillars, their development and growth, consequently leading to changes in the abundance of the population of the pest. The large amount of needles devoured in forest stands without lupin, as well as the larger weight and more rapid development of caterpillars, point to the occurrence of better food conditions for *Dendrolimus pini* here. On the other hand, the mortality of caterpillars was higher, in proportion to the improvement of growth conditions of the pine and the increase of soil fertility (Fig. 8.40), since under these conditions pine needles contain a lower amount of mono- and disaccharides (the only sugars available for caterpillars). These data have been statistically confirmed.

In conclusion in this discussion of the influence of the physiological condition of plants on the phytophagous species which feed on them, it should be noted that the influence of fertilizers operates by means of a change in the biochemical and physical properties of the assimilation apparatus. Nitrogen mineral fertilizers and green (lupin) manures applied to very poor sandy soils exercise the most distinct influence on insects. Populations of phytophagous insects may react to fertilization by changes in the index of mortality as well as by changes in the quantitative sex proportion and fertility. Changes in food quality increase the abundance of insects only when other environmental conditions are fulfilled.

The more or less favourable development parameters of insects due to the physiological condition of nutrient plants may not correlate with the general environmental conditions optimal for the increase of abun-

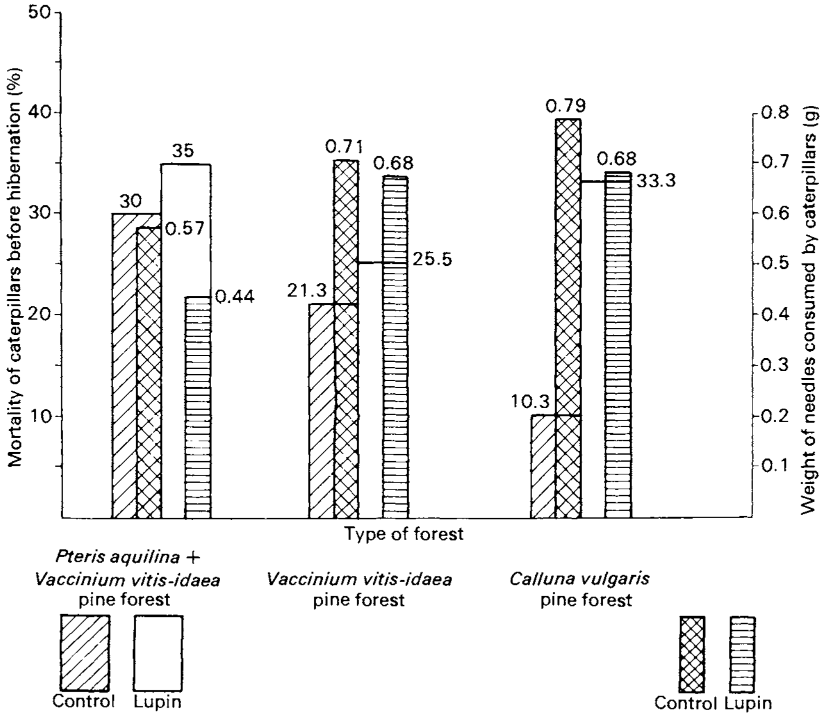


Fig. 8.40 Influence of lupin manuring of forest soils on caterpillars of *Dendrolimus pini* (L.) (after Vorontsov & Izhevskii, 1966)

dance of populations since this increase in influenced by other, frequently decisive, factors.

Studies performed under various conditions by a number of authors (Ronde, 1957, 1960; Huhta *et al.*, 1967, 1969: Axelsson *et al.*, 1973) indicate that the fertilization of forest soils both in nurseries and plantations, as well as in older pine forest stands, evokes violent changes in the abundance of populations of various soil organisms. After the application of mineral fertilizers in large doses amounting to 300 kg per 1 ha, a decrease of abundance of insects generally occurs. After 2–3 years their abundance rises abruptly and after 5–6 years it regains its original level. This is true for *Collembola* and probably also *Diptera* larvae which play a significant role in the decomposition of plant remains in the forest soils environment. No distinct influence of fertilization on imagines and larvae of *Coleoptera* was observed.

A contradictory opinion has been advanced by Leśniak (1975) who studied the influence of Ca+NPK mineral fertilization in doses of about

100 kg of pure component per 1 ha in pine forest stands in the fresh coniferous forest habitat. Under such conditions the abundance of *Carabidae* diminished after fertilization by 50% in the first year and regained its level in the third year. The fertilization limited particularly large zoophages.

Organic fertilizers, such as compost and sewage containing organisms associated with putrefaction processes, may limit the development of the forest soil entomofauna. A limiting influence may also be due to mineral compounds such as lime used for deacidification of soil with poor litter decomposition. It appears that under these conditions intensive liming limits fungi and changes microbiological processes and this negatively influences the density of soil animals. On the other hand, moderate application of lime may favour the active development of the soil entomofauna which takes part in humification and plays an indirect role in mineralization of plant remains, liberating the hitherto unaccessible nitrogen compounds in a form available for arborescent plants (Górny, 1975b).

9 Problems of the development of entomocenoses under reforestation conditions

9.1 Waste-heaps and dumping grounds

The course of the recultivation of post-industrial areas depends on their origin and configuration, as well as on the chemical and physical properties of the material. The most frequently employed method is forest recultivation, which is generally preceded by a preliminary restoration of the soil substrate by technical or agrotechnical methods used depending on the toxic properties of heaps or dumping grounds. In the primary phase of afforestation or tree-planting, recultivation is based on pioneer crop species such as the grey alder, poplar, *Robinia* and others, whereas later the composition of pioneer crop species is extended to forest-forming species such as oaks.

Forest recultivation measures initiate the natural succession of fauna and this leads to the development and intensification of soil-forming processes. Sometimes the recultivation measures also take into account the introduction of animal species which propagate slowly and play an important role in the formation of humus.

The development of soil on heaps and dumping grounds is primarily a biological process. Dunger (1968), who studied the course of the invasion of the recultivated heaps and dumping grounds of lignite quarries in the environs of Görlitz and Leipzig, by soil fauna, distinguished the following four stages of ecological succession: first pioneer, second pioneer, meadow and pre-forest.

The first pioneer stage occurs on heaps and dumping grounds with no recultivation measures or in the first years of recultivation. It is characterized by extremely xerothermal conditions and an absence of humus. The soil fauna forms only partially organized pioneer communities with minimal respiration during the year. *Proisotoma minuta* (Tullberg) and *Entomobrya lanuginosa* (Nicolet) predominate in the edaphic and epedaphic communities of *Collembola* respectively. All *Collembola* occurring here are xerothermophilous or are known from open areas of low humidity. Because of their ecological requirements they occupy sites on the heaps and dumping grounds characterized by a suitable microclimate such as slopes or depressions. Among *Carabidae* field stenovalent species (*Broscus cephalotes* (L.), *Harpalus rufipes* (De Geer), *Pterostichus cupreus* (L.)) and field euryvalent species (*Harpalus aeneus* (F.), *Carabus cancellatus* Illiger) prevail and belong mostly to the autumn developmental type (with hibernating larvae) and are active at night. As regards their food requirements zoophages as well as phytophages and euryphages occur here. On recultivated heaps the first pioneer stage lasts up to three years. On Tertiary debris of dumping grounds it persists for at least 20 years and on recultivated dumping ground for up to nine years.

