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# PLANT ECOLOGY IN THE MIDDLE EAST



AHMAD HEGAZY & JONATHAN LOVETT-DOUST

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We dedicate this book to our students, and are deeply grateful to our spouses for all of their help and support during its preparation.

We also dedicate this book as a message to all the people and countries of the region: may we all work together to build peace and conservation, stability and prosperity for the region.

# Preface

The Middle East has a rich natural history; however study of the diverse flora of the region has been intermittent, and usually localized. Human activities over time have both enriched and damaged biodiversity. Early on, medicinal plants and crops in the region were domesticated; on the other hand, environmental pollution, rampant coastal development, and overgrazing have all negatively impacted ecological functioning, while warfare and disputed borders have delayed systematic study, and to many outsiders the Middle East seems exotic, even mysterious. We believe a better understanding of the plant ecology of the region will allow us to understand and anticipate the effects of climate change in arid and semi-arid regions worldwide, and for that reason as well as the inherent fascination the region holds as a "cradle of civilization," a book on the current state of knowledge seems timely. Our goal is to provide a solid baseline and stimulate further research.

We have taken a "plant's-eye perspective" on the Middle East and include all the biogeographic regions contributing species. For us, the Middle East includes parts of Africa, Europe, Asia, and Arabia, covering some 13.5 million $km^2$. We integrate plant geography, and evolutionary and population ecology with information on the life histories of species found in the deserts, mountains, and coastal regions of the Middle East. We hope this integrative, empirical approach to the region's plant ecology, set in a context of plant evolution and adaptation to unpredictable resources, may be of interest to dryland specialists, ecologists, conservation biologists, and climate change researchers everywhere.

Chapter 1 introduces the several major elements of the book's scope that will help us understand the present day distribution and abundance of plants across the Middle East. We overview previous studies of the flora then outline the general nature of deserts and importance of water in these dryland environments. We explore effects of long-term climate change and the formation of "climate relicts," (the plants of the Middle East have experienced climate change in the past, too) and effects of heterogeneity in time and space on a species' "regeneration niche" (the particular environment that is necessary for successful seed germination and *juvenile* survivorship). In the Middle East various iconic tree species exist as stands of aging individuals that are simply not being replaced through natural regeneration. The region includes many precious and unique sites, for example vestigial "valley-forest" in Arabia, many of which have been reduced to a few highly degraded remnant populations in the southwest (exemplifying the urgency of regional conservation strategies to protect the flora of the Middle East).

Chapter 2 offers a tour of the region, outlining the plant ecology of some 24–25 countries, including parts of Africa and Eurasia as well as the Arabian Peninsula, with many mountain ranges, plains, plateaux, and some islands—not least the botanically fabulous Socotra. The tour is intended to give some overall sense of the entire region—a vast place with many different kinds of habitat. Some, like the montane cloud forests of Oman, Yemen, and Egypt, for example, are biodiverse and spectacular. Others are more homogeneous—often with few species because conditions are more extreme. . . these sites are typically hotter, flatter, and drier, as in for example, the sparse communities of the "Empty Quarter" of Saudi Arabia.

Chapter 3 shows how the Middle East and its plants came together as a product of geological "deep time," starting with major geological events at least some 23 million years ago. The plant

populations and communities we have today represent remnants of their past. We explore in some detail examples of ancient forest relicts—the spectacular Dracaena forests of Socotra, various oak-laurel forests, the refreshing juniper forests of the coastal areas, and the Djibouti Bankoualé Palm.

Chapters 4 and 5 explore the constraints of living in desert and dryland ecosystems, in particular dealing with unpredictable water supplies and spatial heterogeneity. These in turn generate habitat diversity and specialized plant forms, developing succulence, water-conserving photosynthesis and other adaptations to deal with excessive drought and salt in the environment. Given the significance of mountains throughout the region we discuss effects of elevation and isolation on plants and regional patterns of species richness and endemism.

Chapters 6–8 focus on plant reproduction in the dryland world. To succeed in this unpredictable environment plants need to be able to sense the environment and respond to opportunities with speed; it is easy to see how such life history strategies can be seen as evidence of plant "intelligence"—these organisms are integrating different stimuli and protecting their descendants through strategic seed dispersal and dormancy. In such environments plants often have complex "secondary chemistry," producing many anti-herbivore compounds and others that inhibit competitors. Chapter 9 explores the domestication of plants in the region and the many reciprocal effects of agriculture and its early development on plant ecology there.

Chapter 10 outlines the major challenges to plant conservation in the region and proposes strategies for successful conservation, starting with the major Middle Eastern "biodiversity hotspots." A final chapter draws together some general conclusions about the plant ecology of the region. As a general note on spelling and transliteration from the Arabic: is a mountain range here to be *gebel, jabal*, or *djebel*, etc.? Is the thirsty, stimulating plant *Catha edulis* to be described as *khat* or *qat*, etc.? For the most part we have simply adopted the style used by our sources; we generally do not hyphenate the definite article, but again follow precedent, thus Al Ain and El-Keblawy. . .

We are grateful to many people who have kindly helped us in various ways to produce this book. Perhaps first and foremost we thank the many colleagues and students with whom we have been fortunate to work over the years; they have helped shape our thinking on the elements of plant ecology. This includes Drs. H. Adawy, M. Cadotte, A. El-Keblawy, N. Gomaa, M. Imam, A.-H. Khedr, H. Murphy, M. K. Okla, O. Sharashy, E. Badawi, and J. Vanderwal. We appreciate all the kind help given by Drs. Hanan Kabiel and Sanad Al-Sobeai at various stages of the book's preparation.

We are particularly grateful to Dr. Abdel Aziz Assaeed, Dr. Saud Al-Rowaily, and Dr. Magdy El-Bana who showed us so many interesting habitats and locations during field trips in Saudi Arabia, and shared photos and source materials. Special thanks go to friends among the local residents there: Mr. Naser Al Shedwy, his son Osama Al Shedwy, and Dr. Riyad Basahi who all provided valuable logistic support and acted as field guides and instructors during field trips in the western and southern mountains of Saudi Arabia. Without their help many otherwise inaccessible places in that wonderful mountainous landscape could not have been reached.

We are grateful to our taxonomic colleagues, especially Drs. Fahd Al Hemaid, Ibrahim El-Garf, Jacob Thomas, and Wafaa Amer for help in species identification and nomenclature, and for sharing source materials.

We are very grateful to the following individuals who generously gave their time to review some or all of the book in early stages: Peter Sale, who plowed through the entirety of an early draft and provided many useful insights and helpful suggestions; Marc Cadotte, Ali El-Keblawy, and Carl Freeman who all read early material and prompted us toward helpful improvement. Lesley Lovett-Doust very kindly read nearly everything, sometimes more than once, and made many important suggestions at all stages of the book's production.

We thank everyone who has granted us permission to include previously published materials. We are particularly grateful to Drs. Avi Shmida and Bruno Mies for their kind encouragement and permission to use selected material from their published work on Middle Eastern phytogeography and ecology.

Leo Lovett-Doust helped greatly with the preparation of figures and tables and with the book's digital coordination. Dr. Mohamed El Hag kindly helped with drawing the maps.

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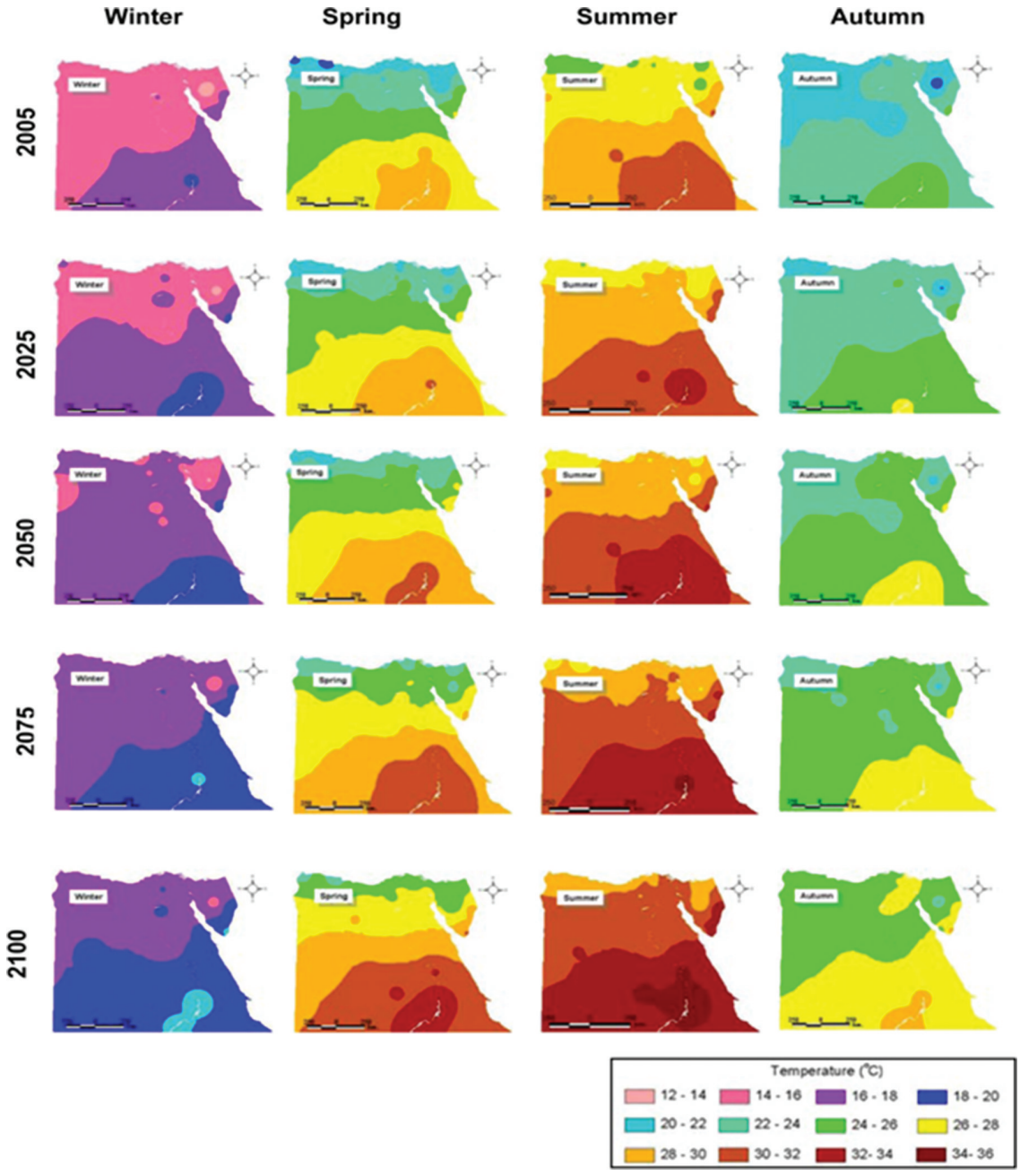



**Plate 1** Seasonal air temperature distribution in Egypt during the year 2005 and the projected years 2025, 2050, 2075, and 2100 due to the expected climate change in the twenty first century (after Hegazy et al. 2008b) (see also Figure 1.6 on page 13).

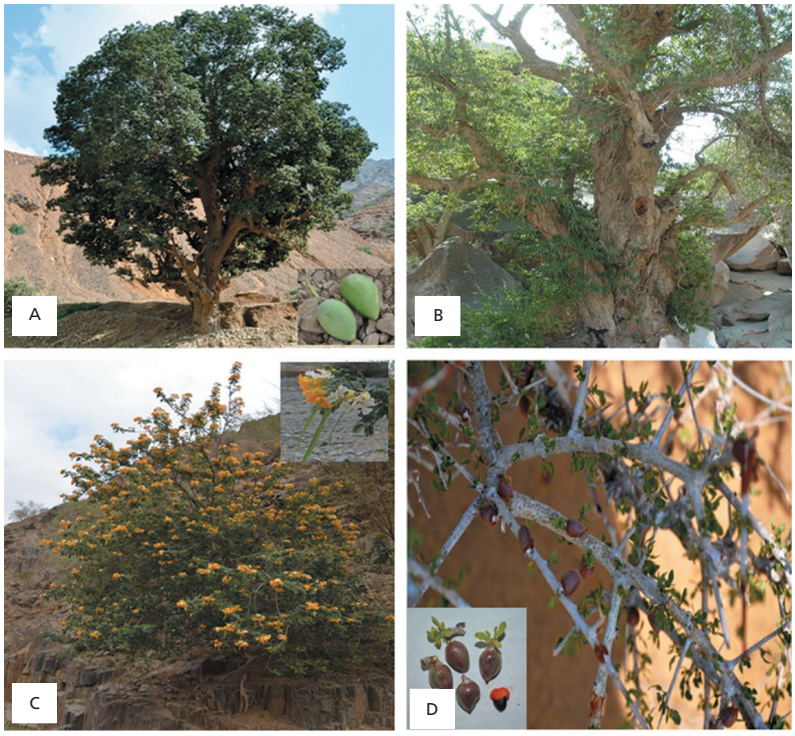



**Plate 2** (A) Giant tree of *Mimusops laurifolia* in the mountain escarpment, Jizan region, southwest Saudi Arabia, elevation 985 m. Two fruits shown in lower right side. (B) An old tree estimated to be *c.* 400 years old *Breonadia salicina* in Shada Mountain, southwest Saudi Arabia, elevation 1200 m. (C) *Delonix elata* in Shada Mountain at elevation 600 m, southwest Saudi Arabia. Reproductive branch in the upper right side. (D) *Commiphora myrrha* fruiting branches. Fruits and seed in lower left. Photo was taken from the coastal dunes of the Tehamah Plain, near Jizan, southwest Saudi Arabia (see also Figure 1.7 on page 24).

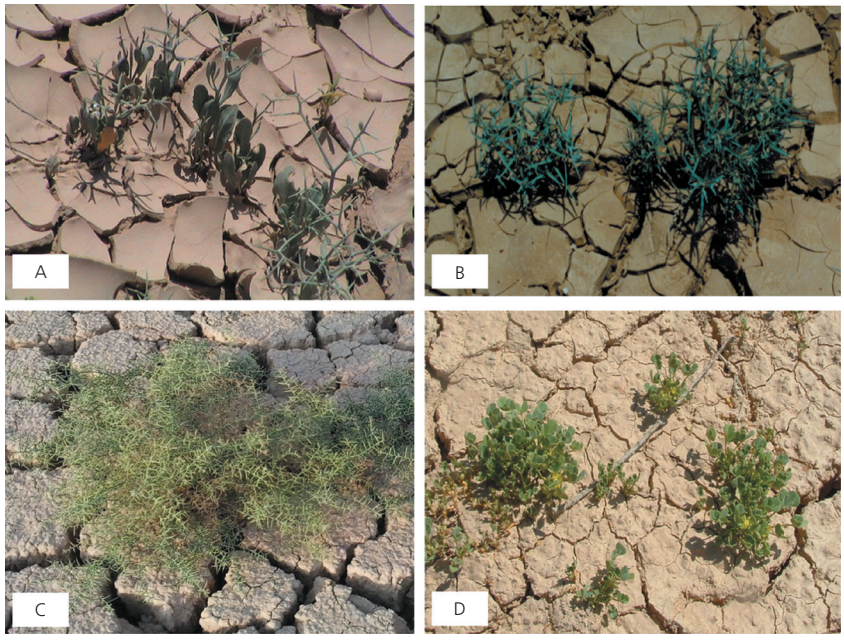



**Plate 3** Desiccation cracks in shallow depressions in arid deserts supporting the establishment of many species. (A) *Zilla spinosa*, (B) *Euphorbia retusa*, (C) *Alhagi graecorum*, and (D) *Trigonella stellata*. Photos A and B from Eastern Desert of Egypt; C and D from Central Saudi Arabia (see also Figure 2.2 on page 30).




**Plate 4** Vegetation of Jabal Al-Akhdar (A, B, and C) in northeast Libya, and Jabal Nafusa (D) in northwest Libya. A = Wadi El-Aker, B = Wadi El-Kouf, and C = Birccess in Jabal Al-Akhdar; D = Meslatah National Park in Jabal Nafusa Mountains (see also Figure 2.4 on page 32).

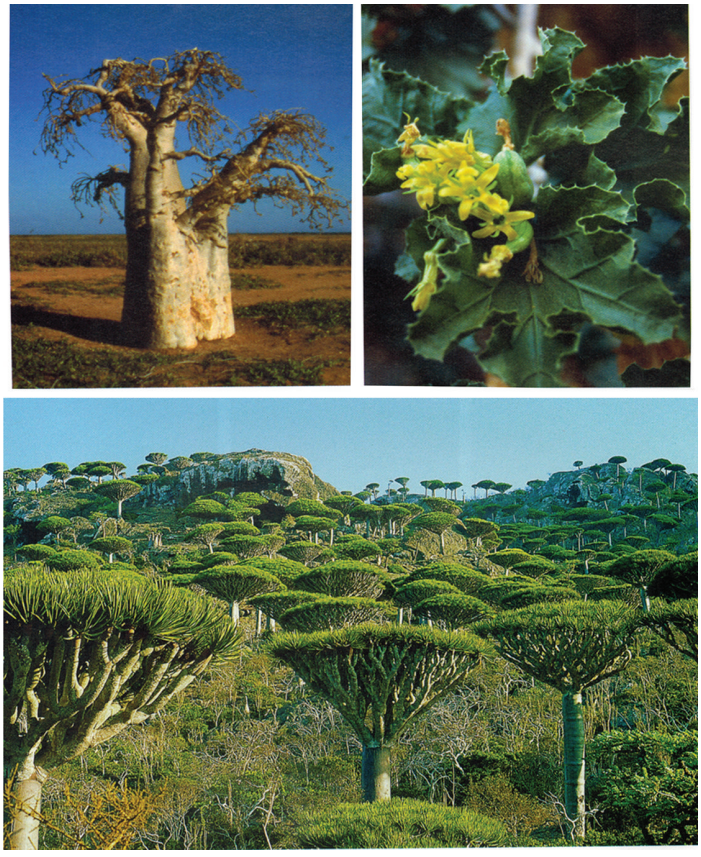


**Plate 5** The cucumber tree *Dendrosicyos socotrana* (upper left) and flowering-fruiting branch (upper right), and the dragon's blood tree *Dracaena cinnabari* (bottom) in Socotra island archipelago. Reproduced with permission from A. Miller (see also Figure 2.11 on page 47).

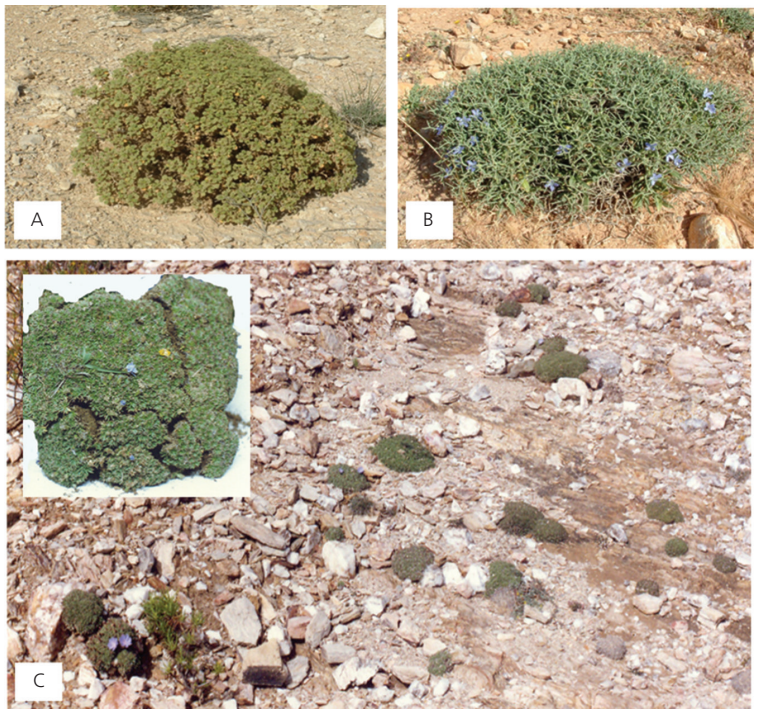



**Plate 6** Cushion plants growth form and specialized habitat types. (A) The aerial cushion form of *Cleome droserifolia*, Eastern desert, Egypt. (B) The aerial cushion plant *Cichorium spinosum*, Mediterranean coast, Shahat, Libya. (C) Population of the closed cushion plant *Cichorium bottae* on dry windy slope at elevation 2900 m, in Alsodah, south west Saudi Arabia. In the top left corner a close up view of an individual plant showing the filling material in the cracked crown under the canopy active surface layer (see also Figure 4.6 on page 109).




**Plate 7** (A) The mangrove plant *Avicennia marina* in the shoreline of Gazerat Sherifah, Red Sea, Saudi Arabia. Viviparous seed appears in the top left corner. (B) Sand mounds (nabkhas) of *A. marina* in Nabq, South Sinai, Egypt. (C) Single tree of *A. marina* growing in the intertidal zone with horizontal rhizomes radiating from the base and upward-growing pneumatophores. (D) Small tree of *Rhizophora mucronata* with one viviparous seed still attached (left side). (E) Single tree of *R. mucronata* (front) bearing viviparous seeds in Shalatin mangrove stand, southeastern Egypt. Note the dense establishment of *R. mucronata* plants under the large tree (see also Figure 4.12 on page 118).




**Plate 8** Dryland plant adaptations. (A) shedding of cortex in *Halopeplis perfoliata* in coastal salt marshes of Farasan Island, Saudi Arabia. (B) Heterophylly in *Artimisia monosperma* in Central Saudi Arabia. (C) *Adenium obesum* in Shada Mountain, southwestern Saudi Arabia at elevation 1750 m (flower and fruits are shown at lower right) (see also Figure 5.1 on page 132).

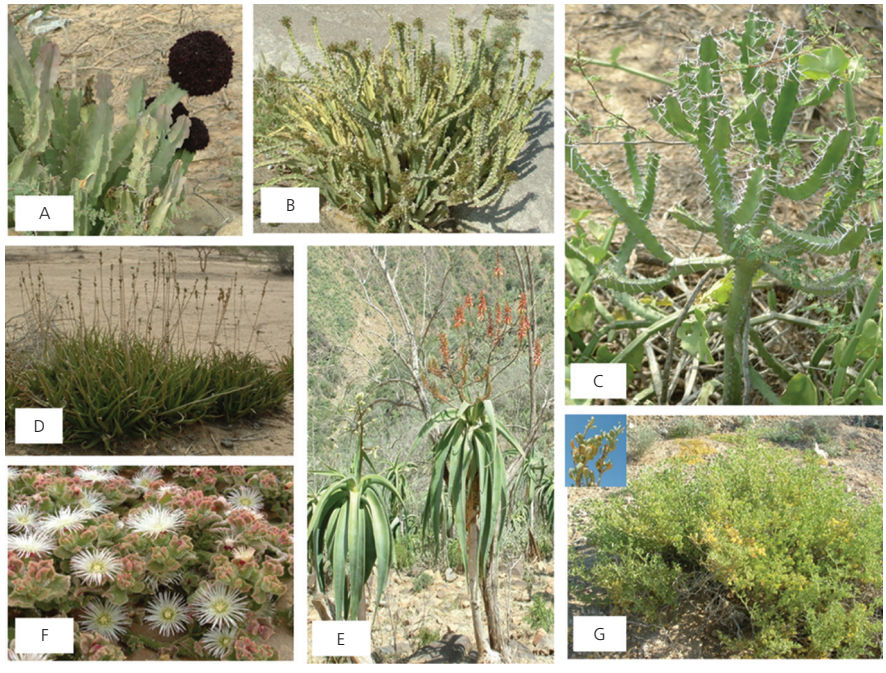



**Plate 9** (A) The succulent plant *Desmidorchis retrospeciens* at the foot of mountain escarpment near Taif, Saudi Arabia. (B) *Desmidorchis penicillatus* in foothills, Ad Darb, southwestern Saudi Arabia. (C) *Euphorbia fractiflexa* in Tehamah plain, Jizan, southwestern Saudi Arabia. (D) *Aloe vacillans* in Tehamah plain, Jizan region, southwestern Saudi Arabia. (E) The leaf succulent *Aloe sabaea* in the Raidah escarpment, northwest of Abha, Saudi Arabia. (F) The annual succulent *Mesembryanthemum crystallinum* in coastal sandy habitats near Sert city, west of Benghazi, Libya. (G) The perennial leaf succulent *Zygophyllum decumbens* in the Eastern Desert, Egypt. Enlarged leaves appear at top left (see also Figure 5.2 on page 134).

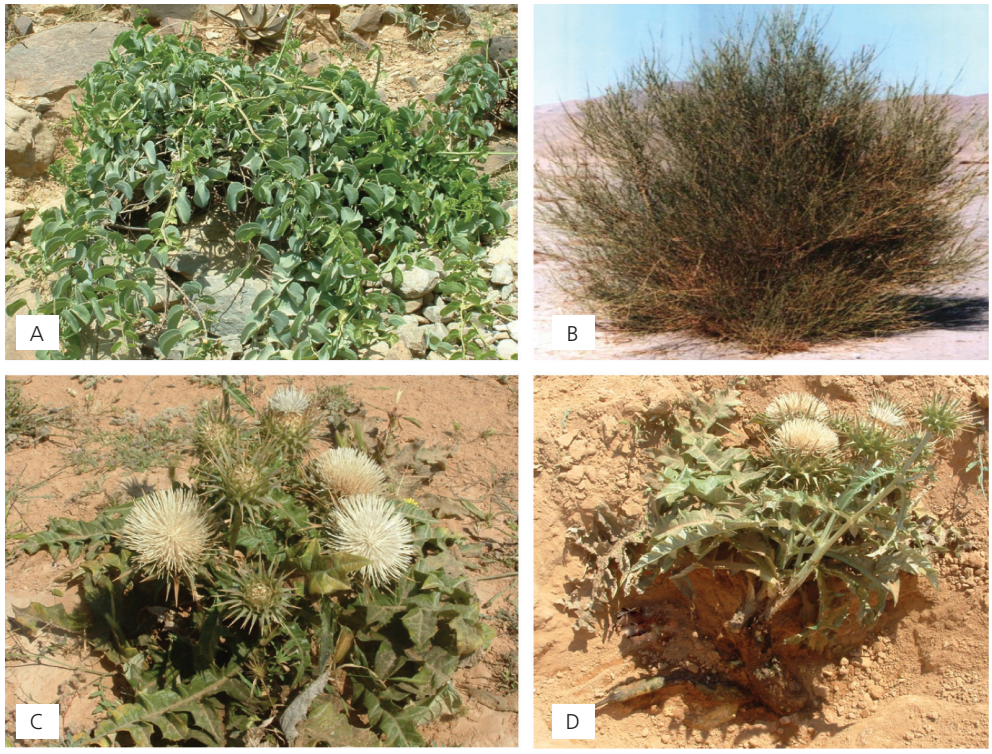



**Plate 10** (A) The stem and leaf succulent *Cissus quadrangularis* (Vitaceae) from the Abha Mountains, Saudi Arabia. (B) The extremely deep-rooted perennial shrub *Leptadenia pyrotechnica* (Asclepiadaceae) from Eastern Desert of Egypt. (C) *Cynara cornigera* (Asteraceae) from northwestern Egypt. (D) Exposed swollen succulent root of *Cynara cornigera* (see also Figure 5.3 on page 139).

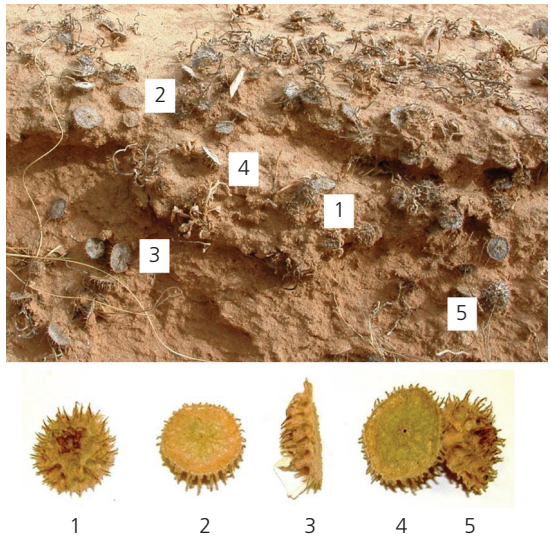



**Plate 11** Orientation of *Neurada procumbens* fruits (diaspores) in the seed bank. (1) Abaxial position (with diaspores lying horizontally on their smooth lower side). (2) inverted position (upside-down) with diaspores lying horizontally on the spinose upper side. (3) vertical position, diaspores vertically on their side. (4) inclined position, diaspores positioned lying inclined at different angles, smooth side upwards. (5) inclined position with diaspores lying inclined spinose side upwards (after Hegazy et al. 2014) (see also Figure 7.2 on page 192).




**Plate 12** (A) Entrance of Karnak temple in Luxor, Egypt. Note *Tamarix nilotica* trees at the entrance; (B) Botanical Garden of Thutmose III at the Karnak temple; (C) Plant and animal reliefs carved on the walls of the Botanical Garden: 1 = *Laurus nobilis*, 2 = *Nymphaea caerulea* var. nouchali, 3 = *Luffa aegyptiaca* (= *L. cylindrica)*, 4 = *Orhis* sp./*Ophrys* sp., 5 = *Cucumis melo*, 6 = *Hordeum vulgare*, and 7 = *Pistacia eurycarpa*; and (D) 1 = *Potomogeton nodosus* and 2 = *Vitis vinifera* (plants identified by Prof. W. M. Amer) (see also Figure 9.1 on page 217).

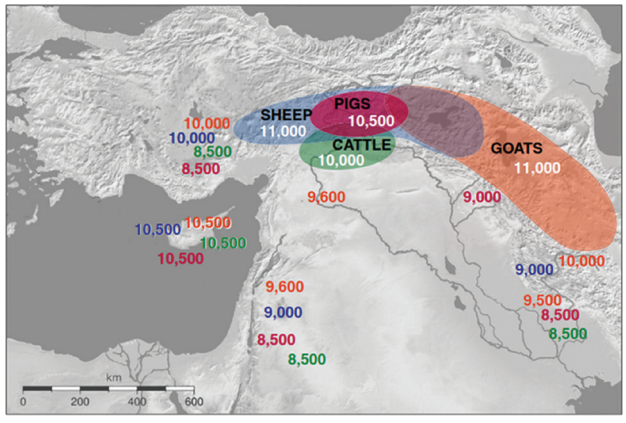



**Plate 13** The origin and dispersal of domestic livestock in the Fertile Crescent. Shaded areas show the general region and approximate dates in terms of years B.P. in which initial domestication is thought to have occurred. Dates outside the shaded areas show the approximate date when a particular domesticate first appears in a region. Orange, goats (*Capra hircus*); blue, sheep (*Ovis aries*); green, cattle (*Bos taurus*); fuscia, pigs (*Sus scrofa*) (after Zeder 2008, used with permission). Copyright (2008) National Academy of Sciences, U.S.A (see also Figure 9.6 on page 224).

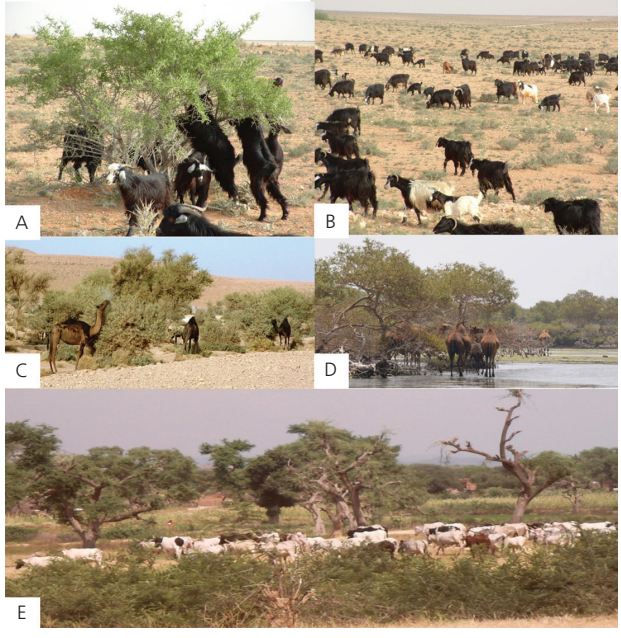



**Plate 14** (A and B) Open grazing of goats on a shrub of *Lycium shawii* and annual and perennial herbs near Kiklah at 760 m, Nafusa Mountains in western Libya. (C and D) Camel browsing of *Acacia gerrardii* in Wadi Huraimla, Central Saudi Arabia, and of *Avicennia marina* mangrove in Herida, Red Sea coast, southwestern Saudi Arabia. (E) Livestock grazing in Sudan and Horn of Africa countries, photo from Darfur, Sudan (see also Figure 10.2 on page 240).

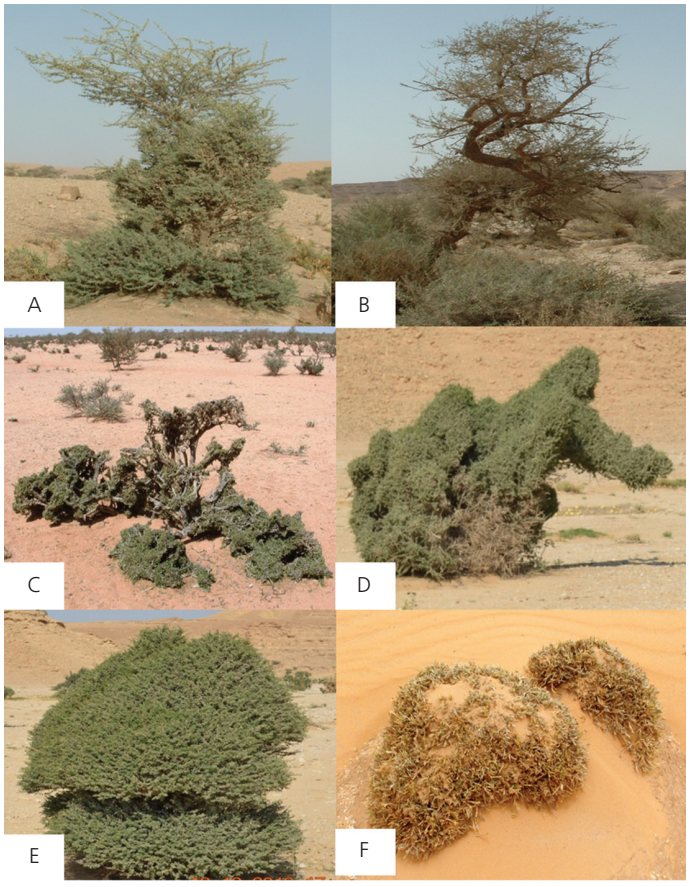



**Plate 15** Deformation of overgrazed plant shoot in arid land of central Saudi Arabia. (A and B) Mild grazing of *Acacia gerrardii* trees result in stratified crowns, the upper stratum is ungrazed, the middle is browsed by camels, and lower stratum by goats and sheep as well as camels. (C) *Acacia tortilis* subsp. *tortilis* tree subjected to overgrazing and trampling resulting in extreme shoot deformations. (D) Overgrazing of *Lycium shawii* resulted in an oddly shaped shoot. (E) an overgrazed *Acacia tortilis* subsp. *raddiana* shrub with shoot shaped like mace or scepter. (F) Overgrazed *Panicum turgidum* in the Saudi Nefud Desert resulting in dome-shape or cushion-like shoots (see also Figure 10.3 on page 241).

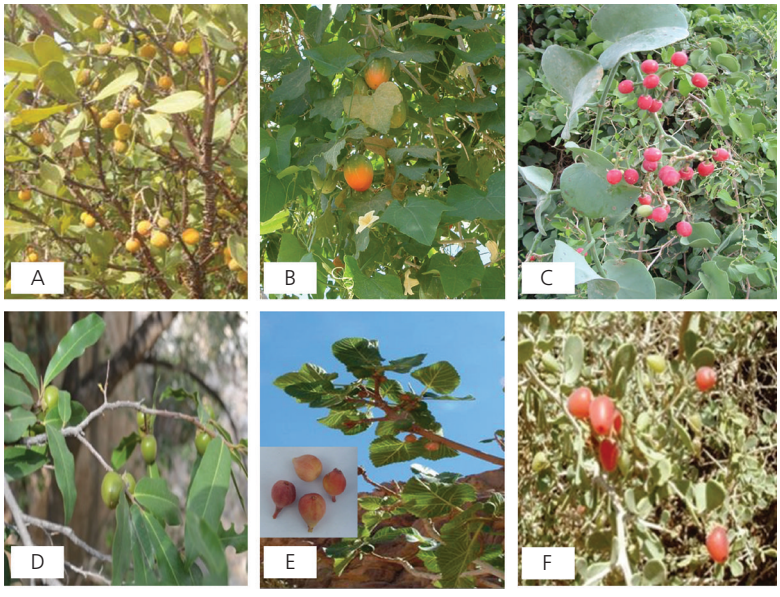



**Plate 16** Edible wild fruits collected by local dwellers. (A) *Arbutus pavarii* in Mount Al Akhdar of Libya. (B) *Coccinea grandis* in Taif, western mountains of Saudi Arabia. (C) *Cissus rotundifolius* in Abha, Saudi Arabia. (D) *Diospyros mespiliformis* in Mount Shada, southwest Saudi Arabia. (E) *Ficus palmata* in Mount Qutar, Eastern Desert of Egypt. (F) *Nitraria retusa* in Wadi Al Reshrash, Eastern Desert of Egypt (see also Figure 10.4 on page 244).

CHAPTER 1

# "*Drylandia*" and the dawn of time

## Introduction to plant ecology in the Middle East

### 1.1 Introduction

Desert plant communities exist in habitats that tend nearly always to be dry, but which may become wet during irregularly occurring, typically brief periods. Predicting or anticipating when these will happen and evolving structures, mechanisms, and behaviors to take advantage of this sudden and unpredictable bounty of water is the desert's existential game. In the beginning is water. Water makes life on Earth possible and is everywhere. Two-thirds of the planet's surface is covered by either solid or liquid water and the atmosphere is moistened by an aqueous vapor able under certain conditions to *precipitate*. Water forms the deep, saline oceans and seas, and a smaller portion makes up the world's freshwater glaciers, ice caps, rivers, lakes and wetlands. In the presence of so much water it may seem surprising that any part of the Earth's surface ever dries out, let alone that it should become inhospitable, dry desert.

But dry deserts do cover nearly a third of the Earth's land area; they range from the rolling steppes of Central Asia and great salty endorheic basins[1] of eastern Iran and its Great Kavir, to enormous dry lake bottoms in Central Australia—to say nothing of windswept sand dune deserts. Interestingly, this desert archetype proves relatively *un*common—even the great sandy Sahara is less than 20% dune sand. And the sandiest desert anywhere, the Rub' al-Khali, extending across some half million km$^2$ of the Arabian Peninsula, is only about one-third sand dunes.

Several chapters of this book explore the proposition that "deserts" and indeed Middle Eastern deserts, in particular, represent a wide range of diverse habitat types, containing many specialized plant communities. Another chapter describes the power of the past—especially the *deep* past of geological time—driving and shaping present-day environments; Chapter 2 provides multiple examples of the interaction between environment and history across the many countries of the Middle East. Throughout the book we will stress the importance of water to life in general and plant ecological life in particular.

The Arabian Peninsula covers some 2.5 million km$^2$, much of it desert dryland—*Drylandia* perhaps—and for our purpose represents the geographic center of the Middle East (see Figure 1.1). The Peninsula is more or less rectangular and tilts gently from its highest parts along the Red Sea in the west, to the Arabian Gulf in the east. It is topographically diverse, ranging from rugged and bare mountains through vast sand and rock deserts, to some luxuriant, mist-covered mountains, and pockets of highly productive, irrigated, and terraced agriculture. Most significantly though, this is a distinctly *dry* place. Most of the rivers and streams are only seasonal; permanent streams are for the most part only found in the highest and wettest mountain regions.

[1] This is a *closed* drainage basin that retains water and allows no outflow to external rivers or oceans, converging instead into lakes or swamps, permanent or seasonal, which equilibrate through evaporation. The bottom of such a basin is typically occupied by a salt lake or salt pan. Alternative names for the dry lake include alkali flat and *playa*. A *playa* lake may cover a wide area, but it is never deep. Most water in it evaporates, leaving a layer of salt on the surface. These salt covered stretches are called salt pans. Other dry lake types include the *sabkha* and the mudflat.

*Plant Ecology in the Middle East.* Ahmad Hegazy & Jonathan Lovett-Doust.
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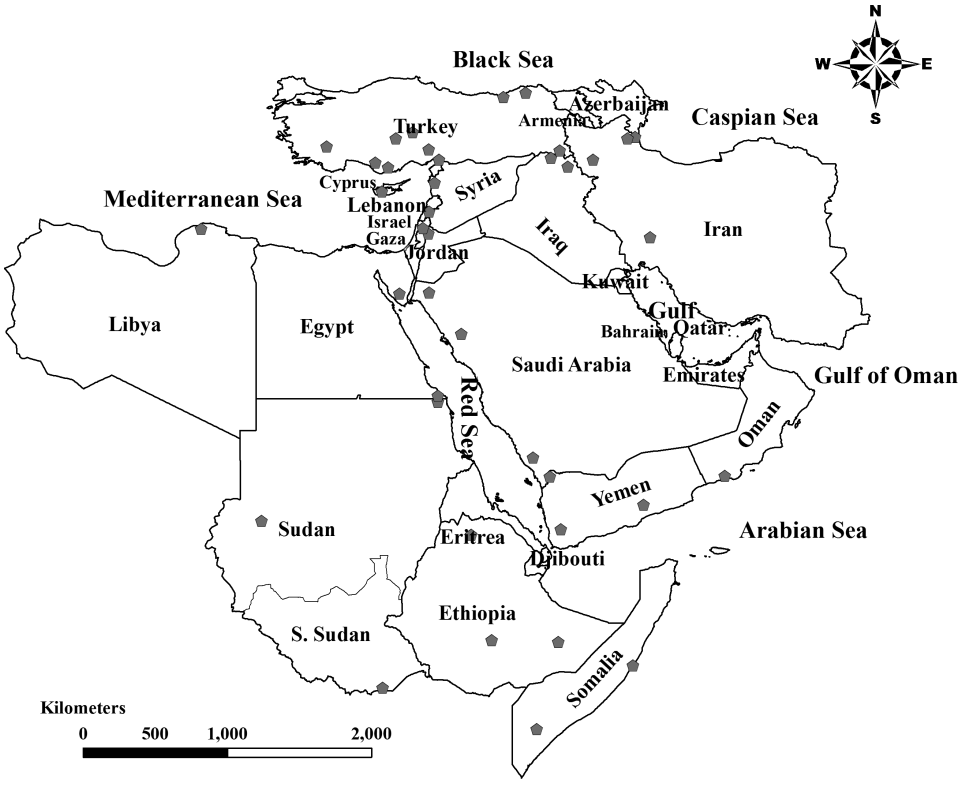



**Figure 1.1** The Middle East political map. Solid symbols represent major centers of diversity.

The *pull* of the desert is strong, with an allure almost primal. Our human ancestors first existed as one vagile hominid species among several, living in an arid land. Early on—some 180 000 years ago—humans first emerged as the modern species in the dry savannas of the Great African Rift, coughed up where the Earth erupted along a tear, or rift, of stretched and fractured crust.

At first, people gathered and hunted and scavenged food as they found it, but later on, beginning perhaps 25–30 thousand years ago (see Section 9.1), they began to discover that they could gather, then *tame* and use plants, leading to a cascade of profound cultural innovations. Then came animal husbandry and further innovation through domestication. Opportunity emerged early on from the benefits of storing dried food—reserves of protein, oils, and carbohydrate able to tide us over seasons when no fresh food was available. And in that dryness, over extended periods of time, people continued to develop the foundations of agriculture. By 9000 or 10 000 years ago we had essentially domesticated most of the plants we still farm to this day; it is striking how relatively few additional species of plant and animal have been tamed by subsequent human generations (Diamond 2002).

As we describe in Chapter 9, gardens (and the act of gardening) were surely the greatest catalyst of human cultural development, on a par at least with our capture and control of fire, and discovery of the benefits of rollers, and moving axles. Gardening moved us from the itinerant condition of hunting and gathering toward the settled state, and brought with it opportunities for social cooperation and development, specialization, and trade. Although it took us a very long time to begin to till, fertilize, plant, water, and weed gardens for food, at some point gardening also became more than just a

utilitarian approach to food production. It also became an aesthetic, creative endeavor and personal expression of the gardener.

With agriculture of course came so much of the rest of human culture, some of it a consequence of the new-found periods of free time brought about by the assurance of stable and stored food reserves, and the seasonal cycles of activity that persist still (in patterns like the academic year, which leaves hands available at harvest). With agriculture, people settled in the Middle East—in the river valleys and plains—and made great cities thousands of years ago. Today across the world most people have left behind the hunting and gathering lifestyles that shaped our ancestors, and in the Middle East only a few, tribal, nomadic Arabian Bedouin remain today as some of the last representatives on Earth of this once dominant human lifestyle (Chatty and Colchester 2002; Hobbs 1989, 2006, 2007).

Supported by agriculture and its benefits, people settled early in the Middle East. As we made our way "out of Africa," desert became scorched into life as early human habitat . . . and indeed hundreds of millions of people continue to live in and around these Middle Eastern lands today. For them, our "primal desert" is still very close and real. By learning more about this region we can travel in the steps of ancient time, following the earliest human passages and trading routes that developed, linking cultures across the expanse of Eurasia and Africa.

The Middle East is also home to a great many livestock, probably too many. Camels, goats, donkeys, and cattle have all acted as powerful selection pressures across the region, and for a very long time (see Chapters 9 and 10). Wildlife, once more numerous, include baboons, ibex (a desert-dwelling goat), and leopards in the southwestern Saudi highlands, which with the Arabian tahr (another wild goat), fox, lynx, and wildcats all once roamed the mountains ringing the entire Arabian Peninsula; there are populations of dugongs and dolphins in the Gulf; and many birds throughout—bustards and buzzards, bulbuls, sunbirds, spoonbills and flamingos, kites, eagles, kestrels, and more.

Fruit trees have been cultivated for thousands of years in the Middle East, while wheat and other cereals were also discovered and invented there, in the region of the Fertile Crescent (see Chapter 9). Among the food plants people have domesticated here are almond, apricot, fig, and palm trees (including the date palm, *Phoenix dactylifera*—first cultivated at least as far back as Egypt's pre-dynastic period more than 5500 years ago, and widely cultivated there still today). In Yemen and the Horn of Africa, coffee and qat (or khat), cinnamon, frankincense, and myrrh were first domesticated and farmed.

The region includes many significant remnants of earlier vegetation—the entire Gondwanan island of Socotra,[2] off the Horn of Africa; the ancient "Hyrcanian" forests of Iran and Azerbaijan (which are among the oldest forests in western Eurasia); relictual Juniper forests in southwestern Saudi Arabia and Sinai; and ancient patches of *Breonadia salicina, Combretum molle*, and *Mimusops laurifolia* as vestiges of "valley-forest" found in southwestern Arabia. Chapter 2 characterizes in more detail these and other ecological fragments of a formerly more moderate, Mediterranean-type regional climate.

## 1.2 *Which* Middle East?

Before the First World War, the term "Near East" was often used to refer to the Balkans and the Ottoman Empire.[3] The term was centered on Turkey and the eastern shore of the Mediterranean (the "Levant")[4] while "the Middle East" referred

[2] This has been rendered as Soqotra and Socotra. We adopt the latter, except in quoting a source.

[3] During the sixteenth and seventeenth centuries, in particular at the height of its power under the reign of Suleiman the Magnificent, the Ottoman Empire (sometimes referred to as the Turkish Empire, or simply Turkey) was one of the most powerful states in the world, controlling much of southeastern Europe, western Asia, the Caucasus, North Africa, and the Horn of Africa. The *political* centers of the major Islamic caliphates—Rashidun, Umayyad, Abbasid, and Ottoman—were located in Medina, Damascus, Baghdad, and Constantinople, respectively (Sardar 2015).The Ottoman Empire was dissolved in the aftermath of World War I; the collapse of the empire led to the emergence of the new political regime in Turkey itself, as well as the creation of modern Balkan and Middle Eastern states.

[4] The Eastern Mediterranean, also known as the Levant, is a geographic and cultural region consisting of the eastern Mediterranean littoral between Anatolia (southern Turkey) and Egypt. The Levant today consists of Cyprus, Lebanon, Syria, the Palestinian territories, Jordan, Israel, and part of southern Turkey.

to Iran, Afghanistan and Central Asia, Turkestan, and the Caucasus. The "Far East" at that time referred to the countries of East Asia (centered on China and Japan). With the disintegration of the Ottoman Empire nearly 100 years ago, "Near East" largely fell out of favor in English, while "Middle East" came to be applied to the re-emerging countries of the Islamic world, an area extending from ancient Mesopotamia to India, that is, basically, the area between the Near East and the Far East.

These days many people apply an expanded, more geopolitical sense to the Middle East, even extending as far as Afghanistan and Pakistan, the Caucasus and Central Asia, as well as Northern and Eastern Africa. This is a fairly recent, largely American-based expansion of a "Middle East" from fewer than 20 countries to more than 30, abandoning the longstanding Eurocentric view that included only Western Asia and North Africa.

From the point of view of physical geography, the larger scope of a "greater" Middle East facilitates

**Table 1.1** Country sizes, floristic richness (flowering plants), and endemism in the countries of the Middle East (after various sources, including Alexander and Miller 1994; Boulos 1997; Davis et al. 1994).

| Country | Land area ($km^2$) | Population number (M) | Number of vascular plants | Number of endemic species | Percentage endemism |
|---|---|---|---|---|---|
| Libya | 1 759 540 | 6.2 | 1750 | 75 | 4.0 |
| Egypt | 1 036 000 | 87.0 | 2100 | 73 | 3.5 |
| Sudan | 2 505 813 | 35.5 | 3132 | 50 | 1.6 |
| Ethiopia | 1 184 000 | 96.6 | 6103–7103 | 600–1400 | 10–20 |
| Eritrea | 101 000 | 6.4 | – | – | – |
| Djibouti | 21 699 | 0.8 | 641 | 2 | 0.3 |
| Somalia | 637 539 | 10.4 | 3028 | 500 | 16.5 |
| Saudi Arabia | 2 401 554 | 27.3 | 2250 | 107 | 4.7 |
| Yemen (excl. Socotra) | 477 540 | 26.0 | 2250 | 300 | 12.0 |
| Socotra | 3625 | 0.044 | 825 | 305 | 37.0 |
| Oman | 271 950 | 3.2 | 1250 | 75 | 6.0 |
| United Arab Emirates | 75 150 | 5.6 | 630 | – | – |
| Qatar | 11 437 | 2.1 | 320 | – | – |
| Bahrain | 661 | 1.3 | 250 | – | – |
| Kuwait | 24 281 | 2.7 | 374 | – | – |
| Jordan | 97 668 | 7.9 | 2450 | 145 | 7.3 |
| Syria | 185 180 | 17.9 | 3100 | 395 | 13.0 |
| Israel, Gaza & West Bank | 20 750 | 12.3 | 2682 | 155 | 6.5 |
| Lebanon | 10 400 | 5.9 | 2600 | 311 | 12 |
| Iraq | 438 446 | 32.6 | 3200 | 195 | 6.1 |
| Turkey | 779 452 | 82.0 | 8650 | 2675 | 30.9 |
| Iran | 1 648 000 | 81.0 | 6500 | 1812 | 27.9 |
| Cyprus | 9240 | 1.2 | 1650 | 88 | 5.2 |
| Armenia | 29 743 | 3.1 | 3200 | 106 | – |
| Azerbaijan | 86 600 | 9.7 | 4500 | – | – |

our exploration of biological phenomena, including phytogeography, patterns of endemism, and ancient dispersal pathways for plants and animals alike, all tracking the Earth's tectonics and changing climates and influenced latterly by human trade and agriculture. For the purposes of this book, we will therefore consider a Middle East that centers on the Arabian Peninsula and includes Turkey and Iran, Armenia and Azerbaijan, as well as much of some seven African countries (Libya, Egypt, Sudan, Ethiopia, Eritrea, Djibouti, and Somalia), and various islands and island archipelagos—Cyprus in the Mediterranean Sea; Qeshm and other Iranian islands in the Strait of Hormuz Archipelago; Bahrain and the Hawar Islands in the Gulf; Socotra (a part of Yemen) in the Indian Ocean (Arabian Sea); and many other, smaller islands in the Red Sea and Arabian Gulf.

The three largest and most populous countries are Egypt (*c.* 16th in the world by population, with *c.* 87 million people), Turkey (17th, with *c.* 82 million), and Iran (19th, with *c.* 81 million)—and together covering nearly 3.5 million km$^2$ of land.[5] Table 1.1 reviews some size and number attributes of these countries and the others, including Iraq (*c.* 32.6 million people), Saudi Arabia (27.3 million), Yemen (26 million), and Syria (17.9 million)—and collectively nearly another 3.5 million km$^2$—as well as smaller countries like Israel (7.8 million people) with the Gaza Strip (1.8 million) and West Bank (2.7 million), Jordan (7.9 million), Libya (6.2 million), the United Arab Emirates (5.6 million), Lebanon (5.9 million), Oman (3.2 million), Kuwait (2.7 million), Qatar (2.1 million), and Bahrain (1.3 million), as well as Cyprus (1.2 million), Armenia (3.1 million), and Azerbaijan (9.7 million).

The narrow separation between Arabia and Africa at the shallow Bab el-Mandeb strait includes many small islands and evidence of active volcanism on both sides. We will consider the influence of tiny Djibouti, with 0.8 million people, and Eritrea (6.4 million), Somalia (10.4 million), and aspects of Ethiopia (96.6 million people, 14th most populous in the world) to the west of these coastal countries and together comprising the so-called Horn of Africa. We will also examine something of Sudan, with 35.5 million people, and which even after its recent referendum and separation of South Sudan (11.6 million) remains the third largest African country by area, with 1.86 million km$^2$; we will focus on the plants of Jebel Marra in western Sudan, as well as those of the northeastern mountains, connecting to Egypt's plant-rich Gebel Elba region. This is all a further land area of some 4.4 million km$^2$ and another 160 million people. Putting all this together the overall area we survey here is some 13.6 million km$^2$, with almost 600 million people, 8.4% of the world's population in its boundaries. It is worth noting that most of these countries are also experiencing crude birth rates (births per 1000 population per year) that are significantly above the global average, so human pressures on the natural and managed environment are likely to continue to increase.

## 1.3 Previous plant studies of the Middle East

Western scientific studies of the Arabian flora began nearly 250 years ago with Pehr Forsskål's successful, but rather ill-fated expedition to "*Arabia Felix*" and the posthumous publication by Niebuhr (1775) of his *Flora Aegyptiaco-Arabia*. Forsskål (1732–1763) was an early Swedish botanist and follower of Linnaeus. He died young, at 31, of malaria—while collecting plants in Yemen, having previously spent nearly two years in Egypt. (Linnaeus later named in his honor one of the plants Forsskål sent home, *Forsskaolea tenacissima*. See, too, Appendix 1.)[6]

Today his book *Flora Aegyptiaco-Arabia* is available free online at Google Books and it is interesting to see the list, in Latin, of the 481 plants identified in Arabia and Egypt. A related resource is F. N. Hepper and I. Friis's *The Plants of Pehr Forsskål's Flora*

[5] Population and land area estimates come from Central Intelligence Agency (U.S.): The World Factbook (accessed August 13, 2014), https://www.cia.gov/library/publications/the-world-factbook/rankorder/2119rank.html.

[6] In the Urticaceae, or nettle family. Following its name, the species is a very tenacious, "tough" plant found in stony soils and road edges, gravel wadis and rock crevices. Common in arid and semi-arid waste lands from sea level to 1200 m, also found in Mediterranean woodland and shrubland, desert, and even extreme desert.

*Aegyptiaco-Arabica* (1994), an annotated catalog of the species collected on that expedition to Egypt and Yemen, 1761–1763. They include 29 "cryptogams," i.e., following older botanical tradition, those plants—in the broad sense including the lichens, algae, ferns and fern allies, even fungi—seen as having "hidden marriages," that is, modes of sexual reproduction which took earlier, less prurient botanists rather longer to understand than did those of the more ostentatious flowering plants.

There has been much interest in the region since Forsskål, but so far no detailed flora of the entire region has yet been completed. This is in marked contrast to the number and richness of studies and completeness of floras for the adjacent (much smaller) Mediterranean basin and region (e.g., Blondel et al. 2010; Thompson 2005). This need calls out for a modern, multi-investigator shared database, to cover the entire region.

Between about 1910 and 1950, several expeditions to Arabia were made by western explorers and collectors, including Wilfred Thesiger (who published *Arabian Sands* [1959] and *The Marsh Arabs* [1964], and inspired many others) and Harry St. John Philby (a British political officer and later adviser to the King of Saudi Arabia).[7] Philby published many books about the region, including *The Heart of Arabia* (1922) and *The Empty Quarter: The Great South Desert of Arabia Known as Rub' al-Khali* (1933). The only botanical work covering the entire Peninsula is Blatter's incomplete *Flora Arabia* (1919–1936).

During the period from about 1960 to 1990, there was a significant flurry of interest in the Arabian flora and several works covering individual countries and smaller regions appeared. The most important are Townsend and Guest's unfinished *Flora of Iraq* (1966–1985), Daoud and Al-Rawi's *Flora of Kuwait* (1985), Batanouny's *Ecology and Flora of Qatar* (1981), Collenette's *Illustrated Guide to the Flowers of Saudi Arabia* (1985, 1999), Mandaville's *Flora of Eastern Saudi Arabia* (1990), Migahid's *Flora of Saudi Arabia* (1978), Miller and Morris' *Plants of Dhofar* (1988), Phillips' *Wild Flowers of Bahrain* (1988), and Western's *The Flora of the United Arab Emirates* (1989). Unfortunately none address in any detail the floristically richest areas in the south and southwest of the Peninsula. The spectacular and rich flora of the island of Socotra has a more complete coverage than any equivalent area on the mainland, thanks initially to Balfour's *Botany of Socotra* (1888) and later works by, e.g., Mies (1998), Mies and Beyhl (1998), Miller and Cope (1996), Miller and Morris (2004), and Knees and Miller (2006).

Wars, political unrest, and security concerns have limited recent ecological science in most of the Middle East, including the basic activities of plant collection and systematic inventories that are so necessary for new interpretations of species distribution and abundance. Fortunately the groundbreaking Flora of the Arabian Peninsula and Socotra project (see Miller and Cope 1996), which was initiated as a joint Royal Botanic Garden Edinburgh and Royal Botanic Gardens Kew pan-Peninsula project, has so far produced the first volume—of six planned—plus part one of a second volume (Cope 2008); remaining volumes are nearing completion and much anticipated.

As for the rest of the Middle East: to the north, the extensive and rich Turkish flora has been described in ten volumes (see, e.g., Davis 1984; Davis et al. 1988). Iran's flora is also very rich and has been characterized in some 176 volumes (see Rechinger 1963–2005). Armenia and Azerbaijani floras are covered to some extent in the surrounding country floras (e.g., Czerepanov 1995). The flora of Israel and Palestine is well described (e.g., Danin 2004), including some 2850 species and these days available online, complete with photographs and ecological highlights of most of the species (http://flora.huji.ac.il/browse.asp?lang=en). Al-Eisawi's (1998) *Checklist* catalogs the plants of Jordan, and Boulos's recent four-volume *Flora of Egypt* (1999–2005) updates the already excellent Tackholm (1974). The flora of Libya was published in several volumes and compiled and edited by Jafri and El-Gadi (1977–1993).

It is clear that the Middle East today is home to many plants, in particular woody plants, which are for the most part characteristic of several different phytogeographic regions. It seems also likely that many of the populations of these species have been there for a very long time, at least since the early Tertiary to early Quaternary (Barron et al. 2010; Rodríguez-Sánchez and Arroyo 2008, 2011).

[7] Also father of a famous British spy, his son Kim.

While floras provide an essential starting point for a species list, so far there have also been relatively few detailed *phyto-*, and *phylo*geographic,[8] demographic, ecological, palynological, or related studies in the region. Nor are we aware of efforts to hind-cast or reconstruct past species distributions using, e.g., niche-based species distribution models. Despite its geographic and historical interest, the Middle East has not been investigated and described as a whole, so the present work is intended to assemble and review several sub-regional studies in order to draft a more complete understanding.

Certain parts of the Middle East experience a Mediterranean climate—the coastal plains of Libya, Egypt, Palestine (Gaza and the West Bank), Israel, Syria, Lebanon, and Turkey—and plants there have been shaped by it for a long time. The adjacent western basin of the Mediterranean region has been rather more thoroughly studied (Blondel et al. 2010; Thompson 2005). The few phylogeographic studies there, which also include populations from the eastern Mediterranean, suggest the Eastern populations were typically much older, and likely gave rise to the populations now present in the west (e.g., Petit et al. 2005; and see Chapter 3). In other words migration of plant species appears to have been mainly from eastern to western Mediterranean, crossing and potentially colonizing parts of the Middle East as range expansions occurred.

## 1.4 Hot, dry, hot and dry?

Deserts tend to be imagined as archetypically hot and dry environments, yet as Ward (2009) made clear in his recent review of desert ecosystems, life in the desert is essentially defined by the *patchy* distribution in time and space of a single resource, namely water. The extremely arid conditions of so much of the Middle East correspond well to Noy-Meir's (1973) classic definition of the desert ecosystem as a "water controlled ecosystem with infrequent, discrete, and largely unpredictable water input."

Much of the Darwinian "struggle for existence" in the desert is a struggle to gain access to—and take advantage of—water. Desert environments have both low amounts of annual precipitation and high variation, making it unpredictable in both space and time. For example, Ward (2009) showed there is a strong negative correlation between the median annual rainfall and the coefficient of variation of rainfall. In other words where there is already very little rain, its distribution in time and space is even more unpredictable! Desert life forms have adapted to survive and persist *despite* the drought; to ensure that at least some of their progeny are well adapted to survive *despite* the statistical significance of that negative correlation and daunting size of the coefficient.

We will develop the theme that it is this lack of reliable precipitation and not high temperature alone which makes a desert. The Darwinian struggle is especially intense in deserts because living cells are 75–90% water, with plants typically having higher water content than animals since water is a critical resource for photosynthesis, besides being a component of every living cell. Most desert organisms contain about the same amount of water as organisms elsewhere, though as we show below, *succulent* species are especially well adapted for superior water-holding capacity. Other adaptations help plants respond to and *access* rare precipitation, and to retain water once they have absorbed it. Plants have been particularly inventive in their adaptations to water stress and climatic unpredictability (see Chapters 4 and 5).

[8] *Phyto*geography (from Greek *phyto* for plant) is a venerable branch of biogeography concerned with the geographic distribution of plant species. Phytogeography is ultimately concerned with all aspects of plant distribution, from controls on the distribution of individual species ranges to the factors that govern the composition of entire communities and floras.

*Phylo*geography (from Greek *phylo* for tribe or race) is the more recent study of the historical processes that may be responsible for the contemporary geographic distributions of individuals (see Avise 2000). This is accomplished by considering the geographic distribution of *individuals* in light of the patterns associated with particular gene genealogies. The term was introduced to describe geographically structured, genetic signals found within and among species. An explicit focus on a particular species' biogeographic past sets phylogeography apart from classical population genetics and phylogenetics. Past events able to be inferred include population expansion, population bottlenecks, vicariance, and migration. Recently developed approaches integrating "coalescent theory," or the genealogical history of particular alleles, along with distributional information, address the relative roles of these different forces in shaping current patterns (Cruzan and Templeton 2000). Other recent work probes "phylogeographic endemism"—the degree to which the history of recently evolved lineages is spatially restricted, due to fundamental evolutionary processes (e.g., Carnaval et al. 2014).

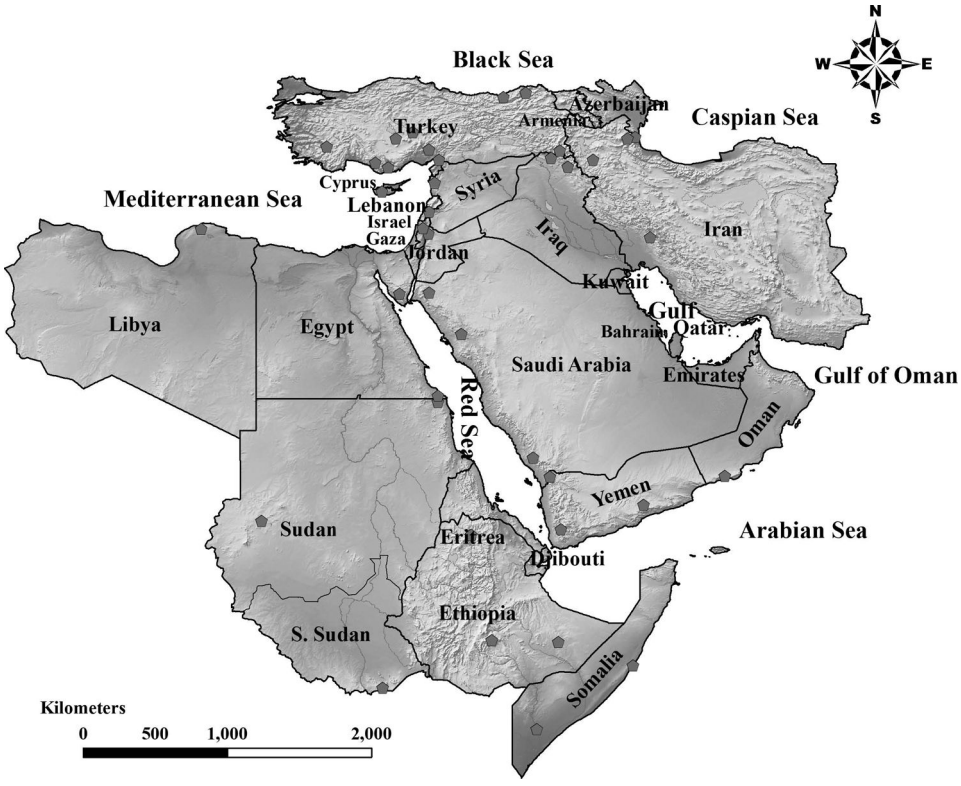



**Figure 1.2** The Middle East topographical map showing centers of plant diversity and endemism. Solid symbols represent the major centers of diversity.

In the desert, patterns of both temporal and spatial variation in annual rainfall are the major drivers of plant ecology and evolution. Rain falls typically in irregular periodic pulses, which are mostly patchy in space. In some coastal deserts, rain may not fall for extremely long periods of time—decades, even centuries (as in the case of the Atacama Desert of northern Chile)—*but* water may also arrive (just as it does in the Atacama) as condensing wet fogs generated by coastal up-wellings.

Consider the summit of Gebel[9] Elba, overlooking the Red Sea in southern Egypt,[10] or of Jabal Fartak, in the mountainous part of the Al-Mahra region of Yemen's coast (see Figure 1.2).

Both locations exist as comparatively luxuriant "mist oases," where a considerable part of the total precipitation arrives as dew or mist and clouds; these often completely enshroud the mountaintops, creating botanically rich ecosystems often associated with striking geological formations. There are similar mist oases at Jebel Al Akhdar in the Dhofar region of southwestern Oman, and in the high Asir Mountains at El Sodah, Jebel Fayfa, and the Black Mountains in southwestern Saudi Arabia, where the sea-facing escarpments are all typically blanketed by moisture-laden clouds (see Figure 1.3A–C). A unique, water-limited seasonal cloud forest exists in these places, surviving the "dry season" when there is no rainfall through near-constant condensation on plant surfaces of water droplets from the fog and clouds, and the trickling of this water down to the soil.

[9] Many variations of words including gebel, gebal, jabal, jabel, jebal, jebel, jbel, djebel, jibal, etc., have been used for the Arabic word meaning "mountain, hill, or slope" (as elevations), and this varies regionally. The words have been used to name many mountains and places throughout the Middle East. In general we use the transliteration of our source material.

[10] Gebel Elba or Elba Mountain is a mountainous landscape overlooking the Red Sea at the border between Egypt and Sudan.

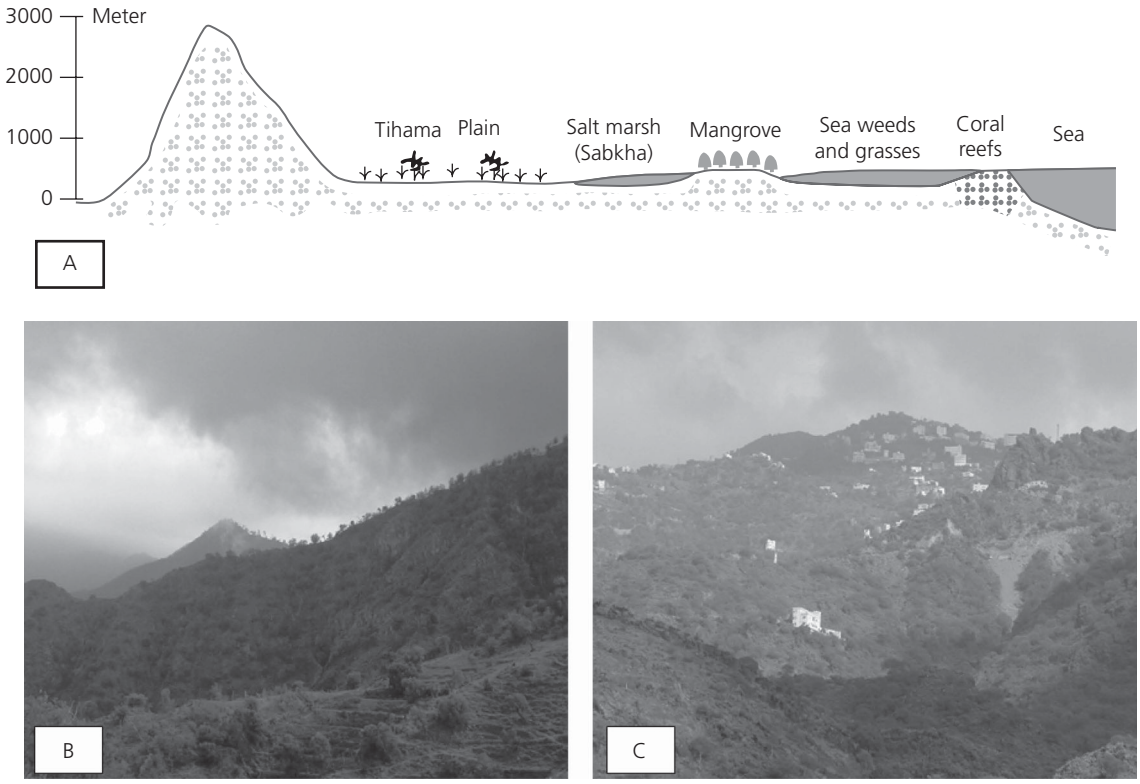



**Figure 1.3** (A) Generalized geomorphological cross section of the southern Red Sea coast of Saudi Arabia showing various environments and habitat types. (B) The foggy Black Mountains. (C) Jebel Fayfa, southwest Saudi Arabia.

The Dhofar mist or cloud oases exist along the southern edge of the Arabian Desert, and are today only a vestige of a once much larger, more moist vegetation belt of ancient, paleo-African origin (Meister et al. 2005; Miller 1994a). As the climate of the Arabian Peninsula became dry, most of the previously moist vegetation became desert. Under the present arid climate, for the most part, the only region where real forests are still to be found is along the southern coast, in places where the desert climate is met in summer by a foggy moist season, immersing the coastal mountains in damp clouds (Hildebrandt et al. 2007).

### 1.4.1 Cloud forests

In general, ecosystems dependent upon persistent seasonal or annual fog are known as *cloud forests*, and are characterized by their typically very high biodiversity, exceptional hydrology, and sensitivity to environmental change, all of which also make them especially vulnerable to climate change (see, e.g., Ray et al. 2006). The bigger the canopy and more surface area available, the more water can condense on the vegetation (this is sometimes referred to as "horizontal precipitation").

These Middle Eastern cloud forests in semi-arid regions are quite different from most of the world's cloud forests whose eco-hydrology have been studied. Mostly they occur in the moist tropics where annual rainfall levels are high (> 2000 mm); there humidity is high and the low transpiration and additional water available from horizontal precipitation do not significantly influence plant water availability.

In contrast, in the semi-arid environment of Arabia, where water is the major limiting factor

to growth, horizontal precipitation and relief from high evapo-transpiration have significant effects on plant growth and metabolism. Indeed, we suggest these semi-arid cloud forests should be clearly distinguished (perhaps by calling tropical, permanent cloud forests "tropical cloud forests" and these semi-arid forests "subtropical" or "seasonal" cloud forests). Figure 1.4A shows a satellite image of the Peninsula with the Omani Dhofar area circled. During the summer season there, moist air from the ocean rises over the mountains, producing orographic clouds and ongoing light drizzle along the mountain range. The upward (vertical) extent of the cloud cover is limited by an overlaying inversion (see Figure 1.4B).

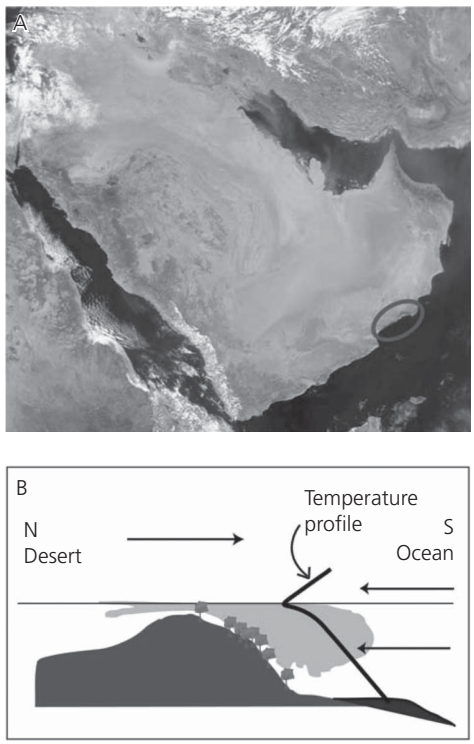



**Figure 1.4** Geography of the area of interest. (A) Satellite image of the Arabian Peninsula. The region of interest is circled; note the half-moon shape of the coastal mountain range. (B) Meteorological situation in Dhofar during the khareef (or southeastern monsoon) (after Hildebrandt et al. 2007). Reproduced with permission from Wiley.

Hildebrandt et al. (2007) studied eco-hydrology in a semi-arid broadleaf deciduous cloud forest in Dhofar and measured the contribution of condensing cloud droplets; about two times as much water was received at ground level (i.e., *net* precipitation) as was falling as rain. Stem-flow, the stream of water coming from condensed cloud on plant surfaces, was estimated using plastic stem-collars. This condensate accounted for about 30% of net totals, as stems effectively directed the water supply to the area immediately around them. The cloudy summer season was associated not only with enhanced net precipitation but also with reduced rates of plant transpiration, allowing for further water storage and subsequent use in drier times.

Despite these areas of seasonal cloud forest, dry deserts and desert ecosystems largely dominate the entire Middle Eastern region. For example, in Egypt the large Eastern Desert covers about a quarter (some 222 700 $km^2$) of the country. It extends along most of Egypt's eastern border and merges into the Nubian Desert to the south. Today most of this desert can be accessed by roads, and indeed since ancient times Egypt has quarried, shipped, and used as building materials the porphyry, granite, limestone, and sandstone found in its desert mountains. The same applies for Egypt's Western Desert and the southern region in Libya, the "Fezzan" (meaning "arid land" in local Arabic) (and see Section 2.6). Or the Saudi Rub' al-Khali expanse, which includes the Great Nafud and Dahna sand deserts (see Figure 1.5). It is not uncommon for extensive areas here to experience multiple consecutive years with no rainfall at all. And yet . . . some plants do live there.

### 1.4.2 Plants of the Rub' al-Khali

Dryland species by definition are usually adapted to climate variability, but there are obviously also limits to their tolerance of persistent drought. Thus the hyper-arid Atacama Desert in Chile supports very little life over much of its extent (Barros et al. 2008; Navarro-Gonzalez et al. 2003). Table 1.2 lists the small flora of the Rub' al-Khali; there are just 21 species and two sub-species despite its great size. In terms of the plant life forms of the

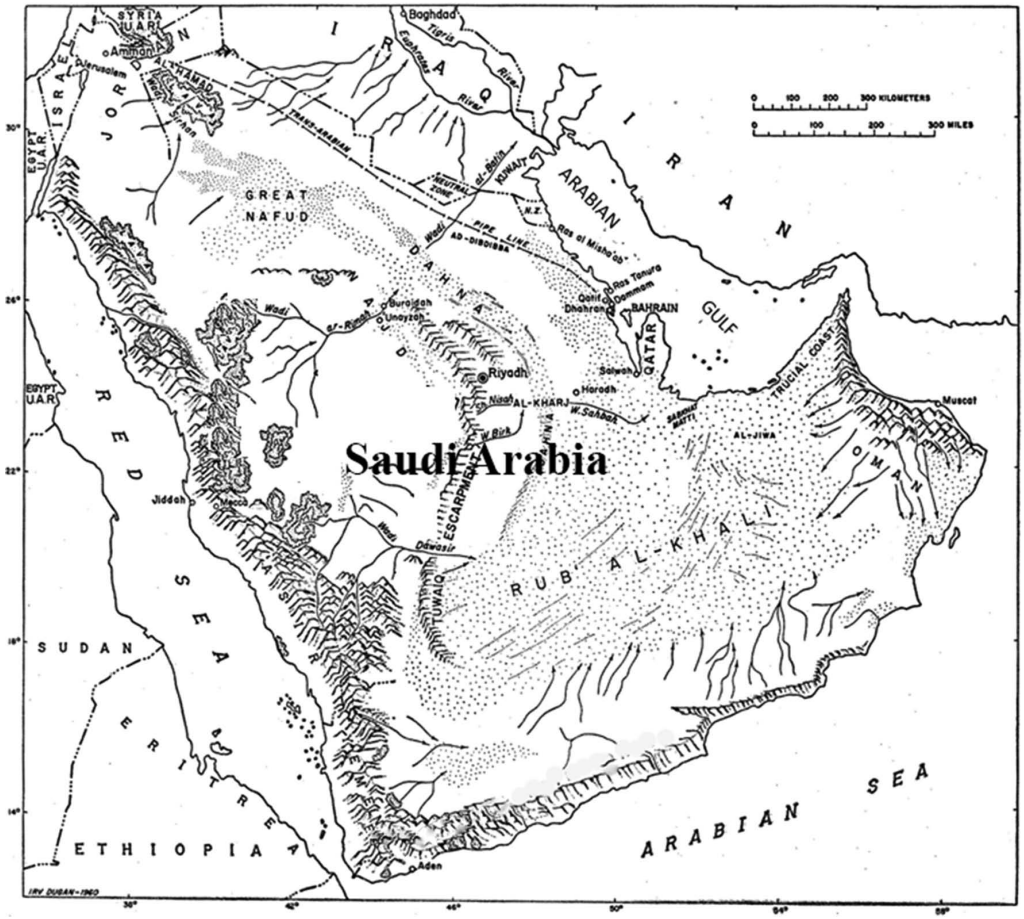



**Figure 1.5** Geomorphology of the Arabian Peninsula (after Holm 1960, used with permission).

early Danish plant ecologist, Christen Raunkiær,[11] these Arabian desert specialists are mostly woody shrubs—distinguished as either chamaephytes (small shrubs) or phanerophytes (trees and shrubs); with therophytes (annuals) contributing a further six. Five of the Rub' al-Khali taxa are endemic to the region (and thus uniquely and specifically connected to that location; see Section 1.9).

[11] Subdivisions of the old Raunkiær system are based on the location of the plant's growth-points (terminal buds) during seasons with adverse conditions (e.g., cold or dry seasons). They include the following (and see Section 5.9).

Phanerophytes: Projecting into the air on stems—normally woody perennials—with resting buds more than 25 cm above soil level, e.g., trees and shrubs like *Lycium shawii*, *Nitraria retusa*, *Tamarix* spp., and *Zizyphus lotus*.

Chamaephytes: Persistent buds on persistent shoots near the ground—woody plants with perennating buds borne close to the ground, no more than 25 cm above the soil surface. For example, cushion plants like *Chamaephyta pulvinata, Cleome droserifolia*, and *Chichorium botti*.

Hemicryptophytes: Persistent buds at or near the soil surface, e.g., tussock-forming *Stipagrostis plumosa, S. ciliata, Lasiurus sindicus, Citrullus colocynthis, Cucumis* spp., and *Tribulus* spp.

Cryptophytes: Persistent buds lying either beneath the surface of the ground or submerged under water. May be further distinguished as Geophytes (in dry ground, may include rhizome, stem tuber, root tuber, bulb, and root geophytes [e.g., *Tulipa, Iris, Ixiolirion*]); Helophytes (in marshy ground [e.g., *Anemone, Ranunculus*]); Hydrophytes (submerged under water).

Therophytes: Annuals that survive the unfavorable season as seeds, and complete their life cycle during favorable seasons (in desert environments sometimes these favorable seasons are very brief, resulting in an "ephemeral" presence of the species). Examples include *Anastatica hierochuntica, Trigonella stellata, Ifloga specata*, and *Diplotaxis acris*.

**Table 1.2** Plants recorded in Rub' al-Khali region (after Al-Hemaid 2002; Mandaville 1990), including species, family, reproductive strategy, life form and phytogeographic region of origin (monocarpic = semalparous; polycarpic = iteroparous).

| |
|---|
| *Cakile arabica* (Brassicaceae); monocarpic, succulent herb; Saharo-Arabian and Irano-Turanian. |
| *Eremobium aegyptiacum* (Brassicaceae); polycarpic herb; Saharo-Arabian. |
| *Savignya parviflora* (Brassicaceae); monocarpic, succulent herb; Saharo-Arabian. |
| *Heliotropium digynum* (Boraginaceae); polycarpic shrub; Saharo-Arabian. |
| *Moltkiopsis ciliata* (Boraginaceae); polycarpic shrub; Saharo-Arabian. |
| *Cornulaca arabica* (Chenopodiaceae); polycarpic shrub; Saharo-Arabian, endemic. |
| *Haloxylon persicum* (Chenopodiaceae); polycarpic shrub; Saharo-Arabian and Irano-Turanian. |
| *Salsola tetrandra* (Chenopodiaceae); polycarpic, succulent shrub; Saharo-Arabian. |
| *Dipterygium glaucum* (Capparaceae); polycarpic shrub; Sudano-Zambezian, Saharo-Arabian and Irano-Turanian. |
| *Monsonia nivea* (Geraniaceae); polycarpic herb; Sudano-Zambezian, Saharo-Arabian. |
| *Limeum arabicum* (Mulluginaceae); polycarpic shrub; Saharo-Arabian, endemic. |
| *Calligonum crinitum* ssp. *arabicum* (Polygonaceae); polycarpic shrub; Saharo-Arabian, endemic. |
| *Neurada procumbens* (Neuradaceae); monocarpic herb; Saharo-Arabian, Sudano-Zambezian and East Mediterranean. |
| *Cistanche phelypaea* (Orobanchaceae); polycarpic, succulent herb; Mediterranean and Saharo-Arabian. |
| *Oligomeris linifolia* (Resedaceae); monocarpic herb; Saharo-Arabian and Sudano-Zambezian. |
| *Tribulus macropterus* (Zygophyllaceae); monocarpic herb; Sudano-Zambezian. |
| *Tribulus macropterus* ssp. *arabicus* (Zygophyllaceae); monocarpic herb; Saharo-Arabian, endemic. |
| *Zygophyllum mandavillei* (Zygophyllaceae); polycarpic, succulent shrub; Saharo-Arabian, endemic. |
| *Centropodia forsskaolii* (Poaceae); polycarpic grass; Saharo-Arabian and Irano-Turanian. |
| *Centropodia fragilis* (Poaceae); polycarpic grass, Saharo-Arabian. |
| *Stipagrostis drarii* (Poaceae); polycarpic grass; Saharo-Arabian. |
| *Stipagrostis plumosa* (Poaceae); polycarpic grass; Saharo-Arabian and Irano-Turanian. |
| *Cyperus conglomeratus* (Cyperaceae); polycarpic sedge; Saharo-Arabian. |

### 1.4.3 Climate change, salt, and endorheic basins

Global climate change will exert increasing pressure on regions that are already subject to low and unpredictable precipitation. For example, Hegazy et al. (2008b) estimated the projected pattern of increase in air temperature for Egypt, using a model based on climatological data for the year 2005. They examined expected increases across the twenty-first century (see map projections, Figure 1.6). There is a strong trend toward increasing air temperature during all four seasons.

In winter 2005, the lowest air temperature recorded was 12–14°C and the highest, 18–20°C. Hegazy et al. predicted fewer areas would experience low winter temperatures, and more of the country would experience higher temperatures, with a change in the range from 12–20 to 14–22°C. Increase in air temperature will be most marked in summer, with increases in Upper, Middle, and Lower Egypt respectively from 30, 28, and 26°C in 2005 to 34, 32, and 30°C in 2100. Obviously these increases in air temperature will in turn affect water availability and plant growth.

The importance of water availability in conjunction with temperature as a limiting factor is well illustrated by Crimmins et al. (2011), who compared the altitudinal distributions of some 64 plant species in California between the 1930s and the present. They found that climate change was associated with a significant *down*ward shift in species' optimum elevations. This downhill shift might seem counter to what would be expected given the

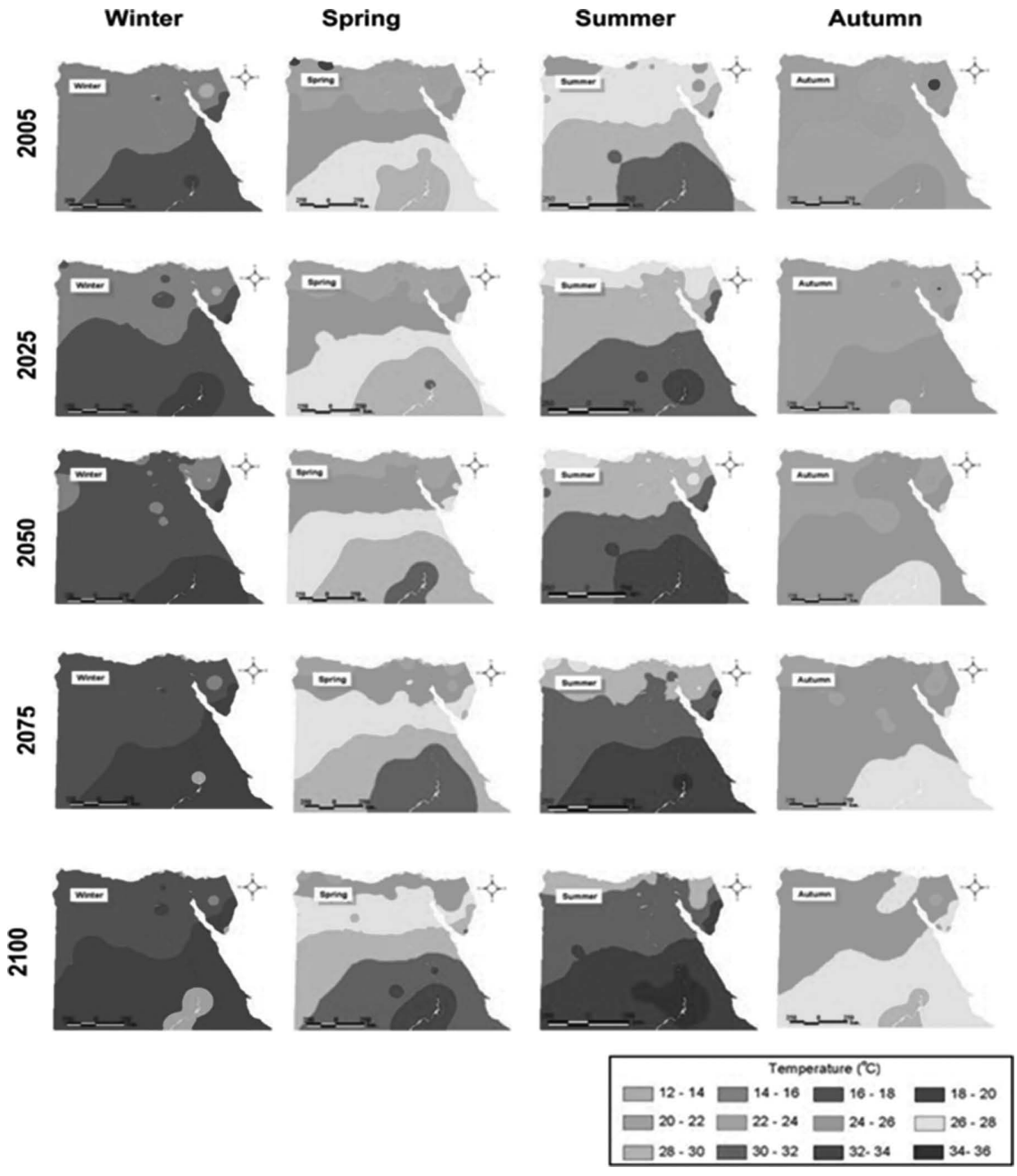



**Figure 1.6** Seasonal air temperature distribution in Egypt during the year 2005 and the projected years 2025, 2050, 2075, and 2100 due to the expected climate change in the twenty-first century (after Hegazy et al. 2008b). [For a color version of this figure, see the color plate section, Plate 1]

twentieth century warming trend, where air temperatures are higher at lower altitudes, but Crimmins et al. showed the downhill migration was tracking regional changes in *water* availability, rather than "seeking" cooler temperatures. Similar downhill shifts can be expected to occur wherever future climate change scenarios project increases in precipitation that outpace evaporative demand. In other words, we can expect that plants in arid environments will continue to "follow the water," in terms of their distribution and abundance.

Arid salty areas occur throughout the Middle East but perhaps nowhere more extensively than in the vast expanses of central and eastern Iran. Landscapes there include large, flat "endorheic" basins called *kavirs* (and resembling North African *shotts*, and American *playas*). Endorheic basins are *closed* hydrologic systems; their surface waters drain to inland depressions where the water evaporates or seeps into the ground, never reaching the sea. Water has been evaporating here and ions accumulating as evaporites over many, many millennia.

Salts interfere with water uptake in plants, so vegetation tends to be limited to the margins of these great saline plains, often showing distinct zonation patterns among progressively more halophytic (salt-tolerant) types,[12] and often with only thin crusts of halophytic archaea and cyanobacteria surviving in the centers of these basins (Breckle 2002). *Halocnemum strobilaceum*, together with *Seidlitzia rosmarinus*, dominates on the most saline sites in Iran and east into Afghanistan. Large areas there occur where mostly only these two shrubby species survive, surrounded by a second belt of vegetation consisting of individuals of *Haloxylon aphyllum* and *Anabasis setifera* growing in large patches on the fringes of the depressions (Breckle 2002).

[12] There has long been a distinction in classical Arabic between *khullah* (sweet plants)—the "glycophytes" of today and *hamdh* (salt plants) or halophytes (see Batanouny 2001). Examples of the more specialized halophytes in the Gulf countries, which tend to be heavily loaded with salt, include *Seidlitzia rosmarinus* (known locally as *shnan*), *Zygophyllum* spp. (*harm*), *Avicennia marina* (*girm*, or *shurah*), and *Aeloropus lagopoides* (*ikrish*). *Most* plants including most crops are glycophytes (i.e., non-salt-tolerant).

## 1.5 Crustal, tectonic effects

Any regional biota will result largely from two influences—*where* species originated, and the degree to which they have managed to persist and adapt to particular, local conditions. The habitats and plants of the Middle East have been shaped over the long term by hugely powerful movements of great geo-tectonic "plates," following the breakup of the supercontinent, Gondwana, and collision of the moving plates with Eurasia.

In terms of their influence on the plant ecology of the Middle East, much of this geological action began during the Oligocene epoch, some 30 million years ago (Ma), when the Arabian Peninsula and later the Sinai sub-plate began to break away from the larger African landmass, physically isolating many species as it did so. This separation is a product of a geological "rifting" process[13]—which goes on still, and which was also responsible for creating the chain of great African lakes from Malawi to Kenya, and continues as far north as Turkey. Tectonic activity has torn a huge extended rift in the Earth's crust, from Ethiopia to Jordan, more than 1600 km long and into which have poured the waters of the Indian Ocean, carrying marine life and creating the Red Sea.

Geologically Africa is "splitting apart at the seams." From the southern tip of the Red Sea south through Eritrea, Ethiopia, Kenya, Tanzania, and Mozambique, the continent is coming unstitched along a zone known as the East African Rift. The Earth's crust is slowly and incrementally ripping apart as molten rock from below pushes up on the solid surface and stretches it thin—sometimes breaking through. Each new slit widens the rift as molten rock—magma—flows in and then solidifies to fill the gap.

[13] Most rifts consist of a series of separate segments that together form a linear rift zone. Segment boundaries often have a more complex structure and generally cross the rift axis at a high angle. These segment boundary zones accommodate the differences in fault displacement between segments and are known as accommodation zones, and can take various forms. For example, in the Gulf of Suez rift, the "Zaafarana accommodation zone" is located where a shear zone in the Arabian–Nubian Shield meets the rift. Other major rifts include the East African Rift, Red Sea Rift, the Baikal Rift, and the Rio Grande Rift in southwestern USA.

### 1.5.1 The Red Sea

The Red Sea resulted from the separation of Arabia and Africa, with Arabia moving initially (~22–10 Ma) in a NE-direction due to rift push, and then (~10–0 Ma) in a N-direction due to slab pull (Abdelsalam and Gao 2009), and all of this occurring *following* the extrusion ~30 Ma of the "Afar mantle" plume volcanism, in Ethiopia. Bohannon et al. (1989) summarized the major geological events that lead to the formation of the Red Sea. These began some 30–32 Ma with much alkaline volcanism and rifting, and affecting only a narrow linear zone in the northeastern Afro/Arabian continent. This was followed by processes of rotational block faulting and detachment faulting, well under way by 25 Ma. Much magma flow and volcanism, as well as fine-grained non-marine sedimentation, then occurred in the rift between 25 and 20 Ma, followed by fine-grained marine sedimentation as the early shelves started to subside during the middle Miocene. Finally, there was some uplift of the adjacent continents (about 3 km) and subsidence of the shelves (about 4 km) between 13.8 and 5 Ma.

The Red Sea has several features that cannot readily be explained as associated with a rift basin beginning with only the horizontal translation of Arabia from Africa (Abdelsalam and Gao 2009). Various vertical effects are also evident. For example, the African and Arabian coasts of the Red Sea do not match up—they are topographically asymmetrical. The Arabian side has well-developed escarpments exceeding ~3000 m in the Asir Mountains, while escarpments on the African side are lower, at about 2200 m in the Gebel Elba mountain group at the Sudano–Egyptian border. Similarly the South Sinai mountains between the Gulfs of Suez and Aqaba have a maximum altitude of about 2640 m (Hegazy and Amer 2002). The Arabian plate also shows a distinct eastward tilt, away from the Red Sea. Moreover, the Sea is asymmetrical in terms of the distribution of magma. Nearly all of the series of magma flows that occurred about 30, 22, and 10 Ma were only along the western margin of Arabia, rather than on both sides, suggesting the rip in the Earth's crust started on the Arabian side of the Red Sea rather than the African.

Comparisons of ancient Precambrian structures exposed on both sides of the Red Sea suggest that it opened essentially at one point in time, along its entire length, without creating significant lateral rifts, following an uplift about 24 Ma (see Bridges et al. 2010).

### 1.5.2 Ongoing activity

Arabia's break with Africa of course continues to this day. For some 30 million years the Arabian tectonic plate has continued to drift and twist away from the African plate at the Red Sea at an average rate of about 2–3 cm/year.[14] Most of the time, though, the plates do not move. For decades and centuries—even millennia depending on the location and context—faults between tectonic plates are locked by friction and do not move. But eventually the stress becomes too great and the fault slips, creating an earthquake and a more substantial widening of the gap.

The violent breakup of the Earth's crust as tectonic plates move apart occurs through intermittent episodes of stretching and cracking, with intrusions of magma "dykes" along rift zones. A dyke is a vertical injection of magma from deep in the Earth's crust. As the magma in the dyke crystallizes, it forms new rock and so fills in the split between the plates. On rare occasions this rifting action has been captured by scientists in real time, in situ.

For example, Keir et al. (2009) used data from the European Space Agency's Envisat radar satellite and also from global positioning systems and seismicity records of the waves of energy created by

[14] The large, great sub-continent of India is believed to hold the continental land speed record (20 cm/year) for a piece of drifting crust (Kumar et al. 2007). About 140 million years ago, the large super-continent of Gondwana began to break apart—with what would become Africa, South America, Australia, Antarctica, and India splitting off in different directions and at different speeds. Movement is caused by huge thermal effects from below—vast internal volcanoes spewing powerful plumes of heat, putting pressure upon and eventually moving the plates on top through convective forces—with India moving away and 50 million years ago crashing into Eurasia (and then slowing down to some 5 to 6 cm/year. Below-ground the Indian landmass continued penetrating for some several hundred km; above-ground the thinner crustal surface buckled, forming the Himalayas). Antarctica is moving hardly at all, and Australia only a little faster than that. The Indian sub-continent is presumed to have traveled so much faster because the thickness of the Indian tectonic plate is only about half the estimated thickness of the rest of Gondwanaland (see Kumar et al. 2007).

earthquakes, to capture the emplacement in Ethiopia of two 10-km-long, 1–2-m-wide dyke intrusions and analyzed how the ground moved, during a 2006 rifting episode.

The Ethiopian event was a vivid demonstration of what seems a phenomenal amount of pent-up potential energy being released by the Earth from time to time, as continents split apart. It is evolutionary geology in present-day action. At that particular point in 2006, the two huge continental plates in Ethiopia moved apart by some 8 m. As they did so, an estimated 2.5 $km^3$ of magma was injected into a vertical crack (the dyke). Detailed observations of the two dyke intrusions from June and July 2006 showed that they were injected along the rift over some four to five hours. As the magma was injected into the upper 10 km of crust, it caused many earthquakes and some faulting.

At the surface, a number of faults moved by several meters and various deep fissures opened up. More than 160 earthquakes were detected in the area during this time. Moreover some 10 000 local people were displaced and, although there were no human casualties, several camels and goats fell into open fissures.

Today a great ring of volcanic activity cordons off the Arabian Peninsula as it pivots away to the east as if hinged, at Jordan, with its western edge also tilting upward and creating a mountain wall down the length of the Red Sea coast. This elongate mountain system is known as the *Hijaz*[15] in Arabic—the *barrier*.

Finally at the extreme southern end of the Red Sea, the Bab-el-Mandeb is a narrow strait only some 25–30 km wide, located between Yemen on the Peninsula and Djibouti and Eritrea at the Horn of Africa. This is one of several Middle Eastern pinch points, this one connecting the Red Sea to the Gulf of Aden and the Indian Ocean. It is very volcanically active.

### 1.5.3 The Gulf

In marked contrast to the Red Sea situation, at the *eastern* edge of the Peninsula the Arabian Gulf is both shallower and younger, and also, unfortunately, more polluted and environmentally degraded. (The name itself remains contentious: "Arabian" Gulf or "Persian"? Because the center of our study region is the Arabian Peninsula, we have called this basin the Arabian Gulf, the name used by the states in the Peninsula and other Arab nations. However for a summary of the naming disputes, with some of the key references and legal decisions, see http://en.wikipedia.org/wiki/Persian_Gulf_naming_dispute).

Earlier on (*c*. 20 000 years ago) the Gulf was just a long, shallow river valley through which the combined waters of the Tigris and Euphrates Rivers flowed toward the Arabian Sea. However as sea levels rose at the end of the last ice age, the freshwater valley became an ocean gulf. Today it remains hypersaline since so little rain falls in its watershed, and the high temperatures promote rapid evaporation. Moreover the connection with the rest of the world's salt water, at the Strait of Hormuz, is comparatively narrow, allowing relatively little exchange with the less salty ocean water.