The second pioneer stage develops from the third year of recultivation under moderate xerothermal conditions beneath the cover of *Artemisia* and herbs and produces humus of moder type. The high cellulolytic activity of the microflora, as well as the activity of the fauna play an important role in the formation of humus. The *Collembola* community in the epedaphon is characterized by the occurrence of the genus *Hypogastrura* as the index of the eutrophization process of the superficial layer of developing soil. Humus of moder type is the product of microphages (*Collembola*, *Oribatei*) and *Diptera* larvae which exhibit the highest density in this stage of succession.

On some heaps *Collembola* and *Diptera* larvae constituted 49% of the entire biomass of soil animals and contributed 31% to the total respiration amounting to 20 kcal per 1 m^2 per year (Fig. 9.1, Table 9.1). The importance of *Diptera* larvae was distinctly lower in further succession stages. The grouping of *Collembola* in the stage under discussion consists of species of ecological requirements resembling those of the first pioneer stage. Nevertheless populations of thermophilous forms exhibit regressive symptoms here. Communities with *Isotomodes productus* (Axelson) and *Micranurida pygmaea* (Börner) (or *Willemia intermedia* (Mills)) as dominant species were distinguished among edaphic *Collembola*. The number of species of *Carabidae* in the second pioneer stage increased from 15 to 51 due to the fact that Pleistocene Tertiary heaps are particularly suitable in this stage for invasion by these beetles.

Neumann's (1971) studies indicate that under similar conditions, as well as in young tree plantations on heaps, the number of species and individuals of *Carabidae* may be very high. The further advancing process of development of these plantations reduces this rich community of open areas in favour of less abundantly occurring forest species. Among other species *Bembidion lampros* (Herbst) and *Pterostichus caerulescens* (L.), i.e. diurnal species of the spring type which are also known to invade clear cutting areas, occur here, as well as the subdominant species *Calathus melanocephalus* (L.). Eurytopic forest species such as *Pterostichus oblongopunctatus* (F.) and *P. niger* (Schaller) begin to appear.

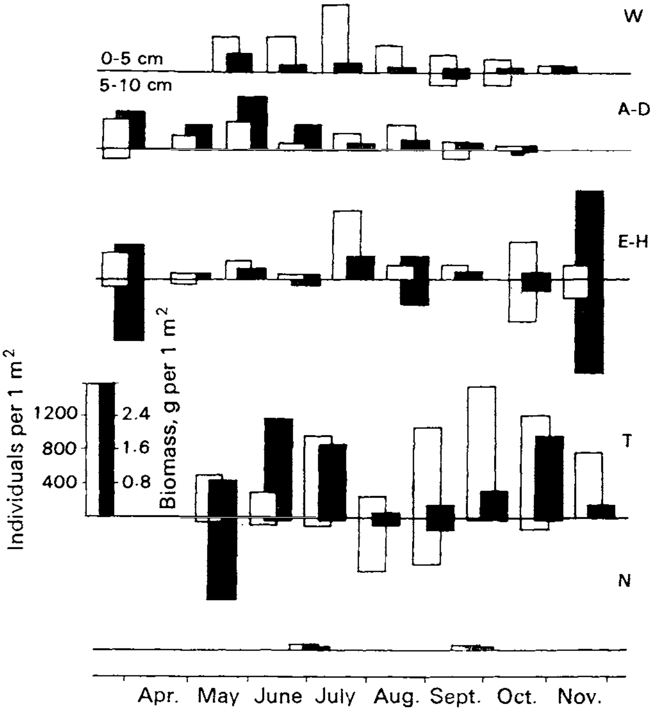


Fig. 9.1 Annual dynamics of density of individuals and biomass of *Diptera* larvae on waste heaps and in the environs of Berzdorf (after Dunger, 1968): W – forest, *Fraxino-Ulmetum* association, A–D – waste heaps in 8th year after afforestation, E–H – in 11th year after afforestation, T – heaps in 3rd year after recultivation with lupin, N – heaps in 1st year after recultivation; dark bars – biomass, light bars – density

Table 9.1 Mean annual amount of biomass of invertebrates on heaps and in the forest (W) near Berzdorf, g per 1 m^2 (after Dunger, 1968).

	Sites				
	N	T	E – H	A – D	W
Insecta	0.03	0.16	0.50	0.10	0.44
Mollusca	–	–	–	+	0.32
Phytophages – total	0.03	0.16	0.50	0.10	0.76
Carabidae	–	0.10	0.05	0.01	0.07
Staphylinidae	0.04	0.13	0.10	0.05	0.12
Arachnomorpha	+	0.07	0.04	0.02	0.04
Chilopoda	–	+	+	0.04	0.22
Parasitiformes	+	0.03	0.03	0.02	0.06
Zoophages – total	0.04	0.33	0.22	0.14	0.51
Lumbricidae	–	0.14	6.67	40.59	32.23
Diplopoda	–	0.03	0.04	+	0.09
Isopoda	–	–	–	–	0.02
Diptera (larvae)	0.01	1.36	1.04	0.41	0.12
Macrohumiphages – total	0.01	1.53	7.75	41.00	32.46
Enchytraeidae	0.02	0.07	0.18	0.10	1.92
Collembola	0.03	0.36	0.28	0.11	0.36
Oribatei	0.07	0.29	0.09	0.05	0.30
Trombidiformes	0.01	0.03	0.03	0.01	0.02
Myriapoda + *Protura*	–	+	0.03	0.01	0.17
Microhumiphages – total	0.13	0.75	0.61	0.28	2.77
Invertebrates – total	0.21	2.77	9.08	41.52	36.48

Note: sites N, T, E – H, A – D arranged according to the progress of the heap recultivation.

The community of *Formicidae* initiated by *Lasius niger* (L.) and further supplemented by *Formica fusca* L. and *Myrmica laevinodis* Nylander develops on waste tips in the second pioneer stage. On these heaps this succession stage generally occurs during the third to fifth year after recultivation whereas on dumping grounds it lasts longer.

The meadow stage develops about seven years after recultivation and exhibits a xerothermo- and mesophilous character. Meadow elements contribute abundantly to the floral composition, whereas the production of humus of moder or mull type is associated with the dominance of *Lumbricus* sp. in the litter fauna while the microflora exhibits a limited cellulolytic activity. The mode of formation of humus distinctly differentiates the meadow stage from the pioneer stages. Annual respiration amounts to about 50 kcal per 1 m^2. The epedaphic *Collembola* are represented by the community with *Lepidocyrtus cyaneus* Tullberg which, depending on the differentiation of the environments of recultivated heaps, may form variants with the distinguishing species *Lepidocyrtus* spp. or *Tomocerus vulgaris* (Tullberg). The edaphic communities of these insects acquire a specific character depending on local conditions due to the occurrence of *Isotomodes productus* (Axelson), *Micranurida pygmaea* Börner and *Friesea mirabilis* (Tullberg). Besides the meadow species, those typical of clear cutting areas as well as field species also play an important role here. The number of forest species of *Carabidae* is almost the same as in the second stage due to the lack of full shading of the ground by the shrub and young tree layer, although meadow elements such as *Carabus granulatus* L. also appear here and *Amara fulva* (Müller) occurs on insolated sandy sites.

The meadow stage invariably occurs during the 9th–11th years after recultivation.

The pre-forest stage is characterized by the growth of planted trees leading to essential changes in the microclimate of heaps recultivated during the course of ten years. Because of this, conditions favouring mesophilous species appear. Humus of mull or moder type is formed due to the contribution of soil *Lumbricus* sp., whereas the cellulolytic activity of the mocroflora is higher here than in the third succession stage. Respiration, which already has a considerable contribution from microsaprophages, amounts to 80 kcal per 1 m^2 yearly.

As a result of the environmental transformations described above, the *Collembola* community of the earlier stages disappears, although the new community of these insects, with *Lepidocyrtus paradoxus* Uzel and *Orchesella quinquefasciata* (Bourlet), still does not exhibit a forest character. The community of *Carabidae* also has a more ecotonic than forest character, which is also manifested by the predominance of *Pterostichus vulgaris* (L.), this being a species characteristic of field and forest edges. Of forest species occurring here the subdominants include *Pterostichus oblongopunctatus* (F.) and *P. niger* (Schaller), as well as *Cychrus caraboides rostratus* (F.) and *Carabus nemoralis* Müller.

It is noteworthy that on sites on which the recultivation was per-

Table 9.2 Comparison of occurrence of *Carabidae* on dumping grounds, afforested heaps and forest areas (after Neumann, 1971).

Community of *Carabidae* in succession order	Dumping grounds and heaps		Early forest recultivation				Afforestation about 20 years after recultivation					Natural forest	
			Sites										
	K_0	K_3	P_2	P_3	P_5	P_7	P_{11}	R_{28}	P_{28_z}	P_{25}	P_{28}	B_k	E_k
1	2	3	4	5	6	7	8	9	10	11	12	13	14
Pioneer community Species of heaps and young afforestations													
Bembidion femoratum (Sturm)	7	120	123	1	12	–							
Broscus cephalotes (L.)	7	26	4	48	25	–							
Harpalus psittaceus (Fourcroy)	3	1	25	37	4	–							
Harpalus affinis (Schrank)	4	9	21	4	2	–							
Harpalus rufipes (De Geer)	2	–	19	22	1	–							
Calathus ambiguus (Paykull)	3	16	6	11	41	–							
Calathus erratus (C.R. Sahlberg)	2	2	14	1	519	2							
Amara cursitans (Zimmermann)	26	–	–	–	–	–							
Pioneer community Species of young afforestations													
Pterostichus cupreus (L.)		2	24	1055	17	5							
Pterostichus caerulescens (L.)		2	1	612	5	101	13						
Calathus melanocephalus (L.)		–	4	152	15	8	–						
Bembidion obtusum Audinet-Serville		–	3	117	–	134	–						
Carabus violaceus L.		–	1	49	1	1	–						

Transitory community													
Species of afforestation of mean age													
Agonum obscurum (Herbst)				–	–	–	164	–	–	–	–	–	–
Pterostichus oblongopunctatus (F.)				–	3	16	232	8	1	48	–	7	12
Calathus piceus (Marsham)				–	–	–	45	–	2	1	7	–	–
Stomis pumicatus (Panzer)				2	–	–	20	4	3	–	8	–	–
Species occurring on all sites													
Trechus quadristriatus (Schrank)	28	3	12	21	16	52	28	–	–	4	1	–	1
Carabus problematicus Herbst	2	50	74	104	128	76	30	14	1	121	95	127	72
Pterostichus niger (Schaller)	–	–	36	5	19	7	5	7	–	4	14	38	14
Carabus coriaceus L.	–	–	–	11	–	–	20	4	24	9	82	39	61
Cychrus caraboides (L.)	1	–	–	–	1	–	–	7	4	4	9	1	–
Forest community													
Species of older afforestations and natural forests													
Abax parallelepipedus (Piller et Mitterpacher)								10	3	171	412	639	430
Carabus nemoralis Müller								3	1	86	64	25	140
Abax parallelus (Duftschmid)										9	15	5	69
Pterostichus madidus (F.)										1	11	94	29
Forest community													
Species of natural forests													
Abax ovalis (Duftschmid)												7	179
Molops piceus (Panzer)												25	4

formed by the introduction of coniferous species, the development of populations of forest insects was delayed and the thermophilous species of open areas, *Harpalus rubripes* (Duftschmid), played the role of dominant or subdominant in the community of *Carabidae*. According to Dunger (1968) the succession of the entomofauna on waste tips does not end at the fourth stage. The climax stage is, however, reached in a period considerably longer than the 14-year process of forest recultivation observed by this author. This succession exhibits an even longer course on dumping grounds of Tertiary rock debris.

This opinion has also been confirmed by the results of the studies published by Neumann (1971) quoted above. This author observed no coincidence of *Carabidae* communities of dumping grounds and heaps near Kiel (German Federal Republic) in the 28th year of recultivation with analogous communities on forest areas (Table 9.2). Both authors quoted above agree that the invasion of post-industrial waste-land by the entomofauna took place in the process of its migration from neighbouring biotopes and that the rate of invasion depended on the distance of tips and dumping grounds from forest areas. Because of this, the contribution of species not capable of flying increased and that of winged forms decreased in the composition of *Carabidae* with advancing recultivation and the development of plantations (Fig. 9.2).

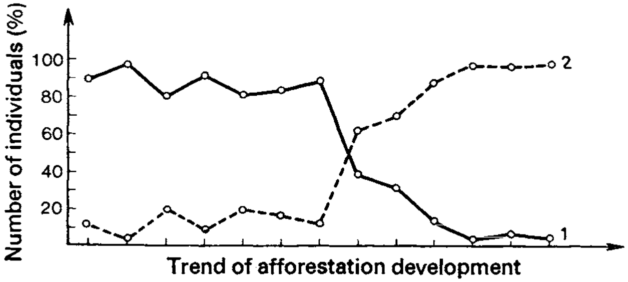


Fig. 9.2 Contribution of winged *Carabidae* in the course of afforestation of waste heaps (after Neumann, 1971): 1 — winged forms, 2 — wingless forms

The introduction of the fauna together with compost and plants plays a certain role in the invasion of the environments studied. Moreover, certain earth-worms were purposefully introduced here (Dunger, 1968).