At the start of the Holocene the Gulf was almost completely dry, so its history as a marine environment is only some 15 000 years old (see Reynolds 1993; Sheppard et al. 2010). It is shallow, less than 30 m for most of its depth, with a maximum depth of about 60 m. According to Sheppard et al., seabed areas which are presently 4–6 m deep have been submerged for only 3000–4000 years, so benthic habitat development there is comparatively young. In terms of reef-building corals, the Gulf contains an impoverished subset of the Indian Ocean biota (Sheppard 1998), ranking 24th out of 26 regional (Indian Ocean) sites in terms of species richness.[16]

[15] Also rendered as Hejaz. This region in western Saudi Arabia includes the Islamic holy sites of Mecca and Medina and so has great significance in the Arab and Islamic historical and political landscape. The Hejazi people (or Hegazis) remain fiercely proud of this heritage.

[16] There are also reefs on the Iranian side; however little is known as to their condition (possibly they are in better shape there, on that rockier, less developed and less well studied side of the Gulf). The aquatic environment of the Gulf as a whole is extremely harsh—*c*. 36°C water temperature (making diving to study the coral and coral reef fisheries there especially dangerous due to heat exhaustion, since a diver cannot cool off under water and it is typically 40°C+ out of the water). Salinity also runs high—37 to 38 ppt vs 34 to 35 in most tropical oceans (Peter F. Sale, personal communication). These reefs are species-depauperate but, amazingly, some species of fish and coral *are* able to cope with these conditions—of course what they cannot cope with is the wildly expansive coastal development, and chronic, severe overfishing.

Mangrove habitat in the Gulf has unfortunately also become greatly reduced in recent decades (see Section 4.6), as have the fisheries and populations of marine mammals. In Dubai much of the coastline was originally fringed by relatively dense coral growth (e.g., Purkis and Riegl 2005). However, in the late 1990s construction began there on the grand "Jumeirah Palm" resort project, and in 2004 on the "Jebel Ali Palm"—all built in what was previously the Gulf's second most biodiverse and well-documented ecosystem (Sheppard et al. 2010).

As we describe in Chapter 10, a combination of warfare, oil pollution, and mega-development projects has caused the Arabian Gulf's marine environment to become seriously damaged. The fact the Palm developments can be seen from space surely signals a mixed message; it demonstrates the impressive capacity of human beings to find the resources and skills to create massive structures, at the same time as we destroy nature's treasures.

## 1.6 The more recent past

According to one major hypothesis of human geography, the strait of Bab-el-Mandeb featured in the earliest migrations of modern humans out of Africa, beginning at least 60 000 or as much as 125 000 years ago (e.g., Armitage et al. 2011; Petraglia et al. 2010). At those times sea levels were much lower and the straits even shallower, enabling a series of emigrations and expansion that continued along the southern coastline of Asia, to India and beyond.

Clearly the Arabian Middle East represents a major zone of contact among three global regions—African, Asian, and European. Isolated on a vast peninsula, Arabia's plants had the opportunity to evolve in isolation from their origins, just as the ancient and deep-water Red Sea marine life, which was similarly isolated in a long and ancient strip of water, also developed to be quite distinct from its origins in the Indian Ocean.

The climate of Arabia and of the rest of the world has fluctuated considerably during the past two million years, and we expect the composition of the flora and fauna to have "tracked" these variations. We can also expect some remnants, or "ghosts of climates past" to persist to this day, as a result of local adaptation in small patches of suitable habitat. As recently as about 9000 years ago, for example, the Middle Eastern region had a much cooler, more humid Mediterranean-type climate. Although conditions have since become significantly more arid, many of the species which first appeared in or colonized Arabia have adapted and continue to survive there. We explore this using examples of mature forest vegetation, once more widespread and which has since become localized and rare or threatened (see Section 3.1).

Countries like Libya, Egypt, and Saudi Arabia are today largely arid countries, in places even hyperarid, but their climates were significantly *wetter* in the past. Still, Murray (1951) concluded that *regular* rainfall ceased over Egypt below the 500 m contour line some time about 0.75 Ma. The last time the climate of the Arabian Peninsula was "wet" was during the period of about 13 000 BP–9000 BP. The present desert climate of Arabia probably first developed sometime after that and has since become progressively drier.

The Latvian–German botanist and explorer (and early authority on African textile archaeology), Georg August Schweinfurth (1883, cited in Zahran and Willis 2009), discovered an ancient dam built across Wadi Garawi in the Eastern Desert of Egypt. The dam was later dated back to the third or fourth Dynasty, about 4665 BP. This dam would have retained and regulated the intermittently torrential waters of the wadi. Another dam, the ancient Marib in present-day Yemen, was built more than 2000 years ago and finally collapsed during the seventh century. It had long been used—by the celebrated Queen of Sheba among others—to support a centuries-long trading empire, an economy founded on high-value natural plant products, mostly frankincense and myrrh. We discuss dams and hydro-politics in Chapter 10.

In general much of the vegetation in the Middle East may best be seen as comprising fragments, and/or subsets of, or sequels to, the vegetation of this formerly wetter climate. In Chapter 3 we look in more detail at ancient climates and evidence from regional plant paleoecology.

## 1.7 Climate relicts and the "regeneration niche"

A major consequence of the current trend of rising global temperatures is that many plant and animal species, worldwide, are moving toward higher elevations and latitudes (e.g., Parmesan 2006). Moreover as we are now realizing, climate change is nothing new—it has been a recurrent phenomenon throughout the history of the Earth, and can be traced in terms of shifting species ranges. What is remarkable in the current episode is the speed of change, and the limited ability to respond by migrating to more suitable regions. One major result is a "climate relict." Gorchakovskii and Zolotareva (2006) have identified relict stands of 66 plant species in three species-rich mountain-steppe ecosystems in the southern Urals, and Danin (1999) has reported that hundreds of "typically Mediterranean" species have survived in the shelter of rock outcrops in the deserts of the Middle East.

At the receding edge of a species range, migrating retractions are often incomplete, leaving behind isolated populations as relicts. Such climate relicts are populations left behind during climate-driven changes in range, able to persist in pockets of suitable conditions within an otherwise inhospitable regional climate. Hampe and Jump (2011) have usefully reviewed the evidence for climate relicts worldwide and developed a general framework for describing them. They distinguish among relict habitats, abiotic and biotic constraints on population dynamics, and mechanisms promoting population persistence. Three major climate relicts were identified: populations (sometimes species) primarily constrained by climate-driven abiotic factors; those restricted to areas inaccessible to competing species for climatic reasons; and those requiring a "host" (or "nurse") species that modifies the microclimate, which is itself limited by climate (see too Section 4.7).

Hampe and Jump pointed out that virtually *all* extant species are likely to have experienced periodic changes in range over their history. Thus whether a taxon is considered a relict or not seems to depend largely on the *severity* of range reduction, over a given timeframe. This in turn is ultimately arbitrary (see, too, Rodríguez-Sánchez and Arroyo 2008, 2011). Furthermore, classification of a species as a climate relict implies that climate is the primary factor causing the permanent reduction in their distribution, though this often cannot be clearly demonstrated.

Traditional biogeographic notions of climate relicts have tended to focus on species and higher taxonomic levels, though most species have their distribution limited by climate only in *some* parts of their range, and may thrive and expand in others (e.g., Franco et al. 2006; Parmesan 2006).

A simple record of species distribution does not address the intra-specific level—the variety of environments that different populations will have experienced, as well as all of the genetic variation, adaptation, and phenotypic plasticity that differentiate each locally adapted population over its particular evolutionary trajectory. Studies at the population level may reveal aspects of microevolution and potential avenues useful for conservation, in the face of the rapidly changing climate of the Anthropocene (see Section 10.1). We need a population-level approach in order to further analyze and better understand climate relicts (Hampe and Jump 2011).

Grubb (1977) made the fundamental point that environments favoring the *seedlings* of plant species function as ecologically vital "regeneration niches." The regeneration niche of any species describes its fundamental requirements for successful establishment. Indeed, the regeneration niche is probably more relevant for assessing the *long-term* viability of populations living at the edge of their climatic tolerance than is the niche space of current adult individuals (e.g., Jackson et al. 2009). This argues for the importance of looking at the age structure of relict populations, and, in particular, assessing whether the age structure is stable, with successful juvenile recruitment, in order to evaluate the potential for long-term population sustainability.

Numerous studies have highlighted the importance of climatic constraints on seed production (e.g., Fisher 1997; Gimenez-Benavides et al. 2007; Hampe 2005; Montesinos et al. 2010), and early stages of plant recruitment (e.g., Ramirez et al. 2006). Many of these were performed in regions with seasonal water shortage so it is perhaps predictable that water deficit was identified as the most frequent cause of recruit mortality.

An adequate water supply during germination and the first year of life may enhance an individual's resistance to drought in subsequent years. This implies that even irregular wet years may allow long-lived polycarpic species to survive and reproduce successfully, as they can amortize reproduction over many years. Year-to-year variation in early recruitment can impact later life stages; for example, Hampe and Arroyo (2002) used dendro-chronological data to demonstrate that the abundance of sapling age-classes in five relict populations of alder buckthorn (*Frangula alnus*) was positively correlated with the amount of precipitation in the year of their germination.

### 1.7.1 Facilitative interactions (and "plants helping plants")

Climate relicts may benefit from biotic interactions if these help mitigate local environmental conditions (most notably through "facilitative" effects—shading, cooling, moistening, and otherwise ameliorating the microclimate, etc.). Indeed many studies in semi-arid regions have shown that successful recruitment of relict species often relies heavily on facilitation (at least initially) by so-called nurse plants (e.g., Ramirez et al. 2006; Valiente-Banuet et al. 2006; and Section 4.7). Many ecologists have described the importance of such effects for climate relicts.

The general proposition is that such facilitation becomes increasingly important as environments become more "stressful" (Holmgren et al. 1997), so we expect it should be a widespread phenomenon in "abiotically limited relicts,"—species whose distribution and growth are limited primarily by climatic factors like high temperatures and water deficit. So far no systematic assessments have been made of Middle Eastern floras for evidence of climate relicts or the relative role of facilitation; however, we expect many such species to be identified (e.g., Danin 1999).

Facilitative interactions have been shown to promote diversity of the regeneration niche and maintain plant species richness (Valiente-Banuet and Verdu 2007, 2013a). For example, it has been shown experimentally that nurse species enabled specialized ecotypes of *Brachypodium distachyon* originating from the more mesic Mediterranean extreme of the Dead Sea—Jordan Valley gradient—to grow and reproduce in the arid desert extreme (Liancourt and Tielborger 2011). This suggests facilitator plants may "expand" the regeneration niche not only for stress-intolerant species, but also for particular ecotypes (locally specialized populations), promoting their colonization of new environments. Facilitation may indeed play an important role in range expansion for some plants, providing some relaxation of intense selection pressures while adaptation to the new conditions occurs (e.g., Calloway 2007; Valiente-Banuet and Verdu 2013a).

It is becoming sadly clear that the Middle East is steadily *losing* its regeneration niche. Too many populations of too many different tree species prove to consist largely of *older* individuals. The once abundant juvenile stages are simply missing. Regarding these populations of mature trees, the world in which they germinated—often hundreds of years ago—has changed dramatically. We see powerful evidence of this problem in the elderly stands of Socotra's dragon's-blood trees (see Section 3.3); populations of *Moringa peregrina* in Egypt and the Emirates; and the Bankoualé Palm, *Livistona carinensis* of Djibouti (see Section 3.4); the Phoenician Juniper (*Juniperus phoenicea*) and endemic shrub, *Arbutus pavarii* in the coastal mountains of Libya (Kabiel et al., 2015 a, b), and many others.

## 1.8 Water as a trophic currency

Albeit that fresh water is essential to terrestrial life, surface water is a scarce commodity on Earth, and very little is available to plants (Winter et al. 1998). Moreover it is even less common in the arid, semi-arid, and dry sub-humid ecosystems (or "drylands" of the world), and in any ecosystem experiencing drought (Reynolds et al. 2007). Perhaps the most important point is that, for plants, water is not simply the solvent in which cellular biochemistry occurs. In combination with carbon dioxide it is also the primary resource used to form sugars through photosynthesis . . . the foundation of most ecosystems on Earth.

Water is obviously an essential ingredient for life on Earth and clearly important in driving ecological interactions, yet too little is known about how it

functions as a *trophic* currency—as a unit of value in determining species interactions in terrestrial food webs (but see Allen et al. 2014). Water availability *has* been shown to influence interactions between plant species (McCluney et al. 2012; Nippert and Knapp 2007; Scholes and Archer 1997), animal physiology and behavior (Ostrowski et al. 2006; Tracy and Walsberg 2002), as well as significantly influencing latitudinal biodiversity gradients (Hawkins et al. 2003).

For all that neighboring plants may assist seedling establishment as modifiers of microclimate, plant–plant interactions in arid ecosystems can readily shift between facilitation and competition, as water availability changes. Such interactions are mediated by multiple interacting factors, including plants acting as resource-rich "islands" in an otherwise empty sea, and neighbor-induced changes in microclimate and soil water availability. Hence increases in soil moisture, reduced physiological stress provided by the shade of nurse plants, and enhanced soil fertility all serve as primary drivers underlying positive effects of grasses and shrubs on shrub and tree seedling establishment in Mediterranean environments (see McCluney et al. 2012).

The nature of the interaction may switch from positive to negative—from facilitation to competition—as individuals transition to different life-history stages. For example, the giant saguaro in the Sonoran Desert, *Carnegiea gigantea*, requires a nurse plant (e.g., *Cercidium* sp.) for establishment but then later out-competes its nurse plant as it matures (McAuliffe 1984).

Various models exist to predict how species interactions change along gradients of ecosystem productivity and resource availability. Among these the "stress-gradient hypothesis" (Bertness and Callaway 1994) has been one of the most influential. It predicts that facilitation should be especially common in communities developing under high physical stress, and significantly less in those in more benign environments. Despite its popularity, support for the stress-gradient hypothesis remains equivocal (see review in McCluney et al. 2012; and see Section 4.7).

Plants in desert environments are clearly important resources for the animals that live there. The fraction of surface water contained in plant tissues can be an important resource for animals living in dryland habitats (McCluney et al. 2012). Allen et al. (2014) conducted field studies at some twenty-seven 625 $m^2$ plots along an aridity gradient in southeastern Arizona, near the Upper San Pedro River. They used water manipulation experiments to observe its effects on primary consumers (crickets) and their predators (spiders and lizards). Consumers increased in abundance in response to added surface water and groundwater, which was presented in the form of additional moist leaves in treatment plots. Predators also increased in abundance in response to added surface water, despite the presence of a river, an abundant source of flowing surface water. Moreover the relative magnitude of organism responses to the water supplement was greatest at the most arid site and lowest at the least arid site, mirroring cricket recruitment (which was greatest at the least arid site and lowest at the most arid).

Relatively little is known about the details of comparative plant hydro-ecology, the availability of soil water and patterns of water use by species, in relation to the influence of rainfall on seasonal and annual patterns of water use. In water-limited biomes like those of so much of the Middle East, rainfall is likely to dictate when plants will consume most water; thus in a "strategic" sense, water use should be greatest in the wet season, declining with soil water availability during the dry season, despite the fact that this will be the period of greatest evaporative demand, thereby limiting canopy desiccation. *Acacia tortilis* is a dominant tree in the Arabian Peninsula and other deserts, surely a "keystone" species ecologically (see Sections 6.8 and 11.6), and as such also represents a potentially efficient and useful model of plant drought adaptation.

Do et al. (2008) tracked water use by mature *Acacia tortilis* ssp. *raddiana* trees, a semi-evergreen or drought-deciduous species in Sahelian Africa, by making continuous recordings over four years. In the northern Sahel, the full canopy stage of this species lasts between six and eight months, including the three-month "rainy" season and part of the dry season.

Do et al. determined that both the annual amount and pattern of tree water-use were remarkably stable from year-to-year, *despite* between-year and

seasonal variations in soil water availability in the upper soil layers. Do et al. studied closely the physiology of adult trees in a population of approximately 30 individuals. Plants transpired readily throughout the year except for one month, during the dry season (when defoliation was greatest). The highest rate of water use (about 23 liters (dm sapwood area)$^{-2}$ day$^{-1}$) was recorded at the end of the wet season. While trees still had foliage in the earlier part of the dry season, the decline in water use was modest at around 30%. Analysis of the deep soil profile revealed living roots at 25 m, and showed that soil moisture levels were low (-1.6 MPa) down to the water table at a depth of 31 m.

Obviously for desert plants there is an important trade-off between the need to present leaf lamina to capture carbon dioxide and radiant energy, and the need to limit the loss of precious water molecules. This trade-off is apparent in terms of various structural and physiological adaptations. The finding that *A. tortilis* transpired readily during all but one month of the year, even though water levels in the upper soil layers were extremely low for eight to ten months of the year, implies significant reliance on moisture from the deep soil layers. Do et al. found living roots at 25 m depth, confirming the trees had access to deep soil water.

Further work is needed to better understand these patterns of water use in the desert, and it is important to note that this species benefits from long-standing symbiotic partnerships with arbuscular mycorrhizae (AM) and the nitrogen-fixing bacterium *Rhizobium*. The AM provides an extensive mycelial network that greatly enhances access to soil moisture, and the fungal tissues often act as a reservoir of resources for their higher plant associates. Interestingly it has been shown that the presence of AM in the root system of *A. tortilis*, in turn, enhances the degree of nodulation with the nitrogen-fixing *Rhizobium* (André et al. 2003).

## 1.9 Endemism and species range

The Middle East has a complex geography that includes several large landmasses, bordered by the Arabian, Red, Black, Caspian, and Mediterranean Seas. It includes the Arabian Gulf and the Gulfs of Oman, Aden, Aqaba and Suez, and several large, fairly isolated peninsulas—the massive Arabian Peninsula itself and smaller Sinai, Qatar, and Musandam peninsulas which it contains. There are several huge mountain ranges—the Taurus, the Zagros, the Elburz—as well as the only slightly smaller Pontic and Asir, Hijaz and Hadhramawt[17] ranges, the Anti-Lebanons and others.

This huge region that is today largely dry land is a meeting point, or area of conjunction for five phytogeographic regions: the Irano-Turanian, Sudanian, Mediterranean, Saharo-Arabian, and Euro-Siberian regions (Zohary 1970, 1973). Zohary's classic work showed clearly how this converging, merging, and mixing of different floras makes the Middle East so botanically fascinating. At the same time, modern plant communities in the Middle East are in part a result of individual plant populations having advanced and retreated in range over time. These populations provide the background ecological theatre and working cast for the great Middle Eastern play, a rich tapestry of centers of endemism and changes in distribution, with much evidence of non-trivial human involvement over the history of these floras.

Endemism is in a sense an extreme form of stenochory, or highly restricted distribution. It has several nuances of meaning and has been taken to convey different degrees of limited distribution (e.g., Brown and Lomolino 1998) but, most simply "endemic" means occurring nowhere else other than a particular place. Of course "place" is magical and also exists at a variety of spatial scales. Moreover plants may be endemic because they *originated* in that place and never dispersed, or because they are relicts of a formerly more widespread species that became confined to a specific area or locality (Cadotte and Lovett-Doust 2002).

The minimum area used by ecologists as a criterion of endemism varies greatly, ranging from "continental endemics" (species limited to a particular continent), to "extreme local endemics" which may be limited to tiny areas as small as 1 km$^2$, or even a few 100 m$^2$. Endemism can also be applied at higher taxonomic levels, for example, to genera or families that are only found in a particular part of the world (cacti in the New World, for example). Endemism

[17] Also rendered as Hadramawt.

is given special significance in attempts to identify the world's top "biodiversity hotspots" (see Section 10.15), five of which are in the Middle East, so it would be helpful to establish a more quantitative approach to measuring the significance of endemism . . . for example, to measure the amount of unique phylogenetic "information" that is represented by individual species, or closely related groups, and compare that between and among taxa and organisms.

From a conservation and natural resource perspective, a "phylo-rare" plant species, existing as the sole representative within a particular rank (a monotypic plant *order*, for example), contains significantly more unique phylogenetic information than another representative species, say one in an otherwise large genus, large family, large order. The phylo-rare species is, to a much more urgent degree, the last of its kind. It is important to acknowledge that so far no standard has been developed for genetic differentiation between taxonomic ranks and among different kinds of organism; taxonomy and genetic distance are not necessarily at all aligned.

If we take the instrumental, anthropocentric perspective of regarding other species as sources of new genetic material, then extinction and loss of a phylo-rare endemic should be more worrisome than loss of a species with many surviving close relatives.

**Table 1.3** List of sites identified as centers of plant diversity and endemism (from Davis et al. 1994). See also Figure 1.2

| Country | Site |
|---|---|
| Libya | Al Jabal al Akhdar |
| Egypt | Southern Sinai & Gebel Elba |
| Sudan | Gebel Elba; Imatong Mountains & Jebel Marra |
| Ethiopia | Bale Mountains & Simen Mountains |
| Eritrea | – |
| Djibouti | – |
| Somalia | Cal Madow; Southern fixed dune vegetation; Hobyo; Nugaal valley & Limestone woodland (Ogaden) |
| Saudi Arabia | Highlands of Southwestern Arabia (Asir); Northern Hijaz & Harrat Al-Harrah |
| Yemen | Socotra; Dhofar Fog Oasis; Hadramaut; Jebal Areys & Highlands of Southwestern Arabia |
| Oman | Dhofar Fog Oasis |
| Emirates | – |
| Qatar | – |
| Bahrain | – |
| Kuwait | – |
| Jordan | Levantine Uplands |
| Syria | Levantine Uplands |
| Israel (incl. Gaza & West Bank) | Levantine Uplands |
| Lebanon | Levantine Uplands |
| Iraq | Mountains of Northern Iraq |
| Turkey | Anti-Taurus Mountains and Upper Euphrates; Tuz Golu; Mountains of Southeast Turkey, Isaurian, Lycaonian Taurus region; Southwest Anatolia; Levantine Uplands; Northeast Anatolia & Ulu Dag |
| Iran | Touran biosphere reserve; Zagros Mountains; Hyrcanian forests; Mountains of Northwest Iran |
| Cyprus | Troodos Mountains |

Endemism has been examined by many workers including, e.g., Brown and Lomolino (1998); Davis et al. (1994); Quézel (1978); Shmida (1985); Thompson (2005); Wickens (1976); and Zohary (1973). The collective total number of vascular plant species in the Middle East could add up (when overlaps in nationally or regionally based lists are resolved) to some 35 000–40 000 species (see Table 1.1). A total of 8780 endemic species has been identified so far. It would be useful to determine accurate sub-regional totals for the greater region, and such an inventory calls out for further study.

The extreme desert is not a *particularly* favorable habitat for endemics, though any relatively humid habitats within it (such as in mountains, oases, or wadis) are excellent locations for speciation and preservation (Shmida 1984). Areas of especially high endemism include the Socotran archipelago, the Dhofar fog oases in Oman and Yemen, and the highlands of southwestern Saudi Arabia and Yemen (all lying in sub-regional Somali-Masai and Afromontane phytogeographic centers of endemism, that correspond to the ancient African and Arabian plates of Gondwana).

Likewise, rich Irano-Turanian centers of endemism (which represent the former *northern* supercontinent's contribution to the Middle East) include the Touran Reserve in central Iran, the Anti-Taurus Mountains and upper Euphrates regions in Turkey, and the mountains of southeastern Turkey, northwestern Iran, and northern Iraq. An Eastern Mediterranean center exists in the Isaurian-Lycaonian region of central Anatolia, and in Cilician Taurus and southwestern Anatolia (all in Turkey), as well as the Levantine uplands in Turkey, Syria, Lebanon, Jordan, and Israel. The Euro-Siberian center extends to the rich Hyrcanian forests in Iran, Azerbaijan, and northeast Anatolia (see Figure 1.2 and Table 1.3), which are among the oldest forests in western Eurasia.

## 1.10 Primal forest in Arabia and conservation

Hepper and Wood (1979) first suggested that during the Miocene (between 23 and 5 Ma), an ancient "valley-forest" covered much of southwestern Arabia, though only small fragments survive today. These remnants are found in splendid isolated southwestern valleys between 500 and 1000 m, mostly running west/southwest and receiving locally high levels of orographic rainfall (Hall et al. 2009). Here (as introduction and example) we briefly characterize the rare and endangered valley-forest ecosystem.

Arabian valley-forest vegetation includes some 18 species that are now largely restricted to these areas. In Yemen and Saudi Arabia, Wood (1997) and Hall et al. (2008) considered these 18 as *indicators* of valley-forest. The major recorded sites are at Jabal Raymah, Jabal Melhan (Milhan), and Jabal Bura, all in Yemen, and at Jabal Fayfa and Lejib Gorge in Saudi Arabia (Al-Turki 2004; Hall et al. 2008, 2009).

According to Al-Abbasi et al. (2009), common valley-forest trees in southwestern Arabia include *Combretum molle, Terminalia brownii, Mimusops laurifolia, Tamarindus indica, Trichilia emetica, Diospyrus mespiliforms, Delonix elata, Commiphora myrrha*, and the Arabian endemic *Acacia johnwoodii*. Large riparian tree species such as *Ficus ingens, F. vasta, F. sycomorus*, and *Breonadia salicina* are frequent along wadi channels. Common shrubs include *Carissa spinarum*, a number of *Grewia* species including *G. schweinfurthii, G. tembensis*, and *G. villosa*, several species of *Maytenus, Ehretia cymosa*, and *E. obtusifolia, Premna resinosa*, and *Teclea nobilis* (Figures 1.7A–D). Underneath the dense tree and shrub cover is a mostly sparse, but diverse, ground flora. Studies in Yemen recorded approximately 170 species from the valley-forest habitat, making it one of the most diverse communities in the region (Hall et al. 2008).

Canopy species include Arabian endemics, Sudano-Zambezian, Somali-Masai, Afromontane, and widespread Afrotropical species. M. Hall and A. Miller and their colleagues—who have been key to identifying this and other "at risk" ecosystems in Arabia—recognize various "transitional" species present in the valley-forest. Floristically it represents a mesic refuge for diverse plant elements from several different regional centers of endemism. Although similar forests occur across the Red Sea, in Eritrea for example, there are significant differences in the composition of northeast African and Arabian valley-forests (making these Arabian forests unique—see Hall et al. 2009).

A particular defining feature of Arabian valley-forest sites is the presence of the regionally restricted

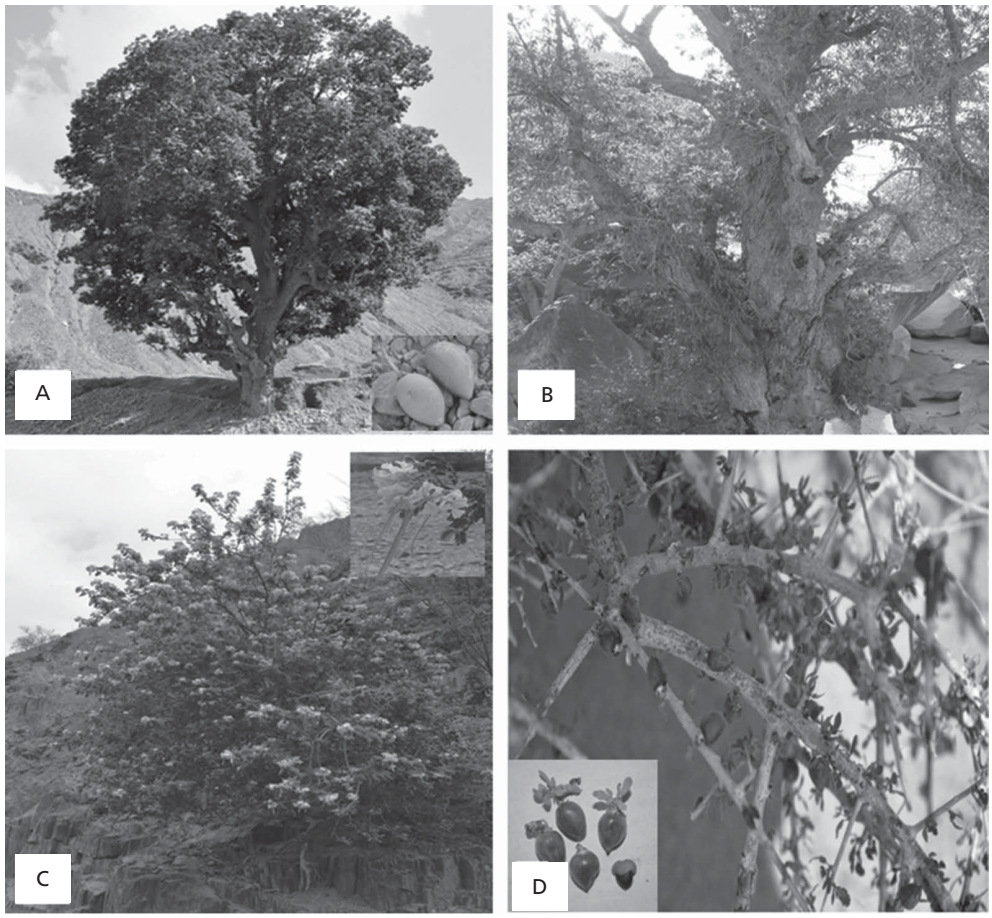



**Figure 1.7** (A) Giant tree of *Mimusops laurifolia* in the mountain escarpment, Jizan region, southwest Saudi Arabia, elevation 985 m. Two fruits shown in lower right side. (B) An old tree estimated to be *c.* 400 years old *Breonadia salicina* in Shada Mountain, southwest Saudi Arabia, elevation 1200 m. (C) *Delonix elata* in Shada Mountain at elevation 600 m, southwest Saudi Arabia. Reproductive branch in the upper right side. (D) *Commiphora myrrha* fruiting branches. Fruits and seed in lower left. Photo was taken from the coastal dunes of the Tehamah Plain, near Jizan, southwest Saudi Arabia. [For a color version of this figure, see the color plate section, Plate 2]

tree *Mimusops laurifolia* (Sapotaceae) (Figure 1.7A), which is found in both Arabia and northeast Africa (Djibouti, Eritrea, Ethiopia, and Somalia). According to Friis (1992), the species represents part of an important phytogeographic element restricted to the ecological transition zone between Afromontane and Somali-Masai plant elements. Hall et al. (2010b) estimate there are only about 100 mature individuals of *M. laurifolia* remaining in Arabia, and only four wadi sites from which ten or more individuals have been recorded (Jabal Gedu, in Wadi Tawila; Jabal Bura, in Wadi Rijaf; Wadi Basal; and Wadi Jawrah). The largest population of *M. laurifolia* occurs in the most extensive area of valley-forest on Jabal Bura, in Yemen, where approximately 40 trees have been recorded.

At sites in Yemen such as Jabal Melhan and Jabal Raymah, the forest is generally heavily degraded (Hall et al. 2009). *Mimusops* has been used as a building material and populations have declined rapidly of late (Hall et al. 2010b). In Saudi Arabia, Al-Turki (2004) noted that the valley-forest at Jabal Fayfa was also heavily degraded and that *M. laurifolia* was threatened with local extinction. As a result of its

fragmented distribution and declining habitat, *M. laurifolia* has been identified on the IUCN Red List as Regionally Endangered (Hall et al. 2010b).

Bafeel et al. (2012) determined the DNA sequence for rbcL (ribulose-1, 5-bisphosphate carboxylase/oxygenase large subunit) in *M. laurifolia*, and assessed the current phylogenetic status and RAPD (Random Amplification of Polymorphic DNA) fingerprinting pattern of *M. laurifolia*[18] and some related species in the Sapotaceae. Overall sequence similarity among the 18 species of Sapotaceae was very high (99.8%). The sequence for *M. laurifolia* was identical to that of *M. zeyheri*. *M. laurifolia* also showed high similarity to *Argania spinosa*. Seeds of *M. laurifolia* are well known to produce at least nine different kinds of saponins (Eskander et al. 2006). Ironically this endangered species is becoming popular after extracts have begun to be used in cosmetics, bath formulations, and detergents.

A new botanic garden at Wadi Jawrah, in Saudi Arabia, is envisioned as a unique resource for both *in situ* and *ex situ* conservation efforts (Al-Abbasi et al. 2009). The garden will focus on conserving both species and habitats. It is also the first conservation site in the new Arabian Important Plant Area program (see Al-Abbasi et al. 2009). The presence of many large *Mimusops* at Wadi Jawrah indicates the area once supported a significant cover of valley-forest. One long-term goal of the new garden will be to restore a broadly based valley-forest community there. To this point there has been no natural regeneration of *Mimusops* at Wadi Jawrah but the site represents a large stand of this regionally endangered tree species. This species would clearly benefit from investigation of its regeneration niche in terms of conditions favoring germination and establishment; followed by protected, coordinated, multi-species plantings and a program of restoration ecology.

From a demographic perspective, the *Mimusops* situation is really very similar to that of Socotra's rare and iconic dragon's-blood trees—*Dracaena cinnabari* (Dracaenaceae). There, individual trees may live up to 600 years (see Section 3.3). But unfortunately there too, seedlings are rare and there are too few juveniles, resulting in an unstable age structure with few potential recruits to the population. This means the populations are on track for demographic death and local extinction, once old individuals reach the end of their lifespan.

## 1.11 Summary

This chapter overviews the region and introduces the plant ecology of the Horn of Africa, the Arabian Peninsula, Turkey, Iran, and thereabouts. For all organisms, water has become a limiting resource, unpredictable in space and time. It is a limiting resource and trophic currency for which competition is intense. Across the region endorheic drainage basins progressively build up salts that become toxic to life.

Plants adapt to drought and salt in a variety of ways. Patterns of endemism and the high frequency of facilitative interactions are noted (many of the endemic species are climate relicts). Phylogenetically some families have fared better than others in adapting to the desert, yet at the same time, regionally, many plants are losing the struggle for existence through having too few recruits. Long-lived tree species are losing their juvenile "regeneration niche." Species-rich cloud forest and valley-forest habitats are localized, vulnerable treasures, hostages to drought.

[18] Plastid rbcL is the most commonly sequenced single gene used for plant phylogenetic studies (Schuettpelz et al. 2006) and RAPD provides quick and easy molecular characterization of taxa, with some limitations (e.g., Penner et al. 1993).

CHAPTER 2

# The lay of the land

## Plant geography in the Middle East

### 2.1 Boundaries

In his own book about plants in the deserts of the Middle East, Batanouny (2001) asked, "East of where and Middle of what?" As discussed in Section 1.2, there are many different perspectives on what constitutes "the Middle East." Here we describe landscapes and vegetation across a broad sweep of countries centered on the Arabian Peninsula, with the goal of identifying major patterns. For each country we summarize the major elements of endemism and characteristics of the flora. In subsequent chapters we address factors accounting for and impacting upon these larger-scale patterns.

In their survey of biological diversity in the Mediterranean basin, Blondel et al. (2010) used a bioclimatic approach to delineate territories they would include, combining climatic factors (temperature and precipitation) with biological, vegetation-based ones. These were defined in terms of two or more dominant trees or shrubs whose combined presence characterized vegetation zones representing particular altitudes, latitudes, and slope exposures. Using this approach, Blondel et al. included some 2.3 million km$^2$ spread over 24 countries. They included parts of a number of countries also in the Middle East: namely Turkey, Cyprus, Syria, Lebanon, Israel, the Palestine territories, Egypt, and Libya.

In both Libya and Iraq small but significant areas of Mediterranean-type woodland do occur, and Blondel et al. noted that if the broad isoclimatic region first identified by Emberger (1930) were adopted, then all of Libya and much of Iraq should really be included as "Mediterranean." By contrast the combined bio-climatic approach that they took reduced significantly (to about 500 km$^2$) the part of Libya included.

### 2.2 Geological characteristics

The region represented here includes a huge land area, with a great deal of structural and topographic variation and much active geo-tectonic movement. The presence of many relatively young mountain ranges reflects the forces of ongoing collisions among Arabian, Anatolian, and Eurasian plates. Powers et al. (1966) described how fold-and-thrust belts have formed mountain ranges and elevated plateaux in the region; mountains continue to rise along the Bitlis suture zone in southern Turkey and the Zagros suture zone in western Iran.

The Anatolian plate is being slowly pushed westward as the Arabian and Eurasian plates collide, creating a high plateau (*c*. 1500 m) in eastern Turkey and northwestern Iran. The Dead Sea Fault, between the Sinai part of the African plate and the large Arabian plate, exists because the Arabian plate is rotating in a slow, counter-clockwise direction while moving northward. Meantime new ocean floors are opening up to the south, along the Red Sea coast and Gulf of Aden.

Water circulation and movement in the Middle East are constrained by several narrow straits, control of which has been of great significance throughout history. The Strait of Gibraltar controls access to the Mediterranean from the Atlantic; shipping between the Mediterranean and Black Sea is controlled at the Bosporus and Dardanelles. Other critical waterways include the Suez Canal, linking

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the Mediterranean to the Red Sea; the narrow Bab el Mandeb, separating the Red Sea from the Indian Ocean; and the narrow Strait of Hormuz, between the Arabian Gulf and Indian Ocean. Coastal areas tend to experience a more moderate climate than the interior, due to water's greater capacity to absorb heat; this in turn moderates the amplitude of temperature variation and provides water vapor that can condense at higher altitudes or at night when air temperatures are lower.

## 2.3 Coastal and desert environments

A perception of Middle Eastern environments is that they are mostly just arid deserts. However, there are also mesic, irrigated oases, coastal areas, river valleys, steppes, mountains, and highland plateaux. Indeed some areas, such as the southwestern corner of the Arabian Peninsula, eastern Mediterranean, and northern Turkey, regularly receive up to 1000 mm of rain per year and, while the entire region typically has hot summers, nearly half of it may also have occasional snow in the winter, particularly in the eastern Mediterranean, northern Turkey, and northern Iran.

Today the Sahara Desert extends across North Africa, limiting major settlements to the Mediterranean coastline and, in Egypt, extending up the floodplain of the Nile valley. Likewise the vast Arabian Desert is dry and largely uninhabited. Areas along riverbanks (like the Nile, Tigris-Euphrates, and Jordan) and along the Mediterranean coast have for millennia supported productive agriculture. Mountain regions are cooler and also support grazing land, while coastal marshes form a productive interface between land and sea and often provide external inputs supporting productive nearshore ecosystems.

Extensive coastal salt marshes occur along the Mediterranean, Red Sea, and Arabian Gulf. Despite considerable differences some general features are evident, including fairly low species diversity. Major halophytic genera include *Arthrocnemum, Halocnemum, Suaeda, Halopeplis, Limonium, Aeluropus, Cyprus, Sporobolus, Juncus, Mesembryanthemum, Halimione, Avicennia*, and *Rhizophora*.

Coastal marshes are subject to regular periodic flooding due to both tidal and non-tidal effects on sea level. Vegetation is mainly herbs, grasses, and low shrubs. Mangrove systems in contrast are dominated by small trees, and in some areas salt marsh and mangroves may grade into each other. *Avicennia marina* mangroves often form a low shrubland that may be even shorter in stature than common salt marsh undershrubs, like *Arthrocnemum glaucum* or *Halocnemum strobilaceum* (see Figure 2.1).

Most deserts of the Middle East are "subtropical" (see Section 4.1), where the aridity is a consequence of the downward movement of cooling, dry air circulating from the Earth's equatorial region. The huge Arabian Desert is an extensive wilderness which occupies most of the Arabian Peninsula (see Figure 1.5), extending from Yemen to the Gulf and Oman to Jordan and Iraq (*c*. 2.3 million km$^2$). The Nafud Desert is one part of it, famous for its gigantic sand dunes sometimes reaching over 30 m high. The Rub' al-Khali is another vast segment of the Arabian Desert, with single dunes extending sometimes for tens of kilometers. The Dahna is the northern expanse of the Arabian and connects to the Nafud. The Syrian Desert represents another extension, covering about 0.5 million km$^2$ in parts of Syria, Jordan, Saudi Arabia, and Iraq. Meantime the Dasht-e Kavir plateau of north-central Iran (*c*. 77 000 km$^2$) is often referred to as the "Great Salt Desert." It is the largest desert in that country and is a mostly uninhabited, barren region covered with crusty salt ridges (and see Section 2.26).

A common desert feature is the presence of shallow depression habitats of different depth. Whenever rain falls these collect surface run-off loaded with fine-textured alluvial sediments. As water evaporates, the drying soil develops distinctive "desiccation cracks" (Harris 1957, 1959; White and Law 1969). These have different shapes and thicknesses depending on attributes of the sediment and extrinsic conditions such as temperature and rate of desiccation (Corte and Higashi 1964). Common species establishing in these habitats are *Trigonella stellata, Schismus barbatus, Anastatica hierochuntica, Zygophyllum* species, *Zilla spinosa, Euphorbia retusa, Plantago* species, *Aizoon canariense*, and *Mulva parviflora* (see Figure 2.2).



**Figure 2.1** Transition zone between mangrove habitat with *Avicennia marina* and salt marsh with *Arthrocnemum glaucum* and *Halocnemum strobilaceum* in Alwagh on the Saudi Red Sea coast (upper), and in Al-Qerma Island, Arabian Gulf, Saudi Arabia (bottom).

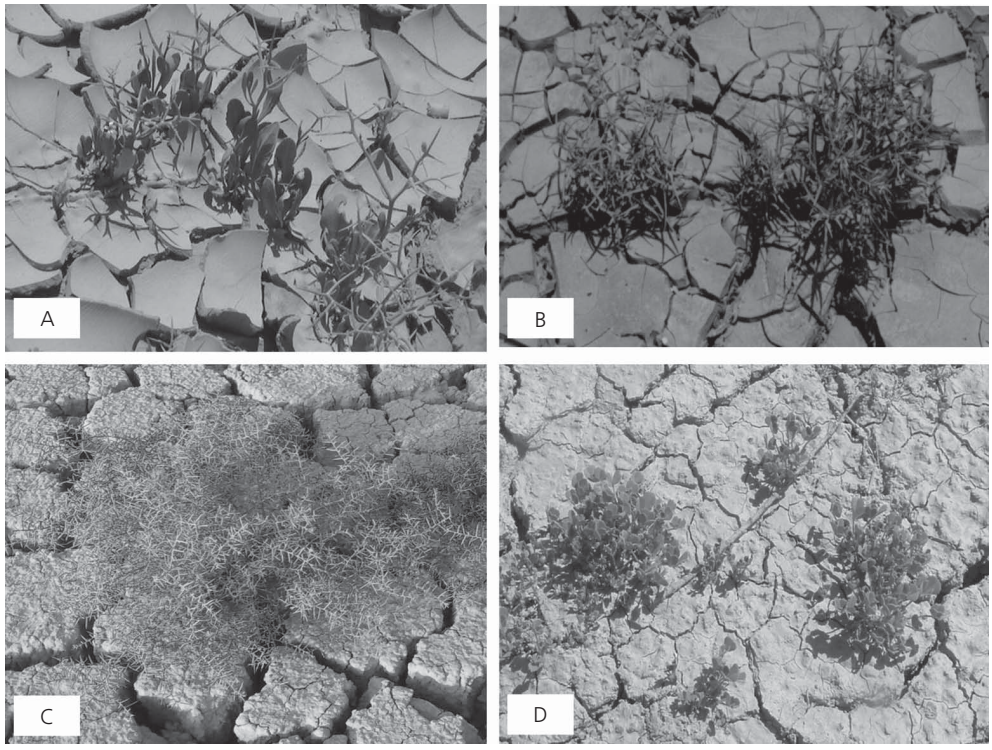



**Figure 2.2** Desiccation cracks in shallow depressions in arid deserts supporting the establishment of many species. (A) *Zilla spinosa*, (B) *Euphorbia retusa*, (C) *Alhagi graecorum*, and (D) *Trigonella stellata*. Photos A and B from Eastern Desert of Egypt; C and D from Central Saudi Arabia. [For a color version of this figure, see the color plate section, Plate 3]

## 2.4 Mountains and plateaux of the Middle East

Tall mountain ranges rise throughout the Middle East, with individual peaks reaching as high as 5800 m. These all play a significant role in the region's climate. Rainfall tends to be significantly greater on the windward side of a range than the leeward edge. This creates good conditions for growth—moist and fertile agricultural zones on the former, and arid zones with little vegetation, in the rain shadow of the latter.

Many mountainous areas in the Middle East are still geologically active, with frequent earthquakes, mudslides, and volcanic activity. These ranges have often become the relatively ill-defined boundaries between nations; they tend to impede travel and transportation and are less subject to political controls. Montane regions also provide an abundance of refugia, for both human minority communities and many plant species which once were more widespread but can no longer survive in the extreme environments at lower altitudes.

The Asir and Hijaz run along Saudi Arabia's Red Sea coast and are more than 3000 m at Al Sodah (see Figure 1.5). The Elburz Mountains[1] extend for almost 1000 km along Iran's northern border; these are jagged peaks that average over 2700 m, the highest being Mount Damavand, a dormant volcano (5670 m).

The Taurus chain extends across southern Turkey to the borders with Iraq and Iran. Mount Ararat is in the Eastern Taurus range, an extinct volcano and according to legend the peak where Noah's Biblical ark was landed. The Koroglu and Pontic ranges extend along the Black Sea coast of northern Turkey.

[1] Also rendered as Alborz, Albourz, Alburz, etc.

The Anatolian Plateau is a barren, arid plateau in central Turkey. Extreme temperatures in both summer and winter make agriculture and animal herding there challenging.

The rugged Hajar[2] Range in northern Oman rises to *c*. 3000 m. The low range of the Hadhramawt, in Yemen, averages about 1067 m, with its highest peak at 2440 m. Dasht-e Lut–the Lout Desert in eastern Iran—an arid, wind-blown desert—is completely surrounded by mountains. In the summer it is one of the hottest and driest spots on Earth; in some areas rain has never been reported.

The mountainous landscape in Sudan and the countries of the Horn of Africa supports most of the endemic flora and what remains of formerly more extensive forest vegetation. The mountainous landscape in southwestern Arabia and northeastern Africa is part of a formerly continuous phytogeographic entity sharing some 5000 plant species (see Sections 2.8 to 2.10).

## 2.5 Rivers

The Middle East is one of the most politically volatile parts of the world and many conflicts have been fought, at least in part, over water and its control. There are only a few major river systems and some temporary, seasonal streams. The Tigris and Euphrates[3] both originate in the eastern Taurus Mountains and are fed by snowmelt as they flow toward Iraq. The Euphrates flows from the Caucasus Mountains of Armenia, moving southwest across Turkey, then southeast through Syria and Iraq, ending in the waters of the Gulf. It joins with the Tigris in southern Iraq and continues as the Shatt al Arab. Overall, the Euphrates is some 3600 km in length. The Tigris arises in the mountains of southern Turkey, flows southeast through Iraq, and is almost 1900 km long. Many deep and wide valleys with only seasonal flow—wadis—occur across the region (see Sections 2.18 and 2.22).

The Nile River is a dominant feature for all aspects of life in the northeastern corner of Africa. Indeed it is the lifeblood to continued human existence, at least in Egypt and northern Sudan. The river runs south to north a distance of 6740 km, crossing 35° of latitude. It has two main tributaries: the Blue Nile, which begins near Lake Tana in Ethiopia; and the White Nile, flowing from Lake Victoria, one of the largest lakes in Africa. The Nile is essentially arheic—going great stretches with no further tributaries contributing to flow. Indeed no tributaries join below the Aswan High Dam. The total basin covers about 3.3 million km$^2$ and spans four different climate zones—including equatorial, tropical, subtropical, and Mediterranean, which vary greatly in their rainfall patterns (see Section 2.8.1).

The Jordan River begins on the southwest slopes of Mount Hermon (also Jabel Al-Sheik) on the northern part of the Golan Heights. From there the river drops and flows more slowly through Lake Huleh, a swampy area that was mostly drained in the 1960s. The river flows south into Lake Tiberias (Sea of Gallilee) and is joined downstream by its most significant tributary, the Yarmouk. The Jordan empties into the Dead Sea (with a salt concentration ten times that of the Mediterranean). Total length of the Jordan is 360 km and these days annual inflow to the Dead Sea is negligible (see Section 2.20).

The Sefidrud River in Iran is some 780 km long and the largest river flowing to the Caspian Sea in terms of sediment load, draining some of the Zagros Mountains and nearly all the Elburz belt, including much of central Iran (*c*. 62 000 km$^2$) (Kazanci and Gulbabazadeh 2013).

## 2.6 Libya

Libya extends over about 1.76 million km$^2$. About 90% of the country is the arid Libyan Desert, though there is extensive (*c*. 1770 km), fairly fertile, Mediterranean coastline where orchards (peach, apricot, apple, pomegranate, plum, olive, and grape) and other forms of vegetable, forage and cereal cultivation occur. Major landforms include large sand formations (the great sandy Sea of Calanscio and Rubiana Sand Sea in the east, and the Ubari and Murzuq Sand Seas in the southwest) as well as gravel and rocky desert depressions, saline soils, wadis and runnels, escarpments, and mountainous regions. Three phytogeographic regions are recognized: Tripolitania, Cyrenaica, and Fezzan.

[2] Also rendered as Hajjar.
[3] In Arabic the *Dijlis* and *Furat*, respectively.

Tripolitania covers the northwestern corner of the country and includes the Nafusah mountain region (see Figure 2.3). Cyrenaica is the largest, covering the entire eastern half of the country and including Jabal Al-Akhdar (the Green Mountains). The Fezzan includes the land south of Tripolitania and is mostly hot, dry desert, including the northwestern Sahara (Hegazy et al. 2011a).

The total number of vascular plants in Libya is estimated at 1750 species (744 genera/118 families) (Qaisar and El Gadi 1984), with some 75 endemics (*c*. 4%) recorded. The greatest affinity of the flora seems to be with eastern Mediterranean vegetation, rather than neighboring regions of North Africa (Boulos 1972; El-Kady 2000; Le Houérou 1997).

The major natural forest occurs at Jabal Al-Akhdar, in the northeast of the country; the region is estimated to include about 1000 vascular plants, with some 50 endemics (Kabiel et al. 2015 a, b). Other small patches of forest and woodland exist

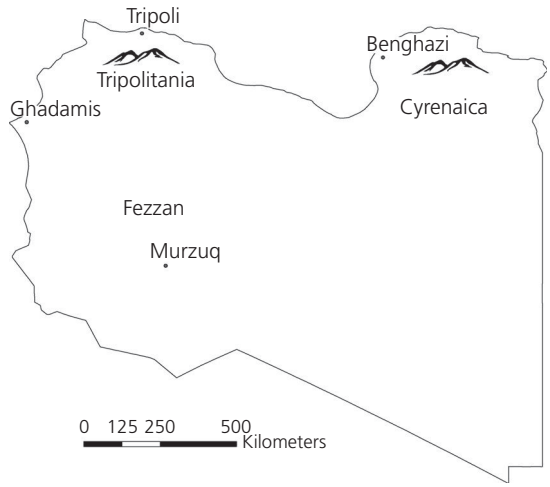



**Figure 2.3** Country map of Libya with major cities and mountain ranges.

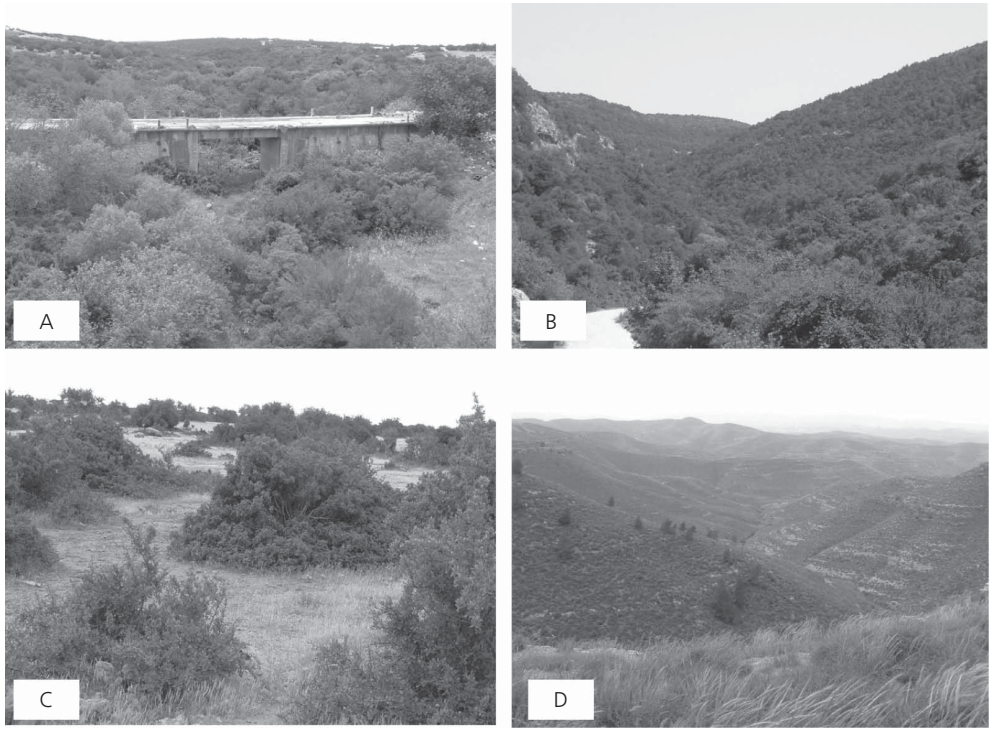



**Figure 2.4** Vegetation of Jabal Al-Akhdar (A, B, and C) in northeast Libya, and Jabal Nafusa (D) in northwest Libya. A = Wadi El-Aker, B = Wadi El-Kouf, and C = Birccess in Jabal Al-Akhdar; D = Meslatah National Park in Jabal Nafusa Mountains. [For a color version of this figure, see the color plate section, Plate 4]

around Jabal Nafusa, in the west (see Figure 2.4). Total forested area at Jabal Al-Akhdar was once *c.* 500 000 ha, but at least a third of this has long since been converted to agriculture. According to Al-Idrissi et al. (1996) and Hegazy et al. (2011a) the major botanical resources in the Al-Akhdar area include the following, distinguished by rainfall.

- Humid forests, confined to areas with > 600 mm annual rainfall; these occupy an area of about 200 km$^2$. Significant species include *Quercus calliprinos, Laurus nobilis, Arbutus pavarii, Olea europaea, Ceratonia siliqua, Quercus coccifera*, and *Cupressus sempervirens*.
- Sub-humid forests, in areas receiving between 400 and 600 mm of annual rainfall. Major species include *Juniperus phoenicea, Pinus halepensis, Olea europaea*, and *Arbutus pavarii*.
- Semi-arid forests, in areas receiving 300–400 mm of annual rainfall. The important species of this forest are *Sarcopoterrium spinosium, Pinus halepensis, Juniperus phoenicea, Pistacia lentiscus, Rhus tripartitum*, and *Periploca laevigata*.
- South Jabal Al-Akhdar forests, found in the zone north of the Benghazi plain and in the hills south of Jabal Al-Akhdar. This area receives 200–300 mm of rainfall. Major tree species here include *Rhus tripartitum, Pistacia lentiscus*, and *Periploca laevigata*.

Vegetation in the region spanning the Chad frontier is mainly restricted to wadis and sandy depressions (Hegazy 1999a). Common plants include *Centropodia forsskalii, Stipagrostis plumosa*, and *Monosonia nivea*. Desert savanna vegetation occurs in wadi terraces in the southeast of the plain, depressions, and escarpments. Among the common woody species are *Acacia raddiana, Balanites aegyptiaca*, and *Ziziphus mauritiana*, which grow interspersed with perennial grasses such as *Cymbopogon schoenanthus, Lasiurus scindicus*, and *Panicum turgidum*.

## 2.7 Egypt

Egypt is perhaps the most arid country in a very arid North Africa—though to be sure, this large country (*c.* 1.04 million km$^2$) includes Mediterranean biomes and the southernmost fifth of the country lies well within the subtropics. In the subtropical region rain seldom falls; average annual rainfall over the country is < 100 mm, and in the more extreme desert regions is < 50 mm. Temperatures are modulated by the effects of the Mediterranean and Red Seas. Higher elevations create lower temperatures in the highlands of southern Sinai, and along the Red Sea coast. Summers are generally hot, winters warm or mild.

El Hadidi and Hosni (2000) described three climatic provinces: First, a semi-arid Mediterranean coastal belt (Egypt has extensive coastline to the north and east, more than 2900 km along the Mediterranean Sea and the Red Sea); second, a northern inland arid belt running parallel to the coastal province (including the northern reaches of Egypt's Eastern and Western deserts, extending into Sinai and the Red Sea coastal plain along the Gulf of Suez); and third the arid southern province, which includes the Gebel Elba region and extends west to the Arabian Desert.

Egyptian plant ecology is in large part a product of its transcontinental location. Bordered by Libya, Sudan, and Israel (see Figure 2.5), there is a former land bridge (the Isthmus of Suez) between Africa and Asia which today is crossed by a navigable waterway, the Suez Canal. This connects the Mediterranean Sea with the Red Sea and Indian Ocean.

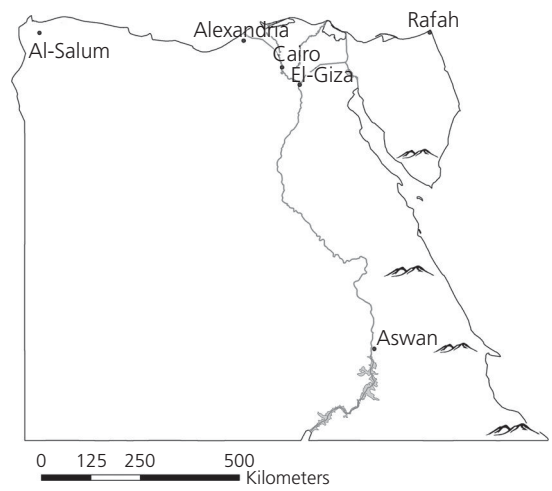



**Figure 2.5** Country map of Egypt with major cities and mountain ranges, and Nile River System.

**Table 2.1** Vegetation types, land area, and number of plant species in the phytogeographic regions of Egypt (El-Hadidi and Hosni 2000). Numbers in parentheses indicate the number of species restricted to that region.

| Phytogeographic region | Approximate area (km$^2$) | Number of recorded species | Vegetation types in each region |
|---|---|---|---|
| Mediterranean | 16 500 | 1060 (321) | Desert, Salt marsh, Sand dune, Farmland, and Aquatic |
| Deserts | 890 699 | 842 (91) | Desert, Salt marsh, Mountain, and Sand dune |
| Nile land | 25 000 | 712 (142) | Farmland and Aquatic |
| Oases | 10 900 | 348 (16) | Desert, Salt marsh, Sand dune, Farmland, and Aquatic |
| Mount Sinai | 28 000 | 540 (152) | Desert, Mountain, Farmland, and Aquatic |
| Red Sea | 11 000 | 284 (18) | Desert, Salt marsh, and Aquatic |
| Gebel Elba | 10 000 | 427 (80) | Desert and Mountain |
| Uweinat & Gilf El Kebir | 9500 | 72 (0) | Desert and Mountain |

The vegetation has been well reviewed by Zahran and Willis (2009). Freshwater aquatic vegetation is concentrated in the Nile and its extensive irrigation and drainage systems, and agricultural weeds are common in farmland. Wetlands of the northern lakes (Bardawil, Manzala, Borollos, Idku, and Mareotis) and the extensive man-made lake of the Aswan High Dam (Lake Nasser) as well as the Nile River system provide significant wetland habitat (e.g., Khedr and Lovett-Doust 2000, 2001). Mountain vegetation occurs along the Red Sea coast, in the mountains of southern Sinai, and in the Uweinats in the southwest Western Desert. Although these mountains are surrounded by extremely dry deserts, orographic rainfall provides a favorable climate for plant growth, particularly in the south Sinai Peninsula and Elba Mountains at the border with Sudan.

The Egyptian mountain flora typically includes the genera *Caralluma, Cocculus, Dodonaea, Dracaena, Moringa*, and *Rhus* (Zahran and Willis 2009). At high elevations in the Sinai (El-Maghera, Yelleq, and Halal), air temperatures are the coldest in Egypt, falling below 0°C in winter. Some species more typical of cold temperate regions also occur there, e.g., populations of *Juniperus phoenicea* continue to live in these refugia representing once-richer, more extensive juniper woodlands (see Section 2.10).

El-Hadidi and Hosni (2000) described the major phytogeographic regions in Egypt (see Table 2.1). Desert (> 90%), aquatic, and salt marsh habitats are the most common, and represented in nearly all the regions. At the same time deserts clearly present a formidable barrier to dispersal (see Chapter 7), as a total of some 820 species of the total flora (*c.* 2088) are confined to a few, specific regions.

Although Egypt has only half the landmass of Saudi Arabia it has approximately the same number of species (Boulos 1999–2005). Egypt's flora—like that of Saudi Arabia—contains much "monotypy" (i.e., orders, families, or genera which are represented nationally by single species). For example, of the 120 Angiosperm families represented in the country fully 30—a quarter—are monotypic (Khedr et al. 2002). Some 17 of these are also reported as either "very rare" or "rare" in terms of their distribution and abundance in Egypt (Tackholm 1974). The flora includes some 742 genera, of which more than half (354) proved monotypic (and over 70% of *these* species are reported as either rare or very rare in their national distribution and abundance).

Khedr et al. (2002) concluded that a relatively small number of families contained much of the

phylogenetic "information" represented in the flora of Egypt. At the next higher taxonomic level, of the 51 orders represented in the flora four are monotypic, each with a single species (Ebenales: *Euclea schimperi*; Podostemales: *Tristicha trifaria*; Haloragales: *Myriophyllum spicatum*; Orchidales: *Epipactis veratrifolia*). As regional targets for recognition and conservation, such monotypic order-level and family-level species are likely among the most significant single species, worthy of national protection. Intuitively, such "phylo-rarity" should increase the level of priority for species conservation. The importance of phylo-rarity seems under-valued as a measure of biological rarity, especially compared to the more traditional assessments based on a species' distribution and abundance. We call this more traditional concept "geo-rarity."

Based on extensive field studies some 457 Egyptian vascular plants have been identified as endangered, vulnerable, or rare and subject to the threat of extinction (El Hadidi and Hosni 2000). These included ten rare pteridophytes (e.g., *Equisetum ramosissimum, Ophioglossum polyphyllum, Pteris vittata, Anogramma leptophylla, Marsilea minuta*); two endangered gymnosperms (*Juniperus phoenicea* and *Ephedra pachyclada*); as well as fully 383 rare or endangered dicotyledonous angiosperms and 62 monocots.

## 2.8 Sudan: the Red Sea Hills and Jebel Marra ranges

Sudan was once the largest country in Africa in terms of area, at *c*. 2.5 million km$^2$ but recently split into two as northern and southern jurisdictions (see Figure 2.6). Topographically the country is a vast plain broken only by the Red Sea Hills in the east, the Marra range in Darfur to the west, the Nuba Mountains in South Kordofan, and the Imatong Mountains in the southeast of South Sudan, extending into Uganda. This latter range has an equatorial climate and once supported dense montane forests and a diverse wildlife.

Unfortunately, most of Sudan's former forest has been severely degraded by clearance and subsistence farming, leading to extensive erosion of steep slopes. In the south a vast swampy region, known as the Sudd, has grown up around the White Nile.




**Figure 2.6** Country map of Sudan with major cities and mountain ranges, and the Nile River system.

The Sudd is one of the world's largest wetlands and the largest freshwater wetland in the Nile basin. It was designated a Ramsar Wetland of International Importance[4] in 2006. Juba, the capital of South Sudan, represents the southernmost navigable point in the Nile system.

According to Bari (1968), desert covers vast areas of northern Sudan, comprising more than a third of the total area. There, annual rainfall is less than 75 mm. Woody vegetation around the Nile and seasonal watercourses includes mainly *Acacia tortilis, Ziziphus spina-christi, Boscia senegalensis*, and *Cadaba farinosa*. In southern areas where annual rainfall is

[4] The Ramsar Convention (on Wetlands of International Importance, especially as waterfowl habitat) is an international treaty for the conservation and sustainable utilization of global wetlands, intended to stem wetland loss, emphasizing the fundamental ecological functions of wetlands and including economic, cultural, scientific, and recreational values. It is named after the city of Ramsar, in Iran, where the convention was signed in 1971.

higher, species like *Indigofera bracteolata* and *Fagonia cretica* often occur. Trees along the southern Nile include *Acacia nilotica, A. seyal*, and *Faidherbia albida*.

Semi-desert makes up about another fifth of the country. There, annual rainfall ranges from 75 mm in the north to 300 mm in the south. The scrubby vegetation includes *Acacia tortilis* and *Maerua crassifolia* as dominants, and *Acacia radiana, Caparis decidua, Ziziphus spina-christi, Balanites aegyptiaca*, and *Salvadora persica* as sub-dominants.

Dry woodland savanna covers about another quarter of the country, with clay or sandy soils and annual rainfall between 300 and 800 mm. In clay areas the main species are *Acacia mellifera, Acacia seyal, Commiphora africana, Faidherbia albida, Boscia senegalensis, Balanites aegyptiaca, Sclerocarya birrea, Dalbergia melanoxylon, Combretum hartmannianum, Anogeissus leiocarpus, Boswellia papyrifera*, and *Sterculia setigera*. Major grasses include *Pennisetum glaucum, P. pedicellatum*, and *P. polystachium* (see Figure 2.7).

In sandy areas the major species include *Acacia raddiana, Faidherbia albida, Adansonia digitata, Acacia Senegal, Maerua cassifolia, Combretum cordofanum, Dalbergia melanoxylon, Albizia* spp., *Sclerocarya birrea, Terminalia* spp., and *Tamarindus indi*ca.

The flora has a significant southern tropical element, including equatorial and mountain species. There is also a more northern flora, appearing as widespread species in central and northern Sudan and the Red Sea coastal region. At least 300 Sudanese species are known to occur also in Saudi Arabia, with two-thirds of those occurring in the southern Hijaz Mountains (Hassan 1981a, b).

Among the richest regions floristically is Jebel Marra (3057 m), located in Darfur province (see Figure 2.6) and including nearly 1000 species (Wickens 1976). Other diverse and floristically rich

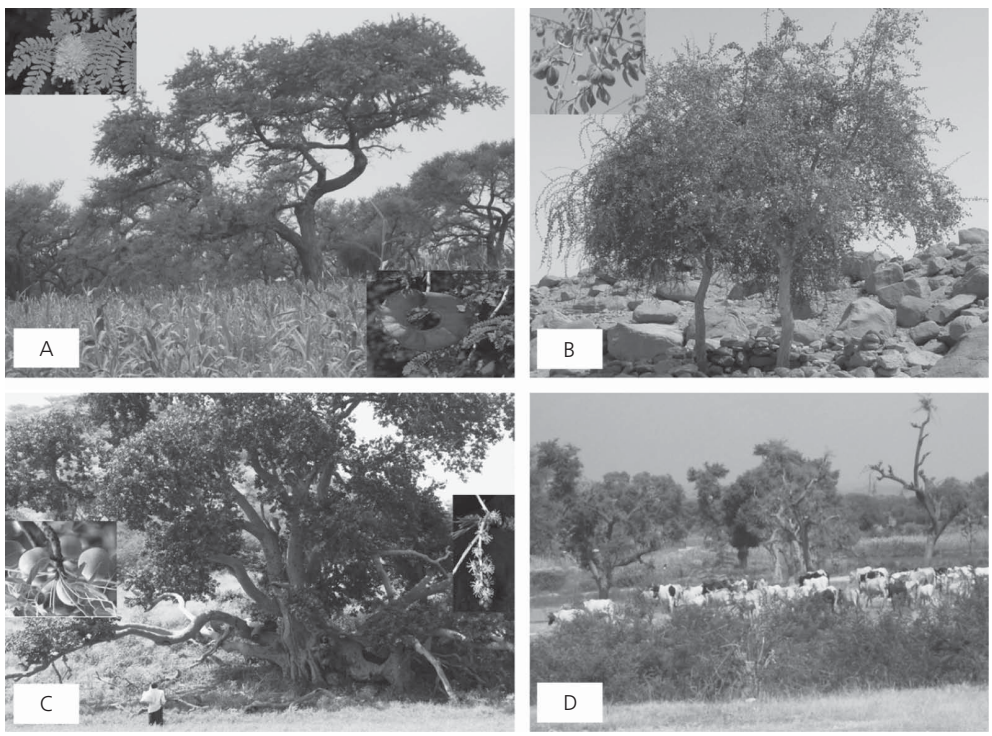



**Figure 2.7** Dry woodland savanna species. (A) *Faidherbia albida* (flowering and fruiting branches in the corners) in *Sorghum dura* fields. (B) *Balanites aegyptiaca* (fruiting branch upper left). (C) *Sclerocarya birrea* (flowers and fruits at the sides). (D) Grazing cows in woodland savanna. Major grasses include *Pennisetum glaucum, P. pedicellatum*, and *P. polystachium*. Photos from Wadi Saliah, Darfur, Sudan.

areas include the Imatong (3100 m), Dongotana (2600 m), and Dedinga regions, where more than 1400 species have been recorded (Sommerlatte and Sommerlatte 1990).

All these ranges support Afromontane[5] vegetation on their upper slopes. In the northeast of Sudan is the Gebel Elba region (1549 m), bordering the Red Sea between Egypt and Sudan and occupying a transitional zone between Afrotropical and other floristic realms. The mountain flora accounts for about a third of the country's total (Davis et al. 1994) though it occupies less than 1% of the country's area; it shows striking affinities with plants in the rest of the Middle East (and see Section 2.10).

Although some Afromontane enclaves are widely separated, they often share a similar mix of plant species, quite distinct from surrounding lowland regions. Podocarps—*Podocarpus* and *Afrocarpus*—are important characteristic trees here, along with *Prunus africana, Hagenia abyssinica, Juniperus procera*, and *Olea* species. In the higher mountains Afromontane woodland transitions into shrubland or grassland.

Two families—Curtisiaceae and Oliniaceae—are Afromontane endemics, and the Barbeyaceae is a near-endemic. Tree genera like *Afrocrania, Balthasaria, Curtisia, Ficalhoa, Hagenia, Leucosidea, Platypterocarpus*, and *Trichocladus* are all Afromontane endemics or near-endemics.

Jebel Marra itself includes many endemics, which Wickens (1976) suggested were all mostly relicts of formerly more widespread species. This flora includes many species otherwise more characteristic of distant centers of diversity, including the Ethiopian Highlands, the western Saharan Massifs, the Mediterranean coast, and southern Africa. This is especially striking and perhaps unexpected for such an isolated flora, located in the midst of an arid area far from other areas of high plant diversity (see Elsiddig 2007).

Thus herbs such as *Hypericum perforatum* from the Mediterranean, and *Swertia abyssinica* from the Afromontane flora of Ethiopia, Cameroon, and Nigeria are both known at Jebel Marra. The semi-aquatic and wetland species *Equisetum ramosissimum* is more characteristic of Asia and the Americas but occurs at Jebel Marra and nowhere else in Sudan or western Africa; it is also known from scattered localities in east and southern Africa. These are examples of species with *disjunct*, or discontinuous distribution, where the nearest relatives are all from very distant regions (see too Figure 5.2, and Sections 3.3 and 7.9).

Other important plants around Jebel Marra include trees typical of mixed savannas such as *Faidherbia albida, Afzilia abyssinica, Albizia zygia, Boswellia papyrifera, Khaya senegalensis*, and *Stercula setigera* (Elsiddig 2007; Wickens 1976). Trees like *Azanza garkeana, Vitex doniana, Combretum mole, Cussonia arborea*, and the figs *Ficus palmata* and *F. sur* are also present, perhaps more representative of other parts of Africa. Finally the flora of Jebel Marra is unusual for a Middle Eastern montane region in that it has so few conifers.

### 2.8.1 Sudd swamps

The Sudd region of swamps in the Nile basin of Sudan is one of the largest wetland areas anywhere (*c*. 5.7 million ha, or an area extending about 600 km by 600 km). The *sudd* (in Arabic "barrier"[6]) proved highly difficult to explore, and indeed the early quest to find the "source of the Nile" was only achieved by John Speke's expedition in 1858 when he bypassed the Sudd, approaching Lake Victoria and the upper reaches of the river from the central African coast across from Zanzibar. The habitat is a large, dynamic system of changing river channels, lagoons, and inundated areas, all interacting and highly variable in time and space (Petersen et al. 2007). The rich and productive vegetation of

[5] The Afromontane region includes the mountains of Africa and the southern Arabian Peninsula. The Afromontane regions of Africa are discontinuous, separated from each other by lowlands and are sometimes referred to as the Afromontane "archipelago" as their distribution is analogous to a series of islands. Afromontane forests are generally cooler and more humid than surrounding lowlands. The Afromontane archipelago mostly follows the East African Rift from the Red Sea to Zimbabwe, with some of the largest areas being in the Ethiopian Highlands.

[6] Like the *Hijaz*, but different. This barrier prevents the flow of water in the river. Similarly the Arabic for "dam" is *Sadd* (pl. *Suddoud*).

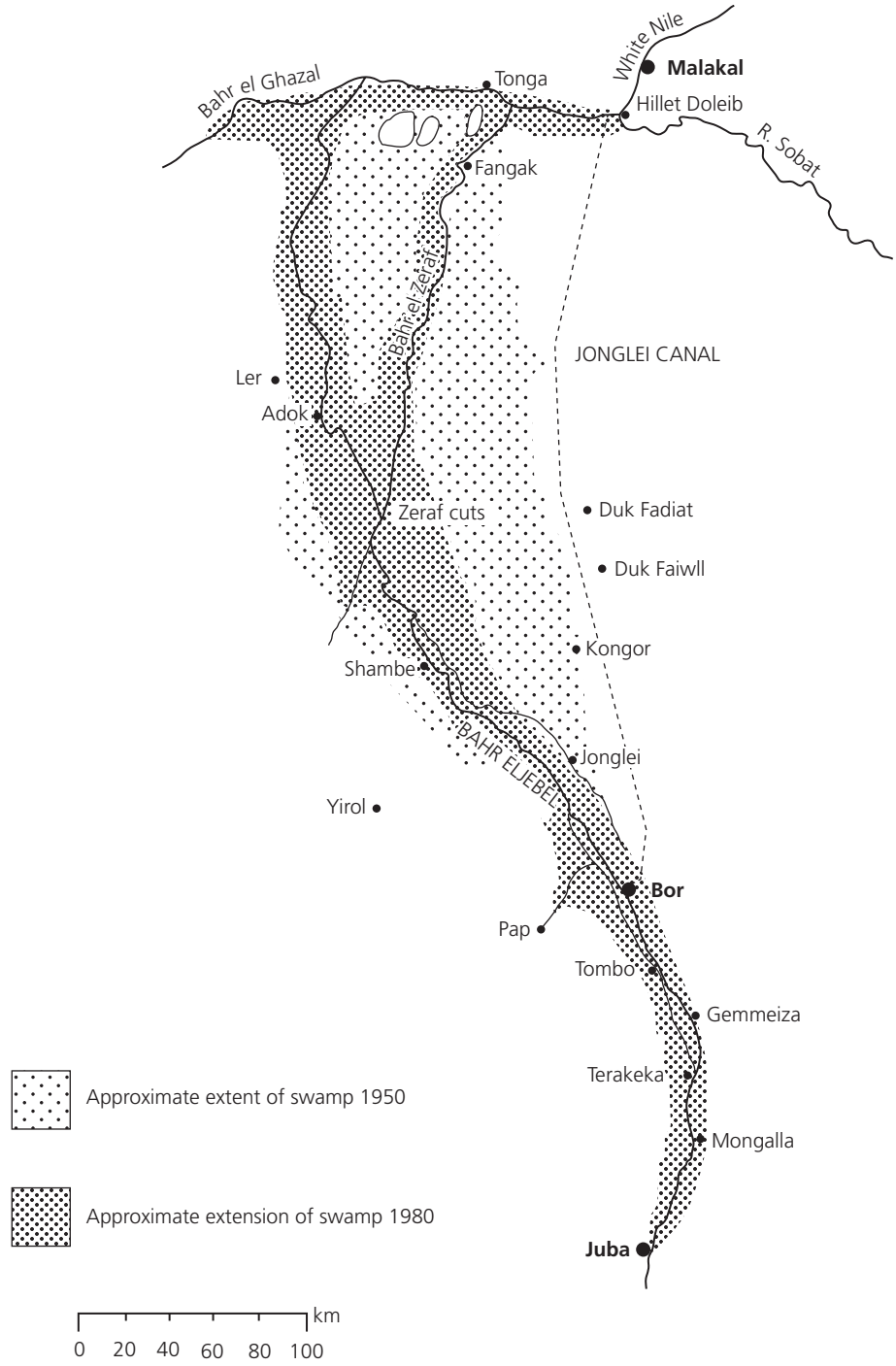



**Figure 2.8** Location map of the sudd and proposed Jonglei canal in Sudan (after Sutcliffe and Parks 1987). Reproduced with permission from Taylor and Francis.

the Sudd is significantly influenced by both water level and flow velocity.

Evapotranspiration in the swamps effectively loses much of the outflow from Lake Victoria. At present only about half the inflow of the White Nile at Mongalla emerges from the extended "tail" of the swamps (see Figure 2.8); the remainder has been lost to evapotranspiration (Sutcliffe and Parks 1987). Average annual regional rainfall is *c*. 850 mm, while open-water evaporation averaged 2150 mm/year. Evapotranspiration in areas covered with vegetation greatly exceeds that in open-water areas. As it enters the Sudd, the river carries large volumes of water laden with inorganics, nutrients, and salts but these mostly get filtered out by the sudd vegetation. These extensive wetlands also influence downstream flooding by absorbing excess water in time of high water availability. The Sudd area loses about half the water that enters it from the White Nile and almost all the water of the Blue Nile through evapotranspiration.

Hughes and Hughes (1992) reported that, since 1961, inflow to the Sudd had increased, presumably due to increased rainfall around Lake Victoria. The inflow was 26 831 billion $m^3$/year prior to 1960, but from 1960 to 1980 it averaged 50 324 billion $m^3$/year. The extent of the wetland consequently increased dramatically up to 1980, though more recent trends are not known.[7]

The dense sudd vegetation causes channel blockages resulting in impounding in many areas and increased flow in others. Sudd vegetation is generally distributed according to flooding depth and duration, with Lake Victoria outflow being the ultimate driver (Migahid 1948; Petersen et al. 2007).

Five major vegetation types have been described in the Sudd wetlands:

1. Open water vegetation: Dominated by free-floating plants like *Eichhornia crassipes, Lemna gibba, Azolla nilotica*, and *Nymphaea lotus* as well as floating rooted species like *Trapa*, and submersed vegetation, e.g., *Potamogeton* and *Ceratophyllum* species, found in both flowing water and lakes. Denny (1984) estimated the fresh mass of *Eichhornia* in the White Nile at *c*. 70 kg $m^{-2}$.
2. Permanent marsh vegetation: The deep open water in the marsh is surrounded by a permanent marsh zone (flooded throughout the year). Vegetation is dominated by emergents such as *Cyperus papyrus, Typha domingensis, Phragmites communis, P. karka, Oryza barthii*, and *Vossia cuspidata*. These species occupy areas where the depth of flooding does not exceed 1.5 m.
3. Seasonally flooded grasslands: These areas are flooded to varying extents by the river. During the rainy season the plains of this river section are often marshy and completely covered with luxuriant growth of tall grasses. Common species include *Oryza longistaminata* and *Echinochloa pyramidalis*, growing in areas where the flood depth is less than 1.2 m for at least a month a year, and soils remain water saturated through the rest of the year. Sedges, herbs like *Desmodium hirtum*, and other grasses such as *Sporobolus pyramidalis* are associated with the *Oryza* grassland. During the dry season semi-woody herbs, e.g., *Sesbania rostrata* dominate this wet grassland. As reported by Denny (1984), emergents like *Phragmites, Typha*, and *Cyperus* can reach well over 4 m; Denny estimated fresh mass of the shoots of *Phragmites* at 18.5 kg $m^{-2}$ and of *Cyperus* at 11.0 kg $m^{-2}$.
4. Rain-flooded grasslands (rain-fed wetland): These habitats are seasonally inundated and occur on seasonally waterlogged clay soil, and are also heavily grazed by livestock. It is dominated by *Echinochloa haploclada, Sporobolus pyramidalis, Phragmites, Sorghum*, and *Hyparrhenia ruffa*. These grasslands also serve as a local source of fibers collected for string and thatching.
5. Wooded grassland (scrubland): These are well-drained areas around the river's floodplains. They are rain-fed with open, mixed *Acacia* forest, several species of tree and shrub and a luxuriant growth of grasses. Trees are dominated by *Acacia seyal, A. sieberiana*, and *Balanites aegyptia*ca. This land is used for grazing, particularly during the wet season, and is often cleared for crop cultivation.

[7] The planned "Jonglei" canal project there (including a canal 75 m wide, depth between 4 and 8 m, and length >360 km) is considered one of the most important shared projects between Egypt and Sudan. The primary objective of this project is for the freshwater supply to bypass the Sudd wetland region; the goal is to ensure a flow of 4.7 billion $m^3$ of Nile water annually (with a minimum of 20 million $m^3$ per day) to be distributed between Egypt and Sudan.

## 2.9 Ethiopia and the Horn of Africa

In Section 1.10 we described the regionally restricted tree *Mimusops laurifolia* (Sapotaceae), present in Arabia and the Horn of Africa, i.e., Djibouti, Eritrea, Ethiopia, and Somalia (see Figure 2.9). *Mimusops laurifolia* can attain heights up to 40 m; it is the tallest and one of the most attractive indigenous trees in both Yemen and Saudi Arabia (see Figure 1.7A). Friis (1992) described *M. laurifolia* as part of an ancient phytogeographic element from Africa's central highlands, one which with many others expanded out of Africa into Arabia. Regrettably it seems that at all known sites for this species there is no longer any successful recruitment of juvenile trees (e.g., Friis 1981, 1992; Kilian et al. 2004). This means that these populations are not self-sustaining and suggests there is a great need for pro-active conservation initiatives, such as identification of the necessary conditions for the regeneration niche of this species and planting of juveniles that are offspring of the aging adult individuals around them.

The several countries of the Horn together possess one of the richest floras in the continent. The land is mountainous and geologically active. Afromontane upland habitats and Somali-Masai savannas have combined with other habitats to create a unique floral richness and high level of endemism (e.g., Davis et al. 1994; Friis et al. 2001; Thulin 2004). The dominant vegetation type is *Acacia-Commiphora* bushland, although variants such as evergreen bush, succulent shrubland, dry evergreen woodland, semi-desert grassland, and low-growing dune and rock vegetation also occupy portions of the region.

There are estimated to be more than 8000 species in the region of the Horn as a whole, of which about a quarter are regarded as endemic to the region due to isolation and resulting speciation (Friis

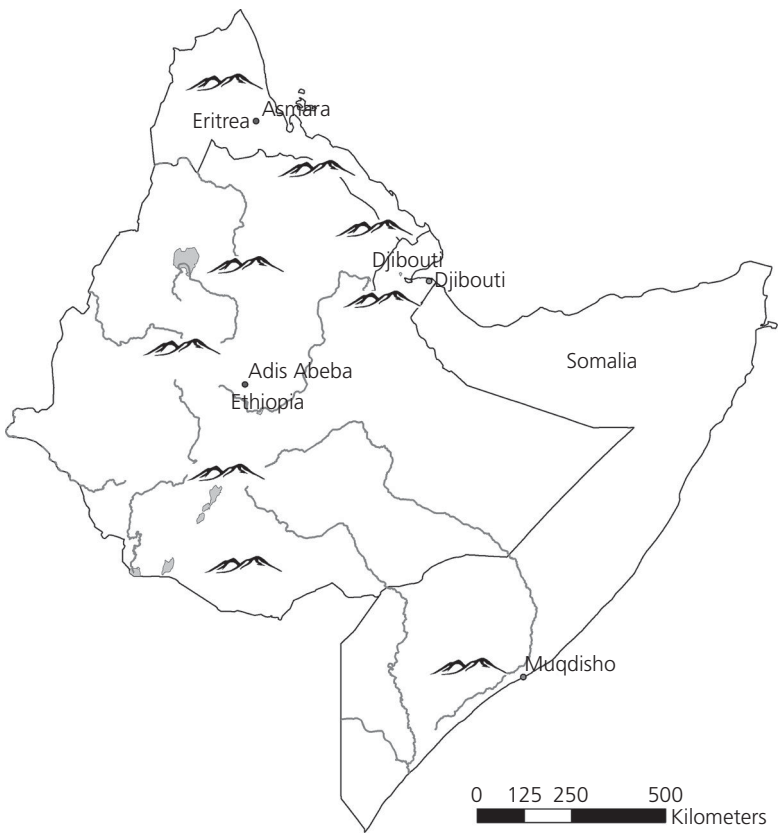



**Figure 2.9** Horn of Africa country maps of Ethiopia, Somalia, Djibouti, and Eritrea.

et al. 2003). The region is also rich in economically significant species, including many agricultural and medicinal plants and their relatives (Berhan 1991; Harlan 1969; Tewolde; Zohary 1970). Where they do still occur, trees are of particular significance in this region of otherwise low forest cover.

For historical reasons the plants of Ethiopia and Eritrea have been studied together (e.g., Edwards et al. 1995, 1997, 2000; Hedberg and Edwards 1989). Together these countries have a flora comprising some 7000 species (Vivero et al. 2005a), including an estimated 1100 trees (Demel et al. 2000). There are also 107 tree and 321 shrub species identified as endemic to Ethiopia and Eritrea. *The Red List of Endemic Trees & Shrubs of Ethiopia and Eritrea* recognizes 135 threatened species (31 trees and 104 shrubs), representing some 13% of the total woody plant flora there (Vivero et al. 2005b).

Environmental degradation and deforestation here have been taking place for centuries at least. High rates of habitat destruction due to natural hazards, civil conflicts, and subsequent human displacement and migration have been particular problems in recent years. With mounting demographic pressure on diminishing natural resources, trees are still being cleared at a great rate opening land up for agriculture and livestock production. Tree-cutting for fuel and lumber is also significant. More than 90% of the total energy consumed in the two countries comes from biomass, with wood the greatest component (Vivero 2001).

Ethiopia also has one of the largest populations of livestock in Africa; grazing pressure has intensified the rate at which the region's trees and shrubs are disappearing, largely as goat browse. In this region species extinction processes may be exacerbated by the narrow distribution and limited ecological tolerance of some of the plants, but it is also worth noting that this region has been affected by the presence of humans for far longer than anywhere else in the world, indeed since the origin of our species.[8]

[8] These are after all the Afari people (also known as the Danakil), living mainly in Eritrea, Djibouti, and the Afar region of Ethiopia, just down the road from where the earliest hominid remains were found, those of *Australopithecus afarensis*, nicknamed Lucy.

Much of the tiny country of Djibouti exists as a threatened, regional landscape—for example, the Forêt du Day—a degraded juniper cloud forest found in the Ditilou, Bankoualé, and Randah Valleys. The endangered endemic Bankoualé Palm, *Livistona carinensis*, coexists here with the critically endangered Djibouti Francolin, *Francolinus ochropectus*, a ground-dwelling pheasant whose natural habitat is high altitude, subtropical or tropical dry forest, composed primarily of African juniper trees, *Juniperus procera*. These forests are in widespread regional decline so the francolin is found in other habitats, such as box-tree (*Buxus hildebrandtii*) forest.

According to Fisher et al. (2009) there is evidence of heavy grazing everywhere, both within and beyond the forest—with an abundance of cattle, camels, donkeys, and goats, often untended. The Forêt du Day is a diminishing resource—it has shrunk from 2300 ha in 1949 to about 900 ha more recently. Although large-scale clearing of timber trees for export or for local house construction has stopped, some cutting of both *Juniper* and *Buxus* persists. Fisher et al. recommend an ecosystem approach to conservation of the forest, with special measures to address the fragile conditions of both the francolin and juniper.

*Livistona carinensis* is an Indo-Malayan plant element, native in Djibouti, northern Somalia, and Yemen (Kilian et al. 2004), and classified in the IUCN Red List as Endangered. It is also recognized as the largest indigenous palm tree in the adjacent Arabian Peninsula (see Section 3.4). At least 90% of the < 2000 remaining individuals occur in Yemen (Kilian et al. 2004).

## 2.10 The Red Sea and Gulf of Aden Basins

The Red Sea Basin occupies an area of *c*. 810 000 km$^2$, including essentially all of the Red Sea coastal plains (210 000 km$^2$) and the seaward slopes of highlands bordering them on both sides (600 000 km$^2$) (see Figures 1.2 and 2.9). The southwestern Arabian Peninsula and northeastern region of Africa are part of a common phytogeographic entity, sharing some 5000 plant species. The highlands of Yemen and Saudi Arabia alone

have more than 2000 species (Davis et al. 1994). Several different labels have been suggested for this phytogeographic region, including Eritreo-Arabian, Somali-Masai, and Somalo-Arabian (see Le Houérou 2003).

The territory shows a great deal of unity in both the nature of the flora and the kinds of plant communities found in both highlands and lowlands. The highlands on both sides of the Red Sea share many Mediterranean-like vegetation types, including sclerophyllous evergreen forest, bushland, and scrubland (Hegazy and Amer 2002). According to Le Houérou, this is largely attributable to retention of vestigial *Podocarpus gracilior* and *Juniperus procera* primeval forests. Earlier Le Houérou called these sclerophyll formations "false garrigues" or "pseudo-garrigues" and regarded them as physiognomically reminiscent of, and botanically akin to, Mediterranean shrublands (garrigue, maquis, etc.).

Le Houérou (2003) described a flora of more than 330 montane species, predominantly sclerophyllous evergreens. Of these, *c*. 80% were present in Ethiopia, 70% in Somalia and Eritria, 60% in Yemen and Djibouti, 50% in Oman (Dhofar region) and Saudi Arabia, and *c*. 30% in Sudan and Egypt's Nubian Mountains. In addition to these sclerophyllous and succulent glycophyte[9] species (i.e., salt-intolerant plants), there are at least another 3000 non-sclerophyllous savanna species present on both sides of the Red Sea, including more than 20 species of *Acacia*, and at least 100 different halophytes (Le Houérou 2003).

Le Houérou noted in particular the presence of a large number of succulent glycophytes in this flora, particularly striking cactoid and coralloid tree and shrub spurges, many of them endemic *Euphorbia* (>30 species: especially subgenera *Diacanthium, Pachychladium, Tirucalli*, and *Tithymalus*). Also in this flora are many other endemic CAM[10] species, such as *Caralluma* spp. (>20), *Aloe* (>20 endemic species in Saudi Arabia alone), *Kalanchoe* spp. (>10), *Ceropegia* (10), *Huernia* (six), *Sarcostemma* (five), *Duvalia* (four), *Rhytidocaulon* (four), and many other Asclepiadaceae, Crassulaceae, Agavaceae, and Aloeaceae, as well as *Dracaena ombet* (= *D. schizantha*), *D. serratula, D. cinnabari, Pandanus odoriferus, Sansevieria* species, and *Kleinia* species.

Another feature of this "Somalo-Arabian" flora is the remarkable expansion of Burseraceae, many highly aromatic species, particularly the kind of incense known as frankincense, *Boswellia sacra* (= *B. carteri*) and *B. frereana* (which is a Somali and eastern Ethiopian endemic), and other more common species such as *B. papyrifera*. Le Houérou pointed out this latter species is common in the lowlands of Kenya, Ethiopia, and Djibouti as a pioneering species of recent lava flows (though it is not a source of incense). The favored commercial frankincense species (largely *B. sacra* and *B. frereana*) live in the fog and mist zones of the Arabian Peninsula (especially the mist valleys of Hadramaut and Dhofar), and in the mid-elevations of the huge escarpment overhanging the Red Sea in Somalia (Le Houérou 2003).

Among other aromatic Burseraceae, it is difficult to estimate the number of *Commiphora* (or myrrh species) in this region with certainty, but there are at least 80 of them. According to Le Houérou there are over 70 species of myrrh in Somalia alone; Kenya has *c*. 45, South Africa 35, southwestern Arabia *c*. 12, Ethiopia 10, Djibouti 12; but only two species exist in the three million km$^2$ of the Sahel, between Khartoum and Dakar.

## 2.11 Yemen (and Socotra)

*Arabia felix*—literally "Lucky" or "Fortunate" Arabia—was the name the Romans gave to the lands on the southern fringe of the Arabian Peninsula, some of which much later became the Aden Protectorate and, most recently, Yemen. Today much of that southern plateau is arid desert, but at the same time there were many reasons for the Romans to believe southern Arabia was indeed a "blessed land" in particular in terms of valuable plant spices, some produced locally and others imported from India and the Horn of Africa. A

[9] "Glycophyte" includes any plants that are not salt-tolerant and which are easily damaged by high salinity; this includes the large majority of all plant species. Typically used in contrast with "halophyte" or salt-tolerant species.

[10] Crassulacean Acid Metabolism, see Section 5.5.

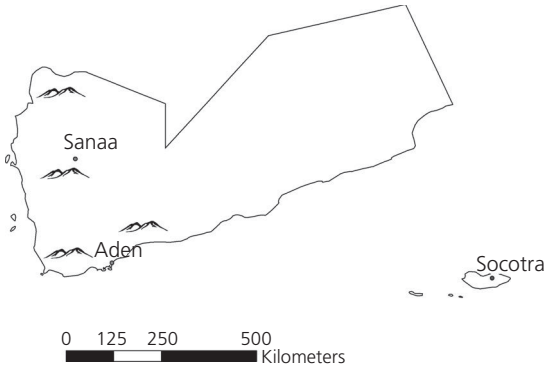



**Figure 2.10** Country map of Yemen with major cities and mountain ranges.

general lack of knowledge about the country persists today.[11]

Yemen lies at the southwestern corner of the Peninsula, with Saudi Arabia to the north, Oman to the east, the Red Sea to the west, and Gulf of Aden to the south (see Figure 2.10). A number of Red Sea islands, including the Hanish Islands, Kamaran and Perim, as well as the large and floristically highly significant Socotra, in the Arabian Sea, also belong to Yemen. Many of these islands (but not Socotra) are volcanically active, reflecting ongoing tectonic events associated with the movement of the Arabian plate and lava flow through the thin crust in the region, as the sea and gulf grow wider.

At *c*. 525 000 km$^2$, Yemen is roughly a quarter the size of Saudi Arabia yet still vast. Ecologically there are four main regions: the coastal plains in the west and south, the western highlands, the eastern highlands, and the Rub' al-Khali desert in the east.

The Tihamah[12] ("hot lands" or "hot earth") make up the very arid western coastal plain, composed of extensive, large crescent-shaped sand dunes. Despite a lack of rainfall, the presence of many tidal lagoons makes the region marshy (and a breeding ground for malaria-bearing mosquitoes). Evapotranspiration is so great that streams from the highlands never reach the sea, though they do contribute to extensive fresh groundwater reserves, which are used agriculturally.

The Tihamah ends abruptly at the escarpment of the western highlands. This area, today heavily terraced for agriculture, receives the highest rainfall in Arabia, rapidly increasing from *c*. 100 mm/year at the leading edge of the escarpment to *c*. 750 mm in Ta'izz, and over 1000 mm in Ibb (Vogel 1987). This is again a direct benefit of orographic rainfall, where winds from the sea cool as they move up the seaward slope and can no longer hold moisture.

The southern mountains of the Arabian Peninsula stretch along the southern coast as far as eastern Dhofar in Oman, where they end in the dramatic escarpment of Jabal Samhan. In the Hadhramout region they culminate on the seaward side in elevations over 2000 m. Further inland they decline more gradually, dissected by a great labyrinth of gorge-like wadis leading into the desert of the Rub' al-Khali. In promontories along the coast, seafacing escarpments form the magnificent "fog oases" or cloud forests (see Section 1.4) (Miller 1994a; in German the "*Nebeloasen*" of Troll, 1935). These shelter a mesic, tropical flora, rich in paleo-African plant elements (*sensu* Zohary 1973). Norbert Kilian and his colleagues have documented this important, endangered flora (e.g., Table 2.2). Kilian et al. (2004) point out that these grand wadi systems often end in breath-taking, vertical falls ranging from several hundred to nearly 1000 m. Such sharp relief

[11] What led to the name was the great wealth and importance of *Arabia felix* in the ancient world. This came very largely from *plants* and the region's near-monopoly of the trade in cinnamon and other valuable spices. In earlier centuries this civilization—known as *Saba* in Arabic and Sheba in English—was exceptionally wealthy. Saba's riches came from its role as a trans-shipment point for Eastern luxury goods being traded to the West, and from the collection and sale of two rare and expensive aromatic resins—frankincense and myrrh—highly desired in the ancient world. (It was of course this same strategic location in the world between East and West, and particularly as the gateway to the Suez Canal, that Great Britain capitalized on from 1838 until 1963, when it controlled the area with military bases in the Aden Protectorate. The canal was nationalized by Egypt in 1956; in 2014 Egypt began digging a second, parallel canal to increase through-flow).

The aromatic resins were used by ancient Egyptians in embalming, and burned as offerings to the gods of East and West. Moreover they were valued as medicines from first-century Rome to eleventh-century Persia, and perfumed the state occasions of royal and imperial courts throughout the known world, well into the early Middle Ages. Yet the plants producing these resins grew, almost exclusively, in southern Arabia and the Horn—and were a vital factor in the prosperity that earned the area its name.

[12] Also Tihama.

**Table 2.2** Vegetation of the Maderan fog oasis in the Jabal Urays range, Yemen. Representative plants of the upper escarpment and lowermost plateau region (*c.* 800–1200 m)—the region most frequently and intensively affected by the cloud bank; the vegetation is a semi-evergreen Afromontane *Olea europaea* ssp. *cuspidata*—*Tarchonanthus camphoratus* woodland. (Data from Kilian et al. 2004.)

| | |
|---|---|
| **Representative tree species** | *Rhamnus staddo* var. *deflersii* |
| *Acokanthera schimperi* | *Ruellia grandiflora* |
| *Cordia monoica* | *Ruellia geminiflora* |
| | *Ruellia patula* |
| *Euclea schimperi* | *Ruttya fruticosa* |
| *Olea europaea* ssp. *cuspidata* | *Sageretia thea* |
| *Tarchonanthus camphoratus* | *Tarenna graveolens* subsp. *arabica* |
| *Searsia flexicaulis* | |
| *Rhus flexicaulis* | **Climbers** include: |
| *Rhus glutinosa* ssp. *abyssinica* | *Coccinia grandis* |
| | *Jasminum grandiflorum* ssp. *floribundum* |
| **Major shrubs** | |
| *Adenia venenata* | **Herbs** include: |
| *Dodonaea angustifolia* | *Asphodelus tenuifolius* |
| *Dyschoriste longicalyx* | *Crossandra johanninae* |
| *Euphorbia cuneata* | *Geranium trilophum* |
| *Forsskaolea griersonii* | *Geranium ocellatum* |
| *Grewia tembensis* | *Iphigenia olivieri* |
| *Grewia trichocarpa* | *Justicia flava* |
| *Hildebrandtia africana* ssp. *arabica* | *Launaea massauensis* |
| *Jatropha spinosa* | *Scadoxus multiflorus* |
| *Lantana viburnoides* | *Silene schimperiana* |
| *Maytenus senegalensis* | *Viola cinerea* var. *stocksii* |
| *Pavonia somalensis* | *Volutaria albicaulis* |

Nearby gorges included others trees, such as *Clerodendrum myricoides, Ficus ingens, Mimusops laurifolia, Nuxia oppositifolia*, and the climbers *Clematis hirsuta, Dregea schimperi, Ipomoea ficifolia*, and *Rhoiocissus revoilii*. Also noteworthy was *Adiantum balfourii*, a rare fern and regional endemic, also known from Socotra and the Horn of Africa region.

features and the nearby ocean make the area an outstanding botanical and ecological resource.

Unfortunately knowledge about the flora of Yemen as a whole is scattered, and little integrative work has yet been carried out (but see, e.g., Al-Khulaidi et al. 2010; Gabali and Al-Gifri 2008; Kilian et al. 2002; Miller and Cope 1996–2008; Wood 1997). In particular, long periods of drought have prevented botanists from collecting annuals and short-lived species from the field, so there is perhaps a bias in terms of recognition of perennials, especially adult trees (and see Chapter 10).

According to Al-Khulaidi et al., a total of about 2800 species have been identified in the country, belonging to 173 families and 1006 genera, and of which some 415 species are endemic. Dominant families include the Poaceae, Asteraceae, Euphorbiaceae, Lamiaceae, and Scrophulariaceae. The largest genera include *Euphorbia* (>40 spp.), *Indigofera* (>28), *Caralluma* (>26), *Heliotropium* (>23), *Aloe* (>23), *Crotalaria* (>20), *Eragrostis* (>20), *Sporobolus* (>20), *Acacia* (>18), also *Cleome, Pulicaria, Barleria, Pennisetum, Stipagrostis, Tephrosia, Solanum, Brachiaria, Commicarpus, Fagonia*, and *Cyperus*.