Thus, the process of forest recultivation of waste heaps and dumping grounds becomes a technical-biological phenomenon in which the con-

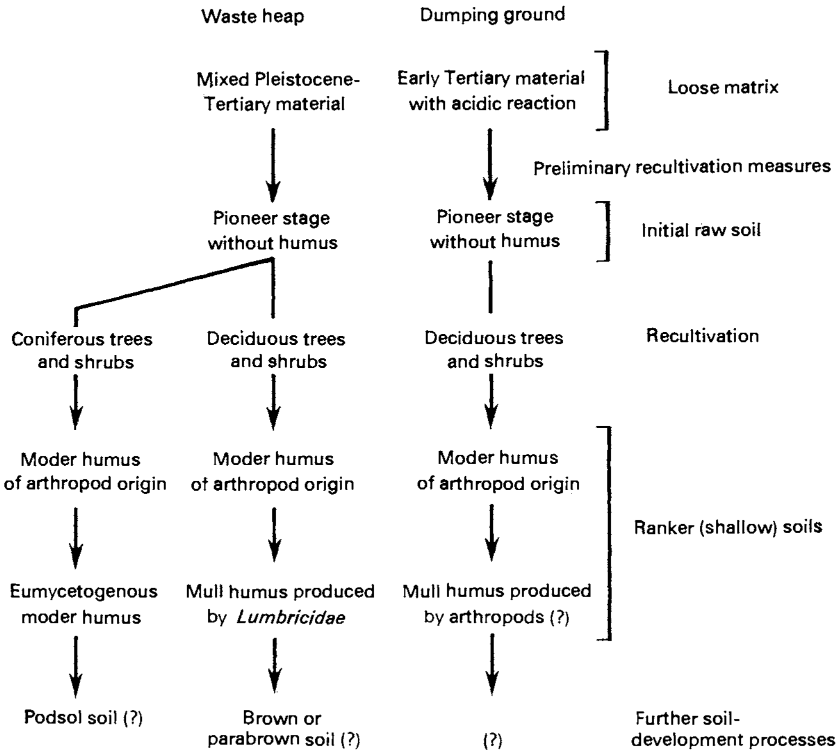


Fig. 9.3 Development of soil on recultivated soils on waste heaps of lignite exploitation (after Dunger, 1968)

tribution of fauna, consisting also of insects belonging to the orders *Collembola* and *Diptera*, is indispensable for a proper course of the formation of readily decomposable humus (Fig. 9.3).

9.2 Areas poisoned by industrial air pollution

The influence of the recultivation of soils poisoned by the Nitrogen Fertilizer Works in Puławy on the fauna was studied, especially with respect to *Lumbricus* spp., *Enchytraeidae*, saprophytes and ants (Górny *et al.*, 1974; Pętal *et al.*, 1975).

The need to recultivate soils poisoned by pollution produced by the Nitrogen Fertilizer Works in Puławy was determined by the degree of destruction between 1967–1971 in the neighbouring forest stands (Table 9.3) and aimed at the transformation of the industrial desert into a zone

Table 9.3 Dynamics of forest destruction in the zone of influence of pollution by nitrogen industry (after Siuta, 1974).

Year	Zone of pollution			Total
	complete and intensive	mean	weak	
1967	29	28	62	119
1968	64	100	116	280
1969	146	98	315	559
1970	470	670	3800	4940
1971	672	728	4000	5400

Table 9.4 Mean annual sedimentation of pollutants emitted by the Nitrogen Fertilizer Works in Puławy in 1971 (after Pętal *et al.*, 1975).

Pollution	Tons per 1 km^2 per year
$N-NH_4$	271.00
$N-NO_3$	37.20
$S-SO_4$	31.70
$S-SO_2$	6.30

of high biological activity (Siuta, 1974). The essential difficulty in this respect consisted of the progressive accumulation of toxic compounds in the soil (Table 9.4), as well as the complete disappearance of the buffer reaction of the soil to poisoning. Because of this, the following measures were taken into consideration in recultivation: organic and mineral fertilization, irrigation and the introduction of cultivated plants or shrubs. Particular concern was given to phosphorus-potassium fertilization determining the amount of nitrogen adsorbed by plants from industrial pollution, as well as to liming and the development of the humus layer (Siuta, 1974).

Recultivation measures influenced the abundance of all the animals studied but to different degrees. The effect of recultivation depended on the kind of measure adopted (the process of water spraying of the soil was particularly important) and the group of animals under consideration.

Changes in the ant population were distinct (Table 9.5). Data summarized in Table 9.5 indicate that the density of ant-hills of *Myrmica* spp. distinctly increased after recultivation due to fertilization. The density of populations of species belonging to this genus increased 20 times, the amount of biomass 19 times and the production about 27 times.

Table 9.5 Changes in the ant population under influence of recultivation measures (after Pętal *et al.*, 1975).

Index of population	Destructed zone	Recultivated zone
Number of species	2	3
Density of ant-hills per 1 m^2	0.008	0.034
Myrmica spp.	0.001	0.020
Lasius niger (L.)	0.007	0.007
Surface of ant-hill, cm^2 per 1 m^2	0.006	0.027
Amount of biomass, mg dw per 1 m^2	2.05	9.67
Myrmica spp.	0.46	9.12
Lasius niger (L.)	0.50	0.25
Production of biomass mg dw per 1 m^2	0.94	2.29
Myrmica spp.	0.08	2.18
Lasius niger (L.)	0.86	0.11
Index of growth of young generation		
Myrmica spp.	0.62	0.50
Lasius niger (L.)	0.80	0.63

On the other hand, the density of *Lasius niger* (L.) was reduced although the number of its ant-hills remained unchanged.

The index of growth of the young generation of both species is higher in the damaged zone and this may be the result of biological adaptation since the development of ant larvae is confined to the period of the maximum stock of plant and animal food. In the damaged zone this period ends as early as June while in the recultivated zone it persists longer (Pętal *et. al.*, 1975).

The data given above indicate that of both populations of ants compared, *Lasius niger* exhibits a weaker or even negative reaction to recultivation. This is due to the fact that, as a result of the activity of the microflora of ant-hills, this species is more resistant to environmental poisoning, therefore recultivation measures cannot affect the indexes characterizing its population.

9.3 Dune areas

Dune areas occupy a considerable part of Poland. Particularly vast areas are occupied by them in old river valleys of large rivers and on vast sandr plains (Fig. 9.4). They are of preglacial and postglacial origin. Coastal dunes occupy small areas but have a specific entomofauna.

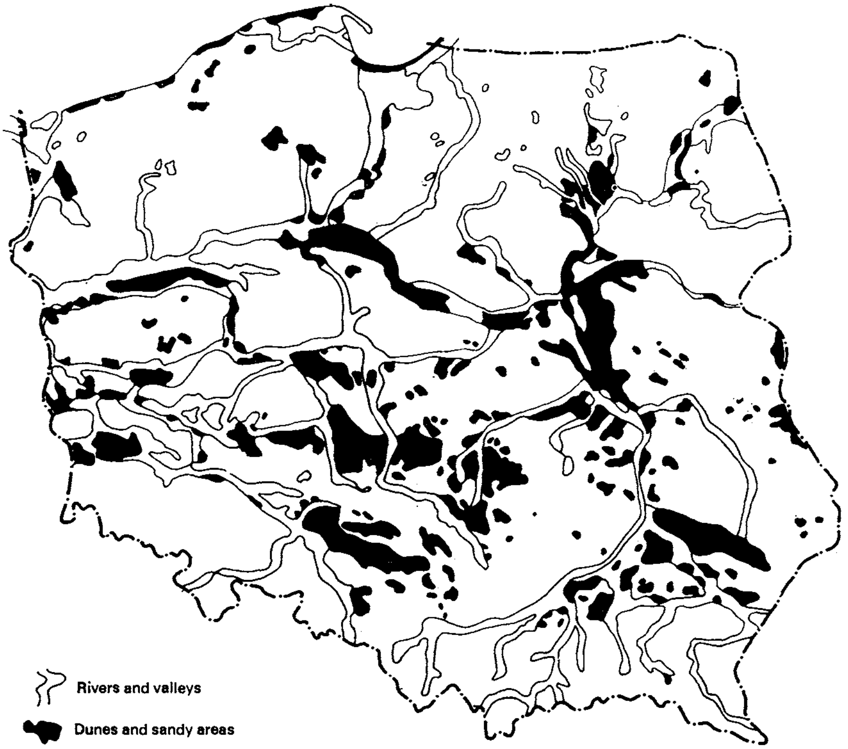


Fig. 9.4 Distribution of sandy areas in Poland (after Burzyński, 1971)

The appearance of inland dunes in the last centuries was due to the felling of forests overgrowing sandy soils and leaving the cutting areas without regeneration. This resulted in the sand being blown by winds and the formation of quicksands.

The high permeability, poor water capacity of sands, lack or deficiency of humus and many mineral components, high heating of sand by the sun and wide diurnal temperature amplitudes in the vegetation period are the main factors limiting the occurrence of plants and animals on sandy dunes. Only few insect species are able to survive under such conditions. They include *Cicindela hybrida* L., *Philopedon plagiatus* (Schaller), *Formica cinerea* Mayr, *Lasius alienus* (Foerster), *Myrmeleon formicarius* (L.), *Oedipoda caerulescens* L., *Melanimon tibiale* (F.), *Polyphylla fullo* (L.), *Asilidae* and *Therevidae* (Burzyński, 1971). *Cicindela arenaria viennensis* Schrank is a specific dune species.

The recultivation of dunes consists of forest recultivation with the use of the common pine (less frequently other tree species) as a potentially forest-forming species and certain shrubs such as the Caspian willow or grasses as plants stabilizing the quicksands. Afforestation of dunes is generally accompanied by fertilization. The process of the introduction of selected plant species onto dunes is accompanied by the invasion of this area by various insect species resulting from changes in the microclimate, soil factors and nutrient stock on the area of dune sands.

Unfortunately the course of succession of the entomofauna accompanying afforestation, as well as its differentiation from changes in the entomofauna under conditions of forest regeneration, has not been sufficiently studied in Central Europe. Certain data in this respect may be found in Jahn's (1951) work which presents the changes which occur in associations of soil animals, as well as in Burzyński's (1971) work on insects damaging the pine on dune areas and on some other rather randomly selected representatives of arthropods.

The number of animals (*Myriapoda*, *Collembola*, *Acarina*, *Psocoidea* were studied) increased systematically together with the growth of the first forest generation on dunes afforested with *Pinus nigra*. The density of these invertebrates increased both in the litter and in mineral soil, in parallel with a decrease in the ratio of the number of individuals occurring in the soil to that occurring in the litter (Table 9.6).

Table 9.6 Occurrence of soil *Arthropoda* on afforested dunes. Abundance in thirteen 1-litre samples. In brackets data concerning *Collembola* (after Jahn, 1951).

Layer	Dune	Thicket 14 years old	Pole-sized forest 46 years old	Forest stand 92 years old
Litter	–	1379	3320	10 236
		(353)	(413)	(617)
Soil	88	2100	2924	3 623
		(451)	(540)	(531)
Total	88	3479	6244	13 623
Soil: litter	–	1.5 : 1.0	1.0 : 1.1	1 : 2.8

Thus, the intensive accumulation of litter, which conditions the formation of soil, determined the process of its invasion by animals. The predominance of soil animals over litter ones declined in the 46 year-old forest stand when an adequate litter layer had developed. The abundance of *Collembola* also increased with the growth of the forest stand, particularly in the litter, but their contribution to the total number of animals decreased during this period. This seems to indicate that just as on other recultivated areas on afforested dunes, *Collembola* play a more important role in pioneer associations of soil fauna. In later succession stages their functions are intercepted by more climax communities generally consisting of invertebrates of larger body size and different metabolism.

An increased abundance of invertebrates was observed not only in the litter, but also in the superficial soil layer. The abundance of organisms in these layers was compared with that occurring in deeper layers. The ratio of the number of invertebrates in the superficial soil layer to that in deeper layers was 1.7:1 in thickets, 3.2:1 in pole-sized forest stands and 3.9:1 in timber forest. Furthermore, the abundance of animals varied in individual layers of the litter and soil depending on the season of the year as a result of the influence of changes in soil humidity and temperature (Jahn, 1951).

An important role is played in the process of biological recultivation of dunes by ants, especially *Formica cinerea* (Mayr) and *Lasius alienus* (Forster) which occur both on deforested dunes and in older forest stands. Their influence on soil-forming processes is particularly distinct from the period of plantation up to the tree age of 30 years. The abundance of ants then decreases abruptly. *Formica cinerea* is characterized by a high mobility and a considerable density of ant-nests. Even on bare dunes it builds underground nests with a system of galleries. The activity of this ant, which consists of the removal of sand of higher compactness than on the surface from deeper ground layers and its interspersing with small fragments of grasses and pine needles in the closest vicinity of the galleries and inlets, leads to a hardening of the substrate and prevents the movement of sand. According to Burzyński (1971), the system of galleries of a single nest stabilized 0.75 m^2 of the dune while in the closest vicinity the sand was blown away to a depth of 15 cm. Moreover, the ramified galleries contribute to the aeration of the soil whereas the fragments of plants accumulated in them undergo decomposition forming small agglomerations of humus. Such agglomerations of the remains of grasses and needles of a volume of about 3 litres were found at the depth of 20–50 cm (Burzyński, 1971).

The stabilization of the dune is frequently associated with the appearance of *Cladonia*, the patches of which stretch between planted tree seedlings or junipers originating from natural regeneration. A community of *Staphylinidae* with the characteristic species *Oxypoda togata* (Erichson) Szujecki, 1972a and the dominant species *Stenus geniculatus* Gravenhorst and *Quedius boops* (Gravenhorst) occur under such conditions in the association *Arctostaphyllo-Callunetum* in Masovia. *Cymindis vaporariorum* (L.) and *Miscodera arctica* (Paykull) are characteristis species in the carabid community here.

Myrmeleon formicarius L. and *Oedipoda caerulescens* L., originating from the period of deforested dunes, remain in young plantations. *Coleoptera* larvae occur in the soil (*Scarabaeidae*, *Curculionidae* and *Tenebrionidae*), as well as predacious larvae of *Diptera* such as *Asilidae* and *Therevidae*.

Adult tenebrionids belong to the characteristic entomofauna of the period of afforestation under discussion. *Melanimon tibiale* (F.) and *Opatrum sabulosum* (L.) are widely distributed, whereas the occurrence of *Phylan gibbus* (F.) is confined to coastal dunes (Burzyński, 1971).

The xerothermophilous soil entomofauna, as well as the epigeic entomofauna of bare dunes and young plantations, is almost completely replaced between the seventh and thirtieth year of the life of the trees by a typical forest entomofauna in which larvae of *Athous subfuscus* (Müller) and *Dalopius marginatus* (L.) are distinguishable. Nevertheless, this entomofauna also exhibits a considerable contribution of psammophilous forms such as *Harpalus latus* (L.) and *Anisodactylus binotatus* (F.).