The qat[13] plant (*Catha edulis*, Celastraceae) is an evergreen shrub whose leaves and buds are used today as a stimulant by many Yemeni. It contains cathinone, an amphetamine-like compound. A remarkable 40% of the country's water supply is estimated to go toward irrigating qat, with production recently reported increasing by 10–15% per year (Filkins 2011). The plant is also widely used in Ethiopia and elsewhere (Lemessa 2001; and see Box 9.1).

### 2.11.1 Endemism in Yemen

According to various authors (Davis et al. 1994; Gabali and Al-Gifri 2008; Groombridge 1992), about 12% of mainland Yemeni species are estimated to be endemic (on the island of Socotra the figure is even higher, at 37%). Five major mainland Yemeni centers of endemism have been identified (including at least four endemic genera).

1. Hujariyah, a mountainous area south of Ta'izz: After Socotra it is the richest location for plants, with 99 national endemics (Miller et al. 1991), and at least eight species that are restricted to this region (including *Kickxia woodii, Crotalaria squamigera, Centaurea yemense*, and *Blepharispermum yemense*).
2. Ibb: These western escarpment mountains also have many endemics, including *Acacia jonwoodii, A. yemenensis, Gymnocarpus dhofarensis, Croton confertus*, and *Pulicaria nobilis*, found mainly around Sumara Pass at altitudes above 2800 m.
3. Hadhramaut Jol: This is at the top of the large limestone escarpment, on a plateau that is dissected by many wadis. Regional endemics include *Anogeissus bentii, Schweinfurthia latifolia, Cucumus canoxyii, Euphorbia applanata*, and *Echidnopsis globosa*.
4. Jabal Areys: A volcanic massif that is frequently mist-covered, lying 150 km east of Aden on the southern coast. Many endemics are found here, including *Cystostemon kissenioides, Salvia areysiana*, and *Kleinia deflersii*.
5. Jabal Fartak or Ras Fartak: This is the mountainous part of Al-Mahra on the southeast coast, Gulf of Aden. It receives significant dew condensation at night supporting many endemics; these include the Combretaceae tree species *Anogeissus dhofarica* and *A. bentii*; as well as *Aloe dhofarensis, A. mahraensis, Blepharis dhofarensis*, and the genus *Isoleucus*. Jabal Fartak is also one of the last recorded sites in Arabia having remnants of the ancient valley-forests which formerly covered much more of the southern peninsula (see Section 1.10).

In summary, one of the richest regions for plant endemism in Arabia is the mainland of Yemen. The island archipelago of Socotra stands in a class of its own (see Section 2.11.2). In terms of overall plant diversity, Hujariyah to the south of Ta'izz is possibly the most species-rich area in all Arabia. Despite the fact we know of the region's importance, to this point the flora of Yemen has not been adequately inventoried and even the distributions of recognized endemics, though recorded, are little known.

### 2.11.2 Socotra

The Socotran archipelago is one of the most isolated landforms on Earth that is a fragment of the earlier continent of Gondwana. Despite this modern isolation, in past millennia Socotra was a cosmopolitan trading center for Greeks and Romans, Arabs and Indians—Boggs (2009) described it as a kind of "Dubai of the ancient world." The archipelago is believed to have become separated during the early Miocene, as a result of the same set of rifting events that opened the Gulf of Aden, to the northwest (Powers et al. 1966; White and Law 1969). Suffice that Socotra has been a separate island for tens of millions of years, having its ancient flora and fauna augmented by further plant propagules, flying birds, and insects transported by wind and water ever since.

The archipelago is in the Indian Ocean, slightly closer to the eastern tip of the Horn of Africa than to the southern Arabian Peninsula (see Figure 2.10). It consists of the main island of Socotra[14] (3625 km$^2$),

[13] Also khat; see Box 9.1.

[14] The name is thought to be derived from the Arabic "suq qatir" meaning market-place of dragon's blood, after the brownish-red resin of the endemic dragon's-blood trees (*Dracaena cinnabari*) (see Section 3.3). Socotra is also sometimes called the Island of Enchantment (or Bliss, Tranquility, Phoenix, or Jinn . . .). The old Egyptian name of Socotra is "Pa"-anch' or "Panchaia" symbolizing an island paradise brimming with spices, and perhaps too the mythical Land of Punt (Grant 2005).

with at least 30 000 inhabitants, plus the three smaller islands of Abd al Kuri, Samhah, and Darsa, and a number of uninhabited rocky outcrops that attract roosting seabirds. The large island of Socotra has three main parts: narrow coastal plains, a limestone plateau permeated with large karst caves, and the ancient granitic Hagghier Mountains, rising to 1500 m.

In 2008, Socotra became the fourth region in Yemen to be included on UNESCO's World Heritage list. According to UNESCO,[15] the site is of global importance because of its rich biodiversity. It has a very distinct flora and fauna: 37% of Socotra's 825 plants (and as many as 90% of its reptiles and 95% of its land snails) are endemic, found nowhere else on Earth. The archipelago includes at least three critically endangered, and 27 endangered plant species (Miller and Morris 2004). In terms of island biogeography and rates of endemism, only Madagascar, Hawaii, and the Galapagos have comparably higher rates than Socotra.

### 2.11.3 The Socotran flora

With over a third of its plants endemic (Mies 1998; Miller and Morris 2004), the almost inaccessible archipelago has attracted botanical expeditions since the late nineteenth century, mainly because of the abundance of these fascinating "living fossils" or "paleoendemics" whose closest relations have for the most part already gone extinct on the African and Arabian mainland (Balfour 1888; Mies 1998; Popov 1957).

Mies (1998) showed how closely the Socotran flora resembled that of the neighboring Eritreo-Somalian and Arabian mainlands. *Cocculus* (Menispermaceae), *Grewia* (Tiliaceae), *Trigonella* (Fabaceae), and *Helichysum* (Asteraceae) are all examples of Socotran genera sharing a wide palaeotropical distribution. The Myrrhs (*Commiphora*) and *Acacia* species are all abundant in the island's bushland and adjacent areas. Likewise, the frankincense genus (*Boswellia*) includes Socotran species that are also found in northeastern Africa and Arabia.

[15] http://whc.unesco.org/pg.cfm?cid=31&mode=table

Mies also described a series of vicariant[16] taxa linking Socotra and other, more disjunct regions. He showed that the island's flora relates closely to those of ecologically comparable zones in northeastern Africa/Arabia, South Africa, Madagascar, and India, and argued these species were all common descendants of a more ancient, continuous, and arid, southern Tethyan[17] belt of vegetation. We consider this further in Section 3.3.

In general, although there is a sequence of vegetation zones from the coast to the peaks of the Hagghier range, true high-altitude "forest" is not present. The shrubby vegetation of the highlands includes Euphorbiaceae, Rubiaceae, Buxaceae, Hypericaceae, and other Palaeotropical families. At high altitudes only lichens are found. The dry coastal lowlands are mainly covered with different species of "featherduster bush" mostly Euphorbiaceae and Acanthaceae; as well as shrubs like *Croton socotranus, Jatropha unicostata*, and *Trichocalyx* species, all forming thickets of umbrella-shaped shrubs (De Sanctis et al. 2012; Mies 1998).

Within the plains vegetation and lower limestone slopes many succulent shrubs occur, including *Cissus hamaderohensis, C. subaphylla* (Vitaceae), *Caralluma socotrana* (Asclepiadaceae), and many *Euphorbia* species. The vegetation of the lowlands and plains has been heavily impacted by overgrazing from goats and sheep (Mies 1998).

On the slopes, vegetation varies according to rock type. In the lowlands, on limestone gravel plains and rocky slopes, Mies found many examples of

[16] Vicariance is a process by which the geographical range of an individual taxon (or whole biota) is split into discontinuous parts by the formation of a physical barrier to gene flow or dispersal. Vicariance of whole biotas occurs following large-scale events such as the uplift of a mountain chain, or separation of continental landmasses through geo-tectonic activity. (See too Sections 3.3 and 7.9.)

[17] The Tethys Ocean is a paleo-ocean that existed between the two "super continents"—Gondwana and Laurasia—during much of the Mesozoic, before the opening of the Indian and Atlantic oceans during the Cretaceous period. It is also referred to as the Tethys Sea. (The name comes from the Greek mythological figure Tethys, sister and consort of Oceanus, and mother of all the great rivers and lakes of the world.) See too Chapter 3.

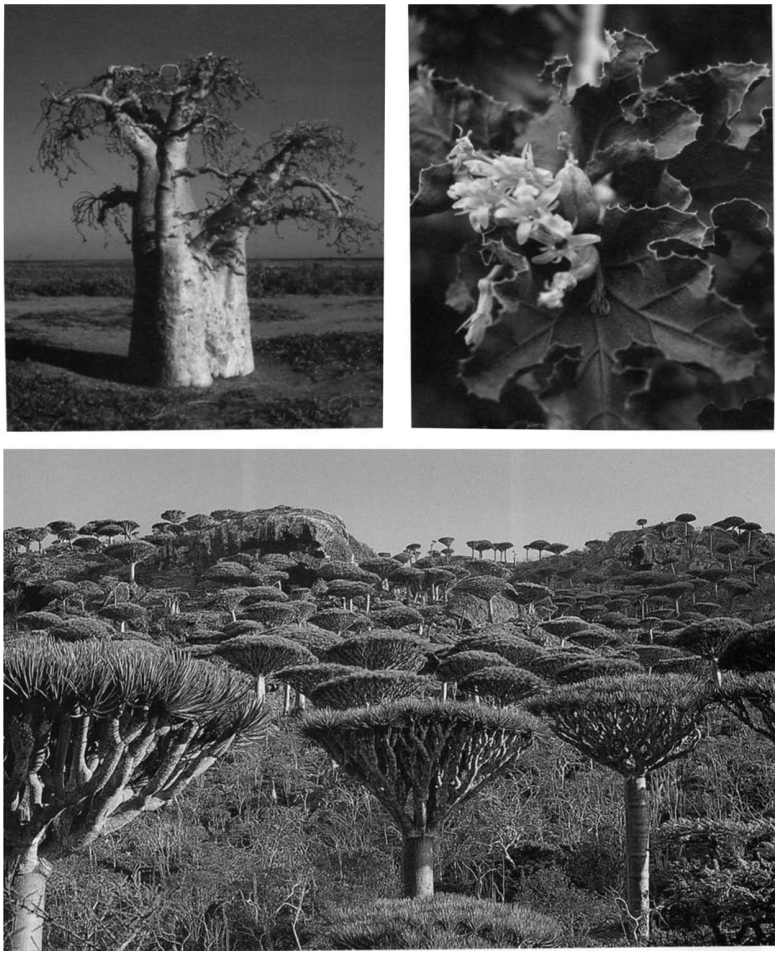


**Figure 2.11** The cucumber tree *Dendrosicyos socotrana* (upper left) and flowering-fruiting branch (upper right), and the dragon's blood tree *Dracaena cinnabari* (bottom) in Socotra island archipelago. Reproduced with permission from A. Miller. [For a color version of this figure, see the color plate section, Plate 5]

the famous "caudiciform succulents",[18] including the bottle-trees ("pachycaul" succulents) *Adenium socotranum* (Apocynaceae), *Dorstenia gigas* (Moraceae), and *Dendrosicyos socotrana* (the cucumber tree, Cucurbitaceae) (see Figure 2.11). Mies reported that whereas *A. socotranum* and *D. gigas* were both still fairly abundant at the time of his study, the cucumber tree was already fast losing ground, largely due to preferential grazing by goats and sheep and the practice of herders using these trees as "drought fodder," feeding it to livestock during times of extreme drought.

*Dracaena cinnabari*, the iconic Dragon's blood tree, a fascinating new member of the Asparagus family (see Figure 2.11) occurs frequently at elevations above 400 m (see, too, Section 3.3). According to Mies, the inland valleys are rich in other species with striking arborescent or tree-like forms, including *Ziziphus* spp. (Mimosaceae), and endemic trees in the Burseraceae, like *Boswellia* spp. and *Commiphora* spp., in addition to *Euclea* spp. (Ebenaceae),

[18] The caudex (plural: caudices) of a plant is a specialized stem, particularly a basal stem structure from which new growth arises. The term "caudex" is often used to describe the stem base of plants that have a different stem morphology from the typical dicotyledonous stem, such as palms, ferns, and cycads. In the Middle Eastern context the related term *caudiciform*, literally stem-like, is sometimes used to refer to pachycauls, or thick-stemmed trees. Pachycauls are succulent woody plants with a disproportionately thick trunk for their height, and few branches.

*Rhus thyrsiflora* (Anacardiaceae), and *Sterculia africana* ssp. *socotrana* (Sterculiaceae).

Dwarf forest survives in the highlands of the Hagghiers above 800 m, composed of Box trees *Buxus hildebrandtii* (Buxaceae), *Cephalocroton socotranum* and *Euphorbia socotrana, Hypericum* spp. (Hypericaceae), *Ficus socotrana* (Moraceae), and understory shrubs such as *Gnidia socotrana* (Thymelaeaceae). Mies described the peculiar *Cocculus balfourii* (Menispermaceae) at this altitude, with its specialized "cladodes" forming thorny stem clusters, essentially impenetrable to livestock seeking the more delicate herbaceous plants growing within. This "tangled thicket" is another example of the frequent interspecific facilitative interactions, where one species provides a protected and often moist microhabitat allowing germination and the regeneration of another species. Such cases occur with high frequency in drylands (see Sections 1.7, 4.7, and 11.4).

At least eleven genera are endemic to Socotra and there is one near-endemic family (Dirachmaceae). The limestone plateau and Hagghier Mountains are the richest areas for endemism but endemic plants occur throughout the island. Due to habitat fragmentation and environmental degradation through overgrazing, many endemics here are endangered.

The endemic and monotypic *Dirachma socotrana* is considered vulnerable by IUCN, while *Croton pachyclados* survives in only one known location. The striking and endangered *Dendrosicyos* is the only representative of the cucumber family that is a tree. *Euphorbia abdelkuriensis* grows only on the island of Abd al Kuri, at Socotra. This endangered species is a euphorb known for its unusually *spineless* columnar stems. In total, IUCN has so far placed 52 endemic Socotran plants on its *Red List of Threatened Species*.

## 2.12 Oman

Oman is associated with some of the earliest human civilizations. A site in the Dhofar region contains stone tools dated at 106 000 years, supporting the proposition that early humans moved into Arabia during the late Pleistocene (Rose et al. 2011). The oldest known settlement is Dereaze, in the city of Ibri, which dates back at least 8000 years to the late Stone Age. By 2000 B.C.E., Oman was already famous for the production of copper, in the north, and frankincense in the south. Oman was an early adopter of Islam (in the seventh century, during the lifetime of the Prophet Muhammad), and most Omanis today are Ibadi Muslims, belonging to one of Islam's earliest fundamentalist movements, distinguished by their conservative doctrine. Oman remained influential as a center of East-West exchange until competing British and Portuguese empires overtook its maritime trade in the early 1800s.

The Sultanate lies between Yemen and the United Arab Emirates in the southeast of the Peninsula and covers a total area *c*. 250 000 km$^2$ (see Figure 2.12). The Musandam Peninsula, extending into the Strait of Hormuz, is separated from the rest of Oman by the easternmost section of the Emirates. Valleys and desert cover more than 80% of the land mass; the rest is mountainous or narrow coastal plain.

The country is very isolated—physically it is flanked by the Gulf of Oman, the Arabian Sea, and the Saudi Rub' al-Khali. Historically the country's




**Figure 2.12** Country map of Oman with major cities and mountain ranges.

contacts with the rest of the world, and indeed communication among its own coastal towns, were by sea. The Rub' al-Khali remains extremely difficult to cross, even with modern transport, and this vast dryland forms a long-standing barrier between Oman and the Arabian interior. Similarly the Al Hajar Mountains, extending from the Musandam to Oman's easternmost point, form another barrier (see Figure 1.2).

Natural features divide the country into some seven fairly distinct areas. There is Ru'us al Jibal, including the northern Musandam Peninsula; the Al Batinah plain, running southeast along the Gulf of Oman coast; the Oman interior behind the Al Batinah coast, comprising the Al Hajar Mountains, their foothills and desert fringe; the coast from Muscat-Matrah around the Ras al Hadd point, and down the Arabian Sea; the offshore island of Masirah (*c*. 649 km$^2$); and the barren coastline running south, to the fertile Dhofar region. (Masirah, off the east coast, is an important hatching ground for loggerhead sea turtles, similar in importance to the beaches at Ras al Hadd and nearby Ras al-Jinz—the easternmost point of the Arabian Peninsula—which serve as hatching grounds for green sea turtles).

Except for the foggy and fertile Dhofar region, to the west, all of the coast and lowlands around the Al Hajar are part of a Gulf of Oman desert and semi-desert ecoregion, with the mountains themselves also distinct (Davis et al. 1994). An earlier, more temperate flora in Oman was similar to that of the Zagros, across the Gulf in southwestern Iran. At altitudes above 2000 m, the Omani flora includes many temperate species. It seems likely they crossed fairly recently on the land bridge between Oman and the Zagros, near Bandar Abbas (see Figure 2.12).

The flora includes at least 1250 species (see Table 1.1). Of these, 1182 are angiosperms, comprising 568 genera and 119 families. There are also three gymnosperms and 22 vascular cryptogams. As seems true for much of the region, mono- and oligotypism is high. Thus some 39 families in Oman are represented there by single species, and there are at least 372 monospecific genera. Only two genera have more than 20 species.

The southern and northern mountain ranges of Oman are the most species-rich regions, with some 72% and 60% of the total species, respectively. The Jabal al-Akhdar massif in the northern Hajars has been recognized as a local hotspot with some 17 endemic species (Ghazanfar 2003; Miller and Nyberg 1991). This region is also an important part of the larger (total area *c*. 470 000 km$^2$) WWF Global 200 ecoregion "Arabian Highlands, Woodlands, and Shrublands" identified in Oman, Yemen, Saudi Arabia, and the UAE, and given vulnerable status (Ghazanfar 1998; Olson and Dinerstein 2002). About a third of the country's plants occur in northern Oman, above 1500 m, including at least 14 national endemics (Patzelt 2008). Other centers of endemism include the following:

1. The escarpment woodlands of Dhofar, where some 63 species are either nationally or regionally endemic. Two of these are monotypic genera (*Cibirhiza*, Asclepiadaceae and *Dhofaria*, Capparaceae); another is the dominant forest tree *Anogeissus dhofarica*, as well as some 60 other species from the sea-facing slopes of the fog-oases there (see Section 1.4.1).
2. The limestone plateau of central Oman where at least 12 species are endemic. Among these the shrub *Ochradenus harsusiticus* (Resedaceae) and the perennial herb *Hyosyamus gallagheri* are both quite common.

Brinkmann et al. (2009) described vegetation patterns along an altitudinal and grazing gradient in the northern al-Akhdar range. Samples were collected between 2150 and 1000 m. Above 1500 m, some 329 species were found, with 34 on the Omani Red List, representing some 10% of the local flora. These authors concluded all Omani regions require more conservation effort, as overgrazing by domestic animals threatens large areas, and in particular threatens regeneration of significant endemic tree species.

Unfortunately, collection data for species in Oman remain incomplete, and sharp declines in the populations of many species (often apart from weedy and unpalatable ones) have been noted, for example, in the hills of Dhofar (Davis et al. 1994). Unless grazing is controlled, there will be no tall grassland left in these tropical, monsoon-affected areas. At present the dominant tall grasses appear to be abundant, but only in areas where grazing has

been limited or that are inaccessible to livestock. The first country-wide Red List of plants at risk was only recently completed (Patzelt 2008) and much basic conservation work needs doing there.

## 2.13 United Arab Emirates

It is now well established that Africa was the original homeland of the human species—of modern *Homo sapiens*—but the dates and particular pathways taken by early humans out of Africa remain an open question. Recently Armitage et al. (2011) described evidence for a human presence 125 000 years ago at Jebel Faya, in what is now the United Arab Emirates. They found stone tool assemblages buried in sediment dating from that period. The tools are remarkably similar to those made by anatomically modern humans living in Africa at that time. This supports an early dispersal of *H. sapiens* along a direct route passing from the Horn of Africa to southern Arabia, across a land bridge that later became the Bab el-Mandeb Strait.

Armitage et al. (2011) suggested that modern humans left Africa by crossing the Bab el-Mandeb and moving along the southern margin of Arabia to reach Jebel Faya. They speculate that during dry periods, migrants would have moved eastward along river valleys that are today submerged in the Gulf. It is clear humans also entered Arabia from northeastern Africa, crossing the Sinai and eventually reaching, for example, the Es Skhul and Qafzeh caves in Israel, where other ancient human fossils have been found. By either route human populations would have eventually reached India, where they could have interacted with archaic *Homo,* representing earlier iterations of the journey "out of Africa" (and see Petraglia et al. 2010).

As is the case for several other places in the Middle East, the linked emirates of the UAE form a kind of pinch-point nexus (see Figure 2.13). The Gulf and Iran to the northeast, an isolated portion of Oman to the east and Saudi Arabia to the south and west. Located along the northern approaches to the narrow Strait of Hormuz, the Emirates today represent a vital transit point for shipping out the greatest portion of the world's crude oil supply. The UAE shares a (disputed) 19-km border with Qatar to the northwest and a (recently disputed) 530-km border with Saudi Arabia to the west, south and southeast, and a 450-km border with Oman to the

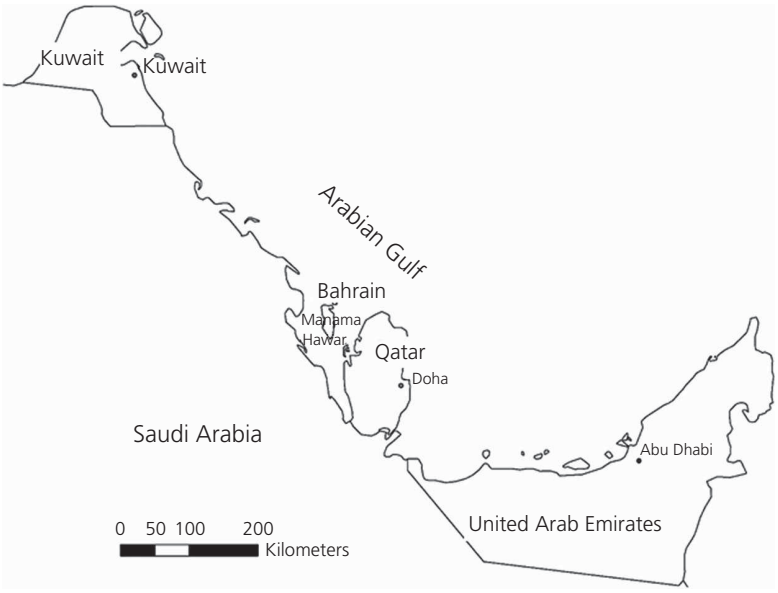



**Figure 2.13** Country map of United Arab Emirates, Qatar, Bahrain, and Kuwait.

east.[19] Numerous islands lie offshore in the Gulf and ownership of some of these, too, has been the subject of international disputes (with Qatar and Iran). Middle Eastern countries are still mostly quite young, albeit in an ancient land.[20]

The UAE is a federation of seven sheikhdoms that united in 1971. They include Abu Dhabi, Dubai, Sharjah, Ajman, Fujairah, Umm Al Quwain, and Ras Al-Khaimah.[21] All have their major city centers located in coastal areas. The UAE has a very long coastline stretching 1318 km, most of it facing the Arabian Gulf and a shorter section along the Gulf of Oman.

Total area is approximately 76 000 km$^2$, with the largest emirate, Abu Dhabi, accounting for some 87% and the smallest, Ajman, having an area of only 259 km$^2$ (see Figure 2.13). Tiny Dubai has developed the largest, most spectacular, and most disruptive coastline modification projects in the world; some of the conservation challenges which have arisen as a result are considered in Chapter 10.

Situated as it is among a confluence of Indo-Asian and Afro-European phytogeographic regions, the UAE has a relatively rich biodiversity including more than 630 higher plants (Brown and Sakkir 2004). As well as great expanses of flat, salty *sabkha* (most characteristic of the largest emirate, Abu Dhabi), the UAE also contains parts of two of the Global 200 most biologically distinct terrestrial and marine ecoregions: the Arabian Highlands, Woodlands, and Shrublands (see Section 10.15), and the Arabian Gulf and Sea (Olson and Dinerstein 1998).

Coastal Abu Dhabi also includes great expanses of seagrass beds, mangrove forests, and coral reefs, as well as the extensive sabkhat, or salt flats. It encompasses the largest marine protected area in the Gulf, the Marawwah Marine Protected Area (designated a UNESCO Marine Biosphere Reserve in 2007). The site provides habitat to endangered species such as green and hawksbill sea turtles, and a large population of threatened dugongs.

The coastline extends for about 90 km along the Gulf of Oman, forming the Al Batinah coast. The Western Al-Hajars separate the Al Batinah coastal area from the rest of the UAE. Beginning at the UAE–Oman border on the Gulf coast of the Musandam, the Al-Hajars curve southeastward for about 150 km to the UAE–Oman border, on the Gulf of Oman. The range continues as the Eastern Al-Hajar Mountains for more than 500 km into Oman. In many places steep mountain slopes run all the way down to the shore. Taken together, these northern emirates on the Arabian Gulf and Gulf of Oman are part of the Gulf of Oman Desert and Semi-desert Ecoregion (Olson and Dinerstein 1998).

### 2.13.1 Plants of the UAE

Much of the western coast consists of Abu Dhabi's saline sabkha flats, and sandy plains dotted with shrubs like *Salsola imbricata, Zygophyllum mandavillei, Seidlitzia rosmarinus*, and occasional stunted *Tamarix* trees (see Brown and Sakkir 2004). All these halophytes show the usual adaptations to highly saline soils (see Section 5.8). *Tamarix* excretes salt on its needlelike leaves, while the succulents accumulate salts and water in the fluid of their swollen leaves and stems.

The Gulf coastline north of 26° N is mostly flat and sandy. Dense local beds of *Juncus maritimus* alternate with patchy swards of *Aeluropus lagopoides*, and *Cressa cretica* is abundant in the open places (Satchell 1978). Hard areas of coral sand support *Limonium axillare*, and *Panicum turgidum* forms thick tussocks on sandy hummocks. The coastal plains of grit and gravel support a sparse perennial vegetation mostly dominated by the shrubby chenopod *Anabasis setifera*.

Tidal creeks and swamps have developed around some of the offshore islands and lagoons. Dominant plants there include the succulent salt-marsh shrub, *Arthrocnemum glaucum* (Chenopodiaceae),

[19] Part of the UAE lies between the Musandam Peninsula and the rest of Oman, with a small area in between which is claimed by Oman.

[20] Examined closely, many international boundaries have a great deal of happenstance, sometimes some absurdity. Most of the modern Middle East emerged from the political death throes of the nearly 500-year-old Ottoman Empire (see Section 1.2). Various European influences during World War I filled any immediate political vacuum, and following that war a great deal of boundary-making occurred (sometimes involving secret agreements)—the Syria–Lebanon–Israel "tri-border" region (Kaufman 2014); Syria itself; Iraq; Jordan. Later on Israel, Saudi Arabia, and the Trucial States were formed, and then in the early 1970s the emergence of the Emirates itself took place.

[21] Ras Al-Khaimah joined the federation in 1972.

and mangrove trees *Avicennia marina* (Acanthaceae) (see Section 4.6).

In raised areas, grasses such as *Panicum turgidum* and *Pennisetum divisum* become abundant, and *Haloxylon salicornicum* occurs throughout most of the coastal and inland sandy plains (Brown and Sakkir 2004). Around sandy areas of Dubai, bushes such as *Cornulaca monacantha, Crotalaria persica, Calotropis procera*, and *Taverniera spartea* may occur. Toward the mountains, high gravel plains include stands of the abundant introduced mesquite, *Prosopis juliflora* (Western 1989). Smaller weeds, many native to Europe, also occur, including *Vicia sativa* and *Galium setaceum*. Under cover of overhanging boulders, tiny plants like *Vicoa pentanema* and *Spergula fallax* co-occur with *Anthemis odontostephana* and *Matricaria aurea*. The most conspicuous plants of these high inland plains are the thorny *Astragalus spinosus* bushes, Arabian almond, *Amygdalus arabicus*, and the beautiful pink-flowering *Moringa peregrina* trees (Western 1989) (see Figure 2.14).

Throughout the central Hajars (e.g., near Hatta), wadis create opportunities for wells (known as *birs*), permanent pools and dripping aquifers. These all provide habitat for fragile ferns like *Adiantum capillus-veneris,* which occurs here in conjunction with the only orchid in the UAE, *Epipactis veratrifolia* (Brown and Sakkir 2004). Other species include *Centaurium pulchella, Lippia nodiflora, Sida urens*, and *Bacopa monnieri*. There are also luxuriant stands of the cosmopolitan weedy monocots *Phragmites australis, Imperata cylindrica*, and *Typha domingensis*, as well as the colorful wild oleander, *Nerium mascatense*.

### 2.13.2 The eastern UAE and Musandam Peninsula

All of the Gulf's densely populated and predominantly sandy, low-lying coastal regions seem especially

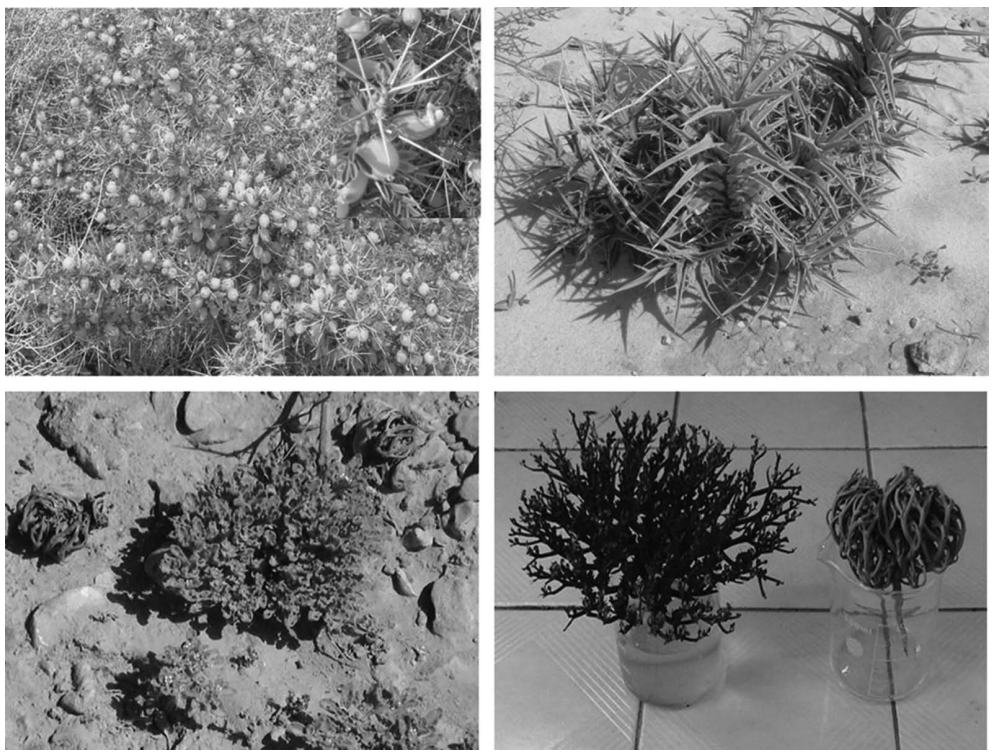


**Figure 2.14** The thorny *Astragalus spinosus* (upper left) with magnified part in the upper right; *Blepharis ciliaris* (upper right); live green and dead dry skeletons of *Anastatica hierochuntica* (bottom left) and the hygrochastic dry curled and wet uncurled skeletons (bottom right).

vulnerable to the impacts of rising sea-levels, either through direct inundation and/or erosion and salt water intrusions. Extensive coastal development, in particular in Dubai, has brought increasing demand for cement and other raw material (rock, aggregate, limestone), all of which have been taken from the country's mountain regions. Aggregate crushing and quarry licenses have dramatically increased in the eastern emirates of Sharjah, Ras al Khaimah, and Fujairah, providing materials for these massive coastal developments.

Fujairah is the only Emirate that faces the eastern (Gulf of Oman) coast, and is a mixture of mountain, alluvial plain, and coastal habitats. Like the other Emirates though, it too is beginning to experience the pressures of tourism and development (Tourenq et al. 2011). Wadi Wurayah, in eastern Fujairah, lies within the Hajars and contains many species typical of arid Middle Eastern mountain habitats, including associations of *Acacia tortilis, Lycium shawii*, and other woody perennials—*Euphorbia larica, Tephrosia apollinea*, and occasional trees such as *Moringa peregrina* (Tourenq et al. 2011). *Ficus cordata* and *Ziziphus spina-christi* occur in the wetter wadi beds (*Moringa* and *Ziziphus* are both highly prized here as sources of nectar for the production of very valued local honey). Among the rare and endangered animals in this region are the Arabian tahr (*Arabitragus jayakari*), Arabian leopard (*Panthera pardus nimr*), Blanford's fox (*Vulpes cana*), Caracal lynx (*Caracal caracal schmitzi*), and Gordon's wildcat (*Felis silvestris lybica*)—all of which once roamed the mountains ringing the entire Arabian Peninsula (Tourenq et al. 2011). Unfortunately feral goats and donkeys are still widespread.

The Hajar cover all of the eastern UAE and northern Oman, running parallel to the coast of the Gulf of Oman for *c*. 600 km. They divide broadly into Eastern and Western ranges, situated respectively to the east and west of the Jebel Akhdar range (see Figure 2.13). The whole region includes various smaller ranges and many individual massifs (e.g., Jebel Akhdar, Jebel Aswad, Jebel Abyadh). The mountains of the Musandam—the Ru'us al-Jibal—are located in the north of the Hajar Range. These rugged mountains are known as a local center of endemism in eastern Arabia (Miller and Nyberg 1991; Patzelt 2008). For example, the Jebal Akhdar massif alone contains about a third of all Oman's vascular plants, many of which are nationally endemic (Patzelt 2008).

The Ru'us al-Jibal and their outwash plains are essentially the northeastern edge of the vast Empty Quarter; temperatures are high and rainfall low, and there are two seasons. Prolonged, hot dry summer from May to October, and mild-to-warm winter with occasional rain, from November to April. Monthly mean summer maxima are 41–45°C, and in winter 12–15°C. Temperatures at higher elevations are lower and occasionally frost or light snowfall occurs above 1700 m (see El-Keblawy 2014).

Feulner (2011) estimates at least 75 species are locally endemic, confined to the high mountains of the Ru'us al-Jibal, mostly at medium-to-high elevation. El-Keblawy (2014) emphasized the distinctiveness of this flora and need for regional, landscape-level conservation. Many or most of these species have their ranges centered in Iran or neighboring central Asia. Common species include *Artemisia sieberi, Astragalus fasciculifolius, Centaurea wendelboi, Convolvulus acanthocladus, Cymbopogon jwarancusa, Ephedra pachyclada, Prunus arabica*, and *Teucrium stocksianum*; less commonly *Aegilops kotschyi, Dianthus crinitus, Leontice leontopetalum*, and *Salvia mirzayanii* (El-Keblawy 2014; Ghazanfar 1998).

As suggested, the most recent glaciation in eastern Arabia peaked about 17 000–18 000 years BP. Sea level was some 120 m lower then and the Gulf was largely dry, with the shoreline located beyond the Strait of Hormuz (Glennie 2005; Parker et al. 2004). This allowed dispersal between Arabia and southern Iran and southern Baluchistan (southwestern Pakistan). The similarity of the Hajar mountain flora, in particular that of the cooler Ru'us al-Jibal, to that of southern Iran and the Makran region in particular, is well known and warrants further study (Ghazanfar 1998). Some of the most common species of the Ru'us al-Jibal are more common in Iran than other regions of Arabia (Feulner 2011).

Elevation has a significant modulating and sometimes protective effect on vegetation. Potential evapotranspiration rates, aspect, and particular geological landforms and substrates all intersect with elevation in influencing plant ecology. Working in the rugged northern Emirates, El-Keblawy and colleagues studied effects of landforms and

other habitat factors on plant ecology. At the Wadi Al Helo Protected Area, El-Keblawy et al. (2015b) probed effects on some 216 plant species among 15 habitats. Species richness values were unimodal, with most species occurring at intermediate elevations. Substrates consisted largely of exposed rocks on steep slopes with almost no soil cover, and only sparsely vegetated. Large boulders, small stones, and gravel were the substrate in steep runnels. The wadi bed consisted mainly of gravel and boulders, with exposed rocks coming as wash from floods.

El-Keblawy used results of multivariate techniques (TWINSPAN and DCA) to characterize communities in the wadi bed and elsewhere. Wadi-bed sites tend to concentrate runoff and act as conduits; they also have low evaporation compared to other locations. *Forsskaolaea tenacissima* and *Rhazya stricta* occurred mainly on the raised bars of wadi beds. *Tephrosia apolina* and *Notoceras bicorne* were found in wadi channels, while *Acacia tortilis* and *Fagonia indica* tended to occur on terraces. Sixteen of eighty stands sampled came from canyons or gorges where the dominant species included *Dodonaea viscosa, Lavandula subnoda*, and *Moringa peregrina*.

In related work El-Keblawy et al. (2015a) looked at the abundance of long-lived trees and shrubs in relation to particular soil/landform characteristics. Based on a large sample of stands, they found strong associations among landforms and certain indicator species and other dominant xerophytes. Results of TWINSPAN and DCA aggregated four groups of landforms. One set included inter-dune areas, sand sheets, and sabkha sites, having *Zygophyllum qatarense* and *Prosopis cineraria* as indicators. A second group consisted of alluvial fans, alluvial plains, terraces, and piedmont, with *Acacia tortilis* and *Haloxylon salicornicum* as indicators. A third included flats, sand dunes, sand ramps, and deflation plains, with *Cyperus conglomeratus, Calotropis procera*, and *Leptadenia pyrotechni*ca. The fourth group represented wadis and was dominated by *Acacia tortilis*.

*Moringa peregrina* is a significant desert tree found in particular in certain arid mountain locations; unfortunately because of severe drought and overcutting for firewood it is threatened in much of its range (Hegazy et al. 2007, 2008a). It is often found in deep canyons and gorges. Hakham and Ritte (1993) reported *M. peregrina* was rare in Israel and very sensitive to grazing pressure. The ground where *M. peregrina* grows is most often covered with coarse, rocky debris, characteristic of the upstream runnels at mountain bases and slopes.

Plants living in gorges may be protected from some of the effects of global warming. Gorges and canyons get shaded for most of the day, reducing total solar radiation and rates of evapotranspiration. El-Keblawy and Khedr (2015) considered the impact of topographic factors on *Moringa peregrina* (165 individuals, in 12 gorges) at Hafit Mountain, UAE. They concluded gorges were particularly important in maintaining *M. peregrina* under the high temperature and low rainfall there at its northwestern range edge. Like other trees there, e.g., *Pistacia khinjuk* and *Cordia* species, *M. peregrina* populations may be sustained through recruitment from plants growing in the protection of cliffs or ledges in gorges and canyons (see, too, Feulner 2011). The Hafit trees were generally small, but more abundant and larger at mid-altitudes (75% of the trees were at 300–500 m; 22% at lower elevation and only eight individuals occurred at the highest elevation [>500 m]). Large trees produced more fruits than small and medium-sized ones, and the larger trees at middle altitudes produced most of the fruits overall. Results suggested the many deep canyons and gorges there play an important role as source populations, maintaining *M. peregrina* in the most hyper-arid parts of its range. Moringa trees were also associated with an understory of grasses and small shrubs—but few other large shrubs or trees beneath their canopies.

## 2.14 Saudi Arabia

To a large degree, Western perceptions of Saudi Arabia as the *parched* Kingdom are shaped by the imagery of the barren expanse of the Empty Quarter. It was on the fringes of the Empty Quarter that oil was first discovered in the 1930s, and it was through experiences among the nomadic Bedu there that twentieth-century explorers introduced Western audiences to the beauty and uniqueness of Arabia.

The country is very large—some 2.4 million km$^2$—and bordered by Jordan and Iraq to the north and northeast, Kuwait, Qatar, and the United Arab

Emirates to the east, Oman to the southeast and Yemen to the south (see Figure 2.15). It is also connected to the tiny island kingdom of Bahrain in the Gulf by a bridge. Saudi Arabia occupies about 80% of the Arabian Peninsula and though it has no permanent year-round rivers or freshwater lakes, its marine coastline extends for some 2600 km. The Red Sea has a rich marine life and world-class coral reefs (see Sheppard et al. 1992).

For example, the Farasan Bank is a great marine shoal, 100 km wide and stretching 800 km along the Saudi Red Sea coast. It is part of the Peninsula's continental shelf, dropping from an average depth of *c*. 40 m to some 600 m at its outer edge. There are more than 100 coral islets of varying size and some 20 large islands; among these the Farasan Island Archipelago, off the southern port of Jizan are the largest. These limestone islands were built up from coral deposited over the past 8000 years, as sea levels rose following the last ice age. Hall et al. (2010a) have described the plants of these islands.

At least a third of the interior of Saudi Arabia is desert, including the Rub' al-Khali, Nafud Al Jafurah and Ad Dahna (see Figure 1.5). East of the narrow Red Sea coastal plains there is a steeply rising mountain range, the Hijaz, averaging *c*. 2100 m. The highest region is at Jabal Sodah, near Abha in the southwest (3015 m). These mountains have steep western escarpments and more gently sloping interiors, or dips. Further to the east is an extensive central desert plateau, with a highland terrain including mesas, buttes, and lava fields (see Section 4.5).

The great basaltic lava fields, called "harrats," have resulted from active volcanoes in the west and northwest. Harrats cover about 180 000 km$^2$ and extend from Turkey to Yemen. They largely lack vegetation except for scattered microhabitats that can support plant growth (El-Ghanim et al. 2010; Seddon 1996). Examples of plants in the Harrat al Harrah Protected Area include *Haloxylon salicornicum, Artemisia monosperma, Cymbopogon schoenanthus, Asphodelus fistulosus, Psiadia punctulata, Artemisia sieberi, Achillea fragrantissima, Ephedra aphylla, Capparis spinosa*, and *Zilla spinosa* (see Figure 2.16).

Southwestern Saudi Arabia has the country's greatest overall plant richness, including some remnants of primal forest having many affinities to Mediterranean and African floras, in particular the latter (e.g., *Commiphora myrrha, Mimusops laurifolia, Moringa peregrina*). The southwest also shows the greatest concentration of endemism, despite the

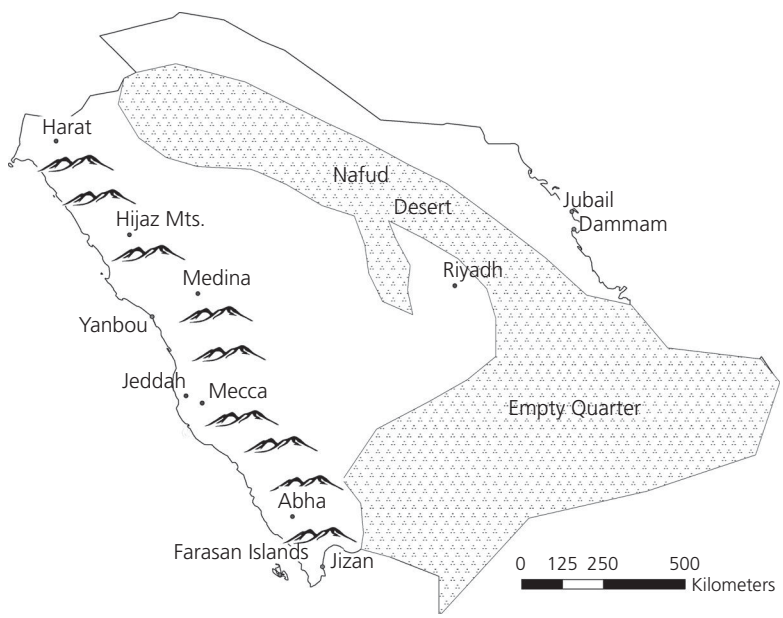



**Figure 2.15** Country map of Saudi Arabia with major cities and mountain ranges



**Figure 2.16** Species growing in harrat habitat: *Zilla spinosa* (upper left with magnified corner); *Achillea fragrantissima* (upper right with magnified corner); and *Ephedra aphylla* (bottom left), and female and male flowers of *E. aphylla* (bottom right).

fact these high altitude areas have been settled by humans since ancient times. Western Saudi Arabia as a whole is relatively rich in natural vegetation compared to the center and east. The northwestern mountains also have many affinities to European/Mediterranean and North African regions (Al-Nafie 2008).

Al-Nafie (2008) suggested Saudi mountains above *c*. 1800 m should be regarded as outliers of Afro-montane regional centers and included some of the wetter slopes and peaks of the As Sarawat mountains (over 2800 m) (see Figure 1.3) where there are pockets of Afro-alpine species. Among these higher altitude plants are *Juniperus procera, J. phoenicea, Olea europaea, Mimusops laurifolia, Rubus asirensis, Rhus natalensi, R. abyssinica, Dodonaea angustifolia, Rumex nervosus, Rosa abyssinica, Euphorbia schimperi*, and *Campanula edulis* (see Figure 2.17). These more elevated ecoregions include many temperate-Mediterranean relicts as well, survivors of the cooler, wetter, earlier era.

Jabal Aja' is the most prominent mountain range of Najd, the central upland region of the Arabian Peninsula. Llewellyn et al. (2011) recently described the flora of this area and designated the site an "Important Plant Area"[22] in the peninsula. They report a total of 355 species in the area of the Aja' mountains and adjoining sands of the Nafud. Jabal Aja' is a maze of pink granite formations, providing a refuge for many Mediterranean and Irano–Turanian species. It is the only known locality for the endemic *Trisetaria chaudharyana* and *Erysimum*

[22] An Important Plant Area program has been initiated for the Arabian region by the IUCN Arabian Plant Specialist Group. The aim of this program is to assess hotspots of plant diversity in the region and designate the most important as Important Plant Areas. These assessments are conducted on the basis of specific criteria (Al-Abbasi et al. 2010).

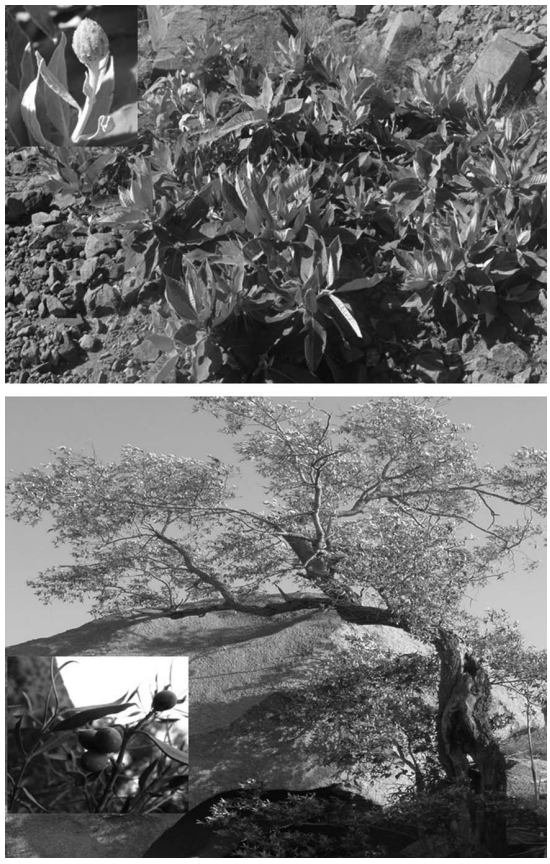


**Figure 2.17** The endemic perennial herb, *Centaurothamnus maximus*, in the Al Sodah heights at 2800 m (upper), flower head appears in upper left; and the wild *Olea europaea* ssp. *africana* at Shada Mountains (1250 m), southwest Saudi Arabia (bottom), fruiting branch appears at left.

*hedgeanum*, and one of only three sites where the endemic *Phagnalon viridifolium* var. *omanense* is found. Due to their very limited endemic ranges and the local threats to Jabal Aja,' these latter species are regarded as globally threatened. At least ten other rare taxa are also found on the mountain that are likely to be nationally/regionally threatened, including *Petrorhagia cretica, Thymelaea mesopotamica, Valerianella sclerocarpa, V. oxyrhyncha, Vulpia muralis*, and *Noaea mucronata*.

With many abandoned ancient agricultural terraces, Jabal Aja' is also recognized as a reservoir for wild crop relatives and land races such as barley, oats, and dates, as well as of medicinal plants. The area is considered to be more important in this regard than any other in the north of Saudi Arabia. There are no known traditional *hemas* or protected areas there (see Section 10.3); however, the planned Jabal Aja' Biosphere Reserve has been proposed as a conservation hema by WWF (Kilani et al. 2007).

### 2.14.1 Plant resources and endemism in the Saudi flora

The country includes a total of some 2250 species of flowering plants, belonging to 149 families and 840 genera. According to Hassan (1981a), nearly half the plant families in both Saudi Arabia and Egypt are cosmopolitan or near-cosmopolitan. In both countries tropical elements are relatively poorly represented (*c.* 7% in Saudi Arabia and 4% in Egypt).

Some 105 species are specialists inhabiting sand dunes, another 90 are halophytes, 75 are trees, and 12 are aquatics. No entire families or genera are endemic but there are 246 species considered regionally endemic and 107 national endemics.

Nearly three-quarters of the flora belong to just 23 families; indeed 42% of all species belong to just three families (Poaceae, Asteraceae, and Fabaceae). The remainder show much monotypy and oligotypy. Of the 149 families, 68 (45.6%) are represented by a single genus per family, and 36 are represented by single species (including the Neuradaceae, Araceae, Aristolochiaceae, and Barbeyaceae) (see Al-Nafie 2008). As in Egypt, the flora is made up of many small genera (840 genera having an average of 2.6 species each).

According to Shmida (1985) the entire Saharo-Arabian region contains many endemic genera that are usually mono- or oligo-typic. All the endemic monotypic genera of the Sahara are common, abundant species, widespread over vast areas. Moreover few endemic monotypic genera in this region have been reported as having a restricted area—which is otherwise a common feature in monotypic-endemic genera in other semi-deserts, such as those in North America and southern Africa (Shmida 1985).

About 20% of the Saudi flora, including many of the rare and endemic species, exist in small populations and are threatened (Collenette 1999; Mandaville 1990). Given the over-grazing of so much Saudi rangeland, and the rapid growth of human

centers in the country's most botanically diverse regions, it seems likely the actual number of threatened species is greater than these earlier estimates suggest.

Although there are some reliable estimates of species richness, other measures of ecological diversity—most importantly systematic determinations of distribution and abundance—have not been widely done for the Saudi flora (or most other Middle Eastern countries). Consequently accurate Red List status reports for plant species are mostly unavailable; indeed the 2000 IUCN Red List of Threatened Species did not include a single record for Saudi Arabia. Even with increased attention to improving knowledge there, the 2012 Saudi Red List only contained some 59 species.

## 2.15 Bahrain

Bahrain is the small island state near the western shores of the Gulf. It is a group of islands, the largest being Bahrain Island (55 by 18 km). Saudi Arabia lies to the west and Iran 200 km to the north, across the Gulf (see Figure 2.13). The peninsula of Qatar sits to the southeast, across the Gulf of Bahrain. Plans exist to build a Qatar–Bahrain causeway linking these two countries in the world's longest marine causeway. Bahrain is believed to be the site of the ancient Dilmun[23] civilization. Much of the evidence of this is in the Hawar Islands, the largest group within the Bahraini archipelago.

The main island of Bahrain contains some five physiographic zones, each with different vegetation types (Hegazy 1999a). Starting from the coast and moving inland these are: (1) coastal salt-affected lands, dominated by *Zygophyllum qatarense, Halopeplis perfoliata, Halocnemum strobilaceum*, and *Schanginia aegyptiaca*; (2) backslopes with soils varying from loose to gravelly sand supporting plant communities dominated by *Anabasis setifera, Sporobolus arabicus, Suaeda vermiculata, Helianthemum kahiricum*, and *Cyperus* species; (3) the escarpment region, an essentially barren zone heavily disturbed due to the presence of gypsum quarries; (4) the interior basin, characterized by rich vegetation dominated by *Zygophyllum qatarense, Heliotropium bacciferum*, and *Helianthemum kahiricum*; and (5) the central plateau, with rocky and gravelly soils, supporting sparse vegetation dominated by *Ochradenus baccatus, Lycium shawii, Erodium bryoniifolium*, and *Glossonema edule*.

[23] Dilmun (or Telmun) was a civilization in ancient Eastern Arabia, regarded as one of the oldest civilizations in the entire Middle East. The Sumerians in the "Epic of Gilgamesh" described Dilmun as a paradise garden. Dilmun was an important trading center which at the height of its power controlled Arabian Gulf trading routes. Although the central location of Dilmun is unclear, Dilmun likely encompassed Bahrain, Kuwait, and coastal regions of the Eastern Province of Saudi Arabia (see Nayeem 1990).

## 2.16 The Hawar Islands

The Hawar Islands[24] are a limestone archipelago of more than thirty islands of various sizes, with a total area *c.* 50 km$^2$. They are flat, desert islands surrounded by shallow water, some 26 km southeast of "mainland" Bahrain, close to Qatar (see Figure 2.13). The flora includes all of the major salt marsh species of the Gulf (*Arthrocnemum macrostachyum, Halocnemum strobilaceum, Halopeplis perfoliata, Suaeda vermiculata*, and others), as well as the characteristic plants of the local Gulf of Salwa region, such as *Zygophyllum qatarense* and *Lycium shawii* (Pilcher et al. 2003). On many of the islands there is a fairly typical salt marsh zonation pattern, with *Arthrocnemum macrostachyum* populations closest to the water line, followed landward by *Halocnemum strobilaceum, Halopeplis perfoliata*, and *Suaeda vermiculata* zones (Pilcher et al. 2003).

Extensive seagrass beds are present in the waters around these islands. Indeed much of the southern part of the Arabian Gulf is home to extensive seagrass pastures, off the coasts of Bahrain, Qatar, UAE, and to a lesser extent the southern coast of Saudi Arabia.

There is only limited documentation of the significance of Gulf seagrasses as critical marine habitats. Yet these marine angiosperms consolidate and stabilize bottom sediments, create and maintain water clarity, oxygenate the water column, and generate food and nursery habitat for many animals, including endangered dugongs, sea turtles,

[24] Politically, nearby Qatar, with Bahrain also claims the main Hawar Island.

and fish. Seagrass beds around the Hawar Islands typically include four seagrass species (*Halodule uninervis, Syringodium isoetifolium, Halophila ovalis*, and *H. stipulacea*), and all are generally associated with relatively fine-grained sediment types (Basson et al. 1997). Most beds are dominated by *H. uninervis*, though more evenly mixed stands do occur (Sheppard et al. 1992).

Seagrass beds surrounding the Hawars are critical habitat for the world's second largest population of endangered dugongs (*Dugong dugong*). Dugongs belong to the phylo-rare monotypic order Sirenia, and are the only herbivorous marine mammals. Significant populations of herbivorous green turtles (*Chelonia mydas*) also depend on Gulf seagrasses. The islands are also notable for the high species diversity of both breeding and annual migratory birds, and are home to bottlenose dolphins (*Tursiops truncates*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) (Pilcher et al. 2003).

## 2.17 Qatar

Until the 1970s, when oil and gas were discovered in commercial quantities, the mainstay of Qatar's economy (and those of other Gulf countries) were the abundant, natural pearls that Qatari divers collected by hand (and at great risk) from under Gulf waters. These jewels get produced by the Pearl oyster, *Pinctada radiata*, through the secretion of calcium carbonate around irritating grains of sand in the mantle, and were highly sought by Indian and European merchants. They had special meaning to the religious faithful, in that the dangers of pearl-diving—ropes, weights, and reliance on a partner to pull the diver up—were said to amount to tests from God, with pearls a reward to the true believer.

The Qatar Peninsula juts into the Gulf from Saudi Arabia and occupies 10 600 km$^2$, its north-south axis *c.* 180 km in length, and east-west width at its widest point 84 km. The country is surrounded by small offshore islands, all uninhabited except Halul Island, which serves as an oil storage center (see Figure 2.13). North of Dukhan lies Hawar Island and to the south-east is the spectacular Khor Al Adaid, a great inland sea of rolling sand dunes around an inlet of the Gulf.

The peninsula has a low, slightly undulating surface, with scattered depressions broken only by a few mesa-type hills (Batanouny 1981). The highest point lies to the west, Qurayn Abu al Bawl, at 103 m in the Jebel Dukhan, a small range of low limestone outcrops running north-south from Zikrit through Umm Bab to the southern border. The lowest part of the country lies at 6 m below sea level, in a large sabkha 15 km southeast of Dukhan (Beheiri and Al-Farra 1977). Indeed most of Qatar is less than 40 m above sea level. Inland and coastal flats occur in various parts of the peninsula at levels below 5 m (Batanouny 1981). The most extensive *sabkhat* are along the eastern coast to the south of Umm Said. Areas below sea level are represented by three large patches, the area east of Dukhan (*c.* 60 km$^2$); north-east of Khor Al-Adaid (*c.* 25 km$^2$); and north-east of Umm Said (*c.* 10 km$^2$). Beware climate change and rising sea levels!

Because of the gentle relief no overall drainage basins have developed; no deep wadis with well-developed tributaries are present in Qatar. Numerous superficial depressions act as catchments receiving intermittent runoff through shallow and poorly developed runnels. Despite the relatively low relief, the landforms of the Qatar Peninsula include conglomerate *hamada*,[25] mesas and buttes, rocky ridges, depressions (*rodat* and *mangaa*), shallow wadis, and runnels (Cavalier 1970) (see Section 4.5). The country is characterized by mild winters and very hot, humid summers.

Vegetation includes both halophytic and non-halophytic types (Batanouny 1981; Obeid 1975b). The major non-halophytic communities are dominated by *Ziziphus nummularia* and occur in depression habitats with alluvial and wind-blown fine-textured soils; *Francoeuria crispa* is also found in shallow depressions with fine-textured deposits. *Acacia tortilis* and *Lycium shawii* and the grasses *Cymbopogon parkeri* and *Panicum turgidum* all occur in depressions and shallow wadis with more coarse-textured, sandy- and gravel soils. The succulent chenopod *Haloxylon scoparium* is found in

[25] Hamada (also hammada; from the Arabic for "barren" or "unfruitful") is a type of desert landscape consisting of high, largely hard, rocky plateaus, with most of the sand removed by wind deflation.




**Figure 2.18** Country map of Iraq with major cities and mountain ranges.

southwestern Qatar on sand deposits; *Pennisetum divisum* is common in shallow wadis and runnels in deep sandy soils, *Rhanterium epapposum* in sandy habitats, and *Chrysopogen aucheri* and *Glossonema edule* in shallow runnels and rocky sites (see, also, Hegazy 1999a). *Zygophyllum qatarense* occurs in various habitats and appears to have a broad ecological range, being one of the most common species in the country.

Typical halophytic vegetation occurs in the many coastal and inland salt marshes. Common species dominating these salty habitats include *Arthrocnemum glaucum, Halocnemum strobilaceum, Halopeplis perfoliata, Suaeda vermiculata, Limonium axillare, Aeluropus lagopoides, Halopyrum mucronatum*, and *Sporobolus arabicus*. Two fairly common species, *Cynomorium coccineum* (Cynomoriaceae) and *Cistanche phelypaea* (Orobanchaceae), are *parasitic* on other plants in the salt marshes and coastal sands.

## 2.18 Iraq

Iraq (total area *c*. 435 000 km$^2$) is a large ancient regional state, bounded by Iran to the east, Turkey to the north, Syria to the northwest, Jordan and Saudi Arabia to the west and southwest, and Kuwait and the Gulf to the south (see Figure 2.18). The country's long axis runs nearly 1000 km from the Turkish border to the shores of the Gulf. The word "Iraq" is believed to trace its earliest origins to the Sumerian city of Uruk, *c*. 6000 years ago. Lower Mesopotamia, as the ancient Greeks called the land between the Tigris and Euphrates Rivers, has been called Iraq (likely from the Arabic for vein or root) since ancient times. In 1921 the three former Ottoman provinces of Baghdad, Basra, and Mosul were united to form the modern state of Iraq (Marozzi 2014).

There are four main ecological regions: the desert west of the Euphrates River; Upper Mesopotamia (between the upper Tigris and Euphrates Rivers); the northern highlands of Iraqi Kurdistan; and Lower Mesopotamia, the large alluvial plain extending from around Tikrit to the Gulf.

The mountains in the northeast are an extension of the great Eurasian alpine system that runs eastward, from the Alps through the Balkans, southern Turkey, northern Iraq, Iran, and Afghanistan, eventually reaching the Himalayas. The desert lies in the

southwest and central provinces along the borders with Saudi Arabia and Jordan.

To the north beyond the agricultural lands of upper and lower Mesopotamia lie the Zagros Mountains, which extend into adjacent Iran. With a total length of 1500 km, the Zagros span the entire length of the western and southwestern Iranian plateau, ending at the Straits of Hormuz directly across from the UAE. The highest points are Zard Kuh (4548 m) and Mount Dena (4359 m).

The Zagros were formed by collisions between the Eurasian and Arabian plates. They are made of sedimentary rocks including many salt domes (trapping petroleum) and large areas of mudstone, limestone, and dolomite (Zohary 1973). Among the habitats in the region are forest- and forest-steppe areas, with a semi-arid but temperate climate and fairly rich flora. Annual precipitation ranges from 400 mm to 800 mm and falls mostly in winter and spring. Winters are cold, with lows often below –25°C; summer and fall are dry.

The Zagros Mountains Forest Steppe is a vast highland ecoregion (see Figure 2.18). In some of the high alpine areas with mountain peaks reaching as high as 3600 m., snow can persist through the summer months. This region is also part of the Irano–Anatolian Biodiversity Hot Spot (see Section 10.15), an area globally important for diversity because of the high rates of endemism there.

The area supports oak-dominated deciduous forest and pistachio–almond woodland, interspersed by a diverse steppe flora. In the northern mountains at lower altitudes (400–500 m) communities are dominated by *Astragalus* and *Salvia* species; higher altitude forests (700–800 m) have *Quercus brantii* and/or *Q. boissieri* up to about 1700 m. Above the timber line (1900–2000 m) is sub-alpine vegetation dominated by *Quercus, Pyrus, Acer*, and *Pistacia* species (Zohary 1973). In Dohuk governorate, a remnant pine forest of *Pinus brutia* exists in Zawita, northwest of Dohuk city, and adjacent to part of the Eastern Mediterranean conifer-sclerophyllous-broadleaf forest ecoregion, which extends slightly into Iraq. The forest becomes more savanna or steppe-like, with scattered shrubs, toward the south side of the Zagros.

The Forest Steppe ecoregion is considered by conservation authorities to be "critical/endangered" (Davis et al. 1994). Certain restrictions relating to resource management (e.g., seasonal fishing bans, controls on hunting and wood cutting) have been established locally through rules enacted by the Kurdistan Regional Government. Unfortunately, large sections of the border zones with Iran and Turkey, mostly higher elevation sites, are heavily covered with land mines, etc., making everything very difficult.

The region's two great rivers, the Tigris and Euphrates, both rise in the eastern mountains of Turkey and enter Iraq in the northwest. After flowing for some 1200 km through Iraq they converge at Karmat Al, just north of Basra, to form the tidal Shatt Al Arab waterway, which flows a further 110 km to enter the Gulf. The alluvial plains of this lower valley region make up about a quarter of Iraq's area. These have existed for millennia as extensive marshland washes and low-lying plains, dissected by slow-moving drainage channels, but unfortunately much of this was recently drained.

The Euphrates has no additional tributaries within Iraq (it is arheic), whereas the Tigris receives four large inputs: the Khabour, Great Zab, Little Zab, and Diyala, all arising in the mountains of eastern Turkey and northwestern Iran and flowing southwest to meet the Tigris. A seasonal river, Al Authaim, rising in the highlands of northern Iraq also flows into the Tigris, and is the only significant tributary arising entirely within Iraq.

Another major ecoregion consists of the upper plains and foothills of the Middle Eastern Steppe region, extending up from the high mountains to the foot of Jabal Hemrin. This forms a transitional zone between the highlands and the desert plains, and consists of mostly open shrub/grasslands extending from western Jordan and south-western Syria to northern Iraq, reaching the Tigris–Euphrates river valleys and ending in the foothills of the Zagros near Iran. Geologically this region includes calcareous Mesozoic and Tertiary rocks and alluvial–colluvial soils in the river valleys, with areas of black basalt in the south-east.

The climate in this steppe ecoregion is continental, with high summer heat and low annual rainfall (< 250 mm), combined with cold winters with periods of frost. The vegetation is representative of the Mesopotamian province of the Irano–Turanian

region (Al-Eisawi 1998). Herbaceous and dwarf shrub sagebrush (*Artemisia* spp.) communities dominate in the deeper, non-saline soils, often in association with grasses. These are important grassland habitats and many Bedouin bring their livestock northward to take advantage of this seasonal spring and summer pasture. This region also contains large areas of barren, hard rocky soils—*hamada* or desert pavement (see Section 4.5) which result when wind has blown away the finely weathered soil particles. The finer grained products get taken in suspension and larger particles are removed through saltation and surface creep, leaving behind only gravel, boulders, and bare rock. In contrast areas all along the Euphrates and Tigris provide richer, riparian vegetation and habitats, with mixtures of woody *Tamarix, Salix*, and *Populus* species, as well as stands of *Typha, Phragmites*, and various small shrubs.

## 2.19 Kuwait

Kuwait is a small country (*c*. 17 600 km$^2$) in the northeastern part of the Arabian Peninsula; it makes up part of the north-western coastal flat of the Gulf (see Figure 2.13) and includes a number of offshore islands of which one, Failaka, is inhabited. Uninhabited islands include Bubiyan, Warbe, Mischan, and Um-Nemmel.

The landscape varies little, from flat to gently undulating, rising to a maximum of *c*. 280 m in the southwest. There the Jal-Az-Zor escarpment extends for some 80 km. Vegetation there is degraded and suffers effects of past militarization, including erosion from heavy traffic and significant ongoing overgrazing by sheep, goats, and camels.

Recent studies indicate there are some 374 species of native and naturalized plants in the country. Shrubs make up about a tenth of the flora, herbaceous perennials a quarter, and the rest are annuals.

Vegetation consists of steppe (treeless plain) or scrub, with only slight variation in terms of the sparse plant cover. Communities are often spatially discontinuous, due to the formation of "phytogenic mounds" or hillocks—*nabkhas*—that have distinct microclimates and soil properties (Schlesinger et al. 1990). El-Sheikh et al. (2010) showed how nabkha formation leads to spatial heterogeneity of soils. Infiltration of rainwater is limited to the area beneath plant canopies, while the more barren inter-plant spaces experience surface flow and soil erosion by wind and water, along with net nutrient losses. The patchiness is caused by the growth of *particular* plants, such as *Nitraria retusa*, acting as "keystone" species and essentially engineering their own ecosystems.

These nabkha plants create, modify, and maintain desert micro-habitats by improving and conserving soil water and nutrient availability in the patches where they are growing; they also promote biodiversity (El-Bana et al. 2002). In essence *nabkhas* are fertile microhabitats created by certain host plants enabling many other plants to persist there too (see Section 4.5). Nabkhas influence not only the community dynamics and survival of species but also prevent soil degradation and erosion (Danin 1996). Brown and Porembski (2000) have shown that nabkhas also provide "safe sites" for plants in the oil-contaminated areas of northern Kuwait.

In contrast to the larger (>1 m high), more stable dunes formed around perennials such as *Nitraria retusa* (Brown 2003), many smaller, less stratified and less nutrient-rich "micro-nabkhas" also exist. An array of similar communities characterizes the desert plain that occupies most of Kuwait (see Figure 2.19) (Brown 2003; Halwagy et al. 1982).

Overgrazing has altered the vegetation in many areas. Brown (2003) suggested that much of the southern half of the country would naturally be covered by a dwarf shrub community, dominated by *Rhanterium epapposum* (Asteraceae). However, locally the sedge *Cyperus conglomeratus* is replacing *Rhanterium* as the key perennial, largely due to overgrazing.

Likewise, northern Kuwait is now largely dominated by *Haloxylon salicornicum* nabkhas, and various authors have concluded this species too has largely replaced *R. epapposum*, mostly as a result of overgrazing and the resulting soil erosion. In some cases the transition to *H. salicornicum* occurs via a *Cyperus conglomeratus* community. According to Brown, *Cyperus* is generally more tolerant of grazing than *Rhanterium*. And while *Haloxylon* seems largely to be avoided by sheep it is a valuable grazing plant for camels. These observations suggest that both the intensity of grazing and some selective grazing

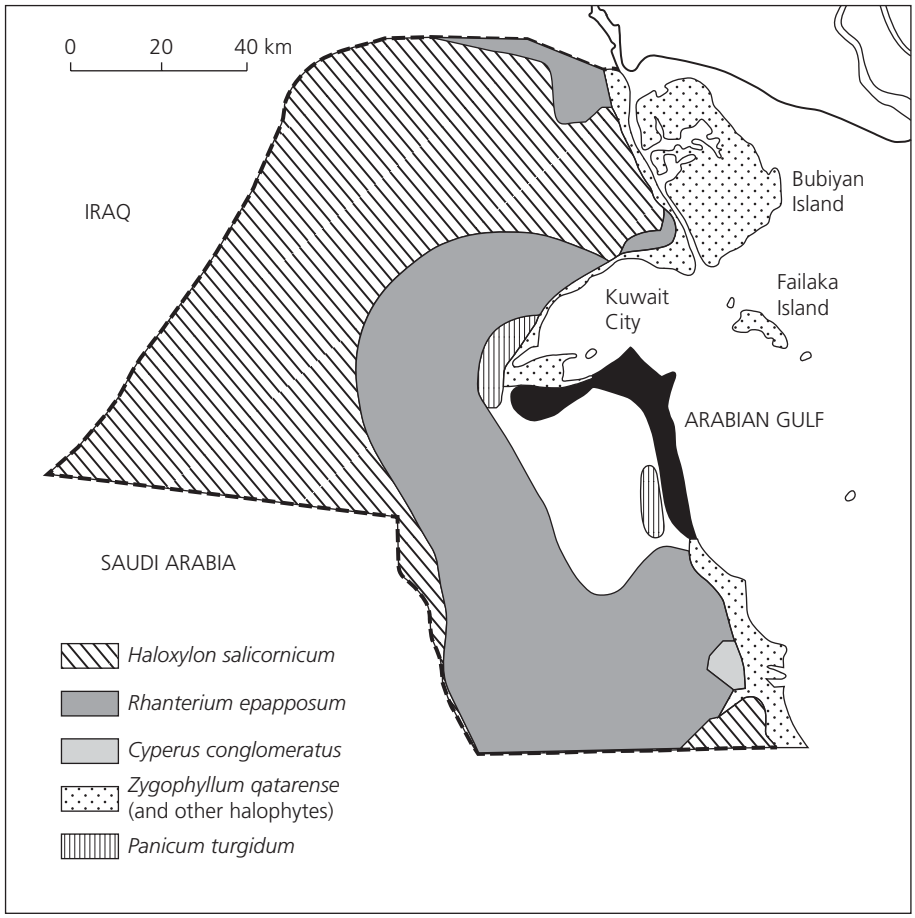



**Figure 2.19** Vegetation map of Kuwait (after Brown 2003, used with permission).

by different herbivores are changing the local flora. Any restoration will obviously require regulation of both the intensity and composition of grazing herds.

Other major communities are dominated by *Panicum turgidum, Zygophyllum coccinium*, and *Stipagrostis plumosa*. The coastal salt marshes and salt-affected lands are dominated by *Salicornia europaea, Juncus rigidus, Halocnemum strobilaceum, Seidlitztia rosmarinus, Nitraria retusa, Tamarix passerinoides, Aeluropus littoralis*, and *Cressa creti*ca.

## 2.20 Jordan

Jordan lies northwest of Saudi Arabia and is landlocked except at its southern extremity where some 26 km of shoreline along the Gulf of Aqaba provide access to the Red Sea. The country is relatively small, covering some 92 000 km$^2$, with a great geological rift running north–south and forming the depressions of Lake Tiberias (or Sea of Galilee), the Jordan Valley, and the Dead Sea (see Figure 2.20).

The country experiences a range of climatic conditions. In the mountainous areas snow regularly falls in winter, and the arid desert areas experience extreme heat in daytime, dropping to near freezing conditions at night (Shehadeh 1985). The mountainous regions around Ajlum and Shobak are rainy and summers tend to be mild, with a maximum monthly average not exceeding 22°C. Annual rainfall averages about 300 mm; and steppe conditions

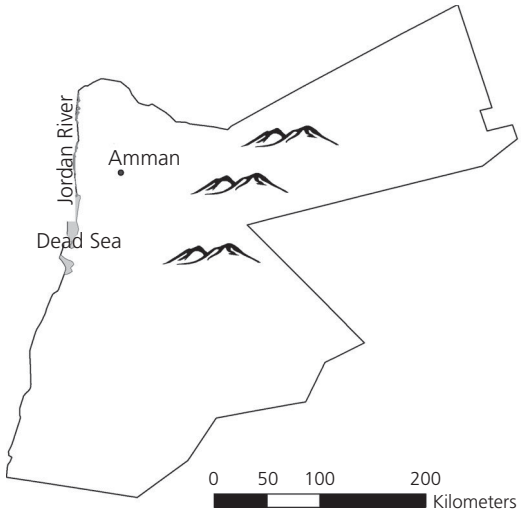



**Figure 2.20** Country map of Jordan with major cities and mountain ranges.

occur along the leeward slopes of the eastern mountains, with rainfall < 300 mm and average temperature in the hottest month of 30°C. The mild desert climate extends eastward across large areas of Jordan, with annual rainfall < 200 mm and maximum monthly average of 36°C. Climatic conditions are reflected in the vegetation across the country, which ranges from dense evergreen forest to only sparse vegetation and barren lands.

Most of Jordan is dry desert. Many areas are endorheic with no drainage to the sea, so sediment and salts accumulate in basins where moisture evaporates or seeps away. To the west the desert rises gradually—the Jordanian Highlands—a steppe country of high, deeply cut limestone plateaux, about 900 m up with occasional peaks reaching 1200–1700 m. These highlands include many long-established agricultural villages where most of the original forest vegetation was cleared very long ago.

The western edge of this plateau forms an escarpment along the eastern bank of the Jordan River–Dead Sea depression and its southern extension. The Dead Sea lies in the deepest depression on the continental surface of the Earth, with its surface some 400 m below sea level. The sense of depth in the depression is accentuated by surrounding peaks.

Wadi Araba is an extended great valley *c*. 170 km long and 5–20 km wide, bounded on the west by mountains of the far Negev desert and on the east by the Edumean Mountains. Elevation of the valley ranges from about –400 m at the southern shore of the Dead Sea to about 400 m, north of the Gulf of Aqaba. The valley represents an extremely dry desert with long dry summers and short winters; average annual rainfall is < 80 mm. Habitats include sand formations, rocky and gravel land, and salt marshes with tough, desert vegetation.

The diverse climate and habitats support a rich array of plant communities (Al-Eisawi 1998, Hegazy 1999a). At higher elevations where snow falls regularly in winter, the Mediterranean climate of the western mountains supports diverse Juniper forest. Major species include *Juniperus phoenicea, Cupressus sempervirens, Globularia arabica, Helianthemum vesicarium, Pinus halepensis, Quercus calliprinos, Fumana arabica, Crataegus azarolus, Asparagus aphyllus*, and *Urginea maritima*. Other Mediterranean vegetation includes communities with *Rhamnus palestinus, Tecrium polium, Noaea macronata, Retama raetam, Capparis spinosa, Astragalus spinosus, Seriphidium herba-alba*, and *Asphodelus ramosus*.

The arid deserts in the east and along the borders with Saudi Arabia and Iraq support different communities depending upon substrate (see Hegazy 1999a). Rocky and gravelly habitats are characterized by *Acacia* species, *Haloxylon scoparium, Zygophyllum dumosum*, and *Helianthemum lippii*. Sandy plains support *Seidlitzia rosmarinus, Anabasis articulata, Ephedra transitoria, Caligonum tetrapterum*, and *Zilla spinosa*. Sand dunes in Wadi Ram and Wadi Araba have sparse vegetation dominated by *Haloxylon persicum, Retama raetam, Calligonum comosum, Panicum turgidum, Pancratium sickenbergeri, Hyoscyamus pusillus*, and *Cakile maritima*. Depressions with fine deposits support many different shrubs, including *Ziziphus spina-christi, Calotropis procera, Ochradenus baccatus, Acacia* species, and *Cocculus pendulus*.

Like those of its neighbors, Jordan's flora is rich in elements from four phytogeographic regions: Mediterranean, Irano-Turanian, Saharo-Arabian, and Sudanian, or Tropical (Al-Eisawi, 1998). Mediterranean species make up the majority (e.g., *Quercus coccifera, Pinus halepensis, Juniperus*

*phoenicea, Cupressus sempervirens, Ceratonia silique, Pistacia palaestina, Arbutus andrachne, Alkana tinctoria, Ononis natrix*, and *Origanum syriacum*). Irano-Turanian examples include *Anabasis syriaca, Noaea mucronata, Salsola vermiculata, Gypsophila arabica, Adonis dentata, Seriphidium herba-alba, Ephedra alata*, and *Lactuca orientalis*.

Saharan species are well represented by the region's typical desert flora, e.g., *Zilla spinosa, Diplotaxis harra, Seidlitzia rosmarinus, Suaeda vermiculata, Astragalus spinosus, Asteriscus pygmaeus, Verbascum transjordannicum, Filago desertorum*, and *Schismus arabicus.*

Sudanian or Tropical elements in the flora are largely limited to the Rift Valley area. Major examples include *Ziziphus spina-christi, Maerua crassifolia, Balanites aegyptiaca, Salvadora persica, Ochradenus baccatus, Acacia tortilis, Acacia raddiana, Reseda muricata, Aerva javanica, Capparis deciduas, Leptadenia pyrotechnica, Abutilon fruticosum*, and *Cocculus pendulus*.

Although degraded, the flora of Jordan is nevertheless highly diverse and reasonably rich, considering the relatively small land area. Recent estimates suggest *c*. 2450 species, belonging to some 720 genera and 122 families (Al-Eisawi 1998). The largest families include the Asteraceae, Poaceae, Fabaceae, Apiaceae, Lamiaceae, Caryophyllaceae, Liliaceae, Boraginaceae, and Chenopodiaceae. Largest genera include *Astragalus, Trifolium, Silene, Euphorbia, Allium, Galium, Centaurea, Medicago, Anthemis, Salvia, Vicia, Trigonella, Ranunculus, Plantago*, and *Erodium*.

Parts of Jordan's flora are well studied; however, like most of the other floras in the Middle East, it has not yet been surveyed systematically (e.g., using standardized 10 km grids, ground-truthing, and field sampling), to build on knowledge from earlier herbarium samples. It has significant affinities with neighboring Israeli and Palestinian patterns, described in Section 2.21.1.

## 2.21 Israel, West Bank, and Gaza

This comparatively well-studied region (see Figure 2.21) is home to some 2682 plant species (Feinbrun-Dothan and Danin 1991; Shmida and Ritman 1985; and see the excellent online Flora of Israel project at the Hebrew University of Jerusalem [http://flora.org.il/en/plants/]). According to Danin (1999), the combined list of plants for Israel, the West Bank, Gaza, and Jordan totals some 2865 species.

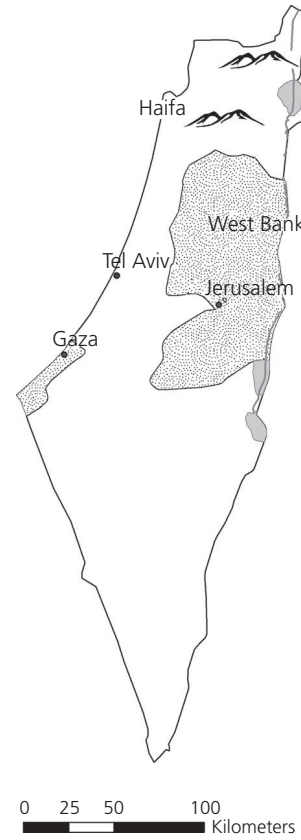



**Figure 2.21** Country map of Israel and Palestinian territories (West Bank and Gaza strip) with major cities and mountain ranges.

In Israel (total area about 22 000 km$^2$) as in the rest of the region, agriculture began long ago to compete with natural forest vegetation. As early as 7000 years ago, people in the eastern Mediterranean began to clear away the natural vegetation and develop agricultural land. Since then many different trees (including olives, *Olea europaea*, and almonds, *Amygdalus communis*) have been domesticated from the native flora. Timber taken from old growth forest and maquis was used in the construction of houses, for tools, and as fuel. The long history of farming, along with grazing by domestic livestock, has all significantly degraded the native flora, and

enabled introduction of many alien and invasive species.

At least 155 endemics are known from Israel (Shmida 1984), comprising about 6.5% of the flora. There is relatively low endemism here as in other desert regions. Of the endemics, many have Irano-Turanian affinities. Endemics occur mostly along the coastal plain, transition zones, and high mountains of the desert.

There are also *c*. 200 species found only in the Mount Hermon area (in Arabic known as Jabal El-Sheikh or Ash Shaykh) of the Golan Heights is in the Anti-Lebanon range and constitutes the southernmost part, running parallel to the Lebanon range on the west. There a montane forest extends from about 1300 to 1700 m, including deciduous trees like *Quercus boissieri, Q. libani*, and *Acer microphyllum*, and several species of *Crataegus, Amygdalus*, and *Prunus*. Ground vegetation includes perennial grasses and other herbaceous species.

Habitat conditions in Israel range from the relatively moist locations in the north to desert in the south. Variation in topography and elevation helps create the warm climates of the Jordan-to-Arava rift valleys and the relatively cold climate of Mount Hermon.

In other areas local climatic variation increases the diversity of habitats and associated plant species. Geomorphological structures here are comparatively small, but the diversity of rock types is high. As a result many distinctive soil types are found over a relatively small area, further increasing the diversity of local conditions to which plants adapt.

### 2.21.1 Vegetation of the mesic parts of Israel and Jordan: Maquis and forest

The major woodlands of Israel are found in the mountains of Judea, Carmel, Galilee, and at the foot of Mount Hermon (Danin 1999); those of Jordan are north of Amman. Forest and maquis, or Mediterranean shrubland dominated by the sclerophyllous evergreen *Quercus calliprinos* and deciduous *Pistacia palaestina* are still found commonly on hard limestone with mineral-rich soil in the Upper Galilee and Mount Carmel regions, and also the Jebel Ajlun area in Jordan (mesic sites), and in the Judean mountains (mostly xeric sites). Other species differ according to soil and rainfall. In the Upper Galilee (the wettest part of Israel), associated species include *Rhamnus alaternus, R. punctatus, Eriolobus trilobatus, Acer obtusifolium, Crataegus azarolus, C. monogyna, Arbutus andrachne, Laurus nobilis*, the vines *Clematis flammula* and *Hedera helix*, and many geophytes and herbaceous species (Danin 1999).

According to Danin, truly mesophytic components rarely occur in the maquis of the Judean Mountains. In the driest stands there are fewer, sparser species and *Rhamnus lycioides* ssp. *graecus* is the only other tree present with *Q. calliprinos*. Typical associated species include *Rubia tenuifolia, Lonicera etrusca, Asparagus aphyllus*, and *Ephedra foeminea*. (See, too, Section 4.8 for a comparison of patterns from Israeli and Californian maquis vegetation.)

### 2.21.2 Open forests of *Quercus ithaburensis*, and other vegetation

The Tabor oak, *Quercus ithaburensis*, is often found associated with *Styrax officinalis*, sometimes *Pistacia atlantica*, and nearly always with a large group of herbaceous species. Where this community develops on chalky ground, the few semi-shrubs are mainly *Majorana syriac*a. According to Danin this type of forest, once common on the Sharon Plain, is now mostly limited to isolated oak trees, and an ecological reserve located between Haifa and Tel Aviv. Large oak forests are still present in the Lower Galilee and Golan, at elevations below 500 m. At the same time Tabor woodlands in northwestern Jordan are fairly well conserved, covering considerable areas of rocky terrain west of Irbid, at the western escarpments of the Jordanian plateau (to about 500 m).

*Ziziphus spina-christi*, the Christ's thorn jujube, is a low, spiny tree with edible fruit, common in Israeli grasslands along with abundant, large-seeded annuals like wild wheat, barley, and oats. These grow on the warm, stony-rocky slopes of Galilee, Golan, Gilead, and Samaria, descending to the rift valley at and below sea level (Danin 1999). *Ziziphus spina-christi* also dominates in true savannas across Africa, where it is often associated with Sudanian perennial grasses.

On windward slopes of the peaks of Mount Hermon (above 1900 m), the vegetation is dominated by shrubs that look like spiny cushions. This is often

called "tragacanth" vegetation, based on the presence of several species of the genus *Astragalus*, section *Tragacantha*. Other species of tragacanth/*Astragalus* occur in areas far from Mount Hermon and the Eastern Lebanons. *Astragalus bethlehemiticus* is often part of steppes and rocky vegetation in the shrub-steppes of the Negev Highlands and southwestern Jordan; *A. echinus* is found at the high elevations of the southern Sinai (Danin 1999).

These species and others (e.g., genus *Acantholimon*) are part of the "cushion-plant" communities found in many Mediterranean parts of the Middle East (Shmida 1977) (and see Section 2.26). The cushion growth form is associated with cold winters and high wind speeds; precipitation that comes mainly in the form of snow; dry summers; and sometimes intense grazing pressure from domestic animals. Because of the short growing season and harsh environment, only a few annual species tend to occur among these perennial cushion plants.

Semi-shrubs (see Section 4.1) are scattered across most of the Negev Highlands, Judean Desert, the Sinai and southwestern Jordan, all areas with 80–250 mm mean annual rainfall. Common dominants in these shrub-steppes are *Artemisia sieberi, Noaea mucronata*, and *Gymnocarpos decander*. The biomass of annuals in communities that develop on the shallow, stony-rocky soils there is typically low compared to in fine-grained and deeper soils. Salts (at concentrations of 8 ppm) carried by clouds and rain from the Mediterranean Sea remain in the soil and accumulate. Soil often becomes too dry or saline for the growth of annuals.

According to Danin, nearly monospecific stands of semi-shrubs occur in the Negev, Sinai, and southwestern Jordan shrub-steppe regions, typically a single species adapted to the local saline conditions. Common dominants include *Reaumuria hirtella, R. negevensis, Salsola vermiculata, Bassia arabica*, and *Atriplex glauca* on richer chalk- and marl-derived soils; *Anabasis syriaca* and *Haloxylon scoparium* on loess soils. In moist years, annuals can establish here; sometimes in high salinity areas there may be monospecific patches of salt-resistant annuals. During moist years in the shrub-steppe regions, conspicuous geophytes including species of *Tulipa, Iris, Ixiolirion, Ranunculus*, and *Anemone* also bloom in abundance (Danin 1999).

At lower elevations a few other trees—*Acacia raddiana, A. pachyceras, Tamarix nilotica*, and *T. aphylla*—occur, as well as many of the species listed earlier. Many small springs arise in the limestone hills of the western Sinai and sandstone hills of southwestern Jordan. Their location is often signaled by the presence of date palms (*Phoenix dactylifera*), which are usually restricted to sites with a high freshwater table. Date palms in turn, acting like giant nabkhas, are often associated with *Nitraria retusa, Juncus arabicus, Phragmites australis*, and *Cressa creti*ca.

Shmida and Aronson (1986) looked closely at the 116 species which are considered (phytogeographically) as Sudanian. These all occur in the Dead Sea Rift Valley. Although paleo-macrofossils are nearly non-existent in the area, other evidence (including the low degree of endemism, disjunctiveness, and adaptations to aridity and long-distance dispersal) suggested that most of the Sudanian elements in the Dead Sea Rift were of recent origin (i.e., post-Pleistocene).

## 2.22 Syria

As a large and largely desert country (area 185 180 km$^2$), Syria is situated at the eastern end of the Mediterranean, bordered by Iraq, Israel, Lebanon, Jordan, and Turkey (see Figure 2.22). About two-thirds of its land area is arable, either irrigated or rain-fed. The climate is greatly influenced by the Mediterranean, with rainfall decreasing from west to east. The coastal plain may receive rainfall of up to 1000 mm or more in a year, but toward the inland desert in eastern Syria, the average annual rainfall decreases to < 80 mm. Mean annual temperature is about 20°C, with min–max temperatures ranging from 0 to 47°C (see Hegazy 1999a).

For at least 4000 years the "fertile crescent" between the Tigris and Euphrates has supported sophisticated agriculture. (According to the estimates of Moore (2000), the agricultural settlement at Abu Hereyra in modern Syria, supported a population of *c*. 10 000, between 15 000 and 6000 years ago). Today much of Syria is at risk of desertification.

The large Syrian Desert is bounded to the west by Mount Hermon and the Eastern Lebanons, with peaks at 2700 m. The region includes an array of vegetation types including species typical of the

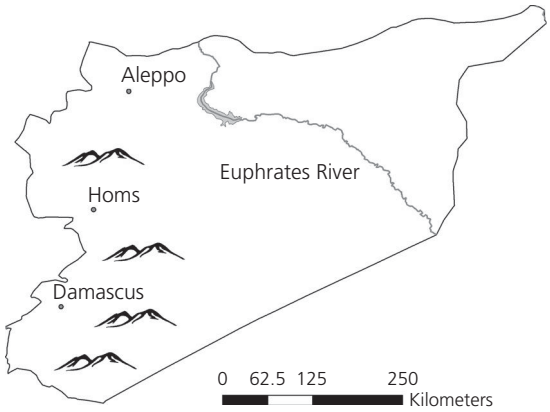



**Figure 2.22** Country map of Syria with major cities and mountain ranges.

adjacent Mediterranean, Irano-Turanian, Saharo-Sindian, and Sudano-Deccanian[26] phytogeographic regions (Zohary 1973). There are also relictual endemics typical of the northerly Euro-Siberian flora, like *Anthemis cassia, Pyrethrum cassium*, and *Allium calyptratum* (Zohary 1973).

Syria contains some 3100 species of plants, of which 395 (13%) are regarded as endemic (Davis et al. 1994). Greatest endemism occurs for Irano–Turanian species of the following genera: *Astragalus, Onobrychis, Anthemis, Cousinia, Acantholimon, Silene, Allium, Salvia*, and *Iris*. These are mostly "point" endemics restricted to particular areas.

Topographically much of the country is a great plateau, at an average altitude of about 700 m, and gently sloping to the east and southeast where the Syrian Desert begins. The mountainous northwestern region includes the country's highest peak (Mount Akra 1730 m); the lower land to the south also has mountains, including Mounts Seir (1600 m), Jbal (1400 m), Moab, Gilead, and Golan (*c.* 1300 m). East of the Golan is the fertile Bashan plain and mountainous Jebel Druz, with summits reaching 1900 m. The mountains are cut by a small number of rivers and streams that flow to the Mediterranean.

The western slopes in Syria support various species of *Quercus, Acer*, and *Juniperus*, as well as *Ostrya carpinifolia, Fraxinus ornus, Pyrus syriaca*, and *Eriolobus trilobatus*. The eastern slopes of the Anti-Lebanons throughout the Baqa valley (including Homs, Hama, and Aleppo) all support several species of *Amygdalus, Gundelia tournefortii, Asphodelus microcarpus, Rhamnus palaestinus*, and *Pistacia atlantica* (Hegazy 1999a; Zohary 1973).

Although for the most part the Syrian Desert has fairly continuous cover, communities are not especially rich. Such species-poor vegetation may be a result of the intensity of human impacts over so long a time, particularly in the south which was part of the earliest ("Silk Road") trading caravan routes between ancient Persia and Egypt.

In the north, from El-Haseke to Cerablus, the vegetation is dominated by *Phlomis burguieri, Centauria balsamitoides, Oliveria orientalis*, and *Cousinia chaborasica* (Sankary 1977). In the northwest, from Aleppo to Hama, the vegetation is dominated by *Poa sinaica* and *Carex stenophylla*. The east has mostly gypsum and sandy soils and plant communities dominated by *Salsola spinosa, Scabiosa olivieri, Astragalus mosselensis, Erodium glaucophyllum, Achillea conferta, Cornulaca setifera*, and *Aristida plumosa*.

In the southeast, calcareous and sandy soils support highly degraded vegetation, dominated by *Haloxylon articulatum, Anabasis aphylla*, and *Poa sinai*ca. The southern region from Damascus to Suweida has species of *Linum, Anabasis setifera*, and *Halogeton alopecuroides*. The inland salt marshes and saline habitats are characterized by *Halocnemum strobilaceum, Salicornia herbacea, Aeluropus littoralis, Juncus maritimus*, and *Tamarix* species (Sankary 1986). In the west, common species include *Haloxylon articulatum, Peganum harmala*, and *Stipa parviflora*.

## 2.23 Lebanon

Lebanon is a small, mountainous country in the Levant, bordered by Syria and Israel, with an area *c.* 10 400 km$^2$ (see Figure 2.23). The flora includes many

[26] The category of "Sudano-Deccanian" was proposed by Eig (1931/1932), and is also known as the North African Steppe element, and the Tropical and North African–Indian Desert element. The Deccan Plateau is a large plateau in India that makes up most of the southern part of the country. It rises to 100 metres in the north, and more than 1 km in the south, forming a great raised triangle of former lava flow, within the larger, downward-pointing triangle of the Indian subcontinent.

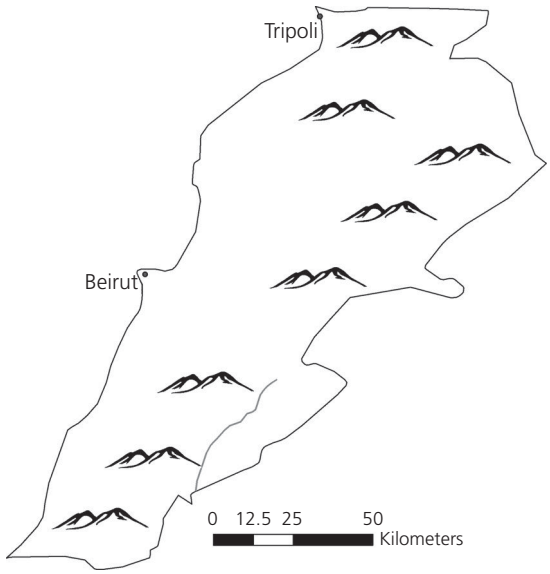



**Figure 2.23** Country map of Lebanon with major cities and mountain ranges.

Euro–Siberian relicts in "Oro-Mediterranean"[27] and higher subalpine regions. Irano–Turanian species tend to occur on the summits and eastern slopes. The relatively rich flora (as species per unit area) includes some 2600 vascular plants, of which 311 (12%) are endemic (Davis et al. 1994).

The main mountains are the Lebanons, with their highest peak (3090 m) in the north; the Eastern Lebanons (also called the Anti-Lebanons) run east of the Lebanons; and to the south, Jabal El-Sheikh (Mount Hermon) with its peak at 2700 m, south of the Eastern Lebanons. All the Lebanese mountains are under threat from climate change, and the regional habitat has been given high priorities in a conservation plan to preserve this ecosystem (Victor 2012).

Notable plants include various members of the montane forest flora. The iconic "Cedar of Lebanon," *Cedrus libani*, is one of the most celebrated trees of the Old World and its recorded history goes back to Biblical times. Forests in the eastern Mediterranean have suffered extensive damage; what remains is estimated to represent barely 5% of the original area (Boulos 1985). The finest remnant cedars in Lebanon grow between 1500 and 1800 m. Other conifers associated with the cedars are *Juniperus excelsa, J. oxycedrus*, and *J. drupacea*.

To the north, *Abies cilicica* replaces *J. drupacea*. Two coastal oaks, *Quercus coccifera* and *Q. infectoria* also occur there along with other oaks and a variety of trees and shrubs, such as *Styrax officinalis, Sorbus umbellata, Cotoneaster nummularia*, and *Lonicera nummulariifolia*.

Sand dune communities along the Mediterranean support large populations of *Ammophila arenaria* and *Retama raetam* (both of them able to produce adventitious roots on stems that get covered by sand). In the mountains elevational banding occurs, with a lower western belt of vegetation at 200–300 m, including *Hyperrhenia hirta, Myrtus communis*, and *Pinus brutia* communities. Above this "Eu-Mediterranean"[28] belt and extending up to about 1500 m elevation is an "Oro-Mediterranean" belt, temperate Mediterranean vegetation typically including beech trees (*Fagus sylvatica*) over calcareous soil. In Lebanon this includes *Quercus calliprinos, Pistacia palaestina*, and various species of pine. At elevations of 1500–2000 m, cedar forests are common, with *Cedrus libani, Abies cilicica*, and *Juniperus excelsa*. Above 2000 m, subalpine and alpine belts are characterized by cushion plants including species of *Astragalus* and *Acantholimon armenum*, also *Salsola canescens, Minuartia libanotica, Festuca pinifolia*, and *Marrubium libanoticum*. Above 2500 m the vegetation is generally poorly developed, with only sparse cover of *Heracleum humile, Cistopteris fragilis, Oxyria digyna, Potentilla geranioides, Ranunculus* species, and *Scorzonera alpina*. Western slopes generally support true "Mediterranean" vegetation, eastern slopes less so (and see Section 4.8).

## 2.24 Cyprus

Most of the islands in the Mediterranean, including Cyprus, are continental in origin, essentially

[27] Oro-mediterranean is a middle-elevation Mediterranean life-zone (temperate zone, 1100–1450 m).

[28] Eu-mediterranean is another Mediterranean life zone (lower subtropical belt, 0–400 m). Other species at this lower level include Holm oak (*Quercus ilex*), Kermes oak (*Quercus coccifera*), and Olive tree (*Olea europaea*). More humid habitats have Bay laurel (*Laurus nobilis*) and Oleander (*Nerium oleander*) communities.

fragments of land that became "separated" from the adjacent mainland areas due to changing water levels. Cyprus is the third largest island in the Mediterranean, with a land area of 9255 km$^2$. It is 60 km from the southern coast of Turkey and 120 from Syria (see Figure 2.24). The island has two mountain ranges, separated by a region of low plains.

The limestone-based Kyrenia Mountains (*c.* 1025 m) lie adjacent and parallel to the northern coast. The igneous, acidic Troodos Mountains (*c.* 1960 m) lie in the central and western parts of the island.

There are some 1650 plant species on the island, of which roughly 5% are endemic (Groombridge 1992). Floristically Cyprus is closely related to southern Turkey and Syria. Irano–Turanian affinities predominate, though many European species occur too (e.g., the clovers *Trifolium pratense* and *T. repens*), together with elements from the east such as *Corydalis rutifolia*; and some 30 species including an endemic species of *Bosea*, regarded as tropical elements in the flora. One genus is endemic, the grass *Lindbergella sintenisii* (Davis et al. 1994; Zohary1973).

The open forest mountain vegetation in the Kyrenia range is dominated by *Pinus brutia* and *Cupressus sempervirens*, while in the Troodos there are forests of the endemic *Cedrus libani* subsp. *brevifolia, Pinus nigra* subsp. *pallasiana, Juniperus foetidissima*, and the endemic *Quercus alnifolius* (Meikle 1977–1985; Thirgood 1981). Most of the central low plains vegetation has been converted to farmland. Communities dominated by *Sarcopoterium spinosum, Pistacia lentiscus, Ceratonia silique, Pinus halepensis*, and *P. brutia* cover the uncultivated low plains.