The introduction of the pine onto sandy dunes creates favourable conditions for the increase of the abundance of phytophages associated with this tree, and this may lead to additional economic problems. Under conditions of water and nutrient deficiency, the pine needles, as compared with those from regenerated felling areas, exhibit on average a 4.5% reduction in the water content and a 0.88% and 0.05% reduction of nitrogen and essential oils respectively. On the other hand their content of sugar is higher by 0.87%. As is already known, this situation may favour the invasion of pines by foliophages and numerous xylophages. *Philopedon plagiatus* (Schaller) and *Strophosomus* sp. most rapidly occur in large numbers in young plantations. Larvae of *Polyphylla fullo* (L.) feed in the soil on pine roots.

Essentially the same pine pests occur on introduced trees of 7–30 years of age as in the case of forest regeneration on forest soils. The following species are most abundant: *Brachyderes incanus* (L.), *Rhyacionia buoliana* (D. & S.), *Exoteleia dodecella* (L.), *Brachonyx pineti* (Paykull), *Pissodes notatus* (F.), *Anthaxia quadripunctata* (L.), *Magdalis frontalis*

(Gyllenhal), *Thecodiplosis brachyntera* (Schwägrichen) and *Aradus cinnamomeus* (Panzer).

Unfavourable conditions of trees growth on dunes reduce the size of buds and therefore eliminate their mass invasion by *Exoteleia dodecella* (L.) and *Rhyacionia buoliana.* A natural protection of buds develops against the mass invasion of pests and a possibility arises of the protection of the tree layer which further may perform its definite function in the primary production of the ecosystem under discussion. On the other hand, fertilization of plantations on dunes favours the invasion of buds by pests.

Older forest stands on dune areas already exhibit a complete complex of pine pests belonging to the genera *Diprion, Panolis, Bupalus, Tomicus, Pissodes, Phaenops* and others. According to Burzyński (1971), *Barbitistes constrictus* Brunner von Wattenwyl and *Lymantria monacha* (L.) are the most important pests of older forest stands on dunes. They appear in large numbers in the Noteć Forest and the Sandomierz Forest. *Thaumetopoea pinivora* Treitschke is one of the characteristic pine foliophages on coastal dunes.

9.4 Afforested old farmland

Arable sandy soils occupied 7 167 000 ha in Poland in 1970. Of these, 1 613 000 ha consist of loose sands, 2 432 000 ha of slightly clayey sandy soils, 1 579 000 ha of clayey soils and 1 543 000 ha of deficient sandy soils.

Due to the very low biological activity of the poorest sandy soils and the persistent water deficiency, the agricultural production on such soils is realized below the limit of economic efficiency. Together with technological modernization and the reduction of expenses of plant production on a wide scale, the cultivation of the poorest sandy soils will become completely unprofitable (Siuta, 1974). Moreover, owing to the high permeability of sandy soils and their very low absorption capacity, the large amounts of mineral fertilizers applied here are not always biologically bound but, on the contrary, are rapidly washed away. This contributes to the salinity of ground waters and to the intensification of pollution processes and sedimentation in water bodies. The increasing mortality of people and animals due to intensive mineral fertilization of plants on sandy soils is also an imminent phenomenon (Aleksandrowicz, 1972, quoted after Siuta, 1974).

The situation described above justifies the transfer of arable soils of the poorest quality to forest management, the more so since the spatial structure of the landscape of Poland requires an increased contribution of woodland. Water protection, as well as climatic, economic, recreational and other reasons are also in favour of such a decision. This concerns soils developed from loose sands, as well as a part of slightly clayey sandy soils with unfavourable water conditions. Since at present afforested old farmland constitutes about one million ha the total area of forests originating from afforestation in the next 50 years may yet increase to about 15–20% of the forest area of Poland.

This requires the elaboration of methods of reasonable cultivation of the forming forest ecosystems, the more so that the biological conditions of former farmland differing from those in forests, as well as their low productivity negatively affect the growth and health condition of plantations in their older developmental stages.

The symptoms of growth inhibition of pine forest stands on old fields become most outstanding during the period of the closing of the tree canopy, when the requirement for nutrient substances, mainly nitrogen, is particularly high. Under these conditions *Fomes annosus* (Fries) develops. This is favoured by the horizontal root system of pines due to the agricultural utilization of the soils, which renders the water supply to the trees inaccessible in periods of drought. The trees are weakened or die and this is accompanied by the process of their invasion by secondary pests.

The methods of cultivation of afforested old farmland should also take into consideration the problem of development of the local biocenoses and particularly soil ones, the reconstruction of which may secure the course of forest recultivation.

Hitherto, the development of entomocenoses under the conditions of reafforested former farmland (Fig. 9.5) was a phenomenon occurring in a natural way in which human guidance was confined to the introduction of trees. This leads to the appearance of unsuitable biological systems, both in the layer of forest stands and in the edaphic layer. Moreover, these systems remain in mutual association characterized by correlated dynamics of quantitative changes. Since afforestation is almost invariably limited to pines, particularly typical biological systems arise between diseases of the pine root system and insects feeding under the bark and in the wood of weakened trees. Because of this, the occurrence of secondary pests on afforested areas generally exhibits a focal character resulting from the focal propagation of *Heterobasidion annosum* (Fries) Brefeld and is most intensive in older thickets.

The following phases of the invasion of trees may be distinguished in the foci of *Heterobasidion annosum* (Vorontsov, 1963): invisibly infected trees (they occur on the periphery of the focus of *H. annosum*), infected trees, weakened trees, drying and dry trees (in the centre of the focus). The death of the roots of the trees infected by *H. annosum* is preceded by the internal and external flow of resin isolating the diseased roots from other parts of the tree. The isolated roots die and undergo decomposition. The death of the roots gradually reduces the water supply to the trees, growth is inhibited, many shoots and needles are shorter and the exchange of needles is accelerated. The disease symptoms appear in the pines only when 80% of roots die. Due to the slow process of debilitation of trees by *H. annosum*, the death of trees is virtually determined by secondary insect pests exhibiting a rapid reaction to changes in the physiological condition of their host plants. In pine forest stands these are primarily *Tomicus piniperda* (L.), *T. minor* (Hartig), *Pissodes piniphilus* (Herbst) and *Monochamus galloprovincialis* (Olivier) and in older forest stands also *Ips acuminatus* (Gyllenhal), *Phaenops cyanea* (F.), *Acanthocinus aedilis* (L.) and others (Sierpiński, 1969).