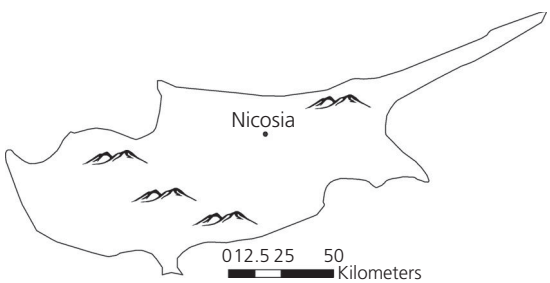



**Figure 2.24** Country map of Cyprus with major cities and mountain ranges.

The island includes forests containing both coniferous and broadleaved trees, including *Pinus brutia* and several species of cypress and oak. Nearly a fifth of the island is woodland and the forests in the Troodos and Kyrenia are still extensive, along with tall shrub communities containing *Quercus alnifolia, Q. coccifera, Arbutus andrachne, Pistacia terebinthus, Olea europaea*, and *Styrax officinalis*. Over most of the island any land not under the plow has a grazed covering of garrigue[29] scrubland. This includes low bushes of *Cistus, Genista sphacelata, Lithospermum hispidulum*, and others.

## 2.25 Turkey

Turkey is a large country (*c.* 780 000 km$^2$) sitting at the nexus of Europe and the Middle East, Central Asia and Africa (see Figure 2.25). Its location—as much as its geologically active mountains and the fact it is surrounded by three great seas—has resulted in very high levels of terrestrial-, fresh water-, and marine biodiversity. Most of Turkey is included within three rich, global biodiversity hotspots—the Caucasus, Irano–Anatolian, and Mediterranean—and there are nearly 9000 native vascular plants, of which almost a third are endemic. Its major wetlands lie on one of the three principal migration routes for Eurasian birds overwintering in Africa (see Şekercioğlu et al. 2011; Waldron et al. 2013).

Despite its international recognition as an ecological hotspot, Turkey faces significant challenges in regard to the conservation of its rich biodiversity. Like the rest of the region, Turkish Anatolia was an early locus of human civilization and millennia of human activities there have significantly altered the original ecosystems. Nevertheless, according to Şekercioğlu et al. (2011) the greatest threats to biodiversity have developed since about 1950 and particularly in the most recent decades. Whereas Turkey's total forest area increased by 5.9% from 1973 to the present, the endemic-rich Mediterranean maquis,

[29] Garrigue (or phrygana) is a type of low, soft-leaved scrubland ecoregion and plant community found in the Mediterranean forests, woodlands, and scrub biome. It occurs on limestone soils around the Mediterranean Basin, generally near the coast, where the climate is ameliorated but where annual summer drought conditions obtain. See too Section 4.8.

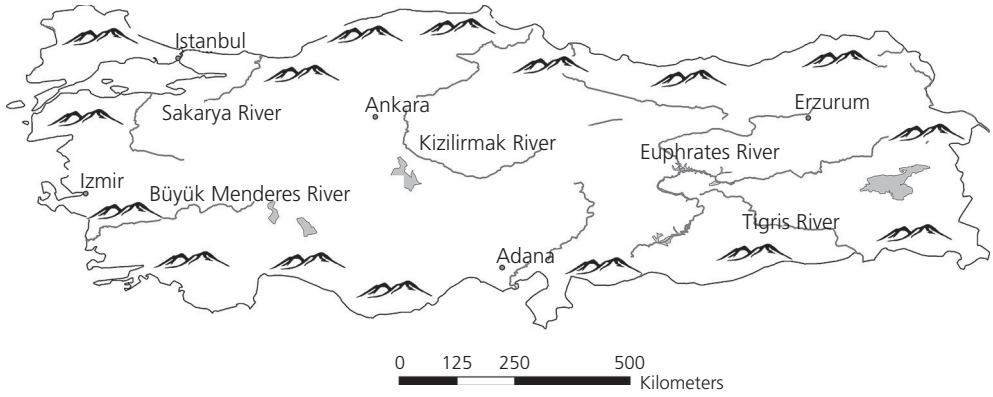



**Figure 2.25** Country map of Turkey with major cities and mountain ranges.

grasslands, coastal areas, wetland, and riverine floras are all fast disappearing. At the same time, overgrazing and widespread soil erosion degrade the vast steppe- and rangelands.

Turkish landforms are among the most complex of all Middle Eastern countries. The variously oriented mountain chains, deep valleys, and plateaux are of course major factors generating the original diversity of vegetation and richness of the flora. Its large area has two asymmetric parts. Most of Turkey is made up of Anatolia, a great semiarid central plateau, rimmed by hills and mountains connecting to Eurasia. The westernmost 3% of Turkey, known as Thrace, is separated by the Bosporus, the Sea of Marmara, and the Dardanelles straits, connecting the Black Sea to the Aegean and Mediterranean (see Figure 2.25).

Most of Turkey is rough and mountainous. The terrain becomes particularly complex in the east where two ranges converge, much of it above 1500 m, reaching a high point along the eastern borders with Armenia, Azerbaijan, and Iran. Mount Ararat, at 5137 m, is situated in Turkey near where the boundaries of these four countries come together.

Except for a relatively small portion of its territory near Syria which is a continuation of the Arabian Platform, most of Turkey is part of the great Alpine belt of mountains extending from the Atlantic to the Himalayas. This was formed during the Tertiary as Arabian, African, and Indian continental plates began to collide with Eurasia. The region remains one of the world's most seismically active, experiencing frequent earthquakes and occasional volcanic eruptions.[30]

The flora is among the richest in the Middle East, with some 8650 species, and 2675 endemics (30.9%) (Davis et al. 1994). This is exceptionally high endemism. The country is of special interest as a global center of plant diversity. Zohary (1973) concluded the flora contained a large number of "giant" genera, highly speciose and rich in species including e.g., *Isatis, Draba, Alyssum, Astragalus, Alcea, Phlomis, Salvia, Scrophularia, Verbascum, Veronica, Anthemis, Allium, Iris*, and *Quercus*.

Within Turkey four major regions have been recognized as centers of plant diversity and endemism. These are the Taurus mountain range; southwestern Anatolia; northeastern Anatolia; and the Levantine Uplands (see Figure 2.25). According to Zohary (1973) and Davis et al. (1994), at least 2500 species occur in the Isaurian, Lycaonian, and Cilician Taurus regions, and of these some 520 are endemic to Turkey. Southwestern Anatolia has *c.* 3365 species of which some 675 are endemic. The northeast of Anatolia has at least 2460 species and 300 endemics.

[30] The most severe earthquake in Turkey in the twentieth century occurred in 1939, in Erzincan (causing *c.* 40 000 deaths) and the more recent, 1999 Izmit earthquake, close to the Bosporus, may have killed as many as 45 000.

The plant-rich Levantine Uplands region includes southern Turkey (and Hatay province[31]) as well as neighboring northwestern Syria (Jebel an Nusayriyah and associated hills, including Latakia), the whole of Lebanon, and parts of northern Israel and Jordan as far as Mount Carmel. It has an approximate total area of 97 000 km$^2$, and some 4160 species are known from the region. These are distributed among 146 families and *c*. 950 genera. Overall some 635 (14%) are endemics, and while there are no endemic families, seven monotypic genera are endemic to the region—*Astoma, Chaetosciadium*, and *Synelcosciadium* (Apiaceae), *Mosbeovia* (Scrophulariaceae), *Postia* (Asteraceae), and *Pilgerochloa* and *Lycochloa* (Poaceae).

Zohary (1973) early on showed that the Turkish flora was the richest in the Middle East in terms of both endemics and tree species. Native trees and shrubs comprise representatives of many genera, including *Sorbus, Pyrus, Malus, Crataegus, Amygdalus, Prunus*, and *Cerasus*. Many of these fruit trees were first domesticated here and indeed Turkey remains a major center of tree fruit horticulture (in particular cherry, plum, apple, pear, almond, and olive). The rich alpine flora shows many affinities with similar environments in central and southern Europe and central Asia (Zohary 1973).

In the central Anatolian plateau there are wide west-to-east valleys where endorheic depressions form undrained saline flats and lakes. The largest is the saline Lake Tüz Gölü. This inland sea, 130 km southeast of Ankara, has an area of about 1100 km$^2$ and is at an altitude of about 900 m. It is very shallow, mostly < 1 m in depth (Davis et al. 1994). The flora around the lake is rich in dryland specialists, with at least 12 endemics, including *Kalidiopsis wagenitzii*, an endemic genus. There are at least 35 species of Chenopodiaceae including six endemics and 14 species of Plumbaginaceae (three endemics) (Davis et al. 1994; Zohary 1973). Surrounding halophytic vegetation includes *Artemisia fragrans, Salsola inermis, Limonium iconium, L. gmelinii, L. globuliferum, Aeluropus lagopoides, Halocnemum strobilaceum, Frankenia hirsuta, Petrosimonia birandii, Puccinellia distans, Juncus maritimus*, and *Salicornia europaea*.

[31] Neighboring Syria has long had a claim to this province.

## 2.26 Iran

There are three main physiographic regions in western Iran—the Mesopotamian Lowland, Interior Plateaux, and Zagros Mountains. The climate there is mostly Mediterranean, with most precipitation coming in the fall, winter, and spring. Summers are dry and hot, up to 35°C in Esfahan. The Zagros form a major barrier to any moisture-bearing storms from the Mediterranean; as a result the very dry Interior Plateaux lie in their rain shadow (see Figure 2.26). Annual precipitation in the Zagros is 400–1000 mm, in the Lowlands 300–400 mm, and in the Interior 200–300 mm.

The dominant vegetation in the western part of Iran includes four main community types (Hedge 1985; Zohary 1973).

1. Mesopotamian lowland steppe, at 200–600 m: This is desert steppe with shrubs such as *Paliurus spina-christi* and abundant *Artemisia* species.
2. Forest steppe and savanna of Zagros foothills and mountains of the Interior Plateaux, at 500–700 m: Native trees and shrubs include *Amygdalus scoparia, Pistacia atlantica*, and *Ziziphus spina-christi*. Unfortunately much of this vegetation has largely disappeared as a result of human activity, mainly clearing for grain production.
3. Zagros oak forest, 700–800 m up to 2500 m: It includes *Quercus brantii, Q. infectoria, Pyrus syriaca, Acer cinerascens, Pistacia atlantica*, and *Fraxinus rotundifolia*. The open forest has been heavily disturbed or destroyed, by charcoal production, livestock grazing, and clearing for grain production.
4. Alpine area and Interior Plateau steppe, above 2000 m in the Zagros: The Alpine zone consists of extensive snow beds, and very short turf in windswept areas. This is also found in areas further east, with < 300 mm rain per year, and includes *Artemisia* steppe vegetation between 1400 and 2500 m.

Like Turkey, Iran's flora is also very rich. The comprehensive Flora Iranica is not limited in its remit to the current political boundaries of Iran but rather covers all of Iran as well as Afghanistan, Northern Iraq, the mountains of Turkmenistan, small parts of Azerbaijan (Talesh), and western Pakistan to the

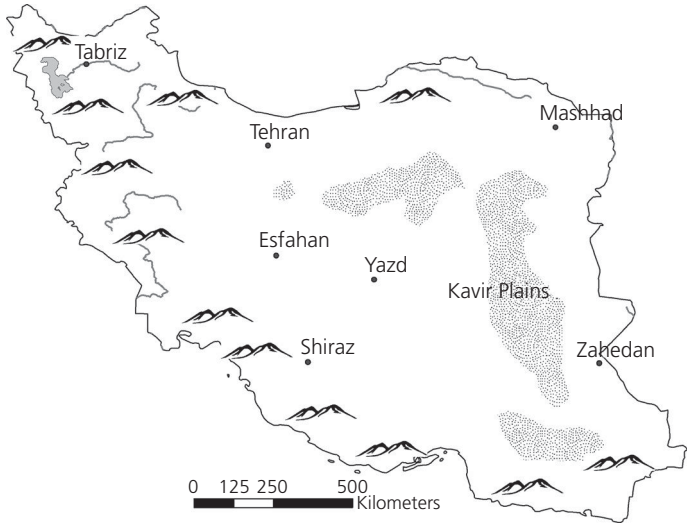



**Figure 2.26** Country map of Iran with major cities and mountain ranges.

Sind River (Rechinger 1963–2005; and see Ghahreman and Attar 1999). The large flora (and expanded area) includes some 176 volumes, listing (as of 1999) some 6417 species, in 1215 genera and 167 families. There are at least 1812 known endemics and 1420 rare species. Since 1850 about 100 species are known to have become extinct (Ghahreman and Attar 1999; Hedge and Wendelbo 1978). Iran's flora is likely the richest in the Irano–Turanian, distinctly Middle Eastern regional center of endemism (Davis et al. 1994). Several endemic genera are known, including *Acanthocardamum, Pseudofortuynia, Straussiella*, and *Zerdana*, all in the Brassicaceae.

The Great Iranian "Kavir" is a vast and spectacular expanse of inland plains and endorheic basins in the center and east of the country. Despite the severe, semi-arid climate, the Touran protected area/biosphere reserve there (18 640 km$^2$) offers a remarkable center of specialized, salt-tolerant plant diversity (Davis et al. 1994). The area extends across northeast and central Iran and is characterized by typical arid landforms. The southern part of the protected area includes a corner of the Great Kavir, the largest salt desert in the world. It is estimated this area contains about 1000 vascular plant species. Significant diversity is found in certain genera in particular: *Astragalus* (32 species), *Salsola* (18), and *Heliotropium* (12), for example. Most of the flora is Irano–Turanian and many species are endemic to central or eastern Iran including *Anabasis calcarea*, a striking succulent found on gypsiferous marl deposits (Freitag 1986). Also *Salsola abarghuensis*, a shrub found in wet salt marshes, and the sand dune shrub *Astragalus kavirense*.

Kavir National Park is a smaller, related dryland-protected zone which includes desert, semi-desert, dry steppe, and semi-desert mountains. The park is located in Semnan province, south of Tehran, and sits on the western end of one of Iran's two major deserts, the Dasht-e Kavir (or Great Salt Desert). The park is dominated by Daracheh-ye Namak (Salt Lake), a huge white saltpan just beyond the park boundaries. This is actually a salt marsh, with water flowing slowly into the lake from the north via the Qom River, which also flows through the northern part of the park. The Qom is one of the few year-round rivers in the entire desert expanse of Iran; nevertheless the river never reaches the sea but rather drains one of the many endorheic basins. Typically the area receives around 150 mm of rain a year, mostly between November and May.

Some 283 species of higher plants have been found in the Kavir Park area, more than half of them annuals (Rechinger and Wendlebo 1976). The most highly represented family is the Chenopodiaceae (35 species) (see, too, Section 4.2). Perhaps as harbinger of what is to come, Breckle (2002) compared this region with the dried former seabed of

the Aral Sea, in the expanding Aralkum Desert, an area of *c*. 40 000 km$^2$ where, since 1960, some 270 terrestrial plant species have invaded, including 70 chenopod species.

The vegetation of the endorheic basins of the Kavir is finely adapted to drought and salt. To reduce water loss and deter grazing, many species grow leaves with thorns (see Section 5.6). Chenopods continue to dominate most of the communities on non-sandy areas with annual precipitation < 150 mm. According to Breckle, they often exhibit the peculiarity of flowering during the arid season and being active in terms of growth during most of the dry summer.

Akhani (2004) investigated endemism in southwestern Iran and concluded the majority of endemics there have Irano–Turanian origins. Akhani argued there seems to have been relatively little south-eastward movement of biota, but abundant westward expansion, at least in regard to the highland vegetation.

Most of the nearly forty endemics studied by Akhani were restricted to the western foothills of the Zagros, in southwestern Iran and adjacent Iraq—the "Persian foothills" of Rechinger (1972) and Rechinger and Lack (1991)—and noted for their biogeographic significance. The ranges of some species also extend to suitable microhabitats at other altitudes. According to Akhani this transition zone separates the higher altitude of the Zagros Mountains, with its essential Irano–Turanian flora to the west and northwest, from Khuzestan and the lowlands of Iraq, with a more Saharo–Sindian flora to the south and southeast.

Species such as *Oliveria decumbens, Cousinia stenocephala, Phlomis bruguieri, Scabiosa leucactis*, and *Brassica aucheri* dominate the entire western foothills of the Zagros. Many are calcicoles or "gypsophilous" species, favoring the limestone and gypsum-rich (CaSO4) environments that are common in Iran (Akhani 1996).

The lowland flora of the region is strongly influenced by Saharo–Sindian and Somali–Masai elements. As mentioned by Rechinger and elaborated by White and Léonard (1991), the Saharo–Sindian flora generally has few endemic taxa, with most of them also being widely distributed (which was why White and Léonard described southwestern Iran as Saharo–Sindian).

Akhani (2004) also noted that in the southern and southwestern parts of Iran, warfare and other internal conflicts, plus heavy grazing pressure and an absence of any adequately protected areas or national parks leave the flora under significant threat. At the same time, the traditionally nomadic people of the region depend on plants for fuel and it is difficult to manage or regulate their practices and use of local plant resources.

The genus *Dionysia* (Primulaceae) exemplifies the adaptive radiation and remarkable diversification that can happen in Iranian mountain environments. In general the dionysias are tuft-forming obligate chasmophytes, another kind of cushion plant (see Section 2.21); these live in rock crevices on vertical limestone cliffs, from about 1500 m to over 3500 m. There are at least 49 species of *Dionysia*, mainly centered on Iran and Afghanistan, but also in Iraq and Pakistan.

The comparatively large-leaved and loose-tufted species, with well-developed inflorescences, are considered to be the more primitive member of the genus and are frequently found in the mountains surrounding the Iranian highlands. Other species form dense to compact tufts and have comparatively thick, often pubescent leaves with strongly reduced venation, and an inflorescence typically reduced to a single, sessile flower per leafy rosette. These latter, newer, phylogenetically more advanced species occur in the inner, drier ranges of the country (Wendelbo 1971). Reductions in leaf size, venation, and size of inflorescence, as well as the formation of dense tufts, are all adaptions to aridity (see Chapter 5 and Figure 2.27 A–E).

Liden (2007) described many species of *Dionysia* in the western Zagros. All were growing in crevices in vertical limestone or conglomerate cliffs, often under small rocky overhangs where there was some protection as well as a steady "drip feed" of moisture from the limestone rocks above. All were endemic to Iran and all seemed to occur in restricted geographical areas within the Zagros. According to Liden it was rare to see individuals of two species sharing the same cliff. At the same time, sheltered among the rocky habitats of southern Arabia, there is a single endemic Omani *Dionysia, D. mira*, growing directly across from the Zagros on the other side of the Gulf, in Oman's Hajar Mountains (Deil and al Gifri 1998).

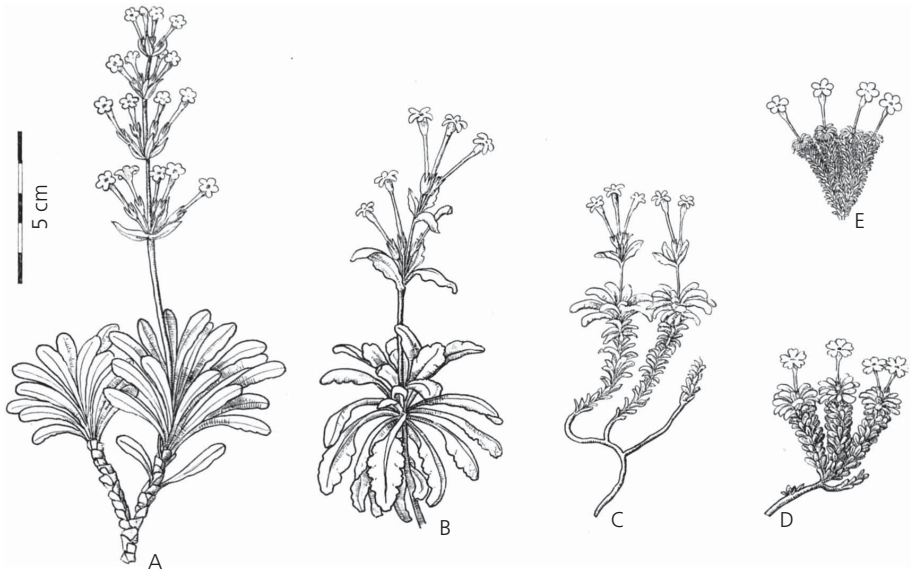



**Figure 2.27** Species of *Dionysia* sect. *Anacamptophyllum* showing the gradual reduction from large-leaved and loose-tufted species with well-developed inflorescences to small-leaved, densely tufted species with one-flowered inflorescences (after Wendelbo 1971, used with permission).

Perhaps the most interesting of all the major regions of Iranian plant diversity are the ancient Hyrcanian[32] Arcto-Tertiary relict forests. These extend in an arc along the southern shore of the Caspian Sea from the Talish region of Azerbaijan to Gorgan in Iran, an area of approximately 50 000 km$^2$, mostly in Iran and including the northern slopes of the Elburz Mountains (see Figure 2.26). "Hyrcania" writ large is the largest and widest portion of the low plain along the shores of the Caspian. It is one of the most biodiverse parts of the Middle East and includes habitat in both mountains and plains. The dominant vegetation is a mesic, broad-leaved deciduous forest (Zohary 1973).

According to Akhani et al. (2010) the alluvial plains on the coast of the Caspian have vegetation dominated by *Populus canescens, Pterocarya fraxinifolia*, and *Alnus* and *Salix* species. A broad-leaved deciduous forest vegetation occupies the dry habitats from sea-level to *c.*1000 m, with *Quercus castaneifolia, Carpinus betulus, Fraxinus excelsior, Acer insigne, Parrotia persica, Zelkova carpinifolia, Alnus subcordata, Albizia julibrissin*, and *Juglans regia* as dominants. The zone from 1200 to 2000 m is occupied by beech forest dominated by *Fagus orientalis, Quercus castaneifolia, Acer insigne, Ulmus glabra*, and *Tilia rubra.* The low forest or shrubland sites at 1800–2500 m are mostly dominated by *Quercus macranthera, Cotoneaster racemiflora, Sorbus boissieri, Crataegus pentagyna*, and *Pyrus boissieriana*.

The diversity of tree species decreases at higher elevations, where the subalpine forests and scrubs are replaced by alpine grasslands on the north-facing slopes, and the Irano–Turanian thorn-cushion steppe on the exposed summits and south-facing slopes. To this point, some 3234 Hyrcanian species belonging to 856 genera and 148 families of vascular plants have been reported from the northern provinces of Iran and Talish in the Republic of Azerbaijan (Akhani et al. 2010).

[32] *Hyrcania* is the Roman form of an Old Iranian word for the region of Gorgan in North Iran. Hyrcania was the name of a principality located in the territories of present-day Gilan, Mazandaran, and Golestan provinces of Iran and part of Turkmenistan, all lands south of the Caspian. To the Greeks the Caspian Sea was the "Hyrcanian Sea" (the name "Caspian" comes from the Casps people, from Transcaucasia). The Mazanderan Sea is the modern name used by Iran to refer to the Caspian Sea.

The ancient Caspian forests are among the oldest forests in western Eurasia and also among the most threatened ecosystems in Iran, largely due to human encroachment, timber removal, and grazing pressure. In terms of conservation, the fact that about half of all known species in Iran (3234 out of about 6300 species) occur in only 6% of the Iranian land area is of obvious significance. This is another major Middle Eastern hotspot (see Section 10.15). Some 280 species are endemic or sub-endemic to the Hyrcanian area and about 500 are Iranian endemics. The Hyrcanian cliff flora and vegetation is also distinctive and supports many endemics and relict species, such as *Crucianella platyphylla, Ferula laseroides, F. glaucopruinosa, Viola spathulata*, and multiple *Dionysia* species.

## 2.27 Armenia

Like the rest of the region, Armenia has a venerable and ancient heritage. Sometimes called "the first Christian nation," the Kingdom of Armenia was established in the sixth century BC. By the nineteenth century, the traditional Armenian homeland was divided between the Ottoman and Russian empires. The modern Republic of Armenia became independent in 1991.

The Republic (population *c*. 3.3 million) is landlocked in the South Caucasus. Located between the Black and Caspian Seas, the country is bordered by Georgia and Azerbaijan to the north and east, and Iran and Turkey to the south and west (see Figure 2.28). It has an area of 29 743 km$^2$ and is located in mostly mountainous terrain (rising to 4000 m), with fast flowing rivers and few forests. The climate is highland continental, with hot summers and cold winters.

The flora is rich and includes some 3200 species and at least 106 endemics, though more study is needed. The flora is especially diverse being located between the rich Caucasian and Iranian geobotanical provinces (Czerepanov 1995). Habitats include semi-desert, mountain steppe, mountain meadow, and alpine. Grassland—including cereal and stipa steppes—is replaced by meadow steppes and alpine meadows in the high mountains.

Woodland occurs mostly in the northeast. There, many deciduous, broad-leaved trees can be found, with oaks, beech, and hornbeams predominant, along with lindens, maples, and ash trees. Poplars, walnuts, and wild fruit-trees are frequent (apple, pear, cherry, plum, cornelian cherry, and dog rose). The rocky and stony soils are farmed for almonds, pistachios, and beans, among other crops.

The country faces increasing and intense desertification, including around the capital and largest city, Yerevan. Indeed increasingly arid conditions threaten most of the country, and forests today make up only 8%. It is estimated that in another 20 years the country will have lost nearly all its forest and woodland.

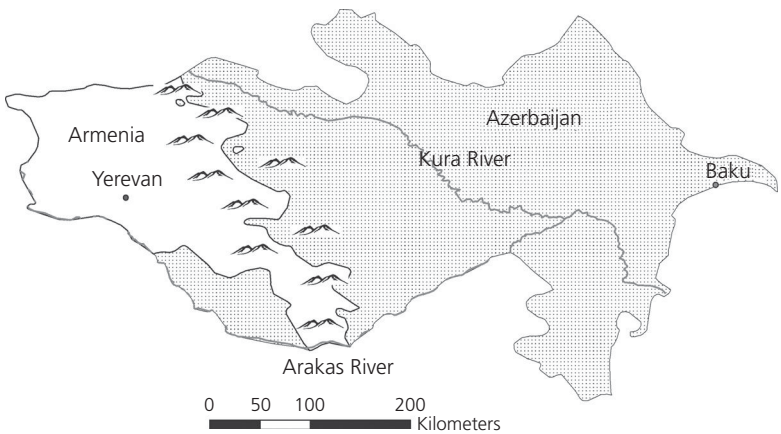



**Figure 2.28** Country map of Armenia and Azerbaijan with major cities and mountain ranges.

## 2.28 Azerbaijan

Baku, on the corner of the Caspian Sea and capital city of Azerbaijan, is another truly ancient and fabulous place, first mentioned in the Egyptian Book of the Dead more than 4000 years ago. Azerbaijan is bounded by the Caspian to the east, Russia to the north, Georgia to the northwest, Armenia to the west, and Iran to the south (see Figure 2.28). The exclave of Nakhchivan[33] is a semi-desert region separated from the main part of Azerbaijan.

Three features dominate the region's ecology: the Caspian Sea whose shoreline forms a natural boundary to the east; the extensive plains at the country's center; and mountains—the Greater Caucasus to the north, the Lesser Caucasus and Talysh Mountains to the south. Indeed mountains cover about 40% of the country. A great many "mud volcanoes" occur where a hot slurry of mud and water warmed by geological activity bubbles to the surface, forming volcano-like structures. The bubbles are mostly methane gas, with some carbon dioxide and nitrogen. Nearly half of all the mud volcanoes on Earth are said to be in Azerbaijan.

The flora is rich and includes more than 4500 species of higher plants, with Talysh in southeastern Azerbaijan an especially rich region (Gadjiev et al. 1979). The tree flora there is the richest in the Caucasus and includes many endemics. Some are relicts of the Tertiary period, extensions of the rich Hyrcanian vegetation of Iran and include Persian ironwood (*Parrotia persica*), Persian pink siris (*Albizzia julibrissin*), chestnut-leaved oak (*Quercus castaneifolia*), Hirkan zelkova (*Zelkova hyrkana*), Oriental persimmon (*Diospyros lotus*), Hirkan butcher's broom (*Ruscus hyrkanus*), Alexandrian laurel (*Danae racemosa*), Hirkan box-tree (*Buxus hyrkana*), Caspian honey-locust (*Gleditsia caspica*), Hirkan fig (*Ficus carica*), and Hirkan maple (*Acer hyrcana*). Hirkan National Park (with a total area of 21 435 ha) was established in Talysh to conserve the many relict and endemic species of the Tertiary period found in this region. These forests are among the very oldest in western Eurasia. Out of *c*. 1200 plant species found in the park, at least 100 are endemic.

[33] The Nakhchivan Autonomous Republic is a landlocked exclave of the Republic of Azerbaijan (that is, it is separated from the rest of Azerbaijan by Armenia to the north and Iran to the south). The region covers 5500 km². The Zangezur Mountains make up its border with Armenia, while the Aras River defines its border with Iran.

## 2.29 The mountainous Caucasus

Overall, the large Caucasus region—including, in particular, the forested montane isthmus sitting between the Black Sea and the Caspian—is a significant biodiversity hotspot (Tordoff et al. 2009). It has the greatest biological diversity of any temperate forest region in the world, including more than 6500 plant species, at least a quarter of which are unique to the region. The hotspot (see Section 10.15) spans some 580 000 km² of Eurasian mountains, including all of Armenia and Azerbaijan as well as Georgia, the North Caucasus portion of the Russian Federation, north-eastern Turkey, and part of north-western Iran. Its forests, wetlands, steppes, and semi-deserts likely contain more than twice the plant and animal diversity found in adjacent regions of Europe and Asia, yet it remains greatly understudied.

Several of the many mountain barriers in the Caucasus come together topographically and meet as a giant triangle created by the intersection of the western part of the Greater Caucasus Range (in Georgia and Russia), the western part of the Lesser Caucasus Chain (in Turkey and Georgia) and the Likhi ridge at the Black Sea, and by the Talysh-Elburz Mountains at the southwestern coast of the Caspian. Annual rainfall in the southwest is high, usually exceeding 2000 mm in coastal areas of the Black Sea (rising to 4500 mm), while in the southeastern part of the Caspian coast it rarely exceeds 150 mm.

The vegetation here is especially diverse and interesting because of the extensive mountainous habitat making for abundant speciation, but also due to the particular evolutionary history of the local flora, which includes two major Arcto-Tertiary refugia. One of these centers of very "deep endemism" is the Colchic area in the catchment basin of the Black Sea; the other is the Hyrcanian region at the southeast of the Caucasus, including the eastern

slopes of the Talysh and northern slopes of the Elburz, south of the Caspian (see Section 2.26). All these remnant species and communities are relicts of the floral assemblage which once—tens of millions of years in the past—covered the Northern Hemisphere. That flora was likely more widespread when the global climate was warmer than it is now, when the continents were closer together in late Mesozoic to early Cenozoic times. With the onset of global cooling and periodic Ice Ages, these tropical to subtropical species were left in isolated pockets where the climate was warmer.

According to Zazanashvili (2009), many relicts exist today as local dominants and co-dominants. Examples from the Colchic region include *Quercus pontica, Betula medwedewii, Epigaea gaultherioides, Rhododendron ungernii*, and *Rh. smirnowii*. In some places these diverse forests even become temperate rainforests, with extensive steep slopes in barrier-mountains along coastlines, able to trap humidity from oceanic air masses.

## 2.30 Summary

This chapter focuses on local and regional endemism and the plant ecology and biogeography of the many individual countries in the Middle East. The region includes some areas that are very thoroughly studied, and others that are relatively unknown. There are mountain ranges, steppes, dry deserts, and salt basins, and magical islands, like Socotra, Cyprus, and the Hawar Islands that are rich in unusual endemics. Some special floras have been long recognized—like the Gondwanaland relicts on Socotra; the Dasht-e Kavir plateau of north central Iran (*c*. 77 000 km$^2$) known as the Great Salt Desert; the Red Sea and Aden Gulf Basins (*c*. 810 000 km$^2$), with sclerophyllous evergreens of bush- and scrubland; the Israeli tragacanth; the Caucasus hotspot; and the ancient "Hyrcanian" forests of Iran and Azerbaijan that represent refugia for northern plants as they edged southward to escape the advances and retreats of Eurasian ice sheets.

CHAPTER 3

# Continents in motion and global climate change

## Understanding past and present plant communities

### 3.1 Miocene tectonics (23–5.3 Ma) and present-day plant communities: Ghosts of floras past

We each experience our lives in the here-and-now, i.e., in *present* time. This experiential bias extends to our understanding of climate, vegetation, even life in general. We have a natural inclination to over-emphasize the present—the importance of the here-and-now, so to speak—at the expense of understanding the past and how we got to where we are. A plant's life, like a human life, is an ongoing, continuous process and the external pressures of natural selection *never* let up. Individual organisms are here only because their ancestors survived and successfully reproduced. Some plants in the Middle East represent the "living dead"—not the plant version of a zombie apocalypse, but simply old individuals that, when they germinated, conditions were fine . . . and over their sometimes very long lifetimes the climate changed, such that their progeny can no longer survive the perils of seedling and juvenile life at the same location . . .

Over the span of our own lives (in the authors' case from about 1950 to the present) the human population has more than doubled, from fewer than 3 billion to more than 7.3 billion. This exponential growth (and its consequences) has changed the world . . . Across *any* individual organism's lifespan the availability of critical resources, including temperature and light, water and mineral nutrients may change significantly (see, e.g., Cavender-Bares and Bazzaz 2000). This is *especially* true for plants, and long-lived plants in particular. It is not unusual in the Middle East to find trees that may be hundreds of years old. Regional distributions of adult individuals will be a product of all their responses to past conditions (whether resource-related, climatic, or otherwise). Furthermore, being sessile and rooted to the spot, individual plants are mostly unable to move to more favorable sites or track necessary resources (though progeny may get there). *Young* individuals (i.e., seedlings and juveniles) will necessarily reflect a more immediate response to the *present* environment and more recent prior experiences. Life in the here-and-now.

Thus, for example, mature juniper trees (*Juniperus excelsa*, some reaching 750 + years in age [e.g., Sass-Klassen et al. 2008]) at Omani, Sinai, and southwestern Saudi mountaintops; or the ancient Dragon's-blood trees in Socotra where some individuals are estimated to be 500 to 600 years old (Habrova et al. 2009), and the Ombet (*Dracaena ombet*) scattered in Djibouti, Sudan, Uganda, and Egypt; or old *Mimusops* trees in southern Yemen and Saudi Arabia, *all* face dramatically different life conditions and local environments today compared to what they experienced when they first germinated as seedlings, hundreds of years ago. Major changes today include much more intense browsing by goats and other livestock, and greatly increased direct effects of human activities (especially farming and development), as well as the increasingly arid conditions which plants currently experience in the region.

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These harsh ongoing realities—*selection pressures*—extend beyond individual life spans and it is important to acknowledge that variation and change in environmental conditions have always been a feature of life on Earth. Large-scale effects of climate change have been shaping the distribution and abundance of every species, reaching back through the generations into deep, geological history. In itself it is nothing new. Yet most climatologists believe the *rate* of change is particularly intense, reminiscent of the five earlier mass extinctions that have occurred on Earth, that were due to planet-wide catastrophes and climate change. The rate of change is so rapid that adjusting species distributions to find and colonize new locations is particularly challenging for plants, where range expansion is mostly local and incremental.

Potter and Szatmari (2009) reviewed global Miocene tectonics and showed that significant paleogeographic, geomorphic, oceanic, and climatic changes took place during what they described as a *dynamic* Miocene epoch (23–5.3 Ma).[1] They show nicely how those Miocene changes shaped the geological foundation of our present-day world. Potter and Szatmari proposed that the single major immediate cause for all these events was *mountain-building*—the broadly simultaneous activity of two, great convergent orogenic belts, having a total length of about 29 000 km—the 13 000 km Eurasian chain of the Alpine–Carpathian–Zagros–Himalayas, running from Spain to Vietnam; and the Andean–Cordilleran belt about 16 000 km in length, in the western Americas.

Potter and Szatmari suggested all the continents of today would be readily recognizable by the Early Miocene, though with some differences. All the present mountain belts formed in the Paleozoic and Mesozoic eras would be easily identifiable in general outline, if not in geomorphic detail. Many of today's large river systems did not exist then; conversely, many older ones have long since vanished. The Late Oligocene–Early Miocene world also had a more uniform, warmer climate. Aridity was much more restricted than today; the mountain belts were lower—which meant less severe rain shadows to the leeward side of coastal mountain ranges (see Chapter 4).

Potter and Szatmari also described some significant differences from today's world. North and South America were then still separated from each other, and Greenland was still connected to Canada. Perhaps most important from the perspective of the Middle East, the great Tethyan Ocean[2] at that time existed with deep water extending from India and Pakistan across to the Atlantic; the Mediterranean had not closed off on the eastern side. Southern Europe was an archipelago and there was also a shallow sea in much of southern Russia extending into Kazakhstan. Widespread mountain building and continental uplift began at the beginning of the Middle Miocene and changed these areas into the lands we recognize today.

Throughout the Cenozoic, large tectonic plate movements were gradually both opening and closing several great, global "gateways" (see Figure 3.1). The net effect was to significantly change patterns of oceanic heat transfer, from a rather more unified and connected, circulating equatorial "Greenhouse" climate system where ocean currents absorbed and distributed heat more evenly, into the more segmented, "icehouse" system of today (Potter and Szatmari 2009). This change in global heat transfer systems coincided with a buildup of landmass in northern latitudes (i.e., Eurasia and North America), all of which, taken together, promoted global cooling.

According to these models, three new gateways were opened to deep-water flow and three others became closed during the Miocene. The three that closed were the Tethyan Seaway of the Middle East

[1] The Neogene is a geological period and part of a system in the International Commission on Stratigraphy (ICS) Geologic Timescale, starting 23.03 ± 0.05 million years ago and ending 2.588 million years ago. The Neogene Period follows the Paleogene Period as the second period within the Cenozoic Era and is succeeded by the Quaternary Period.

The last epoch into which the Paleogene Period is subdivided is its Oligocene Epoch. The Neogene Period is subdivided into two epochs, the earlier, *Miocene* Epoch and its succeeding Pliocene Epoch. The first epoch into which the Quaternary Period is subdivided is its Pleistocene Epoch.

[2] A paleo-ocean also known as the Tethys Sea or Ocean, which during its greatest extent separated the northern continent, Laurasia, from the southern, Gondwana (or Gondwanaland).

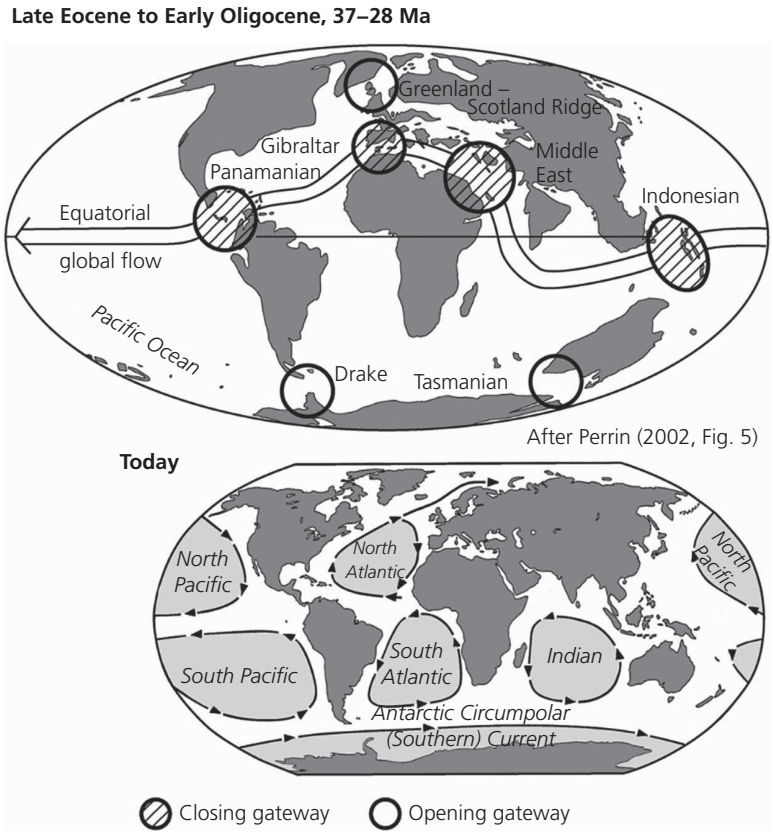



**Figure 3.1** Late Eocene to Early Oligocene (37–28 Ma) equatorial, warm water flow and its contrast with the major surface oceanic current systems of today's well-ventilated, cooler global ocean. Notable is the closing of four great equatorial gateways and the opening of three polar ones (after Potter and Szatmari 2009, used with permission).

(until then the partition between the two supercontinents, Laurasia and Gondwana, which in turn had been previously united as the single continent of Pangea), the Indonesian Gateway, and the Isthmus of Panama (see Figure 3.2). All of this came largely from the final breakup of Gondwanaland—and northward movement of its African, Indian, and Arabian fragments toward Eurasia. As ocean gateways closed, they blocked the equilibrating circulation of the Tethys Sea's greenhouse-style equatorial system.

Along with the northeastward impact of Arabia against Eurasia came a key closing in regard to Middle Eastern ecosystems. In effect, the global "air-conditioning and humidifier systems" were slowly becoming clogged. Whereas in the early Miocene there was still good connectivity between the

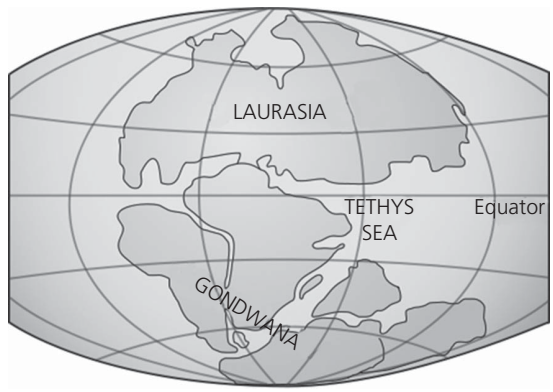



**Figure 3.2** The Tethyan Seaway in the Triassic 200 million years ago (from http://en.wikipedia.org/wiki/Tethys_Ocean).

Mediterranean Sea and Indian Ocean, by the middle Miocene that connection was only intermittent, varying with sea-level, and final closure occurred during the early-late Miocene, at about 10–11 Ma (see Rögl 1999).

From that point on, mid-latitude desertification proceeded on all the continents and in the rain shadow of mountains rising in the middle and late Miocene. A combination of rising mountains and the progressive closing of the Tethys, coincided with an increase in aridity from Moldavia to Lake Baikal and eastward into northern China (Zhang et al. 2014). Forests became grasslands and grasslands became deserts (Medeanic 2002; Ramstein et al. 1997; Velichko 2005). The Sahara became progressively more arid, reaching desert conditions during the late Miocene (Schuster et al. 2006).

Meantime significant Miocene events in eastern and southern Africa included the *extension* of most of the trans-African rift system southwestward, as well as the maximum widening of the Red Sea and uplift of much of southern and eastern Africa (see Section 1.5). Present-day Africa, Italy, Arabia, and India all accelerated northward toward Eurasia during the middle and late Miocene. At the same time, the Alpine–Carpathian–Zagros–Himalayan chains were rejuvenated and uplifted, and the former Tethyan Ocean shrank to become the present Mediterranean, Black, and Caspian Seas, and residual epicontinental lakes such as the Aral "Sea" and the Balkhash in Kazakhstan.

## 3.2 Relictual vegetation

Landscapes of the former Gondwana continents are residual—paleo-landscapes or "survivor landscapes" perhaps—rich in paleoforms, many dating from the Tertiary and some from the early Mesozoic (e.g., Squires 1988). Since these areas were never covered by Pleistocene continental ice sheets, and experienced relatively few mountain-folding events during the late Tertiary, these landscapes tend to exist as high plateaux, lower residual mountains, and lowlands.

In marked contrast *glacial* landscapes are widespread in much of North America and northwestern Eurasia; there continental glaciers replaced many long-established large river systems, often carving out new ones and generating a distinctly morainic-, ice-scoured landscape. The ice ages in effect pressed a "reset" button on the plants, and while some relict populations of a species might survive at altitudes above the advancing or retreating ice sheet, for the most part northern vegetation was left to re-colonize terrain as the glaciers retreated. Present-day plant communities exist as outcomes—"ghosts" indeed—of several great prehistorical sorting events.

These include the climatic shift just mentioned, from the "wet" Tertiary period to the unusually dry Quaternary, during which most of the present day deserts of the world developed (see Sections 3.7 and 4.1). Thus vegetation in the Middle East includes clusters of species that joined the flora at different times and under different ecological conditions. Present day vegetation is a composite of species, survivors, and joiners of past floras.

So far since the groundbreaking work of Zohary (1973), and other phytogeographers (e.g., A. Eig, F. White, J. Léonard, J. Lavranos, H. Freitag et al.), there have been few integrative analyses bringing together both large-scale paleo-botanical and finer-scale phylogeographic studies in the Middle East. Indeed there are few field studies in ecology and evolutionary biology that address most of the region. There are some integrative studies of adjacent and nearby regions, such as the (mostly western) Mediterranean basin (Barron et al. 2010), and taken together these studies provide a useful starting point and potential models for understanding plant communities in the Middle East.

Barron et al. (2010), for example, synthesized paleo-botanical, phylo-geographic, and paleo-ecological studies of the Cenozoic vegetation of the Iberian Peninsula (present day Spain and Portugal). They showed that starting some 65 Ma the region had tropical/subtropical rainforests, mangrove swamps (including *Nypa* along the shores of the Tethys), as well as an array of laurophyllous (ancient evergreen, broad-leafed) forest and leguminous-sclerophyllous plant communities. Later, during the Miocene, these regions experienced significant climatic change, particularly the cooling and aridification already mentioned. Open, dry grasslands developed toward the interior, and

ancient, northern "Arcto-Tertiary" elements (see Sections 2.26 and 11.3) invaded mountainous and riparian ecosystems (such as Iran's Hyrcanian forest), often coexisting with or becoming part of the evergreen, broad-leaved forests that today include many Paleotropical species.

From the late Miocene onward the Iberian forests lost entire taxa; survivors endured further directional-environmental change, and further invasion by Arcto-Tertiary species expanding their ranges from the north. Nevertheless some Paleotropical taxa persisted through the environmental and climatic changes of the Miocene and Pliocene, to remain a part of the modern flora of the region (e.g., *Juniperus, Erica, Ocotea*, as well as the olives and laurels) (see Figure 3.3).

As we describe here, the laurel forests that developed in the Mediterranean were important in ancient Cenozoic landscapes, and by the late Eocene, at least in Iberia, they appear to have replaced the former tropical forests in the whole region. Barron et al. showed the significance to present-day plant communities of these "edaphically mediated" laurel forests, and suggested a broad ecological tolerance in such species lets them continue to persist both in mountain ranges and near the sea. These ancient forest species were the main progenitors of the plant families that became the modern flora we regard as characteristic of the western Mediterranean.

Valiente-Banuet et al. (2006) concluded that fleshy-fruited species dating back to the Tertiary have been an important constant in the Mediterranean region. Fleshy fruits help direct dispersal away from the parent plant to nutrient-rich understory locations, because birds deposit highly disproportionate numbers of seeds where they perch (e.g., Herrera 1984). Indeed seed deposition in the understory by birds and other dispersers is advantageous not only for shrubs but also *any* of the Tertiary species as the canopy species provide a modified, more moist, and nutrient-enriched habitat.

Many benefits have been noted to accrue largely through the *facilitative* effects on seedlings of shade, maintenance of soil moisture, and local recycling of

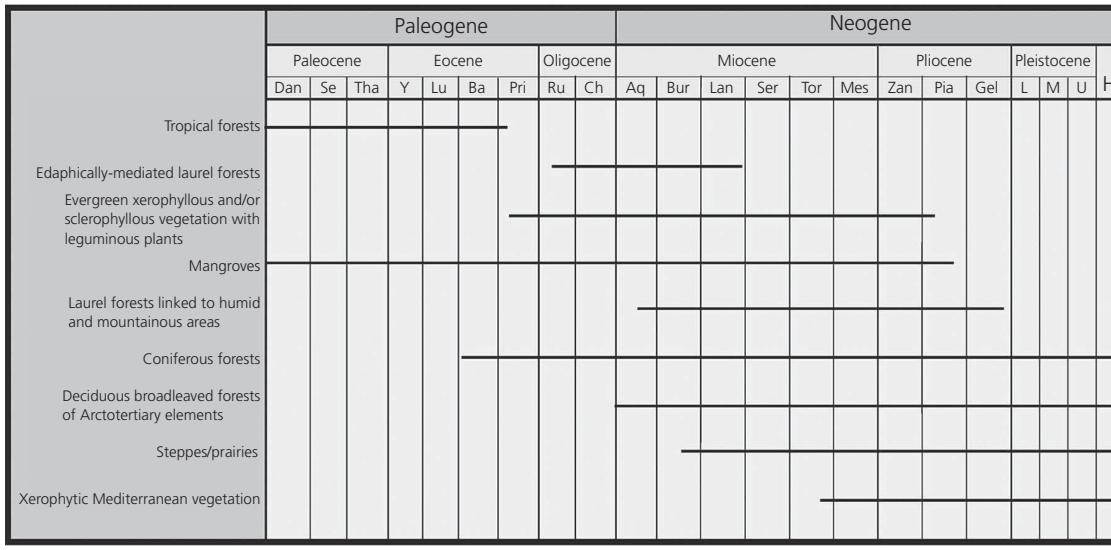



**Figure 3.3** Composite range chart of the main types of vegetation in the Iberian Peninsula during the Cenozoic. The appearance and disappearance time of these vegetation types is shown. Abbreviations: Dan = Danian, Se = Selandian, Tha = Thanetian, Y = Ypresian, Lu = Lutetian, Ba = Bartonian, Pri = Priabonian, Ru = Rupelian, Ch = Chattian, Aq = Aquitanian, Bur = Burdigalian, Lan = Langhian, Ser = Serravallian, Tor = Tortonian, Mes = Messinian, Zan = Zanclean, Pia = Piacenzian, Gel = Gelasian, E = Early Pleistocene, M = Middle Pleistocene, L = Late Pleistocene, and H = Holocene (after Barron et al. 2010, used with permission).

nutrients from leaf litter and animal waste (Valiente-Banuet et al. 2006; and see Keeley 1992 and Section 4.7). Valiente-Banuet et al. argue that a large number of ancient Tertiary species in present-day Mediterranean-climate ecosystems appear to have been assisted in their persistence by facilitative effects of modern Quaternary species. "Nurse" plants tend mostly to be woody, providing a protective and enriched structural micro-environment, thereby promoting an understory of more sensitive species.

In general, the amplitude of any climatic changes experienced by plant populations should increase as the period of observation increases. Hence recent Holocene relicts may often be found in relatively small and environmentally uniform areas such as mires or talus slopes (Hampe and Jump 2011), whereas those that have survived at least one complete glacial oscillation essentially *in situ*—sometimes referred to as pre-Last-Glacial-Maximum (pre-LGM) relicts—are almost exclusively found in patchy, heterogeneous landscapes allowing persistence under very different regional climates. Pre-LGM relicts survive through changes in altitude or slope orientation, etc. (Hampe and Petit 2005). It is unclear the extent to which these species either had broader ecological tolerances (i.e., sufficient phenotypic plasticity to allow acclimation), and/or some greater genetic capacity to evolve and adapt to the new conditions. Further work on this would be useful.

In their review of climate relicts, Hampe and Jump concluded the particular regions of the world where climate was both stable through time and patchy in space have tended to harbor disproportionately high concentrations of climate relicts, as well as greater biodiversity and endemism (see Denk et al. 2001; Fjeldså and Lovett 1997; Qian and Ricklefs 2000; Rodríguez-Sánchez et al. 2008). Such localities—and this would seem to embrace many Middle Eastern mountain ecosystems—should be seen as representing potential conservation hotspots (see Section 10.15) as well as being critical locations for generating *de novo* biodiversity. Taking this a little further, they may also be of value for the restoration of genetic diversity in disjunct populations of a species, or close congeners.

## 3.3 Socotran Dragon's-blood trees and other relicts of Mio-Pliocene Laurasian subtropical forests and climate change

Charles Darwin's great friend, J. D. Hooker, first proposed (1878) that the Dragon's-blood tree (see Figure 2.11), together with other species of the Macaronesian[3] laurel forest, was probably a relict of an ancient vegetation that once existed in north-western Africa.

A century later, Axelrod (1975) provided the evidence for a xerophytic sclerophyllous "Madrean–Tethyan" flora, that is including plants with hard leaves and short internodes (the distance between leaves along a stem). Such plants are characteristic of the more seasonal climates that ranged along the ancient Tethyan coast, from North America to southeast Eurasia and North Africa (Figure 3.2). Fossil evidence shows sclerophyllous taxa entering the record in the Early Eocene and forming a broad belt across southern North America and Eurasia, until it was disrupted by increased climatic cooling and drying, at the end of the Oligocene (Axelrod 1975). Axelrod proposed that subtropical elements including *Dracaena* (Asparagaceae) and *Sideroxylon* (Sapotaceae), found refuge in eastern and western North Africa as a consequence of desertification of the Sahara, during the late Oligocene.

[3] The Macaronesian biogeographic region refers to three volcanic island groups off the coast of Europe and Africa: the Canary Islands, Madeira, and the Azores (having a collective total surface area of 10 372 km$^2$). Major habitats include coastal locations, upland vegetation, and evergreen forests—remnants of humid evergreen broad-leaved forests (and dry evergreen pine forests in the Canary Islands). The introduction of grazing animals, especially rabbits, has been devastating and fragile forest systems have been irreversibly degraded. The original vegetation of low-lying islands (including *Juniperus, Phoenicea*, and *Dracaena draco*) is no longer present.

The humid evergreen laurel forest (and dry evergreen forest, now confined to the Canaries) are regarded as characteristic for the region. The most ancient elements, including endemics, occur in the laurel forest. The "laurisilva" forest developed in areas with reduced solar radiation, moderate temperatures, high precipitation (500–1200 mm), and fog, and is especially rich in the deeper ravines. Dominant trees include Canary laurel (*Laurus azorica*), Madeira mahogany (*Persea indica*), and Acotea (*Ocotea foetens*). In Madeira the forest is also characterized by endemic lily-of-the-valley trees (*Oxydendrum arboretum*) while the laurel forest in the Azores has juniper (*Juniperus brevifolia*) and Azorean heath (*Erica azorica*).

The Socotra Archipelago was declared a UNESCO Biosphere Reserve in 2003, included on their World Heritage List in 2008 and then designated as one of the "Global 200" priority natural habitats by the World Wildlife Fund (see, too, Section 2.11.3). Groves of the endemic *Dracaena cinnabari*, magnificently odd, ancient monocotyledonous[4] "trees" that can live up to 600 years, greatly contribute to the uniqueness and ecological value of the islands. These trees are signature conservation elements that dominate the landscape of Socotra, across an altitudinal range from 250 m to the highest parts of the mountains (Habrova et al. 2009).

Most *Dracaena* species[5] grow as shrubs or geophytes (perennials that survive the adverse season by producing below-ground buds and storage organs—rhizomes, corms, tubers, bulbs, etc.). However, six species are trees (*D. cinnabari, D. ombet, D. serrulata, D. schizantha, D. draco*, and *D. tamaranae*) (see Marrero et al. 1998). All these species exist as remnants of the Mio-Pliocene Laurasian subtropical forests, now almost extinct because of the climate changes of the late Pliocene that caused the desertification of North Africa.

Habrova et al. (2009) analyzed population dynamics in stands of *Dracaena cinnabari*, using multiple methods of age determination (obviously more difficult in monocots, which lack true wood formation). They concluded that many individuals at Socotra were at least several hundred years old, and that young individuals—absolutely vital as recruits to the population—were exceedingly rare, although flowering and seed production continued to take place among adult trees.

Habrova and colleagues also concluded that the higher elevation, or "mountain populations" represented a distinct ecotype from the lowland form. Mountain plants had smaller crown and stem dimensions and larger branch sections. Individuals from the lowlands branched more uniformly, had shorter branches (20–30 cm), denser crowns, and differences in flowering phenology. The mountain form typically had longer branches (40–50 cm) but produced sparser crowns and different flowering times. Habrova suggested such differences in flowering season could promote genetic differentiation between highland and lowland populations. The highland form was less common and appeared limited to places inaccessible to herbivores (which otherwise appeared to be decimating juvenile individuals).

The midlands of Socotra, with their various exposures to both the SW and NE monsoon and its strong rainfall (Scholte and de Geest 2010), have diverse vegetation dominated by succulent shrubland. The spectacular appearance of the bottle trees here—the Desert-rose, *Adenium obsesum* and Cucumber-tree, *Dendrosycios socotranum*—may mitigate Le Houérou's earlier (2003) suggestion that midlands in the Eritreo-Arabian phytogeographic domain "lack originality" (see Scholte and de Geest). Also striking in the Socotran midlands are the mountain cliffs with fog- and mist-catching microhabitats. There frankincense trees are able to regenerate, probably because, like the *Dracaena*, they are protected on these cliffs from goat grazing as much as from the drought. These protected mountain cliff sites have surely continued to serve as refugia during times of aridification up to the present day.

Scholte and de Geest (2010) suggest the winter precipitation makes the Socotran midlands more comparable to their slightly closer African counterparts (in Eritrea, Djibouti, and Somalia) than to adjacent parts of the Arabian Peninsula. This is illustrated by the dominant evergreen shrub *Buxanthus hildebrandtii*, the box, which Socotran midlands share with these eastern African edges. Any

[4] In many respects Dracaenas are exceptional even among monocotyledonous plants. A distinctive feature of the arborescent, or tree-like *Dracaena* group is its growth habit—called "dracoid" by aficionados (e.g., Bos 1984) and regarded as the type case for species showing the distinctive "Leeuwenberg model" of plant architecture (Hallé et al. 1978). This growth form is known from plants of several families and was present in extinct *Lepidodendron* sp., *Bothrodendron* sp., and *Sigillaria* sp. of the Carboniferous period (Stewart and Rothwell 1993).

*D. cinnabari* bears its leaves exclusively at the end of the youngest branches, arranged in clusters ("rosette trees") like other dracoids. According to Adolt and Pavlis (2004), in *D. cinnabari* the oldest leaves seem to be shed at the same time, en bloc every three to four years with simultaneous maturation of new leaves, influenced by continuous growth of the branch at its tip. Other dracoids shed all their leaves each year at the beginning of the dry period.

[5] The genus *Dracaena* includes somewhere between 60 (Mabberley 1990) and 100 species (Bos 1984). According to the APG III classification it is best placed in the Asparagaceae, subfamily Nolinoideae (formerly the family Ruscaceae) (Chase et al. 2009). Other treatments have placed it in the family Dracaenaceae, and Agavaceae (now Agavoideae).

contrasts with the seasonal cloud forest vegetation in Dhofar and Hawf described in Section 1.4.1 (in Oman and Yemen, respectively) may be due to the fact that fog only occurs there during the summer, whereas on Socotra significant amounts of fog also occur between the summer dry and winter rainy seasons.

Even where there is severe habitat loss, connecting corridors can provide pathways for dispersal and range extension. This process will be slower than for more mobile organisms, since plant movement occurs only generationally, through the dispersal of seeds and other propagules. Dispersal corridors and larger, more regional considerations are developed in Sections 4.10 and 4.11.

One such corridor likely occurred during most of the Paleogene and early Neogene periods, when broadleaved evergreen sclerophyllous vegetation like Axelrod's Madrean–Tethyan flora covered low- and mid-latitudes of the Northern Hemisphere; this offered a viable Early Tertiary migration route between the Asian, African, and North American tropics. These subtropical forests were mostly dominated by thermo-hygrophilous (warmth loving) woody plants, including representation from tropical families like the Lauraceae, Myrtaceae, and Arecaceae (palms) (Rodríguez-Sánchez and Arroyo 2008). A sustained trend toward cooler and drier climates since the Upper Miocene led to the decline of this unique vegetation.

More recently, for example during the "mid-Pliocene climatic optimum" (*c*. 3 Ma), the climate was still substantially warmer and more moist than at present. At that time relict genera of the Tethyan flora (e.g., *Myrica, Ocotea, Cinnamomum, Persea*) continued to coexist in southern Europe along with ancestors of extant Mediterranean taxa like *Olea, Quercus, Pistacia*, and *Nerium* (Kovar-Eder et al. 2006). The onset of the Mediterranean climate in the Pliocene, with hot and dry seasons, and the glacial–interglacial cycles of the Quaternary with recurrent oscillation between periods of cold and arid conditions, ultimately caused the extinction of many members of the ancient Tethyan flora in Europe and North Africa (see Rodríguez-Sánchez and Arroyo 2008).

The Hyrcanian forests of northern Iran and Azerbaijan are also known as major refugia for many Arcto-Tertiary relict elements (Akhani et al. 2010; Leestmans 2005; Miller 1994b). The occurrence of *Zelkova carpinifolia, Parrotia persica*, and *Pterocarya fraxinifolia*, for example, argues that the Caspian forest region has been an important refugium for temperate broadleaved trees throughout the Quaternary glaciations (see Akhani et al. 2010).

While Quaternary range shifts of many temperate European plants are now relatively well understood (e.g., Hewitt 2004), the actual dynamics of the ancient Tethyan flora remains obscure, due at least in part to the scarcity of fossil data (Kovar-Eder et al. 2006). Predictive distribution models, however, can be used to identify probable refugia and dispersal corridors at a scale that cannot be achieved using fossil data alone. In turn, fossil records and the results of phylogeographic analyses can be used to test these models. Rodríguez-Sánchez and Arroyo (2008, 2011) and Rodríguez-Sánchez et al. (2009) used predictive models and patterns of variation in chloroplast DNA to reconstruct range dynamics in *Laurus*, one of the most informative relicts of the Tethyan flora and found the approach to be valuable. These can serve as useful starting points for more detailed studies in the Middle East.

## 3.4 Djibouti and aging populations of the Bankoualé Palm, *Livistona carinensis*

*Livistona* is one of the most ecologically diverse and widespread genera of palms in the world (Dowe 2009). The Bankoualé Palm, *L. carinensis*, has an unusual, highly disjunct global distribution. It is the only species—of some 36 in the genus—found in Africa. The rest are distributed throughout southeastern and eastern Asia, Malaysia, and Australia. In contrast the Bankoualé is distributed only in the Horn of Africa—in tiny Djibouti and adjacent Somalia—as well as southern Arabia, in Yemen. According to reports on the IUCN Red List (e.g., http://www.iucnredlist.org/details/30402/0), in Somalia only 38 trees in two localities are known; there are approximately 2000 trees in three villages in Wadi Hadjen in the Jol region, South Yemen, and there was no information regarding the status of the population in Djibouti. As a result *Livistona*

*carinensis* was classified as vulnerable in the IUCN/WCMC *World List of Threatened Trees* (1998), and this status has been recently upgraded to endangered (Dowe 2009).

The Bankoualé is a large fan palm capable of reaching 25–40 m, tall and majestic with a trunk that is enlarged at the base and bears prominent leaf scars. The crown carries up to 40 stiff, pointed leaves on barbed petioles over 1 m long (Ford and Bealey 2004). The axillary hermaphrodite inflorescences may be up to 2 m in length, each with hundreds of creamy-colored flowers. Fruits are hard and pea-like, and each contains a single seed.

A reliable water supply is crucial for both germination and establishment of the Bankoualé. According to Ford and Bealey, young palms are nearly always found where the ground is wet, though adults may live in areas that are now quite dry (demonstrating the frequent, unfortunate fate of the Middle Eastern regeneration niche—see Section 1.7). The species' distribution is limited to springs, oases and wadis. Flash floods are particular dangers to both young and old individuals that have established in wadis. In Yemen and Djibouti the Bankoualé is typically associated with the Date Palm *Phoenix caespitosa* and *Phoenix reclinata* (Ford et al. 2008; Lebrun et al. 1989; Welch and Welch 1999).

Shapcott et al. (2009) used microsatellite markers to investigate genetic diversity in the Bankoualé. At the species level *L. carinensis* contained very low diversity. Most variation occurred between samples from Yemen and Somalia compared to those from Djibouti. The Djibouti populations were nearly monomorphic across nine loci tested, suggesting they had gone through a genetic bottleneck where only a few, related individuals contributed to the present population. Individuals from botanic garden collections of Yemeni and Somali populations were more diverse than those from Djibouti field samples.

Careful surveys in Yemen and around the Horn have located nearly all known adult populations and have confirmed a total of <1800 individuals (Ford and Bealy 2004; Welch and Welch 1999). Compared to population estimates from 10 to 20 years earlier, there had been declines of 23–59% across all locations. Primary causes were harvesting of the palms for timber, or clearance for agriculture. There is no active program to conserve this species in either Somalia or Yemen, while some government initiatives are beginning in Djibouti.

The status of Bankoualé populations in Yemen and Somalia is uncertain. Welch and Welch (1999) reported that in Somalia the total population was likely fewer than 38 trees—though Somalia has been understudied for decades—while in Yemen there was evidence that, even though the populations were larger, they were under serious threat. For example, the Welches reported hundreds of stumps that evidenced ongoing harvesting.

Ford and Bealey's (2004) report on the status of the palm in its Djibouti refuge suggested an overall decline of *c*. 23–30%. They concluded population structures at most localities were heavily biased toward mature individuals, with relatively few young plants. This is typical of the unstable age structure of populations that are no longer recruiting new individuals, and include even-aged, ever-aging stands of "doomed" individuals (Harper 1977). In light of the combined threats indicated by the demographic and genetic data, the Djbouti populations are at particular risk.

In Djibouti the Bankoualé persists in sub-populations made up of 3–50 individuals and is found typically in clusters of closely spaced individuals in a wadi bed or spring bank. Populations at the town of Bankoualé appeared in particular danger as there was nearly no regeneration there. The two main sub-populations there had no rosettes or seedlings, and one population of 47 adults was located in the middle of the wadi and therefore in danger of being washed away by flash floods. A single new sub-population of six rosettes was identified (Ford et al. 2008).

Populations of the Bankoualé are clearly "overmature" and consist of adults and older individuals, with few young trees and rosettes, although many plants flower and set fruit freely. This is reminiscent of Socotran *Dracaena cinnabari* and other Middle Eastern tree species. Some of this demographic variation in *L. carinensis* may be due to differences in the timing of observations, as it is clear seedlings and other juvenile stages are highly vulnerable to grazing. This could account for the frequent association with *Phoenix reclinata*, as this latter palm typically forms fairly dense thickets, often impenetrable

to primary grazers—fat-tailed sheep, cattle, camels, and donkeys—and thus may provide shelter during especially susceptible, early growth stages.

The large number of Bankoualé seedlings recorded over time shows that germination *is* a frequent if not annual occurrence. Unfortunately seedlings and small rosettes get carried away in the flash floods that regularly occur in Djibouti. Also plants in transitional demographic stages—the small rosettes and other juveniles—are all heavily grazed. Henry Ford and colleagues (2008) point out that nomadism, with shifting patterns of grazing, is now rarely practiced in the region, so grazing has become more continuous and intense. Protected gardens and *ex situ* genetic cultures may offer the best hope for the future of this fine, statuesque palm tree.

*Ceratonia oreothauma*, a member of the Fabaceae, is another similarly rare and endangered tree known only on the Arabian Peninsula from the western Hajar Mountains (Jabal Aswad) in northern Oman, in Yemen from the summit area of the Kor Seiban in the Hadhramout, and at Jabal Gedu where just a few individuals survive (Hillcoat et al. 1980; Kilian et al. 2004). Outside the Peninsula it persists in isolated localities in the mountains of northern Somalia.

## 3.5 Genetic "footprints" of past vegetation change and current populations of oaks and laurels

Climate fluctuations have obviously occurred at various timescales throughout geologic history, including during the past two million years of the Quaternary period. These fluctuations include glacial and interglacial cycles, driven by changes in the Earth's orbit. The cycling at *c*. 100 000 years is attributed to orbital "eccentricity"—the fact that the Earth has an elliptical orbit due to the gravitational pull of Saturn and Jupiter when they are closer to us. The Earth's tilt on its axis (obliquity) varies from about 22.1° to 24.5° and generates a cycle with a period of about 41 000 years, and also a more marked *c*. 23 000-year-cycle due to "precession of the equinoxes." Basically, because the Earth is slightly pear-shaped rather than a perfect sphere, gravitational tidal forces of the Moon and Sun together apply torque to the Earth's equatorial "bulge" pulling it into the plane of the elliptic . . . this generates a "wobble," as seen in a spinning top.[6] As examples in Sections 3.2–3.4 indicate, many plants have undergone dramatic changes in range and abundance in response to these fluctuations.

During glacial episodes, temperate and boreal tree species were restricted primarily to areas far south of the ice sheets, though small populations of some species apparently also survived in periglacial environments (at the edges of a glacier), and in high-latitude sites that were free of glaciers. Following each episode, refuge populations could respond to climate amelioration and re-expand their distributions to form interglacial populations and communities, including those we see on the landscape today (Hu et al. 2009).

Hu et al. reviewed recent surveys of DNA polymorphisms revealing small tree populations surviving in mid- to high-latitude refugia throughout the Quaternary glacial episodes. In most of the large-scale studies they examined, colonization routes were uncertain. One exception was the study of oaks in the Swiss Alps by Matyas and Sperisen (2001). A large body of chloroplast DNA (cpDNA) data indicated that a lineage of oaks had dispersed across the high mountain passes there, during a postglacial northward expansion. Contrary to perceived wisdom about the role of mountain ranges as barriers to gene flow and plant dispersal, it appeared mountains need *not* necessarily constitute a barrier to migration. This was confirmed by Magri et al. (2006) who concluded that mountain ranges in fact *facilitated* the postglacial re-expansion of *Fagus sylvatica* (Fagaceae) in Europe.

It is becoming clear that when plant samples are gathered at a sufficiently fine level of geographic resolution, genetic data can reveal past demographic processes and mechanisms of range expansion. This is illustrated by Petit et al. (1997) who

[6] The Earth's orbit is elliptical and so there is some wobble to its tilt. The *greater* the tilt to its axis the greater is the contrast between summer and winter temperatures. Major glaciations in the Quaternary appear to have coincided with times when tilt, precession, and eccentricity of orbit all lined up to give the Northern Hemisphere particularly low amounts of summer insolation.

analyzed haplotype variation in cpDNA of *Quercus robur* (pedunculate oak) and *Q. petraea* (sessile oak), at 188 locations over a 200 km by 300 km area in western France.

Petit et al. determined that, over several hundred square kilometers, the spatial distribution of genetic polymorphisms was highly localized and patchy; entire small forests were typically characterized by single haplotypes. It may be that such patches reflect infrequent "founder flushes" from single parents, or sibling females following long-distance dispersal events in recolonization. Petit et al. suggested environmental conditions suitable for seedling establishment occur only rarely, with acorns often coming from single maternal lineages, followed by rapid growth of those newly established populations.

At times during the long glacial episodes of the Quaternary, European forests were considerably more restricted in distribution than in the present interglacial. This is mostly because the Mediterranean Sea, to the south, and unsuitable, ice-covered environments to the north, *limited* temperate tree and shrub taxa to the Iberian, Italian, and Balkan peninsulas.

Petit et al. (2003) tested the hypothesis that glacial refugia harbor a large fraction of the intraspecific biodiversity of present-day floras. They surveyed chloroplast DNA variation in 22 widespread European trees and shrubs, with each species being sampled in the same set of mixed forests mentioned above. Most species proved to be represented by genetically distinct populations in different forests, in particular in those species with a low capacity for seed dispersal. An intriguing finding meriting further study was that the genetically most diverse populations were not those located in the south, but rather those at intermediate latitudes. This is likely a consequence of the greater admixture of divergent lineages recolonizing the continent, coming from separate refugia and inter-breeding in the center of the range (Petit et al. 2003), as well as possible "mid-domain effects" (see Section 4.9.1).

Many ancestors of modern-day Mediterranean taxa originated from Paleotropical floras and had to compete over the past 20 million years or so with northern Arcto-Tertiary elements like the junipers (see Section 3.6), that gradually became increasingly important ecologically (Barron et al. 2010). Elements of each of these floras must have adapted to dry climates throughout the Miocene. During this period the evergreen sclerophyllous–laurophyllous forests were of great importance. Remnant laurel and oak forests still exist today in the eastern Mediterranean (or Levant),[7] and Turkey.

Barron et al. argued that other pre-Mediterranean elements may have been associated with this ancient evergreen laurophyllous vegetation, including species ancestral to the oaks, *Quercus ilex* and *Q. coccifera*, both of which are also found in the Levant and maquis vegetation in Turkey. These workers suggested *Quercus ilex* may have its origins in the holm oaks associated with lauroid elements such as *Q. drymeja, Q. praeilex*, and *Q. praecursor*. That *Q. ilex* might arise from this set of subtropical oaks is also supported by the present distribution of *Q. ilex* ssp. *ilex* in humid and sub-humid Mediterranean areas (Pons and Vernet 1971).

*Quercus coccifera*, on the other hand, appears to be more closely related to fossil species that developed in more humid–mesic environments, such as *Q. mediterranea*. Barron et al. suggested that during the driest periods of the Neogene this species most likely found refuge in laurel-dominated forests. *Quercus mediterranea* has been identified in the Iberian Peninsula in association with mesophyllous and notophyllous taxa (having leaf surface areas of 45–182 $cm^2$ and 20–45 $cm^2$, respectively).

Despite the essential disappearance of the early laurel forests from European and Middle Eastern localities during the Pliocene, some of the species that belonged to the laurel forest community have managed to survive in refugia, and these are now found in sites and localities that meet their particular temperature and water requirements. According to Barron et al., this is the case in western Europe for species such as *Laurus nobilis, Rhododendron ponticum, Prunus lusitanica*, and *Myrica faya*. Still today *Rhododendron ponticum* is found in Turkey and Lebanon, *L. nobilis, P. lusitanica*, and *M. faya* in the eastern Mediterranean and Turkey.

[7] Known in Arabic as *Bilad al-Sham*.

## 3.6 Relictual junipers in the Middle East

Junipers are coniferous plants in the cypress, or Cupressaceae family. *Juniperus excelsa* ssp. *polycarpos* is found in mountain areas from Turkey to India, including an isolated population on Jebel Akhdar in the northern mountains of Oman. The species appears to have dispersed across the shallow, often dry Strait of Hormuz into Arabia (Farjon 1992; Fisher and Gardner 1995; Kerfoot and Lavranos 1984). This Juniper is not found elsewhere in Arabia but there are populations of the related *J. procera* (which is otherwise East African) and *J. phoenicea* (essentially Mediterranean) in Yemen and Saudi Arabia (Adams et al. 1993; Farjon 1992; Kerfoot and Lavranos 1984). In northern Oman, *J. excelsa* ssp. *polycarpos* is generally the dominant component of woody vegetation above 2100 m, and often co-dominant with the olive tree, *Olea europaea*, below 2300 m (Fisher and Gardner 1995; Ghazanfar 1991; Mandaville 1977).

Fisher and Gardner (1995) suggested that at elevation—above about 2400 m—the Omani juniper woodlands appeared to be regenerating and in reasonably good condition, both on exposed slopes and in sheltered wadis and gullies. However, at lower elevations there was considerable die-back and poor regeneration in many of the woodlands. Poor condition and low regeneration have also been reported in the *J. procera* woodlands of the Forêt du Day, in Djibouti, where no living junipers are observed below c. 1300 m (Fisher et al. 2009). It is also reported to be in poor condition in the mountain forests of the Raydah Reserve of Saudi Arabia (Hajar et al. 1991) and in some, but not all, areas of the *J. excelsa* forests in Baluchistan, Pakistan.

If poor growth at these lower elevations were due to any long term change in climate, both tree status and regeneration would be expected to be poorer in drier habitats, rather than lower altitudes. While investigating the general decline in Omani junipers, Fisher and Gardner (1995) surveyed a 32 ha area of Hayl Juwari, in northern Oman, analyzing differences in tree status and regeneration at wadis and non-wadi areas (i.e., relatively more xeric sites).

Approximately a third of the Omani trees surveyed were dead, and analysis of plant height, condition, regeneration, female cone production, preferred germination sites, and spatial distribution all indicated effects of topography, hydrology, and microclimate. Although there were relatively more dead and poor-condition trees in drier locations, there was also no unequivocal evidence that the present distribution of juvenile trees in both habitats could not in future become a stand of larger, sexually mature trees. Fisher and Gardner (1995) speculated the climate at this altitude may be marginal for survival of the juniper woodland and that even small increases in climatic stress could imperil its present status.

*Juniperus procera, J. phoenicea*, and *J. excelsa* are still found growing naturally in the southern hemisphere. The taxon was first described by Christian Hochstetter (1787–1860) and published by the great coniferologist, István László Endlicher (Endlicher 1847), based on material collected in Ethiopia. Junipers grow in East Africa, in mountainous regions at altitudes between 1500 and 2500 m (Hall 1984) in Ethiopia, Kenya, Tanzania, Uganda, Malawi, Zaire, and Zimbabwe (see Figure 3.4). The Zimbabwe

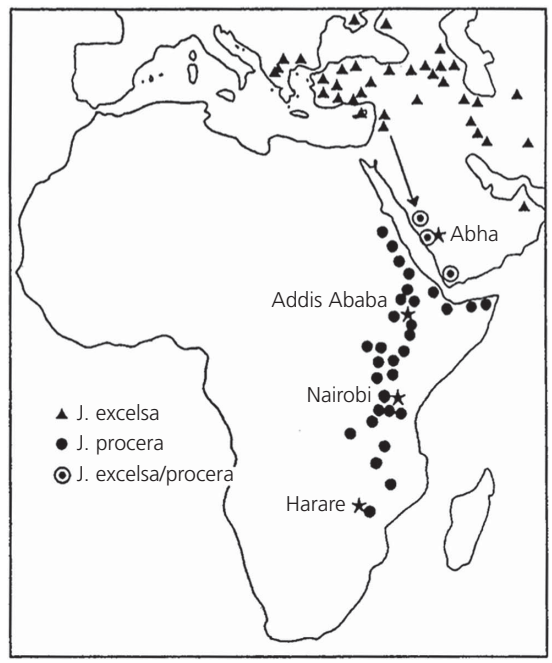



**Figure 3.4** Distribution of *Juniperus excelsa, J. procera*, and the *J. excelsa/procera* junipers of the southwestern Arabian Peninsula. The arrow marks the proposed migration pathway for *J. excelsa* (or pre-*J. excelsa*) plants southward into east Africa (after Adams et al. 1993, used with permission).

site is the southernmost native population of any known juniper (Kerfoot and Lavranos 1984). *Juniperus procera* is also found high (>2000 m) in the Asir mountains of southwestern Saudi Arabia (see Section 2.14).

Kerfoot (1975) postulated that *J. procera* originated from *J. excelsa* in Asia Minor during the Mio-Pliocene, when *J. excelsa* expanded southward along the western mountains of the Arabian Peninsula, across the Red Sea to Ethiopia and on down south along the East African rift mountains as far as Zimbabwe. According to this scenario, junipers in the mountains of the southwestern Arabian Peninsula represent an important corridor and link between *J. excelsa* in Asia and the east African junipers.

Adams et al. (1993) analyzed random amplified polymorphic DNA (RAPDs) as well as volatile terpenoids from leaves to compare the junipers from Abha, Saudi Arabia with *J. excelsa* from Greece and *J. procera* from Addis Ababa, Ethiopia. Both RAPD and terpenoid results clearly identified the Saudi junipers as *J. procera*, but morphologically these junipers are very similar to *J. excelsa*.

El-Bana et al. (2010) recently compared communities of *J. phoenicea* growing in the three mountain regions of northern Sinai: Gabal El-Halal, Gabal El-Maghara, and Gabal Yelleq (as a Mediterranean relict this species has been included in the Egyptian national list as a target for conservation and management). Ordination analysis identified four major vegetation types associated with the junipers. At Gabal El-Halal, *Chiliadenus montanus* and *Zygophyllum dumosum* dominated the slopes of smooth-faced rock outcrops in Wadi Abu Seyal between 350 and 470 m, while *Deverra tortuosa, Ephedra aphylla*, and *Gymnocarpos decander* were present in the soil pockets of north-facing slopes at 600–700 m of Gabal El-Halal. *Stachys aegyptiaca* and *Moricandia nitens* were in the runnels of Wadi Arar (450–560 m) at Gabal El-Maghara, and *Artemisia herba-alba, Atriplex halimus*, and *Reaumuria hirtella* were with the junipers on slope runnels at higher elevations (900–960 m) of Gabal Yelleq.

The two communities at Gabal El-Halal had, on average, greatest species diversity and highest juniper densities and percentage cover values. Juniper did less well at the higher elevations (600–960 m), having a greater proportion of old and recently dead trees there, plus a skewed sex ratio (more maleness, compared to populations at Gabal El-Maghara and Gabal Yelleq). Junipers at lower elevations on Gabal El-Halal were in the best condition, with more living foliage and reproductive branches than at the other sites.

It seems clear that differences in rock type and elevation influence recruitment differentially at these mountain locations, mostly through moisture availability (El-Bana et al. 2010). Results suggested *J. phoenicea* was endangered and that its conservation in the mountains of northern Sinai should be a priority, in particular the habitats at Gabal El-Halal. Changing climate, increasing drought, and high temperatures continue to limit the distribution of these characteristic Middle Eastern trees.

## 3.7 Deserts in the Middle East

Deserts are those places in the world where the limits to biological success are driven by *abiotic* factors—either scarcity of water and extremely high temperature (e.g., arid zones) or insufficiency of heat (cold deserts) at high latitude (arctic) and high altitude (alpine) zones of the world (see Section 4.1). Despite obvious differences between hot and cold deserts they share some basic features (Tivey 1971). In both, the physical environment is harsh and living conditions extremely difficult. Climatic extremes, protracted periods of intense drought and heat or cold usually result in short growing seasons, often of variable duration. Survival in such extreme environments is generally associated with a high degree of adaptation to these conditions (see Chapter 5).

Hot deserts are distinguished by their aridity—the temporal and/or spatial scarcity of water—and by their characteristic vegetation patterns and land use (Walter and Breckle 1986). In arid and semi-arid regions, mean annual evapotranspiration (ET) usually far exceeds mean annual precipitation (P). According to UNESCO's "World Map of Arid Regions," which defines bioclimatic aridity by the ratio of precipitation to evapotranspiration, or P/ET ratio (Wickens 1998; and see Table 10.1), ratios lower than 0.03 roughly correspond to the extreme arid zone, with mean annual precipitation 60–100 mm; ratios of 0.03–0.20 correspond to arid zones,

**Table 3.1** Major desert areas in the Middle East (from Holzapfel 2008; Siegmer-Walter 2002; Wickens 1998).

| Desert | Countries |
|---|---|
| Sahara desert | Libya, Egypt, and lowland Sudan |
| Horn of Africa desert | Southeast Sudan, lowlands of Eritrea, southern Ethiopia, and Somalia |
| Arabian Peninsula desert | Saudi Arabia, Yemen, Oman, Emirates, Qatar, Bahrain, and Kuwait |
| Syrian desert | The coastal eastern Mediterranean strip of Israel-Palestine, Lebanon, and eastern Syria, and the interior deserts of Jordan, Iraq, and Syria. |
| Turkey desert | Coastal Anatolian plateau |
| Iranian desert | Iranian coastal plains and the Dasht-e Kavir (the largest salt desert in the world) |

with precipitation from 60–100 to 150–250 mm. Ratios >0.20 characterize semi-arid regions, with precipitation from 150–250 to 250–500 mm.

In the Middle East desert conditions occur in almost all countries, and much of the landscape is classified as desert (see Table 3.1). Generally desert areas tend to be surrounded by Mediterranean climate and Mediterranean vegetation types, or by grasslands. These in turn may be either dry temperate or tropical grasslands (Holzapfel 2008). Major deserts are as follow.

1. The "Sahara," named from the Arabic for "desert," is the world's most extensive desert, stretching from the Atlantic in the west, across northern Africa to the Red Sea and highlands of Ethiopia. The parts of the Sahara most relevant to this book are in the arid and semi-arid parts of Libya, Egypt, Sudan, and the Horn.
2. The Horn of Africa desert, lying almost entirely below 800 m and corresponding to the Somali-Masai regional center of endemism, extends from southeastern Sudan and the lowlands of Eritrea and southern Ethiopia through Somalia and Kenya south to the plains of northern Tanzania (White 1983; Wickens 1998).
3. The desert of the Arabian Peninsula extends across Saudi Arabia, Yemen, Oman, the Emirates, Qatar, Bahrain, and Kuwait. It is separated from the Sahara by the Red Sea rift and excludes the highlands of the Hijaz and Asir mountains in Saudi Arabia, and the highlands of Yemen and Oman on the Arabian Sea and Gulf of Oman. Basically, aside from these mountain ranges the rest of the Peninsula is desert, including the vast and continuous sandy expanse, the Rub' al-Khali (see Section 1.4).
4. The Syrian Desert has two sub-regions—the coastal strip that includes Israel-Palestine, Lebanon and eastern Syria; and the interior deserts of Jordan, Iraq, and Syria.
5. In Turkey the desert is represented by the semi-arid central Anatolian plateau, which is separated from the Syrian Desert by the Anti-Taurus Mountains. The plateau falls gradually to a treeless depression containing the large endorheic salt lake, Tüz Gölü (see Section 2.25).
6. The Iranian deserts include the coastal plains and kavir deserts. The Iranian coastal plain bordering the Arabian Gulf and Gulf of Oman is characterized by a subtropical climate. The central Iranian plateau, with its very dry climate, includes the Dasht e Kavir or Great Salt Desert, the largest salt desert in the world (and largely devoid of much vegetation (see Sections 2.26 and 5.8).

## 3.8 Desertification and climate warming

The widespread deterioration of dryland ecosystems under the combined pressure of adverse climate change and habitat loss due to human development has been described as "desertification" (e.g., Verstraete 1986). The 1992 United Nations Conference on Environment and Development held in Rio de Janeiro defined it as land degradation in arid, semi-arid, and dry sub-humid regions of the world due to climatic change and variation (e.g., drought), and anthropogenic activities (e.g., overuse of natural resources).

Desertification is inevitably associated with the loss of biodiversity, reduced plant cover, soil erosion, and loss of organic matter; this leads to increased run-off and sand accumulation, all of which lead to progressively more desert-like conditions (Kassas 1977). All the usual forms of desertification are occurring today in the arid regions of Africa and the Middle East, and the process has long

been recognized as a major problem (Dregne 1983; Dregne and Chou 1992).

Large, global circulation models indicate the complexity of several interacting factors that are driving desertification in arid and semi-arid regions. Overgrazing and wood-cutting reduce vegetation cover; this results in increased albedo, which in turn cools the soil. Cooler soils promote subsidence of upper air masses, resulting in increased convection and upper atmosphere cloud formation; this leads to reduced precipitation (Charney 1975; Charney et al. 1977; Whitford 2002). Reduced vegetation also exposes soils to erosion and increases atmospheric dust burdens, which in turn affects surface temperature and provides raindrop-nuclei. Vegetation offers surfaces where condensation can occur during cold desert nights; moisture is "ducted" to the root system for uptake. Night-time condensation declines significantly where plant cover is removed.

Global climate warming is predicted to be causing regional climatic zones to "move" at a mean global rate of 0.42 km per year (Loarie et al. 2009),[8] and species are expected to respond to such changes through shifts in their geographical distributions, tracking suitable conditions (Collingham and Huntley 2000). Estimated warming velocities are highest in habitats like flooded grasslands (1.26 km/year), mangroves, and deserts.

The reported high warming velocities suggest the climates of only 8% of global protected areas have residence times exceeding 100 years. Small protected areas exacerbate the problem in Mediterranean-type and temperate coniferous forest biomes. Creating large protected areas in desert biomes might mitigate this problem (Loarie et al. 2009). Present-day climate change is already impacting the distribution of species' climatic-niche-space (e.g., VanDerWal et al. 2013), and species distributions, with latitudinal and altitudinal range shifts being increasingly documented (Chen et al. 2011; Parmesan 2006; Parmesan and Yohe 2003).

Global circulation models (Williams and Balling 1996) predict lower precipitation for deserts in the Middle East and northern Africa, in conjunction with increasingly frequent drought cycles. Whitford (2002) concluded the end result of these changes will be simply to exacerbate any desertification due to human activities.

In his review of climate change, drought, and desertification, Le Houérou (1996) tried to weigh the relative contributions of direct anthropogenic effects such as grazing and harvesting of vegetation, with the global pattern of climate change, particularly in reference to rainfall and surface temperatures. He concluded he saw no global long-term trend in rainfall change over the period of instrumental record (150 years); but that there *has* been an increase of 0.5°C in global temperature over the past 100 years. He suggested the increase was likely due to effects of urbanization, given no evidence it was a direct result of atmospheric pollution by $CO_2$ and other warming gases ($SO_2$, $NO_2$, $CH_4$, CFH, etc.).

At the same time, Le Houérou pointed out the thermal increase was *uneven*, being more intense at latitudes above 40° N and S. He concluded that the general increase in temperature was only slight or non-existent in subtropical and inter-tropical latitudes, which is where most of the world's arid and semi-arid lands lie.

Le Houérou showed that a possible increase of 1–3°C in arid lands over the next 50 years (e.g., due to a doubling in $CO_2$ content of the lower atmosphere, to 700 ppm—as assumed by most scenarios stemming from general Global Circulation Models–derived scenarios) would increase global potential evapotranspiration (PET) in plants by some 75–225 mm/year. He pointed out that it was not possible at that time to predict the resulting *net* balance between impacts of increased $CO_2$ on plants—the positive effects of boosting photosynthesis (and primary productivity), versus those of increased water use efficiency, coming from reduced stomatal conductance. In summary, Le

[8] Loarie et al. (2009) presented a useful new index of the velocity of temperature change (km/year), derived from spatial gradients (°C/km) and multi-model ensemble forecasts of rates of temperature increase (°C/year) in the twenty-first century. This index represents the instantaneous local velocity along Earth's surface needed to maintain constant temperatures, and has a global mean of 0.42 km/year. Owing to topographic effects, the velocity of temperature change is lowest in mountainous biomes such as tropical and subtropical coniferous forest (0.08 km/year), temperate coniferous forest, and montane grasslands, and highest in deserts. This fits with the general observation that such upland sites have offered safe harbor for species in the past, when subjected to rapid climate change.

Houérou concluded the possible effect of a climatic change—or fluctuation—of the size he envisioned, would have a relatively trivial effect on arid environments, as compared with the effects of humans and their livestock. *We* are the greater problem.

### 3.8.1 Drivers of desertification

The major drivers of desertification in the Middle East include the "mining" of groundwater, livestock overgrazing, and agricultural intensification. When aquifers are drawn off at rates which exceed the rate of recharge, the practice is unsustainable and the groundwater table will steadily fall. This will bring increased surface aridity, and local soils will become a "dustbowl" subject to wind erosion (El-Baz and Hassan 1986). Agricultural monocultures, excessive tillage, and local deforestation all promote soil erosion and loss. Overgrazing occurs when the number of grazing livestock exceeds the carrying capacity of a particular ecosystem. Overgrazing causes plant mortality, which exposes the soil to erosion by wind and runoff. Deterioration of vegetation and declining plant populations destabilize ecosystems, bringing local faunal extirpation and a decline in biodiversity. It's a sad but familiar ecological situation.

Where overgrazing is practiced over a wide area, permanent biodiversity loss can occur (Geeson et al. 2002). National policies that favor settled farming over the more traditional practice of nomadic herding can contribute significantly to desertification in regions more suited to occasional, seasonal, or intermittent grazing.

In general the pressures of an increasing human population on limited cultivated land have led farmers to shorten the fallow period in shifting cultivation cycles, and toward extension into more marginal, drier regions. Many nomadic pastoralists have lost areas that were previously sustainable for grazing because of conversion to permanent cultivation. In many places crops can only be produced once every three or more years, due to unpredictable rainfall in the inland and coastal deserts (Batanouny 1983). In countries like Libya, Egypt, and Saudi Arabia, failures of grain and forage crops dependent solely on rainfall can result in food shortages.

Across the Arabian Peninsula there has been a trend of increasing use of groundwater-based agriculture. Thus in addition to the effects of dry climate, over-exploitation of resources, excessive harvesting of trees and shrubs, and overgrazing, this practice of pumping excessive amounts of groundwater from deep wells has in turn further lowered the water table. Groundwater pumping is typically combined with dam construction over many of the major wadi systems and with establishment of water recharge wells that drain off the collected water (see Section 10.8). These have all caused loss or reduction of vegetation cover and subsequent soil erosion. The growing urban areas across the region are prioritized for access to the scarce supply of freshwater, leaving lower-value brackish or salty water for agriculture (Warren and Agnew 1988), and leading to a downward spiral in the fertility and productivity of agricultural lands.

In eastern Mediterranean countries and the region of Mesopotamia, desertification is a problem with ancient roots[9] (El-Baz 1983). The current climatic shift toward drying coincided with developing agricultural technology (see Chapter 9), over-exploitation of resources, and salt accumulation in irrigated lands. In Ethiopia and the Sahel, the combined effects of drought, increased human population and poor land management had devastating effects during the 1970s and 1980s, when more than 1.3 million people starved to death as a result of desertification and civil war (Darkoh 1998). Even in an otherwise wealthy country like Kuwait, desertification has seriously affected livestock production and negatively impacted the socioeconomic status of local residents, though there is no evidence of starvation (Omar and Abdal 1994).

Salinization and waterlogging of irrigated land is ongoing and widespread in the Nile Valley and North Africa, and elsewhere. In the Nile Valley the estimated reduction in crop yield attributed to salinization has reached about 17%, on more than 80% of the old irrigated lands. In newly irrigated lands east and west of the delta, there is about a 25%

[9] Various authors have suggested that expanding urbanization over once-fertile lands has already contributed to the collapse of major civilizations, including Carthage, and parts of the Roman Empire (Carter and Dale 1974; Ghabbour 2002; Whitford 2002).

yield reduction (Dregne and Chou 1992; Gomaa 2001). Similarly in Iraq, salinization and waterlogging in the irrigated southern part of the country is extensive and the damage is exacerbated by deep, fine-textured soils and nearly flat topography there. These make it difficult to provide enough drainage for a deep enough water table, which would otherwise help prevent surface-level salt accumulation (Dougrameji and Clor 1977).

## 3.9 Summary

This chapter considers Middle Eastern plant ecology as a product of "deep-time" and major geological events, beginning about 23 million years ago and including the loss of the Tethys Sea (this once stretched between the present-day Atlantic and Indian Oceans, but persists today only as the isolated basins of the Mediterranean, Black, and Caspian Seas). Plant populations and communities today are typically *remnants* of their past; any regional vegetation is always in a sense relictual, a product of its history and ongoing reality. Examples include the Socotran Dragon's-blood trees and other Socotran species, the Junipers of the Middle East, and the Bankoualé Palm, *Livistona carinensis*.

The many deserts of the Middle East are all growing in size as desertification proceeds apace. Global climate change and human activities are accelerating this process, and plants are unfortunately disappearing.

CHAPTER 4

# The desert as a heterogeneous environment

## 4.1 Introduction: Deserts and desert vegetation types

Deserts exist on every continent and cover about a fifth of the Earth's land area, if somewhat unevenly. Indeed deserts occupy *much* of the Middle East, extending through the Sahara of North Africa to Arabia and Iran, before essentially swinging northeast to the great cool deserts of Central Asia (Shmida 1985). In contrast to these African-Arabian-Eurasian desert-lands, the extent of both warm and cool desert to be found in the "New World" of the Americas is much less, for a variety of reasons.[1] Broadly speaking, deserts can be classified into five major types according to the *causes* of their dryness.

*Subtropical deserts* (sometimes called Trade Wind deserts): These are caused by the global circulation patterns of large air masses and occur along the Tropic of Cancer, between 15 and 30° N, and the Tropic of Capricorn, between 15 and 30° S. Hot, moist, equatorial air rises into the atmosphere; as it rises it cools, and so has reduced water-holding capacity. Precipitation falls as heavy tropical rains. The resulting cooler, drier air-mass circulates away from the Equator. As it approaches the tropics the air descends. The descending air is already dry and on re-warming, increases its capacity to hold water. This makes it unlikely clouds will form, so more sunlight directly heats the land and little rain falls.

The North African Sahara is the world's largest hot desert, covering some 4.6 million km$^2$ and is a subtropical desert that often experiences temperatures as high as 55–57°C. Other examples include the Arabian Desert and the deserts of southern Iran, the Kalahari in southern Africa, and the Tanami in northern Australia.

*Coastal deserts*: Coastal deserts are relatively complex because they occur where terrestrial, oceanic, and atmospheric systems meet. Onshore winds are chilled by contact with cold water currents running along the coast. This produces a layer of fog which drifts onto land. Winter fogs produced by upwelling cold currents frequently blanket coastal deserts and block solar radiation. Coastal deserts are generally found on the western edges of continents near the Tropics of Cancer and Capricorn. Local wind systems dominate so these tend to be less stable than other deserts. The Atacama of South America is the Earth's driest desert. There measurable rainfall of 1 mm or more of rain may occur as rarely as once every 5–20 years and some parts have gone for centuries without any. Other coastal deserts are found in Egypt, Libya, the Arabian Peninsula, and Iran. Some coastal deserts have little or no measureable rainfall yet they may be quite moist due to fog condensation.

*Rain shadow deserts*: Rain shadow deserts exist on the lee side of certain mountain ranges, away from prevailing winds. In general, as moisture-laden air

[1] First, the Americas are much smaller continents than Eurasia and little of the North American landmass lies in the subtropical latitudes, where deserts typically develop. Indeed much of what in America is called "desert" is, strictly, semi-desert—where annual precipitation is generally between 150 and 300 mm (Shmida and Whittaker 1979). The North American cool semi-desert is smaller, and historically younger than the huge, ancient arid center of continental Asia (Shmida 1985).

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hits a mountain range it is forced upward and cools. Since cold air holds less moisture, clouds form and drop precipitation on the windward (wind-facing) slopes. When the air moves over the mountaintop and begins to descend the leeward slopes, there is usually little moisture left. Also as it descends the air warms up and can hold more moisture, so clouds are unlikely to form.

Death Valley, in the rain shadow of the Sierra Nevada Mountains in California and Nevada is a rain shadow desert, the lowest and driest place in North America. Rain shadow deserts in the Middle East occur on the lee sides of coastal mountains in the western and southern Arabian Peninsula, and Iran.

*Interior deserts*: These occur in the centers of continents, beyond the reach of moisture-bearing winds. By the time coastal air-masses reach the interior, they have lost all their moisture. Prominent interior deserts are Rub Al-Khali and central Saudi Arabia, the large Syrian Desert, and the central Iranian desert. The Gobi in China and Mongolia lies hundreds of kilometers from the ocean, and is also in the rain shadow of the Himalayas, to the south.

*Polar deserts*: Parts of the Arctic and Antarctic are also defined as desert. Despite an abundance of water, most of it is in a solid state in glaciers and ice sheets; there is little water *available* to support plant growth. Thus the largest desert in the world is also the coldest (most of Antarctica being a polar desert, experiencing little precipitation).

Despite obvious differences between hot and cold deserts, they share an extreme (hot or cold) climate with protracted periods of intense heat or cold. This results in a short growing season of variable duration. Under such harsh conditions survival requires a high degree of adaptation and acclimation (and possibly plant "intelligence," too; see Section 8.1).

In his very useful and wide-ranging overview of desert floras worldwide, Shmida (1985) identified three desert ecosystems, focusing on annual precipitation rather than climate as the criterion.

*Semi-deserts* have precipitation between 150 and 300 to 400 mm per annum.

*True deserts* are regions receiving rainfall below 120 mm per annum.

*Extreme deserts* have rainfall below 70 mm per annum.