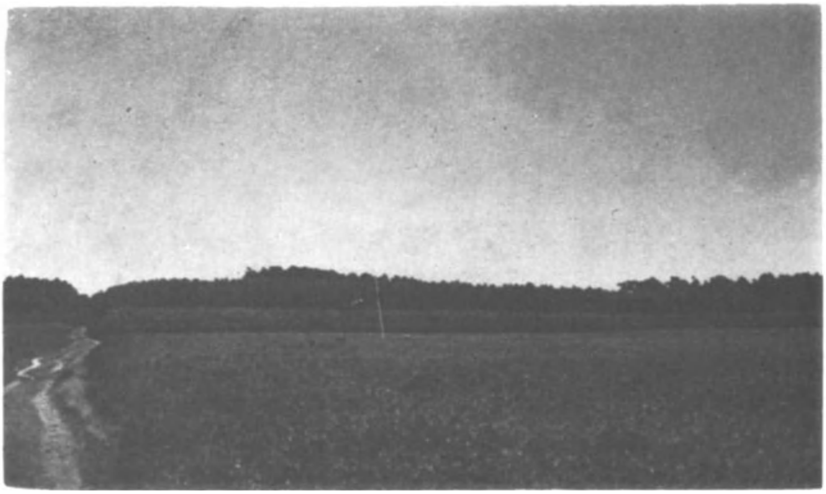


Fig. 9.5 Afforestation of former farmland (photo by the author)

Damages of tree roots due to larvae of *Brachyderes incanus* (L.), the population of which in younger and middle-aged classes of plantations on former farmland is invariably abundant, may favour a further propagation of *Heterobasidion annosum*. These larvae occur in the superficial soil layer, a dozen or so centimetres thick, in which an excessive accumulation of superficial pine roots occurs and may play the role of vectors of *H. annosum*. Adults of *Brachyderes incanus* are among the most abundant insects feeding on needles in pine plantations and thickets. They are generally accompanied by *Strophosomus capitatum* (De Geer), *Brachonyx pineti* (Paykull) and others.

The course of the invasion of afforested areas by *Tortricidae* and *Exoteleia dodecella* (L.) depends to a high degree on the distance of these areas from plantations on forest soils. This is probably one of the causes of the extreme differences in the intensity of invasion of pine plantations on old farmland by *Tortricidae* variously interpreted in the literature. It should be stressed that, despite the considerable interest in the occurrence of noxious insects on afforested areas, there are no methodically correct comparative studies on the formation of entomocenoses on afforested farmland and the analogous phenomenon in regenerated forest soils. The results given in numerous elaborations devoted to the formation of insect communities in protective forest belts in the steppe and semi-desert zone of the Soviet Union (Vorontsov, 1963) include no data useful for the evaluation and characteristics of the similar process on afforested areas. Elaborations devoted to the soil fauna of afforested areas in Poland are of little value in this respect.

The course of the formation of associations of the forest soil fauna under the influence of afforestation of old farmland on the western edge of the Bory Tucholskie Forest (Człuchów Forest) was the subject of team studies performed by the Institute of Forest and Wood Protection, Agricultural University, Warsaw (Szujecki, Szyszko, Mazur & Perliński, 1975, 1977).

Invasion of old farmland by the fauna takes place in the form of secondary succession while on forest felling areas it represents the character of regeneration of animal associations temporarily eliminated. Due to the different character of the formation of entomocenoses on former farmland and the case of forest regeneration, the community of insects during the periods of plantation and thicket of these environments differs widely. The essential process of invasion of former farmland by the forest entomofauna occurs in the period of older thickets and pole-sized forest stands and lasts until age class V, when it seems that the faunae of soil forests and old farmland exhibit no distinct differences as regards their species composition and dominance structure.

Different taxons (generally families) stabilize the composition of forest species in various periods of development of the introduced trees.

The communities of large epigeic predatory carabids stabilize most rapidly, i.e. already in old thickets. The longest course of stabilization is observed in larvae of *Diptera* which make up the communities in 50–70 year-old forest stands. Ants of the *Formica rufa* L. group not observed in the first generation of trees introduced onto the area studied do not reach stabilization.

The complete scheme of succession of soil microfauna on afforested areas and the cyclic changes in communities of microfauna on forest areas are illustrated in Fig. 9.6. The course of changes in the entomofauna on afforested areas exhibits a succession character with a number of links superceding each other with the growth of the forest stand and the formation of the typical forest entomofauna.

The period of plantations is characterized by the occurrence of the xerothermophilous entomofauna of forestless areas in which a high contribution of phytophages, mainly larvae of *Elateridae*, is distinguished. These include *Selatosomus aeneus* (L.), *S. latus* (F.), *S. impressus* (F.), *Agriotes ustulatus* (Schaller), *A. obscurus* (L.) and others. Moreover, characteristic or dominant larvae of *Malthodes* (*Cantharidae*), *Scarabaeidae*, *Chironomidae*, *Itonidiidae* and *Petauristidae* are present, whereas on the soil surface the adults of the staphylinids: *Philonthus nitidulus* (Gravenhorst), *Stenus atratulus* Erichson and *Ocypus picipennis* (F.), as well as the ants *Tetramorium caespitum* (L.), *Lasius niger* (L.), *Formica cunicularia* Latreille and *Lasius alienus* (Foerster) also occur. On the other hand, larvae typical for forest soils such as *Ampedus balteatus* (L.), *Cardiophorus ruficollis* (L.) and *Bibionidae*, and many adults of *Coleoptera* such as *Bradycellus caucasicus* Chaudoir and *Mycetoporus lepidus* (Gravenhorst) are absent (or rare).

The period of thickets is characterized by a high density of individuals and biomass of phytophages among which larvae of *Brachyderes* and *Strophosomus* predominate, as well as those of *Selatosomus* and *Agriotes*. Zoophages, particularly epedaphic *Carabidae* and *Staphylinidae* such as *Oxypoda togata* Erichson and *Quedius boops* (Gravenhorst), are active and exhibit a high density. On the other hand, soil saprophages, among which larvae of *Orthocladiinae* (*Chironomidae*) are most abundant, exhibit a low biomass. Abundant populations of *Tetramorium caespitum* (L.) play an important role here. Species of the period of plantation gradually disappear, although the entomofauna still represents a xerothermophilous character. Forest species are few but

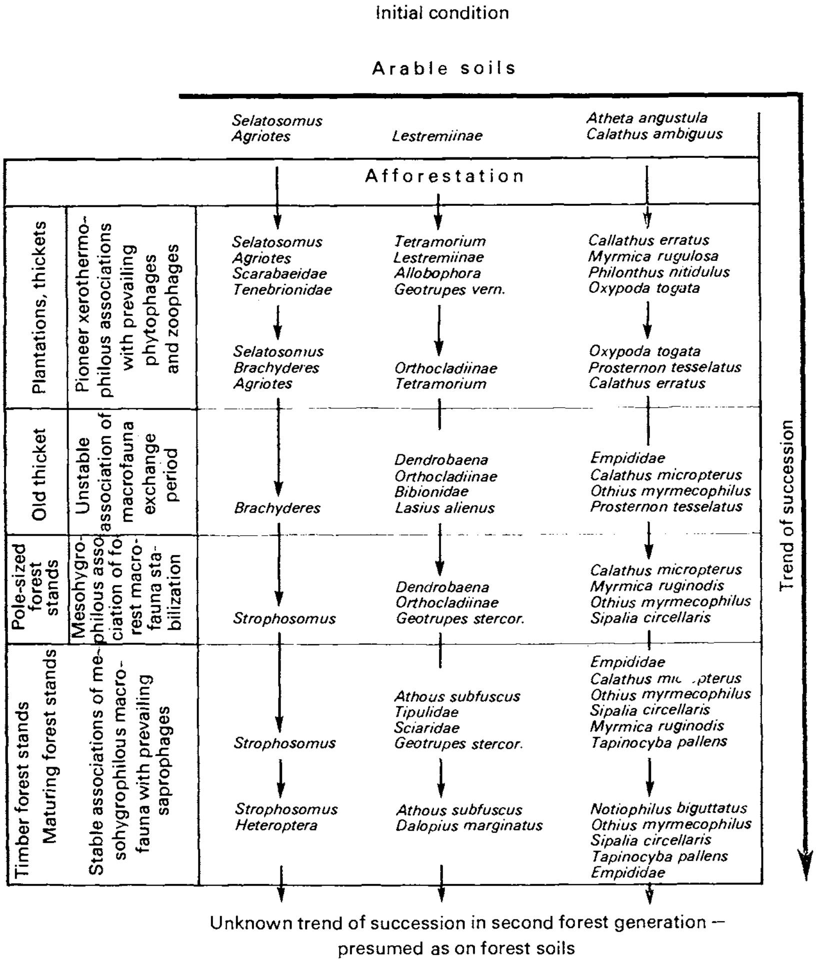


Fig. 9.6 Scheme of succession of soil macrofauna on afforested old arable land (after Szujecki *et al.*, 1977)