Figure 4.1 shows the major desert ecosystems. For organisms in a desert environment, the

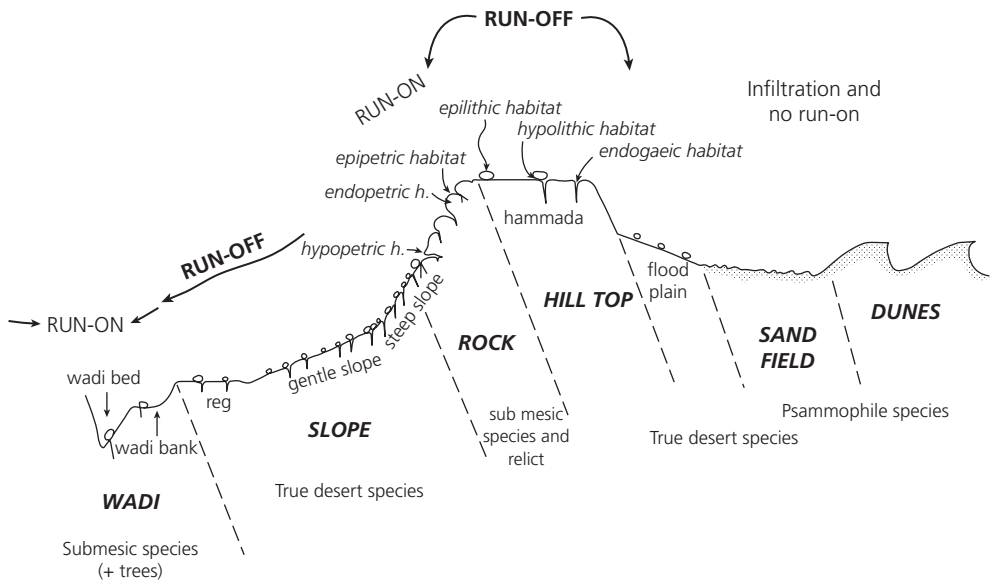



**Figure 4.1** Schematic diagram of the major desert ecosystems (after Shmida et al. 1986, used with permission).

concentration and availability of both water and nutrient resources all tend to vary greatly over time and space, both within and among years and significantly influencing the plant ecology of the region. From an animal's perspective, plant life is surely mostly very, very slow. As Shmida et al. (1986) showed, short periods of water and nutrient availability do occur after rains but their timing, duration, and extent are all very variable and highly unpredictable.

An *arid* regional ecosystem tends to combine both extreme and true deserts, while a semi-arid system corresponds to semi-desert. Shmida (1985) showed how confusion can result from inconsistency of terms such as desert, steppe, savanna, etc., and in what follows we use his definitions and synonymy. In practice, most plant communities or "formations" tend to be identified mainly by the *tallest* growth-form present. This has led to a certain amount of typological nomenclature associated with plant growth form ("dwarf shrub," "low shrub," "semi-shrub," "shrublet," "nano-phanerophyte". . .).

*Contracted desert*: This is an environment where perennial plants are restricted to wadis (= valleys or washes). In good years, when there is abundant rainfall, annual plants also grow on the slopes and hamadas[2] between wadis (see Figure 4.1).

*True desert*: Where the cover by perennial plants is < 10%. Vegetation is generally dominated by sparse dwarf-shrubs (chamaephytes) or a few true shrubs. In the rainy season a flush of annuals covers the ground. Overall coverage, even in the best years, is < 50%.

*Steppe* (= chamaephyte semi-desert): Here dwarf-shrubs cover > 10% (usually 10–30%) of the ground. Perennial grasses (and in the Americas, cacti) can grow among these *suffrutescent* shrubs (having a woody, perennial base), but the grasses tend not to dominate.

*Grassland*: Semi-desert vegetation dominated by perennial grasses. This includes the spinose tussock grassland of the Australian semi-desert and many plant communities in Middle Eastern desert wadis and sand plains, which are dominated by perennials and annuals of various genera, e.g., *Panicum, Pennisetum, Lasiurus, Cymbopogon, Cynodon, Sporobolous, Stipagrostis, Stipa, Aegilops, Hordeum, Aristida, Bromus*, and *Dactyloctenium*.

Arboreal plants (including trees and shrubs > 1 m high) are generally absent from all of the previously mentioned communities because they are unable to survive with such limited water supplies. Trees and shrubs *can* be found, even in extreme deserts, but they are usually restricted to the wetter parts of wadis (or other channels and *arroyos secos*). When trees occur in rows along a wadi bed, this is sometimes referred to as a "gallery forest" (Zohary 1973).

*Shrubland*: This kind of vegetation is dominated by shrubs (> 0.5 m and up to 2 m high) covering > 30% of the ground. If shrubs are more sparse, *c.* 3–30% cover, the formation is usually regarded as an "open shrubland" (or desert chaparral; Barbour and Major 1977). This latter is the major vegetation type in much of eastern Arabia (see Section 4.4).

Shrubs may be evergreen or deciduous. If most are broad-leafed evergreens, the vegetation corresponds to the Mediterranean "matorral" (also called chapparal, maquis, mallee, etc.; see di Castri et al. 1981 and Shmida 1981). If the shrubs have long, slender leaves—"leptophyllous" evergreens—the vegetation is described as heath (Specht 1979). If the shrubs are drought-deciduous or partially drought-deciduous, then the vegetation may be described in terms of other, less well-defined communities (such as scrub or thicket).

*Woodland*: An open arboreal community in which trees (and sometimes shrubs) are > 2 m and plant cover ranges between 20 and 80%. Woodlands are usually found in the temperate zone and are composed of cold-deciduous, broadleafed species (e.g., oaks), and conifers (e.g., junipers).

If the woodland becomes sparse (< 20% cover), it is regarded as "open woodland," sometimes called

[2] Hamada (also hammada) is a common desert landscape consisting of high, largely barren, hard, rocky plateaux with most of the sand removed by deflation (aeolian, or wind-driven, removal of the fine products of weathering) (e.g., Gautier 1935). The related terms *Reg* (in the western Sahara), *Serir* (eastern Sahara), *Gibber Plain* (Australia), or *Saï* (Tarim Desert, central Asia) also describe a high sandy plain or broad depression largely covered by lag gravels or angular boulders, from which the finer soil and sediment has been stripped by wind action.

steppe forest in Asia (Walter 1973; Zohary 1973), or savanna (Griffin 1977).

*Savanna*: This is an open tropical woodland in which trees are usually thorny and have a facultatively deciduous microphylly—their small leaves may drop during dry periods (see Chapter 5). According to Shmida savanna usually has a grass layer among the trees (especially in Africa), but not always (as in the Sonoran, in the southwestern United States). In the New World this kind of vegetation is often called thorn-wood, spinose suffrutescent scrub, sub-tropical thorn scrub, etc.

As Shmida pointed out, many semi-arid plant communities simply do not fit any of these categories. Many transects show a continuum from one vegetation "type" to another, and other growth-forms may be dominant in the landscape (including cacti, succulents, and rosette shrubs). Succulents are an important growth-form in the Middle East and elsewhere and can become dominant in some formations—e.g., the succulent chamaephyte semi-desert of Baja California, the succulent savanna of the Sonoran (Mooney 1977; Whittaker 1975), or the Succulent Karoo of southern Africa.

Succulents are dominant or co-dominant in many different habitats. They belong to various families and have different growth forms and may be stem or leaf succulents and more (see too Sections 5.1 and 5.2).

### 4.1.1 Trees and shrubs in the global desert flora

According to Shmida, the legumes (family Fabaceae) are the most important group of trees and shrubs in the world's subtropical deserts (including those in the Saharo-Arabian region, the Thar in India, deserts in Australia, South America, southern Africa, and the Sonoran). *Acacia, Cassia*, and *Prosopis* are dominant genera in many of the semi-desert savannas. They extend to the true desert in wadis, sometimes creating a gallery forest. Both *Acacia* and *Prosopis* are mostly thorny, microphyllous multi-stemmed trees, with leaves which are often facultatively drought deciduous (Shmida 1985).

The genus *Juniperus* (with scaly micro-leaves) is common in the semi-deserts of temperate areas such as the Irano–Turanian and Great Basin regions. Junipers also form a huge steppe forest of very open woodland in the cold semi-deserts of the Middle East (at elevations above 1000 m), as well as Central Asia and North America (Shmida 1985).

### 4.1.2 Low shrubs and chamaephytes

Generally speaking as conditions get drier, the dominant plants become smaller. Dwarf shrubs (= suffrutescent chamaephytes), semi-shrubs, and low shrubs (chamaephytes and some nanophanerophytes[3]) are the most *conspicuous* growth form in the arid environment (Shmida 1985). Under semi-arid conditions dominant shrub genera include *Artemisia* (in particular in the Irano–Turanian region, and also in North America), *Atriplex* (Irano–Turanian, North America, and Australia), *Cassia* (Australian), *Ephedra* (Irano–Turanian and North America), *Larrea* (North and South America), and *Retama* (Sudano–Arabian region) (Shmida 1985).

In areas with < 120 mm annual rainfall (i.e., in the true and extreme deserts) dwarf-shrub communities are dominant where vegetation occurs. These plants have a small, perennial arborescent form and each year part of their canopy is shed. According to Shmida, genera such as *Anabasis, Hammada, Salsola*, and *Suaeda* (all in the Chenopodiaceae) and *Fagonia* and *Zygophyllum* (Zygophyllaceae) are very abundant in the extreme deserts of the Saharan and Irano–Turanian parts of the Middle East, and elsewhere. *Astragalus* (Fabaceae) and Asteraceae (e.g., *Achillea, Anvillea*, and *Asteriscus*) are also important in the region.

## 4.2 Desert phytogeography

The global flora has been broadly classified into six great floristic *realms*—Holarctic, Paleotropic, Neotropic, Australian, Cape, and Antarctic (Engler and Drude 1896; Good 1964; Walter 1973). Aside from the Australian and Central Asian deserts, it is noteworthy that all the other deserts in the world are located in transitional areas, or "vegetation tension zones" between one and another of these realms (see Figure 4.2).

[3] Any woody perennial between about 25 and 200 cm in height.

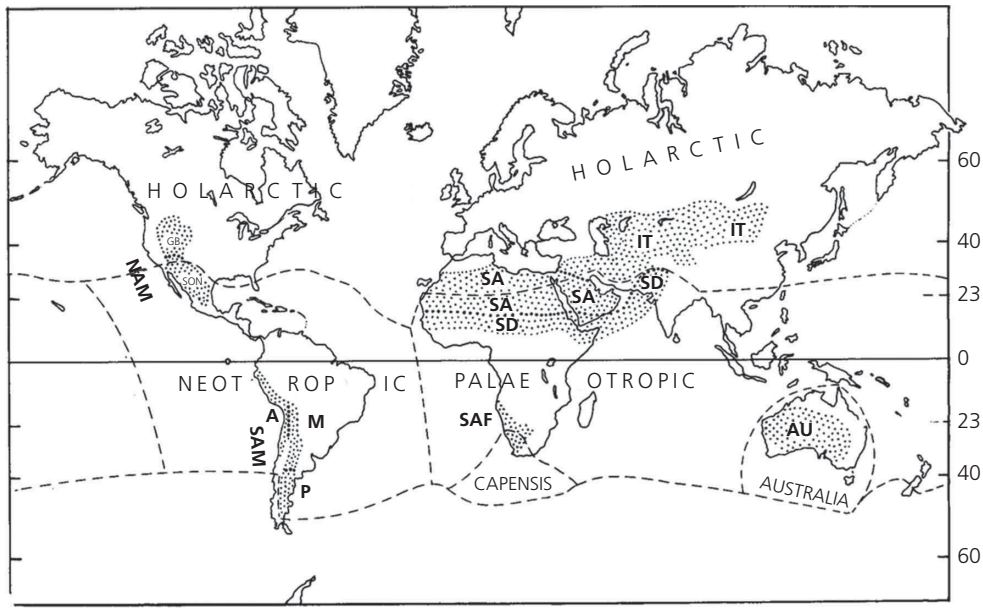



**Figure 4.2** Phytogeographical regions of the arid environments of the world. Dashed lines: borders of the six main floristic realms of the world (Engler and Drude 1896 Walter 1973). This shows that most of the desert phytogeographical regions are in the transition zone between temperate floristic realms and tropical realms. Legend: *AU* = Australia region; *SAF* = southern African region; *SAM* = south American region (*P* = Patagonia, *A* = Atacama, *M* = Monte); *NAM* = North American region (*SON* = Sonoran region, *GB* = Great Basin (Artemisian) region); *IT* = Irano–Turanian region; *SA* = Saharo–Arabian region; and *SD* = Sudano–Deccanian region (after Shmida 1985, used with permission).

Shmida (1985) showed how this geographic reality gets reflected in the floristic composition of those desert regions. For example, in the Middle East, the Saharo-Arabian phytogeographic region shares major elements with both the Holarctic and Paleotropical realms. North American deserts have both Holarctic and Neotropical elements; South African deserts have large plant components representing the Cape and the Paleotropics.

These global realms have been divided into hierarchically ranked, phytogeographic regions, using measures of their floristic dissimilarity (usually expressed by the Jaccard coefficient)[4], as well as the presence of any endemic higher category taxa (e.g., new plant families having special features, such as succulence, Crassulacean acid metabolism, salt tolerance, etc.) (See Chapter 5.)

Figure 4.2 and Table 4.1 summarize the most important floristic nodes of the world's desert floras, and the major plant families involved. All the different desert regions of the world can be assigned to the following phytogeographic regions:

1. Australian region
2. Southern African region
3. Monte–Patagonian region
4. South American (Peru–Chile) region
5. Sonoran region
6. Artemisian (Great Basin) region
7. Irano–Turanian region
8. Saharo–Arabian region
9. Sudano–Deccanian region

The Middle East is represented by the last three: Irano–Turanian, including all the Central Asian and mid-Asian deserts; Saharo–Arabian, including the extreme deserts of Sahara and Arabia; and

[4] The Jaccard coefficient, also known as the Jaccard similarity index, is a statistic used for comparing the similarity and diversity of sample sets. The coefficient measures similarity between finite sample sets, and is defined as the size of the intersection divided by the size of the union of the sample sets (e.g., Qian et al. 2008; and see, too, Alroy 2015).

Sudano–Deccanian, which includes the Sahel[5] and savanna vegetation types south of the Sahara, as well as the Thar desert on the border between India and Pakistan.

According to Good (1964), only three phytogeographic regions are characterized mainly by their *arid-adapted* flora. These are the central Australian; the western and central Asian—or Irano–Turanian region (*sensu* Eig 1931/1932; Zohary 1973); and the African–Indian region (Saharo–Sindian region *sensu* Eig 1931/1932).

Shmida (1985) described a general, global north-to-south (occasionally west-to-east) desert macro-gradient, in which winter rains diminish and summer rains increase. When deserts are large there is an extreme desert area in the center, and almost no overlap between winter and summer rains. This is the case in the Sahara and Rub al-Khali drylands. This macro-gradient includes a temperature continuum from lower in the north to higher in the south.

Plant life and the associated vegetation patterns tend to follow this large-scale gradient, with temperate elements in the north being replaced by more tropical ones in the south. Thus cold, deciduous temperate-forest elements such as *Fraxinus* and *Populus* decline toward the south, while thorny, microphyllous savanna species taper toward the north (e.g., *Acacia, Balanites, Bursera, Commiphora, Prosopis*) (Shmida 1985).

As shown in Figure 4.3, this pattern is particularly pronounced in the Saharo–Arabian deserts, where mostly temperate families like the Apiaceae, Brassicaceae, Linaceae, Ranunculaceae, and Rosaceae all decline toward the south, whereas tropical families, including the Asclepiadaceae, Cucurbitaceae, and Euphorbiaceae increase. Only two families are typically *richer* in taxa in deserts than elsewhere—the Chenopodiaceae and Zygophyllaceae, both of which have clearly managed to exploit the desert environment and adapt highly successfully (see Figures 4.4 and 4.5).

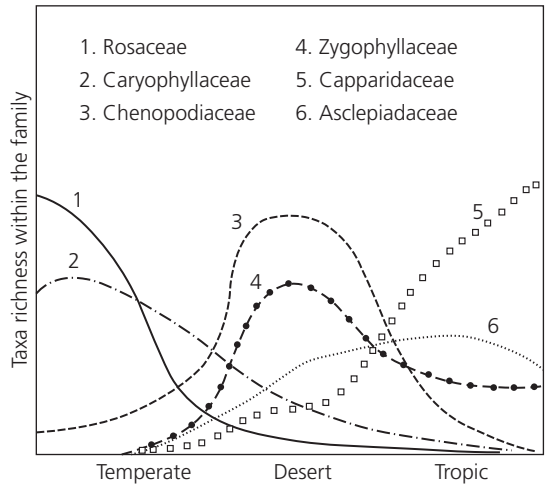



**Figure 4.3** Number of species in representative families along the geographical catena from the temperate/Mediterranean through the subtropical desert to the tropics (after Shmida 1985, used with permission).

Table 4.1 lists the ten dominant plant families in different desert regions. Shmida concluded the Chenopodiaceae was the single most important family among the world's desert flora[6] (see Figure 4.4). In terms of extent, it is the most widespread family within the very large Irano–Turanian region; it is also very important in the Sahara, as well as in the deserts of North America, Australia, and South America.

As shown in Table 4.1 the Brassicaceae (formerly Cruciferae), the Caryophyllaceae, and to some degree the Polygonaceae are all also abundant in the deserts of the Holarctic realm. Brassicaceae are most abundant in the Sahara and Caryophyllaceae in the Asian, Irano–Turanian deserts. According to Shmida these are both dominant, temperate, herbaceous plant families that have successfully expanded into adjacent desert areas. The Polygonaceae have a distribution with two eremic centers, one in Asia (including chiefly the genus *Calligonum*) and the other in North America (especially *Eriogonum*).

[5] The Sahel is the semi-arid zone of transition in Africa between the Sahara Desert to the north and the Sudanian savanna to the south, and stretches between the Atlantic Ocean and the Red Sea.

[6] It should be noted that this long-standing family-level name has since been subsumed within an expanded Amaranthaceae by the Angiosperm Phylogeny Group (APG II, 2003; APG III, 2009).

**Table 4.1** The main dominant/abundant families (as percentage of species number) of some desert regions of the world (*desert family; families preferential for a region are set in italics, exclusive families in bold face) (after Shmida 1985, used with permission).

| **Australia** | | **South Africa** | | **Irano–Turanian** | | **Middle East** | |
|---|---|---|---|---|---|---|---|
| 630 | | 748 | | 623 | | 608 | |
| (63 introduced) | | | | | | (3 introduced) | |
| Asteraceae | 23.2 | Asteraceae | 20.2 | Poaceae | 13.8 | Asteraceae | 14.0 |
| *Chenopodiaceae | 11.6 | *Aizoaceae* | 15.0 | Asteraceae | 11.6 | Poaceae | 8.2 |
| Poaceae | 11.4 | *Liliaceae* | 8.3 | *Brassicaceae* | 10.4 | *Chenopodiaceae | 7.4 |
| Fabaceae | 9.2 | Poaceae | 6.4 | *Chenopodiaceae | 7.9 | Fabaceae | 7.4 |
| **Myrtaceae** | 5.0 | *Crassulaceae | 5.6 | Fabaceae | 7.5 | *Brassicaceae* | 5.6 |
| Brassicaceae | 3.2 | Scrophulariaceae | 5.2 | *Caryophyllaceae* | 4.6 | *Caryophyllaceae* | 5.4 |
| **Goodeniaceae** | 3.2 | Fabaceae | 4.0 | Boraginaceae | 4.3 | Liliaceae | 4.8 |
| Solanaceae | 2.4 | Iridaceae | 3.3 | Polygonaceae | 3.0 | Boraginaceae | 3.8 |
| Liliaceae | 2.2 | *Geraniaceae* | 2.9 | Lamiaceae | 2.7 | *Zygophyllaceae | 3.0 |
| Malvaceae | 1.9 | Chenopodiaceae | 2.7 | Liliaceae | 2.4 | Lamiaceae | 3.0 |
| **Proteaceae* | 1.8 | *Zygophyllaceae | 2.3 | Crassulaceae | 1.8 | | |
| **Epacridaceae** | 1.8 | Euphorbiaceae | 2.3 | Scrophulariaceae | 2.6 | | |
| *Zygophyllaceae | 1.6 | Asclepiadaceae | 2.0 | Rosaceae | 2.4 | | |
| **Myoporaceae** | 1.6 | *Oxalidaceae* | 1.5 | | | | |
| *Aizoaceae | 1.4 | | | | | | |

| **Sahara** | | **Indian Desert (Thar)** | | **North America** | | **World** | |
|---|---|---|---|---|---|---|---|
| 674 | | 592 | | 632 | | 225 000 species | |
| | | (45 introduced) | | (26 introduced) | | | |
| Poaceae | 11.1 | Poaceae | 15.0 | Asteraceae | 19.3 | Asteraceae | 11.1 |
| Asteraceae | 11.0 | Fabaceae | 14.0 | Poaceae | 7.0 | Orchidaceae | 7.8 |
| Fabaceae | 10.7 | Asteraceae | 6.4 | Fabaceae | 6.1 | Fabaceae | 7.6 |
| *Brassicaceae* | 3.2 | *Convolvulaceae* | 5.6 | Polygonaceae | 4.9 | Poaceae | 4.0 |
| *Chenopodiaceae | 3.4 | Malvaceae | 4.6 | Boraginaceae | 4.6 | Rubiaceae | 3.3 |
| *Zygophyllaceae | 2.8 | Cucurbitaceae | 3.2 | **Polemoniaceae** | 4.1 | Euphorbiaceae | 2.6 |
| Caryophyllaceae | 2.6 | *Acanthaceae* | 2.7 | Brassicaceae | 4.0 | Lamiaceae | 2.0 |
| Boraginaceae | 2.3 | Euphorbiaceae | 3.4 | **Hydrophyllaceae** | 3.1 | Scrophulariaceae | 1.8 |
| Capparidaceae | 2.3 | Scrophulariaceae | 2.4 | ***Cactaceae** | 2.8 | Cyperaceae | 1.8 |
| *Aizoaceae | 2.1 | *Amaranthaceae* | 2.4 | Scrophulariaceae | 2.8 | Melastomataceae | 1.7 |
| Plumbaginaceae | 1.8 | *Zygophyllaceae | 2.3 | *Chenopodiaceae | 2.4 | *Chenopodiaceae | 0.7 |
| Lamiaceae | 1.7 | *Chenopodiaceae | 1.0 | **Onagraceae** | 2.2 | *Zygophyllaceae | 0.1 |
| Geraniaceae | 1.4 | Capparidaceae | 1.4 | **Loasaceae** | 1.3 | *Aizoaceae | 1.0 |
| | | | | **Agavaceae** | 1.0 | *Cactaceae | 0.1 |
| | | | | Fouquieriaceae | 0.1 | Asclepiadaceae | 1.5 |
| | | | | | | *Crassulaceae | 0.7 |

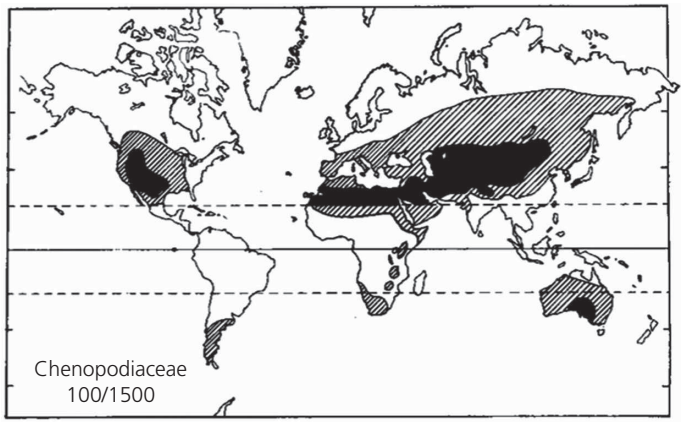



**Figure 4.4** Distribution map of the Chenopodiaceae (100 genera, 1500 species). The most widespread and representative family of saline habitats and deserts throughout the world. One of the only two families actually having their center in the desert (black patches) (after Shmida 1985, used with permission).

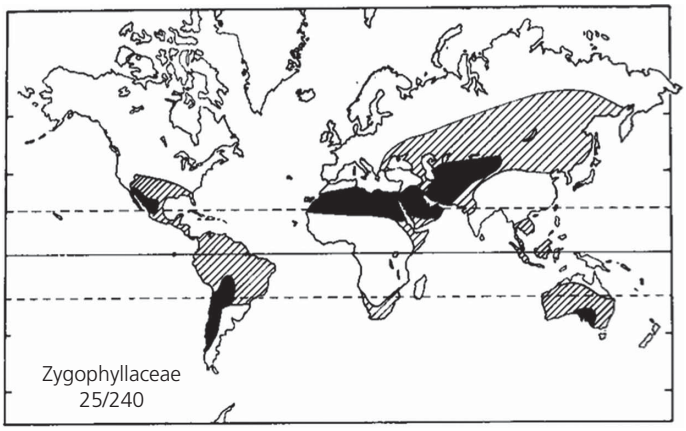



**Figure 4.5** Distribution map of the Zygophyllaceae (25 genera, 240 species). One of the most typical cosmopolitan desert families and one of the only two families which are actually centered in arid regions (black patches) (after Shmida 1985, used with permission).

Two common desert families—the Aizoaceae (including the mesembs, "ice plants" or "stone plants" which resemble rocks and pebbles) and the Liliaceae—are shared between the Sahara and southern Africa. These families and many other shared genera (see Shmida 1985), all show the mutual influence of these two desert regions.

In general the Aizoaceae, along with the other major succulent lineages—the chenopods and amaranths, brassicas and crucifers, caryophs and euphorbs—present a wide array of succulent morphologies. Their growth forms suggest water relations are a more important limiting factor for survival and reproduction than simple carbon gain through photosynthesis. Many of these drought- and salt-resistant species have Crassulacean acid metabolism, or CAM photosynthesis (see Section 5.5), or are physiologically flexible and able to switch to CAM. Ice plants and these other specialists successfully manage the suite of desert selection pressures . . . low and sporadic rainfall, intense solar irradiation and high temperature, high salinity, and much windy sandblasting. Low temperatures appear to limit the distribution of the mesembs, but most of the other succulent lineages—certainly those from mountain regions in the Middle East—have become cold adapted, too.

## 4.3 Desert growth forms and Cactaceae

According to Shmida and Whittaker (1979), the Old World deserts and semi-deserts—from the

Sahara to central Asia—have a fairly limited array of plant growth-forms; conventional shrubs and semi-shrubs predominate. They point out that some striking growth-forms that are common in the relatively small North American semi-desert area are essentially *absent* from the far larger, "Old World" arid regions.

1. Cactoids—massive stem-succulents as in the Cactaceae, which are restricted to the New World. They are almost the only common exclusive family shared by the two continents of the New World. According to Shmida (1985), *Rhipsalis* is the only cactus that grows widely in Africa and this is probably a result of long-distance anthropogenic dispersal.[7] *Opuntia ficus-indica* is raised for its fruit in Egypt and elsewhere.
2. Tall columnar green-stemmed plants, both succulents (giant cacti) and woody non-succulents (especially Fouquieriaceae).
3. Rosette shrubs with succulent or semi-succulent leaves—*Agave, Yucca, Nolina*, and *Dasylirion* in North America.
4. Semi-desert ferns and clubmosses. In North America a number of clubmosses (*Selaginella* spp.), and a few genera of ferns (*Cheilanthes, Notholaena, Bomeria, Pityrogramma*) are adapted to desiccation of their foliage during the dry season and recovery in the rainy season. Such pteridophytes are more limited in the Old World.

At the same time, Old World deserts have some species with life history strategies not seen, or which are significantly less common in the New World. Shmida and Whittaker give several kinds of examples:

- Annual species that are tumbleweeds, rolling in the wind as a means of seed dispersal (see Section 7.6). They are abundant in Asia and were largely absent in America until recent Eurasian introductions occurred (e.g., *Salsola tragus*, the tumbleweed of frontier Western movies, and *Kochia indica*).
- Giant spiny annuals are common in the Old World, and absent but introduced as weeds in the New (and distinct from the spiny biennials/short-lived perennials like *Cirsium*, that are common ruderals and agricultural weeds in both Old and New).
- Shrubs with slender, succulent green stems are more widespread in the Old World (in particular members of the Chenopodiaceae, which are common dominants across the Middle East).
- In mountains, a special form of Middle Eastern dwarf-shrub occurs—the tragacanth (gum-producing legumes in the genus *Astragalus*, including *A. adscendens*, *A. gummifer*, *A. brachycalyx*, and *A. tragacanthus*), first highlighted by Shmida (1977, 1985; see Section 2.21). Although the genus is found throughout the Northern hemisphere, these drought-resistant, low, intricately branched and spinose, cushion shrubs of the alpine semi-desert and desert are not found in North America.

The arid region of central Asia is ancient, as a result of a long-extant cold and arid climate, in the interior of a huge landmass. Great dry salty basins which remained, along with the Aral and Caspian Seas as the Tethys receded, have clearly been excellent nurseries for the evolution of succulent-stemmed halophytes and salt-tolerant trees such as *Tamarix* (Shmida and Whittaker 1979).

## 4.4 Desert plant communities

In most Middle Eastern deserts but in particular in the great deserts of eastern Arabia, many of the more important plant communities—often covering hundreds or even thousands of square kilometers—are characterized by woody dominants of *single* species. According to Mandaville (1990), these open shrublands have diffuse perennial cover that usually totals less than 15%; the spaces between shrubs remain bare for much of the year but for a few weeks or months each year they produce a ground layer of rainy-season ephemerals.

The list of plant species that make a significant contribution to primary productivity in a desert is typically fairly short. As an example, Table 4.2 lists 50 species that Mandaville determined to be most important in terms of their abundance and

[7] About 36 *Rhipsalis* species are native to America. *Rhipsalis baccifera*, the mistletoe cactus, is an epiphytic species native to America that crossed to the Old World (Africa, Madagascar, and Sri Lanka) possibly on trading ships and associated bird dispersal (Cota-Sanchez and Bomfim-Patrício 2010).

**Table 4.2** Principal contributors to plant biomass in eastern Saudi Arabia (after Mandaville 1990).

| **Dominant perennials** | *Lasiurus scindicus* | *Trigonella stellata* |
|---|---|---|
| *Haloxylon salicornicum* | *Dipterygium glaucum* | *Trigonella hamosa* |
| *Rhanterium epapposum* | *Anvillea garcinii* | *Launaea capitata* |
| *Calligonum comosum* | *Zilla spinosa* | *Launaea mucronata* |
| *Calligonum crinitum* | | *Cutandia memphitica* |
| *Cornulaca arabica* | **Annuals** | *Savignya parviflora* |
| *Haloxylon persicum* | *Plantago boissieri* | *Arnebia linearifolia* |
| *Anabasis lachnantha* | *Plantago ovata* | *Brassica tournefortii* |
| *Zygophyllum qatarense* | *Astragalus tribuloides* | *Emex spinosa* |
| *Zygophyllum mandavillei* | *Picris babylonica* | *Horwoodia dicksoniae* |
| *Seidlitzia rosmarinus* | *Stipa capensis* | *Erodium laciniatum* |
| | *Eremobium aegyptiacum* | *Senecio glaucus* |
| **Abundant perennials** | *Schismus barbatus* | *Hippocrepis bicontorta* |
| *Cyperus conglomeratus* | *Neurada procumbens* | *Lotus halophilus* |
| *Stipagrostis drarii* | *Schimpera arabica* | *Reichardia tingitana* |
| *Stipagrostis plumosa* | *Ifloga spicata* | *Ononis serrata* |
| *Moltkiopsis ciliata* | *Astragalus hauarensis* | *Asphodelus tenuifolius* |
| *Pennisetum divisum* | *Medicago laciniata* | *Astragalus annularis* |
| | | *Aaronsohnia factorovskyi* |

contribution to biomass across eastern Arabia. Mandaville suggested this was also an indication of the relative importance of each species as a grazing resource supporting any animal life there.

It is obvious the dominant shrubs in these eastern Arabian communities quite effectively *modify* the habitat for annual plants, primarily through soil-stabilizing effects. According to Mandaville the eastern Arabian annuals often congregate around and under woody species, which are able to trap wind-driven seeds and propagules, collect rain, and provide shelter from the wind (see Sections 1.7 and 4.7). Many of the seasonal annuals are opportunistic and lack any close community integration.

Of the ten most important perennials in Table 4.2, five are Chenopodiaceae, two Zygophyllaceae, two Polygonaceae, and one Asteraceae. Of the next nine, four are grasses (Poaceae) and there is one representative from each of the Cyperaceae, Boraginaceae, Capparaceae, Asteraceae, and Brassicaceae. Among the 31 ephemerals the most important families are the Fabaceae (9 species), Asteraceae (7), Brassicaceae (5), and Plantaginaceae (2).

These fifty species predominate in what is a relatively small set of major plant communities in the region. They often include various species and genera of chenopod "saltbushes." There has been significant morphological convergence among the various saltbushes[8] and they can be difficult to

[8] These Middle Eastern chenopod saltbushes should not be confused with various other plants elsewhere, commonly called "saltbush." Examples include the following.

*Atriplex*, distributed nearly worldwide from subtropical to temperate and subarctic regions. This genus shows lots of speciation in Australia, North America, South America, and Eurasia. Many species are halophytes and adapted to dry environments with salty soils.

*Chenopodium hastatum*, commonly called berry saltbush, found in open areas of eastern Australia.

*Chenopodium nutans*, commonly called climbing or nodding saltbush, native to Australia. The small leaves are semi-succulent.

*Sarcobatus vermiculatus*, native to North America, a halophyte usually found in sunny, flat areas around dry lake margins (*playas*).

distinguish. As described in Section 5.8, saltbushes are mostly defined by their ability to excrete significant amounts of salt from their leaves.

Saltbush species are also unusual in their seasonal development, as many tend to undergo active growth in summer and produce fruit in the fall. Thus these species are mostly flowering in September–October and have mature fruits in late-October to mid-November. Mandaville interprets their pronounced winter die-back as a possible hold-over adaptation to harsh winters in an ancient Irano–Turanian homeland to the north. Meantime species in some other saltbush genera, such as *Salsola* and *Halothamnus*, have spring or summer fruiting seasons.

Several Middle Eastern parasitic plants use saltbushes as host species. For example, *Cynomorium coccineum*, a monotypic genus in the Cynomoriaceae, parasitizes the roots of most of the major saltbushes, including both *Halophyllum salicornicum* and *Haloxylon persicum* in eastern Arabia (Collenette 1985; Mandaville 1990). (Other parasitic species include *Cistanche phelypaea, C. tubulosa*, and many species of *Orobanche*, including *O. cernua, O. hypertomentosa*, and *O. pubescens* all of which parasitize a wide range of desert plant hosts.)

According to Mandaville the following are the dozen or so most important eastern Arabian plant *communities*.

*Rimth* saltbush shrubland: This is open shrubland dominated by the *rimth* saltbush, *Haloxylon salicornicum*, and likely covers more area than any other community in northeastern Arabia. It occurs on low sandy soils where the water table is close to the surface. According to Halwagy et al. (1982), *Haloxylon* should probably not be classified as a strict halophyte, as it is not generally found on the *most* saline sabkha margins (where instead two other chenopods, *Seidlitzia* and *Suaeda* occur). *Haloxylon salicornicum* does, however, tend to dominate the plant community surrounding sabkhas at slightly higher elevations (Mandaville 1990).

'*Arfaj* Shrubland: This open shrubland is dominated by *Rhanterium epapposum* (Asteraceae), known as '*arfaj*. It is best developed in northern Saudi Arabia, Iraq, and Kuwait. This vegetation is found on better-drained soil on higher ground where bedrock is close to the surface, and provides a significant winter, spring and early summer grazing resource. There are generally more annual species here than in *rimth* shrubland, with *Plantago boissieri* (Plantaginaceae) typically the most frequent and abundant annual, and *Picris babylonica* (Asteraceae) and *Neurada procumbens* (Neuradaceae) other important members of the community.

*Thumam* grass shrubland: This community is dominated by the perennial tussock grass *Panicum turgidum*, or *thumam*, and is widely distributed in the central coastal lowlands of eastern Arabia. Woody associates include *Lycium shawii* (Solanaceae), *Leptadenia pyrotechnica* (Asclepiadaceae) and, most frequently, *Calligonum comosum* (Polygonaceae) which can often become co-dominant with the *Panicum*.

*Ephedra* shrubland: Essentially pure stands of the dioecious shrublet, *Ephedra alata* (Ephedraceae), are found occasionally all the way from the south coastal lowlands up to the north of Arabia. This community is often associated with gypsaceous soils (high in calcium sulfate).

*Achillea-Artemisia* silt basin association: This is a northern community type distinguished by its highly aromatic dominants, *Achillea fragrantissima* and *Artemisia sieberi* (both Asteraceae). The association is more common in the northwest, in the Hajarah and al-Widyan regions outside the Eastern Province of Saudi Arabia (see Figure 4.1). Patches also occur on heavy silts and clay basins in the Northern Plains and Summan regions.

'*Abal-'Adhir* sand shrubland: This community type typically includes *Artemisia monosperma*, as well as widely spaced but well-developed shrubs of *Calligonum comosum* and tussocks of the perennial grass *Stipagrostis drarii*, the sedge *Cyperus conglomeratus*, and in the south, *Limeum arabicum* (Aizoaceae). The community includes a wide variety of annuals, such as the very common *Plantago boissieri*, plus *Plantago psammophila, Eremobium aegyptiacum* (Brassicaceae), and *Cutandia memphitica* (Poaceae).

*Ghada* shrubland: This community is dominated by the large shrubs/trees—*Haloxylon persicum* and *H. salicornicum*, or *ghada.* These are the largest of the saltbush species, often more than 2–3 m in height, and widely used as a desert firewood—see Section 10.2. *Ghada* shrubland often forms "islands" or patches within a larger region of *rimth* shrubland. In the Rub' al-Khali it may also border on *hadh* shrubland, another saltbush association.

*Hadh* saltbush shrubland: This community and its dominant species *Cornulaca arabica* (Chenopodiaceae) is endemic to the Rub' al-Khali; it is one of that region's most important vegetation types.

Rub' al-Khali '*Abal* shrubland: This is another widely spaced shrub community of the Rub' al-Khali, where *Calligonum crinitum* ssp. *arabicum* replaces the *Calligonum comosum* of the northern sands communities. The dominant shrub is usually associated with *Cyperus conglomeratus* and often *Stipagrostis drarii* and *Limeum arabicum.* In the far east of the Rub' al-Khali, on the great massifs of the "Sand Mountains" this community includes *Tribulus arabicus* (Zygophyllaceae).

Succulent halophyte associations: These are distinctive, often sharply zoned halophyte communities, found typically in and around coastal salt marshes and sometimes around inland *sabkhas*. They are often dominated by succulent chenopods, including *Bienertia cycloptera, Halocnemum strobilaceum, Arthrocnemum macrostachyum, Suaeda vermiculata*, and *Seidlitzia rosmarinus*. Mangrove forests (*Avicennia marina*) occur in a few protected Gulf embayments (see Section 4.6).

Shrubless community types: There are wide tracts of desert with virtually no woody plants; these may represent the final stages of desertification and land degradation due to overgrazing and other disturbance. Vegetation there is essentially limited to temporary flushes of annuals (see Table 4.2) following winter rains.

Micro-communities: These are specialized associations often occurring as patches within other community types. Examples include the "*Ziziphus* basins" found scattered throughout sparse saltbush shrublands. Here, in rounded, clay-floored basins often associated with rain pools, are well-developed stands of *Ziziphus nummularia* (Rhamnaceae), sheltering species such as *Ephedra foliata* and *Sisymbrium erysimoides* (Brassicaceae). According to Mandaville these small patches tend to attract birds and other wildlife out of proportion to their small area.

Associated marine angiosperm communities: Seagrass beds sometimes occur on the underwater sediments of coastal Gulf and Red Sea waters, in protected bays and to a lesser extent along the open coast. These are important habitats for many marine organisms, and are characterized by high primary productivity. The extreme seasonal variations in temperature and salinity in the Gulf are tolerated by three opportunistic seagrasses (*Halodule uninervis, Halophila stipulacea*, and *H. ovalis*). The rich, complex communities supported by these seagrasses are now at risk from activities that include land reclamation, desalination, and construction of powerplants (Erftemeijer and Shuail 2012).

Four to six species of marine angiosperm occur in Gulf coastal waters (see Section 2.16). One, *Ruppia maritima* (Ruppiaceae), is typically found in shallow beach waters. Others, such as *Halodule uninervis* (Cymodoceaceae), *Halophila stipulacea*, and *Halophila ovalis* (Hydrocharitaceae) are found in deeper waters, in more or less dense beds. Some 500 species of marine animals have been identified from these communities, including the pearl oyster *Pinctada radiata*, and assorted shrimps (see Basson et al. 1981). Larger animals associated with these beds include the green sea turtle and one of the world's largest populations of dugongs (once estimated at about 5800 individuals), both of which feed largely on the flowering plants themselves.

## 4.5 Desert ecosystems and specialized habitats

Desert plant success is often dependent upon the substrate, and various different substrates exist.

There are rocky surfaces, hamada, erosion pavements, gravel deserts, slopes, cliffs, and sand—obviously a great deal of sand. Each substrate in turn has its characteristic vegetation. Zahran and Willis (2009) described for Egyptian deserts some of the variability in these communities. For example, the rocky surface of a desert plateau is extremely arid offering little opportunity for plant growth. The "chasmophytes," or plants that can grow on fissures, extend their roots into these rocky crevices and collect mineral nutrients, e.g., *Capparis spinosa* (Capparaceae), *Stachys aegyptiaca* (Lamiaceae), *Cocculus pendulus* (Menispermaceae), *Iphiona mucronata* (Asteraceae), and all the various "cushion" plants.

"Cushion" plants are perennial chamaephytes forming dome-shaped, spherical, hemi-spherical, or convex canopies close to the soil surface (see Figure 4.6). This growth form minimizes the proportion of foliage exposed to direct sun while the interior of the cushion creates a relatively shaded, water-holding microclimate (e.g., Krivonogova 1960). Cushion plants are usually found in exposed, dry, and windy mountain slopes, and in sandy or rocky desert plains. A more open version of this growth form occurs in *Cleome droserifolia* in the eastern desert of Egypt and central Saudi Arabia, and in *Cichorium spinosum* in the eastern Mediterranean coastal plain of Libya (see Figure 4.6A and B) (Hegazy 1990a; Hegazy et al. 2011a). Some individuals have a denser growth form, with a closed canopy surface that includes dead plant leaves and branches, trapping fine inorganic matter and coarse soil particles, e.g.,

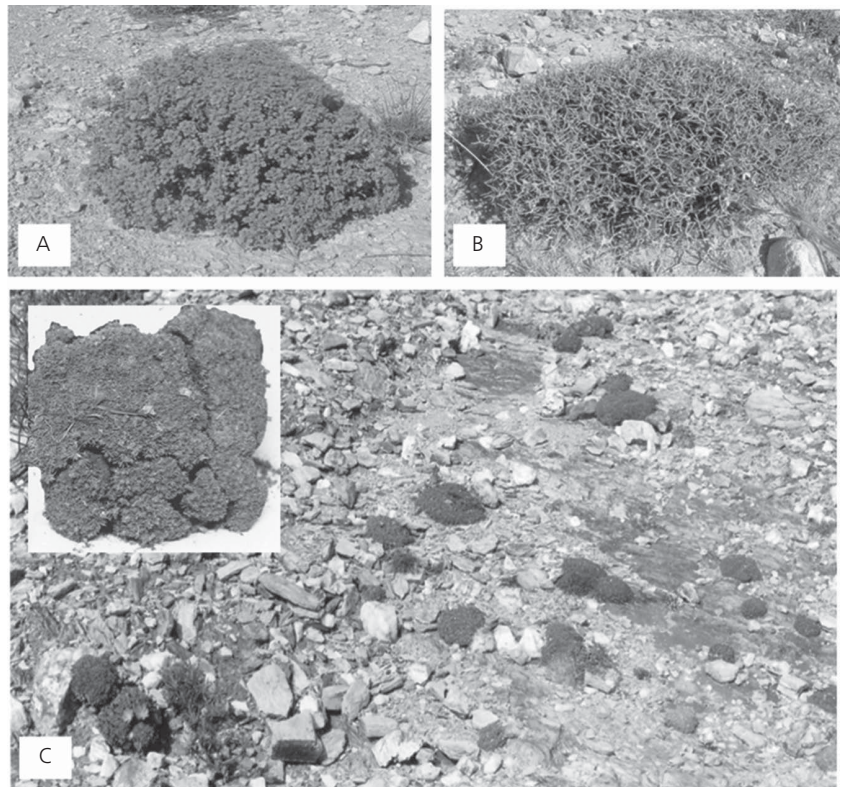



**Figure 4.6** Cushion plants growth form and specialized habitat types. (A) The aerial cushion form of *Cleome droserifolia*, Eastern desert, Egypt. (B) The aerial cushion plant *Cichorium spinosum*, Mediterranean coast, Shahat, Libya. (C) Population of the closed cushion plant *Cichorium bottae* on dry windy slope at elevation 2900 m, in AlSodah, south west Saudi Arabia. In the top-left corner a close up view of an individual plant showing the filling material in the cracked crown under the canopy active surface layer. [For a color version of this figure, see the color plate section, Plate 6]

*Cichorium bottae* in the Asir Mountains of southwest Saudi Arabia (see Figure 4.6C). This growth form facilitates moisture retention under conditions of extremely high day-, and low night temperatures, and the powerful desiccating effect of wind on mountain slopes.

Erosion pavement provides a rocky surface overlain by a layer of soft rock waste and boulders (Zahran and Willis 2009). Run-off water collects in drainage channels. In primary channels, with more water and soil, the vegetation tends to be evergreen and richer, e.g., *Zilla spinosa* (Brassicaceae) and *Zygophyllum coccineum* (Zygophyllaceae), and associated ephemeral species. In secondary channels with shallower soil and more limited water the vegetation includes ephemerals such as *Pteranthus dichotomus* (Caryophyllaceae), *Anastatica hierochuntica* and *Diplotaxis acris* (both Brassicaceae), and *Rumex vesicarious* (Polygonaceae) along with perennials having a summer-deciduous growth form, e.g., *Asteriscus graveolens* (Asteraceae), *Farsetia aegyptiaca* (Brassicaceae), *Iphiona mucronata* (Asteraceae), and *Diplotaxis harra* (Brassicaceae) (Zahran and Willis 2009).

In gravel deserts the surface is composed mostly of transported material (in contrast to the *in situ* deposits of erosion pavement) (Zahran and Willis 2009). The gravel cover is mostly barren but some plants do manage to appear in some of the gaps, especially in the rainy season, e.g., *Aizoon canariense* (Aizoaceae), *Centaurea aegyptiaca* (Asteraceae), *Mesembryanthemum forsskaoli* (Aizoaceae), and *Polycarpaea repens* (Caryophyllaceae).

The extended flats of gravel deserts receive and accumulate wind-borne materials, which in turn often create sand sheets where ephemeral plants can grow. Over time there is accumulation and as the sheet becomes deeper more species appear. Common founder or "host" species include *Hammada elegans* (Chenopodiaceae), *Panicum turgidum*, and *Zilla spinosa*. Associated plants often include *Artemisia monosperma, Astragalus spinosus* (Fabaceae), *Convolvulus lanatus* (Convolvulaceae), and *Lasiurus hirsutus* (Poaceae).

Slopes are typically covered with rocky detritus and little associated plant growth. A key determinant is the aspect, or direction the slope is facing. Moreover on high mountains with gentle slopes, plant cover often shows zonation in relation to altitude (see Sections 4.9 and 4.9.1). In Egyptian deserts species characteristic of wadi slopes include *Diplotaxis harra* (Brassicaceae), *Fagonia kahirina* (Zygophyllaceae), *Gymnocarpos decander* (Caryophyllaceae), and *Salsola volkensii* (Chenopodiaceae).

Cliffs represent a particular dry habitat that can only be colonized by chasmophytes rooting in ledges and fissures, able to catch and hold rain-splash and condensation. According to Zahran and Willis, the most common of these cliff species in Egypt is *Capparis spinosa* (Capparaceae); others include the climbing dioecious shrub *Cocculus pendulus* (Menispermaceae), *Fagonia mollis, Iphiona mucronata*, and *Zygophyllum coccineum* (see Figure 4.7).

### 4.5.1 Nabkhas

The specialist plants of sand drifts and dunes—*psammophytes*—often form mounds of accumulated wind-borne material around them but from time-to-time they may also be buried by sand deposition. These species are effective sand-collectors and soil-binders, producing so-called phytogenic mounds, hillocks, and dunes, locally called "*nabkhas*"[9] (see Figure 4.8). Examples of such species include *Anabasis articulata, Atriplex farinosa, Cornulaca monacantha*, and *Hammada elegans* (all Chenopodiaceae), *Ammophila arenaria* (Poaceae), *Halopyrum mucronatum* (Poaceae), *Nitraria retusa* (Nitrariaceae), and *Tamarix aphylla* (Tamaricaceae), *Panicum turgidum* (Poaceae), *Calligonum comosum* (Polygonaceae) and *Retama raetam* (Fabaceae).

[9] Phytogenic hillocks were first reported in the Middle East by Comyn (1911) in the western desert of Sudan. There he observed entire trunks and main branches of individual Acacia trees buried by sand mounds, and named them "Selima" mounds (from the Arabic name of *Acacia ehrenbergiana*—"Salam"). El Hadidi (1980) reported widely dispersed "islands" identified as huge mounds of Selima in the region of Kharga Oasis (Nubian Desert) in western Egypt. Whole trunks and main branches were buried and concealed by 10–20 m high mounds of sand. The vegetative green plant parts form an active layer at the surface of the sand mound, covering a circular area of 30–50 m diameter (see Figure 4.8, upper). El Hadidi suggested some mounds may be very old, perhaps 1000 years. Similarly we have observed sand mounds of *Calligonum comosum* in Wadi Araba, in the Eastern desert of Egypt where at least two-thirds of the shrubs are buried by the mound (A. K. Hegazy, unpublished) (see Figure 4.8, lower).

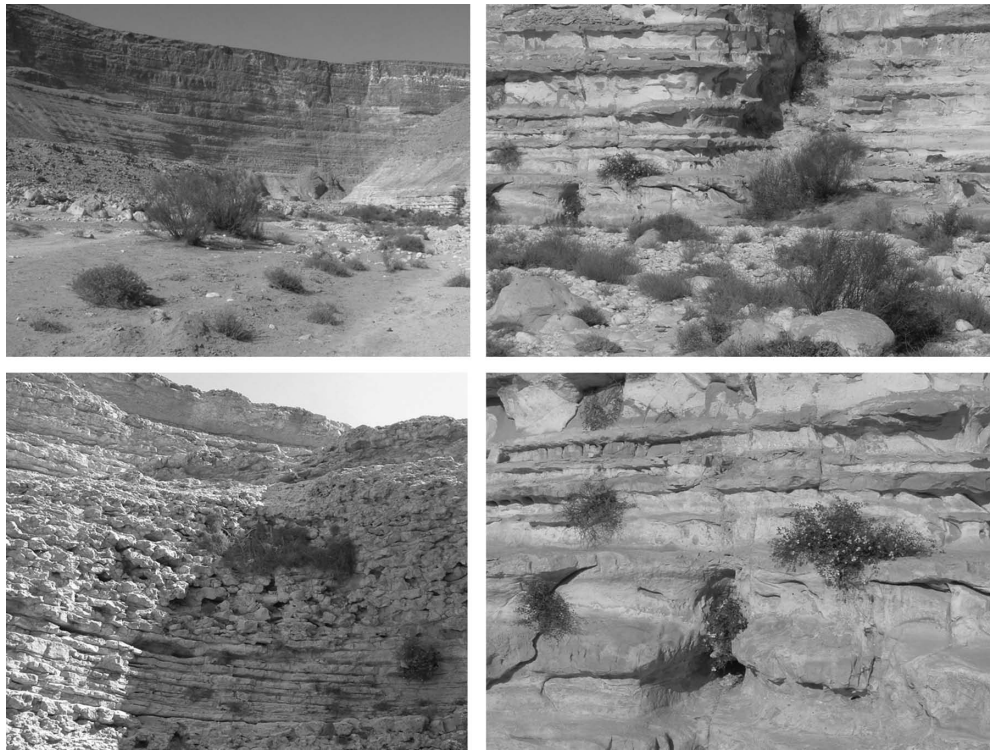


**Figure 4.7** Cliff habitat and community in Wadi El-Reshrash, an arid wadi in the Eastern Desert of Egypt. The wadi bed and about 300 m side cliff (upper left) and close up on the wadi bed and lower part of the cliff (upper right). Vegetation in the wadi bed is dominated by *Retama raetam, Zygophyllum coccinium, Achillea fragrantissima*, and *Zilla spinosa*. Close up on the side cliff with vegetation dominated by *Capparis spinosa* and *Cocculus pendulus* (bottom left) and close up on *Capparis spinosa* on the cliff (bottom right).

The features of nabkhas are well illustrated by El-Sheikh et al. (2010) as sand mounds formed by a host plant species, in most cases trees and shrubs. The size, height, width, and length vary with host. The base of the individual nabkha may be circular, giving it a dome-shaped or elongated appearance (see Figure 4.9). The elongated nabkha has a "nose" (windward end) and tail (leeward) and varies in length, with the host plant positioned at the highest point.

Nabkhas represent significant ecological opportunity. They are significant islands of organic matter representing potential resources for many lowland desert species. These in turn influence longer-term, local vegetation dynamics and ecosystem processes (Danin 1996). El-Bana et al. (2002, 2003) and Quets et al. (2013) described how particular host species, e.g., *Nitraria retusa, Zygophyllum qatarense, Haloxylon salicornicum*, and *Panicum turgidum*, are all especially adept at forming nabkhas because of their ability to produce *adventitious* roots from buried vegetative organs, allowing new shoots to replace those buried by accumulating sand. They also possess an intricately branching shoot system. *Haloxylon salicornicum* is so effective at recovering from sand burial and providing microhabitat for other species that Brown and Porembski (2000) described these shrubs as "ecosystem engineers" and obvious keystone species.

Interactions between and among nabkhas and their environment were examined by Quets et al. (2013) in two contrasting landscapes. One, a highly dense New Mexican mesquite (*Prosopis glandulosa*) and snakeweed (*Gutierrezia sarothrae* and *Gutierrezia*

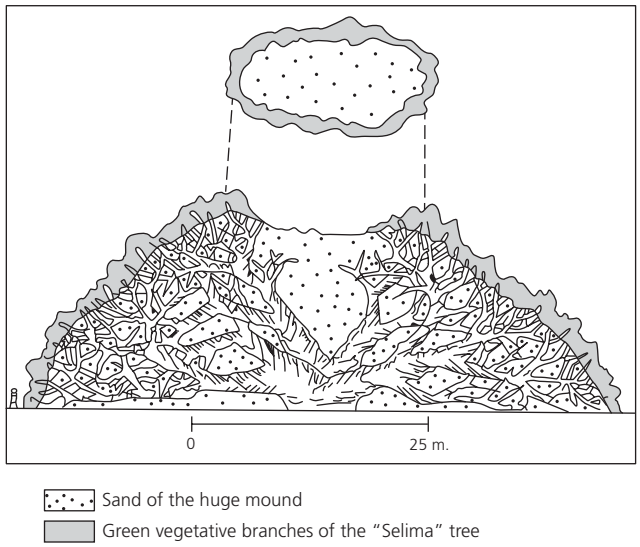





**Figure 4.8** Upper image: Cross-section of a "Terbal" at Kharga Oasis, Egypt showing the trunk and main branches of giant *Acacia ehrenbergiana* tree buried in the sand while vegetative branches breach the mound surface (after El Haddidi and Hosni 2000). Lower photo: Sand mounds of *Calligonum comosum* in Wadi Araba, Eastern Desert of Egypt. Note barren land surrounding *C. commosum* sand mounds.

*microcephala*) system; the other a low-density mixed *Tamarix aphylla* and *Calligonum comosum* community in central Libya. Quets et al. tested three hypotheses for nabkha pattern formation: (i) biologically induced recruitment suppression zones; (ii) biologically induced recruitment favoring zones; or (iii) spatial distribution not biologically driven. Results suggested that biologically induced suppression zones surround many adult mesquite nabkhas. The configuration of *Calligonum* and *Tamarix* nabkhas, in contrast, appeared to be driven by spatial dynamics not caused by nabkha interactions. They concluded both biotic and abiotic drivers can shape nabkha spatial patterns.

Certainly nabkhas act as "safe sites" for many plants in sand-depleted and oil-polluted areas, producing patches of relatively high productivity and diversity in arid and semi-arid land. From the

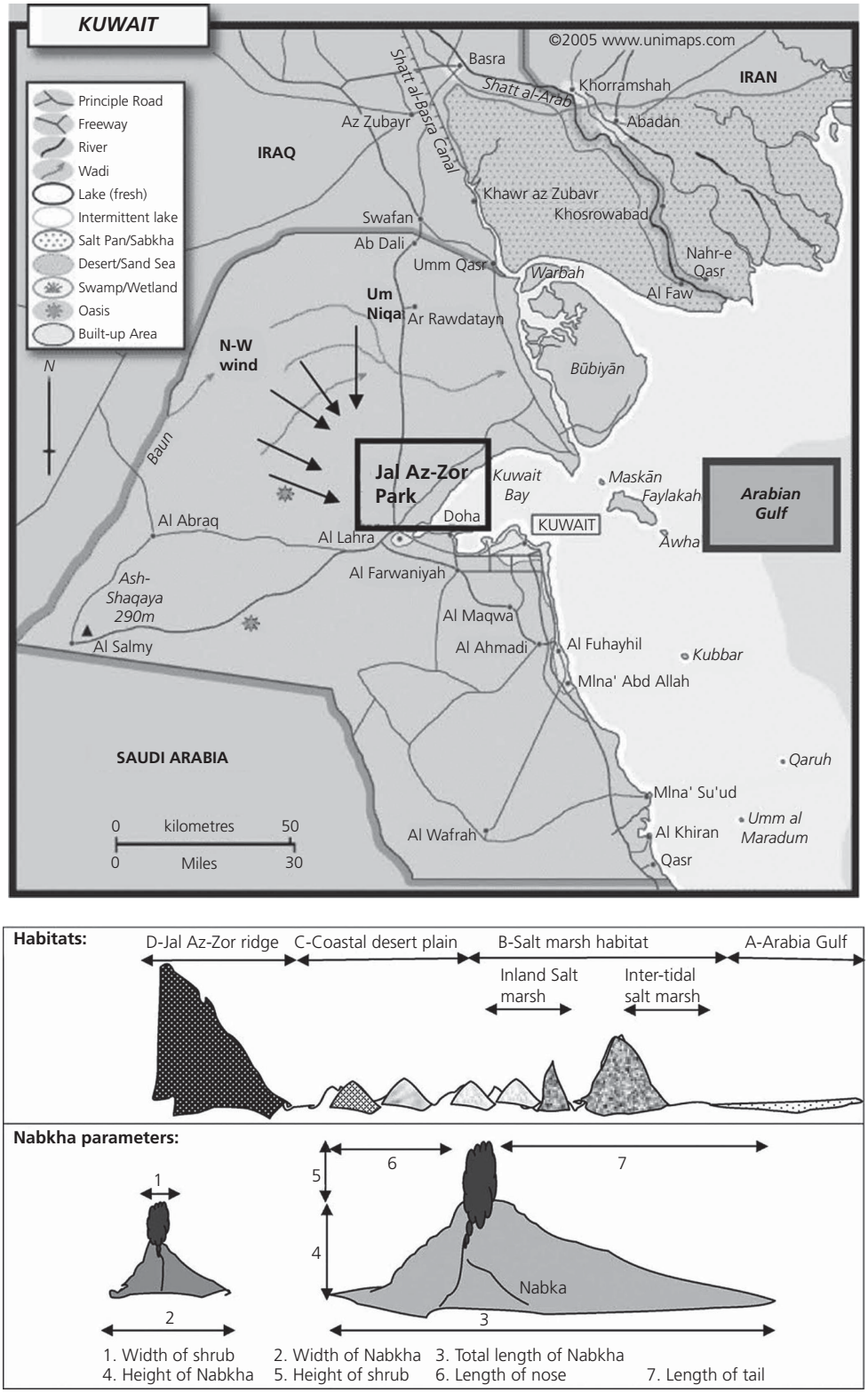



**Figure 4.9** Nabkha traits as described in the coastal area, northwestern Kuwait. (A) Location map of Kuwait showing the study area. (B) Sketches of nabkhas along a Gulf coastal transect (after El-Sheikh et al. 2010, used with permission).

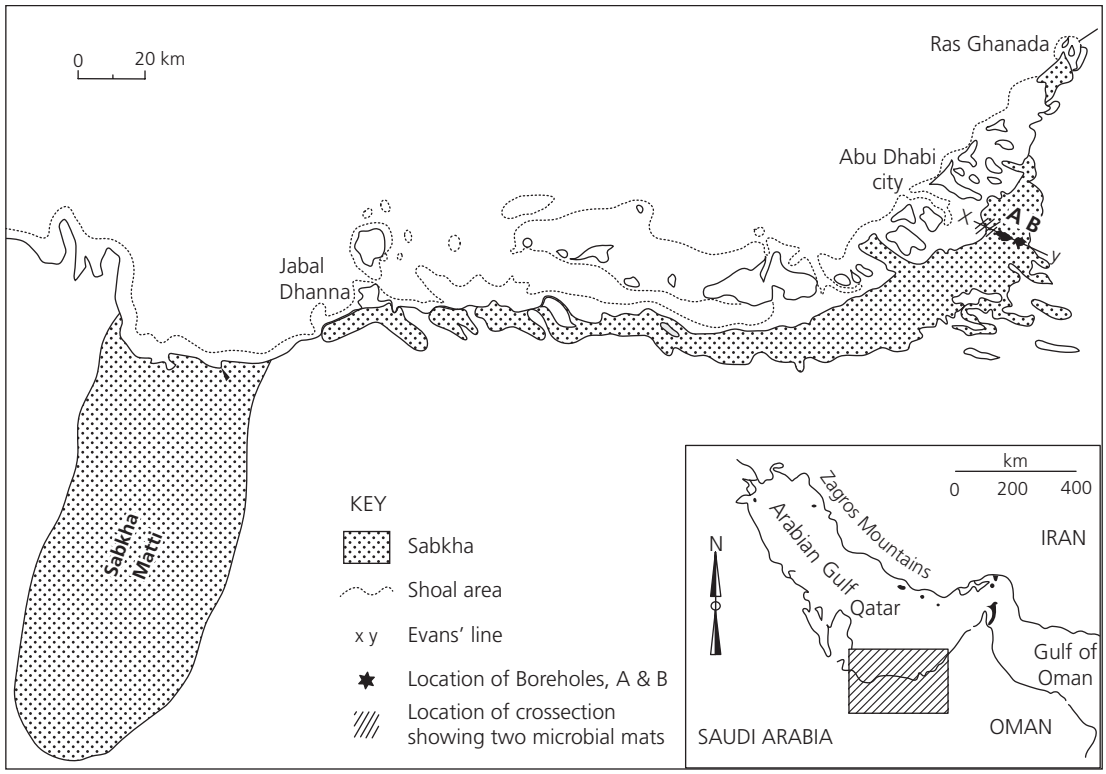



**Figure 4.10** Location of Sabkha in the United Arab Emirates (after Evans and Kirkham 2002).

perspective of plant diversity, nabkhas were among the most species-rich sites in Jal Az-Zor Park, in Kuwait, and contained about half of the 62 species present (El-Sheikh et al. 2010).

### 4.5.2 Sabkhas

Much of the coastline of Abu Dhabi is formed by a chain of offshore barrier islands, enclosing an extensive complex of lagoons (see Figure 4.10). Bordering these lagoons on the mainland is an extended flat plain with a salt-encrusted surface, the *sabkha*,[10] with its surface just above the tidal high-water mark (Evans and Kirkham 2002).

[10] *Sabkha* is an Arabic term for flat, salt-crusted desert. In the Arabian Peninsula sabkha is present as extensive barren, salt-encrusted, and periodically flooded coastal and inland sites (see also Barth and Boer 2002).

Coastal sabkhas around the Gulf are all periodically flooded by seawater (e.g., coastal Qatar and Iran; see Sections 2.17 and 2.26). As a result of the saltwater wedge which infiltrates coastal groundwater, it is saline, as are most sabkha sediments. Coastal sabkhas are often completely devoid of vegetation but where there is a thin layer of sand on the surface of the salty crust some halophytes, including, e.g., *Halopeplis perfoliata*, *Arthrocnemum macrostachyum*, and *Halocnemum strobilaceum* (Chenopodiaceae), can establish and form extensive stands. These coastal sabkhas are mostly *aeolian* in nature—that is, their sandy substrate has been blown there by the wind; they are also flooded with salt water twice daily (Barth and Boër 2002). This is in marked contrast to the inland sabkhas that are only flooded from time-to-time, by precipitation, and that have become salty due to the fact that they are endorheic, and

evaporation and evapotranspiration exceed fresh water inputs.

### 4.5.3 Wadi ecosystems

In wetter parts of the region, wadis[11] represent one of the most important desert ecosystems. Clearly a wadi is a drainage system, gathering water from a more extensive watershed and includes significant microhabitat variation (e.g., Gomaa 2014). Typically a wadi's water supply is greater than that of individual surrounding slopes, which gets reflected in higher-than-average biotic richness and abundance there. In some locations there may be enough moisture to support forest vegetation. Within the wadi, distinct vegetation types occur along the channel, lower ledges, and side slopes. Although some moisture may be flowing (possibly intermittently) in the channel, inputs can also come from condensation of winter mist and orographic rainfall.

There is no simple generalization to make about wadis and their vegetation, even in different parts of the same country. Plant communities seem highly variable but always strongly moisture related. For example, vegetation in the wadis of Al-Jabal Al-Akhdar (the Green Mountains) of northeastern Libya is quite different from that in the hyper-arid Fezzan region in the southwest. Average rainfall in the Green Mountains reaches 250–600 mm and mean temperature is *c*. 20°C. The wadis in Al-Jabal Al-Akhdar are noted for their rocky substrates, with many crevices and prominent valleys. In contrast the wadis of the Fezzan are mainly oases at the foot of escarpments, and generally covered by sand. The vegetation of Wadi El-Kouf in the Green Mountains (at 400 m) has been described by Hegazy et al. (2011a) as composed of herbs (37% of species), shrubs (48%), and trees (15%). Dominants included *Juniperus phoenicea, Arbutus pavarii, Phlomis floccosa, Sarcopoterium spinosum, Cupressus sempervirens, Ferula marmarica, Cistus parviflorus, Cistus salvifolius, Serratula cichoracea*, and *Asphodelus aestivus*. These all have more affinity with the flora of the eastern Mediterranean than adjacent North and East Africa, and the region is considered an important center of plant diversity (Davis et al. 1994; Hegazy et al. 2011a).

The large Wadi Araba in the Eastern Desert of Egypt separates two limestone plateaux (250–1500 m), namely Galala El-Bahariya (North Galala) and Galala El-Qibliya (South Galala). The associated tributaries and drainage runnels from the catchment area of the wadi dissect the two highlands (see Figure 4.11). Studies in the wadi identified at least 14 different plant communities (see El Hadidi and Hosni 2000) all mostly dominated by *Acacia tortilis, Centaurea scoparia, Fagonia arabica, Hammada elegans, Launaea spinosa, Pulicaria crispa, Panicum turgidum, Pennisetum divisum, Retama raetam, Zilla spinosa, Calligonum comosum*, and *Euphorbia retusa*. Many of the plants in the wadi belong to Saharan regional phytochoria.[12] One endemic species, *Podonosma galalensis* (Boraginaceae), is restricted to these plateaux.

The valley-forest communities of the southwestern mountains of Arabia are dominated by dense evergreen trees that may reach more than 30 m in height. These include many species also found in tropical Africa, in tropical families including, e.g., Anacardiaceae, Bignoniaceae, Ebenaceae, Moraceae, and Sapotaceae. The valley-forest of Jabal Bura (Yemen) is dominated by *Combretum molle* and *Terminalia brownii* (Hall et al. 2008, 2009; Scholte et al. 1991; Wood 1997) and includes many endemics and rare species (see Section 1.10).

Floristically the valley-forest trees represent Sudano-Zambezian, Somali-Masai, Afromontane,

[11] In Arabic *wadi* means valley.

[12] The old term phytochorion has been used to characterize consistent vegetation "types." It is usually based on classifications following the early methodology of J. Braun-Blanquet, which placed emphasis on the presence or absence of particular species. In phytogeography, a phytochorion is a geographic area with a relatively uniform composition of plant species. Adjacent phytochoria tend to have soft boundaries, including many species from both regions. In some schemes, areas of phytochoria are classified hierarchically, e.g., in floristic (phytogeographic) kingdoms, regions, and provinces, while others do not rank areas, referring to them simply as regions or "phytochoria."

Systems used to classify vegetation can be broadly divided into those which use physiognomic-environmental parameters and characteristics, and those that are based on floristic relationships. Phytochoria are defined by their taxonomic compositions, while other schemes (e.g., phytophysiognomies, formations, biomes) may depend on the apparent characteristics of a community (e.g., dominant lifeforms), environmental characteristics, associated fauna, human factors, or conservation issues.

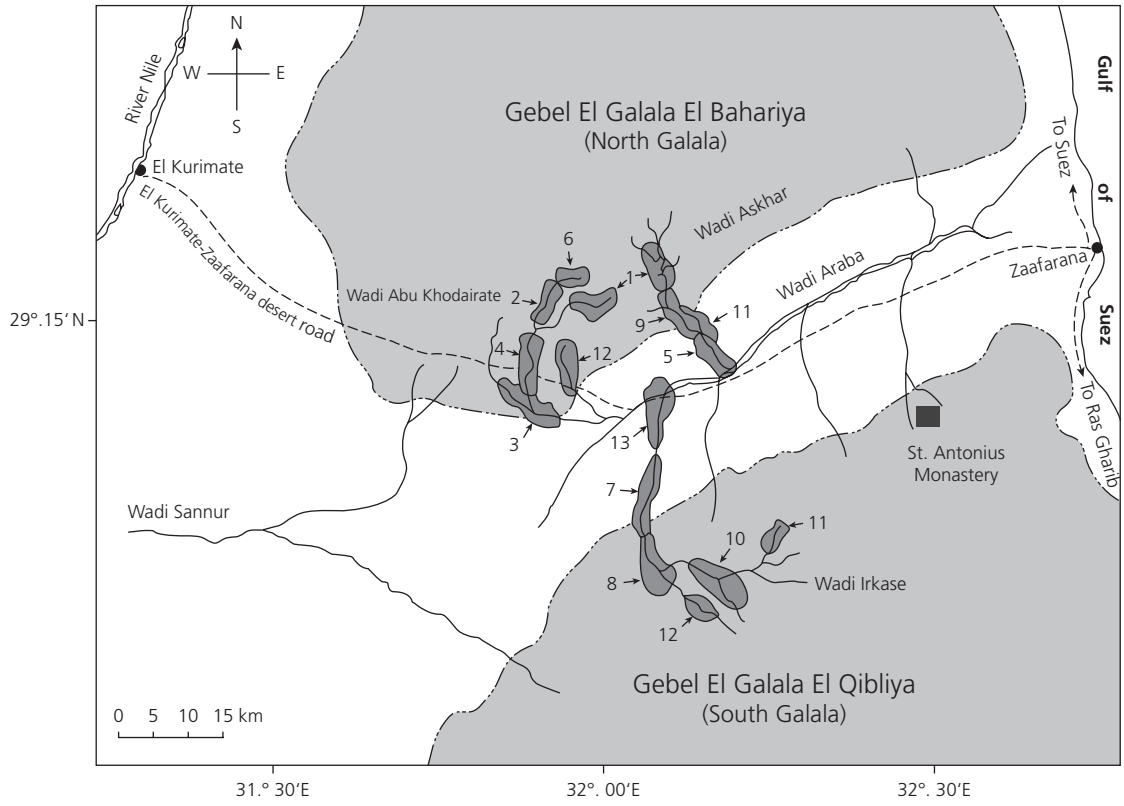



**Figure 4.11** Distribution of plant communities in the western sector of Wadi Araba showing 14 communities dominated by: 1. *Acacia tortilis*, 2. *Centaurea scoparia*, 3. *Fagonia arabica*, 4. *Hamada elegans,* 5. *Launaea spinosa*, 6. *Pulicaria crispa,* 7. *Pulicaria crispa-Hamada elegans*, 8. *Panicum turgidum*, 9. *Panicum turgidum-Pulicaria crispa*, 10. *Pennisetum divisum*, 11. *Retama raetam*, 12. *Zilla spinosa*, 13. *Zilla spinosa-Euphorbia retusa*, and 14. *Zilla spinosa-Launaea spinosa*. (After El Hadidi and Hosni 2000).

and many Afrotropical and transitional species, suggesting the vegetation is a relict forest, where little change or diversification has occurred since the available migration corridors between Africa and Arabia were cut off (Hall et al. 2008). Southwestern Arabian valley-forests are in certain ways comparable to the Eritrean "xerophilous open woodland" and "gallery forest" of Jabal Marra, in the Darfur region of Sudan (Friis 1992; Hepper and Wood 1979; Wickens 1976).

## 4.6 Coasts and mangroves

Coastlines of the Red Sea, Gulf of Aden, Gulf of Oman, and Arabian Gulf are all mostly very dry, often devoid of plants except for a few species of halophyte and mangrove. Mangrove ecosystems tend to have comparatively high structural and biological diversity. They occur in the Middle East along some of the most arid coastlines, where temporary influxes of fresh water may be limited to just a few days a year.

Mangroves typically create extended longitudinal communities, often associated with spreading, alluvial fans as the sediments get trapped. These form in scattered locations at the mouths of intermittent wadis, along tidal creeks or inlets (*khors* or *khwars*), and behind barrier islands. Mangroves are often found in association with adjacent salt marsh communities. Four species are known from the Middle East, including *Avicennia marina* (Acanthaceae) and *Rhizophora mucronata, Ceriops tagal*, and *Bruguiera*

**Table 4.3** Mangrove area, plant species, and approximate mean tree height of *Avicennia marina* in Middle East countries. Values between brackets are maximum *A. marina* tree heights reported. Data extracted from national statistics given in Spalding et al. 2010.

| Country | Mangrove area (km$^2$) | Plant species | Mean tree height (m) |
|---|---|---|---|
| Bahrain | 0.65 | *Avicennia marina* | ? |
| Djibouti | 9.96 | *A. marina, Rhizophora mucronata, Ceriops tagal, Bruguiera gymnorhiza* | 9 (13) |
| Egypt | 5.12 | *A. marina, R. mucronata* | 3 (7) |
| Eritrea | 101.93 | *A. marina, R. mucronata, C. tagal* | ? (10) |
| Iran | 192.34 | *A. marina, R. mucronata* | 4 (6) |
| Kuwait | 0.05 | *A. marina* | 1.5 (2.5) |
| Oman | 10.88 | *A. marina* | ? (8) |
| Qatar | 12.27 | *A. marina* | 2.5 (5) |
| Saudi Arabia | 204.00 | *A. marina, R. mucronata* | 4 (8) |
| Sudan | 9.80 | *A. marina, R. mucronata, C. tagal, B. gymnorhiza* | 4 (8) |
| United Arab Emirates | 68.21 | *A. marina* | 5 (9) |
| Yemen | 9.27 | *A. marina, R. mucronata* | ? |
| Total | 624.48 | | |

*gymnorhiza* (all Rhizophoraceae), but only *A. marina* is widespread (Hegazy 1998, 2003; Khan et al. 2010; Spalding et al. 2010).

World-wide, mangrove ecosystems are estimated to cover *c*. 181 000 km$^2$, and of this only about 625 km$^2$ are in the Middle East, with about a third of this in Saudi Arabia (see Table 4.3) (Spalding et al., 2010). Djibouti and Sudan include all four species, followed by Eritrea with three species. Other countries have one species, *A. marina*, or two—*A. marina* and *R. mucronata*. The mangroves at Nabq on the Gulf of Aqaba in the Sinai represent the northernmost limit of naturally growing *A. marina*. Populations exist in various habitats, including inter-tidal, shoreline, salt flats, and sand mounds (see Figure 4.12A and B).

*Avicennia marina* is a small tree characteristically producing multiple "pneumathodia" (or "pneumatophores") which rise up from horizontal rhizomes, often in straight lines radiating from the plant base (see Figure 4.12C). These erect, leafless stems are believed to oxygenate the root environment (Mandaville 1990). *A. marina* is the major species in the Middle East and is also found along Africa's east coast, in southern Asia and Australia.

A second species, *Rhizophora mucronata*, is found in the southernmost section of the Red Sea including the shorelines of many offshore islands; neither species is found on the Mediterranean coast. Typical habitat is the shallow, salty water along the southern Red Sea and the Arabian Gulf shorelines. The tidal mud of mangrove vegetation is typically grey or black, rich in decomposing organic matter and often richly foul-smelling.[13]

Although recognized as valuable and to some degree protected, in most countries where they occur, active mangrove protection is minimal. Increasing coastal development and related wastewater management issues are big problems. Development generates emissions and pollution, fishing and aquaculture, as well as tourism and its pressures. It is important that the relevant countries of the region recognize the significant "goods and services" which mangroves bring by absorbing excess nutrients and providing habitat (Saenger 2002a,b). These make major contributions to the maintenance of shrimp fisheries and support diverse mammalian, fish and crustacean, mollusc, and bird communities.

[13] One difference noted by Zahran and Willis (2009) between tidal mud colonized in southern Red Sea locations by *Avicennia* compared to that by *Rhizophora* was a lower content of calcium carbonate in the former (4.5–19.5%), compared with the more highly calcareous mud (80%) of the latter.

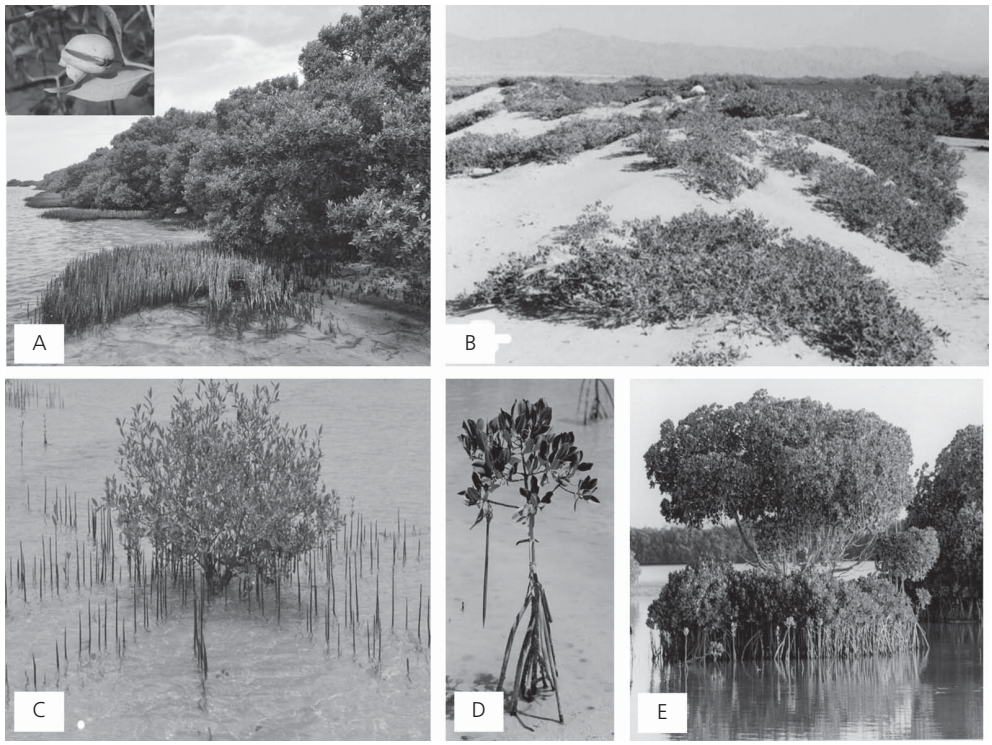



**Figure 4.12** (A) The mangrove plant *Avicennia marina* in the shoreline of Gazerat Sherifah, Red Sea, Saudi Arabia. Viviparous seed appears in the top-left corner. (B) Sand mounds (nabkhas) of *A. marina* in Nabq, South Sinai, Egypt. (C) Single tree of *A. marina* growing in the intertidal zone with horizontal rhizomes radiating from the base and upward-growing pneumatophores. (D) Small tree of *Rhizophora mucronata* with one viviparous seed still attached (left side). (E) Single tree of *R. mucronata* (front) bearing viviparous seeds in Shalatin mangrove stand, southeastern Egypt. Note the dense establishment of *R. mucronata* plants under the large tree. [For a color version of this figure, see the color plate section, Plate 7]

Mangrove loss is doubly unfortunate given they are such important *facilitators* of biodiversity. Bishop et al. (2013) showed how individual traits of the mangrove, in conjunction with the density of interacting species, together promote and maintain a "facilitation cascade" in mangrove systems. Working in an Australian mangrove Bishop et al. showed how the pneumatophores in *A. marina* trap the free-living alga, *Hormosira banksii*, which in turn supports dense and diverse assemblages of epifaunal mollusks.

*Avicennia marina*, *Rhizophora mucronata*, and other halophytes living in tidal marshes also have what may be another adaptation to its severely saline, oxygen-depleted habitat, namely the habit of "vivipary" (see Farnsworth 2000). Viviparous seeds germinate and send out root initials *before* they are even detached from the parent plant. Such "still-attached" or "live-birth" seedlings likely receive additional nutrient and water resources through the point of attachment. Viviparous seeds of *Rhizophora mucronata* are shown in Figure 4.12D.

Viviparous seed germination occurs in a number of mangroves and other halophytes. When mangrove seeds/fruits get dispersed normally they can get carried away by low tides to the deep sea and lose any chance for success. When germination begins while the seed is still attached to the maternal parent the radicle grows straight down and gets embedded in the mud, or the developing seedling drops and a new tree begins to grow close to the parent. This can lead to development of thick mangrove vegetation. In *R. mucronata* (see Figure 4.12E) the developed hypocotyl and terminal radicle of the

embryo point down, out of the fruit, and when they are about 50–60 cm long the seedling drops down and becomes fixed in soft mud. At that point the developing seedling grows rapidly. This all seems to be a useful adaptation enabling salt marsh seedlings to avoid the effects of salinity at the most sensitive early stages of establishment.

## 4.7 Facilitation effects and the regeneration niche

The extent of association between annual species and woody shrubs/trees in semi-arid and arid areas depends, ultimately, on the balance between various negative and positive effects on these contrasting plant life forms. The balance will range between the effects of interference and facilitation, an interplay of costs and benefits that has become an important theme in community ecology (e.g., Bruno et al. 2003; Butterfield et al. 2010; Callaway 2007). Various workers have argued that positive interactions among plants are stronger in more stressful sites, while negative interactions, or interference and competition, will dominate in less stressful situations (Bertness and Callaway 1994; Callaway and Walker 1997) (Butterfield et al. 2010).

Holzapfel et al. (2006) analyzed variation in the annual plant–shrub interactions along a steep climatic gradient in Israel ranging from arid desert to mesic Mediterranean regions, where water was the major limiting resource. In the three relatively more moist locations (of four studied), the semi-globular dwarf shrub *Sarcopoterium spinosum* (Rosaceae) was selected for analysis. *Artemisia sieberi* (Asteraceae) was used as the representative in the *most* arid site, where *S. spinosum* did not grow.

Permanent quadrats were established with corresponding "open area" quadrats in the open areas next to each selected shrub. In each location five blocks with five quadrat pairs were monitored. In order to test the net effect of shrubs on annual plants, performance of the annuals was compared between different neighbor conditions using a Relative Interaction Intensity (RII) index:

$RII = (P_{+N} - P_{-N})/(P_{-N} + P_{+N})$; where P is a measure of performance of annuals in the presence (+ N), and absence (–N) of shrubs (and see Armas et al. 2004).

Holzapfel et al. found good evidence that in arid environments presence of a shrub had both positive and neutral net effects (i.e., positive RII) on associated annuals, and strong negative effects in more mesic environments. Holzapfel and colleagues determined that at the arid end of the environment, above-ground productivity, species richness, seedling and seed bank densities of the annual plant populations were all generally higher under shrubs than in the open areas between shrubs, though values were significantly lower at the humid end of the gradient. This is in line with the predicted shift from positive to negative net interactions with decreasing environmental stress. There was no assessment of localized adaptation on the part of the shrubs to the different moisture regimes at each site. Possibly a reciprocal replant–transplant experiment involving the four locations would give useful information on the relative importance of competitive vs. facilitative effects.

In a different ecosystem—the Sonoran Desert—and using three different scales of experimental resolution, Tewksbury and Lloyd (2001) probed the importance of a particularly long-lived desert tree—ironwood (*Olneya tesota*: Fabaceae)—in structuring plant communities and promoting desert diversity. This tree is a monospecific genus believed to be the longest-living tree species in the Sonoran, with some individuals living > 800 years. Trees develop a canopy that may be >12 m in diameter and retain their leaves throughout the year. As a result they provide a large area buffered from temperature extremes, which persists over many generations of understory species. Tewksbury and Lloyd assessed the positive effects of *Olneya* canopies of different sizes on plant communities in mesic and xeric habitats throughout the central Gulf Coast sub-region of Sonora, Mexico.

In xeric sites, *Olneya* canopies had strong positive effects on plant richness and abundance, and only small but significant positive effects on the size of understory plants, underscoring the role of facilitation in extreme environments. In mesic sites *Olneya* canopies had very little effect on perennials and a negative effect on ephemeral species richness, suggesting predominantly competitive effects in this less-stressful environment. At the largest—landscape—level of analysis, facilitative effects of

*Olneya* canopies were at first completely masked by differences in water stress. However, when large-scale differences in moisture availability were controlled, plant communities under *Olneya* canopies proved to be consistently different from those in control plots, despite large differences in community composition.

Tewksbury and Lloyd determined that size of the *Olneya* canopy was a major contributing factor. Larger canopies had a positive effect on larger perennials in both xeric and mesic sites. Facilitative effects of long-lived "host" species like *Olneya* will typically change as the trees grow and age, and competitive effects among understory plants may begin to exclude establishment of new individuals. Tewksbury and Lloyd argued that larger trees have had more time to accumulate nutrients through trapping dead organic matter, leaves, and soil. They have also had more time to gather a larger seed bank of other species by trapping wind-dispersed seeds and accumulating seeds through bird foraging behavior, dispersing seeds beneath the canopy. It is not surprising larger trees have larger plants beneath them.

So-called nurse- or host-protégé interactions constitute one major category of ecological facilitation. These are common across diverse environments but are most frequently reported in arid and semi-arid environments. Early reports (Shreve 1931, 1951) suggested that larger desert trees like *palo verde* (*Cercidium* spp.), mesquite (*Prosopis* spp.), and *Olneya tesota* were all able to facilitate the germination and seedling survival of other species.

Flores and Jurado (2003) surveyed the literature on plant facilitation (some 296 papers) and found more than half (158) focused on arid and semi-arid zones. However, because of the large number of different nurse species (147, from 98 genera and 40 families) and protégé species (429, from 273 genera and 84 families) described across a diversity of environments, Flores and Jurado concluded that more than one driver is likely selecting for nurse-protégé interactions in arid and semi-arid environments.

Flores and Jurado probed various hypotheses to explain these facilitative desert interactions. Of the several identified, seed trapping seemed to have the strongest support (e.g., El-Bana et al. 2002), followed by the benefits of locally increased nutrient levels. The notion of nutrient safe-sites includes nurse plants as "fertile islands" (Garner and Steinberger 1989) where seedling establishment and survival opportunities increase.

Further to the nutrient hypothesis, it is noteworthy that many nurse plants are legumes (40 of 147 in the analysis of Flores and Jurado), capable of fixing atmospheric nitrogen through bacterial symbiosis in their root nodules. Most of these species (29) were in the Fabaceae, ten Mimosaceae, and one Caesalpiniaceae. Since other, non-nitrogen-fixing families also frequently include nurse species in arid environments (e.g., Asteraceae [15 species] and Euphorbiaceae [7 species]), factors other than this particular form of nutrient enrichment are likely also involved. Other hypotheses include protection from herbivores (especially when the canopy species has thorns or prickles that prevent herbivores from accessing the ground vegetation beneath them), and water availability. As Flores and Jurado pointed out, experiments designed to test specific hypotheses will shed useful light on the factors favoring these plant–plant facilitations.

It is important to consider that many patterns of plant behavior could reflect traits which are simply a continuation of the traits of ancestors, rather than necessarily reflecting current, immediate selection pressures. Thus it seems likely that closely related species with disjunct distributions will have maintained their fundamental niche features[14] through evolutionary time (Wiens and Graham 2005). Growing evidence suggests the plant niche—like that of animals—evolves in a conserved manner showing "phylogenetic niche conservatism" (Valiente-Banuet and Verdu 2013a), and represents the natural tendency of lineages to maintain their ancestral ecological features. This may include important features such as the separate habitat preferences of juveniles (the regeneration niche) and adults, an issue of vital importance in the Middle East where

[14] Hutchinson (1957) distinguished between the fundamental and realized niche of a species. The former referred to the abiotic conditions under which a species persists, the latter to conditions including the presence of competitors and predators. These days modern "niche-parsing" is proving very fruitful in climate-change research (e.g., Bateman et al. 2013; VanDerWal et al. 2009).

the regeneration niche of many long-lived species seems to have disappeared (see Section 1.7).

As one example of retention of ancestral traits, Ricklefs and Latham (1992) showed that herbaceous species that diverged between 10 and 30 Ma had similar habitat distribution patterns in both Asia and North America. They interpreted this as conservation of ecological features affecting the current distribution of the species. Clearly a good understanding of past selection pressures and evolutionary adaptations can help explain the present and perhaps the future.

The demography and patterns of diversity observed in *current* communities are a consequence of historical "sorting events" and quite likely include mixtures of different floristic elements originating in different times. Wolfe (1995) carried out paleoenvironmental reconstructions using leaf traits and concluded that many of the floristic elements he studied had evolved under quite different ecological conditions, yet have persisted through major changes in climate. One of the most important sorting periods affecting Middle Eastern communities happened during the shift from the wet Tertiary to the unusually dry Quaternary—the time when most deserts developed (Valiente-Banuet et al. 2006).

Valiente-Banuet et al. (2006) argued that many species—including those in dryland communities—may therefore today exist in environments which are less than optimal. Valiente-Banuet et al. suggested that species cannot always "do it by themselves"—i.e., surviving and successfully reproducing—but rather may manage to persist as a result of various beneficial interactions including the effects of ecological facilitation.

Valiente-Banuet et al. concluded most of the woody taxa present in Mediterranean ecosystems today—originating during the Tertiary and evolving in woodlands—likely recruited juveniles through facilitation under the canopy of shrubs. They suggest facilitative interactions were especially critical during the transition from the Tertiary to the Quaternary. Such a change from wet to dry could promote the evolution of new taxa having increased tolerance of water stress and an ability to regenerate in areas lacking vegetation (Verdu and Pausas 2013). These more-recently evolved taxa generate more benign micro-environments beneath their canopy, which in turn favor the subsequent regeneration of ancient Tertiary species in the understory.

Results for Mediterranean ecosystems were consistent with the fact that facilitative interactions tend generally to increase in intensity and importance as *abiotic* stress levels increase (e.g., Hacker and Gaines 1997; He et al. 2012; Valiente-Banuet and Verdu 2013b). Facilitation increases biodiversity by modifying harsh environments at the microclimate scale (Gómez-Aparicio et al. 2004; Valiente-Banuet and Ezcurra 1991). In terms of niche theory, these effects are achieved through expansion of the realized niche of the less tolerant species (Bruno et al. 2003; Valiente-Banuet and Verdu 2013a).

Valiente-Banuet and Verdu (2013a, b) emphasized that in order to better understand how facilitation promotes biodiversity, we need to move beyond the study of relatively simple, pairwise interactions and begin to consider multi-species systems, since many species often interact simultaneously.

Phylogenetic relationships among co-occurring species have also been useful in predicting individual plant performance and species coexistence. For example, Castillo et al. (2010) showed experimentally that growth and survival of the cactus, *Neobuxbaumia mezcalaensis*, inhabiting multi-species patches had a complex, temporally dependent relationship having several different drivers. Thus an individual seemed to depend, sequentially, upon the phylogenetic distances first to its "nurse," then its nearest relatives, and then to all its neighbors. Seedling establishment of *N. mezcalaensis* increased under more distantly related nurses, especially as a result of the low number of seedlings emerging under conspecific nurses (and consistent with the comparative rarity of "self-facilitation" in nature [Bonanomi et al. 2011]). When facilitated seedlings grew up, the phylogenetic distance to the nurse became irrelevant and the important factor driving plant performance became the distance to neighbors in the more crowded, multi-species patch.

Over the first three years of life, the growth of established cactus seedlings proved positively correlated with phylogenetic distance to the nearest closest relative, suggesting stronger competition with closely related neighbors, which could be attributable to greater niche overlap. The survivorship of juveniles (3–14 years) was not dependent on

the nearest relative but on interactions with all its neighbors with the result that survival was maximized in a phylogenetically diverse neighborhood.

Verdu and Valiente-Banuet (2008) also examined Mexican desert communities as networks of host species interacting with their variously facilitated species. Hosts and facilitated species did not interact randomly but rather had highly nested patterns, in which a few generalist hosts facilitate a large number of other species, while the remainder of the hosts facilitate only a smaller subset. Because generalist hosts tend to be the most abundant species in the desert community, Valiente-Banuet and Verdu (2013a) predict the nested pattern of interactions confers a certain *robustness* against extinction in communities governed by facilitation.

This further supports an evolutionary role for facilitation buffering older lineages from extinction through the Tertiary–Quaternary climate change (Valiente-Banuet et al. 2006). Positive interactions help form complex networks that contribute to both the persistence of biodiversity and a decrease in the rate at which species go extinct. Such networks include positive interactions in addition to those of host-protégé plants—for example, mutualisms between seed dispersers and plants, and between pollinators and plants (Bascompte and Jordano 2007). The nested nature of the network's structure seems to help buffer communities against extinction (Memmott et al. 2004).

## 4.8 Comparing desert and Mediterranean ecosystems

The "Mediterranean" climate—hot, dry summers and cool, wet winters[15]—has generated similar plant associations in all five of the widely scattered regions of the world where this climate occurs (Raven 1971). It gets different names, including "chaparral" in California, "fynbos" in the Cape province of South Africa, "matorral" in Chile, "mallee" in south and south-western Australia, and "maquis" in the Mediterranean basin. It is worth noting that these five regions occupy less than 5% of the earth's surface, yet contain almost 20% of the world's plants. The evergreen sclerophyllous vegetation characteristic of ecosystems having Mediterranean-type climates consists mostly of short shrubs and trees (1–3 m high) and broad-leafed sclerophyllous species, with 40–100% coverage by woody vegetation.

According to Raven, plant associations in these five world regions are extremely similar, both in physiognomy and in the morphology and physiology of the plants, mostly dominated by low, evergreen, sclerophyllous trees with short thick trunks and twisted, often spreading branches. Sclerophyllous plants occur in many parts of the world but are most typical of the matorral/chaparral biome (see Section 5.3).

At the same time interesting differences do exist, depending on the region. Regarding the Mediterranean region of the Middle East, Shmida (1981) compared the major Mediterranean vegetation types of California and Israel (the latter taken as representing more broadly eastern Greece, Turkey, Syria, and Lebanon). Vegetation types include woodland, matorral, phrygana, montane belts, riparian vegetation, and transitions to desert. Shmida described significant differences in life form spectra, physiognomy of the vegetation, species richness, fire adaptations, leaf traits, and the altitudinal sequence of montane belts (estimating average timberline in the Middle East to be 1900 m, and in California 2400 m).

With regard to the predominant matorral/maquis vegetation, in Israel this was significantly poorer in woody species than equivalent Californian chaparral. By three measures—community species richness, differential diversity, and regional richness—California proved significantly richer and more diverse. Life form spectra also differed broadly between matorral formations at the two locations (see Table 4.4). California had a significantly smaller proportion of annuals and geophytes and a greater proportion of shrubs and trees. Shmida suggested Old World annuals may be especially aggressive on introduction to western North America simply because they are being placed in a relatively empty adaptive zone for which they are especially well-suited . . . and that this may explain the success of invasive European

[15] And memories of school mnemonics regarding Mediterranean climates—W[5]: warm, wet, westerly winds in winter; with major food products FLOGWOG: figs, lemons, oranges, grapefruit, wheat, olives, and grapes.

**Table 4.4** Growth form spectra of some Mediterranean floras of chaparral in Israel and California (after Shmida 1981, used with permission).

| Growth forms[1] | Israel | | California | |
|---|---|---|---|---|
| | No. taxa | % | No. taxa | % |
| Annuals, all | 823 | 53.1 | 178 | 43.8 |
| Introduced | | | 107 | 29.3 |
| Facultative annuals | 52 | 3.3 | 12 | 2.9 |
| Biennials + facultative perennials | 75 | 4.8 | 4 | 1 |
| Geophytes | 114 | 7.3 | 10 | 2.5 |
| Hemicryptophytes, all | 307 | 19.7 | 89 | 21.9 |
| Chamaephytes, all | 104 | 6.7 | 38 | 9.4 |
| Subshrubs | 9 | 0.6 | 17 | 4.7 |
| Suffrutescent | 64 | 4.1 | 10 | 2.4 |
| Nanochamaephyte | 31 | 2 | 11 | 2.3 |
| Shrubs (0.5–2.0 m), all | 41 | 2.6 | 41 | 9.8 |
| Trees (> 2.0 m), all | 45 | 2.9 | 33 | 8.2 |
| 2–4 m tall | 15 | 1 | 21 | 5.3 |
| 4–8 m tall | 24 | 2.5 | 1 | 0.2 |
| > 8 m tall | 6 | 0.4 | 11 | 2.7 |
| Climbing vines | 23 | 1.5 | 7 | 1.7 |
| Parasites | 22 | 1.4 | 2 | 0.5 |

[1]Life form categories are modified from those of Raunkiaer (1934).

and Asian weeds in North America (see too Stebbins 1974).

Phrygana vegetation—called coastal sage in California, and batha, low matorral, or phrygana in the Old World—was much more widespread throughout the Mediterranean region of Israel than in California. Shmida suggested this reflected the major difference in intensity of human activities in the two regions. He postulated a late Pleistocene in which widespread desertification took place at subtropical latitudes and the desiccation spread into Mediterranean regions. At that time many mesic forest climax species became extinct. The evergreen, understory sclerophyllous shrubs, however, survived and developed into the present matorral communities. Human development has significantly degraded the mixed evergreen forests and woodland at both locations; however, this process was much longer and more profound in the Middle East, with rather more time there as a "Cradle of Civilization" than California.

Fire adaptation by serotinous diaspores and burls or lignotubers[16] is typical in California and almost absent in Israel. Serotinous diaspores that require heat scarification are generally common in chaparral, but closed-cone conifers or other taxa having serotinous diaspores are absent from Israel. Shmida suggested that maquis vegetation there—in

[16] A burl is a woody swelling of the root crown containing buds from which new stems may arise. The ability to sprout from the stump following crown removal is common in both maquis and chaparral, but these swollen "lignotubers" are absent from Israeli taxa (Shmida 1981). Burls are a powerful adaptation to fire; these meristematic areas contain multiple buds from which new stems may sprout, as well as stores of starch, able to support a period of growth in the absence of photosynthesis. Many of these species grow in a shrubby, "lignotuberous" habit, with multiple stems arising from the lignotuber.

**Table 4.5** Numbers and percentages of spinescent taxa by growth forms in the Mediterranean floras of California and Israel (after Shmida 1981, used with permission).

| | Spiny leaves | | Spiny + rigid stem | | Total spiny species | | Total no. of species studied | |
|---|---|---|---|---|---|---|---|---|
| | No. | %[1] | No. | %[1] | No. | %[1] | %[2] | |
| **Israel** | | | | | | | | |
| Annuals | 20 | 4.4 | | | 20 | 4.4 | 23.3 | 451 |
| Perennial herbaceous | 32 | 18.9 | 2 | 1.2 | 34 | 20.1 | 39.5 | 169 |
| Suffrutescents | 1 | 1.4 | 3 | 4 | 4 | 5.4 | 4.7 | 74 |
| Low shrubs | | | 3 | 23 | 3 | 23 | 3.5 | 13 |
| Arboreal | | | | | | | | |
| Shrubs | 1 | 4 | 19 | 76 | 20 | 80 | 23.3 | 25 |
| elements | | | | | | | | |
| Trees | | | 5 | 15.2 | 5 | 15.2 | 16.6 | 33 |
| Total | 54 | 7.1 | 32 | 4.2 | 86 | 11.2 | 100 | 765 |
| **California** | | | | | | | | |
| Annuals | – | – | – | – | – | – | – | 166 |
| Perennial herbaceous | 3 | 2.7 | – | – | 3 | 2.7 | 12.5 | 110 |
| Suffrutescents | 3 | 7.9 | – | – | 3 | 7.9 | 12.5 | 38 |
| Low shrubs | 2 | 10.5 | 3 | 15.8 | 5 | 26.3 | 20.8 | 19 |
| Arboreal | | | | | | | | |
| Shrubs | 4 | 12.1 | 5 | 15.1 | 9 | 27.2 | 37.5 | 33 |
| elements | | | | | | | | |
| Trees | 2 | 7.6 | 2 | 7.6 | 4 | 15.2 | 16.6 | 26 |
| Total | 14 | 3.6 | 10 | 2.6 | 24 | 6.1 | 100 | 392 |

[1]Percentage of spiny plants relative to total number of species in this growth form category.

[2]Percentage of spiny plants relative to total number of all spiny species in the assemblage.

the absence of a fire-type climate with frequent, dry lightning strikes—has not become adapted to burning.

Spines on leaves are generally interpreted as herbivore deterrents. Compared to Californian chaparral the Middle East maquis contained fewer spiny trees and shrubs, but many more spiny hemicryptophytes and annuals (see Table 4.5). Some 10.3% of chaparral overstory taxa have spiny leaves (e.g., some *Prunus, Quercus, Rhamnus, Ceanothus* species), and 12.8% have spiny stems. In Israel 32% of the arboreal element of the maquis flora have spiny stems, while only 2% have spiny leaves (see too Section 5.6 on spinescence).

In another, quite different kind of comparison of otherwise similar plants, Aronson et al. (1990) surveyed the variability in plant size at reproduction for plants living in either a Mediterranean or desert climate. Twelve species were studied and pairwise comparisons made of ephemerals[17] from different

[17] An ephemeral plant is one marked by a short life cycle (see Section 5.9), and can refer to several distinct growth strategies. The first, "spring ephemeral" refers to perennials that emerge briefly in the spring and die back to underground parts after a short phase of growth and reproduction (only *appearing* to be ephemeral, as the individual persists). "Desert ephemerals" are short-lived species adapted to exploit brief wet periods in arid climates, completing their life cycle from

Mediterranean and desert sites in Israel. Aronson et al. explored the notion that at the extremes of gradients of increasing aridity and rainfall unpredictability, ephemeral species in particular have adapted through changes in the norm and variability of *developmental* traits, as well as through shifts and trade-offs in the relative allocation to reproduction. Aronson et al. proposed that in ephemerals the importance of phenotypic plasticity and genetic variability as a whole gets maximized.

In two of the parameters studied, plant height and total-above-ground biomass, Mediterranean populations had significantly greater variability than corresponding desert populations. Moreover the greater variance was not due simply to greater plant size in the Mediterranean region, since in some cases the desert plants were of equal or greater size at comparable stages. Aronson et al. argued the greater variability in size in Mediterranean individuals was due to the far greater density and intensity of competition there. They described representative 1 $m^2$ plots in the Mediterranean region having 7000–12 000 seedlings, while in the desert an average 1 $m^2$ plot supported only 40–400 seedlings.

Developing a theme, Aronson and his colleagues proposed that in the highly unpredictable desert environment major plant fitness benefits may come from spreading risk through *time*, mainly as dormant seeds delaying germination both between- and within-years (see too Chapter 7). In contrast in Mediterranean habitats, where there are higher plant densities, the ability of individuals in a given cohort to exploit resources in *space* seemed the preferred strategy.

Aronson et al. suggested the greater variability in size at reproduction could also be a consequence of the simultaneous flowering of cohorts emerging following *different* rain events during the Mediterranean growing season. In both Mediterranean and desert regions non-dormant seeds germinate soon after strong rainfall (15–20 mm). However, major rain events are obviously less frequent in the desert. In the Israeli desert, in some years, only one to two effective rains occur during the entire winter season. Because in the Mediterranean region multiple rainfall events allow ongoing germination from about the end of November through the end of January, several different cohorts of seedlings may be produced each season. In marked demographic contrast, in desert the flowering of ephemeral species occurs simultaneously, since it is generally *induced* (or triggered and enhanced) by the relatively low temperatures of early winter and progressively longer days of late winter and early spring (Aronson et al. 1990).

Finally, in a third Mediterranean comparison, Valiente-Banuet et al. (1998) compared a diverse array of ecological and botanical features of an unburned evergreen sclerophyllous vegetation known as *mexical*, in south-central Mexico under a wet-summer climate, with those of Mediterranean regions. They considered the general notion that plant characters at community and population levels—often claimed to "converge" under Mediterranean climates around the world—are the *same* as those in the plant communities and populations in south-central Mexico living under non-Mediterranean climate. They determined using multiple traits and correspondence analysis that the *mexical* did not differ significantly from plants in the evergreen sclerophyllous parts of Chile, California, Australia, and the Mediterranean basin. Moreover they concluded that all of the vegetation and floristic traits of the *mexical*, as well as its distribution along the rain-shadowed mountain parts of Mexico support its origin in the Madrean–Tethyan hypothesis of Axelrod (1975) (see Section 3.3). This all supports a general expansion of the "convergence paradigm" for Mediterranean-type vegetation, an integrative view whereby a general trend to aridity could explain floristic and adaptive patterns detected in all these environments.

Similarities between the *mexical* and plants from Mediterranean regions suggest the *mexical* represents the same kind of vegetation as that which traditionally has been considered as only associated with Mediterranean climates. In addition to classical views of evergreenness and sclerophylly as adaptations to environmental constraints, Valiente-Banuet et al. suggested the results support expansion of the convergence paradigm. They argue these

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germination and reproduction to death quickly. "Mud-flat annuals" take advantage of brief periods of low water-levels. In areas subject to recurring human disturbance such as plowing, weedy ephemerals are very short-lived plants whose entire life cycle takes less than a growing season. In each of these cases, the species has a life cycle well timed to exploit a brief moment when resources are freely available.

dryland systems can best be seen in the context of an extended paleo-climatic trend toward greater aridity. Of course at the same time, once the Mediterranean climate developed, i.e., gradually after the late Cenozoic in the five different world regions, plants under a summer-wet climate gradually adapted physiologically to the new conditions.

## 4.9 Elevation and warming

Global climatic warming over the past century has led to a variety of responses from biota including changes in the *timing* of development—the phenology of leafing out, flowering, and fruiting in plants (Cleland et al. 2007; Doi and Katano 2008). Other changes include pole-ward latitudinal shifts in the distribution of species (Hickling et al. 2005; Parmesan et al. 1999) and in general migration to higher elevations (Konvicka et al. 2003; Moritz et al. 2008). Such shifts in response to historical warming are well documented, leading us to expect the trend to continue. During the last ice age relict mountaintop populations sometimes persisted and survived simply because there they were above the inexorable plow of the ice sheet.

Hegazy et al. (1998) studied an altitudinal gradient in southwestern Saudi Arabia and showed how interactions among environmental factors changed in relation to elevation. They described variation in habitat types and the particular suite of plant communities, and also fairly distinct regional belts of vegetation. At low elevations (0–500 m), the Tihamah coastal marshes, plains, and foothills had fairly discrete plant communities corresponding to discontinuous substrates and habitat types. Similarly at higher elevations (> 2500 m), the Asir highlands had many distinct plant communities, largely determined by aspect and the topographic mix of slopes, ridges, and crests. Intermediate elevations (500–2500 m) had more continuous communities, with greatest overall species richness and diversity along with relatively high evenness values.

Obviously elevation per se is not the only factor: soil depth, water flow, orographic rainfall, aspect, etc., are all important. Lovett-Doust et al. (2009 and see Hegazy et al. 2009) examined correlated effects of elevation on abundance-occupancy in the northwestern Red Sea region, comparing both regional- and individual habitat levels. Some 58 stands (and 66 species) were studied using ten quadrats (10 × 10 m) per stand. The relation was positive and significant at both scales. "Niche-breadth" was estimated as the number of habitats occupied regionally by a species and was significantly related to both individual abundance and percentage occupancy of quadrats. Niche breadth explained only 10.1% of variation in abundance, but some 56% of variation in occupancy.

It is a truism of biogeography and life on Earth that in general, climate becomes colder with increasing latitude. Temperature also drops with increasing elevation. These two factors combined—elevation and latitude—can generate very low temperatures and wide diurnal ranges. Large water bodies, with their high latent heat and specific heat act as air-conditioning systems . . . the closer a particular location is to the sea or a large lake, the more temperate in general is the climate and the less the difference between seasons and between day and night temperatures.

### 4.9.1 Patterns of species richness, elevation, and the "mid-domain effect"

It is widely agreed that the distribution of the world's vegetation is largely controlled by climate—chiefly water and energy availability (e.g., Currie and Paquin 1987)—but it is also influenced by particular historical constraints such as limitations upon dispersal, and on a more local scale by environmental constraints interacting with biological processes, including a species' capacity to reproduce and disperse. In particular, a simple response to climatic and/or energy-related factors is considered the primary explanation for the observed decline in plant species richness with increasing latitude or elevation (Allen et al. 2002; Currie and Paquin 1987; Hawkins et al. 2003; Leathwick et al. 1998).

Differences in species richness at different locations are *also* a simple consequence of the shape and size of individual land masses. Colwell and Hurtt (1994) first showed that such "non-biological" gradients in richness can arise simply from the assumption of a random one-dimensional association

between the size and placement of species' ranges. Colwell and Lees (2000) labeled this geometric theory of species richness gradients the "mid-domain effect" (MDE) and defined it as "the increasing overlap of species ranges toward the center of a shared geographic domain, due to geometric boundary constraints in relation to the distribution of species range sizes and midpoints."

The MDE has since received much attention as a way to explain patterns in species richness over large areas. The most common terrestrial mid-domain models have been 1-D latitude or elevation models, and 2-D latitude–longitude models. VanDerWal et al. (2008) took this a step further and described a mid-domain model incorporating 2- and 3-D combinations of latitude, longitude, and elevation, reflecting a more realistic geometry of natural landscapes and the shapes of species ranges. Their results successfully explained patterns of species richness in amphibians, birds, mammals, and tree species in North America.

More recently Murphy et al. (2011) examined the contentious issue of the *relative* explanatory power of MDE effects versus standard environmental factors such as climate variables. The use of both traditional "global" regression models as well as geographically weighted regressions ("local" models) allowed measurement of the relative contributions of traditional climatic effects and separate MDE effects, to species richness across the domain. Using data on some 500 North American tree species and their ranges, Murphy et al. showed that for many species the contribution of MDE to patterns of species richness was substantial, and in most cases a combination of MDE and climate best predicted tree species richness.

Although broad-scale factors like MDE and climate may determine the botanical composition and related species richness of any particular location, a major modifying factor is elevation. Altitude has a particularly significant influence upon the structure of vegetation in the Arabian Peninsula, with species richness reported to be greatest in elevated areas from 1000 to 1480 m (Deil and Al Gifri 1998). Changes in species richness along altitudinal gradients have been the subject of numerous studies worldwide (e.g., Lomolino 2001; Murphy et al. 2011) with most reporting a "humped" distribution, and peak species richness in the mid-altitude part of the slope (Rahbek 1995, 2005).

## 4.10 Regional ecology: Plant metapopulations and landscapes

Ecological analysis at large spatial scales has emerged as a subject of two quite separate subdisciplines: metapopulation ecology and landscape ecology. The former provides one framework for understanding population dynamics—that is as consequences of migration, colonization, and local extinction events, all set within "spatially structured" matrices of suitable and unsuitable habitats (see, e.g., Hanski and Gilpin 1997). In theory metapopulations represent the organisms inhabiting regional landscapes—the reef fishes, butterflies, and dragon's blood trees, say—each experiencing its environment at unique, species-specific scales of space and time.

At the same time, the study of landscape ecology considers a similar variety of subjects, including population dynamics. Its general focus is often summarized, though, as the "effects of landscape structure and spatial configuration on ecological processes" (Turner 2005; Turner et al. 2001).[18] Lives and fates of actual living organisms on the ground are often treated as "secondary" to landscape definitions and parameters.

The major models in both landscape- and metapopulation ecology assume a kind of *binary* landscape composed of "habitat" and "matrix" (i.e. non-habitat areas that surround suitable habitat patches). Metapopulation models have focused almost exclusively upon the habitat-patch component, rather than the matrix (Ricketts 2001). This is an important distinction compared to the spatially explicit population approach of landscape ecology, which tries to take more account of characteristics of the non-habitat, or matrix portion of the landscape (e.g., Ims and Yoccoz 1997).

[18] Ecological processes of course continue to act *through* the activities and success or failure of individual organisms. For example, landscape-level effects have been shown to influence patterns of individual plant developmental instability and fluctuating asymmetry in leaves across the North American range of Honey Locust, *Gleditsia triacanthos* (Fabaceae) (Murphy and Lovett-Doust 2004b, 2007).

Landscape-based models usually assume that movement between patches depends on aspects of the matrix, which may influence dispersal mortality and/or movement direction. Both these emergent sub-disciplines would benefit from the integration of some of the approach of the other. Murphy and Lovett-Doust (2004a) argued that such an integrated perspective promotes understanding of large-scale spatial dynamics in plants, in particular those due to dispersal.

The overriding importance of dispersal has long been recognized as an influence on patterns of distribution and geographic range in plants (Reed et al. 2000). The mobility of the recruitment stage is expressed primarily through dispersal of seed and fruit propagules, and via pollen movement (Bullock et al. 2002). Of course it is inherently difficult to track single seeds as they disperse from individual parent plants to their final site of deposition, and in particular it is hard to follow those rare, longer-distance dispersal events required to colonize new habitats (Greene and Calogeropoulos 2002). Such difficulties are even more challenging for tracking *pollen*-mediated dispersal events (but see, e.g., Waser et al. 2000).

Plants differ from animals in several fundamental features of their life history. They are *non-unitary* organisms, modular, and essentially "stand still" for much of their lives,[19] and so must be capable at least of enduring, *persisting*, in some local environment. At all spatial scales, suitable environments are interspersed in a matrix of more or less inhospitable space (Eriksson and Ehrlen 2001). This means that for most plant species a *fragmented* habitat tends to be the arena within which population dynamics, ecological processes, adaptation, and evolution occur (e.g., Cadotte et al. 2002).

Persistence requires coping with temporally and spatially unpredictable resources. Many plant features, including dispersal structures, seed size and dormancy patterns, and forms of clonal propagation can all be interpreted in this context—in conjunction with sessility and the rootedness of individuals, necessary for gathering and capturing the many diffuse resources of plant existence—i.e., molecules of water and mineral nutrients in the soil, $CO_2$ in leaves.

The existence of long-lived stages including both seeds (genets) and vegetative shoots (ramets, or offsets) means that local populations and even individuals can persist for a long time, even though a habitat patch may have become less than suitable. This is clearly happening in long-lived trees and shrubs such as those on Socotra. Ehrlen and Eriksson (2003) argued that successful dispersal and recruitment in plant populations may typically be very sporadic, and therefore recolonization is unlikely after local population extinction. Plant dispersal over long distances appears to be governed by significant stochasticity. Moreover while the definition of "long distance" may differ markedly between species, it is typically only rarely more than a few hundred meters, often much less for most species (Cain et al. 2000).

It was perhaps not surprising that a major conclusion from the several reviews of plant metapopulation prevalence in nature—e.g., Bullock et al. (2002); Freckleton and Watkinson (2002); and Husband and Barrett (1996)—was that many plants appear *not* to be organized as metapopulations. Hence other frameworks may be necessary to understand large-scale, plant regional dynamics above the population level (and possibly also in other organisms sharing similar life history features).

Freckleton and Watkinson (2002) showed that regionally some species do appear to exist as metapopulations in the classic sense, where regional persistence is governed by the recursive processes of patch colonization, extinction, and recolonization. However, many other species exist as *regional ensembles*, or systems of essentially unconnected local populations persisting in an ill-defined mosaic of suitable and unsuitable habitat patches (e.g., the tree, *Moringa peregrina* (Hegazy et al. 2008a). Still other species exist as spatially extensive populations, essentially a single, large population occupying large tracts of suitable habitat but whose regional dynamics represent simple extensions of local dynamics. Many desert perennials—including the several nabkhat-forming saltbushes—appear to fit this category and seem worthy of further study in this regard.

[19] . . . "waiting to be counted," as the plant biologist J. L. Harper (1977) put it in his book demonstrating the importance of plant demography in understanding their evolutionary ecology.

It seems clear that plants in the desert mostly just "follow the water." When distinctions between habitat and non-habitat (background "matrix") are fairly clear, as seems the case in desert environments, then identification of distinct habitat patches is relatively easy and species dynamics can be described in terms of the attributes of those patches. Suitable habitat is readily defined for obligate epiphytes growing on tree trunks, or hemiparasitic mistletoes living in tree canopies, or parasitic *Cynomorium coccineum* living on saltbush roots. By extension, in the desert the presence of water is an obligate attribute of habitat.

In contrast for many species, in particular those with relatively broad physiological tolerances, there may be no clear distinction between habitat and matrix so delineating habitat patches becomes difficult or impossible (Freckleton and Watkinson 2002). Identification of "empty" but suitable patches is even more difficult and there are still only a few experimental studies that have been designed to estimate occupancy (the proportion of suitable patches which are in fact occupied) in plants (Ehrlen and Eriksson 2000).

As far as the suitability of habitat is concerned, most plants surely respond to *gradients* of resource quality rather than simple presence/absence of a resource, as would be the case for, say, specialized herbivores (With et al. 1997). As a result, for plants suitable habitat lies along some environmental continuum, from optimal habitat through suitable, to sub-optimal and unsuitable . . . with many biotic and abiotic parameters likely contributing to suitability. Where a species does not perceive sharp and distinct boundaries—say gradual moisture gradients—patch properties become less important and the nature of the overall landscape mosaic likely becomes increasingly significant (Thomas and Kunin 1999).

The assumption in metapopulation ecology that properties of the matrix are unimportant is perhaps only true for terrestrial organisms inhabiting oceanic islands. This sits at one extreme of a continuum extending from situations such as true islands like Socotra, where the marine matrix is completely inhospitable and quite homogenous, through the more paradigmatic metapopulation landscape in which discrete, suitable habitat is separated by a homogenous matrix that is not suitable for colonization but that is also not fatal to dispersers (Ims and Yoccoz 1997). Finally at the other extreme is continuous habitat in which the matrix nature is essentially indistinguishable from the patch. The metapopulation—landscape debate seems to echo the early ecological discourse about either identifying discrete "stands" of vegetation, as proposed by Clements (1916), or interpreting vegetation as a continuum (Gleason 1926). As is often the case, it depends on the particular vegetation being examined and the scale at which observations are made, or patterns recognized, as to which models make most sense.

## 4.11 Connectivity and the background matrix from a plant perspective

At present there is no single, commonly accepted measure of connectivity. Metapopulation ecologists measure connectivity mostly at the patch scale, while landscape ecologists measure it as a species-specific attribute of the landscape, and both groups *use* these measures in different ways. Yet the underlying process is the same: we seek to measure the movement of individual plants—here including ramets and disconnected shoots, seed-bearing tumbleweeds, dispersed fruits, seeds, and pollen—across a regional landscape.

Terrestrial habitat patches tend to be surrounded by a complex mosaic of other landcover types, and these likely differ in their resistance to the movement of individuals among patches. However, the landscape matrix has mostly been regarded as uniform by metapopulation biologists, and most connectivity metrics in population ecology are based on simple nearest-neighbor distances (Moilanen and Neiminen 2002), or negative exponential distances, with population size or patch area as weighting functions (Hanski 1999).

The relatively high species richness in south Sinai has been attributed to its location at the nexus of four phytogeographic regions: Mediterranean, Irano–Turanean, Saharo–Arabian, and Sudanian (Hegazy and Amer 2002). The moist mountain sites on both sides of the Red Sea likely act as a tropical corridor that facilitated the stepwise migration of many tropical species onto the Sinai Peninsula. Among the tropical species are *Acacia tortilis, Moringa peregrina, Salvadora persica*, and *Suaeda monoi*ca.

To develop a more comprehensive model of landscape matrix effects on connectivity, especially as it relates to large scale dynamics in plants, requires better understanding of the movements of the animals that disperse seeds, most commonly birds, mammals, and ants, as well as the agents, biotic and abiotic, that move pollen (see Chapter 7).

In animal-pollinated plants, reproductive success may be negatively related to the distance between flowering patches. Various studies have documented lower success in isolated or fragmented populations (Aizen and Feinsinger 1994; Groom 2001). Moreover even when pollinators successfully travel long distances between patches, the *quality* of the pollen transferred may decline. Thus generalist pollinators may visit a variety of species when travelling longer distances, and other species' pollen may act to clog stigmas and reduce reproductive success (Groom 2001). Chapter 6 explores reproductive ecology in the environments of the Middle East in more detail.

## 4.12 Summary

This chapter develops the concept of "desert" beyond the simple perception of endless sand dunes to describe an extensive heterogeneous dryland habitat. Vegetation types are discussed and specialized habitats such as nabkhas, coastal sabkhas (salt flats) and mangroves are described. Desert phytogeography and the major plant families are introduced—including the ice plants and other large succulent lineages like the chenopods and amaranths, brassicas and crucifers, caryophs and euphorbs. Mountain regions are important in the Middle East and effects of elevation on plants are discussed, as well as regional patterns of species richness and endemism, problems of landscape connectivity and other issues pertaining to plant metapopulations and genetic isolation. Finally, the many instances of ecological facilitation (plants "helping" plants) in desert ecology are explored from several different perspectives.

CHAPTER 5

# On growing up dry

There is sometimes a certain circularity—as in Kipling's "Just So Stories"—in discussing adaptations to what *we* regard as "extreme" conditions (such as life in a sweltering dry desert). It is always important to note that desert species are present today only because their ancestors had traits which helped them survive and successfully reproduce there. In this chapter we consider several general traits, including photosynthesis and physiological resistance to salt and drought, as well as sclerophylly (having small, hard leaves and short internodes) and water storage systems—noting here at the outset that these latter two traits are rarely binary, or present/absent, and especially in the case of water storage, may manifest to varying degrees.

## 5.1 Introduction to dryland plant adaptations

Desert plants are in a sense "sitting ducks." The water and nutrients contained in a perennial plant body represent sessile resources *waiting* to be found by animals which, like plants, require water and nutrients for survival. Desert plants have evolved an array of structural armor—spines and barbs of many forms—which discourage animals from eating them (Section 5.6). These structures often do double duty, providing surfaces on which night dew can condense and reducing evapotranspiration in the heat of the day. Desert plants have also evolved chemical defenses—including a rich diversity of secondary metabolites, more or less toxic compounds that serve in defensive and sometimes competitive roles (see Section 8.1).

Many adaptations exist, mostly attending in some way or other to the general problem of water shortage. Such adaptations include an array of features that increase absorption by roots, for example involving changes in anatomical differentiation, and other features of root systems. Examples include more rapid seedling root growth, abundant root extension, and low shoot/root ratios, and a capacity for adventitious[1] root formation (i.e., shoot-borne roots), e.g., in sandy mounds and hillocks. Other adaptations help plants to reduce water loss—many reducing or minimizing transpiring surfaces. Lots of succulent species appear shiny and light in color; this reflects rather than absorbs sunlight, reducing the surface temperature and rate of evapotranspiration.

The green leaf cortex is the transpiring and photosynthesizing tissue of a plant and in many dryland species some or all of this tissue may be abscised as conditions become progressively drier. This happens in e.g., *Haloxylon salicornicum, Anabasis setifera, Arthrocnemum macrostachyum, Zygophyllum qatarense, Z. coccineum*, and *Halopeplis perfoliata* (see Figure 5.1A). In all these species the core of the young branches during the rainy season consists only of a central cylinder containing vascular bundles surrounded by the cortex (Batanouny 2001). So long as water is available these cortical tissues remain green, actively transpiring and photosynthesizing. As soil water becomes scarce, water continues to be lost through transpiration; then cork is formed, separating the cortex from the main plant body. When the cortex is cut off from the water supply it dries

[1] Adventitious roots in general may originate from stems, branches, leaves, or old woody roots. They commonly occur in monocots and pteridophytes, but also in many dicots, e.g., *Trifolium*. Most aerial roots and stilt roots are adventitious (e.g., *Rhizophora mucronata*). In some conifers, adventitious roots may form the largest part of the root system.

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**Figure 5.1** Dryland plant adaptations. (A) shedding of cortex in *Halopeplis perfoliata* in coastal salt marshes of Farasan Island, Saudi Arabia. (B) Heterophylly in *Artemisia monosperma* in Central Saudi Arabia. (C) *Adenium obesum* in Shada Mountain, southwestern Saudi Arabia at elevation 1750 m (flower and fruits are shown at lower right). [For a color version of this figure, see the color plate section, Plate 8]

out and is abscised (Batanouny 2001). Batanouny also described how many species were able phenotypically to reduce their transpiration rates, either on a daily or seasonal basis.

Orshan (1953) early on distinguished four main patterns based on the plant organs that were abscised or "shed" and those left in place, exposed to drought during the dry season. In many ways this is analogous to Raunkiaer's system of life forms, in that the categories describe which tissues are abscised and which remain as dormant buds surviving the adverse season.

1. Leaf shedders: plants that drop their leaves and inflorescence shoots (e.g., *Zilla spinosa* is leafless in the dry season; *Retama raetam, Leptadenia pyrtechnica*, and *Calligonum comosum* are leafless almost year-round).
2. Branch-shedders: e.g., many chenopods drop parts of their branches seasonally.
3. Whole-shoot shedders: these lose all their aboveground parts each season.
4. Annuals: plants that die each year, surviving the period of severe drought as a dry seed or propagule.

In some cases plants have reduced their leaves completely, either producing no leaves at all or reduced, dry scales, or sometimes making only small, seasonal leaves ("microphylls") in the short period just after it rains, e.g., *Deverra tortuosa*. Microphylly—extending to a complete absence of leaves—reduces water loss during photosynthesis. Meantime leafless green stems can still conduct efficient photosynthesis, using well-positioned stomata that open only at night to allow carbon

dioxide molecules into the plant's air spaces. "Heterophylly," where individuals produce two or more distinct types of leaf, is also adaptive in the desert, e.g. *Artemisia monosperma* (see Figure 5.1B) in central Saudi Arabia produces both simple elongate leaves and small microphylls (A.K. Hegazy, personal observations). Another example is in the "desert rose," *Adenium obesum* (or the "fat" adenium, referring to the grossly thickened trunk) (see Figure 5.1C). The species stores water in the soft swollen stem and uses it to survive during extreme drought.

Waxy cuticles secreted on stem and leaf surfaces are reflective, reducing heat absorption and water loss. Summer leaves of *Capparis aegyptiaca* are coated with wax, giving them a lighter color than the winter leaves (Danin 1983). The lighter color and shiny surface reflects radiation and so leaves absorb less heat, reducing water loss through evapotranspiration.

## 5.2 Succulence

Succulence—the storage of available water, most often in leaves but also in stems and other specialized parts—allows plants to remain active photosynthetically during seasonal water shortage, and is common under semi-arid and arid conditions, i.e., where annual precipitation is less than potential annual evapo-transpiration. Some include in their definition plants that store water in underground roots and modified stems; others exclude these and classify them as "geophytes," producing underground organs such as bulbs, corms, and tubers, often fleshy with water-storing tissues.

The term "succulent" itself dates from 1619 when it was first applied to a group of plants by the Swiss botanist Johann (Jean) Bauhin.[2] He was referring to plants having thick, juicy leaves (and see too, Rowley 1987).

Succulence has radiated successfully in at least three major families, each comprising about 2000 species (Arakaki et al. 2011). These are the Cactaceae ("stem" succulents which are almost completely restricted to the Americas); the Crassulaceae ("leaf" succulents, occurring in both the New and Old World); and the Mesembryanthemaceae (leaf succulents originally restricted to the Old World and today regarded as part of the Aizoaceae, or Ice Plants [e.g., Figure 5.2]).

We consider the Crassulaceae in Section 5.5, as eponymic first family of Crassulacean acid metabolism (CAM) and the associated *kranz*-type anatomical adaptations ("CAM *mit kranz*").[3] There are also many succulent species in the very large Spurge family, Euphorbiaceae *s.l.*, which globally includes four giant genera and a combined total of over 5000 species (not all succulents) (see Section 5.7 on *Euphorbia*).

Regarding the Mesembryanthemaceae, Ihlenfeldt (1994) indicated that about 90% were native to southern Africa and indeed to a relatively tiny region there—known as the "Succulent Karoo" (this region is about 200 000 km$^2$ in area, and is the geographic epicenter of the lineage). According to Ihlenfeldt up to 53 different genera or subgenera (note here not *species*) may occur in a single degree square (*c.* 100 by 100 km) in the Karoo. Over vast areas this single lineage may represent more than 50% of the species and up to 90% of the biomass of vegetation. The radiation of succulent Mesembryanthemaceae is all the more remarkable as the ecological niche of ice plants—arid, with winter rainfall and moderate temperatures—first opened up only five million years ago, making this among the fastest known rates of evolution in the flowering plants (Ihlenfeldt 1994).

[2] In his posthumously published classification *Historiae plantarum universalis* (1619), Bauhin grouped a number of plants together as the Succulentae, on the basis of being "herbae crassifolia et succulentae" ("thick-leaved and juicy herbs"). His Succulentae embraced taxa of the modern genera *Agave, Aloe, Portulaca, Crassula, Rhodiola, Sedum*, etc., and was specifically restricted to leaf succulents. "Succulentae" was in continued use as a group in plant classification well into the second half of the eighteenth century, and later also included the cacti. With time however, the Succulentae became more and more a hodge-podge phylogenetically, and the "taxonomic" grouping soon disappeared in favor of evolutionary systematics, though the term remains as a useful descriptor.

[3] Most C4 plants have a characteristic leaf anatomy, called *kranz* anatomy from the German word for "wreath." Their vascular bundles are surrounded by two rings of cells. The inner ring (bundle sheath cells) contains starch-rich chloroplasts lacking grana, different from those in the mesophyll cells present as the outer ring. This provides a site where $CO_2$ concentrates, and avoids photorespiration. To help maintain higher $CO_2$ in bundle sheath cells than in mesophyll, the boundary layer of the *kranz* is often impregnated with suberin, which slows or prevents $CO_2$ diffusion (and see Section 5.5).

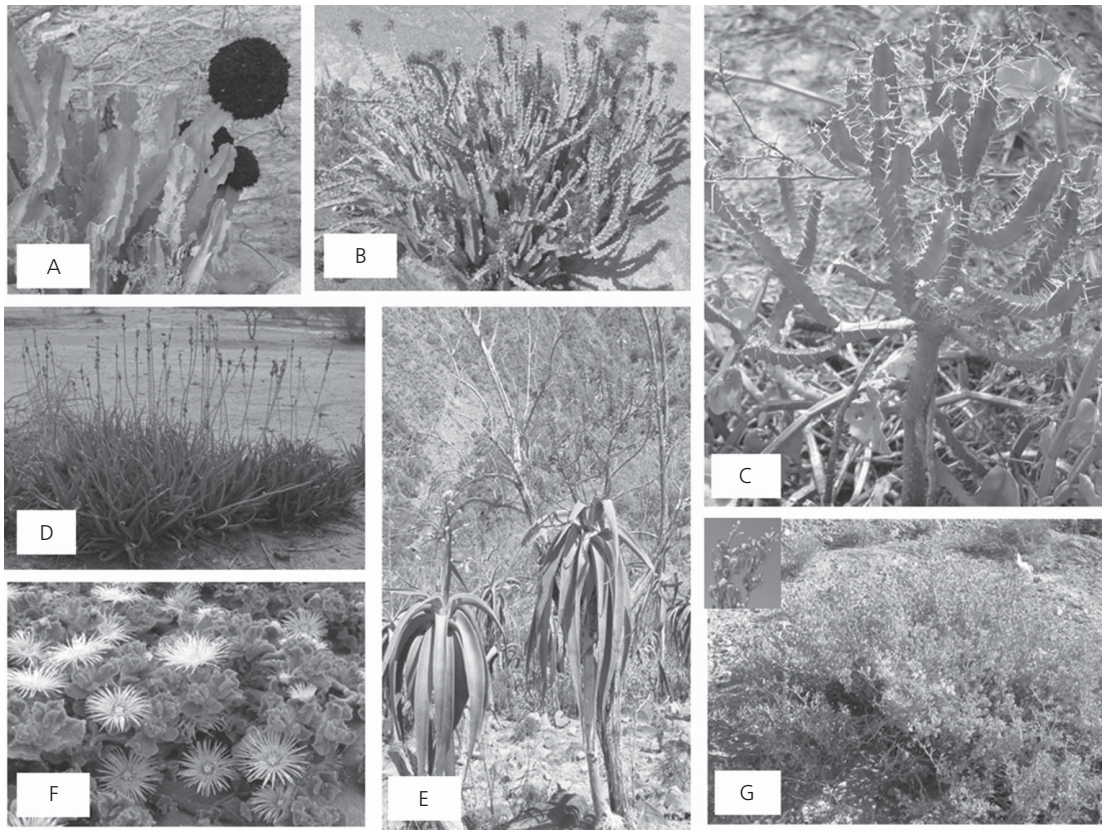



**Figure 5.2** (A) The succulent plant *Desmidorchis retrospeciens* at the foot of mountain escarpment near Taif, Saudi Arabia. (B) *Desmidorchis penicillatus* in foothills, Ad Darb, southwestern Saudi Arabia. (C) *Euphorbia fractiflexa* in Tehamah plain, Jizan, southwestern Saudi Arabia. (D) *Aloe vacillans* in Tehamah plain, Jizan region, southwestern Saudi Arabia. (E) The leaf succulent *Aloe sabaea* in the Raidah escarpment, northwest of Abha, Saudi Arabia. (F) The annual succulent *Mesembryanthemum crystallinum* in coastal sandy habitats near Sert city, west of Benghazi, Libya. (G) The perennial leaf succulent *Zygophyllum decumbens* in the Eastern Desert, Egypt. Enlarged leaves appear at top left. [For a color version of this figure, see the color plate section, Plate 9]

Arakaki et al. (2011) used a hybrid phylo-genomic approach and more than a hundred representative chloroplast genomes to interpret the evolution of the world's major succulent lineages. They concluded that the cactus lineage diverged from its closest relatives about 35 Ma, with major diversifications in cacti happening more recently. Most species-rich cactus clades appear to have originated during the late Miocene, about 10–5 Ma.

These cactus radiations occurred at the same time as did those of the South African ice plants and North American agaves; this was simultaneous diversification among several of the world's major succulent plant lineages, across multiple continents. It also coincides with the time when most of the C4 plants emerged and there was a global rise of C4 grasslands. The endemic Didiereaceae of Madagascar—sometimes called the "cacti of the Old World"—are stem succulent trees and shrubs of the spiny-thicket forests whose diversification occurred *c*. 17–11 Ma. There is a convincing body of evidence that global expansion of dryland environments during the late Miocene was associated with new ecological opportunities, especially for succulent and C4 species.

At the same time others have argued there was a substantial decline in atmospheric $CO_2$ (from about 425 ppm to 200 ppm), around 15–8 Ma (e.g.,

Tripati et al. 2009). As Arakaki et al. point out, this too would have strongly favored C4 evolution and expansion of C4-dominated grasslands. Lowered atmospheric $CO_2$ would also substantially exacerbate any plant water-stress in arid and marginally arid environments, providing any pre-adapted succulent species there with significant advantage, and promoting their rapid diversification.

Succulence is a complex syndrome involving aspects of plant morphology, physiology, and behavior. These often include a shallow but extensive root system giving rapid uptake of unpredictable precipitation; a thick, waxy cuticle that minimizes water loss; swollen or near spherical leaves (if present) that reduce surface-to-volume ratios and water loss, and Crassulacean acid metabolism, allowing cooler, night-time uptake of atmospheric $CO_2$ that will be used for photosynthesis over the next day. The core feature of succulence is the ability of water storage tissues to support physiological function in the absence of an ongoing water supply (Ogburn and Edwards 2012). The general mechanism by which any succulent plant avoids drought at the cellular level is perhaps best represented in the eco-physiological trait of *hydraulic capacitance* (C), the change in volume of a cell or tissue per unit change in water potential ($\psi$) (e.g., Nobel 1988):

$$C = \Delta V / \Delta \psi$$

Succulence appears to be governed primarily by the relative hydraulic capacitance, but also by absolute volume. Thus sometimes succulent qualities seem to be associated simply with the absolute *volume* of water storage tissues, such that some, clearly "succulent" taxa, may not even have especially high relative capacitance values, instead relying on high absolute capacitance from the total volume of storage tissues of the individual (e.g., North American *Agave deserti*, Calkin and Nobel 1986; and *Ferrocactus acanthodes*, Hunt and Nobel 1987).

The ability to hold changing volumes of stored water (capacitance) involves a certain amount of elasticity in the cell wall. Succulent cells or tissues, such as specialized hydrenchyma cells, tend to have high values of C (Ogburn and Edwards 2010), and will take up or lose large volumes of water for a given change in $\psi$, relative to cells or tissues that have lower values of C. Table 5.1 shows C values for representative species.

Succulent tissues are able to gain or lose relatively large volumes of water across small gradients in water potential. Ecologically this means that for a given volume lost, succulent tissues maintain relatively high water potentials, allowing them to prolong photosynthetic activity in periods of drought. Moreover, differences in capacitance between neighboring cell types, for example between "high-C" (high capacitance) water storage tissues and lower-C chlorenchyma tissues within a leaf, can generate a passive mechanism ensuring transfer of water from storage tissues to actively photosynthesizing cells (Ogburn and Edwards 2012).

Water potential is a measure of the free energy of water; it is central to plant water relations for two reasons. First, water spontaneously moves from adjacent regions of high to low $\psi$, and gradients in $\psi$ throughout the plant provide the driving force for the movement of water along the soil–plant–atmosphere continuum. Second, $\psi$ decreases as plant tissues desiccate, so the assessment of $\psi$ also gives a general indicator of tissue water status (or stress) (Ogburn and Edwards 2010). Plant water potential has two components: Osmotic potential ($\psi$ osmotic), which is a negative quantity determined by solute concentration; and turgor pressure potential ($\psi$ turgor), determined by the pressure of the protoplast against the cell wall, which is equal and opposite to the wall pressure (the reciprocal positive pressure of the cell wall on the protoplast): $\psi$ = $\psi$ osmotic + $\psi$ turgor.

In fully hydrated tissues these two components are balanced and tissue $\psi$ is usually at or near zero, with the exception of halophytes, which have very low values of $\psi$ osmotic even when fully hydrated and thus may never reach total $\psi$ of zero (Ogburn and Edwards 2012). As tissues dehydrate, $\psi$ osmotic and $\psi$ turgor both drop with decreasing water content. The drop in $\psi$ osmotic is due to increasing solute concentration (that is *decreasing* water, or solvent concentration), and the drop in $\psi$ turgor is due to diminishing turgor pressure. Periodically measuring $\psi$ during tissue dehydration and graphing values as a function of relative water content, RWC (RWC = $\Delta V$ /V) produces a characteristic curve known as a pressure–volume curve

**Table 5.1** Hydraulic capacitance values for some Middle Eastern plants (after Ogburn and Edwards 2010, used with permission).

| Taxon | Organ | Relative capacitance ($MPa^{-1}$) | ε (MPa) | SI | Method used |
|---|---|---|---|---|---|
| *Sabal Palmetto* | Leaf | 0.007 | | | Pressure bomb |
| *Hemizonia luzulifolia* | Leaf | 0.08 | | | Thermocouple psychrometer |
| *Ferocactus acanthodes* | Stem | 0.11 | | | Pressure bomb |
| *Polypodium phyllitidis* | Leaf | 0.14 | | | Psychrometer |
| *Limeum africanum* | Leaf | 0.16 | 7.5 | 11.18 | Thermocouple psychrometer |
| *Polypodium crassifolium* | Leaf | 0.17 | | | Psychrometer |
| *Mollugo verticillata* | Leaf | 0.17 | 8.2 | 9.59 | Thermocouple psychrometer |
| *Mirabilis nyctaginea* | Leaf | 0.18 | 6.5 | 8.24 | Thermocouple psychrometer |
| *Lycium californicum* | Leaf | 0.18 | 4.1 | | Thermocouple psychrometer |
| *Arthrocnemum subterminalis* | Leaf + Stem | 0.23 | 3.16 | 11.87 | Thermocouple psychrometer |
| *Talinum triangulare* | Leaf | 0.28 | 3.23 | 15.4 | Thermocouple psychrometer |
| *Suaeda taxifolia* | Leaf | 0.3 | 2.56 | 17.52 | Thermocouple psychrometer |
| *Rhipsalis baccifera* | Stem | 0.45 | | | Psychrometer |
| *Epiphyllum phyllanthus* | Stem | 0.55 | | | Psychrometer |
| *Hemizonia luzulifolia* | Leaf | 0.68 | | | Thermocouple psychrometer |
| *Argyroxiphium grayanum* | Leaf | 0.7 | | | Thermocouple psychrometer |
| *Portulaca oleracea* | Leaf | 0.79 | 0.9 | 16.92 | Thermocouple psychrometer |
| *Ferocactus acanthodes* | Stem | 0.81 | | | Psychrometer |
| *Opuntia acanthocarpa* | Stem | 0.96 | | | Psychrometer |
| *Opuntia basilaris* | Stem | 1.04 | | | Psychrometer |
| *Sabal Palmetto* | Stem | 1.07 | | | Vapor pressure osmometer |
| *Anacampseros lanceolata* | Leaf | 1.14 | 0.62 | 53.27 | Thermocouple psychrometer |
| *Echinocereus engelmannii* | Stem | 1.35 | | | Psychrometer |
| *Opuntia ficus-indica* | Stem chlorenchyma (droughted) | | 0.97 | | Psychrometer |
| *Opuntia ficus-indica* | Stem chlorenchyma (well-watered) | | 0.85 | | Psychrometer |
| *Opuntia ficus-indica* | Stem hydrenchyma (droughted) | | 0.37 | | Psychrometer |
| *Opuntia ficus-indica* | Stem hydrenchyma (well-watered) | | 0.34 | | Psychrometer |

(P–V curve) which can effectively document plant water responses to changing conditions (see Tyree and Hammel 1972).

While succulence and its physiological consequences have often been estimated using parameters derived from P–V curves, applying this technique to succulent tissues is difficult, time consuming, and generally not suitable for large datasets. Ogburn and Edwards (2012) analyzed P–V curves on leaves of 25 taxa from across the succulent order Caryophyllales, and compared results with direct measures of saturated water content (SWCmeas), the ratio of water mass at full saturation to tissue dry mass for the same taxa. SWCmeas was significantly related to relative capacitance, the most physiologically relevant parameter describing tissue succulence.

Ogburn and Edwards developed a linear model describing SWCmeas as a function of relative capacitance and leaf volume; this was also supported

when accounting for the phylogenetic relationships among taxa. These results suggest that SWCmeas is a suitable proxy for succulence, and that both cellular properties and variation in gross morphology contribute toward a plant's relative water storage capacity. Ogburn and Edwards argue that quantifying SWCmeas across succulent taxa offers a useful avenue for exploring the evolutionary dynamics of this important ecological adaptation; use of SWCmeas may also provide an effective tool for measuring plant responses in the field.

### 5.2.1 Succulence and altitudinal differentiation in Yemen's Haraz Mountains

A useful transect which focused on the presence of succulents in the Haraz Mountains was reported by Ricanek and Hanacek (1998). Starting on the steep cliffs and other rocky habitats at the highest parts of the Haraz, in Yemen, the only succulents present belonged mainly to the Crassulaceae, Mesembryanthemaceae, or Aloaceae, and included for example many massive specimens of *Aloe rubroviolacea*. Succulent asclepiads and euphorbias do not tend to survive in the high-altitude parts of Yemen, such as in the Haraz west of Sana'a, where some peaks reach *c*. 3000 m. However, these high altitude sites *do* include the only *Aeonium* representative growing outside of the Macaronesian[4] area—*Aeonium leucoblepharum*, a disjunct member of the Crassulaceae (= *Sempervivum leucoblepharum*) (Ricanek and Hanacek 1998).

Moving down the Haraz Mountains, Euphorbias begin at *c*. 2600 m, with the candelabra-like *Euphorbia ammak*, more than 2 m tall, and a little lower down, large populations of *Euphorbia cactus* and *E. parciramulosa* dominate the vegetation. At *c*. 2000 m, Ricanek and Hanacek recorded clumps of *Euphorbia fruticosa* and at Wadi Al-Hadud several stapeliad members of the Asclepiadiaceae, including *Caralluma cicatricosa, Caralluma* cf. *wissmannii, C. penicillata*, and *Sarcostemma forskaolianum*. On shady, rocky outcrops some less common succulents including *Carulluma deflersiana, C. shadhbana, Rhytidocaulon macrolobum*, and *Ceropegia* species were observed.

[4] See too Sections 3.3 and 7.9.

Lower down in the foothills of the Haraz, *Euphorbia inarticulata* and *E. cactus*, along with the striking "desert rose," *Adenium obesum* (Apocynaceae), with swollen stem bases (or caudices) ranging from 10 to 50 cm in diameter, occur among the dominant Acacia trees. Another stem succulent was *Adenia venenata*, with its distinctive bottle-shaped stem. *Sansevieria ehrenbergii* (and to a lesser degree *S. abyssinica*) made up the rest of this region's succulent vegetation.

Succulent asclepiads found along the baking hot Yemeni coastal Tihamah, included *Caralluma shadhbana* and *C. sinaica*, both growing near Al-Barh, a town that was once an important coffee port but is now a tiny village on the Red Sea coast (Ricanek and Hanacek 1998).

## 5.3 Succulence and sclerophylly, foliage angles, and other strategies for dealing with drought

Although succulence is first noted in terms of gross anatomy—fleshy leaves and stems, etc., the *physiology* of succulence is happening mostly at the cellular level.[5] The cells of highly succulent tissues have taken water storage to an extreme, producing enlarged vacuoles that can occupy 90% or more of cell volume (Gibson 1982; von Willert et al. 1992). In many taxa apoplastic[6] mucilage (Nobel 1988; Nobel et al. 1992) or special pectic compounds (Carlquist 1974) can contribute to extracellular water storage.

Sometimes photosynthetic organs also contain an internal, non-photosynthetic parenchyma tissue, with a high water storage capacity (Gibson 1996). Succulent species typically have a relatively low "specific leaf area" (SLA: the extent of light-catching surface area per unit photosynthetic dry

[5] Development of a large cell vacuole, capable of storing water and other substrates, was an early and important event in the evolution of land plants (Becker 2007). This facilitated water homeostasis and buffered the plant against vagaries of an external water supply (Larcher 2006).

[6] This is the free diffusional space *outside* the plasma membrane. It is interrupted by the Casparian strip in roots, by air spaces between plant cells and by the plant cuticle. Structurally it is a continuum of cell walls of adjacent cells as well as the extracellular spaces. Moreover the "apoplast" forms a tissue level comparable to the "symplast."

mass), along with high leaf thickness and high leaf water content. Vendramini et al. (2002) analyzed associations among these three traits as indicators of water use strategy in 77 species from drylands in central-western Argentina, where succulent species are common. In addition to looking at succulent species they also looked at *sclerophyllous* species, which have "tough," "fibrous," or "leathery" leaves as an adaptation to drought.

Vendramini and colleagues found that both sclerophyllous and succulent species had low values of specific leaf area, but that this was accompanied by low values of leaf water content in sclerophyllous species and high values in succulent species. When all species were considered together, leaf area and water content were not significantly correlated. All high-SLA tender-leafed species showed high leaf water content (LWC). Low SLA, however, was associated with *both* low LWC (i.e., sclerophyllous species) and high LWC (in the case of the succulents). When succulents were excluded, the association between SLA and LWC was significant and positive.

Thus specific leaf area and leaf thickness—but not leaf water content—were significantly correlated with a species' score along a multivariate axis of plant resource-use strategy. Vendramini et al. suggested that because of its straightforward ecological interpretation and applicability across floras, SLA would be a prime attribute for inclusion in any future, large comparative flora databases.

Succulence and sclerophylly are clearly two quite different ways of dealing with low water availability, with succulents being more dependent on—or better able to take advantage of—relatively sudden *pulses* of water supply (Schwinning and Ehleringer 2001). However, the two traits represent converging strategies in terms of carbon assimilation and nutrient conservation—both succulence and sclerophylly are associated with significant allocation to storage and defense, at the expense of additional growth (Vendramini et al. 2002).

Evergreen, sclerophyllous species living in dry and nutrient-poor habitats tend to have thicker or tougher leaves than species from more favorable conditions. They also converge toward higher leaf mass per unit area, which requires greater investment per unit leaf area, and also a more rapid response to water stress (Niinemets 2001). In a group of Australian dryland species, Cunningham et al. (1999) found that leaves tended to become thicker, denser, and narrower along gradients of both decreasing rainfall and decreasing soil phosphorus content. This was consistent with worldwide correlations of specific leaf area, photosynthetic capacity, and leaf longevity documented by Reich and Walters (1992) and Reich et al. (1997).

Sclerophyllous leaves are advantageous under a wide range of environmental conditions, and much debate has concerned whether sclerophyllous leaves—with their thick cross-sections, thick cell walls, and abundant mechanical tissue—are primarily an adaptation to *drought*, or low soil nutrient levels, or to both (see, e.g., Chabot and Hicks 1982; Salleo et al. 1997).

Under the hypothesis that morphological and physiological features of a plant should change as a function of its location on a water deficit gradient, Barchuk and Valiente-Banuet (2006) predicted that with increasing water stress, leaf orientation (away from the horizontal) would be greater and mean values of the leaf mass per unit area (that is, specific leaf mass) would increase with the gradient.

These leaf traits were compared in an investigation of *Aspidosperma quebracho-blanco* (Apocynaceae) at three locations along a water deficit gradient, extending from humid chaco vegetation, or plains, through semi-arid chaco to the arid chaco of Argentina (crossing a rainfall gradient from 350 to 1200 mm). Plants in the study showed a variable phenotypic response in leaf-angle distribution and leaf-mass per unit area, in response to the gradient in water deficit.

Foliage angle distribution is likely one of the most important components of canopy architecture, affecting as it does both direct and diffuse light penetration into the canopy, as well as water loss by transpiration. In many species the time stomata are open during the day is reduced to diminish water loss, but this can increase leaf temperature and would also reduce daytime $CO_2$ uptake. There is an obvious trade-off between energy gain through photosynthesis and water loss through transpiration; some species optimize that tradeoff by reducing the interception of solar radiation (and evapotranspiration) by orienting their leaves at angles that depart from the horizontal.

Falster and Westoby (2003) provided the first wide-ranging cross-species evidence that steeper leaf angles reduce exposure to excess light levels during the peak of the day, despite the theoretical advantage of being horizontal and, in theory, maximizing carbon gain.

## 5.4 *Degrees* of leaf, stem, and caudex succulence

It is estimated that about 4% of all Angiosperms are succulents, and it features as a habit for a great many Middle Eastern species (see Figure 5.3). It is clearly a successful strategy for resisting periodic drought and has evolved separately on multiple occasions, occurring in at least 30 out of some 50 Angiosperm orders (Eggli and Nyffeler 2009).

According to Mies and Beyhl (1998), Yemen's large island of Socotra is home to a wide range of succulent forms. These include leaf succulents (*Aloe* spp., *Kalanchoe* spp.), "green" stem succulents (*Caralluma* spp., *Euphorbia* spp., *Cissus* spp., *Kleinia scottii*), and "caudiciform" succulents, which have developed the caudex—a massively enlarged portion of the stem axis and in some cases the roots—toward water storage (*Adenium socotranum, Dendrosicyos socotrana, Dorstenia gigas, D. socotrana*). The thickened, swollen stems of *Boswellia* spp., *Dracaena cinnabari, Euphorbia arbuscula*, and *Sterculia rivae* all serve as water reservoirs. The Socotran Federbush, *Euphorbia balsamifera* ssp. *adenensis* accumulates water in its short, thick stem caudex. Mies and Beyhl described formation of a caudex as an *especially* Socotran form of succulence. The swollen

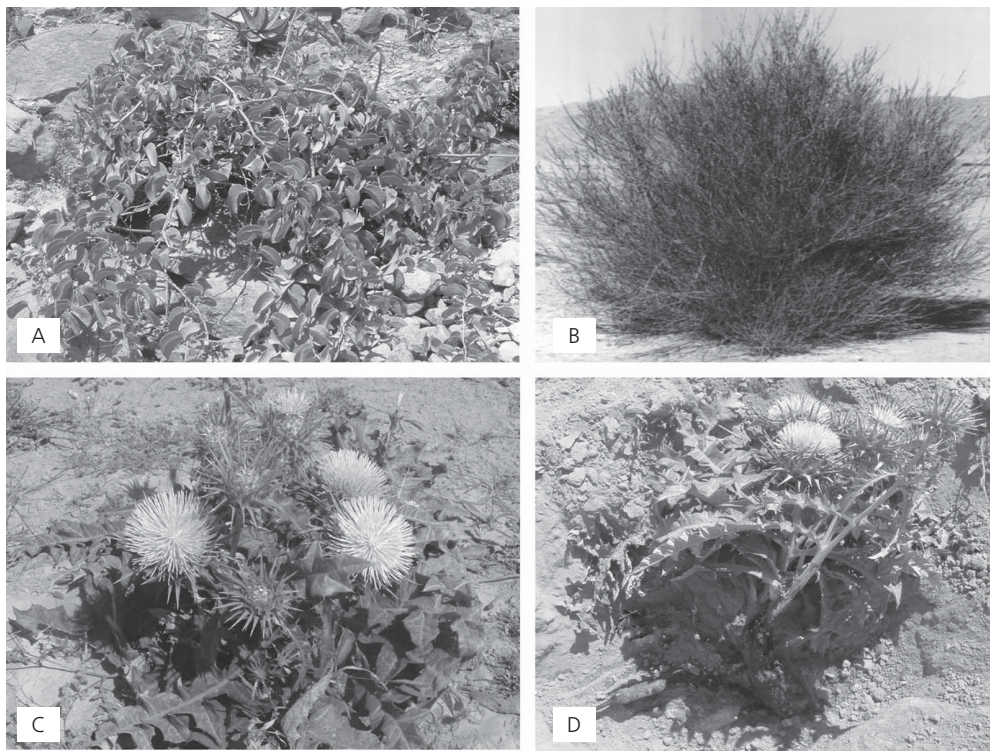



**Figure 5.3** (A) The stem and leaf succulent *Cissus quadrangularis* (Vitaceae) from the Abha Mountains, Saudi Arabia. (B) The extremely deep-rooted perennial shrub *Leptadenia pyrotechnica* (Asclepiadaceae) from Eastern Desert of Egypt. (C) *Cynara cornigera* (Asteraceae) from northwestern Egypt. (D) Exposed swollen succulent root of *Cynara cornigera.* [For a color version of this figure, see the color plate section, Plate 10]

root, hypocotyl, and epicotyl form a large water storage organ (e.g., the "bottle" trees). This gives a very unusual but characteristic appearance known technically as "pachycauly" to these plants. The wild artichoke (*Cynara cornigera*, Asteraceae) that grows in northwestern Egypt and in the southern part of Al-Akhdar mountain landscape of Libya, even has fleshy, succulent roots (see Figure 5.3).

Succulence is more commonly found in plants of semi-desert or semi-arid scrub communities than in extremely dry environments (Shmida 1985). The length of time between precipitation events appears to be limiting to highly succulent species, which need to be able to renew their water stores periodically. Succulent taxa tend to become less abundant as dry seasons become longer. There is also a gradient in terms of growth form, with stem and root succulents in general persisting longer along such dry-season gradients than leaf succulents (see von Willert et al. 1992).

All dryland plants (both as individuals and species) must persist in one way or another through periods of drought. Succulence is an evolved response to seasonally dry climates, though it is often only a matter of *degree* or extent of physiological response that distinguishes a population (see Eggli and Nyffeler 2009). Many authors have recognized a continuous gradient of increasing succulence *within* species as conditions become more xeric. Thus authors include descriptions like "leaves are more than usually fleshy" and plants in a particular species may have a "complete series of life forms present, from mesophytes . . . to highly xerophytic succulents" (Eggli and Nyffeler 2009). Clearly if a continuum in succulence can be observed within a single species, there is no distinct or categorical separation between succulence and non-succulence.

### 5.4.1 Drought survival strategies

Various drought survival strategies have been described and there exists a welter of jargon, which has all been usefully reviewed by Eggli and Nyffeler (2009). We follow Ogburn and Edwards (2010) in using the spectrum of "drought tolerance" through "drought avoidance" as a backdrop to considering these strategies.

Tolerance and avoidance relate directly to the experience and response of cells and tissues during drought, primarily at the site of photosynthesis. While persistence in dryland environments is commonly seen as requiring drought tolerance, at the *cellular* level any detrimental effects of drought may be largely avoided (and for most life forms staying alive is *ultimately* cellular). Drought-avoiding succulents, with their considerable water stores, are often able to do just that. They essentially amortize their total water resources, bridging and smoothing the variance in external supply.

Desert ephemerals show another approach to drought avoidance by quickly completing their short, "fast and furious" life cycles from germination through reproduction to death, within a brief window of environmental opportunity (see Section 5.9.1). There are trade-offs involving traits that promote such rapid growth and reproduction and other traits relating to tolerance of water and heat stress in the desert (Smith et al. 1997). Thus many desert ephemerals have high stomatal conductance enabling rapid growth when moisture is available, yet such a trait is highly maladaptive in dry conditions (which the desert ephemeral survives as a seed).

Drought avoidance also occurs in woody perennials. Deep-rooted plants or "phreatophytes" like *Prosopis glandulosa* (Fabaceae), and the perennial shrub *Leptadenia pyrotechnica* (Asclepiadaceae) (see Figure 5.3), have adapted to aridity by producing extremely deep root systems that access more moist soil horizons or tap in, even deeper, to the water table, thereby avoiding direct effects of local drought (see Smith et al. 1997). Batanouny and Abdel Wahab (1973) investigated the root system of *L. pyrotechnica* in Egypt's Eastern Desert. The roots of a 1.6 m tall shrub were found to penetrate to a depth of 11.5 m, while lateral roots extended for up to 10 m. Given the extent of this rhizosphere and the moisture content of the soil, the water available for exploitation by this individual was estimated to be about 23 000 liters. Annual water output from this shrub was estimated at 5700 liters, suggesting the water available in the soil occupied by the root system would, in theory, be enough to supply the plant for a period of four years without additional contributions from rainfall. Of course in reality the

interaction between moisture and roots is more complex, and soil moisture may be recharged from rain falling elsewhere in the watershed. Perhaps the most striking aspect of this study is the considerable investment this shrub makes in root biomass as opposed to stem biomass, which only underscores the significance of water to individual survival.

Species of *Tamarix* also have deep and extensive rooting, and Danin (1999) suggested that the distribution of *Tamarix* trees could be used as an indicator of deep water reserves. Likewise, Chatterjee and Bhaskar (1977 [cited in Shukla and Chandel 1989]) listed other plants and plant communities as ecological indicators of ground water, in Indian deserts. These (with typical rooting depths) included *Euphorbia caducifolia* (12–18 m), *Salvadora persica–Tamarix* species (6 m), *Salvadora oleoides–Prosopis cineraria* (10–20 m) and *Crotalaria burhia–Leptadenia pyrotechnica* (6–20 m).

Another effective tactical response to dry conditions is to be "drought deciduous," facultatively dropping leaves during dry periods. This occurs in many perennials, such as the shrub *Encelia farinosa*.

"Avoidance" strategies such as these involve either tolerating high levels of cellular desiccation and low water potentials (as seen in extremely *poikilohydric*[7] taxa, and evergreen shrubs) or avoiding unfavorable periods through tissue dormancy (drought-deciduous shrubs). In contrast *succulence* generally confers an ability to avoid drought at the cellular level while still maintaining metabolic activity, through having the stored water *available* for access during the driest periods.

[7] According to Evenari (1985), *homoiohydric* plants maintain their water status at the cellular level within a very narrow range, and rapidly experience irreversible cell damage followed by subsequent death, whereas *poikilohydric* plants equilibrate their water content with that of the environment. They can even dry out completely, at which point they enter a state of "anabiosis"—see Evenari (1985)—yet they can continue to live and grow when rewetted (e.g., as seen in lichens, and *Selaginella* spp.). Relatively few Angiosperms appear to have this ability. The tactic of *poikil*ohydric metabolism can be switched on and off multiple times in reaction to availability of water. "Tolerance," in contrast, is largely due to modifications at the cellular and metabolic levels. Tolerance of the effects of water shortage is seen in terms of increased desiccation tolerance and is exemplified by poikilohydric "resurrection plants."

Succulent plants often have thick water-storing tissues in their main photosynthetic organs, letting photosynthesis continue while avoiding desiccation when the soil is dry. Although some of the best-known succulent plant families are phylogenetically close (e.g., Cactaceae, Chenopodiaceae, Aizoaceae, and Portulaceae are all in the order Caryophyllales) succulence is, as mentioned, widespread and appears in various unrelated clades (see APG 2003 2009; Eggli and Nyffeler 2009).

*Stem* succulence (and the so-called cactus life form) provides a fine example of convergent evolution (Eggli and Nyffeler 2009; Niklas 1997). Many of these plants develop swollen storage organs that contain nutrient and water reserves and are able to survive, where other plants would die in the drought. Stem succulence is widespread, occurring in about 4000 species, which is about a third of all succulents (Eggli and Nyffeler 2009).

It is often stated that many succulents use Crassulacean acid metabolism (CAM) but as Eggli and Nyffeler (2009) pointed out, although CAM is the most common photosynthetic adaptation associated with succulence, succulence is not exclusively connected with any particular photosynthetic pathway; indeed all known pathways (C3, C4, and CAM; see Section 5.5) occur in different species of succulents.

Depending on species, most of the different kinds of stem tissue may be involved in specialized water storage. This includes (working from the center outward): the pith, xylem (wood), cortex, phelloderm (if present), hypodermis (if present), epidermis in dicots, and primary parenchyma in monocots. The sheer array of structural solutions for water storage is impressive and surely indicates the power of this selection pressure (see many examples in Eggli and Nyffeler 2009).

Over the years there has been some debate over whether caudiciform and pachycaul plants, with their swollen stem bases or trunks, should be regarded as succulents. Gibson (1996) concluded that the heterogeneous assemblage of caudiciforms and pachycauls—specializing in water storage primarily or exclusively in the stem or stem-root axis—were indeed succulents; Newton (2006) in his survey recommended that caudiciforms and pachycauls should be regarded as "honorary succulents," together with bulbs and orchids.

Today the poster children of pachycauls include the ancient bottle trees of Socotra and the Horn of Africa; several *Adansonia* species—the Baobabs; the Malagasy *Moringa* species; and in the southwestern United States the Elephant trees (*Bursera microphylla*). Bottle trees are a remarkable and striking feature of the Middle Eastern and African landscape. Various succulent tree species live on Socotra, most of them endemic to the island. The "giant" bottle trees include the following:

*Adenium socotranum* (= *A. obesum* ssp. *socotranum*) of the periwinkle family, Apocynaceae, is prevalent on lower mountain slopes of Socotra. Like other members of the family these trees produce whitish, irritating or poisonous latex. This 'milk' likely protects against browsing animals as it contains a number of alkaloids and is exuded from cuts or wounds (Mies 1999). The phenology and cycles of flowering and growth of *A. socotranum* seem well adapted to the climate, in that it flowers after the rainy season in March and April and only when they are well past flowering do the fruits release their airborne seeds, leaving them then to be dispersed by the heavy storms of the southwest monsoon. Then the seasonal drought begins with—as estimated by one expert, Bruno Mies—perhaps a million *Adenium* specimens on Socotra waiting for the next rainy season (Mies 1999).

*Dendrosicyos socotrana*: The cucumber tree (Cucurbitaceae) belongs to a striking endemic genus in Socotra. Individuals exhibit gigantism, reaching a height of 5 to 6 m (this is the only tree in the family). According to Mies (1999), this species was once very common and well established in the island's *Croton socotranus* bushland in the alluvial plains, but it has become very rare as a result of persistent overgrazing by domestic animals. Its white bark reflects radiation, reducing over-heating (Mies and Beyhl 1998). Mies reported only small numbers of specimens remaining in the limestone screes of coastal escarpments, associated with the then still common *A. socotranum,* and suggested *Dendrosicyos* represented an unhappy example of local extinction of a once more-widespread regional species.

## 5.5 Dryland photosynthetic variability

Most succulent plants are perennial, with water content of 90% or more in fully hydrated tissue. They also often have Crassulacean acid metabolism as their main photosynthetic pathway (Gibson 1996). Accordingly their photosynthetic organs consist of chlorenchyma (photosynthetic cells containing chloroplasts); these are large, rounded cells that have a large vacuolar storage space available to hold carboxylic acids and water. The presence of these conspicuous vacuoles and large intercellular air spaces results in comparatively few chloroplasts per unit surface area (Kluge and Ting 1978).

CAM is a photosynthetic mode common in drought-avoiding succulent plants, as well as some aquatic plants that experience severe diurnal variation in $CO_2$ availability (Keeley and Rundel 2003). CAM is essentially a modification of the standard C3 photosynthetic pathway.

In CAM photosynthesis, stomata open at night to collect $CO_2$ and store it as malate ($C_4H_4O_5^{2-}$). This in turn is used as a source of $CO_2$ for photosynthesis in the day, when stomata are closed to reduce evapotranspiration. The first step of $CO_2$ fixation is carried out by the enzyme phosphoenolpyruvate (PEP) carboxylase. $CO_2$ forms 4-carbon compounds, mostly molecules of malate, stored in the enlarged vacuoles. During the day these 4-carbon acids are shuttled to the chloroplast, where they get decarboxylated. The released $CO_2$ is then refixed by RuBisCO (ribulose-1, 5-bisphosphate carboxylase oxygenase, the initial enzyme of the photosynthetic Calvin cycle, and the compound regarded as the single most abundant protein on Earth). Synthesis of sugars then proceeds via the regular C3 pathway. CAM significantly increases a plant's *water-use-efficiency* (the ratio of carbon fixed photosynthetically to water lost through transpiration), compared to those of the C3 and C4 pathways because nocturnal evapotranspiration is lower, while the $CO_2$ gradient remains largely unchanged.

In C4 photosynthesis (i.e., using the so-called Hatch-Slack metabolic pathway) $CO_2$ is fixed by PEP carboxylase in the daytime, mainly in peripheral green mesophyll tissue. The malate produced is moved to green cells of the bundle sheaths where it is decarboxylated and the $CO_2$ produced is refixed

and assimilated via RuBisCO. Because PEP carboxylase has a *c*. 60-fold greater affinity for $CO_2$ than does RuBisCO, this overall process results in an approximately six- to eight-fold increase in the $CO_2$ concentration in bundle sheaths compared to the air outside.

A conspicuous trait of C4 plants is the so-called Kranz anatomy in which the green cells involved in C4 photosynthesis become more differentiated as green mesophyll tissue and bundle sheaths. In contrast the Kranz cells are not green but contain chlorophyll-free plastids that can transform malate into other carbohydrates. This anatomy is typical for many grasses and members of the Amaranthaceae.[8]

CAM is a particularly *flexible* photosynthetic system, in terms of both degree of expression and pathway variations found in different species. While some taxa, such as the major clades of cacti, are considered obligate CAM plants, many other taxa exhibit facultative CAM in response to drought, switching back to C3 photosynthesis when the stressor is removed (Kluge and Ting 1978). Winter et al. (1978) described this phenomenon in *Mesembryanthemum crystallinum*.

In other species CAM may be irreversibly induced by drought or salt stress, or simply as a function of ontogeny (Ogburn and Edwards 2010). CAM "cycling" is another adaptation, where $CO_2$ from cellular respiration is internally recycled for photosynthesis. An example is *Talinum calycinum* (Portulacaceae) from rocky outcrops in Missouri. Martin et al. (1988) showed that plants could adjust the level of $CO_2$ recycling in response to temperature and drought stress, and were able to conserve from 5 to 44% of daily water loss through the process.

Patterns of carbon isotope distribution in plant bulk tissues, and in particular in leaf waxes, are often used to evaluate the relative use of different carbon fixation pathways across species. According to Feakins and Sessions (2010), C3 species (using the standard "Calvin-Benson" cycle) produce leaf wax *n*-alkanes that have $\Delta^{13}C$ values of *c*. –35, while C4 plants, using the Hatch-Slack pathway, generate values of –20. Succulent plants capable of CAM have extremely variable $\Delta^{13}C$ values for bulk tissue, but typically intermediate between those of C3 and C4 species, possibly reflecting the facultative nature of this metabolism.

There is ample evidence that CAM-capable species use CAM or C3-like pathways to varying degrees (Osmond et al. 1989). Feakins and Sessions characterized patterns of hydrogen isotope fractionation during biosynthesis of leaf wax *n*-alkanes in CAM-capable plants. They measured stable carbon- and also hydrogen isotopic compositions ($\Delta^{13}C$ and $\Delta D$ [Deuterium], respectively) of individual *n*-alkanes in 20 succulent species from around the world. They assessed interspecific differences in net deuterium/hydrogen fractionation between source water and leaf wax products, with plants grown under greenhouse conditions and irrigated with water of constant Δ-Deuterium value. They reported a wide (*c*. 90%) range of $\Delta D$ values between species, from –193‰ to –107‰.

Two results seem clear. First procedurally, given the flexible metabolism of CAM-capable species, both carbon *and* hydrogen isotope measurements can be used to assess the amount of CAM occurring, and therefore to infer climatic conditions based on the interpretation of hydrogen isotopic fractionation. This could be useful in paleoenvironmental reconstruction of environments like those in the Middle East, where many species are CAM-capable. Second, compound-specific measurements by Feakins and Sessions revealed the same pattern of hydrogen isotopic enrichment as observed in CAM cellulose (compared to that in C3 plants) was also found in individual leaf wax compounds (*n*-alkanes). This suggests a common metabolic pathway associated with the photosynthetic flexibility of CAM plants is also involved in hydrogen isotopic enrichment.

## 5.6 Spinescence (and keeping the grazers at bay)

Many Middle Eastern plants are a tough, thorny lot. Lev-Yadun (2003) among many others has argued that over the past several millennia the vegetation of the Middle East has suffered a continuous and increasing selection pressure from grazing animals,

[8] APG III (2009) combined the former Chenopodiaceae and Amaranthaceae families into a new, enlarged family Amaranthaceae.

especially domestic livestock. Under these conditions thorny plants, which were consumed less than undefended ones, became more common (and see Zohary 1962). Sheep, goats, and cattle are the major Middle Eastern grazing mammals, while horses, donkeys, and camels have been of mostly secondary importance (Sasson 1998, and see Section 10.3).

Ecologists envision a kind of trophic dance involving plants and the animals that eat them. This is a kind of ongoing "arms race" in which, over evolutionary time, plants are selected to develop better defenses while herbivores adapt to partly or fully overcome them. On the plant side, species have evolved an extensive array of both chemical (see Chapter 8) and morphological defenses. Spinescence—which is the production of spines (botanically, a sharp part of a leaf), thorns (a sharp stem/branch), and prickles (a sharp emergence from the cortex)—acts against grazers by wounding an animal's mouth-parts and digestive system (e.g., Janzen 1986; Myers and Bazely 1991). Spines may also inject pathogenic bacteria and fungi into large herbivores (Lev-Yadun and Halpern 2008). In general, spinescence not only slows the rate of feeding in the canopy of a spiny-leaved plant by reducing the size of ingested parts, but also provides overall advantage to such plants over non-defended ones (Ronel et al. 2010). (This effect may *also* protect otherwise palatable species growing under or within the canopy, a benefit that is sometimes interpreted as facilitative; see Section 4.7).

Spiny plants are more abundant in arid than humid regions (e.g., Carlquist 1974; Grubb 1992; Shmida 1981). Ronel et al. (2010) compared the flowering phenology of spiny and non-spiny native species from three major families in Israel (Asteraceae, Fabaceae, and Lamiaceae). These families include the highest numbers of spiny species in the flora of Israel. The *peak* of flowering (when the highest number of species flowered) proved to be 4–8 weeks later for spiny species than for non-spiny. The relatively less-defended non-spiny species grow and flower in spring there; spiny plants flower later on, during the hot and dry summer. As a result, spiny plants enjoy a longer pre-reproductive growing season, which may help to offset the costs of producing spines, among other things.

The 195 non-spiny species of Asteraceae had their flowering peak at the beginning of April while the 92 spiny species had it at mid-June. The 270 non-spiny Fabaceae had their peak at mid-April, while the 28 spiny species peaked in mid-May. The 114 non-spiny Lamiaceae peaked at the beginning of May, while the 13 spiny species peaked in mid-May. An overall comparison of all 113 spiny species of these families with all 589 non-spiny species showed that the peak in flowering of the spiny species was at the beginning of May while that of the non-spiny species was in late March.

Ronel et al. argue that—given the nature of the Mediterranean climate (short, mild, and wet winter, and a contrasting long, dry, and hot summer)—the phenological differences in flowering times reflected the interacting effects of climate and herbivory. Spinescence was associated with flowering during a time of greater grazer impact (selectively depleting more palatable species earlier in the season) and greater drought stress. Each growing season, as the summer progresses, any non-spiny and non-poisonous plants gradually disappear due to grazing (Gutman et al. 1990; Noy-Meir 1990). These trends fit the general pattern of greater anti-herbivore investment in slow-growing plants in habitats with limited resources (e.g., Coley et al. 1985).

Ronel and Lev-Yadun (2012) further analyzed associations between life form and plant part/organ and spininess, characterizing the spiny, thorny, and prickly organs in the entire wild flora of Israel (294 such species). Of these, 63.3% defended their reproductive organs (the most-defended part) and 67.0% defended various non-reproductive organs. Ninety-three species defended both their reproductive organs and at least one other part; 48.3% defended leaves; and 36.4% their stems and branches. Spiny wings defended stems and branches only in herbaceous species (annual or perennial).

There were some clear differences among life forms. Annual and perennial herbs mostly defended reproductive organs (96 and 83%, respectively), dwarf shrubs defended mostly their leaves (54%) and shrubs and trees mostly their branches (90 and 76%, respectively). Ronel and Lev-Yadun also noted spine, thorn, and prickle *colors* for 167 species, with yellow, red, orange, and white predominating, supporting hypotheses about spines

being visually aposematic—that is *advertising* their presence.

Early on Harper (1977) proposed that the association of unpalatability with visual signals (as in, e.g., the white leaf-mark polymorphism in *Trifolium repens*) might be responsible for selection of much of the considerable variation in leaf form and variegation. More recently Lev-Yadun (2003) described the rosette and cauline leaves of the highly thorny winter annual, *Silybum marianum* (Asteraceae), as resembling "green zebras" due to the variegation. Lev-Yadun reported significant correlation between spininess and the strength of white–green variegation and suggested this was a special, plant case of aposematic, or warning coloration.

Lev-Yadun and Ne'eman (2004) developed this notion in their analysis of grazed areas across the Negev, in Israel, where like the other deserts of the Middle East, the landscape is largely devoid of green plants during summer. At that time most of the annuals, geophytes, and hemi-cryptophytes are either dormant in the soil or have already been eaten by grazing animals. Many shrubs are summer deciduous or enter summer dormancy with minimal canopy. Lev-Yadun and Ne'eman made a good case for visual signaling by the small number of common plants that are present and green in the desert, during the long, dry summers.

They point out these summer-green species are also typically poisonous or thorny, as protection against grazing. Lev-Yadun and Ne'eman proposed that in arid ecosystems, when most plants are dry or leafless, green color is conspicuous and contrasts with the yellow desert, or leafless background. The green color itself could act aposematically. Certain of the poisonous summer-green plants, e.g., *Calotropis procera, Datura innoxia, D. stramonium, Nicotiana glauca, Ricinus communis*, and *Thymelaea hirsuta*, also have specific strong odors, supporting a hypothesis of *olfactory* aposematism in poisonous plants (Eisner and Grant 1981, and see Lev-Yadun and Ne'eman 2004). This warrants further work.

Finally Lev-Yadun (2001) showed that two types of *conspicuousness* in thorns are typically present in many different species coming from several continents and various families. (1) Colorful thorns; and (2) white spots and stripes, being associated with thorns, leaves, and stems. Both phenomena are highly frequent in the globally spiniest taxon—the Cactaceae—in which *c.* 90% of species have white markings associated with their colorful thorns. Many other examples exist in the genera *Agave* and *Aloe*. In the genus *Euphorbia*, colorful thorns and white or whitish variegation, or white markings associated with thorns, also predominate (Lev-Yadun 2001).

## 5.7 *Euphorbia* and the Middle Eastern cactus niche

A major Middle Eastern genus is *Euphorbia*, a large,[9] widely distributed, highly variable group of species able to survive well in hot and arid conditions. Sometimes Euphorbias are mistaken for cacti, though they originated in Madagascar while cacti are native to the Americas. Although there are many species of *Euphorbia* native to the New World, the reciprocal is not so true for the Cactaceae as only a few members of the family have colonized the Middle East.

One way to distinguish is to cut the plant open. If the liquid inside is clear, it is more likely a cactus. If the liquid is whitish and milky it is a euphorbia (another plant in the family is *Hevea brasiliensis*, the Rubber tree, whose sap is especially thick). The milky latex in *Euphorbia* likely evolved as a deterrent to herbivores,[10] and is generally interpreted as a defense against insect herbivores rather than vertebrates (e.g., Agrawal and Konno 2009).

*Euphorbia* was one of several genera noted by Charles Darwin as having endemic species in the Galapagos (Darwin 1845). Among some eight species of *Euphorbia* collected there by Darwin, seven were confined to the archipelago and no species was found on any two of the islands.

Steinmann and Porter (2002) circumscribed *Euphorbia* as the plant clade including all species with

[9] What makes a genus or family highly speciose? It is worth noting that *Euphorbia* is the fourth largest plant genus anywhere (with 1836 species), and *Croton* (also Euphorbiaceae) is 11th (1223 species). (*Astragalus* is the largest plant genus, with some 3270 species.)

[10] These plants should be handled with caution and any latex on the skin washed off immediately. Members of the family and genus are often referred to as *spurges* from a Middle English/Old French word meaning "to purge," due to use of the plant's sap as a powerful purgative.

"cyathia" or "false flowers" which are really inflorescences made up of bracts, nectar glands, a much reduced female flower, and typically five groups of highly reduced male flowers (and see Section 6.7). They also established the presence of four major sub-clades. Bruyns et al. (2006) formally recognized these as subgenera: *E*. subg. *Esula, E*. subg. *Rhizanthium* (= *Athymalus*), *E*. subg. *Chamaesyce*, and *E*. subg. *Euphorbia*. The genus is extremely diverse in succulent growth forms, and most of the diversity in succulence (in terms of number of species) is found in subg. *Euphorbia* and subg. *Rhizanthium*. Even so, in subg. *Chamaesyce* stem succulence has also evolved independently at least six times.

*Euphorbia* subg. *Euphorbia* is the largest subgenus (> 650 species) and includes the full range of growth form diversity present in the genus—herbs, geophytes, woody shrubs, understory, and canopy trees, stem succulents that range from dwarf shrubs to candelabriform trees, and the unusual growth form of pencil-stemmed plants (e.g., *E. decorsei*). Dorsey et al. (2013) recently showed the subgenus itself to be made up of four highly supported clades, including one early derived New World clade and multiple independent lineages in Madagascar. Old World species are distributed in Africa, Asia, and Madagascar, with most of them in warm, arid climates. Highly succulent photosynthetic stems have evolved in *E*. sect. *Monadenium* and *E*. sect. *Euphorbia*. The defining character for this latter clade is the spine-shield—a horny pad of tissue subtending or surrounding each leaf base, typically bearing two or four spiny outgrowths.[11]

Dorsey et al. concluded the evolutionary "switch" to stem-based (rather than foliar) photosynthesis, as happened in *E*. sect. *Euphorbia* and in all the pencil-stemmed species, likely involved several steps. These included an increase in stem stomatal density, delaying or abandoning bark initiation, increasing the volume of cortex for water storage, and development of the CAM system (see, too, Edwards and Donoghue 2006; Nobel 1988).

Dorsey et al. argued that given the frequency with which stem-based photosynthesis has evolved in *E*. subg. *Euphorbia*, these may be relatively "easy" transitions in this group. Edwards and Donoghue (2006) showed in Cactaceae that *Pereskia* species—believed to be the closest relatives to the core cacti—have high water use efficiency and some level of CAM photosynthesis. This may have been "pre-adaptive" for the transition to the succulent-stemmed cactus life form. CAM has been inferred in most stem photosynthetic species (in *E*. subg. *Euphorbia*), but close relatives of the pencil-stem species all have C3 metabolism (Horn et al. 2012), suggesting CAM is not a necessary prerequisite for the evolution of highly succulent, photosynthetic stems.

Subgenus *Esula* includes approximately 400 herbaceous and shrubby species primarily distributed in temperate regions of the Northern Hemisphere. Southwestern Asia and the Iranian highlands are major centers of diversity in *E*. subg. *Esula* sect. *Paralias*. In Iran nearly all of the rare and endangered, endemic, and complex *Euphorbia* species belong to this subgenus (Pahlevani et al. 2011).

Phylogenetic reconstructions suggest that Macaronesian species of *E*. subg. *Esula* section *Aphyllis* have their closest relatives in the Horn of Africa, southern Africa, and the southern Arabian Peninsula (see Figure 5.4) (Barres et al. 2011). Recent molecular dating puts the time of split between African–Arabian and Macaronesian species at *c*. 5 Ma. Barres et al. (2011) argue this supports a vicariance scenario, where the aridification that occurred during the late Miocene–Pliocene in northern Africa was an important ecological barrier. The arid belt would have fragmented the formerly continuous subtropical flora in this area and left two relict distribution centers in refugial areas, explaining the present disjunct distribution of sect. *Aphyllis* (and see Section 7.9, on Socotran *Euphorbia*).

*Euphorbia* subg. *Chamaesyce* is the second most species-rich subgenus, with around 600 species. It includes the largest New World radiation within this otherwise Old World-centered genus. The subgenus is well known for its leafy, non-succulent ornamentals including the Christmas Poinsettia (*E. pulcherrima*), one of the most profitable potted plants in the world. *E.* subg. *Chamaesyce* is highly diverse in growth forms, including annual and

[11] These are usually interpreted anatomically as a pair of stipular spines and a pair of prickles (Carter 1994).

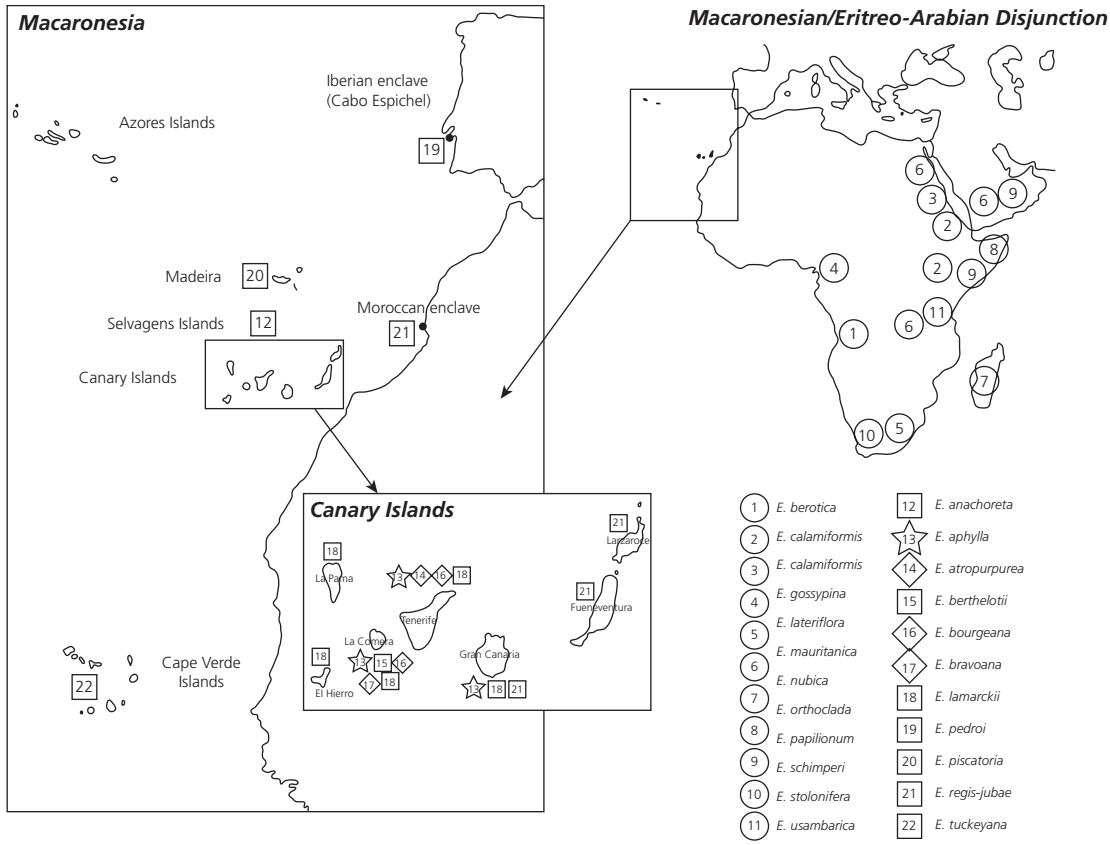



**Figure 5.4** Molecular phylogeny of *Euphorbia* subg. *Esula* sect. *Aphyllis* (Euphorbiaceae) inferred from nrDNA and cpDNA markers with biogeographic insights. The traditional groups previously considered within section *Aphyllis* are indicated as: circle, sect. *Tirucalli*; square, subsect. *Pachycladae, Euphorbia lamarckii* complex; rhombus, subsect. Pachycladae, *Euphorbia atropurpurea* complex; star, sect. *Aphyllis* (after Barres et al. 2011).

perennial herbs, shrubs, trees, and pencil-stem succulents. According to Webster et al. (1975), it is the only plant lineage at or below the level of genus known to include all photosynthetic types: C3, C4, and CAM photosynthesis, showing multiple adaptations to warm and dry habitats.

The genus *Euphorbia* and the other spurges show a wide array of life history strategies. Many are annual and perennial herbs that retain their leaves throughout their active periods. At its simplest, in a number of species in the *Chamaescyce* group, seeds germinate and individuals grow, branch dichotomously, flower, fruit, and die, all in a matter of weeks. Such "tachyplants" have been recognized as useful experimental models, lending themselves to short-term experiments that can be completed in the classroom.[12]

There are also leafy shrub and tree species of *Euphorbia* which may reach 20 m. A large number of euphorbias are succulent, with thickened, photosynthetic stems and very ephemeral leaves if leaves are present at all. Many succulents are in turn thorny, and some have well-developed underground tubers for additional storage. One of the

[12] One such tachyplant, *Arabidopsis thaliana* or rock cress, has become the Drosophila of the plant kingdom, being used for many fundamental studies of plant physiology and development, and was the first plant to have its complete genome sequenced (see, e.g., Plant Genome and Systems Biology [pgsb.helmholtz-muenchen.de/plant/athal/].)

many unusual euphorbs endemic to Socotra is *Euphorbia arbuscula*, a tree with dichotomous branching and terminal growth, expressing Crassulacean acid metabolism (Mies and Beyhl 1998).

## 5.8 Halophytes and living with *salt* as a compounding variable

Succulence is often discussed in relation to arid environments but it is also a common feature of plants growing in saline soils. Although they may resemble drought-avoiding succulents at the macro scale, *halophytic* succulents use water in very different ways. Saline soils present plants with two distinct stressors: osmotic stress due to low soil water potential; and ionic stress from the uptake into cells of cytotoxic salts, especially Na + and Cl – (Munns and Tester 2008). Osmotic stress has traditionally been considered as a form of drought, even for plants growing in inundated conditions[13] (Waisel 1972).

Halophytes have specializations allowing them to tolerate long-term uptake and storage (or excretion) of salts while protecting metabolic functions (Flowers 1985). They are typically characterized by slight increases in growth rate at low-to-moderate soil salinities, relative to their performance in normal, "non-saline" soils (Munns and Tester 2008).

Ogburn and Edwards (2010) identified several traits that appear to underpin the ability of halophytes to persist in saline habitats. Thus these plants can accumulate and store cytotoxic salts in large vacuoles; they also synthesize organic solutes such as proline, glycine, betaine, and sucrose, which are maintained in the cytosol and help keep its osmotic potential in balance with that of the storage vacuoles. They also filter and exclude excess inorganic ions in roots (Scholander et al. 1962), modulating osmotic potential and maintaining a fairly constant water potential gradient with the soil.

Breckle (2002) has described the typical "zonation" effect of salt gradients on surrounding vegetation. Some zones are narrow and over just a few meters one may encounter distinct gradients in vegetation and salinity. In other areas changes in salinity may be more gradual and fairly distinct vegetation zones may extend over several kilometers. Breckle distinguished the following types of halophyte, based on morphology and ecophysiology.

Stem-succulents (S); Leaf-succulents (L); Recreto-halophytes, i.e., plants which recrete (= secrete and excrete) salts out of special glands by some active mechanism (X); Pseudo-halophytes (P); and non-halophytes (N).

According to Breckle, broadly speaking across much of central and eastern Iran and adjacent Afghanistan, a fairly consistent pattern occurs in the vegetation. Across a 1000-fold gradient in salinity from highly saline to salt-free soil, the dominant stem-succulents are gradually replaced by leaf succulents; these are replaced by recreters and at even lower salinities these are replaced by pseudo-halophytes. On almost salt-free soil, the non-halophytes predominate (see Table 5.2). Breckle suggested the S-L-X-P-N sequence corresponded to the relative adaptive advantages accruing to halophytes under more extreme ecological conditions, where competition would exclude species that could neither tolerate nor avoid the negative effects of high salinity. In contrast, these traits would no longer provide special advantages in less saline soils where halophytes would be out-competed by non-halophytes.

Breckle (1986) used *Flora Iranica* and *Flora Europaea* to compare the occurrence of halophytic angiosperms in the two regions. In the area covered by *Flora Iranica*, some 5.7% of all species were identified as halophytes (354 of 6166 recorded species), and 14.1% of genera (121 of 860) contained halophytes. In Europe the corresponding figures were 4.6% of species (303 of 6551), and 9.1% of genera (77 of 845).

Breckle investigated many desert saline areas and determined that large parts of the desert have a complex pattern of ion composition and salinity. The various saline environments proved relatively rich in species and in each case were particularly rich in certain families, as shown in Table 5.3. Families are listed in order of the number of halophytic species reported for *Flora Iranica* and compared with those from western, central, and southern Europe.

[13] Eggli and Nyffeler distinguished "xero-halophytes" (or halophytes from dry climates) from "hygro-halophytes," or halophytes that do not experience annual water shortage—such as *Salicornia* spp. from coastal salt marshes. For xero-halophytes, aridity is essentially *both* climatological in the sense of low rainfall, and edaphic caused by soil salinity.

**Table 5.2** Percentage values of calculated abundances of different halophytic types (S, L, X, P, N) arranged according to salinity levels (salt content in soil: logarithmic intervals,% NaCl of dry soil), averages from eight halophytic catenas in Iran and Afghanistan (after Breckle 2002). See text p.148 for definitions of halophytic types.

| | **15** | **10** | **10–5** | **5–3** | **3–2** | **2–1** | **1–0.5** | **0.5–0.2** | **0.2–0.1** | **0.1–0.05** | **0.05–0.02** | **0.02–0.01** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S | 71 | 63 | 51 | 18 | 3 | 12 | 7 | 4 | 11 | 10 | 0 | 0 |
| L | 29 | 32 | 30 | 72 | 30 | 56 | 51 | 18 | 35 | 18 | 10 | 0 |
| X | 0 | 5 | 19 | 0 | 60 | 27 | 28 | 41 | 4 | 9 | 0 | 2 |
| P | 0 | 0 | 0 | 5 | 7 | 5 | 15 | 23 | 24 | 45 | 68 | 10 |
| N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 26 | 24 | 22 | 88 |

**Table 5.3** List of families and numbers of genera and species of halophytic seed-plants in the *Flora Iranica* region and corresponding figures for east, south, and central Europe. In brackets: total number of genera and species of the respective area. (After Breckle 1986.)

| No. | Plant Family | Flora Iranica Area | | | | Europe | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | genera | | Species | | Genera | | Species | |
| 1 | Chenopodiaceae | *c.*30 | (50) | *c.*100 | (150) | 16 | (34) | 68 | (154) |
| 2 | Poaceae | *c.*15 | (157) | *c.*50 | (1000) | 14 | (155) | 43 | (862) |
| 3 | Asteraceae | *c.*15 | (140) | *c.*25 | (1200) | 7 | (181) | 16 | (1614) |
| 4 | Plumbaginaceae | 3 | (8) | 19 | (192) | 3 | (8) | 70 | (146) |
| 5 | Brassicaceae | 5 | (126) | 16 | (465) | 6 | (108) | 14 | (651) |
| 6 | Cyperaceae | *c.*3 | (10) | *c.*15 | (100) | 4 | (12) | 19 | (263) |
| 7 | Tamaricaceae | 2 | (3) | *c.*15 | (45) | – | (3) | – | (9) |
| 8 | Polygonaceae | 3 | (9) | 14 | (123) | – | (9) | – | (96) |
| 9 | Zygophyllaceae | 5 | (8) | 14 | (30) | 1 | (6) | 3 | (9) |
| 10 | Fabaceae | *c.*2 | (70) | *c.*10 | (1200) | 2 | (74) | 6 | (845) |
| 11 | Caryophyllaceae | *c.*4 | (40) | *c.*10 | (400) | 5 | (37) | 14 | (655) |
| 12 | Boraginaceae | *c.*5 | (46) | *c.*9 | (367) | 1 | (37) | 1 | (263) |
| 13 | Capparaceae | 3 | (5) | 8 | (30) | – | (2) | – | (4) |
| 14 | Orobanchaceae | 1 | (3) | 7 | (55) | 1 | (4) | 2 | (50) |
| 15 | Gentianaceae | 2 | (9) | 6 | (44) | 2 | (9) | 8 | (72) |
| 16 | Apiaceae | *c.*4 | (120) | *c.*6 | (400) | 6 | (110) | 9 | (431) |
| 17 | Juncaceae | 1 | (2) | 5 | (31) | 1 | (2) | 9 | (84) |
| 18 | Convolvulaceae | 2 | (6) | 5 | (65) | 1 | (6) | 1 | (51) |
| 19 | Frankeniaceae | 2 | (2) | 4 | (4) | 1 | (1) | 6 | (6) |
| 20 | Amaranthaceae | 2 | (7) | 3 | (17) | – | (4) | – | (18) |
| 21 | Plantaginaceae | 1 | (1) | 3 | (28) | 1 | (2) | 7 | (36) |
| 22 | Aizoaceae | 2 | (5) | 3 | (7) | – | (7) | – | (10) |
| 23 | Thymelaeaceae | 2 | (6) | 2 | (13) | – | (2) | – | (29) |
| 24 | Malvaceae | 2 | (15) | 2 | (108) | 2 | (14) | 4 | (50) |
| 25 | Primulaceae | 2 | (9) | 2 | (65) | 2 | (14) | 2 | (101) |
| 26 | Portulacaceae | 1 | (1) | 1 | (5) | – | (2) | – | (5) |
| 27 | Linaceae | – | (2) | – | (22) | 1 | (2) | 1 | (37) |
| | Total | 121 | 860 | 354 | 6166 | 77 | 845 | 303 | 6551 |
| | % | 14.1 | | 5.7 | | 9.1 | | 4.6 | |

It is evident from the 27 families included that the percentage of halophytes is significantly higher for Iran than Europe.

Breckle gave estimates of ions present in the various salty species which he studied (Tables 5.4 and 5.5). He emphasized Chenopodiaceae (Table 5.4) though other families were also included (Table 5.5). Species were arranged according to their Na/K ratio, within the various chenopod genera. He concluded some species are more "sodiophilic" while others show "potassiophily" (Breckle 1986). Clearly within this group of species there are

**Table 5.4** Ion pattern in various species of Chenopodiaceae from stands in northern (N), and central and eastern (C) Afghanistan (n is number of samples; ion concentrations in% of dry matter; ion-ratios are equivalent-ratios; B is ppm dry matter). (After Breckle 1986.)

| No. | Species | Region | n | $Na^+$ | $K^+$ | $Cl^-$ | $SO_4$ | B | Na/K |
|---|---|---|---|---|---|---|---|---|---|
| 1 | *Anabasis macroptera* | C | 1 | 7 | 0.33 | 4.98 | 1.56 | 16 | 34.9 |
| 2 | *Salsola brachiata* | C | 1 | 8.7 | 0.87 | 3.66 | 0.54 | 285 | 16.9 |
| 3 | *Halimocnemis mollissima* | N, C | 7 | 11.5 | 1.27 | 6.95 | 6.43 | 44 | 16.2 |
| 4 | *Salicornia europaea* | *C* | 1 | 5.8 | 0.63 | 10.8 | 2.35 | 156 | 15.7 |
| 5 | *Halocnemum strobilaceum* | N | 2 | 12.2 | 1.36 | 17.3 | 0.77 | 23 | 15.2 |
| 6 | *Gamanthus commixtus* | N | 2 | 12.7 | 1.31 | 8.6 | 15.5 | 28 | 14 |
| 7a | *Salsola orientalis* | C | 1 | 9.9 | 1.16 | 2.76 | 3.43 | 19 | 13.8 |
| 8 | *Gamanthus kelifii* | C | 1 | 7.8 | 1.18 | 10.7 | 4.23 | 38 | 11 |
| 9 | *Salsola longistylosa* | N | 3 | 12.9 | 2.06 | 10.5 | 5.8 | 28 | 10.2 |
| 10 | *Seidlitzia rosmarinus* | N | 3 | 13.2 | 2.68 | 2.44 | 9.96 | 39 | 8.3 |
| 11 | *Halocharis hispida* | N | 4 | 12.3 | 2.3 | 4.04 | 12.5 | 64 | 8.2 |
| 12 | *Halostachys caspica* | N | 1 | 10.1 | 2.17 | 5.4 | 3.82 | 160 | 7.6 |
| 13 | *Salsola dendroides* | N | 1 | 11.1 | 2.52 | 0.96 | 11.2 | 65 | 7.5 |
| 14 | *Suaeda transoxana* | N | 1 | 9.8 | 2.22 | 11.4 | 3.43 | 222 | 7.4 |
| 15 | *Halocharis afghanica* | N | 2 | 16.5 | 3.8 | 6.7 | 15.2 | 46 | 7 |
| 16 | *Anabasis eriopoda* | N | 1 | 6.6 | 1.62 | 2.04 | 0.26 | 25 | 6.8 |
| 17 | *Anabasis turkestanica* | N | 1 | 10 | 2.35 | 3.9 | 0.27 | 50 | 6.7 |
| 18 | *Salsola bungeana* | N | 1 | 5.5 | 1.58 | 4.2 | 2.62 | 69 | 5.8 |
| 7b | *Salsola orientalis* | N | 3 | 6 | 1.88 | 4.9 | 3.66 | 57 | 5.7 |
| 19 | *Salsola sclerantha* | N | 7 | 8.9 | 2.88 | 13.3 | 3.87 | 68 | 5.5 |
| 20 | *Salsola maracandica* | C | 3 | 7.2 | 2.2 | 1.75 | 2.35 | 44 | 5.5 |
| 21 | *Londesia eriantha* | N | 2 | 4.7 | 1.58 | 2.06 | 7.8 | 83 | 5.2 |
| 22 | *Anabasis bamianica* | C | 1 | 2.9 | 1.01 | 2.02 | 1.68 | 12 | 4.8 |
| 23 | *Aellenia subaphylla* | N | 4 | 7.7 | 3.25 | 1.64 | 0.72 | 46 | 3.9 |
| 24a | *Suaeda altissima* | N | 1 | 6.9 | 3.33 | 3.67 | 0.39 | 22 | 3.4 |
| *25* | *Halocharis violacea* | C | 3 | 2.9 | 1.51 | 7.5 | 2.31 | 49 | 3.3 |
| 26a | *Atriplex turcomanica* | N | 1 | 7.9 | 4.9 | 15.4 | 0.81 | 177 | 2.7 |
| 27 | *Salsola aperta* | N | 1 | 6.9 | 4 | 9.4 | 0.42 | 22 | 2.4 |
| 28 | *Halogeton glomeratus* | C | 4 | 9.1 | 7.05 | 5.5 | 1.02 | 35 | 2.2 |
| 29 | *Atriplex flabellum* | N | 1 | 5.6 | 4.7 | 11.6 | 3.18 | 144 | 2 |
| 30 | *Atriplex griffthii* | C | 2 | 4.2 | 4 | 7.9 | 1.62 | 105 | 1.91 |
| 31 | *Girgensohnia oppositiflora* | N | 1 | 1.35 | 1.32 | 1.34 | 1.44 | 86 | 1.75 |
| 26b | *Atriplex turcomanica* | C | 2 | 2.65 | 2.43 | 5.8 | 2.03 | 93 | 1.68 |
| 24b | *Suaeda altissima* | *C* | 1 | 8.1 | 8.2 | 6.5 | 5.7 | 255 | 1.67 |
| 32 | *Salsola richteri* | N | 3 | 3.2 | 4.9 | 0.9 | 0.39 | 52 | 1.12 |
| 33 | *Salsola gossypina* | C | 1 | 1.3 | 2.06 | 3.64 | 5.18 | 51 | 1.08 |

*continued*

**Table 5.4** *Continued*

| No. | Species | Region | n | $Na^+$ | $K^+$ | $Cl^-$ | $SO_4$ | B | Na/K |
|---|---|---|---|---|---|---|---|---|---|
| 34 | *Camphorosma lessingii* | C | 4 | 1.01 | 2.2 | 1.1 | 0.55 | 153 | 0.79 |
| 35 | *Horaninowia ulicina* | N | 1 | 1.09 | 2.42 | 1.13 | 0.64 | 84 | 0.77 |
| 36 | *Noaea mucronata* | C | *2* | 1 | 2.41 | 1.82 | 0.29 | 52 | 0.71 |
| 37 | *Haloxylon persicum* | N | 3 | 0.79 | 1.51 | 0.53 | 0.37 | 46 | 0.69 |
| 38 | *Arthrophytum griffithii* | C | 1 | 1.18 | 3.86 | 1.36 | 0.41 | 22 | 0.53 |
| 39 | *Panderia turkestanica* | C | 1 | 2.02 | 9.35 | 2.2 | 0.91 | 28 | 0.37 |
| 40 | *Arthrophytum leptocladum* | N | 3 | 0.7 | 3.6 | 0.69 | 0.44 | 67 | 0.36 |
| 41 | *Ceratoides papposa* | C | 2 | 0.2 | 3.48 | 0.24 | 0.95 | 52 | 0.088 |
| 42 | *Ceratocarpus utriculosus* | C, N | 2 | 0.036 | 1.11 | 0.21 | 0.52 | 68 | 0.056 |
| 43 | *Agriophyllum latifolium* | N | 1 | 0.056 | 1.98 | 0.59 | 0.17 | 28 | 0.048 |

different physiological solutions possible when it comes to surviving in a salty environment, and this warrants further investigation.