they already contribute to the communities. Due to these factors, many taxocenes exhibit a quantitative depression here (*Elateridae*). On the other hand, other groups of the entomofauna attain a specific composition and abundance corresponding to that of forest soils in the period of old thickets and young pole-sized forest stands. These are *Carabidae*, *Staphylinidae* and *Formicidae* (but not quantitatively, ants are invariably more abundant on forest soils). Other more important taxocenes stabilize their specific composition and dominance structure in later life periods of forest stands. These are larvae of *Elateridae* (older pole-sized forest stands) and larvae of *Diptera* (maturing forest stands).

Thus the development of communities of the entomofauna on old farmland is attained primarily by epigeic predacious species (obligatory or facultative zoophages), whereas the conclusion of the development of communities of hemi- and euedaphic saprophages is retarded by about 20 years as compared with the former group. In view of this only 60–100 year-old forest stands on former farmland become similar to stands on forest soils as regards their specific composition and dominance structure, as well as the amount of biomas of the soil entomofauna.

The course of succession as regards the dominance of important ecological groups of animals, here resembles that occurring for instance on recultivated waste heaps and dumping grounds, due mainly to the important role of *Carabidae* in the second stage of succession and to the delayed attainment of dominance of various groups of saprophages. This indicates that the process of formation of soils with biological properties of forest soils is also hardly realized on these sites and may take place only with a high contribution of fauna.

The amount of biomass of the microfauna in the litter and mineral soil layers exhibits a course somewhat different from that of the succession. Former farmland essentially differs from forest soils in this respect. The biomass of the microfauna of former farmland is higer than that in forest soils only in the period of plantations. Since, in the period of thickets, the biomass of the macrofauna of former farmland is on the average lower by 25% as compared with the analogous biomass in forest soils, the density of microfauna is also lower here. The distribution of the biomass of saprophages in the litter and mineral soil of the soils compared is interesting. In the period of plantations and thickets the biomass of saprophages in the litter of former farmland is lower than that on forest soils. This ratio is inverse in later life periods of the forest stands. Since the biomass of the macrofauna of the superficial 10 cm layer of mineral soil does not increase with the development of the planted trees as intensively as in forest soils, the ratio of biomass of the macrofauna of the litter to the biomass of the microfauna of mineral soil on old farmland steadily increases since the period of younger pole-sized forest stands up to the period of timber forest whereas on forest soils this value approches equilibrium (Fig. 9.7).

This allows us to establish that reafforestation of old fields does not secure the complete functioning of the soil macrofauna. Its biomass is

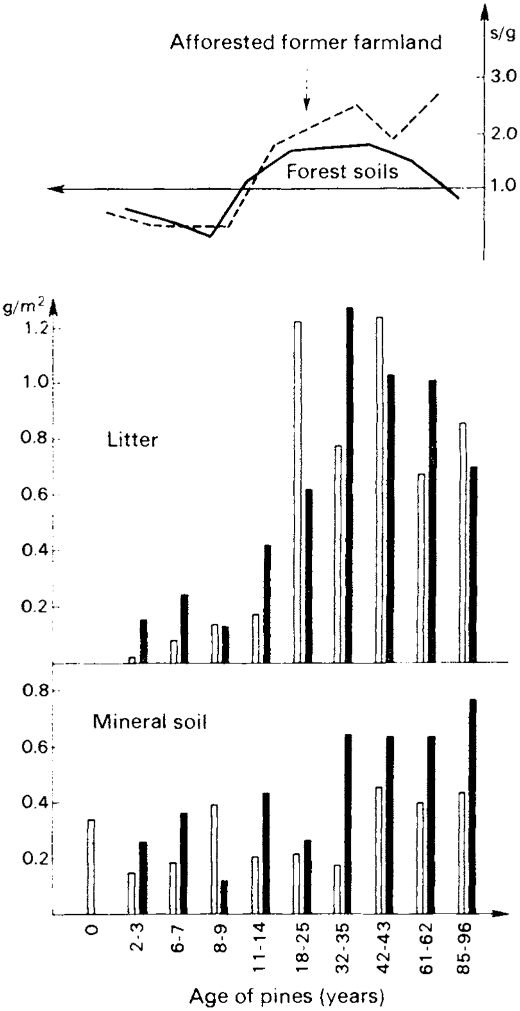


Fig. 9.7 Biomass of saprophages in litter and mineral soil and ratio of biomass of macrofauna in the litter to biomass in mineral soil in forest soils and on afforested old arable land (after Szujecki *et al.*, 1977): s/g — weight ratio of macrofauna in litter and mineral soil; dark bars — forest soils, white bars — afforested old arable land

smaller and its role in soil-forming processes occurring in the layer of soil formerly utilized in agriculture is insufficient. Parallelly predacious epigeic insects exhibit a high mobility on former farmland and this may indicate that their nutrient resources are deficient.

The biomass and density of phytophages during the period of thickets to pole-sized forest stands in the litter, are lower on old farmland than on forest soils. This is due to the lack of the rich herb layer in forest stands on old fields such that soil larvae of *Curculionidae* prevail here, whereas bugs and larvae of *Lepidoptera* which appear abundantly on forest areas overgrown by the blueberry and cowberry are deficient.

Analysis of the layered distribution of the macrofauna indicates that the differentiation of this system, as compared with forest soils, corresponds in time to the period in which the growth of forest stands originating from afforestation is inhibited, the trees undergo the pathogenic influence of *Heterobasidion annosum* (Fries) Brefeld and secondary pests.

It is probable that both these phenomena are causally associated. The recultivation of old farmland would thus require measures biologically activating the superficial soil cover in the period of plantations and thickets as well as the superficial layer of mineral soil in a later period.

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Index of latin names of Invertebrata

(Page numbers marked with an asterisk are connected to illustrations, photos and tabels)

Subject index

ERRATA

Page, line	For:	Read:
79_7	= *Melasoma*	(= *Melasoma*)
82^{11}	= *Chrysomela populi* L.	(= *Melasoma*) *populi* L.
114^2	first half	second half
353_2	Vast spruce	Vast pine
424_5	Kieych	Kierych
523_{21}	*Fomes annosus* (Fries)	*Heterobasidion annosum* (Fries) Brefeld

A. Szujecki, *Ecology of Forest Insects*.