Many of the chenopods appear to be typical succulents, having high concentrations of sodium and inorganic ions, mainly $Cl^-$, in their cells. Such plants have been called chloride-halophytes (e.g., Breckle 1982). Other chenopods as well as genera from other families (such as *Ephedra*), tend to replace the high $Cl^-$ content with organic anions such as oxalate (see Table 5.4). In these cases the cation/anion ratio tends to be considerably greater than one (e.g., *Halogeton*). In other species—*Londesia eriantha, Salsola gossypina*, or *S. dendroides*—the sulfate content of the leaf sap is greater than that of chloride (Breckle 1986). These have been called sulfate-halophytes and Albert and Kinzel (1973) reported that this physiotype was common in cruciferous halophytes (Brassicaceae).

The non-chenopod species (Table 5.5) present in saline habitats include a number of "recreting" halophytes, i.e., species both secreting *and* excreting salts through special glands using an active (energy-dependent) process. According to Breckle (1986) these halophytes also have mechanisms for maintaining their water balance; some are sulphate-halophytes and some are chloride-halophytes, and many Zygophyllaceae accumulate potassium ions ($K^+$). Among chenopods the recreting process appears to be less important than succulence per se. Recreting chenopods are known mainly from the genera *Atriplex, Halimione*, and *Chenopodium* (Breckle 1986). In all these cases recretion is achieved using tiny hair-like structures known as vesiculated trichomes. Each trichome has a stalk and a balloon-like tip, the bladder cell. Leaves accumulate $Na^+$, $K^+$, and $Cl^-$ in the bladder as a very concentrated brine, using active transport to remove these ions from mesophyll cells. When the bladder cells rupture, the salts are released back into the environment.

The salty-halophytic habitat is one of the most extreme in the world (Chapman 1977) and inhabitants include members of only a few families (e.g., Chenopodiaceae, Frankeniaceae, Plumbaginaceae, and Tamaricaceae). All are noted for their habitat specificity as well as their cosmopolitan distribution (Shmida 1985). Many species are distributed in more than one global region and Shmida argued this is due at least in part to long-distance dispersal, rather than ancient land bridges as others have argued. Shmida estimated that among the 154 genera Thorne (1973) had listed as sub-cosmopolitan, about a quarter were halophytes.

Shmida suggested that once eco-morphological adaptation to extremely salty habitats had evolved, the strategy spread about the world. The observation that halophytic families are so few and widely distributed argues that—at least

**Table 5.5** Ion patterns in various species from non-chenopod families, from various sites in northern (N), and central and eastern (C) Afghanistan. (n = number of samples; ion concentrations in% of dry matter; ion-ratios are equivalent-ratios; B = ppm dry matter). (After Breckle 1986.)

| No. | Species | Region | n | $Na^+$ | $K^+$ | $Cl^-$ | $SO_4$ | B | Na/K | C/A |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Spergularia marina* | C | 2 | 3.390 | 1.15 | 5.75 | 5.35 | 80 | 5.500 | 0.90 |
| 2 | *Aeluropus littoralis* *§ | N | 1 | 0.700 | 0.31 | 1.21 | 0.22 | 85 | 3.800 | 1.08 |
| 3 | *Alhagi sparsifolia* | N, C | 2 | 1.200 | 0.73 | 2.30 | 5.84 | 223 | 2.800 | 0.77 |
| 4 | *Tamarix* sp. *§ | N | 1 | 1.010 | 0.75 | 2.86 | 2.74 | 79 | 2.300 | 0.67 |
| 5 | *Crypsis aculeata* * | C | 3 | 1.280 | 1.11 | 1.50 | 1.75 | 29 | 1.970 | 1.58 |
| 6 | *Limonium otolepis* *§ | N | 2 | 1.230 | 1.07 | 1.54 | 3.49 | 95 | 1.950 | 1.31 |
| 7 | *Tamarix karakalensis* *§ | N | 1 | 1.090 | 0.99 | 3.26 | 8.42 | 54 | 1.880 | 0.53 |
| 8 | *Cressa cretica* *§ | N,C | 2 | 1.210 | 1.10 | 4.73 | 2.14 | 50 | 1.870 | 0.56 |
| 9 | *Limonium reniforme* *§ | N | 1 | 0.960 | 0.95 | 1.50 | 6.88 | 93 | 1.720 | 0.86 |
| 10 | *Glaux maritima* * | C | 1 | 1.380 | 1.59 | 3.07 | 2.62 | 34 | 1.470 | 1.01 |
| 11 | *Lepidium latifolium* § | N | 1 | 1.130 | 1.63 | 0.84 | 8.78 | 250 | 1.180 | 1.30 |
| 12 | *Populus euphratica* | N | 1 | 1.350 | 2.14 | 1.94 | 1.25 | 101 | 1.080 | 1.86 |
| 13 | *Ephedra pachyclada* | N | 2 | 0.480 | 1.05 | 0.27 | 0.22 | 19 | 0.990 | 5.49 |
| 14 | *Artemisia kurramensis* | C | 1 | 0.800 | 1.59 | 0.88 | 1.22 | 98 | 0.860 | 2.42 |
| 15 | *Peganum harmala* | N,C | 3 | 1.270 | 4.25 | 4.48 | 1.63 | 161 | 0.590 | 1.21 |
| 16 | *Calligonum caput-medusae* | N | 4 | 0.210 | 0.91 | 0.32 | 0.45 | 55 | 0.390 | 2.75 |
| 17a | *Zea mays*, cult. (yellow, salty) | N | 1 | 0.290 | 1.60 | 2.13 | 1.61 | 300 | 0.310 | 0.78 |
| 17b | *Zea mays*, cult. (green, normal) | N | 2 | 0.039 | 1.79 | 0.89 | 0.40 | 144 | 0.037 | 1.75 |

*—Recreting halophytes

§—Analysed leaves washed twice with distilled water

in such an environment—the likelihood of long-distance dispersal across ocean barriers is greater than the probability of another salt-adapted taxonomic novelty evolving independently on another continent.

At least for the Chenopodiaceae and Tamaricaceae, their center of origin appears to have been in Central Asia (Zohary 1973). There these families have the greatest center of diversity (most species, genera, and tribes), and the greatest number of primitive genera (Shmida 1985). As for *Tamarix*—essentially the only tree in the world that grows in salt marshes—its distribution covers the arid and salty regions of Asia and Africa (Shmida 1985). A few species live in Europe, either in salt marshes or near the coast, and fairly recently it was introduced to the deserts of North Africa, likely sometime in the nineteenth century (Shmida 1985).

Finally, Table 5.6 summarizes taxa that are distributed in salty or sandy habitats of both desert and coastal areas in Israel (see Shmida 1985). It shows most of these taxa belong to the desertic—halophytic families (Aizoaceae, Chenopodiaceae, Frankeniaceae, Plumbaginaceae, Poaceae, Tamaricaceae, Zygophyllaceae), and that the genera are mostly cosmopolitan in distribution.

## 5.9 Desert life forms, demography, and dynamics

Desert vegetation is often dominated by species that have natural lifespans of decades, centuries, or even millennia (Goldberg and Turner 1986; Vasek 1980). This results in slow rates of population turnover and as a result, there have been few quantitative assessments of desert plant community and

**Table 5.6** List of taxa in Israel occurring in both coastal and desert locations; Med. = Mediterranean; SA = Saharo-Arabian; IT = Irano-Turanian; AU = Australia (after Shmida 1985, used with permission).

| Genus name | Family | General distribution of the genus | Corresponding species coast–desert | General distribution of the species | Main habitat of the species |
|---|---|---|---|---|---|
| *Aeluropus* | Poaceae | Old World | *A. littoralis* | Med. -SA | salt marshes |
| | | | *A. lagopoides* | | |
| *Artemisia* | Asteraceae | cosmopolitan | *A. monospermia* | Med. -SA | arid climates |
| *Atriplex* | Chenopodiaceae | cosmopolitan | *A. halimus* | SA, (Med.) | deserts |
| *Arthrocnemum* | Chenopodiaceae | cosmopolitan | *A. macrostachyum* | Med. -SA | salt marshes |
| *Cressa* | Convolvaceae | cosmopolitan | *C. cretica* | Old World | salt marshes |
| *Frankenia* | Frankeniaceae | cosmopolitan | *F. pulverulenta* | Old World | salty eastern deserts |
| *Limonium* | Plumbaginaceae | cosmopolitan | *L. sinuatum* | Med. -SA | salty coasts |
| | | | *L. thouinii* | | |
| *Lycium* | Solanaceae | cosmopolitan | *L. schawii* | | |
| | | | *L. schweinfurthii* | | |
| *Mesembryanthemum* | Aizoaceae | SAF (SA, IT, AU) | *M. nodiflorum* | African deserts | deserts |
| | | | | Med. coasts | "salty coast" |
| *Pancratium* | Amaryllidaceae | Paleotropic | *P. maritimum* | Med. -SA | coasts |
| | | | *P. sickenbergeri* | | |
| *Salicornia* | Chenopodiaceae | cosmopolitan | *S. europaea* | Med. -SA | Salt marshes |
| *Salsola* | Chenopodiaceae | cosmopolitan (introduced?) | *S. kali* | Med. | steppe, salt coast |
| *Spergularia* | Caryophyllaceae | cosmopolitan | *S. marina* | cosmop. -SA | salty habitat, |
| | | | *S. diandra* | | desert weed |
| *Sporobolus* | Poaceae | cosmopolitan | *S. virginensis* | Med. -SA | salt marshes (desert) |
| | | | *S. arenarias* | | |
| *Suaeda* | Chenopodiaceae | cosmopolitan | *S. vera* | Med. -SA | deserts, salt marshes |
| *Tamarix* | Tamaricaceae | Old World | *T. nilotica* | SA, (Med. -IT) | salt marshes (washes in desert) |
| *Zygophyllum* | Zygophyllaceae | Old World-AU | *Z. Album* | SA | deserts (salt marshes) |

population dynamics. McAuliffe (1988) investigated shrub communities in the arid Sonoran where many communities consist of simply two species, *Ambrosia dumosa* and *Larrea tridentata*, and found that different communities show completely different recruitment patterns and rates of turnover. In places where there is a lot of bare ground, *Ambrosia* readily colonizes the open spaces. Recruitment in *Larrea* is less frequent and largely limited to areas beneath the canopies of larger, older *Ambrosia* individuals.

There are interesting parallels in the dynamics of more species-rich communities, in some less xeric parts of the Sonoran. One shrub in particular, *Ambrosia deltoidea*, is capable of colonizing large open spaces, whereas for most other species recruitment is largely limited to areas beneath the canopies of other plants, in particular *A. deltoidea*. According to

McAuliffe, even in the simple two-species systems it is likely that no individual mechanism, such as competition, or seed distribution and fate, can be singled out as predominant drivers of population dynamics, and hence of community structure.

Plant *longevity* in conjunction with certain rare climatic extremes can complicate the observation of plant population dynamics and its interpretation (Drechsler et al. 1999; Silvertown et al. 1996). Miriti et al. (2007) suggested that desert vegetation may even "beguile" observers into a kind of "simplistic uniformitarianism" where observations made over a few years *appear* to reflect processes across much longer periods of time. They argued the potential extreme longevity of the adults of certain conspicuous species, combined with certain rarely observed, individual adult mortality events were examples of the highly significant, albeit very rare processes *actually* driving desert plant population dynamics.

In a study of common species using thousands of individual long-lived perennials, tagged and monitored over 20 years in the Colorado Desert of California, Miriti et al. reported periods of high mortality in response to episodes of severe regional drought. Their long-term results highlight the disproportionate effects of *rare* extreme events like floods (Gutschick and BassiriRad 2003), in terms of both changes in species richness of a long-standing desert community and the opportunity for ecological succession or transition to a different stage, in desert ecosystems.

Regional histories of desert localities often show extended periods of severe drought, as well as periods with several years of unusually high precipitation (known as "pluvials"). Such patterns are well known in the Middle East. It is quite possible that many species, established much earlier, perhaps in previous centuries, simply cannot successfully reproduce in the plant community or under the environmental conditions that are present in such dry times. Permanent sites established across the Middle East for long-term studies of the vital statistics of plant birth, death, and population persistence, would be very useful to better understand desert vegetation and population responses to both long-term and short-term environmental factors.

Danin (1983) classified life forms according to Raunkiaer's five types (Figure 5.5; and see Section 1.4). Raunkiaer's original focus was on how plants survived cold winters, but the concept has been applied to plants living in arid regions where the adverse season is the period when drought is most severe.

A. Therophytes. These are annuals or ephemerals; they are short-lived "drought-escaping" species that complete their (seed-to-seed) life cycles over a very short time, often just a few weeks. During dry periods they survive as seeds and fruits and at the beginning of a rainy season seeds germinate, grow, and reproduce. Typically size and fecundity depend on the amount or duration of rainfall (e.g., Hegazy and Kabiel 2010). Death occurs toward the end of the wet period or in the course of the following season. Common desert therophytes include *Ifloga spicata, Trigonella stellata, Schismus barbatus, Zygophyllum simplex, Plantago ovata, Anastatica hierochuntica*, and *Asteriscus hierochunticus*.
B. Geophytes. The perennating stock (rootstock or underground stems) and food reserves of these plants survive the adverse season with underground dormant buds, often protected by a layer of dry scale leaves. Aerial shoots die back in the dry season and underground buds sprout as water availability improves. These stems become aerial shoots that die back again in the following dry season. Examples of perennating structures in geophytes include bulbs (*Allium* species), corms and tubers (*Arisarum vulgare*), and rhizomes (*Phragmites australis, Arundo donax*).
C. Hemicryptophytes. Perennials that produce dormant buds at the soil surface. The above-ground parts die back in the dry season and the new buds sprout following winter rain. Examples include *Cynara cornigera* (Figure 5.3C), *Peganum harmala*, rosette plants like *Limonium narbonense*, and prostrate or decumbent plants such as *Tribulus* and *Citrullus* species.
D. Chamaephytes. These are the low-growing perennial plants (under-shrubs, shrublets, semi-shrubs) whose buds are borne just above the ground surface (typically no more than 25 cm). During the dry season upper branches (or parts of them) die back and are dropped, maintaining the dwarf stature of these shrubby plants. After

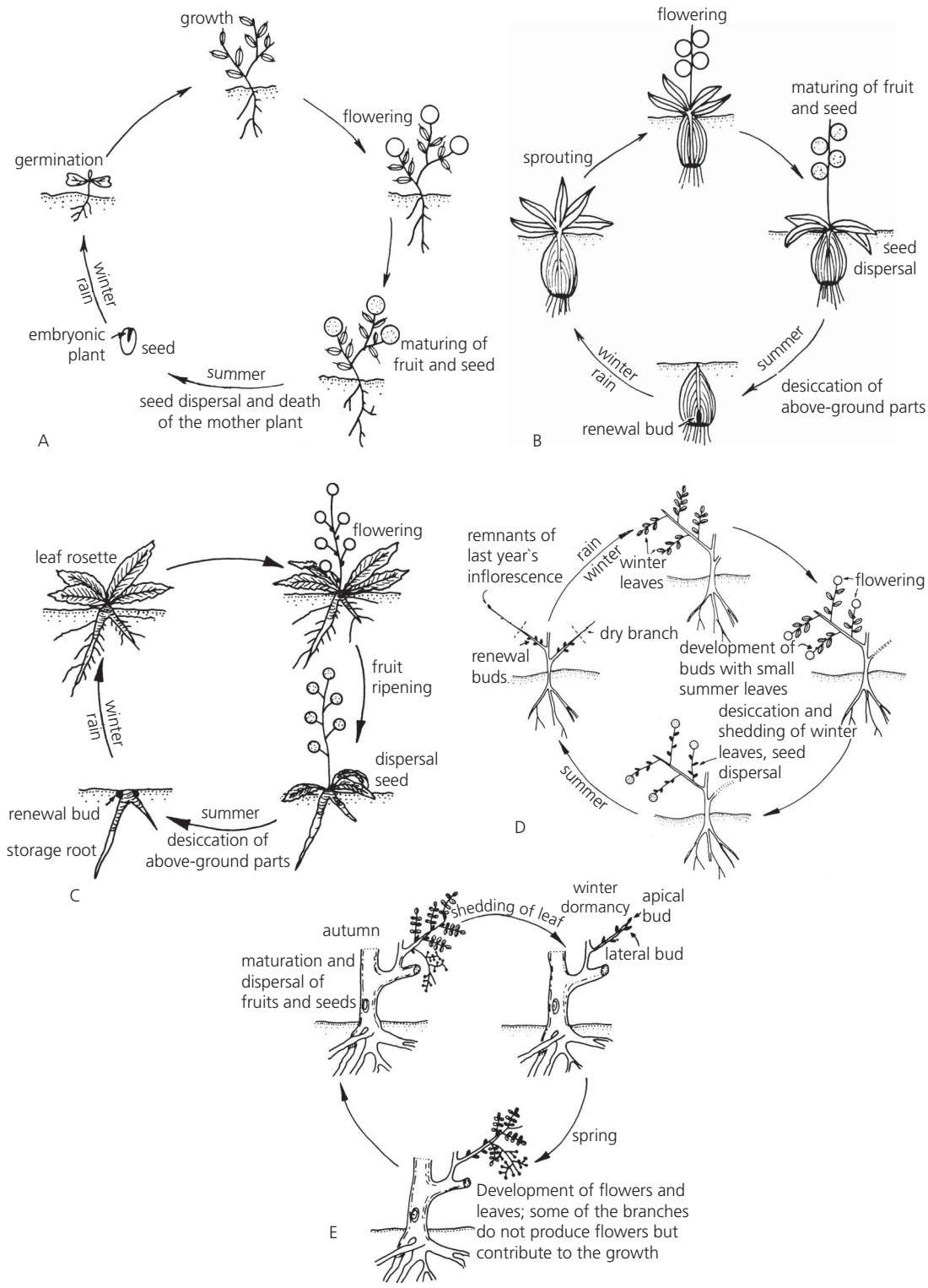



**Figure 5.5** Life cycles of different plant life forms (after Danin 1983) A=therophytes; B=geophytes; C=hemicryptophytes; D=chamaephytes; E=phanerophytes.

the start of the rainy season the renewal buds sprout and flourish, producing new branches, e.g., *Cleome droserifolia* and *Ebenus armitagei* (Hegazy and Eesa 1991).

E. Phanerophytes. These include the trees and shrubs that produce new buds at various heights above the ground. Older woody branches are typically not shed, but rather leaves may be abscised during the dry season and sometimes some parts of the newly formed branches may also be shed, depending on the degree of drought. New branches, leaves, flowers, and later fruits are produced over the rainy season. Examples include *Acacia, Retama*, and *Ochradenus* species. Deep-rooting "phreatophytes" can access deeper soil horizons, or even subsoil water tables (Smith et al. 1997). Many other perennials, such as the shrub *Encelia farinosa* are "drought deciduous" and may facultatively abscise leaves during unfavorable periods.

### 5.9.1 Life history variation and life-tables

More recent classifications are less concerned about the location of surviving buds and meristems and more about other, more demographic variables, like lifespan and frequency of reproduction (Schaffer and Gadgil 1975; Silvertown et al. 1997). A life history can be characterized as some overall pattern of limited resource allocation toward major sinks: typically competition, defense, reproduction, and basic maintenance.

Species in which individuals have a single reproductive period followed by death are monocarpic or "semelparous." This is sometimes referred to as "big bang" reproduction, especially in perennials such as agaves or century plants, and some bamboos which may wait many years, growing larger every year—sometimes mostly underground—and finally flowering, setting seed, and dying in a relatively sudden "bang" (Section 7.4). In contrast, plants having repeated reproductive sessions and living for multiple years are perennials and termed polycarpic, or "iteroparous." Annuals germinate, flower, set seed, and die in one year. "Biennials" are semelparous, living from one to several years vegetatively, growing and storing resources until becoming reproductive, and then dying.

Disturbance and other factors causing unpredictability in environments can remove competing populations, reduce adult survival, and otherwise create temporary habitats with available resources. In general this favors a strategy of rapid growth and reproduction. Find an opportune moment, exploit it, then die. These are annuals and short-lived perennials that occupy disturbed or otherwise ephemeral habitats. *Boerrhavia repens* in the Sahara develops from germinating seed to new, next-generation seed in as little as ten days (Cloudsley-Thompson and Chadwick 1964); *Anastatica hierochuntica* can complete its life cycle in as little as three weeks (Hegazy 1990b; Hegazy et al. 2013c).

Another life history classification uses the general nature of selection pressures present in contrasting environments, or r- and K-selection (MacArthur and Wilson 1967). The former refers to an organism's intrinsic rate of natural increase, while K-selection refers to the environmental carrying capacity and theoretical maximum number of individuals of a species able to co-exist in a particular location. Species experiencing r-selection tend to occupy temporary habitats in relatively unpredictable environments. Accordingly they maximize fitness by rapid growth and short life-spans, utilizing early and abundant reproduction followed by death. In contrast, K-selected species are more resistant to environmental fluctuations and maximize fitness in more predictable habitats in which their life-spans extend for multiple years and have multiple reproductive sessions (see Table 5.7).

The larger classification of Philip Grime (2001) includes three distinct strategies, essentially dependent upon the intensity of two major selection pressures, disturbance, and stress (see Figure 5.6). In the strategy for specialists in "low disturbance–low stress" environments, known as the competition strategy, plants have the potential to grow well and compete strongly for resources. These "competitors" tend to dominate in resource abundant, reasonably predictable habitats and allocate resources primarily to growth. In the second strategy, selected in high stress–low disturbance environments and known as the stress-tolerance strategy, plants endure adverse, physiologically stressful conditions and are adapted for exploiting temporary favorable opportunities. Such "stress-tolerant" species

**Table 5.7** Characteristic differences between *r*- and *K*-selected plant strategies (adapted from Pianka 1970).

| Population trait | *r*-selection | *K*-selection |
|---|---|---|
| Habitat type | Temporary habitat types | More stable habitat types |
| Climate | Unpredictable and uncertain | Predictable and more certain |
| Survivorship | Deevey type I and II (see Figure 5.7) | Deevey type III |
| Mortality | Density independent (catastrophic) | Density dependent |
| Population size | Below carrying capacity | At or about the carrying capacity |
| Competition | Often lax | Usually keen |
| Life span | Short and rapid growth | Long and slow growth |
| Reproduction | Sexual and single reproductive period | Sexual and vegetative with multiple reproductive periods |

dominate in resource-limited habitats and allocate resources mostly to somatic, maintenance activities, making for longer lifespan possibility. In the third strategy, selected in high disturbance–low stress environments and known as the "ruderal" strategy, plants have a capacity for rapid growth and completion of the life history in short periods between successive disturbances. Ruderals tend to dominate in resource-abundant, temporary, or disturbed habitats; they allocate resources primarily to reproduction and have very short life span (see Table 5.8).

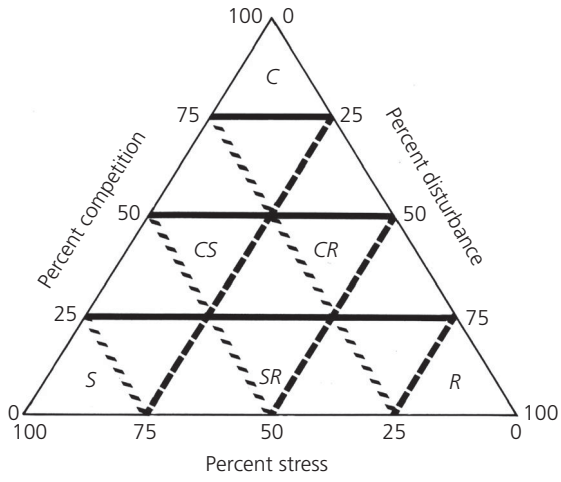



**Figure 5.6** Grime's classification of plant life history strategies based on percentage occurrence of competition (solid lines), disturbance (long dashed lines), and stress (short dashed lines). C = Competitive, S = Stress-tolerant, R = Ruderal, CS = Stress tolerant competitor, CR = Competitive ruderal, and SR = Stress tolerant ruderal. (Redrawn after Grime 1979.)

Life-tables collect systematic information about species and populations, including survivorship, fecundity, reproductive rates, and rates of increase and expectations of future life. "Cohort" life-tables have been used for annuals and short-lived perennials, and are determined by tracking the cohorts of a species life stages, including seeds, seedlings, juveniles, and adults at particular times until all individuals have died. "Static" or time-specific life-tables are used for long-lived perennials, where survival is estimated by sampling at different stages or life intervals and estimating ages (through coring, etc.).

Deevey (1947) described three general survivorship patterns by recording the number of survivors at each age interval against time (see Figure 5.7). Deevey type-I curves are characteristic of short-lived plants having low mortality in younger ages and high mortality in older ones, as in annuals. The Deevey type-II curve occurs where the probability of mortality is approximately the same at any stage regardless of age. Type-III curves occur in long-lived species having high rates of mortality in the younger stages and low mortality in old age classes, as in trees and shrubs. Survivorship curves of some desert species are shown in Figure 5.6.

The desert undershrub *Cleome droserifolia* (see Figure 5.8A) shows a pattern of extremely high seed and seedling mortality followed by linear mortality with age up to about 20 years, then a plateau of low mortality in adults between 20 and 60 years old (Hegazy 1990a). Survivorship in *C. droserifolia* exhibits a combination of all three Deevey curves.

**Table 5.8** Representative features of competitive, stress-tolerant, and ruderal plant strategies (adapted from Grime 1979).

| Character | Competitive | Stress-tolerant | Ruderal |
|---|---|---|---|
| Life form | Herbs and woody plants | Herbs and woody plants | Herbs |
| Shoot and root systems | Extensive lateral and vertical spread | Variable growth forms (wide range) | Limited spreading |
| Life history duration | Long | Very long | Very short |
| Leafiness | Seasonal peaks of leaf production | Various patterns of leaf production | Short phase of leaf production |
| Flowering frequency | Flower each year | Intermittent flowering | High frequency of flowering |
| Resource allocation to seeds | Small | Small | Large |
| Perennation | Dormant buds and seeds | Stress-tolerant leaves, stems, and roots | Dormant seeds |
| Regeneration | Vegetative, seed dispersal, and persistent seed bank | Vegetative and persistent seedling bank | Seed dispersal and persistent seed bank |
| Growth rate | Fast | Slow | Fast |
| Photosynthesis and mineral uptake | Seasonal and coinciding with long vegetative growth period | Opportunistic and uncoupled from vegetative growth | Opportunistic and coinciding with vegetative growth |
| Acclimation | Weak | Strong | Weak |
| Litter accumulation | Copious and persistent | Sparse and sometimes persistent | Sparse and not usually persistent |

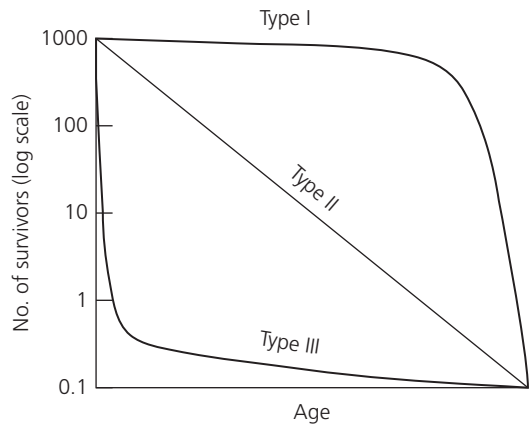



**Figure 5.7** Deevey's three model survivorship curves. Type I for populations having low mortality in the younger stages and rapid mortality in the older age, Type II for populations having the same probability of dying at any age, and Type III for populations having high rates of juvenile mortality and low mortality in the older ages (after Deevey 1947).

Seed and seedling stages coincide with a type III, juveniles and adults up to 20 years match a type II, and adults above age 20 and with truncated mortality above age 60 can be described as a type I.

For *Limonium delicatulum* (= *L. narbonense*), a salt tolerant perennial rosette species (Hegazy 1992), survivorship shows a sharp decline from flower bud to seedling stage, followed by a plateau of low mortality in juvenile and adult stages (see Figure 5.8B). Similar curves were found in *Moringa peregrina* and *Acacia tortilis* populations in Egypt (Hegazy and Elhag 2006; Hegazy et al. 2008a).

Separate sexual and "vegetative" life-tables were constructed for the invasive *Heliotropium curassavicum* (Hegazy 1994). For "vegetative" reproduction the life table used the numbers and fates of ramets, and was based on regular counts of root buds, bud sprouts, and aerial shoot stages; while for sexual reproduction it used the numbers and fates at flower-, fruit-, seed-, seedling-, juvenile-, and adult stages. Survivorship showed a sharp decline during the early stages of growth and reproduction (see Figure 5.8C). A major difference between sexual and vegetative curves was that vegetative stages occurred over a shorter period.

Survivorship in the desert annual *Anastatica hierochuntica* raised under different water treatments is shown in Figure 5.8D (Hegazy et al. 2013c). In the four treatments (equivalent to 100, 200, 500, and 1000 mm rainfall), survivorship fell from a maximum initial value at seed germination to zero at senescence. Under 100 mm water treatment

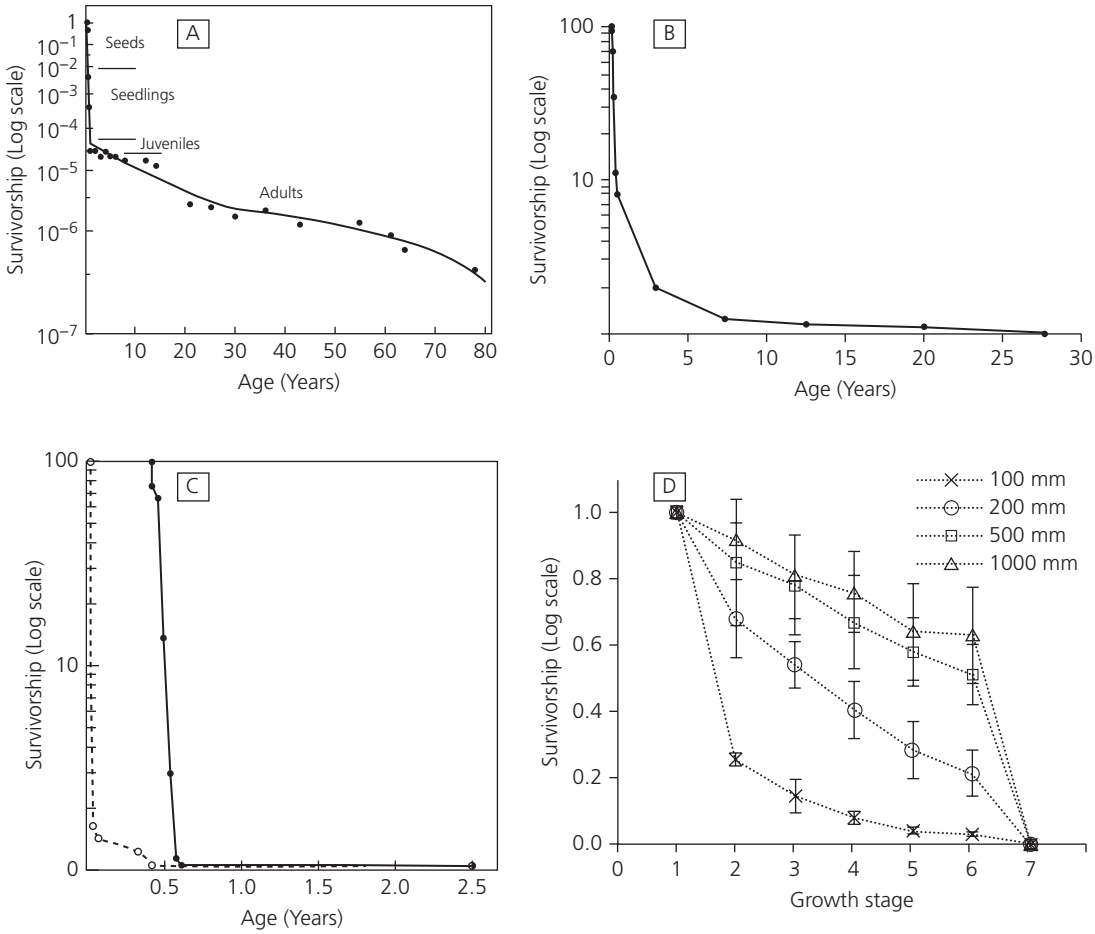



**Figure 5.8** Survivorship curves of some desert species. (A) *Cleome droserifolia*. (B) *Limonium delicatulum*. (C) *Heliotropium curassavicum*, dashed line for vegetative life table and solid line for sexual. (D) A*nastatica hierochuntica* (after Hegazy 1990a, 1992, and 1994; Hegazy et al. 2013).

survivorship matches a Deevey type III, and under 200 mm a Deevey type II. For water treatments equivalent to 500 and 1000 mm, the curves match Deevey type I, with low mortality at early stages and sharp decline during senescence.

A summary of life table data for some desert species is shown in Table 5.9. Expectations of future life and reproductive value of trees and shrubs including *Acacia tortilis*, *Moringa peregrina*, and *Cleome droserifolia*, and the perennial rosette *Limonium delicatulum* are all higher than the values estimated for the annual *Anastatica hierochuntica* (raised under 100 mm rainfall). Net reproductive rates and germination times are all species specific. The perennial ruderal *Heliotropium curassavicum* achieved very high reproductive values, net reproductive rate, and intrinsic rate of increase, and low germination times in both sexual and vegetative life-tables.

## 5.10 Summary

The chapter considers the general phenomenon of succulence and some of the many and diverse forms of plant water storage, along with sclerophylly and other adaptations that reduce water loss. Diversity and flexibility in terms of photosynthesis and

**Table 5.9** Results of life table analysis based on sexual reproduction in six desert species. Numbers in parentheses are based on vegetative reproduction. $E_x$ = expectation of future life, $V_x$ = reproductive value, $R_o$ = net reproductive rate, T = generation time (years), and r = intrinsic rate of increase.

| Species | Life form | $E_x$ range | $V_x$ range | $R_o$ | T | r | Source |
|---|---|---|---|---|---|---|---|
| *Cleome droserifolia* | Undershrub | 0.50–2.95 | 4413–217 521 | 0.99 | 30.12 | $1.33 \times 10^{-6}$ | Hegazy (1990a) |
| *Limonium delicatulum* | Per. rosette | 1.00–2.03 | 557–1624 | 0.36 | 14.39 | –0.07 | Hegazy (1992) |
| *Heliotropium curassavicum* | Per. herb | 1.00–5.01 (1.00–2.06) | 141 205–2 634 949 (9802–203,958) | 119 953 (6730) | 3.43 (3.64) | 3.41 (2.42) | Hegazy (1994) |
| *Acacia tortilis* | Tree | 1.00–6.33 | 284 580–628 168 | 0.281 | 376.24 | –0.003 | Hegazy and Elhag (2006) |
| *Moringa peregrina* | Tree | 1.00–4.54 | 250–609 | 0.004 | 68.23 | –0.08 | Hegazy et al. (2008a) |
| *Anastatica hierochuntica* | Annual | 1.00–1.54 | 19.3 | – | – | – | Hegazy et al. (2013) |

metabolism are common in desert plants, and various combinations of Crassulacean acid metabolism, C4 and C3 photosynthesis can be found. Another constraint in dry habitats is dealing with excess salt. A select few families have become adept at dealing with this. A variety of growth habits, life forms, and life history strategies help individuals "avoid" the worst effects of aridity. Plant structural defense—spinescence—is reviewed for the desert situation using the Israeli flora, where spinescence is associated with delayed flowering. Among toxic plants, possible aposematic or warning coloration is described. The demography of desert species is introduced using life-tables.

CHAPTER 6

# Sex in a hot dry place

## 6.1 The importance of timing!

As we emphasize in regard to other aspects of desert plant ecology (e.g., Chapter 7), the *timing* of certain life-history events can be critical. Reproductive phenology[1] and other seasonal patterns of plant development are especially significant, because the timing of flowering influences subsequent pollination, and fruiting influences any subsequent seed dispersal. The precise timing of developmental transitions will most often be a function of long-term characteristics of particular local environments (Rathcke and Lacey 1985).

In environments that are *unpredictable* from year-to-year, fitness is much less likely to be increased via evolution of fixed, pre-programed patterns of development, than through developmentally labile, environmentally cued responses. Early on Janzen (1967) argued that in the tropical dry forests of Central America, dry-season tree flowering happened "as a result of selection for sexual reproduction at the most opportune time in the year, rather than the result of immutable physiological processes which can only occur at that time of year." Janzen regarded sexual selection as the ultimate cause of flowering time, and particular, local environmental triggers as more proximate causes.

Three environmental triggers for flowering are now fairly well known, namely photoperiod, temperature, and moisture. Rainfall can serve as proxy for estimates of soil moisture, which are often not directly available. The trigger date is the starting point in estimating the minimum number of heat units required for floral development in a species. Heat units are expressed typically as degree-days, i.e., as the sum of the mean daily temperatures above some threshold, base temperature.

Bowers and Dimmitt (1994) emphasized that phenological triggers typically act as physiological/biochemical *switches*, serving to break bud dormancy and initiate particular developmental processes, such as leafing out or the switch from a vegetative apical meristem to a flowering one. Once these physiological processes are set in play, they advance as a function of the local temperature and/or daylength. Bowers and Dimmitt (1994) carefully analyzed flowering phenologies in six woody species in the northern Sonoran Desert.

They determined that in *Larrea tridentata*, a wide-ranging evergreen shrub in the Zygophyllaceae, flowering was triggered by rain. The same was true for four other drought-deciduous shrubs: *Fouquieria splendens* (Fouquieriaceae), *Encelia farinosa* (Asteraceae), *Ambrosia deltoidea* (Asteraceae), and *Acacia constricta* (Fabaceae). In a sixth species, the drought-deciduous tree *Cercidium microphyllum* (Fabaceae), flowering was triggered by photoperiod.

The base temperature for floral development in *L. tridentata, F. splendens, E. farinosa, A. deltoidea*, and *C. microphyllum* was about 10°C. Their mean degree-day requirements ranged from 414 to 719. *Acacia constricta* required 522 degree-days above 15°C. The minimum rainfall triggers ranged from 9 mm for *Ambrosia* to 20 mm for *Encelia*. For *Cercidium microphyllum*, the trigger was a daylength of *c*. 11 hours. At flowering, mean degree-days above 10 °C were 719 ± 72.

Bowers and Dimmitt (1994) concluded that flowering time in *C. microphyllum* was most likely

[1] Phenology is the study of periodic life cycle events and how these are influenced by climate and habitat factors, such as elevation. Historically it has been concerned with the dates of first occurrence, e.g., emergence of leaves and flowers, dates of leaf color change, and fall in deciduous trees, etc.

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a product of phylogenetic constraints, while in *F. splendens* it seemed strongly influenced by pollinator availability. Flowering times for the other four species appeared to be more constrained by climatic than biotic considerations—including phylogeny, seed germination, and competition for pollinators. More generally, these authors concluded that phenological strategies for woody dominants in the northern Sonoran Desert could perhaps best be characterized as a "grab-bag," in that species with a variety of triggers and heat requirements coexisted happily. In this desert habitat, a variety of mechanisms trigger flowering in the species studied and no single "desert strategy" was apparent.

Given the significant correlation between optimal timing of flowering and the probability of successful seed-set, the onset of flowering is an obviously critical developmental switch. Aronson et al. (1992) probed the dynamics of vegetative and reproductive activity in three sets of matched pairs of Mediterranean and desert populations using the following annual species: *Erucaria hispanica* (Brassicaceae), *Brachypodium distachyon*, and *Bromus fasciculatus* (both Poaceae). They investigated plant responses under high and low water availability in a common-garden experiment.[2]

Plants from desert populations appeared adapted to shorter, more compressed growth cycles, leading to earlier dates of seed maturation and plant senescence. Desert plants also showed greater phenotypic plasticity in transitioning to senescence (which became even greater following sustained or repeated water deficits). In contrast the individuals from Mediterranean populations tended simply to delay switching from one developmental phase to the next.

Fahmy et al. (1990) considered the relation between timing and leaf-area-lifespan in three closely related leaf-succulent shrubs, *Zygophyllum album*, *Z. decumbens*, and *Z. coccineum* around the year in the Egyptian desert. In all three species vegetative presence was limited to winter and spring (see Figure 6.1). After yellowing and shedding of leaves (during dormancy), vegetative growth resumed in early November for *Z. decumbens* and in the beginning and middle of December for *Z. coccineum* and *Z. album*, respectively. Flowering began in March, coinciding with peak leaf area index in all three species, and persisting for nearly four months in *Z. album* and *Z. decumbens*, and five months in *Z. coccineum*. These three similar species appear to have much niche overlap, and indeed since flowering time overlaps from March–July they do not appear to be avoiding interspecific pollination (by differential timing). Instead there seems to be much resource *sharing* going on in community pollination dynamics.

Any specialization in flowering phenology may be a product of competition among plants for pollinators and pollination services and we expect, in principle, some evolutionary divergence along a limited resource axis (i.e., resource "partitioning"), which would reduce negative interactions among coexisting species. Hegazy et al. (2012) studied the phenology of some twenty species at Wadi Degla, in Egypt. They argued that hyperarid conditions there promote phenological specialization and diversity, including both spatial and temporal partitioning of the flowering and reproductive niche through the year.

Twenty species representing different life forms were investigated over a period of 36 months (January 2004 to December 2006). Populations were sampled at down-stream, mid-stream, and upstream locations in the large, desert wadi ecosystem. Results were analyzed using TWINSPAN, DCA, and CCA techniques.[3]

Five phenological niches were evident along the wadi: (1) species that flowered all year round with

[2] Common-garden experiments usefully help explore the gene-by-environment interaction; however, the garden is not neutral ground, but rather represents a third habitat. More useful are reciprocal transplant-replant studies, that allow parsing of the extent to which plant performance is a product of conditions in one site and/or the other, while controlling for "transplant shock" (see Lovett-Doust 1981b).

[3] Two-way indicator species analysis (TWINSPAN) is a Fortran-based tool widely used in ecological research. Correspondence analysis (CA) is a multivariate technique, conceptually similar to principal component analysis, but pertaining to categorical rather than continuous data. Like principal component analysis, it provides a means of summarizing a set of data in two-dimensional graphical form. Several variants exist, including de-trended correspondence analysis (DCA) and canonical correspondence analysis (CCA). DCA is a multivariate technique widely used to find the main factors or gradients in large, species-rich but usually sparse data matrices.

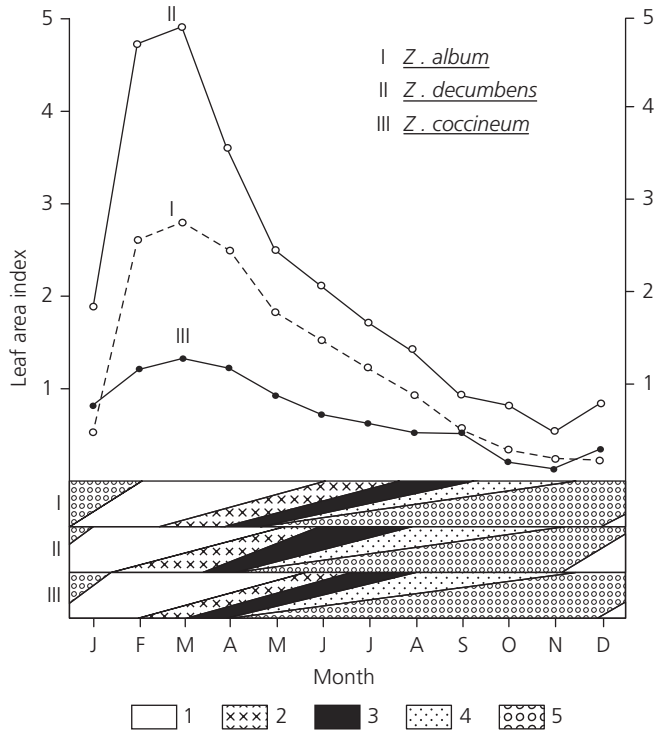



**Figure 6.1** Phenological spectrum and leaf area index of *Zygophyllum album, Z. decumbens*, and *Z. coccineum* in the Egyptian desert (after Fahmy et al. 1990).

peaks in spring and fall, such as *Ochradenus baccatus*; (2) species that flowered during winter, including *Lycium shawii* and *Tamarix nilotica*; (3) species flowering during spring, like *Zilla spinosa, Zygophyllum coccineum*, and *Capparis spinosa*; (4) species flowering during summer, including *Iphiona mucronata* and *Deverra triradiata*; and (5) species flowering during fall, like *Atriplex halimus* and two species of *Anabasis*. Climatic variables including temperature, rainfall, and relative humidity all significantly influenced these temporal niches and inter-species differences.

## 6.2 Pollination syndromes in the desert

Pollination is fundamental to plant reproduction and when carried out by animals is considered a specialized form of mutualism. In temperate regions insects are common pollinators (Moldenke 1975), while in the tropics many species are adapted for bird pollination (see Faegri and van der Pijl 1966). In desert plants it is perhaps not surprising to find that wind-based pollination is most common. Wind pollination is generally more common in floristically depauperate regions with open vegetation, such as subtropical deserts (Bluthgen and Klein 2011; Regal 1983; Shi et al. 2010). Pollination by animals is more complex and requires a series of mutually co-evolutionary exploitative interactions between groups of animals and plants. Plants "reward" pollinators with energy in the form of nectar and pollen. From the plant's perspective, investment in these resources enhances reproductive success by increasing the frequency of pollinator visits (Zimmerman 1988).

It seems clear that at least some of the time, most plants exhibit some pollination failure, suggesting the pollination environment is highly variable (Larson and Barrett 2000; Lee 1988; Lovett-Doust et al. 1987; Stephenson 1981). Sand dunes and other desert habitats provide an unstable, unpredictable environment due to the highly variable weather and sparse resources there. Strong or gusty winds can often impact pollinators negatively (Saunders and Sedonia 2006).

In general in the desert ecosystem, several traits seem necessary for reproductive success. Ma et al. (2007) described a "mass-flowering" pattern, prolonged where there is anthesis under adverse weather conditions, and with flowers opening only under favorable weather conditions.

Desert organisms have been broadly seen as coping with the high seasonality and extreme unpredictability through *generalizing* in their use of a wide variety of resources, which allows them to meet their food needs (in the case of animals) and for plants the satisfaction of their reproductive requirements. Chacoff et al. (2012) carried out a detailed analysis of a four-year plant-pollinator network from the Monte desert in Argentina. The Monte includes various shrub genera that are vicariant in the New World (including *Capparis, Cercidium*, and *Larrea*). The results were complex but consistent with a model of generalized resource sharing.

## 6.3 Breeding systems

Reproductive ecology is extremely important evolutionarily; it determines the extent of self- and cross-pollination, and the distance that pollen and seeds move within populations. Both factors ultimately influence the population genetics and level of inbreeding in populations (Hamrick and Godt 1989; Schoen 1982a, b; Silva-Montellano and Eguiarte 2003a, b). Reproductive ecology also influences the extent of gene flow between and among populations, their effective population sizes, and potential for natural selection to occur (Hamrick and Godt 1989; Parra et al. 1993; Slatkin 1994). Population genetic structure will influence the evolution of reproductive traits and these in turn will depend upon the availability of useful genetic variation in populations, and effective population sizes (Parra et al. 1993).

Silva-Montellano and Eguiarte (2003a, b) studied the relationship between genetic structure and reproductive ecology in populations of *Agave lechuguilla* (Agavaceae), along a latitudinal gradient in the Mexican portion of the Chihuahuan Desert. They showed that floral traits clearly varied along the latitudinal gradient—southern populations had long, tubular, pale flowers that produced large amounts of dilute nectar, and were intensively visited by both nocturnal and diurnal pollinators. In contrast northern populations had shorter, more open, reddish flowers and were less intensively visited. The efficiency of fruit production was also higher in southern versus northern populations.

Despite these differences, and although the overall level of genetic variability was high (expected heterozygosity [He] = 0.394), the levels of genetic variation showed no apparent pattern. Total genetic differentiation among populations was low, although estimates of gene flow (Nm) varied among groups of populations. Southern populations had the lowest levels of differentiation, suggesting high gene flow; northern populations had greater levels of genetic differentiation, suggesting lower gene flow there. Thus the level of pollinator activity can influence floral characteristics, and where pollinator activity is lower the level of gene flow between adjacent populations is reduced.

## 6.4 Semelparous flowering

In Chapter 7 we describe evolutionary "bet-hedging" and show how such a strategy helps explain patterns of dormancy and flexible seed germination, along with patterns of serotinous fruit retention and delayed seed dispersal. Species in the genus *Agave* are monocarpic (semelparous)—that is, individual rosettes have only a single reproductive session and then die (Gentry 1982) (see Section 5.9.1). When flowering begins, agaves and other semelparous species develop a large terminal flowering stalk (or "scape"), as a result of the rapid elongation of the apical meristem following an extended period (up to many decades) of vegetative growth of the basal rosette and root system.[4] One of the major risks faced by long-lived semelparous species is the threat of reproductive failure, which can result from random environmental events. These would reduce the fitness of an individual rosette to zero.

*Agave* flowers produce abundant nectar with which they attract their natural pollinators, including hummingbirds, bats, or insects, depending on

[4] Such "big bang" reproduction is also well exemplified by the synchronized mast flowering seen in many monocarpic bamboos. Janzen (1976) argued this synchrony was due ultimately to the avoidance of seed predation.

the species (Gentry 1972, 1982). Arizaga et al. (2000) pointed out that *paniculate* agaves (i.e., species with branched scapes, belonging to the subgenus *Agave*) are pollinated chiefly by bats. In contrast, spiculate agaves (i.e., species with unbranched scapes and flowers forming directly on the main shoot, belonging to the subgenus *Littaea*) show pollination syndromes suggesting mostly insect-based pollination.

Arizaga and Ezcurra (1995) showed in *Agave macroacantha* that ramets (in this case bulbil-like offshoots, or small rosettes forming vegetatively on lateral meristems of the scape) are produced when pollinators fail to arrive. Having such a "backup plan" is a valuable trait, where failure of flowers to develop seeds in turn relaxes resource demands on the parent, presumably allowing resource reallocation to other tissues. This allows the genet, or genetic individual to persist and reproduce in another year.[5] Arguably this represents a facultative monocarpic strategy, since the process of switching from vegetative to reproductive meristem in this case is not an "all-or-nothing" transition.

The ecophysiology of another monocarpic perennial *Agave*, namely *A. deserti*, a leaf succulent with Crassulacean acid metabolism, has been studied in some depth and is a useful model desert species (see, e.g., Nobel 1987). The plant—commonly called the "desert agave" or "century plant"—grows on dry rocky slopes below 1700 m in much of the Sonoran (Gentry 1982). Even though *A. deserti* mostly propagates vegetatively via clonal ramets, it can produce, generally in spring, a single large inflorescence from the center of a basal rosette of leaves, before dying (Nobel 1987).

Nobel analyzed a wealth of data concerning soil water potential, daily air temperature, photosynthetically active radiation, etc., as well as information about the reproductive activity and size of rosettes. He determined that the percentage of rosettes that flowered each year in his northwestern Sonoran study region, varied *c*. 50-fold over the eight years of the study (maximum lifespan was estimated to be *c*. 55—so not quite a century!) Nobel showed that flowering in the century plant was best predicted by a pair of interrelated factors. First the number of wet days occurring *two years previously* ($r^2 = 0.33$). This suggests inflorescence differentiation was triggered and floral initials laid down *c.* two years before the inflorescence actually appeared. Second, years with a high percentage of flowering tended to alternate with those of a low percentage ($r^2 = 0.64$). Such year-to-year alternations in flowering have also been observed for polycarpic (iteroparous) desert perennials. The two conditions of yearly alternations and wet days two years previously, when taken together accounted for 95% of the year-to-year variation in percentage flowering.

## 6.5 Apomixis (asexuality and a balance between long- and short-term advantage)

*Apomicts* are plants able to produce seeds without undergoing sexual reproduction (that is, seeds in apomicts are produced through mitosis, rather than through meiosis and recombination). These asexually derived seeds are in effect highly mobile *ramets*—units of clonal growth having the enhanced distance-dispersal features of the seed. Some apomicts are facultative in that they can also carry out sexual reproduction. Of these many are polyploid, and nearly all perennials (e.g. *Oxalis dillenii* ssp. *filipes*, Bierzychudek 1987; Lovett-Doust et al. 1985). Apomicts are especially common among Asteraceae, Poaceae, and Rosaceae (Nygren 1967), but also occur in other Angiosperm families.

It is noteworthy that apomicts typically have close relatives that are sexual, often in the same genus or species, and apomictic lineages can outnumber the related sexual taxa by an order of magnitude or more. The blackberry *Rubus fruticosus* agg. is represented in Britain by one sexual form and some 368 distinct apomicts. Ninety percent of

[5] In plants the sexual life cycle proceeds from genet to genet, i.e., one zygote develops through adulthood to produce progeny that are the product, first of meiosis (producing gametes) and then recombination when that gamete is fertilized, to form the new generation of genets (sexually derived progeny). Vegetative propagation (i.e., clonal growth of ramets) involves solely *mitotic* activity and extension of the individual genet in time and space. In different species various specialized organs have evolved, all serving to further the ecological and evolutionary benefits of clonal growth. Such structures include runners and suckers, rhizomes, stolons, corms and cormlets, turions, bulbs and bulbils, root buds, etc.

known dandelion "species" are obligate apomicts (Richards 1973). Clearly the species concept, and indeed the population concept in this context, is inappropriate, as the "micro-species" of apomicts are, really, simply clonal lineages.[6] The existence of such closely related sexual and asexual taxa offers excellent opportunities to compare the long- and short-term consequences, and assess the relative costs and benefits of sex versus asex; it also suggests that apomixis has evolved recently and separately in many taxa (Silvertown and Lovett-Doust 1993).

If asexuality had given apomicts a long-term advantage over sexual taxa we would expect many apomicts to have no living relatives that resemble them. Such relatives should have been displaced by competition from apomicts, or should have diverged during evolution. Apomicts and their related sexual taxa often have distinct geographical distributions, with apomicts predominantly being found in geologically more recent habitats, in regions which were previously glaciated (Bierzychudek 1987). This also suggest apomicts may be better at colonization than they are at long-term persistence, and would match with the greater efficiency of their seed production, essentially making them more r-selected than their sexual relatives.

## 6.6 Sexual specialization and lability in expression

Plant reproductive success is often a direct function of their size. If male and female organs can be separated in time or space, and if the curves of fitness plotted against size for male function and female function intersect each other, the best strategy will be to specialize as one sex when small and the other when large, so natural selection ought to favor a change in sex expression as a plant grows (see Figure 6.2) (Ghiselin 1969). Sex change with size is a fundamental feature of the life history of a number of plants, for example in *Acer grandidentatum* (Barker et al. 1982), *Atriplex* spp. (Freeman et al. 1984), and *Arisaema triphyllum* (Lovett Doust and Cavers 1982c). In all these cases, smaller plants tend to be male and larger ones female or cosexual.

[6] Usually called "agamospecies" (Richards 1986).

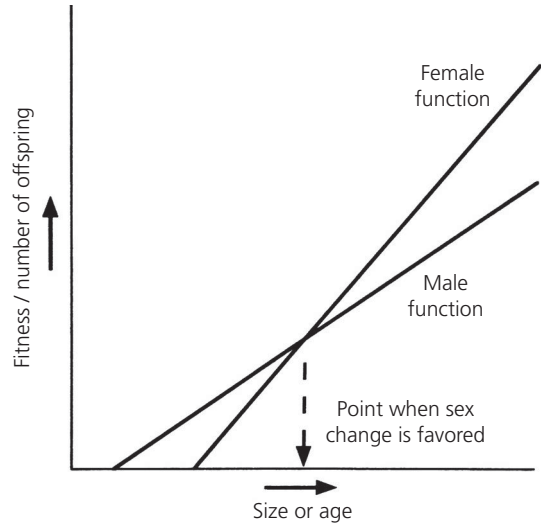



**Figure 6.2** Relationship between fitness returns of male and female function when these are age- or size- dependent and favor a change in sex (after Silvertown and Lovett Doust 1993).

Freeman et al. (1997) present evidence from an array of species suggesting that instances of sex lability, or the presence of an array of sexual intermediates, of sex-switching, and sexual niche differentiation[7] can largely all be explained in terms of the pathway taken in the evolution of a particular dioecious species. Moreover the degree of sexual dimorphism seen in dioecious species is often correlated with the mode of pollination, whether insect- or wind-pollinated (with insect-pollinated species more sexually dimorphic, presumably due to pollinator-driven selection pressures, and other ecological factors).

[7] Niche differentiation between the sexes has been called the "Jack Sprat effect" following the nursery rhyme: "Jack Sprat could eat no fat, his wife could eat no lean, and so between the two of them, they licked the platter clean" (see Cox 1981). Thus in some dioecious species the two sexes may be separated spatially—along gradients of moisture, nutrients, light, temperature, and salinity (Cox 1981; Freeman et al. 1976; Lovett-Doust and Lovett-Doust 1988; Ramadan et al. 1994), with females typically more common under the less stressful conditions. In *Rumex acetosella* (Lovett-Doust and Lovett-Doust 1987) and spinach (Onyekwelu and Harper 1979) females remain alive longer each season, enabling them to cover their greater reproductive costs and even, in the case of *R. acetosella*, ending up ahead of males in terms of clonal growth (Lovett-Doust and Lovett-Doust 1987).

### 6.6.1 *Thymelaea hirsuta*

*Thymelaea hirsuta* is a wind-pollinated, evergreen desert shrub found throughout the Mediterranean region. Sex expression in this species is complex and highly labile (E1-Keblawy et al. 1995, 1997). Observations over several years show that plants fall into one of two classes of sex phenotype: individuals are either stable in their sex expression (i.e., constant over time as males or females) or they are sexually labile (changing sex expression to varying degrees over the flowering season, and/or from year to year).

It is possible that the more "constant" male and female sex morphs in *Thymelaea* are somehow more genetically fixed in their sex expression, while sexually labile individuals are more sensitive to environmental factors influencing sex expression. Alternatively, "constant" males and females may simply represent two extremes of a sexual continuum, where individuals have high environmental thresholds for inducing formation of flowers of the other sex.

The frequency of particular sex phenotypes, the percentage of biomass allocated to reproduction by each genotype, the germination rates of seeds from different genotypes, seedling growth rates, and other aspects of reproduction in *T. hirsuta* all differ among different habitat sites (E1-Keblawy et al. 1995, 1996a, b, 1997; Ramadan et al. 1994). In this species, in Egypt, sexually labile individuals appear to make up the majority of most populations; in contrast it is interesting to note that Dommee et al. (1990) have not so far seen labile sex expression in individuals in populations of the same species in France.

One interpretation of the Egyptian data is that the species is demonstrating some partial niche separation among the sex classes (Ramadan et al. 1994), although the different forms coexist at all sites. For example, the andro-monoecious "phase choice" individuals (see E1-Keblawy et al. 1995) represent only 2.8% of the individuals in coastal dunes but make up more than a third of individuals in the more arid and unpredictable habitat of the inland plateau.

In the coastal dunes, seedlings from protandrous mothers (where male organs were produced first) grew significantly better than seedlings from protogynous mothers (where female organs were produced first), but the reverse was true at the harsher inland sites. It seems reasonable to propose that the inherent unpredictability of the heterogeneous Egyptian desert may maintain this diverse breeding system. It is not clear whether any apparent niche segregation is due to environmental effects on sex expression in gender-labile plants, or to differential selection of individuals that place in different positions along the spectrum of expression between "constant" male and female sex phenotypes. Further work, including transplant experiments and tracking controlled crosses between plants of contrasting sex phenotype is needed to clarify this.

### 6.6.2 *Atriplex canescens*

*Atriplex canescens* is a woody chenopod shrub widely distributed in western North America (Freeman et al. 1984). The species was introduced to some Middle Eastern countries and is now considered a naturalized invasive in sandy habitats (Boulos 2009). Although most systematists now believe that primitive flowering plants were woody, woodiness in *chenopods* is regarded as a derived condition (Cronquist 1981; Stebbins 1974). Evidence for the secondary nature includes anomalous secondary thickening of woody stems and roots, derived C4 photosynthesis in many shrubs but in only a few herbs (*most* herbs use the more common and primitive C3 pathway).

Reproductively, in a number of shrubby chenopods, there appear to be complex sexual systems (McArthur 1989; McArthur et al. 1992; Pendleton et al. 1988; Stebbins 1974). In contrast to those woody shrubs, the majority of herbaceous chenopods either produce perfect flowers or are monoecious (Smith 1982).

*Atriplex canescens* normally produces unisexual flowers and in most populations a few individuals also produce a small fraction of perfect flowers (Barrow 1986; McArthur et al. 1992). Unisexual flowers appear to have evolved early in the history of the family and *Atriplex* species are generally regarded as either monoecious or dioecious. However, much evidence shows that some individuals of *A. canescens* are sexually labile, while others are constant

(genetically determined) males or females, unable to alter their sexual expression.

There has been some argument on how to characterize such forms as the "hermaphrodites" of *A. canescens*. They appear to be categorically different from constant males and females (i.e., they are not examples of the minor deviations that Lloyd and Bawa (1984) described as sexually "inconstant" male and female individuals.) Freeman et al. (1997) argued that true examples of sex inconstancy in plants are found in species which evolved dioecy via gynodioecy. In *A. canescens* and species that developed dioecy via monoecy, the occurrence of sexual intermediates and lability are the rule rather than the exception. The "hermaphrodites" described in *A. canescens* were not a homogeneous group; indeed, like *Thymelaea* and spinach (Wachocki 1992), *A. canescens* can perhaps better be regarded as having multiple morphs.

### 6.6.3 *Ochradenus baccatus*

*Ochradenus baccatus* is a semi-deciduous shrub commonly found in wadis throughout the Judean Desert and Arava Valley in Israel and elsewhere (Wolfe and Shmida 1995, 1997) (see too Amer et al. 2015, and Section 7.7). Although most flowering and fruit production occurs from January through April, large plants may bloom throughout the entire year. These flowers were visited by many different pollinators, including bees, beetles, wasps, and flies, collecting pollen and/or nectar. The inflorescence consists of long, terminal, spike-like racemes loaded with small, yellow flowers and green fruits that become waxy-white when ripe. Wolfe and Shmida described *gynodioecious* populations of *O. baccatus*, where hermaphrodite and female flowers were produced on different individuals in various patterns across the range in Israel.

Gynodioecy often exists in nature as a "subdioecious" or transitional sex habit, typically interpreted as evolving toward some more complete form of dioecy. Charles Darwin was one of the first to see the importance of gynodioecy, in which separate female and cosexual or "hermaphrodite" individuals co-exist in populations. This sex habit has been regarded as a step in the evolutionary pathway from monoecy (with its monomorphic populations composed of individuals producing gametes of both sexes, but in separate flowers), to dioecy (with its dimorphic populations and separately sexed male and female individuals). It is generally believed this transition occurs mostly by invasion of specialized female mutants into previously hermaphroditic populations (Charlesworth and Charlesworth 1978).

Both female and hermaphrodite forms are expected in general to become more specialized and differ in their responses to the effects of pollination, because hermaphrodites can potentially self-pollinate whereas females cannot. Differences are well known to exist between these two sex forms in terms of both seed quantity and quality. Wolfe and Shmida studied sex expression over time in *O. baccatus* and identified sex inconstancy in maleness as a critical variable. They argued ecological constraints of desert life—the severe seasonality and highly unpredictable rainfall—favor the maintenance of sex inconstancy in males, which in turn helps stabilize the gynodioecious habit there.

They argued that typically most growth and reproduction in the desert occurs during and immediately after the rainy season (to the degree there is any rain). However, most large *O. baccatus* individuals remain in bloom all year. Since inconstant males are larger than both females and pure males, inconstant males are disproportionately represented among summer-blooming individuals. During the summer the size of the population and hence the number of potential mates is lower than during the winter. Pollinators are also less abundant in the summer. Wolfe and Shmida suggested it is in precisely this sort of ecological situation (small population size in terms of currently breeding individuals and low pollinator service) that sex inconstancy and the ability to self-pollinate would be most advantageous. They concluded the capacity to reproduce during the hot summer is a further factor maintaining male inconstancy in *O. baccatus*.

Hegazy et al. (2011b) reported an extended reproductive period in *O. baccatus* at Wadi Degla in Egypt, where there were two peaks, one in spring and one in fall. The extended activity was size related and spring performance was greater than autumn. Female individuals compensated for their lower frequency in the population (and likely lower

total pollinations) by producing more fruits, seeds of greater mass, and having a greater percentage germination rate than seeds from hermaphrodite individuals.

### 6.6.4 *Acer negundo*

Although native to North America, *A. negundo* trees were introduced and have become invasive in parts of Europe and Asia. The species quickly colonizes cultivated, uncultivated, and riparian areas; this has led to significant range expansion and it has also become naturalized in many countries and is found in some of the cooler parts of the Middle East.

Dawson and Ehleringer (1993) investigated physiological sex specialization in the deciduous, dioecious *Acer negundo* which, like many dioecious species shows significant, habitat-specific biases in terms of sex ratio. Under both field and controlled-environment conditions, males and females also differed significantly in a number of water-use traits. For example males maintained lower values of stomatal conductance to water vapor, transpiration, net carbon assimilation, leaf internal $CO_2$ concentration (*ci*), carbon isotope discrimination ($\Delta$; an index of time-integrated *ci* and water-use efficiency), and higher values of both instantaneous- and long-term water-use efficiency than females. Moreover male trees had greater stomatal sensitivity to both declining soil water content and increasing leaf-to-air vapor pressure gradients, a measure of evaporative demand. Higher rates of carbon fixation in female trees were correlated with higher stomatal conductance, higher leaf nitrogen concentrations, and greater stomatal densities.

The frequent occurrence of male plants in poorer (drier) habitats and female plants in richer (moister) habitats is now well documented in many dioecious and sub-dioecious species (e.g., Cox 1981; Lovett-Doust and Lovett-Doust 1987), though the role that physiology may play in helping explain this pattern is not well understood. Although sex ratio in *A. negundo* varied along a soil moisture gradient, neither sex demonstrated tolerance to water deficit (males closed their stomata and actively prevented water deficits while females essentially did not establish in xeric sites). Dawson and Ehleringer show how sex-specific physiologies help explain the maintenance of habitat-specific biases in sex ratio, as well as sex-based size differences in plants. Sex-specific physiological differences may have evolved to meet the significantly different, and greater, costs associated with reproduction as a female.

### 6.6.5 *Pinus halepensis*

Pines—as both genus and family—have been viewed as generally well adapted to moderate- to low-fertility habitats and exploitation of open conditions that may be a result of sparse nutrient availability, or by intermittent disturbance especially fire (Keeley and Zedler 1998). Pines are an important tree in the Middle East and it has been suggested that fires—caused both by lightning and human activities—have strongly shaped the evolution of certain pine species, including *Pinus halepensis* (Aleppo pine). Such "pyrophytes" show certain key adaptations related to fire.

Ne'eman et al. (2004) examined 21 life history traits in *Pinus halepensis* and their contributions to either post-fire regeneration and/or to circumstances where there might be no fires (and potentially fewer opportunities for new colonization events). As it turned out the species does well in both these circumstances. Such a "dual strategy"—and the fact that its ability to regenerate after fire is one of its major invasive features—makes it difficult to evaluate the relative contributions of individual traits to this success. Nevertheless Ne'eman et al. showed that most of the 21 traits made positive contributions to post-fire regeneration.

Table 6.1 shows the distribution of traits according to their contribution to post-fire regeneration (18 positive, 2 negative, and 1 neutral). The distribution according to their contribution to invasion in the absence of fire was: 7 positive, 7 negative, and 7 neutral. Twelve traits contributed to both, or to one, and were neutral in regard to the other. Seven contributed positively to post-fire regeneration and negatively to establishment in the absence of fire, and only two traits contributed positively to invasion in the absence of fire and negatively to post-fire regeneration. Overall, the preponderance of traits support post-fire regeneration, and about half of all traits benefit plants in both situations.

**Table 6.1** The contribution of the major life history traits in *Pinus halepensis* to its post-fire regeneration or no-fire invasive ability. + is positive value, 0 is indifferent and – is negative value, * is positive contribution to post-fire and negative to no-fire situations (after Ne'eman et al. 2004, used with permission).

| Life history traits | Post-fire regeneration | No-fire invasion |
|---|---|---|
| *Flammability | + | – |
| Thin bark | + | 0 |
| Non self-pruning of branches | + | 0/– |
| Non self-pruning of empty cones | + | 0/– |
| Early age of first reproduction | + | + |
| Production of female cones first | + | + |
| Winged seeds and long range dispersal | 0 | + |
| *Color change in post-fire dispersed seeds | + | – |
| **Non-serotinous cones** | | |
| Xeriscence (drought-induced cone opening) | – | + |
| *Pyriscence (fire induced cone opening) | + | – |
| **Serotinous Cones** | | |
| Xeriscence (drought-induced cone opening) | – | + |
| *Pyriscence (fire-induced cone opening) | + | – |
| *Higher percentage in young trees | + | – |
| *Higher percentage in post-fire stands | + | – |
| **Germination** | | |
| Effect of light | + | + |
| Effect of temperature | + | + |
| *Seeds from serotinous cones | + | – |
| **Effects of ash** | | |
| pH | + | 0 |
| ammonium | + | 0 |
| Nitrate | + | 0 |
| Relative establishment success | + | 0 |

The typical sex habit of pines is monoecy—that is individuals bear separate male and female strobili (cones) (Mirov 1967). This is usually accompanied by dichogamy, temporal separation in male and female expression. Sometimes dichogamy is female-first (protogyny), sometimes male-first (protandry). In *P. halepensis*, trees typically begin the season as females and later turn bisexual, when they begin producing male cones as well as female.

Shmida et al. (2000) recorded patterns of sex expression at a three-year-old post-fire stand on Mount Carmel, Israel. Some 93% of reproductive individuals were female, 6% were male, and 1% bisexual (see Table 6.2). This protogynous segregation of the sexes contrasts with the general pattern reported in many other monoecious species. Because female success is typically limited by the availability of resources (Charnov 1982; Lovett-Doust and Cavers 1982a, b, c), younger and smaller individuals are typically all male, and female sex expression only follows later when plants are larger.

Arguably, this type of dichogamy is advantageous in a post-fire environment as, in that relatively open habitat, female cones can receive wind-borne pollen from distant pollen parents. In addition fire-induced seed release (pyriscence) is extensive in the species and leads to widespread post-fire recruitment. *Xeriscence*—drought-induced seed release (see Chapter 7)—accounts for the majority of seeds released over a tree's lifetime (Ne'eman et al. 2004). Non-abscission of dead cones and branches, and high resin content in *Pinus* tissues, increases the likelihood of canopy fires and consequent death of adult trees. Collectively these contribute to the fire-related regeneration niche of this species.

In general, species that release their seeds following fire may regenerate either from the soil seed bank or from a serotinous canopy-stored seed bank. In *P. halepensis* there is nearly always high predation pressure on seeds in the soil—on the order of 97%; hence seeds are almost completely absent from the pine forest soil seed bank (see Ne'eman et al. 2004). Young reproductive trees function first as females, with a high percentage of serotinous cones. This seems to be to some degree inducible; the proportion of serotinous cones was higher in post-fire stands that were naturally regenerating than in unburned stands.

Any seeds that do germinate under the forest canopy would produce seedlings that will fail to grow and reproduce in the shade. As a result regeneration in the absence of fire was found to increase significantly with distance from the adult trees. When there is essentially no soil seed bank, *all* post-fire

**Table 6.2** Percentage of non-reproductive (vegetative), female, male and monoecious trees in *P. halepensis* and *P. brutia* at Lahavim (plantation in arid area), Mount Carmel (natural post fire regeneration) and Yoqneam (3 m high understory and open area natural regeneration of a 40-year-old plantation) (after Shmida et al. 2000, used with permission of the author).

| Species and site | Age/height | Veg. | Female | Male | Monoecious |
|---|---|---|---|---|---|
| *Pinus halepensis* | | | | | |
| Lehavim | 4 years | 1 | 56 | 1 | 36 |
| Lehavim | 13 years | | | | 100 |
| Mount Carmel | *3 years | | 93 | 6 | 1 |
| Mount Carmel | 9 years | 13 | 48 | 12 | 27 |
| Yoqneam sunny | 3 m | 8 | 75 | 4 | 13 |
| Yoqneam shaded | 3 m | 12 | 9 | 64 | 15 |
| *P. brutia* | | | | | |
| Lehavim | 8 years | 4 | 13 | 1 | 82 |

*Only reproductive trees were counted

regeneration will depend on canopy-stored seeds, in serotinous and non-serotinous cones.

### 6.6.6 *Diplotaxis harra*

Plant life histories have often been classified in terms of the duration of life span of individuals into annual, biennial, and perennial forms (see Section 5.9). However, these descriptive categories may be more labile than previously recognized. In some species, for example, not all individuals in an "annual" population are necessarily monocarpic; in certain situations some individuals may shift to a repeated-flowering mode and act as short-lived perennials. On the other hand, especially in arid and semi-arid regions, "perennials" may sometimes behave as annuals (e.g., Hegazy 2001; Hegazy et al. 2010). Such diversity may help individuals to persist and delay reproduction in an environment with extended drought.

Reproductive behavior in *Diplotaxis harra* (Brassicaceae) is known to vary according to the amount of rainfall. Three distinct "ecological lifespans" have been identified in Egyptian populations (Hegazy 2001).

1. An "ephemeral" lifespan where plants produce an unbranched stem having a single inflorescence. Individuals are more or less synchronous in their germination, growth, reproduction, and death and the life history typically extends for 6–8 weeks. This pattern dominates when annual rainfall is <50 mm.
2. A "continuous-flowering," but monocarpic life history where plants maintain the potential for continued vegetative growth and sexual reproduction until drought conditions become too great. These plants have branched stems bearing two or more inflorescences. Branches do not flower synchronously but sequentially, and flowering can extend for up to 15 weeks. This pattern occurs when annual rainfall is about 80 mm and plants will continue, facultatively to form new shoots for as long as conditions allow growth.
3. In some circumstances we see a form of herbaceous perennial, polycarpic behavior, when plants maintain a persistent vegetative stump during the adverse season. This pattern is usually seen when annual rainfall is >80 mm and soil moisture remains high during summer. These herbaceous ("coppiced-like") plants may survive up to five years, and their reproductive activity extend for up to five months each growing season. In these individuals the base of the stem forms a thick caudex or crown arising from the upper part of the root, which persists through the adverse season and produces new shoots the following year.

A summary of the forms present in a four-year-old population of *D. harra* at Wadi Hof, in Egypt's Eastern Desert is shown in Figure 6.3. About half (47.6%) of all juveniles reached adulthood. Most adults (72.7%) completed their life span as ephemerals in less than six weeks; 27% extended their growth and life span for 6–8 weeks as branching plants; and only 0.3% persisted in the herbaceous form for up to four years (Hegazy 2001).

Overall total seed production was *c.* $6.7 \times 10^6$ seeds/$m^2$. The branching plants contributed 45.8% of that, the ephemerals 31.2%, and the herbaceous individuals some 22%. The three "strategies" can be seen positioned along the r-K continuum with ephemerals and branched plants more r-selected, and herbaceous individuals more K-selected. This is seen in terms of increased seed output per individual in the case of the herbaceous perennial individuals (see Figure 6.4). Looking at the population overall, the mean number of seeds per plant ranged from *c*. 1760 to 106 980 for r-selected and K-selected forms, respectively.

Ephemeral individuals of *D. harra* allocated about a third of their dry mass to reproductive structures (with values ranging from 27.4 to 52.5%). Meantime allocation ranged from 15.1 to 41.3% in branching plants and 9.5 to 19.1% in herbaceous plants. Minimum reproductive effort of the ephemeral growth form (i.e., reproductive biomass as a fraction of total biomass) was greater than that of the branched, which was in turn greater than that of the herbaceous form. *Ebenus pinnata* also produces these three functional types (see Figure 6.5).

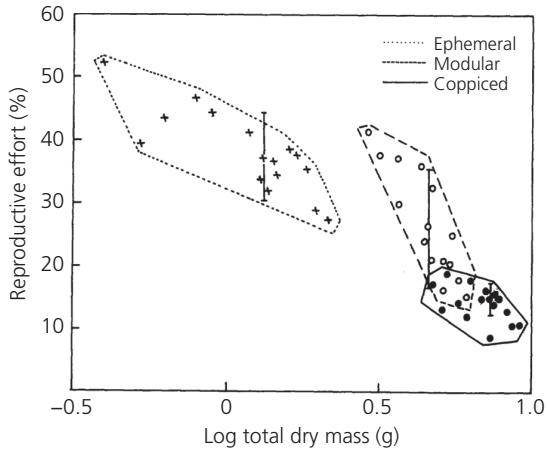



**Figure 6.4** Scatter plot of reproductive effort (%) and log total dry mass per plant in the ephemeral, branching/modular, and herbaceous/"coppiced" plants in *Diplotaxis harra* population. Points with vertical bars are means ± SD (after Hegazy 2001, used with permission).

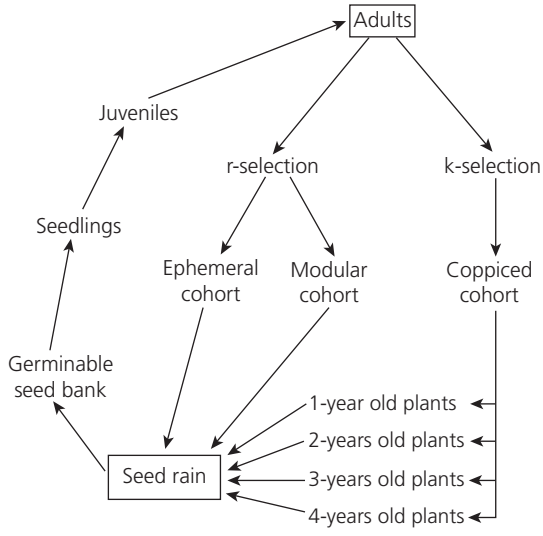



**Figure 6.3** Ecological life cycle of *Diplotaxis harra*. Juvenile plants may give ephemeral, branching/modular, and herbaceous/"coppiced" cohorts of adult plants (after Hegazy 2001, used with permission).

## 6.7 *Euphorbia* species

As with the highly evolved "floral packages" of the aroids, umbellifers, and asters, the evolution of cyathia (or "pseudoflowers") in members of the genus *Euphorbia* (Euphorbiaceae) is associated with significant adaptive radiation. Indeed *Euphorbia* is one of the largest Angiosperm genera, including >1800 species worldwide. It is Old World in origin and is well represented in the Middle East (e.g., Sections 5.7 and 7.9). The genus includes a remarkable diversity of both succulent and non-succulent species that are raised horticulturally, and they also show a great diversity of growth forms. Euphorbias are readily recognized by the milky latex in their stems and organization of the highly reduced flowers into a characteristic inflorescence, the *cyathium*, which acts as a

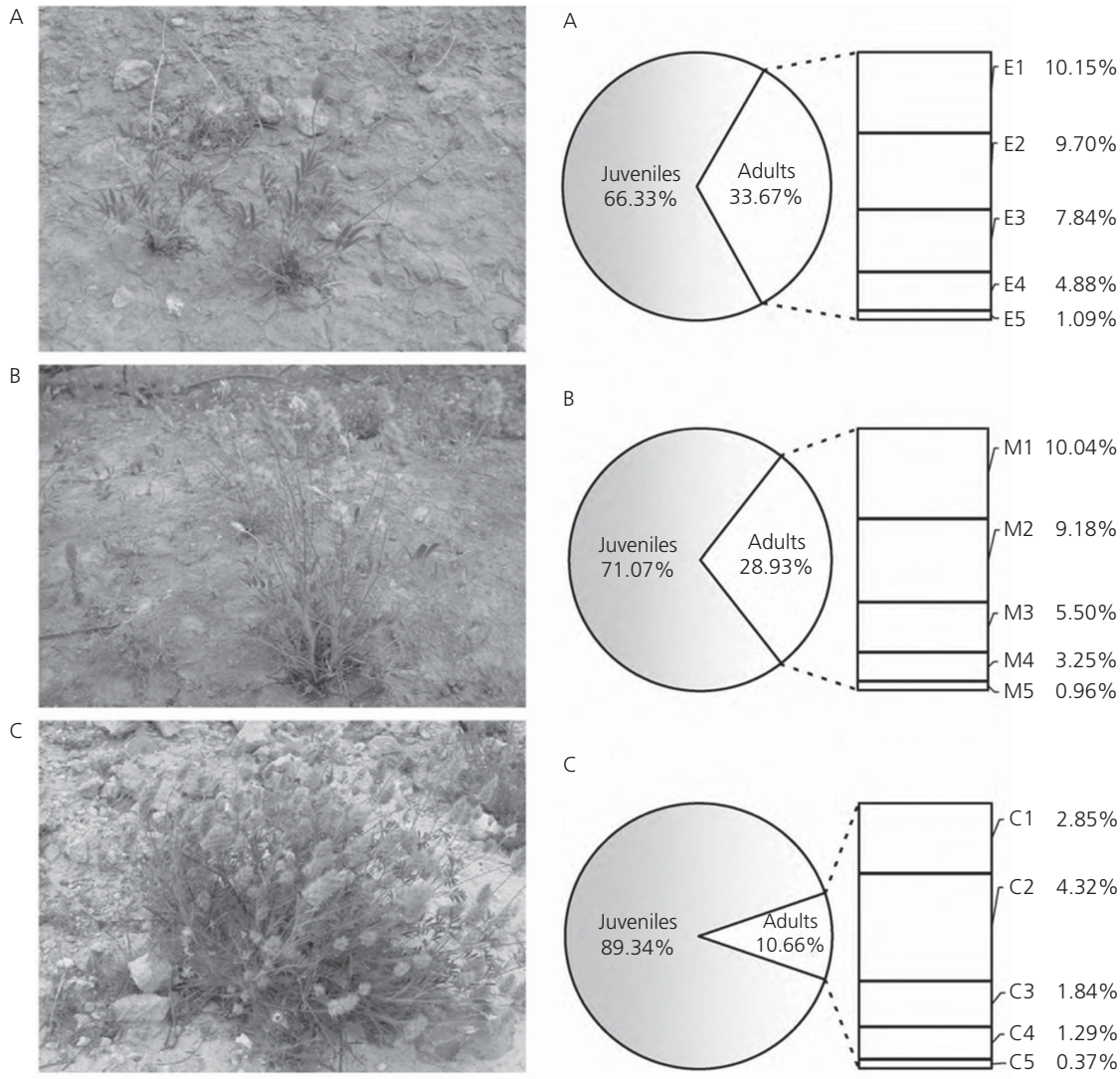



**Figure 6.5** Functional types of *Ebenus pinnata*. (A) ephemeral type. (B) branching/modular type. (C) herbaceous/"coppiced" type. Note different soil textures. Juvenile and adult demography (percent contribution) of the three functional types, based on number of inflorescences per individual. Ephemeral type (A) is represented by plants having 1 (E1), 2 (E2), 3 (E3), 4 (E4), and 5 (E5) inflorescences per individual. Modular type is represented by individuals having <10 (M1), 10–15 (M2), 16–20 (M3), 21–25 (M4), and >25 (M5) inflorescences per individual. "Coppiced" type is represented by individuals having <50 (C1), 50–70 (C2), 71–90 (C3), 91–110 (C4), and >111 (C5) inflorescences per individual. (Adapted from Hegazy et al. 2010.)

pseudanthium (or inflorescence "masquerading" as a flower).[8]

The cyathium consists typically of a single naked[9] pistillate flower surrounded by cymes[10] of naked staminate flowers, each consisting of a single stamen. These individual floral units are all enclosed in a cup-like involucre (or covering) that is typically provided with peripheral nectaries and petaloid appendages, such that the whole aggregation, taken together, closely resembles a single flower. From this basic structure various elaborations have evolved, including development of colorful subtending bracts, cyathial nectary glands with petaloid appendages, and fusion or addition of cyathial glands.

The large *Euphorbia* genus overall is considered as being essentially monoecious in its sex habit, aside from the relatively few dioecious species (separately sexed individuals), mostly in sect. *Tirucalli*. This Old World section of the genus includes species with several growth forms and a diversity of cyathial and fruit characters,[11] but it is distinguished from other clades of the genus by the fact that most species are dioecious. A number of these are found in Africa and the Arabian Peninsula (e.g., *E. tirucalli, E. uzmuk, E. decorsei, E. arbuscula*, and *E. stenoclada*). In monoecious species the pistillate or female flower of the cyathium typically develops before the male—making each cyathium behave functionally just like a protogynous hermaphrodite "flower." The glands usually produce nectar and pollination is mainly by animals.

Narbona et al. (2002) investigated the occurrence of cyathia containing staminate flowers but lacking a pistillate flower, in 17 species of *Euphorbia*. Such "male" cyathia proved to be widespread, present in the majority of these species (88.2%), with the net effect of giving these plants a functional andromonoecy—a sex habit where individuals produce both hermaphrodite and staminate flowers (here cyathia). Andromonoecious sex expression (i.e., the *proportion* of hermaphrodite and male flowers per plant) is in general often highly variable among individuals, populations, and years (e.g., Diggle 1994; Lovett-Doust 1980, Lovett-Doust and Harper 1980). Among euphorbs, sometimes young plants or those growing under unfavorable conditions are male only, and female flowers are only produced as the plant matures or growing conditions improve.

In these specialized male cyathia, female flowers were generally totally absent except for an occasional vestigial flower with non-functional ovary. In annual species there was a trend for production of male cyathia only in the first level of the compound inflorescence, whereas in perennials their production typically occurred up to the fourth level (Narbona et al. 2002).

Why might this widespread habit of andromonoecy have evolved? Male function requires fewer resources than female (Charnov 1982), and in a resource-limited environment spatial segregation may facilitate females persisting in "better" locations where those greater costs could be borne. Narbona et al. observed that the proportion of all-male cyathia varied according to life form, with perennial species producing a significantly greater proportion than annuals. They interpreted this in terms of promoting outcrossing; long-lived species tend to have higher genetic loads and greater inbreeding depression when self-fertilization occurs. It is quite

[8] A pseudanthium is in general a special type of inflorescence, in which anything from a small cluster to hundreds or sometimes thousands of flowers are grouped together to form a single flower-*like* structure. The pseudanthial inflorescence of *Euphorbia* looks superficially like a typical dicot flower, but in developmental terms it is intermediate between a flower and an inflorescence (see Prenner and Rudall 2007). In general individual "flowers" or florets of a pseudanthium are greatly reduced but the pseudanthium itself can sometimes be quite large (as in, for example, the analogous capitula, or heads, of some varieties of sunflower). The structure represents an evolutionary convergence of the inflorescence toward a compressed reproductive unit that may function in pollination like a single flower, at least in plants that are animal-pollinated.

[9] Here botanical nakedness means lacking any petals or sepals around the androecium or gynoecium.

[10] Inflorescences are often classified according to whether they are determinate or indeterminate in their growth. Determinate simple inflorescences are generally called cymose. The major type is the cyme, in which the first flower is the terminal bud of the main stem and subsequent flowers develop as terminal buds of lateral stems. Compound cymes are further divided according to the number of secondary axes: one (a monochasium); two (dichasial cyme); or more than two secondary axes (pleiochasium).

[11] The fruits are three- (rarely two-) loculed capsules, sometimes fleshy but almost always ripening to a woody container which then splits open (typically explosively). Seeds are four-angled, oval or spherical, and in some species have a caruncle, or fleshy appendage.

possible that greater production of male cyathia may be promoting outcrossing.

The entire *Euphorbia* genus has fruits with explosive dehiscence, an effect produced by the differing orientation of cells of the mechanical wall (Berg 1990). In most cases the seeds also have a lipid-rich *caruncle* that functions as an elaiosome, attracting ants and initiating a myrmecochorous secondary dispersal (Berg 1975). Narbona et al. (2005) studied patterns of dispersal in *Euphorbia boetica* and *E. nicaeensis*. Both are perennial shrubs that branch at the base and reach heights averaging 50 and 60 cm, respectively. Each branch forms several pleiochasia or dichasia, which bloom sequentially in the spring.

Both species had an efficient mechanism of explosive dispersal. Seeds of *E. boetica* reached a median distance of 156 cm and a maximum of *c*. 8 m, while seeds of *E. nicaeensis* did not travel quite as far (a median of 132 cm and a maximum of 5 m). Differences appeared to be related to both the mass of individual seeds and retention of the caruncle. Seeds of *E. boetica* shed the caruncle at the time of the explosion, favoring longer distance primary dispersal, while the seeds of *E. nicaeensis* had a larger, strongly attached caruncle so did not initially travel as far, but the caruncle favored their further secondary dispersal by ants (Narbona et al. 2005).

## 6.8 *Acacia*, a keystone tree species in the Middle East

Members of the polyphyletic group *Acacia* (*sensu lato*) share certain reproductive traits typical of successful invasives (Gibson et al. 2011) (and see Sections 7.8.1 and 11.2). Their flowers are attractive to diverse pollinators, and their floral morphologies enable promiscuous pollination (rather than flowers selecting for specialists through long tubular structures or other adaptions that confer preference for certain pollinators). As a result in acacias, most floral visitors could be potential pollinators. These plants also produce large numbers of flowers that persist for a considerable time. They may be able to self-pollinate, and also undergo clonal growth (vegetative propagation). Flowering tends to be induced by similar triggers to those of native species.

All acacias produce small, tubular flowers clustered in spherical or elongate flower heads. Pollen grains in turn are clustered into "polyads"—groups of an indeterminate number, which provide opportunities for increasing pollination efficiency. There are always fewer ovules per ovary than pollen grains per polyad, so one polyad delivered through a single pollination event can fertilize all the ovules in the flower (see Gibson et al. 2011).

In a large survey of the genus, Kenrick (2003) concluded that final pod set (i.e., pods/inflorescence) was relatively low in many Acacias. Morgan et al. (2002) observed that low pod set in *A. baileyana* was offset by precocious flowering and high flower number; this resulted in high seed production and likely facilitates species success. Shorter juvenile periods ensure seeds are produced earlier, a more r-selected strategy of precocious reproduction that is associated with colonization and invasiveness.

Among Australian acacias, species range from being highly self-incompatible to completely self-compatible and autogamous; as a result they may vary greatly in their dependence upon pollinators. According to Gibson et al. (2011) realized outcrossing rates tend to be high; the multi-locus outcrossing rate tm > 0.9 in most species studied. This suggests pollinators do play an important role in their reproduction.

Gibson et al. investigated features of the reproductive biology of Australian acacias particularly associated with invasiveness. Invasive acacias reach reproductive maturity earlier in life and were more commonly able to regenerate shoots following cutting or damage than non-invasive species. Acacia plants can also regenerate vegetatively from root buds and stem bases (Bell et al. 1993; Reid and Murphy 2008).

Munzbergova and Ward (2002) considered the notion that *Acacia* species act ecologically as *keystone* species in the Negev, where three species: *A. raddiana, A. tortilis*, and *A. pachyceras*, are the only trees present and therefore constitute a major ecological factor in southern Israel (Danin 1983) (see, too, Ward et al. 2012, Section 7.8.1). Since many *Acacia* populations suffer high mortality due to water stress, these authors explored the hypothesis that *Acacia* trees in populations that were suffering high mortality would also show diminished beneficial

effects on plant species and soil quality under their canopies.

There is widespread concern about *Acacia* mortality in the Negev. Mortality rates vary widely but reach more than 60% in some populations of adult trees. Mortality is directly linked to water stress which is exacerbated by anthropogenic factors. These include aquifer "mining" (where too much water is removed from an aquifer, and the recharge rate does not keep pace with extraction), and careless road-building practices (Ward and Rohner 1997). Plant diversity in the understory of *Acacia* canopies was greater than in surrounding areas. Species composition differed significantly between sites where *Acacia* was experiencing either high or low mortality. Interestingly and perhaps unexpectedly, there was greater diversity of ground flora in sites where *Acacia* was suffering high mortality, and under trees which were experiencing higher water stress, suggesting *Acacia* trees were normally competing with the understory plants for water. Soil nutrient content was consistently higher under the trees than in the open areas, especially under larger trees and trees with higher water availability, which would be beneficial to understory plants. These results suggest that understory plants experience both positive and negative effects as a result of the *Acacia* canopy, and that negative effects are more intense during times of water stress (Munzbergova and Ward 2002).

## 6.9 Summary

This chapter examines the importance of timing for flowering and reproductive ecology in the desert. Phenological studies show the special significance of reproductive timing in dryland environments and the importance of particular environmental triggers inducing flowering in different species. Accumulation of sufficient heat-units, and particular photoperiods, are well-known triggers. Sex *specialization* toward maleness and/or femaleness, and sexual lability are evident in many desert plants (including, e.g., *Thymelaea hirsuta* and *Ochradenus baccatus*). Two major desert genera, *Euphorbia* and *Acacia*, are also considered in some detail as important, regionally representative species.

CHAPTER 7

# Seed dispersal, dormancy, and "bet-hedging" in desert plants

'A seed is an end and a beginning; it is a bearer of the essentials of inheritance; it symbolizes multiplication and dispersal, continuation and innovation, survival, renewal and birth.'

**W. Heydecker (1973)**

## 7.1 Introduction

Plants long ago solved their "sessile problem" by evolving a variety of long- and short-distance dispersal behaviors (see, e.g., Silvertown and Lovett-Doust 1993). Yet desert species often do neither, instead having a very effective drought avoidance strategy using seed dormancy mechanisms, and germination triggered by rainfall (or rainfall and cold). Moreover for all that individual survival and success is very local, plant politics must often be brought to bear on larger, more regional matters. These are effects of the "lay of the land" and include large-scale factors like landforms, hydro-geology, and elevation. Each influences population biology and the landscape ecology of the flora in major ways (e.g., Lovett-Doust and Kuntz 2001; Lovett-Doust et al. 2003; Turner 2005).

Seeds typically get dispersed from a parent plant to a place—typically not too far away—where they can then remain dormant for a period and then possibly under certain conditions germinate, establish, and grow into adult individuals. Seed ecology is largely concerned with the hazards and opportunities associated with dispersal and subsequent establishment. As a result the scale and degree of spatial heterogeneity are of special importance. Success at this life stage—and particularly successful establishment in the *desert*—seems mainly to involve adaptations which allow plants to live in environments that are highly variable in *time* as well as space. There is a significant premium on rapid, opportunistic germination and development.

In desert environments where temporal variation is high—consider the short-term unpredictability of rainfall patterns, say—organisms have often evolved traits that reduce short-term reproductive success in favor of longer-term risk reduction. This has been described as "evolutionary bet hedging" (Slatkin 1974), implying that evolution proceeds via a trade-off between the *expected* value and the *variance* of fitness, of a genotype or particular life-history strategy (Philippi and Seger 1989).

Evolutionary bet-hedging, or risk-spreading, represents one major solution to the challenge of a highly variable environment and is believed to be widespread biologically (see Childs et al. 2010). The concept is usually defined in terms of a trade-off between the mean value and the variance of some performance factor related to fitness. Thus fitness in the average environment may be sacrificed in favor of lower variation in fitness over the longer term, provided this leads to greater lifetime fitness. For annual plants, one way to spread the risk of establishment is for the seed cohort of an individual plant produced at one time to germinate in different years, even if they are all dispersed into the same local environment at the same time.

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A classic example of bet hedging in plants involves delayed germination and the development of seed banks in desert annuals. Evolutionary bet hedging also helps explain patterns of delayed flowering in monocarpic plants, as well as serotinous[1] fruit retention (allowing *delayed* seed dispersal). There are some interesting patterns that arise when these strategies are combined with complex life-history traits such as size at flowering in semelparous perennials (Childs et al. 2010).

Cohen (1966) first showed that a strategy in which only a fraction of seeds germinate and the rest remain alive but dormant, tends to maximize fitness in environments where the probability of successful establishment is low and varies at random. As we show in this chapter, the high unpredictability of the desert environment favors strategies of bet hedging in a number of different ways, which all involve sacrificing mean fitness for a reduction in the variance of fitness over time, thereby improving the chances of leaving at least some descendants.

## 7.2 Dispersal in the desert

In the desert relatively few species have morphological structures favoring long-distance dispersal (or "telochory"), compared to species from non-desert habitats (Ehrman and Cocks 1996; Ellner and Shmida 1981). According to Ellner and Shmida there are a number of explanations for the rarity of telechory in desert species—and indeed why many desert plants even have adaptations which *hinder* long-distance dispersal—that is they show "anti-telechory."

Ellner and Shmida argue anti-telechory may be best regarded as part of a complex syndrome of characteristics related to *both* dispersal and regulation of germination. Basically the goal is to regulate the timing of seed-dispersal and germination within a given year, and to amortize the germination of each year's seed crop over several years, following death of the monocarpic parent. Thus in a dry desert it may be advantageous to have seeds remain dormant and wait a while before germinating. An advantage would be that even if a dry year followed their production, they might encounter adequate precipitation in another year. Having several different cohorts in the seed bank all increases the genetic diversity among potential mates.

Table 7.1 (and Box 7.1) summarizes the dispersal spectrum of the Mediterranean and desert flora in Israel, as an example.

If long-distance dispersal is reduced, either in the sense that dispersal-enhancing characteristics are absent (atelochory), or structures are present that actually hinder dispersal (anti-telochory), one would predict such species should be more localized in their distribution, and desert communities should show higher frequencies of these strategies in their vegetation. Ellner and Shmida examined this idea by comparing dispersal spectra for two representative Mediterranean and desert communities, shown in Table 7.2. Several interesting patterns emerge.

- *Astragalus* (which is probably the most common legume in Old World deserts) has an indehiscent fruit, that is, the pod does not rupture upon maturation, releasing the seeds,[2] whereas most of the widespread legume genera in the temperate and Mediterranean regions have dehiscent fruits (e.g., *Lathyrus, Lotus, Vicia*) (Ellner and Shmida 1981).
- Basicarpy, where seeds are produced at or near ground level, is regarded by Ellner and Shmida as the most specialized of the anti-telechoric syndromes. This strategy occurred mostly in true desert and was practically absent in non-desert regions. Many of these are tiny, ground-hugging annuals, and retain their seeds or fruits over an extended period, e.g., *Trigonella stellata*. In most of the common basicarpic species the propagule is hygrochasic and dehisces upon wetting,

[1] Serotiny is an adaptation exhibited by some angiosperms, in which seed release occurs in response to an environmental trigger, rather than spontaneously at seed maturation. The most common and best-studied trigger is fire ("pyriscence"). Other triggers include death of the parent plant or branch; wetting ("hygriscence"); and drying atmospheric conditions ("xeriscence").

[2] Dehiscence is the opening at maturity of a plant structure, such as a fruit, anther, or sporangium, to release its contents. Sometimes this involves the complete detachment of a part. Structures that open in this way are said to be dehiscent. *Xerochasy* is dehiscence that occurs upon drying, and *hygrochasy* is dehiscence that occurs upon wetting (see Section 7.6).

**Table 7.1** Dispersal spectrum of the Israeli flora related to the dispersal-distance. Note categories are not mutually exclusive (after Ellner and Shmida 1981, used with permission) See Box 7.1 for definitions.

| | Mediterranean and semi-desert | | Desert | | Total |
|---|---|---|---|---|---|
| | 1560 species | | 604 species | | 2164 species |
| | No. | % | No. | % | No. |
| Synaptochory | 92 | 5.9 | 11 | 1.8 | 113 |
| Synaptostasy | 88 | 5.6 | 60 | 9.9 | 148 |
| Delayed dispersal | 72 | 5.1 | 57 | 9.4 | 129 |
| Ballist-dispersal | 311 | 19.9 | 61 | 10.1 | 372 |
| Synaptospermy | 120 | 7.8 | 51 | 8.4 | 171 |
| Tumbleweeds | 6 | 0.4 | 4 | 0.6 | 28 |
| Basicarpy | 5 | 0.3 | 22 | 3.6 | 27 |
| Hygrochasy | 12 | 0.8 | 17 | 2.7 | 29 |
| Heterocarpy | 11 | 0.7 | 80 | 1.3 | 91 |
| Amphicarpy | 6 | 0.4 | 1 | 0.2 | 7 |
| Geocarpy | 12 | 0.8 | 1 | 0.2 | 13 |
| Zoochory | | | | | |
| • epizoochory | 29 | 1.9 | 4 | 0.6 | 33 |
| • endozoochory | 47 | 3 | 11 | 1.8 | 58 |
| Anemochory | | | | | |
| • wing | 33 | 2.1 | 28 | 4.6 | 61 |
| • pappus or feathery bristles | 91 | 5.8 | 45 | 7.4 | 136 |
| Telechory | 574 | 36.8 | 88 | 14.6 | 662 |
| Atelechory | 780 | 50 | 453 | 75 | 1233 |
| Antitelchory | 25 | 1.6 | 62 | 10.4 | 88 |

a useful opportunistic response to unpredictable rainfall (see Table 7.3 and examples below).

- Epizoochory is long-distance dispersal that involves attaching propagules to the surface of animals; this is relatively rare in the desert, but more common in more mesic sites. The same is true of endozoochory, which is seed dispersal through ingestion and deposition of intact seeds by vertebrate animals (mostly birds and mammals) (and see *Ochradenus*, Section 7.7).
- Heterocarpy (production of more than one morphologically distinct type of seed or fruit by an individual) is usually related to differential dispersal, and is more common in the Mediterranean than in the desert (Table 7.2). Dryland tumbleweeds such as *Bassia indica*, where the entire maternal plant forms a ball of dried up dead tissue, enclosing seeds or fruits which get dispersed by the wind, are concentrated in the semi-desert and almost absent from true deserts.

The dominant desert annuals listed in Table 7.2 show a suite of linked characters. The seeds and/or diaspores lack structures that would facilitate long-distance dispersal (for example, plumose pappi and fleshy fruits are almost absent). Hygrochasy is common, as is matristasy, where propagules are retained on the dried skeleton of the parent (which

**Box 7.1 Glossary (for Tables 7.1–7.3)**

The general classification of dispersal-distances adopted here, following Ellner and Shmida (1981) is:

I. Telechory: seeds or diaspores possess morphological characters facilitating long-distance dispersal of seeds (e.g., barbs, pappi, and fleshy fruits).
II. Proxichory: seeds and/or diaspores lack morphological characters facilitating long-distance dispersal of seeds. This consists of two sub-categories:
   a. Anti-telechory: long-distance dispersal of seeds is hindered by the initial placement of diaspores (at, near, or below the soil surface) or by morphological characteristics of the seeds or diaspores (as delineated in the text).
   b. Atelechory: proxichory without anti-telechoric characters. Insofar as possible our typology of specific dispersal modes follows Pijl (1972).

Aestatiphory: seeds are retained on the skeleton of a winter annual at least until the start of the next rainy season.

Amphicarpy: some, but not all seeds are borne beneath the soil surface.

Anemochory: wind-dispersal of seeds with characters slowing their terminal velocity of descent (e.g., a plumose or many-barbed pappus, bristle, or arista).

Barospermy: dispersal distance of seeds is limited by the weight of the diaspore.

Basicarpy: "compact inflorescences are borne close to the soil surface and whose fruits or fruit aggregates remain attached to the dead parent" (Zohary 1962), and the dead plant is held in place by a strong lignified root.

Bradyspory: dispersal of seeds from the mother plant is delayed and spread out over significant periods of time. For desert plants this refers to spreading dispersal over several rainfalls.

Geocarpy: all diaspores are borne beneath the soil surface.

Heterocarpy: production of two or more morphologically distinct types of diaspore by an individual plant.

Hygrochasy: opening and closing of the dispersal unit (or organ of the mother plant enclosing the dispersal units) as a function of moisture.

Matrispermy: extended attachment of diaspores to the skeleton of the mother plant. This includes:

a. Matrichory: the skeleton of the mother plant with attached seeds facilitates long-distance dispersal (e.g., tumbleweeds).
b. Matristasy: the skeleton of the mother plant hinders long-range dispersal of seeds (via barospermy or attachment to the soil).

Synaptospermy: Two or more seeds (or one-seeded fruits) are joined together to form a compound diaspore.

a. Synaptochory: the diaspore has morphological characters facilitating long-distance dispersal of seeds. In most cases the diaspore is a dehiscent fruit, inflorescence, or part inflorescence.
b. Synaptostasy: the diaspore lacks characters facilitating long-distance dispersal. The weight and size of the diaspore by themselves then hinder dispersal (a form of barospermy).

Trypanocarpy: the form and/or appendages of the seed or diaspore favor burial in the soil at the point of initial contact (e.g., by drilling or wedging into cracks).

Zoochory: dispersal by animals, either internally (endozoochory) or externally (epizoochory).

itself often remains attached to the ground) (see Ellner and Shmida 1981). Hygrochasy, as in *Anastatica hierochuntica*, impedes long distance dispersal by limiting seed release and germination to periods following rainfall (Hegazy and Kabiel 2010). This "built-in rain gauge" helps ensure seeds do not get released or germinate until after suitable rainfall (see also Fig. 2.14, Section 8.6.1).

In general among flowering plants, for most non-woody species and in most of the habitats that have been investigated, the majority of dispersed seeds end up no more than a matter of meters away from the mother plant. This is seen even in the most telechoric species (Harper 1977). Trees, being taller, tend to have slightly greater modal dispersal distances, but still often only on the order of *c*. 10 m. It has been suggested that in closed vegetation, spatially based variation in the density of competitors makes dispersal more advantageous; other proposals to explain the value of progeny distancing themselves from their parents include the Janzen–Connell hypothesis, often cited as an explanation for the maintenance of tree species diversity in the tropics (see Janzen 1970). They proposed

**Table 7.2** Dispersal spectrum (% of species) of representative Mediterranean (Sansan, open maquis) and true desert (Ein-Gedi) communities. Results derived from complete species lists of 1 ha quadrats taken in Spring, 1980 (Sansan) and 1981 (Ein-Gedi), Israel (after Ellner and Shmida 1981, used with permission).

| | Mediterranean (Sansan, open maquis) | Desert (Ein-Gedi) |
|---|---|---|
| Synaptochory | 9.0 | 7.0 |
| Synaptostasy | 5.0 | 30.0 |
| Ballist-dispersal | 21.0 | 14.0 |
| Delayed dispersal | 7.0 | 28.0 |
| Synaptospermy | 14.0 | 37.0 |
| Basicarpy | 0.5 | 18.0 |
| Hygrochasy | 1.2 | 12.0 |
| Heterocarpy | 9.0 | 2.0 |
| Zoochory | | |
| • epizoochory | 7.0 | — |
| • endozoochory | 14.0 | — |
| Anemochory | | |
| • wing | 4.0 | 11.0 |
| • pappus and feathers | 14.0 | 15.0 |
| Telechory | 45.0 | 26.0 |
| Atelechory | 53.0 | 52.0 |
| Antitelchory | 2.0 | 22.0 |
| Total | 100.0 | 100.0 |

a density- or distance-dependent factor in recruitment by adults of tropical tree species was due to host-specific predators or pathogens being clustered around the parent plant. However, in desert habitats the stressors of the *physical* environment seem to act as significantly more powerful pressures than do biotic competitors (Noy-Meir 1979).

Given that in the desert precipitation dictates opportunity, it seems entirely reasonable that desert annuals depend more upon *dormancy*, essentially biding their time until conditions are suitable for germination and establishment, than upon dispersal. They are essentially dispersing in time rather than space, and waiting in the same place for favorable precipitation at a later time rather than trying to "find" water via dispersal in space. It is therefore interesting to look at the trade-off between dispersal and dormancy as bet-hedging adaptations in spatially and temporally varying environments. The work of Lawrence Venable and his colleagues has been particularly useful here (e.g., Venable and Brown 1988; Venable and Lawlor 1980; Venable et al. 2008); and see too Ellner and Shmida (1981).

Venable et al. (2008) quantified seed dispersal in a guild of Sonoran Desert winter annuals, and estimated dispersal curves, or kernals[3] for two species, *Pectocarya recurvata* and *Schismus barbatus*, based on the change in seedling density with distance from the border of herbicide-treated zones.[4] Estimated dispersal distances proved to be very short, with most seeds travelling less than a meter. The adhesive seeds of *P. recurvata* went farther than the small seeds of *S. barbatus*, which had no obvious dispersal adaptation. Venable et al. also concluded that the majority of the dozen or so other desert annuals they looked at did not travel very far. Values were similar to those reported by Willson (1993) in general patterns for herbaceous plants with morphological adaptations for wind dispersal (which averaged 0.92 m), and somewhat greater than that of herbaceous species with no apparent dispersal mechanism (which averaged 0.49 m).

## 7.3 Variable germination in the desert

Venable (2007) described an association between delayed germination and *risk*, using a 22-year data set on demographic variation for ten species of desert annuals. These results are particularly powerful as they are based on direct estimates of *per capita* reproductive success using long-term demographic data. They enable a strong test for any association between greater bet-hedging and greater risk. The seed banks of species with greater variation in reproductive success (i.e., *per capita* survival from

[3] A dispersal curve or "kernal" plots the change in density or numbers of offspring—seeds or recruits—against distance from the source. It provides a useful summary of the spatial patterns of dispersal or recruitment (e.g., Nathan and Muller-Landau 2000).

[4] Venable et al. (2008) quantified ultimate dispersal distance from a boundary. Boundaries were created by spraying herbicide to inhibit reproduction of otherwise intact plants, on one side of an arbitrarily determined boundary in a previously unbounded natural population. In each of an array of transects, seedling densities and inverse modeling were used to infer the average dispersal kernel for individual plants.

**Table 7.3** Dispersal characteristics of the dominant annual plants in the deserts of Israel. Species listed had the highest overall abundance in 230 0.1 ha samples in the Negev (Israel) and Sinai (Egypt) deserts. [–, imperfectly developed, +, + +, + + +, degree of development (least to most, of observations)] (after Ellner and Shmida 1981, used with permission).

| Species name | Family | Heterocarpy | Attached to the ground | Hygrochasy | Skeleton | Stay on the mother plant | Synaptostasy | Ballist | Pappus and bristle (wing) | Immediately opened |
|---|---|---|---|---|---|---|---|---|---|---|
| *Rumex cyprius* | Polygonaceae | | | | | | | | | |
| *Aizon canariense* | Aizoaceae | | + + + | + + + | + + + | + | | | (Wing) | |
| *A. hispanicum* | Aizoaceae | | | + | + | - | | | | |
| *Mesembrianthemum nodiflorum* | Aizoaceae | | | + | - | + | | | | |
| *M. forsskalii* | Aizoaceae | | | + + + | + + | + | | | | |
| *Silene clorata* | Caryophyllaceae | | | | - | | | + | | + |
| *Spergularia diandra* | Caryophyllaceae | | | | | | | + | | + |
| *Pteranthus dichotamus* | Caryophyllaceae | | | | | | + + + | | | |
| *Neurada procumbens* | Neuradaceae | | | | | | + + + | | | |
| *Statice thouinii* | Plumbaginaceae | | | | | | + + + | | | |
| *Salsola inermis* | Chenopodiaceae | | | | + + | + | | | (Wing) | |
| *Nasturiopsis arabica* | Brassicaceae | | | | | | | | | + |
| *Reboundia pinnata* | Brassicaceae | + | | - | + + | - | | | | |
| *Notoceras bicorne* | Brassicaceae | | + + | - | + + | + | | | | |
| *Diplotaxis harra* | Brassicaceae | | | | | | | | | + |
| *D. acris* | Brassicaceae | | | | | | | | | + |
| *Anastatica hierochuntica* | Brassicaceae | | + | + + + | + + + | + | | | | |
| *Reseda muricata* | Resedaceae | | | | | | | | | |
| *Astragalus tribuloides* | Fabaceae | | + | | + + | + | + | | | |
| *A. callichrous* | Fabaceae | | | | | | + + | | | |
| *A. fatemensis (vegelii)* | Fabaceae | | | | | | + + | | | |
| *Lotonomis platycarpa* | Fabaceae | | + | | - | - | | | | |
| *Trigonella stellata* | Fabaceae | | + | - | + + + | + | + | | | |
| *Erodium bryoniifolium* | Geraniaceae | | | | | | | | + + + | |
| *Zygophyllum simplex* | Zygophyllaceae | | | | | | - | | | |
| *Lappula spinocarpa* | Boraginaceae | | | | + | + + | + | | | |

*continued*

**Table 7.3** *Continued*

| Species name | Family | Heterocarpy | Attached to the ground | Hygrochasy | Skeleton | Stay on the mother plant | Synaptostasy | Ballist | Pappus and bristle (wing) | Immediately opened |
|---|---|---|---|---|---|---|---|---|---|---|
| *Linaria halava* | Scrophulariaceae | | | | | | | | | |
| *Blepharis ciliaris* | Acanthaceae | | | + + | + + | + | | | | |
| *Plantago ovata* | Plantaginaceae | | | | | | | | | + |
| *P. cylindrica* | Plantaginaceae | | | | | | | | | + |
| *Ifloga spicata* | Asteraceae | | | | | | | | | + |
| *Gymnarrhena micrantha* | Asteraceae | + + + | + | + + + | + | + | | | | |
| *Pulicaria undulata* | Asteraceae | | | | | | | | + + | |
| *Astericus pygmaeus* | Asteraceae | | + | + + + | + + + | + | | | | |
| *Anathemis melampodina* | Asteraceae | | | | - | + | | | | |
| *Aaronsohnia factorovskyi* | Asteraceae | | | | | | | | | + |
| *Senecio coronopfolia* | Asteraceae | | | | | | | | + + | |
| *Launea nudicualis* | Asteraceae | | | | | | | | + | |
| *Reichardia tingitana* | Asteraceae | + | + | | | | | | + | |
| *Asphodelus tenuifolius* | Liliaceae | | | | | | | | | |
| *Schismus arabicus* | Poaceae | | | | | | | | | + |
| *Stipa tortilis* | Poaceae | | | | | | | | + | |
| *Aristida raddiana* | Poaceae | | | | | | | | + + | |
| *42 species* | | 3 | 9 | 10 | 17 | 17 | 9 | 5 | 7 | 10 |

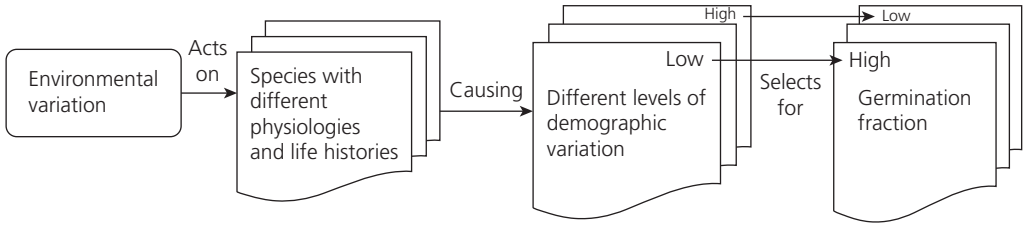



**Figure 7.1** Schematic showing how environmental variation selects for bet hedging (low germination fraction) (after Venable 2007, used with permission).

germination to reproduction, times *per capita* fecundity of survivors) were found to have lower average proportions of their viable seeds germinating each year. Species that experienced greater long-term demographic variation also showed greater sensitivity to year-to-year variation in rainfall.

Figure 7.1 shows schematically how environmental variation can select for bet-hedging (where a low proportion of seeds germinate, spreading the germination of progeny over a longer time). Differences in the variability of *per capita* reproductive success—due in part to differences in sensitivity to precipitation—provide the different levels of risk that select for different levels of bet-hedging in each species.

Venable's study provides a valuable test using the pooled overall fitness of populations of different species. It is particularly interesting that in a guild of co-existing desert annuals we see different levels of demographic variation, accompanied by corresponding bet-hedging in terms of the proportion of the viable seed bank that germinates each year. A reasonable inference might be that differences in the physiology and phenology of each species, likely associated with micro-heterogeneities in the environment are enough to allow continued co-existence.

There seems an obvious parallel here to the limnologist G. E. Hutchinson's ecological "paradox of the plankton"—essentially, in niche theory, why does one single superior competitor not take over a system and dominate? The variability associated with composition of the annual desert plant community is likely due to the *grain* and *heterogeneity* of the environment, with an array of species better able to co-exist by "partitioning" the ecological niche at a relatively fine scale. Also many ecosystems are not "steady-state," but rather undergo changes at various time scales. This influences how we set conservation goals and the strategies we use to protect natural areas. For deserts the challenge is that our human perception of these environments is at a very different scale from that of the annual plant. It would be useful to know more about the role of seed dispersal in maintaining competitive coexistence, in regard to both spatially and temporally based heterogeneity.

In arid ecosystems one typically finds significant year-to-year variability in composition of the annual community. This is largely a consequence of species-specific germination sensitivity, coupled with year-to-year variation in environmental factors (e.g., Pake and Venable 1996). These effects—combined with high persistence of seeds in the seed bank—are a major contributor to species coexistence and have been termed the "storage effect" (Chesson and Huntley 1989). This is in essence an amortization of risk, mediated via the seed bank. If seed dispersal is highly local, then population density for a species can build up at particular, suitable sites (e.g., under the protective microclimate of a shrub's canopy; see Section 4.7 on facilitation effects).

Facelli et al. (2005) studied the annual community of a chenopod shrubland in South Australia. The vegetation was open *Acacia papyrocarpa* woodland with an understory dominated by chenopod shrubs, along with a large number of annuals. Dominant among these was *Carrichtera annua*, a plant introduced to Australia from the Middle East (Gutterman and Shem-Tov 1997).

Sequential analysis of the seed bank showed significant seasonal and year-to-year variability in both numbers and composition. Soil samples incubated

under different temperatures and watering regimes generated different above-ground communities, indicating that species responded differentially in terms of germination rate depending on the combination of conditions. For all species, germination was extremely low at low water availability (and at high temperatures even when there was ample water).

For four out of five species a high percentage of seeds buried in the field remained viable for two years, while the fifth species, the introduced *Carrichtera annua*, experienced a sharp decline in seed viability over the two years, reaching nearly zero survivorship. These results suggest the indigenous Australian annuals have adapted to extend germination of each cohort over at least a two-year period, whereas the introduced weed does not. Because species show different responses to different combinations of conditions, the community composition varies annually.

## 7.4 Serotiny

Unpredictable environments promote not only the evolution of delayed seed germination but also delay of seed or fruit release. This also allows the parent to spread germination of progeny cohorts through time (Philippi 1993 a, b), with increased likelihood that at least some of them will encounter favorable conditions.

Serotinous retention of mature seeds on the parent for more than a year is a behavioral syndrome of adaptive significance in randomly fluctuating environments, such as dry, fire-prone scrubland and other arid ecosystems (Gunster 1992; Hegazy and Kabeil 2010; Lamont 1991; Lamont and Enright 2000; Peters et al. 2009; Rodriguez-Ortega et al. 2006). The most common triggers for release of seeds by serotinous species are death of the whole plant or part of it, fire, or exposure of a dehydrated plant skeleton to moisture. Hygrochastic plants release or disperse seeds after being wetted by rainfall.

Serotiny in *Anastatica hierochuntica* and *Asteriscus pygmaeus* is induced by water availability. Such a relation largely restricts seedling recruitment to years when moisture conditions are suitable (Venable and Lawlor 1980) and spreads germination of a single cohort of seeds over multiple years (see also Figure 2.14). This in turn spreads the risk of reproductive failure across time, in these unpredictable environments. Serotiny is a well-known adaptation to fire in the case of certain tree species, including various pines and cypresses. There, once cones are pollinated and seeds fertilized, female cones remain tightly closed for years following seed maturation and only open when they are exposed to the high temperature of forest fires. Obviously the advantage of this is that offspring will germinate only when the overtopping canopy of adults has been removed by fire.

In the eastern Mediterranean, three pine species—*Pinus halepensis, P. brutia*, and *P. pinaster*—covering a wide range of xeric and lower altitude conditions, all show high levels of serotiny (Keeley et al. 1999; Moya et al. 2008; Ne'eman 1997; Ne'eman et al. 2004; Pausas et al. 2008; Tsitsoni 1997; Tsitsoni et al. 2004). This has been shown to increase the survivorship of seeds released post-fire, as well as seedling establishment.

## 7.5 Dormancy

In areas with winter rain and a hot dry summer, most seed production occurs in late spring to early summer. In contrast, in areas with cold winters and summer rains, seed production typically occurs in the fall. In both cases this means seed dispersal occurs at times that are unsuitable for germination and seedling establishment. As a result, seeds in most species have developed dormancy mechanisms. These may require an after-ripening period of embryo maturation, or leaching of germination inhibitors, or drying and scarification events to break dormancy and allow germination of a new individual.

A corresponding cost is that, for seeds to remain viable for years in the seed bank, the parent must invest more in seed reserves to maintain baseline cell respiration. There may also be investment in thickened seed coats and in some cases synthesis of germination-inhibiting secondary compounds.

According to Murdoch and Ellis (2000) many species in arid and semi-arid regions produce dormant seeds that are able to maintain viability despite having very low moisture content. These seeds have extended longevity and viability even under desiccation up to -350 MPa in dry storage. On the other

hand, seeds of species from more mesic habitats are more often non-dormant and rapidly lose viability if they do not germinate soon after dispersal. Generally their longevity and viability increase under higher levels of moisture. Dryland annual populations often rely on a seed bank for persistence, while those from more mesic habitats that lack dormancy require successful seedling establishment each year.

Dormancy as a general phenomenon provides an interruption of active growth, helping plants avoid adverse conditions. Seed dormancy is a special case of growth cessation, characterized by partial metabolic stasis, initiated through the embryo's response to both endogenous and exogenous controls. Responses are typically regulated by a balance between growth inhibitors and promoters. Initially the balance favors inhibition, shifting later toward promotion.

Several frameworks have been proposed to describe the diverse patterns of dormancy found in plants around the world. Some authors distinguish "constitutive" or endogenous mechanisms, from "exogenous" ones; dormancy has been equated with "quiescence" (*sensu* Sussman and Halvorson 1966), and other approaches include distinctions among "innate," "enforced," and "imposed" dormancy (*sensu* Harper 1977), as well as the "primary" or innate *vs*. "secondary" or induced dormancy characterized by Baskin and Baskin (1998).

Based on the mechanism of inhibition of germination, various categories of seed dormancy were distinguished by the Baskins (Baskin and Baskin 1998).

1. Morphological—where seeds are shed from the parent while still immature and only incompletely developed. Such seeds require time (and often particular conditions such as a period of cold temperature) for the embryo to complete its growth and differentiation before it can germinate.
2. Physiological—caused by a physiological or biochemical inhibition of the embryo that prevents germination. Breaking this requires chemical changes, such as activation of growth regulators through a period of cold stratification, or other effects of temperature, light, or oxygen.
3. Physical—the seed is covered by an impermeable coat (testa, pericarp, etc.) which keeps the embryo dry until the coat is broken or softened and water enters the seed, causing swelling and germination.
4. Chemical—where the seeds do not germinate due to the presence of chemical inhibitors in the pericarp or in the seed itself, inhibiting embryonic growth. This type of dormancy is broken by removing/leaching away the inhibitors.
5. Mechanical—is due to the presence of a hard woody fruit wall which needs to be broken for the seeds to germinate. Typically such seeds also require scarification through ingestion and passage through an animal gut, or exposure to a cycle of freezing and thawing.
6. Morpho-physiological—a combination of morphological and physiological dormancies.

Ecological aspects of germination and dormancy have been well reviewed by others (e.g., Baskin and Baskin 1998; Fenner and Thompson 2005). Here we consider examples with reference to the Middle East, and biomes ranging from tropical and subtropical to Mediterranean and temperate, and where salinity as well as temperature and water availability can complicate seed germination (see Table 7.4).

## 7.6 Annual species

Annual plants are essentially semelparous, having a single reproductive session in their lifetime and producing a single cohort of seeds before death. These seeds may have innate, enforced, or induced dormancy (*sensu* Harper 1977).

In general desert annuals require relatively high water availability to germinate, and tend to have adaptations that allow them to synchronize their seed germination to the most favorable season of the year. They are thereby able essentially to *tune* or align seedling emergence to environmental conditions favorable for germination and subsequent growth and reproduction, through dormancy (Facelli et al. 2005; Gutterman 1994).

Individuals of the winter annual *Asteriscus hierochunticus* (Asteraceae) often stand as dry plant "skeletons" for several years. Skeletons bear reproductive heads holding numerous seeds (achenes) which in turn are enclosed within stiff, involucral

**Table 7.4** Types of seed dormancy in some desert plants. 1 = Morphological dormancy, 2 = Physiological dormancy, 3 = Physical dormancy, 4 = Morphological-physiological dormancy, 5 = Physical-physiological dormancy, 6 = Chemical dormancy, 7 = Mechanical dormancy. Life span: A = annual/monocarpic, B = biennial/monocarpic perennial, and P = polycarpic perennial

| Species | Life span | 1 | 2 | 3 | 4 | 5 | 6 | 7 | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Aegilops geniculata* | A | x | x | | x | | x | | Gutterman (1994) |
| *Aeluropus lagopoides* | P | | x | x | | | | | Khan (1990, 1993) |
| *Aloe asperifolia* | P | | x | | | x | | | Cousins and Witkowski (2012), Smith and Correia (1992), Smith and Van Wyk (2009) |
| *Aloe dichotoma* | P | | X | | | X | | | Cousins and Witkowski (2012), Giddy (1993), Smith and Correia (1992), Smith and Van Wyk (2009) |
| *Aloe greatheadii* | P | | x | | | X | | | Cousins and Witkowski (2012), Smith and Correia (1992), Smith and Van Wyk (2009) |
| *Anastatica hierochuntica* | A | | x | | x | | | x | Gutterman (1972, 1994), Gutterman and Ginott (1994), Hegazy and Kabiel (2007, 2010), Hegazy et al. (2006) |
| *Arthrocnemum indicum* | P | | x | x | | x | | | Gul et al (2013), Gul and Khan (2006), Khan (1990, 1993) |
| *Arthrocnemumm acrostachyum* | P | | x | x | | | | | Gul et al (2013), Gul and Khan (2006), Khan (1990, 1993) |
| *Asteriscus hierochunticus* | A | | x | | x | | | x | Gutterman (1972, 1994), Gutterman and Ginott (1994) |
| *Avena sterilis* | A | x | | x | | | | | Volis (2012) |
| *Blepharis ciliaris* | A/P | x | x | x | | | | | Gutterman (1972, 1994), Gutterman and Ginott (1994) |
| *Calotropis procera* | P | | x | | | | x | | Amritphale et al. (1984) |
| *Cleome droserifolia* | P | | x | | x | | x | | Hegazy (1990a) |
| *Capparis spinosa* | P | | | x | | x | | | Al-Oudat (2008), Al-Safadi and Elias (2011), Olmez et al. (2004) |
| *Cressa critica* | P | | x | x | | x | | | Gul et al. (2013), Gul and Khan (2006), Khan (1990, 1993) |
| *Diplotaxis harra* | A/P | | x | | | | | | Hegazy (2001), Tlig et al. (2008) |
| *Eruca sativa* | A/P | | x | | | | | | Barazani et al (2012), Hanin et al. (2013) |
| *Ferula gummosa* | P | | | x | x | | | x | Nadjafi et al. (2006) |
| *Haloxylon salicornicum* | P | | x | | | | | | El-Keblawy (2013) |
| *Haloxylon stocksii* | P | | x | x | | x | | | Gul and Khan (2006), Gul et al. (2013), Khan (1990, 1993) |

*continued*

**Table 7.4** *Continued*

| Species | Life span | 1 | 2 | 3 | 4 | 5 | 6 | 7 | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Heliotropium digynum* | P | | x | x | | | | | Hunt et al. (2009) |
| *Hordeum spontaneum* | A | x | | | x | | x | | Chen et al. (2004), Gutterman and Gozlan (1998), Gutterman et al. (1996) |
| *Mesembryanthemum nodiflorum* | A | | | x | | x | | | Gutterman (1980, 1981) |
| *Neurada procumbens* | A | x | x | | x | | | x | Hegazy et al. (2014) |
| *Pinus brutia* | P | x | | x | | x | | | Moya et al. (2008), Ne'eman et al. (2004), Pausas et al. (2008), Tsitsoni et al. (2004) |
| *Pinus halepensis* | P | x | | x | | x | | | Moya et al. (2008), Ne'eman et al. (2004), Pausas et al. (2008), Tsitsoni et al. (2004) |
| *Pinus pinaster* | P | x | | x | | x | | | Moya et al. (2008), Ne'eman et al. (2004), Pausas et al. (2008), Tsitsoni et al. (2004) |
| *Prosopis juliflora* | P | | x | | x | x | | | El-Keblawy (2006), Shiferaw et al. (2004) |
| *Pteranthus dichotomus* | P | x | x | | x | | x | x | Datta et al. (1974), Gutterman (1994) |
| *Rubus caesius* | P | | x | x | | x | x | | Wada et al. (2011) |
| *Rubus hoffmeisterianus* | P | | x | x | | x | x | | Wada et al. (2011) |
| *Rubus occidentalis* | P | | x | x | | x | x | | Wada et al. (2011) |
| *Salsola imbricata* | P | | x | x | | x | | | Gul and Khan (2006), Gul et al. (2013), Khan (1990, 1993) |
| *Sporobolus ioclados* | P | | x | x | | x | | | Gul and Khan (2006), Gul et al. (2013), Khan (1990, 1993) |
| *Suaeda fruiticosa* | P | | x | x | | x | | | Gul and Khan (2006), Gul et al. (2013), Khan (1990, 1993) |
| *Teucrium polium* | P | | x | x | | x | | | Nadjafi et al. (2006) |
| *Trigonella arabica* | A | | x | x | | | x | | Gutterman (1978), Gutterman (1994) |
| *Verbascum sinaiticum* | B | | x | | x | | | | Hegazy (2000), Noy-Meir (1973) |
| *Zygophyllum dumosum* | P | | x | | | | x | | Agami (1986), Freas and Kemp (1983) |

bracts. On wetting, these bracts open rapidly and some seeds get released, averaging *c*. 1–10 seeds per year. This is a raindrop-stimulated process that can extend over a couple of decades in this otherwise "annual" species (Gutterman 1972, 1994; Gutterman and Ginott 1994). Each fruiting head (or capitulum) contains *c*. 200 seeds, arranged in 10–12 whorls and protected by two hygrochastic whorls of bracts. There is polymorphism in terms of achene germinability, with those released from peripheral whorls tending to germinate faster than those from inner whorls, i.e., the deeper within the capitulum, the more dormant the seeds. As a rainfall event stops and the plant skeleton dries, the bracts close up once more. . . until the next rain.

*Anastatica hierochuntica* (Brassicaceae) is another small desert annual (see Figure 2.14), with efficient seed dispersal that exploits the hygrochastic nature of the dead plant. After death the small lignified stem branches dry and curl, enclosing the fruits. When wetted by heavy dew or rainfall these branches uncurl. Seeds are released by the force of rain on fruit valves, and the repeated curling and uncurling of branches (Hegazy and Kabiel 2007, 2010; Hegazy et al. 2006). Once released, seeds germinate rapidly, typically within 12 hours. As a result of this curling-uncurling behavior, seeds produced in one season may get dispersed over a period up to a decade or more. This form of bet-hedging allows dispersal and germination risk to be spread out in a manner finely tuned to match the occurrence of rainfall. More plant life in the very *slow* lane . . .

Adaptive bet-hedging was investigated in two co-occurring annual grasses in Israel: *Hordeum spontaneum* (wild barley) and *Avena sterilis* (wild oats). Both are common components of the open, coastal Mediterranean vegetation as well as occurring in the drier desert habitats, wadi beds, and loess depressions (Volis 2012). Seeds are produced in spring and are innately dormant at dispersal, requiring exposure to high temperature and a period of embryonic after-ripening before germination can occur.

In a Mediterranean-desert reciprocal transplant experiment involving these two annual grasses, both species showed similar patterns of seed dormancy across the two environments. In both species a greater proportion of seeds was dormant at the desert location, and in particular in the seeds of desert origin, suggesting both a genetic and facultative—or tactical—aspect to the production of dormant seeds. This likely reflects the significant buffering that seed dormancy brings against an unpredictable desert environment.

An earlier study of germination and desiccation tolerance in xeric- and mesic ecotypes of *Hordeum spontaneum* had also found greater dormancy in xeric- compared to mesic forms (Chen et al. 2004). Testing germination percentage of single seeds (caryopses) with- and without glumellae present, showed that in both ecotypes naked grains had significantly greater germinability than grains covered with glumellae. This suggests these grain coverings are probably exerting both physical and chemical dormancy effects (Chen et al. 2004; Gutterman et al. 1996; Gutterman and Gozlan 1998).

The psammophyte[5] *Neurada procumbens* (Neuradaceae) is another small, wide-ranging annual often found on disturbed sand dunes and sand sheets, as well as alluvial and inter-dune plains, wadis, and rough mountain terrain. It survives in hyper-arid desert environments including the Saudi Empty Quarter (see Table 1.2). Given the species' distribution in environments that are inherently unstable, the seed bank of *Neurada* is especially vulnerable to surface disturbance from both wind and animal action, mixing upper and lower layers and changing soil micro-topography (Hegazy et al. 2014). Given that Neurada seeds are highly asymmetric, there could be a premium to maintaining an optimal position within the substrate profile, and germinating only when the seed is oriented to allow successful germination.

Hegazy et al. (2014) noted that seeds of *N. procumbens* have a rough, spinose upper side and flat, smooth underside, and studied effects of burial depth and seed orientation in this species. Seeds were sown in different positions: (1) lying horizontally on the flat, smooth lower side; (2) lying horizontally on the spinose, upper side; (3) positioned vertically; (4) lying at *c*. 45° with flat, smooth side down; and (5) lying at *c*. 45° with spinose side down (see Figure 7.2).

[5] A desert specialist that manages to thrive even in parched, shifting sand locations.

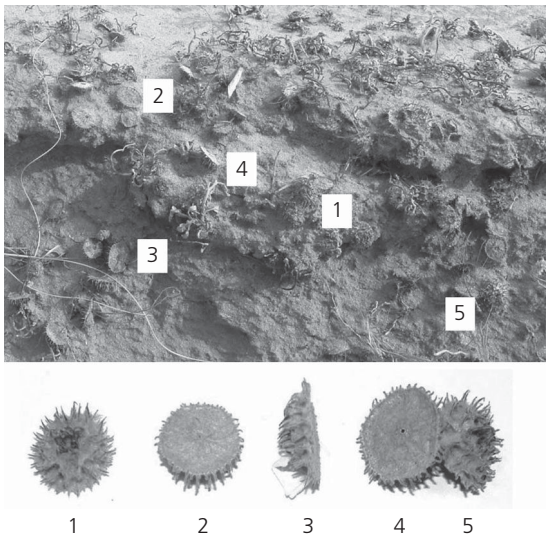



**Figure 7.2** Orientation of *Neurada procumbens* fruits (diaspores) in the seed bank. (1) Abaxial position (with diaspores lying horizontally on their smooth lower side). (2) Inverted position (upside-down) with diaspores lying horizontally on the spinose upper side. (3) Vertical position, diaspores vertically on their side. (4) Inclined position, diaspores positioned lying inclined at different angles, smooth side upward. (5) Inclined position with diaspores lying inclined spinose side upward (after Hegazy et al. 2014). [For a color version of this figure, see the color plate section, Plate 11]

Emergence proved highly sensitive to seed orientation. Greatest emergence (61%) occurred in seeds set with smooth-side down and tightly appressed to the soil surface. This was followed by 41% for seeds set in an inclined position with smooth side down. Emergence was just 8% for seeds at 45° with spinose-side down and negligible to zero in inverted seeds, positioned with their spinose-side down. Seeds near the surface may constitute a more transient (less dormant) component of the seed bank, as few of these remained viable for more than a year.

The vertical distribution of seeds in the soil and presence of a wide range of seed sizes suggest the presence of a fairly persistent seed bank in *Neurada*. Successful germination and establishment result from a combination of burial depth, seed size, and seed orientation. A persistent seed bank implies seeds maintain dormancy while buried in the soil. Secondary dormancy may be induced by burial, which often happens in species with long-lived seeds (Harper 1977). This kind of dormancy may be broken and germination promoted by disturbances that bring buried seeds to the surface.

Seed polymorphism can lead to different seeds in an infructescence having different germinabilities, which can spread germination over several seasons. For example, in *Pteranthus dichotomus* (Caryophyllaceae), terminal seeds within single dispersal units tend to germinate more readily than basal seeds (Datta et al. 1972). In *Aegilops geniculata* (Poaceae), the dispersal unit (spike) consists of 2–5 spikelets. In contrast to *P. dichotomus*, grains in the lowest spikelets of the inflorescence tended to germinate more readily than those in terminal spikelets (Datta et al. 1972). Seed polymorphism within an individual likely also reduces sibling competition by allowing emergence of only some progeny each season (Gutterman 1994).

Seeds of *Mesembryanthemum nodiflorum* (Aizoaceae), when stored dry at ambient laboratory conditions showed an annual cycle of dormancy and non-dormancy that was maintained for many years (Guttermann 1980–1981). Terminal seeds, from the upper part of the capsule, germinated earlier and at higher rates than central and basal seeds, and this effect was maintained even after > 20 years dry storage in the laboratory.

## 7.7 Fleshy-fruited perennial species

In many ecosystems animals play a major role in dispersal; epizoochory (passage on the outside of animals) and endozoochory (dispersal after passage through an animal's gut) are common adaptations, reflecting the importance of plant-animal co-evolution. As we have indicated, epizoochory is relatively uncommon in the desert; endozoochory—with its frequently associated fleshy fruits—is also rare; however, where it does occur in deserts it is of major ecological significance. Examples include the orange, one-seeded berries of the Dragon's blood tree, *Dracaena cinnabari* (Mies and Beyhl 1998), *Ephedra foeminea, Cissus rotundifolius*, and *Coccinea grandis* (Hegazy et al. 2014), and the fruits of *Ochradenus baccatus*.

Willson et al. (1990) concluded that zoochory was associated with greater vertical diversity in vegetation structure, and higher soil fertility. Willson et al.

(1989) reported a significant negative correlation between the proportion of fleshy-fruited species and moisture availability, across Australian and New Zealand plant communities. Moreover because fleshy-fruited plants are typically woody perennials, any patchiness caused by "directed" dispersal often also creates island-like concentrations of fruiting resources, which in turn draw greater visitation by frugivores (Bronstein et al. 2007).

*Opuntia* (prickly pear cactus) forms large, dense stands in parts of arid Mexico (e.g., Janzen 1986). Dispersal of seeds by frugivorous vertebrates there has been well studied (e.g., Godinez-Alvarez et al. 2002; Janzen 1986; Silvius 1995). As in the case of *Ochradenus* (Resedaceae) described in the next paragraph, some of these species can form large, extensive populations.

*Ochradenus* includes six species found in desert, semi-desert steppe, and mountains, from Pakistan to Libya and from Israel and Jordan to Somalia (Miller 1984). *Ochradenus baccatus* is a widespread Saharo–Sindian species and quite often the dominant fleshy-fruited shrub in many hot desert regions in the Middle East (Bronstein et al. 2007). Elsewhere (see Section 6.6.3) we describe its variable sexuality and interesting phenology, with prolonged year-round reproduction, peaking in both the spring and autumn. Regarding dispersal we note that year-round and throughout its range, *O. baccatus* fruits are likely the single most important food for many desert frugivores (Bronstein et al. 2007).

It is clear frugivory plays an important role in the ecology of deserts, helping generate the contagious spatial structure often observed in populations of fleshy-fruited species. Bronstein et al. suggest the effect in fleshy-fruited species may itself be a larger, emergent property of xeric systems, exerting a strong influence on frugivore behavior and creating positive feedbacks through resource-aggregating effects. Bronstein et al. suggest that at least in desert environments, the few, highly abundant, fleshy-fruited species such as *Ochradenus baccatus* should be regarded ecologically as keystone species, and are therefore particularly urgent targets for conservation.

Birds are the most diverse group consuming *O. baccatus* (Bronstein et al. 2007). These include regionally resident bulbuls, grackles, sparrows, and blackstarts, as well as many migrants—e.g., blackcaps, warblers, and lesser whitethroats. In addition several mammals (including foxes) and some reptiles spend significant time feeding on *Ochradenus* shrubs. It is also browsed by larger mammals like camels, gazelles, and ibex.

Bronstein et al. reviewed the extent to which frugivory can influence the island-like patterning of vegetation in desert systems, and the importance in the Middle East of the particular case of *O. baccatus*. They determined that two bird species in particular, yellow-vented bulbuls (*Pycnonotus xanthopygos*; Pycnonotidae) and Tristram's grackles (*Onychognathus tristramii*; Sturnidae), both ingest *O. baccatus* fruits, removing germination inhibitors from the pulp and depositing more germinable *O. baccatus* seeds in their droppings. Perhaps not surprisingly, most of the seed rain for *Ochradenus* is generated under trees. In the Judean Desert, bulbuls and grackles spend most of their time on *Acacia* and *Tamarix* trees, *O. baccatus*, and other shrubs, and largely avoid open spaces. Recruitment in *O. baccatus* is particularly dense under *Acacia* and *Tamarix* (see Bronstein et al. 2007).

## 7.8 Non-fleshy-fruited perennials

### 7.8.1 *Acacia* species—herbivory—bruchid beetle and other biotic interactions

*Acacia* is a cosmopolitan genus containing *c*. 1350 species and comprising three large subgenera, namely subgenus *Acacia* (*c*. 161 species, pantropical distribution), subg. *Aculeiferum* (235 species; pantropical), and subg. *Phyllodineae* (960 species, largely confined to Australia) (see Maslin et al. 2003).

At least a third of all *Acacia* species are trees, and most of them occur in Australia where it is the single largest genus, with over 1000 species (Miller et al. 2011). Miller et al. note that while the legume subfamily Mimosoideae includes a particularly high percentage of invasives, the Australian acacias show the highest rates of all the legumes. Some 23 species of Australian Acacia are now considered invasive outside Australia. Some of these—e.g., *Acacia mearnsii, A. longifolia*, and *A. cyclops*—are invasive in many parts of the world including the Middle East. (Other weedy mimosoid legumes

having large invasive ranges include *Prosopis* spp. [mesquite], *Acacia nilotica* [prickly acacia], *Leucaena leucocephala*, and *Mimosa pigra*.)

In many parts of Africa and the Middle East, *Acacia* trees are widely regarded as keystone species in their ecosystems (see Section 6.8). They are nitrogen fixers and have a positive effect on soil structure and soil chemistry. Moreover most of the desert fauna depend on them either directly or indirectly for food and shade (Hackett et al. 2013; Munzbergova and Ward 2002; Or and Ward 2003; Ward et al. 2012). Acacias hold crucial ecological links to arthropods such as ants, which live on them (Kruger and McGavin 1998; Palmer 2003; Young et al. 1997), and bees, which rely on their pollen (Martins 2004), as well as bruchid beetles that frequently infest seed pods (Rohner and Ward 1999). Recently, Hackett et al. (2013) showed that Acacia trees in the Negev are also of major importance to the large community of insectivorous desert-dwelling bats there.

There has also been significant coevolution over time between Acacia trees and large mammalian herbivores (Coe and Coe 1987; Rohner and Ward 1999). Various large animals act as both predators on and dispersers of *Acacia* seeds. While some seeds get destroyed during passage through the herbivore's digestive tract, others are later egested, unharmed. Ingestion appears to facilitate germination by scarification of the testa, or seed coat, as well as, of course, subsequently also providing localized nutrient enrichment for seedlings (Or and Ward 2003).

Fruits of different *Acacia* species may be either dehiscent—splitting open and releasing seeds which may then get dispersed by wind and gravity—or *in*-dehiscent, producing pods which do not split open, but instead remain on the tree until removed by browsers or mechanical action, or, as in the case of *A. raddiana* and *A. tortilis*, pods may drop off but do not split. Seeds of indehiscent species remain in the pods until they are eaten, stepped on, or degraded by fungal attack (e.g., Miller and Coe 1993).

Seeds and fruits of Acacias are eaten by a multitude of large wild animals, and livestock. According to Or and Ward (2003), African Acacias are eaten by many large herbivores including elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), great eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*), and duiker (*Sylvicapra grimmia*). Other consumers include ostrich (*Struthio camelus*) and many different rodents. In the Middle East dorcas gazelles (*Gazella dorcas*) and ibex (*Capra ibex*) are also important, along with domesticated camels, cattle, and goats.

Many acacias can be infested with seed beetles (Bruchidae, Coleoptera). In small bruchid species, several beetles may infest a single seed; in larger species the larvae may exploit more than one seed, moving to adjacent seeds in a pod. Some pods (e.g., *A. nilotica*) are fragmented (compartmentalized) preventing larvae from moving readily from one seed to another.

It is not always easy to distinguish between vertebrate seed *predators* and vertebrate seed *dispersers*, given that many act as both (Sallabanks and Courtney 1992). Or and Ward (2003) suggested that the *level* of bruchid beetle infestation may be what determines the relative ratio of predation to dispersal. They argued that seeds which have had large fractions of their cotyledons consumed by bruchids end up being digested by herbivores, while hard, intact seeds may be impossible to digest and therefore survive passage through the gut and get dispersed. Although it is now broadly agreed there is an important three-way interaction involving bruchid beetles, Acacia trees, and various large, mammalian herbivores, it is also apparent that these relationships are complex and not yet completely understood (see Or and Ward 2003). There are also other potential dispersers than just the mammals. . .

Many acacias have specialized seed adaptations for dispersal by birds and ants (O'Dowd and Gill 1986), although passive dispersal by water, wind, and gravity is also common. Broadly, biotic seed dispersal in Acacia falls into two categories based on whether seeds have arils (edible outgrowths at the funiculus, or attachment site of the seed) or *elaiosomes* (fleshy structures at the seed attachment that are rich in lipids and proteins). The fleshy arillate appendages in the bird-dispersed seeds, and elaiosomes in ant-dispersed seeds attach the seed to the lining of the seed pod

and make them attractive to various bird and ant species respectively.

Typically ants remove and fairly rapidly bury *Acacia* seeds and their elaiosomes in underground nests, and so transport them on a local scale. Gibson et al. (2011) noted that species described as having a "bird-dispersal syndrome" are often likely to be also dispersed vertically by ants, as myrmecochory (seed dispersal by ants, which occurs even when elaiosomes are absent) accounts for so much of the movement of seed from the litter layer into the deeper seed bank.

Ants appear to be the main drivers of *Acacia* seed bank persistence and maintenance (with gravity and water playing a role when ants are absent). Once seeds have dropped to the ground, ants bury many of them in their nests to allow them to exploit the attached aril (e.g., Milton and Hall 1981). Such seeds benefit by protection from above-ground seed predators and also from fire, besides being moved into the seed bank (Holmes 1990).

Rohner and Ward (1999) suggested that high mortality and poor recruitment in Acacia tree populations were having important cascading effects on Middle Eastern ecosystems. Human activities have caused drastic changes in the water regime and the abundance of wild and domestic ungulates, which in turn may be impacting these trees. Rohner and Ward studied effects of large mammalian herbivores on the establishment of young *Acacia raddiana* and *A. tortilis* in Israel's Arava Valley, between the Red Sea and Dead Sea. Seed accumulation under trees was high when large herbivores were excluded, and direct observations confirmed that ungulates were the main seed dispersers. Bruchid beetles damaged more than 95% of seeds that were not ingested by ungulates. Seed germination was facilitated by gut passage through ungulates. Seedling survival was determined largely by water availability and proved independent of herbivore density.

Rohner and Ward concluded that a sequence of several years of high rainfall was necessary for successful establishment of young trees. Under severe browsing pressure by ungulates, growth in juvenile trees was delayed and smaller sizes became overrepresented because herbivory was limiting the growth of trees that were present. There was no evidence of effects on the long-term demography, perhaps because ungulates benefitted the population by increasing seedling densities, through enhanced germination of seeds. Rohner and Ward also concluded that large mammalian herbivores are essential components of arid Acacia savannas and that wild and domestic ungulates must be included in future conservation plans. They predicted that loss of *Acacia* trees in the Middle East would lead to a significant loss of biodiversity in the region.

### 7.8.2 Other species

Different types of seed dormancy are shown in Table 7.4. A study of dormancy in the desert undershrub, *Cleome droserifolia* (Cleomaceae) showed that, on average, some 44% of seeds were endogenously dormant, 9% exogenously dormant, and 46% readily germinable when there was sufficient rainfall (Hegazy 1990a). Exogenously dormant seeds tend to have mechanisms that delay seed germination until conditions are more suitable for seedling establishment. In contrast, endogenous dormancy prevents synchronous germination of a seed cohort, and the likely greater sibling competition which would result.

Caper, *Capparis spinosa* (Capparaceae), is a native Mediterranean shrub whose distribution stretches across North Africa, southern Europe, and western Asia. Its seeds typically show dormancy and require acid scarification (a treatment partially simulating passage through a vertebrate gut) or surface abrasion to soften the hard testa and break dormancy (Al-Oudat 2008; Olmez et al. 2004). Al-Safadi and Elias (2011) treated seeds by abrasion and soaking in dilute sulphuric acid, both of which increased germination. Sulphuric acid and scratching/abrasion resulted in germination of 32% and 20% respectively, compared to controls which had no more than 5%.

Germination and dormancy in the perennial rangeland herbs, *Ferula gummosa* (Apiaceae) and *Teucrium polium* (Lamiaceae), were tested in Iran by Nadjafi et al. (2006). Seeds of both species have a hard testa. Chemical treatments with 75% sulphuric acid, cold stratification, soaking in gibberellic acid (GA3), washing/leaching in running water and cooling for 14 days, all gave increased germination.

For *F. gummosa*, seed leaching, cold storage, and GA3 all gave better germination than other treatments. In *T. polium*, GA3 and acid treatments produced highest germination.

El-Keblawy (2013) studied germination in two succulent, halophytic shrubs, *Haloxylon salicornicum* and *Salsola imbricata* (Chenopodiaceae). Both species have short-lived seed banks (El-Keblawy and Al-Shamsi 2008; Khan 1993; Zaman et al. 2010). El-Keblawy stored seeds in dry conditions at room temperature (20–23°C), under cold conditions (−4°C), and under warm storage conditions (40°C). Germination in each group was compared with natural storage in situ at an inland desert site in the UAE. Seeds of both species showed highest germination immediately after dispersal, and lost viability after about nine months under natural conditions. Loss of viability could be due to repeated cycles of hydration and dehydration in the field. Seeds held in cold storage for 17 months maintained high germinability (> 80% in both species). After both warm- and room-temperature storage, percentage germination was lower than after cold storage. Stored seeds germinated under a wider range of temperatures than did fresh, unstored seeds. High annual seed output in *H. salicornicum* and *S. imbricata*, even in dry years, likely compensates for the rapid loss of viability in the short-lived seed bank.

Many other halophytes, including *Arthrocnemum macrostachyum, Aeluropus lagopoides, Cressa critica, Haloxylon stocksii, Salsola imbricata*, and *Sporobolus ioclados* have transient seed banks that are depleted a few months after dispersal (Khan 1990, 1993). Some halophytes—for example, *Arthrocnemum indicum* and *Suaeda fruiticosa*—maintain a more persistent seed bank using both innate, and secondary, enforced dormancy. Under saline conditions dormancy may be driven by osmotic equilibria; at lower salinity levels, more water diffuses into seeds enabling more germination. In more moist, temperate regions, halophyte seeds often remain viable after exposure to hyper-saline conditions and maintain large, persistent seed banks. Such species germinate readily during early spring to July, when soil salinity is relatively reduced and temperature is warmer (Khan and Ungar 1986a,b; Ungar 1995).

Mesquite, or *Prosopis juliflora* (Fabaceae) is a Middle Eastern invasive in which the hard seed coat carries with it a physical dormancy (Shiferaw et al. 2004). El-Keblawy and Al-Rawi (2006) evaluated effects of different maturation times and dry storage on dormancy in seeds collected in November ("fall"), February ("winter"), and May ("spring"). Mesquite seeds that matured in fall (i.e., short day and low temperature conditions) had the highest germination among the three groups (and lowest dormancy). At the same time, fall- and winter- produced seeds both germinated better at 40°C in light than at lower temperatures. Dry storage increased overall germination for fall- and winter-collected seeds. Carry-over effects of temperature and light conditions during seed formation became reduced after storage.

In the semi-desert, pastoral lowlands of Ethiopia, Shiferaw et al. (2004) studied the soil seed bank of mesquite and the role of animals in seed dispersal and seed dormancy. Seven treatments were examined: (1) seeds recovered from animal droppings; and seeds that had received (2) mechanical abrasion and scarification; (3) immersion in boiling water; (4) exposure to dry heat; (5) soaking in dilute sulphuric acid; (6) immersion in cold water; and (7) controls with no pre-treatment. Germination was assessed in Petri dishes held at 22°C.

The highest germination rates (100% and 97%) occurred in mechanically scarified and acid-treated seeds, respectively. Seeds recovered from animal droppings showed 37%, 47%, and 4% germination for goats, wild warthogs, and cattle, respectively, compared to 21% for control seeds, while simple soaking in cold water did not improve germination. These results suggest mesquite shows adaptation to endozoochory as a result of the hard testa. Shiferaw et al. concluded that under field conditions, fluctuations in temperature, soil chemistry, abrasion, and ingestion by animals all enhance permeability of the seed coat, promoting germination.

The natural range of the genus *Aloe* covers Sudan, Ethiopia, Somalia, Djibouti, Eritrea, and the southwestern Arabian Peninsula. Typically seed viability in the genus extends for about a year after dispersal (Cousins and Witkowski 2012). However, the seeds of aloes from drier habitats, e.g., *Aloe dichotoma*, *A. asperifolia*, and *A. greatheadii* may remain viable and

dormant for up to three years (Smith and Correia 1992). This could be an adaptation to more erratic rainfall in the drier sites. As reported by Smith and Van Wyk (2009), a shaded microhabitat is typically required after germination for most aloes, since aloe seedlings are very sensitive to heat and desiccation.

*Blepharis ciliaris* (Acanthaceae) occurs in many warm desert areas and has great ecological flexibility (see Figure 2.14). Plants may be mono- or polycarpic, depending on available moisture. Seeds are capable of germinating shortly after dispersal. Some seeds can be dispersed in individual dry skeletons over several rainy seasons and germinate at several occasions (Gutterman 1994; Gutterman and Ginott 1994). No seeds germinate before the soil is wet enough to ensure establishment, while at the same time a seed reserve is maintained on the standing plant skeleton that spreads germination over several years (Gutterman 1972). Field studies showed seeds had successfully germinated just three hours after release, and similar results were obtained under field conditions (Gutterman 1972). High rates of germination were observed for seeds that had been retained, dry on skeletons for up to ten years.

This rapid germination response places *B. ciliaris* near the top in terms of speed of seed germination[6] (Gutterman 1972). The pattern of intermittent seed release in *Blepharis* represents another mechanism (besides dormancy in the seed bank) that offers a bet-hedging strategy enabling the parent individual to spread the risk of progeny germination over time. From the population perspective, this ensures persistence of a diverse (multi-parent) *aerial* seed bank in *B. ciliaris*.

The biennial rosette species *Verbascum sinaiticum* (Scrophulariaceae) is rare in Egypt, with distribution restricted to the Sinai Peninsula. Strictly the species is a facultative biennial, since individual lifespans range from 1 to 2 years; this results in a certain amount of within-population variation

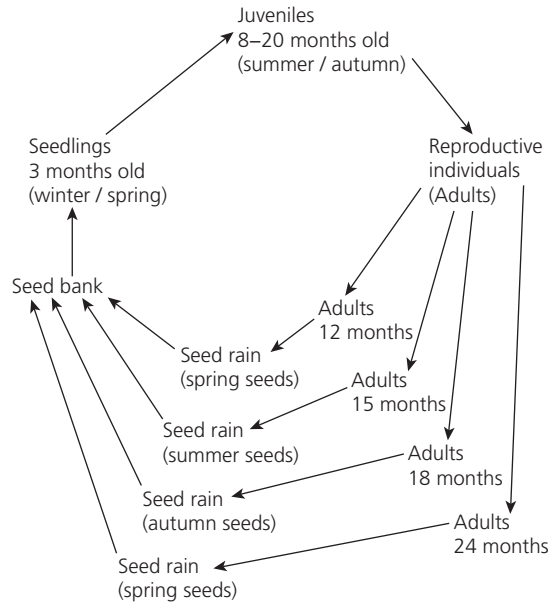



**Figure 7.3** Diagrammatic life cycle dynamics of *Verbascum sinaiticum*. Seedling establishment occurs during spring. Three month-old seedlings enter the juvenile stage. Juvenility extends over summer and autumn where plants reach an age of 8 to 20 months before becoming reproductive. Each cohort of juveniles gives four cohorts of reproductive (adult) individuals. Age of the reproductive individuals ranges between 12 and 24 months. Seed rain (output) may occur in spring, summer and autumn. Seed bank represents about 0.05 to 0.1% of total seed output (after Hegazy 2000, used with permission).

in patterns of resource allocation, seed longevity and viability. The age of reproductive individuals ranges from 12 to 24 months and seed production can occur in spring, summer or fall (see Figure 7.3). The viable seed bank is estimated to represent only 0.05 to 0.1% of total seed output (Hegazy 2000). Plants that flowered at 15 months made the greatest contribution (83.5%) to the seed rain, and also produced seeds that had the greatest viability and germinability.

Seeds of *Eruca sativa* (Brassicaceae) collected from desert and semi-arid habitats had greater dormancy than seeds from the more mesic, Mediterranean environment (Barazani et al. 2012), as the aridity seemed to induce a secondary dormancy. Hanin et al. (2013) investigated the genetic diversity of seeds in the seed bank of arid and semi-arid populations of *E. sativa* in the eastern Mediterranean.

[6] However perhaps the fastest rate may be for *Salsola kali*, where seeds germinated less than half an hour after wetting (Rhoads et al. 1967). This is likely due to the relatively simple uncoiling of what is already a well-differentiated seedling within the seed.

AFLP markers[7] were used to compare the diversity of seeds in the seed bank with that of adult individuals in desert and semi-arid populations. Genetic diversity in the adult population appeared to be structured by continuous recruitment from the soil seed bank. However, the non-dormant seed bank made a greater contribution to the standing population than did the dormant seed bank. Hanin et al. suggested dormant seeds could contribute to the above-ground diversity in following growth seasons.

## 7.9 Vicariance (and scattered vestiges of Gondwanaland in Socotra)

*Vicariance* biogeography also considers dispersal, but at a rather different time scale, probing the relation between species' distributions (biogeography) and continental drift. The slow drifting apart of the Earth's geo-tectonic plates—as described in Chapters 1 and 3—is another aspect of an organism leaving home and dispersing (although vicariance can be a far more violent and transformative process than the phrase "drifting apart" may suggest). Vicariance is an extended process that creates physical separation between populations that once shared a gene pool; this in turn may promote subsequent speciation.

If the splitting of the land and separation of the species living on it happen to coincide, the result will be two closely related species living in similar parts of a formerly contiguous area (an area previously occupied by their common ancestor). This is an example of a vicariance event (meaning a splitting in the range of a taxon); events like this can often help us account for a region's biotic "starting capital."

Before it became distributed as a fruit tree throughout most of the world's tropical countries, the cultivated pomegranate *Punica granatum* (Punicaceae) was originally restricted to the Middle East. (This ancient species is both Biblical and Koranic, being mentioned many times in both holy books.) The only other species in the genus, *P. protopunica*, occurs in Socotra and is believed to be the wild ancestor of the cultivated species. *Punica protopunica* may have previously occurred across a wider area of the Middle East (Balfour 1888), or it may have been exported there from Socotra and developed as a cultivar at a very early date.

Socotra is clearly a significant place biogeographically, one we have used as a touchstone on several occasions, a reference location against which, as with the pomegranate, we may consider the plants of the larger Middle Eastern region as a whole. In the late Cretaceous or early Tertiary, the islands of the Socotran archipelago formed part of the southern continent of Gondwana so its flora includes a variety of ancient taxa, disjunct in their distribution there compared with related taxa which may have "gone their own way" both genetically and spatially during Earth's deep history.

The plant geographer Bruno Mies (e.g., 1998) has considered the flora of Socotra and related the plants there to ecologically comparable zones in northeast Africa and Arabia, southern Africa, Madagascar, and India. He regarded many of the plants of these regions as common descendants of a once continuous, arid southern "Tethyan" vegetation (see Figure 3.2). Thus, for example, xeromorphic[8] *Dracaena* or "Dragon's Blood" tree species have relatives growing on the mountains of southern Arabia (*D. serrulata*), and on those of southern Sudan, Egypt, and southwestern Arabia (*D. ombet*), northern Somalia (*D. schizantha*), and Madagascar, southern Africa, and the Atlantic Macaronesian islands (i.e., the Azores, Madeira, Canaries, and Cape Verde) where the genus is represented by *D. draco*.

On Socotra *Dracaena* is represented by *D. cinnabari* (Sections 2.11.2 and 3.3). This species—with its

[7] AFLP or Amplified Fragment Length Polymorphism is a PCR-based tool using restriction enzymes to digest genomic DNA, followed by ligation of adaptors to the sticky ends of the restriction fragments (Vos et al. 1995). A subset of the restriction fragments is then selected to be amplified. The amplified fragments are separated and visualized on denaturing polyacrylamide gels, either through autoradiography or fluorescence, or automated capillary sequencing instruments.

[8] Xeromorphic characters are developed in plants specially adapted to conserve and store water, avoiding desiccation and maintaining balanced metabolic activities during periods of drought. Xerophytic plants have many structural and physiological adaptations that serve as protection against excessive loss of water (see Chapter 5).

striking arborescent morphology—closely resembles the Atlantic Islands' *D. draco*, growing 8–10 m high, with a single, secondarily thickened trunk, ending in dichotomously branched terminal leaf rosettes that form an umbrella-shaped crown. The leaves are sclerophyllous and both *D. cinnabari* and *D. draco* appear to fix $CO_2$ by opening their stomata overnight and using the CAM pathway (see Section 5.5).

Species in the genus *Dracaena* mostly live in the moist tropical belt of the paleotropics. However, the distribution of the eleven related xeromorphic species shows a remarkable pattern (Figure 7.4). The Atlantic *Dracaena draco* has an isolated distribution, while the remaining ten species occur from Arabia to South Africa along the eastern part of the African continent. Xeromorphic species are not naturally present in the wet Congo Basin and Guinean rain forests, but northern Africa (the Atlas Mountains, Ahaggar, and Tassili) also lacks members of this group.

Mies goes on to describe the *tirucalli*- and *tithymalus*-groups of *Euphorbia* species (see Figure 7.5A and B) as having a very similar distribution pattern to the Dracaenas. More than 20 species occur in South Africa, Madagascar, and east Africa to Socotra and Arabia, stretching as far as the Indian subcontinent. One close relative, *Euphorbia aphylla*, lives in the Canary Islands, and *E. latiflora* in West Africa.

*Euphorbia* is a major genus in the Middle East (see Section 5.7). At Socotra it comprises a large number of stem-succulent specialists, including the following:

- The 0.5 m high *Euphorbia spiralis* and *E. septemsulcata* (Socotra), vicariants of *E. handiensis* (at Lanzarote in the Canaries) with cactoid morphology.
- The peculiar *E. abdelkuriensis* (which lacks any spines—though spines are otherwise highly characteristic of the genus, and possesses a yellow, milky, flavenoid-rich juice), and a size, shape, and habitat preferences that are most similar to those of *Euphorbia canariensis* (at Gran Canaria in the Canaries). Both belong to the section *Diacanthium* of the genus.
- *Euphorbia socotrana* (Socotra) is a related species of the *tithymalus*-group, which comprises a dozen species on the Atlantic islands (see Figure 7.5A). The hemispheric canopy of these individuals is the result of terminal leaf rosettes, closely arranged to form a so-called featherduster-brush shape—a name sometimes applied to these plants. Inside each bush a special microclimate is created wherein the temperature and wind velocity are reduced, decreasing rates of evapotranspiration.
- *Euphorbia arbuscula, E. obcordata, E. oblanceolata*, and *E. schimperi* (Socotra) of the *tirucalli*-group closely resemble *E. aphylla* (Gran Canaria, Gomera, and Tenerife). The terminal green branches contribute to photosynthesis; moreover leaves are only present on actively growing young shoots.

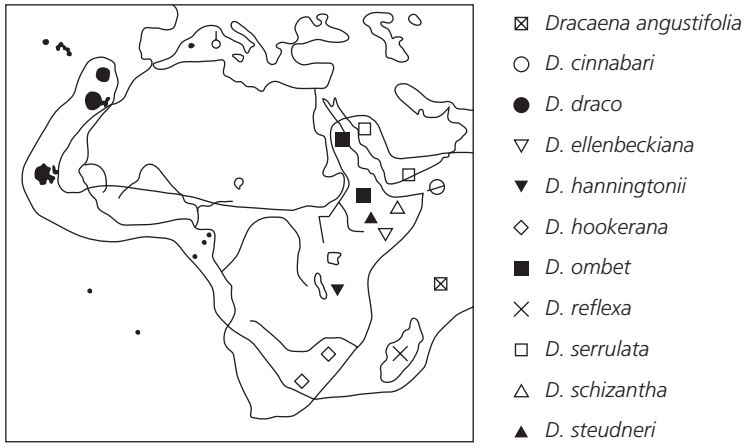
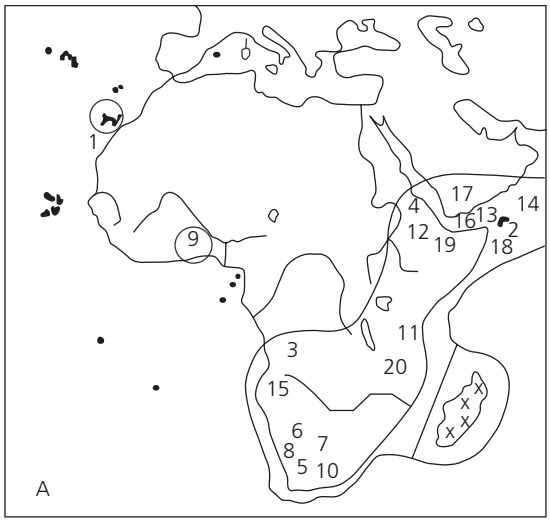
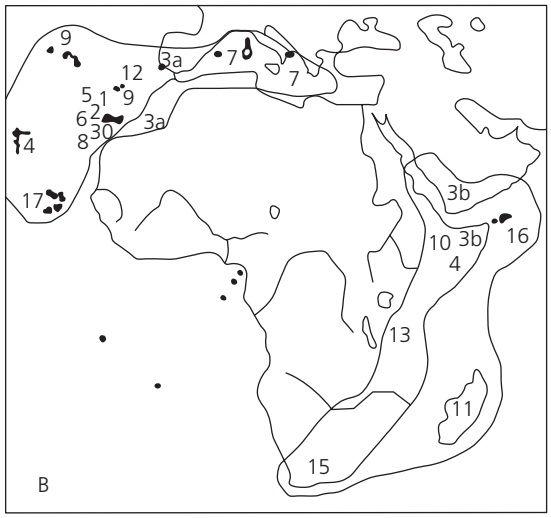



**Figure 7.4** The xeromorphic species of the genus *Dracaena*, indicated as symbols, and the general distribution of the genus (after Mies 1998, used with permission of the author).




1 *Euphorbia aphylla*
2 *Eu. arbuscula*
3 *Eu. berotica*
4 *Eu. consobrina*
5 *Eu. dregeana*
6 *Eu. fleckii*
7 *Eu. gregaria*
8 *Eu. gummifera*
9 *Eu. lateriflora*
10 *Eu. mauritanica*
11 *Eu. merkerii*
12 *Eu. nubica*
13 *Eu. obcordata*
14 *Eu. oblanceolata*
15 *Eu. rhipsaloides*
16 *Eu. schimperi*
17 *Eu. schimperiana*
18 *Eu. schweinfurthii*
19 *Eu. scoparia*
20 *Eu. tirucalli*
× Malagasy species et al.




1 *Euphorbia anachoretea*
2 *Eu. atropurpurea/broussonetii*
3a *Eu. balsamifera*
3b *Eu. bals. ssp. adenensis*
4 *Eu. barbicollis*
5 *Eu. berthelotii*
6 *Eu. bravoana*
7 *Eu. dendroides*
8 *Eu. lambii*
9 *Eu. mellifera/stygiana*
10 *Eu. noxia*
11 *Eu. orthoclada*
12 *Eu. piscatoria*
13 *Eu. pseudograntii*
14 *Eu. punicea*
15 *Eu. quadrata*
16 *Eu. socotrana*
17 *Eu. tuckeyana*

**Figure 7.5** The *tirucalli* (A) and *tithymalus* (B) sections of the genus *Euphorbia* and their general distributions (after Mies 1998, used with permission of the author).

According to Mies, long-distance dispersal of seeds for all these disjunct distributions is improbable if they indeed originated directly from regions as far away from Socotra as South Africa, Australasia, or India. Euphorbiaceae and *Dracaena* species have fruits that are, for the most part, too heavy for significant wind dispersal.

Mies went on to speculate that because there are so many relict species in the Atlantic region with a probable eastern origin, there may have existed a "southern Tethys trail" or dispersal corridor along the shores of the Tethys Ocean for these species. Figure 7.6 shows a general biogeographical distribution type of xeric taxa (e.g., *Senecio*, subgen. *Kleinia*) in areas in and around Africa and Arabia. Taxa related to Socotran and Macaronesian species occur, either in South Africa or along the East African rift valley and mountain-range system. The flora of

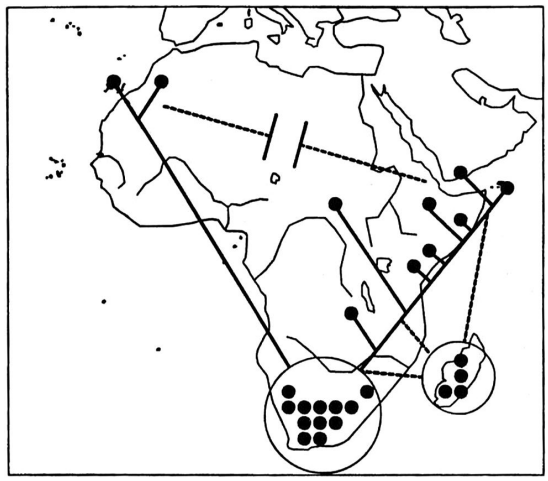


**Figure 7.6** Hypothetical scheme of geographical relations between the species of the genus *Kleinia* in the African paleotropics as "Tethyan trail relics" (after Mies 1998, used with permission of the author).

the Saharan desert region is in general unrelated to the eastern and western islands of the continent—Mies suggests this is because any previous connecting links between the eastern and western islands, presumably along the shores of the former Tethys Ocean, have been lost.

Other, non-Macaronesian vicariant distributions in Socotra include many species exemplifying the earlier, adjacent African connections.

Socotra–Dhofar (Oman/South Arabia): *Cucculus balfourii* (Menispermaceae), *Exacum affine*, and *E. gracileps* (Gentianaceae).

Socotra–Dhofar–Somalia/Djibouti: the Cucumber tree, *Dendrosicyos socotranum* (Cucurbitaceae).

Socotra–Ethiopia–Somalia: *Buxus hildebrandtii* (Buxaceae) occurs in mountainous areas of the region where it receives sufficient precipitation from winter monsoon and dew. *Echidnopsis socotrana* differs in stem morphology from *E. nubica* and *E. scutellata*. The genus *Wellstedia* occurs with *W. socotrana* in Socotra as well as on mountain tops of northern Somalia, where there are also *W. somalensis* and *W. laciniata*.

Socotra–Somalia: *Dirachma somalense* (Dirachmaceae) is the Somalian vicariant of *D. socotrana. Dorstenia gypsophila* is a vicariant species from northern Somalia, expressing a similarly striking "epigaeic caudex" just like *D. gigas*.

Socotra–Africa–Arabia: *Hypericum balfourii* and *H. socotrana* (Hypericaceae) both belong to the section *Campylosporus*, which has an otherwise general African distribution.

## 7.10 Summary

This chapter considers seed dispersal, dormancy, and evolutionary "bet-hedging" as ways of avoiding drought. Cues that induce and release dormancy, and environmental triggers for germination, as well as different styles of seed dormancy are all shaped by local conditions. Frugivory plays an important role in the plant ecology of deserts, often generating a contagious distribution among populations of fleshy-fruited species. This effect may be a larger, emergent property of dryland systems, exerting a strong influence on frugivore behavior and creating positive feedbacks through resource-aggregating effects. The few, highly abundant, fleshy-fruited species such as *Ochradenus baccatus* act as "keystone species" in desert environments and are therefore particularly urgent targets for conservation. Other desert keystones include the Acacias, many of which have specialized seed adaptations for dispersal by birds and ants. Vicariant dispersal and continental drift are discussed using many Socotran examples.

CHAPTER 8

# Chemical ecology in the desert

## 8.1 "Intelligent" plant behavior

Plant behavior at some abstract level surely involves the acquisition and processing of information. Plants gather and integrate information about their environment and then somehow "decide" when and in what direction to deploy resources to roots, shoots, leaves, and flowers. Despite their essential sessility, plants are nevertheless highly *active* and organized agents, responding to environmental cues in ways which seem subtle and adaptive. Plants perceive competitors and are able to grow away from them; in some cases they can even respond to potential competitors before being directly shaded by them (e.g., Karban 2008). Experiments have shown that plants are more "wary" of actual vegetation than of inanimate objects. Plant behaviors are in fact highly sophisticated, but to an animal are either invisible or seem simply (with exceptions) very, very slow.

Silvertown and Gordon (1989) defined plant behavior as the response to internal and external signals, including such developmental phenomena as de-etiolation—the complex cluster of biochemical and developmental effects that take place when a seedling is exposed to light; also flower induction, wind-sway response, regeneration, induced bud break/germination, tropic bending, etc. More recently Trewavas (2003, 2009) has described plant behavior simply as "what plants *do*" and he envisioned it as active, purposeful, and intentional. Related to this, phenotypic plasticity describes the degree to which an organism can be changed (via reaction norms[1]) in response to environmental signals (Schlichting and Pigliucci 1998; Sultan 2000). This developmental adjustment to prevailing conditions has been posited as a kind of plant "intelligence," even suggesting "foresight" to some (Trewavas 2003, 2004, 2009). Phenotypic plasticity may be evident in terms of both morphology and physiology (e.g., Bell and Sultan 1999).

As living organisms, individual plants are obviously highly complex. The fact that there is interdependence and biochemical signaling among different organs and separate, specialized plant parts is well known. Trewavas (2004), for example, reviewed an array of root signals, which in turn can modify shoot development. These include, for example: abscisic acid, which can modify stomatal conductance, flowering, and shoot morphology; cytokinins, which modify leaf expansion, shoot branching, and senescence; and ethylene precursors, which modify shoot nastic responses and stem growth. At the same time *shoot* signals can modify root development. For example, auxin produced by stems can modify root branching, vascular tissue formation, and regeneration around wounds; auxin also causes different responses in the root and shoot tissues of uprooted plants; shoots will tend to grow upward, against

[1] A reaction norm (or norm of reaction) describes the pattern of phenotypic expression of a single genotype across a range of environments. It is best assessed through multivariate experiments using cloned individuals. One use of reaction norms is to describe how different species—especially closely related species—respond to varying environments. But differing genotypes within a single species may also show differing reaction norms for particular phenotypic traits and environmental variables.

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gravity ("negative gravitropism"), and roots will tend to grow downward ("positive gravitropism"), the combination of these two effects will re-establish the upright orientation of the plant. Like a turtle turning over, but different.

At a more subtle scale, mature leaves control the stomatal density of individual, young developing leaves; moreover all leaves communicate external photoperiodic signals to meristems, stolons, and buds, these signals in turn promote flowering, tuberization, and dormancy behaviors. Several weeks of cold temperature can create a stable "memory" (i.e., vernalization) that can last nearly a year. Likewise herbivory can establish a long-term effect, a "memory" of previous grazing attacks that stimulates plant defense mechanisms and increases resistance against further attacks (Baldwin and Schmelz 1996; Karban 2008; Karban and Niiho 1995). Finally the individual effects of previous plant neighbors on phenotypic development may be "remembered" by plants for up to a year following transplantation to a different location (Turkington et al. 1991).

Volatile chemicals (gases) are increasingly being recognized as important signaling compounds in plants, influencing plasticity in growth. Phenotypic modification is well recognized as a response to patterns of humidity (water vapor), carbon dioxide, oxygen, ethylene, ozone, and nitric oxide. More recently Galis et al. (2009) and Dicke (2009) reviewed the larger role of volatile plant compounds in resisting herbivory. Particular combinations of volatile compounds can bypass vascular constraints on systemic signaling—for example, in hybrid poplar (*Populus deltoidea* × *nigra*) intact leaves that lack direct vascular connections can respond, raising their levels of defense chemicals based on a volatile signal from nearby damaged leaves (Frost et al. 2007), while other combinations may signal adjacent plants (Karban 2008). We still await the discovery of a chemical "Rosetta Stone," providing some preliminary translations between plant receptors and environmental signals.

Meaningful plant signals are distinguished by specific receptors, and as Trewavas (2009) made clear, the greater the selectivity of the receptor, in general the higher the quality of information conveyed to the organism. Related receptors help to amplify further elements of the signal, thus families of receptors are not uncommon, for example, phytochromes, cryptochromes, nitrate reductases, auxin receptors, calmodulins, and other calcium receptors, etc. Unfortunately, with the exception of the extensive studies on ethylene, specific receptors for all these various volatiles so far await discovery and characterization.

Lloyd (1980) suggested that flowering in plants consisted of a series of "reassessment" points in which adjustments to the final number of flowers may be made, dependent upon nutritional availability. This process of matching flower production to current (and anticipated) resources could be regarded as a kind of learning and memory. Likewise, in many species if seed imbibition occurs in conditions that are unsuitable for germination, then a more prolonged state of dormancy—secondary dormancy—may be entered (Trewavas 1986). Trial-and-error learning seems to play an essential role in plant behavior, given the complexity and unpredictability of the plant environment.

Herbivory, disturbance, parasitism, mutualisms, and competition from neighbors . . . all these biotic interactions exist to differing degrees in the individual plant's experience, and the plant in turn must produce a response that optimizes its evolutionary fitness. Thus, for example, as Trewavas (2004) described, root systems must *integrate* the signals of soil hardness, stones, light penetration, temperature, invertebrates, the polarized distribution of water, calcium or nitrate, the presence of gases like carbon dioxide, and numerous other, internal signals in order to make critical decisions about the quantity and direction of new root growth. Integration represents higher-order learning.

## 8.2 Allelopathic interactions

Because they are rooted to one spot, plants—in particular long-lived plants—are in a sense "bound to be found" by an array of grazers, granivores, and other herbivores; not to mention parasitic plants, fungi, and pathogens. Plants are also often confronted by competitors—other plants of the same or other species that may exert positive, neutral, or negative effects. However, as suggested, plants have developed a rich arsenal of chemically mediated signals, achieved through the production and

storage of abundant "secondary" compounds (i.e., "secondary" to the essentials of basic existence: cellular metabolism, photosynthesis, and cellular respiration). Plant secondary compounds tend to be highly diverse, both chemically and in terms of their mode of action (Trewavas 2014).

Such chemicals—many of which have been interpreted as "allelopathic" compounds—are typically synthesized at specific organs or tissues, and include short-chain fatty acids, phenolic compounds, terpenoids, alkaloids, steroids, polyacetylenes, and essential oils, tannins, and resins (see, e.g., Whittaker and Feeny 1971).

Allelopathy embraces both chemical mechanisms of plant interference, and also use of chemicals as a means of defense. "Auto-toxicity" differs from allelopathy by having only inhibitory effects, and acts as a kind of inhibitor of other members of the same species, that is individuals likely to be seeking the very same resources as the individual of interest. The larger ecological meaning of many of these compounds remains open, but the phenomenon is often assumed in many desert species. As reviewed by Hegazy (1999b), allelochemicals are sometimes selectively toxic, affecting some plant species but not others. Some plants, e.g., *Anastatica hierochuntica*, produce compounds having both allelopathic "against other plants" and auto-toxic effects (Hegazy et al. 1990).

## 8.3 Interactions between annuals and perennials

Competition is generally a key factor shaping most longer-lived plant communities (e.g., Brooker and Callaghan 1998; Tielborger and Kadmon 1997, 2000). Dryland plants tend to be particularly influenced by their interactions with other plants (see Sections 1.7 and 4.7). Gutterman (2003) showed that shrubby perennials often have multiple, significant effects on the fates of annuals. Desert annuals are often found positively associated (spatially) with particular shrubs, with the nature and extent of associations largely dependent on the overall balance of negative and positive interactions among life forms.

Often the first indication of a role for chemical communication in plant communities is some distinctive spatial arrangement. For example, an "even" spacing of plants, either of the same or different species, may indicate a chemically mediated competition. In some communities positive (facilitative) interactions among individuals will generate positive spatial associations. Where one component is found the probability is high the other will be found as an associate, in a non-random, clumped pattern.

Studies of *Anastatica hierochuntica* (Hegazy et al. 1990, 2005; Hegazy and Kabiel 2007) showed significant variation among microsites, depending on plant size, dispersal mode, and the amount of rainfall—rainfall being associated with the leaching of allelochemicals from plant tissues (see Box 8.1 and Figure 8.1A and B). A clumped pattern of *A. hierochuntica* among small individuals was observed in the fine, sloping runnel microhabitat, likely due to the "batch" mode of seed dispersal where a subset of each cohort of seeds on the dried plant skeleton is released and able to germinate in a brief window of opportunity and sufficient rainfall. Random and over-dispersed patterns, with wide spacing between individuals, were observed among plants in large size-classes in both sand and gravel microhabitats.

Perennial species can sometimes influence the regional community of annuals by limiting them in various ways, e.g., to open spaces where there is less competition, though as we show in Section 4.7 certain shrubs and trees can also create under their canopy a microhabitat that is beneficial in terms of providing shade from the intensity of full sunlight, and enriched in terms of nutrients, moisture, and organic matter.

In a three-year field experiment, Berg and Steinberger (2012) examined annual–perennial interactions in the Negev highlands (elevation *c*. 600 m). The major vegetation there was a mix of perennial shrubs (about 10% of the area) and a diverse, scattered variety of annuals and small geophytes, differing according to micro-topography and position of the water table. Dominant shrubs included *Hammada scoparia*, *Zygophyllum dumosum*, and *Artemisia sieberi*.

Fifty *Hammada* individuals were selected at random, and fifty "artificial plants" that provided the physical shading which would be given by a real

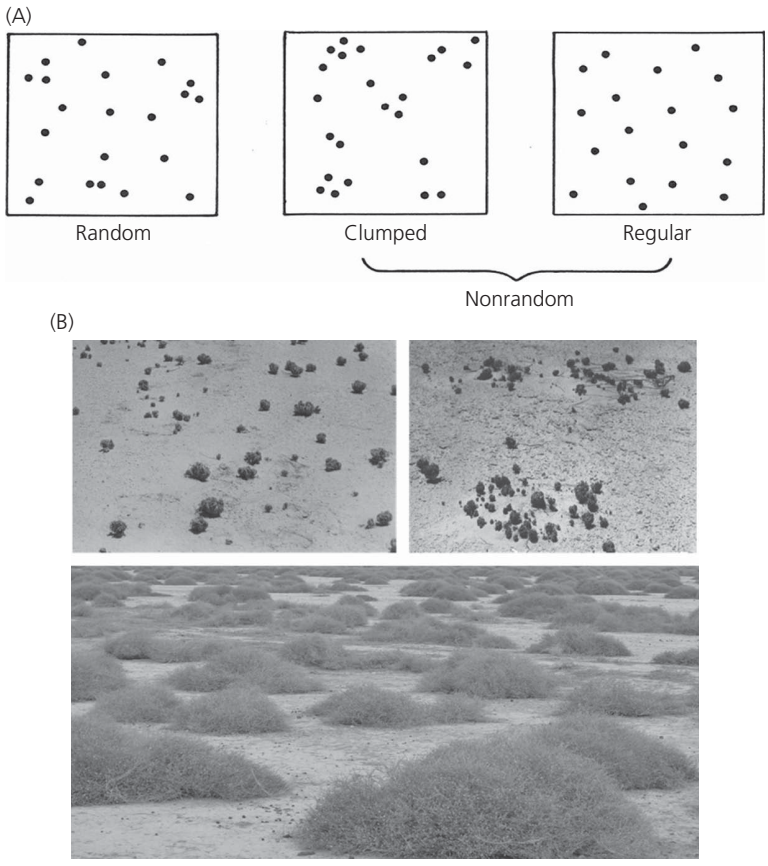



**Figure 8.1** Spatial distributions. (A) Diagrammatic representation of individual plants showing random, clumped and regular patterns. (B) Random (upper left) and clumped (upper right) patterns of *Anastatica hierochuntica* populations in Bahariya oasis, Western Desert of Egypt, and regular pattern of *Rhantherium eppaposum* at the Ibex Protected Area, central Saudi Arabia.

## Box 8.1 Generalized distribution patterns

Distributions in plant populations can be categorized into three basic patterns: random, clumped, and regular (Figure 8.1A and B). A random pattern occurs when individuals have an equal chance of occurring anywhere in the site. In clumped (or "aggregated") patterns any one individual has a high probability of being found in some areas with other individuals of the same species. Alternatively, in the regular (or "over-dispersed") pattern, where any one individual is found there is a decreased probability of finding another individual of the same species, i.e., individuals are uniformly spaced.

Clumped individuals of the same species are usually aggregated as a result of localized reproduction and/or seed dispersal; they may also be clumped because suitable conditions are patchy in their distribution, and establishment meets with different degrees of success (Barbour et al. 1987). Molles (2005) showed that many distribution patterns are produced by a combination of interactions between individuals in the population and the patchy distribution of local environmental conditions. Individuals may "attract," "repel," or "ignore" each other. Mutual attractions tend to produce clumped patterns where individuals are, for example, attracted to a common resource (e.g., greater water supply in a slight depression site). Regular patterns of distribution are produced when individuals repel each other due to antagonistic interactions or localized depletion of resources. Neutral interactions generate random distributions where all individuals have an equal probability of occurring anywhere in a particular area, i.e., neutral interactions between individuals of the population and the (relatively homogeneous) environment.

shrub, but which were obviously not releasing secondary compounds, photosynthesizing, respiring, or creating organic litter, etc. Monthly soil samples were collected and all annual species counted and identified. In the two years of lower-than-average rainfall during the study, plant density, species richness, and the biomass of annuals were all significantly greater in areas that were occupied by the simulated shrubs, compared with those in the neighborhood of living *Hammada* shrubs. These suggest a possible allelopathic effect, where inhibitors may be moving via moisture gradients in the soil surrounding *H. scoparia* plants.

In this situation the few annuals able to tolerate potential allelochemicals underneath perennial shrubs may benefit from having less competition from other annuals, as well as being able to access the nutrient pool and moisture there. Berg and Steinberger found evidence for this in the greater biomass per individual among the few annuals which were able to grow under *H. scoparia* canopies compared with those elsewhere.

## 8.4 Life history strategies

Rhoades and Cates (1976) classified the great array of plant secondary compounds into two broad categories: either "toxin-" or "tannin/resin-" types of compounds. They also showed how these patterns in plant secondary chemistry may be produced by natural selection and related to life history strategies. An array of species were classified as, very broadly, either *r*- or K-selected; then the authors showed these two groups differ significantly in the types of allelochemicals they contain. In general, short-lived, r-selected species tend to accumulate "toxin"- type compounds, made up of relatively simple molecules that tend to be effective in low concentrations, e.g., alkaloids. In contrast in long-lived, K-selected species more complex compounds were found, and these were usually present at higher concentrations and often acted as generalized "digestibility reducers" rather than toxins, effectively reducing the quantity and quality of nutrients that a herbivore could extract from the foliage in its gut.

Toxins accounted for less than 2% of leaf dry mass in the annual species studied by Rhoades and Cates. Perennial plants may contain toxins, but they tend more often to accumulate tannins and resins (which are larger, more complex molecules that may exceed 6% of leaf dry mass). In desert plant communities, annual species often constitute more than 60% of the total flora.

By signaling and otherwise influencing their environments, plants behave proactively, interacting directly with other plants by transmitting, receiving, and responding to chemical compounds released by other organisms. Plants release such compounds to the environment by means of four processes: volatilization, leaching, root exudation, and decomposition in the soil (e.g., Chou 1989). These compounds often suppress growth and development in plants, inhibiting cell differentiation and interfering with basic elements of photosynthesis, respiration, and transpiration.

Sometimes plants can benefit from a kind of "passive interference" that in some ways seems anticipatory, releasing allelochemicals that delay or inhibit development by future competitors (Reigosa et al. 2002). Taking into account that "stress" may be any environmental condition limiting access to essential resources, it seems reasonable to suggest there may be a positive relationship between environmental stress level and allelochemical production. Chou (1989) showed in plants under severe stress that allelochemicals can act as auto-toxicants, reducing population size albeit leaving resources for survivors; and Tang et al. (1995) showed that more secondary metabolites were produced by plants growing in nutrient-poor habitats compared to nutrient-rich ones.

Allelochemical production by invasive species and corresponding low tolerance of these "novel" compounds by native species helps account for the relative success of introduced species (Ridenour and Callaway 2001), and could be a key factor defining the new community that emerges after the invasion process (Hierro and Callaway 2003). Canals et al. (2005) pointed out that auto-toxicity is not uncommon in perennials, where an adaptive advantage to toxin-production is that it inhibits establishment of competitors of its own species in its immediate vicinity, limiting interference. These authors suggested the same rationale would not work for annuals since short-lived auto-toxic plants would be

dead before the next generation established. Ecologically, auto-toxicity in annuals is interesting; is it a simple byproduct of other processes, or does it contribute in some way to the fitness of the individual investing in chemical compounds?

## 8.5 Effects on seed germination and seedling growth

In Qatar Hegazy and Alsubaey (1994) and later Hegazy (1997b) studied allelopathic potential in *Glossonema edule*, a succulent perennial herb with fleshy leaves and soft erect branches that arise from the stem base. Individuals undergo repeated annual cycles of shoot growth and dormancy. During summer the above-ground shoot dries out but not the buried base of the stem. Shoot regrowth begins in winter and flowering and fruiting follow in the spring. Hegazy tested effects of *G. edule* against two annuals (*Plantago ciliata* and *Spergula fallax*) and four perennials (*Farsetia hamiltonii, Lycium shawii, Salvia aegyptia*, and *Savygnia parviflora*). Seed germination and seedling growth were reduced in all target species but the two annual species were significantly more sensitive than the perennials.

The phenology of the life cycle of these annuals is relevant here. Their seeds germinate and plants grow rapidly during the rainy season, when allelochemicals in the soil may otherwise be diluted by the rain. Thus an experiment in which allelochemicals are presented at higher concentrations does not fully capture the chemical experience to which these annuals have adapted. In contrast, perennials are growing throughout the year and unable to avoid exposure to "full concentration" allelopathic compounds. It is therefore advantageous to them to have some level of resistance to the compounds.

Hegazy's studies of seed- and fruit-based allelopathy (Hegazy 1999b) showed the presence of both germination- and growth inhibitors, and that these substances belong to different kinds of chemicals. Studies of natural growth substances in seeds of the Egyptian shrub *Crotolaria aegyptiaca* (Kinawy and Youssef 1971) showed both promoters and inhibitors. Seed extracts acted as growth inhibitors, though not germination inhibitors. Perhaps in *C. aegyptiaca* there is a premium to germinating early and rapidly; the first seeds to germinate will also be releasing inhibitors around them, which will in turn suppress the establishment of close neighbors, even if they have managed to germinate.

*Nymphaea lotus*, an invasive weed in Egyptian rice fields, inhibits the germination, growth, and yield of rice (*Oryza sativa* var. Giza-177) (Hegazy et al., 2001). In an experiment involving potted "targets" (rice) and "neighbors" (lotus), the dry mass and relative growth rate of rice proved significantly dependent on plant age and lotus rhizome density (with decreased growth at higher lotus densities). Field data for infested and non-infested fields showed lower leaf area index and yield for rice in infested fields. Several phenolic compounds were identified in the lotus rhizomes. Allelochemical production by *Nymphaea* depended on their density and is likely aided by the waterlogged condition of the poorly drained, oxygen-deficient soil. Such conditions seem favorable to the production of phytotoxins.

## 8.6 Some case studies

### 8.6.1 *Anastatica hierochuntica*

*Anastatica hierochuntica*, the Rose of Jericho, is a monocarpic annual in which the rolled-up skeletons enclose the mature fruits and often persist as dead dry "tumbleweeds" for a number of years. Hegazy et al. (1990) showed that aqueous extracts of the plant had both auto-toxic and allelopathic effects. The latter were shown against five desert species (*Rumex cyprius, Trigonella stellata, Diplotaxis harra, Cleome droserifolia*, and *Farsetia aegyptia*). In all cases germination and seedling growth were inhibited by the extract of *A. hierochuntica* (see Figure 8.2). An auto-toxic effect was associated with plant death and smaller populations; seed germination and seedling growth were inhibited in the vicinity of established individuals. Survivors produced larger seed cohorts (rolled up in plant skeletons), which in turn allowed the plant to spread progeny release over multiple years. Regarding the mechanism of inhibition, extracts of *A. hierochuntica* had significant mito-depressive effects that increased with increasing extract concentration. At a concentration of 8% the mitotic index was reduced by more than 50% (compared to controls) in *C. droserifolia* and

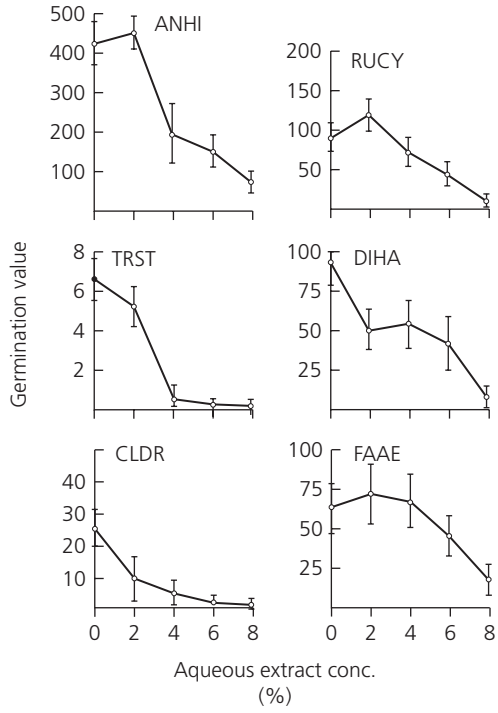



**Figure 8.2** Effect of aqueous extract of *Anastatica hierochuntica* (ANHI) on its own seed germination (auto-toxic effect) and possible allelopathic effects on *Rumex cyprius* (RUCY), *Trigonella stellata* (TRST), *Diplotaxis harra* (DIHA), *Cleome droserifolia* (CLDR), and *Farsetia aegyptia* (FAAE). Vertical bars around the means are standard deviations (after Hegazy et al. 1990, used with permission).

*T. stellata*, by more than 40% in *F. aegyptia* and *A. hierochuntica*, and more than 30% in *R. cyprius*.

Hegazy (Hegazy and Kabiel 2007; Hegazy et al. 2005) used Ripley's K-function to quantify the extent of clumping, randomness, and over-dispersion in *Anastatica hierochuntica* at different wadi microhabitats: runnels, patches, simple depressions, and compound depressions (see Figure 8.3A). The simple depression has a core zone surrounded by an outer zone, while the compound depression is differentiated into a core zone with two surrounding zones. In this approach a derived "L-function" is calculated by normalizing the K-function to obtain a benchmark of zero (see Figure 8.3B). The value of L (d) indicates the degree of clumping or over-dispersion. Values of L (d) > 0 indicate a clumped pattern, with more individuals clustered together than would be expected if the individuals were randomly distributed. L (d) < 0 indicates an over-dispersed pattern, i.e., fewer individuals are within a scale d than would be expected if the individuals were randomly distributed. Results of this survey indicated that plants are consistently "over-dispersed" or clumped in gravel runnels (at all scales from 0 to 50 cm) and are also clumped at a smaller scale (< 25 cm) in sandy runnels. They are largely absent from patches of gravel and sand, and the outer zone of compound and simple depressions, and are only found clustered at the small scale (<10 cm) in the core zones of simple and complex depressions, and intermediate zones (up to 30 cm scale) of complex depressions.

Hegazy et al. (2005) assessed allelopathic effects of *A. hierochuntica* on four target species: *Diplotaxis acris, Plantago phaeostoma, Trichodesma africanum*, and *Farsetia aegyptia*. Mulching with dried *Anastatica* skeletons was associated with decreased photosynthetic efficiency and increased hydraulic conductance and leaf specific conductance in treated plants of all four target species. There was also a general reduction in reproductive output for plants raised in mulched soils.

The degree of clumping (i.e., extent intraspecific aggregation within patch microhabitats) and the density of *A. hierochuntica* both decreased significantly from the core to outer zone of the site, and was lowest outside extent the patch. Meantime the amount of plant tissue produced ($g/m^2$) increased from core to outer zone of the patch. (See Figure 8.4.)

A major dispersal strategy of *A. hierochuntica*, sometimes called "dispersal on the spot" results in a cluster of offspring being established by local regeneration around the (now dead) parent (Friedman and Stein 1980; Hegazy and Kabiel 2007; Hegazy et al. 2013c). This in turn leads to a patchy local distribution. Growth inhibitors in *A. hierochuntica* have some auto-toxic activity, as well as inhibiting other species. This combined inhibition of its own and other species reduces both intra- and inter-specific competition and may explain the largely pure patches of *A. hierochuntica* we often see, with successive generations maintaining a presence in one place for a number of years.

Intra-specific interactions determine the overall dispersion of *A. hierochuntic*a. The spatial pattern

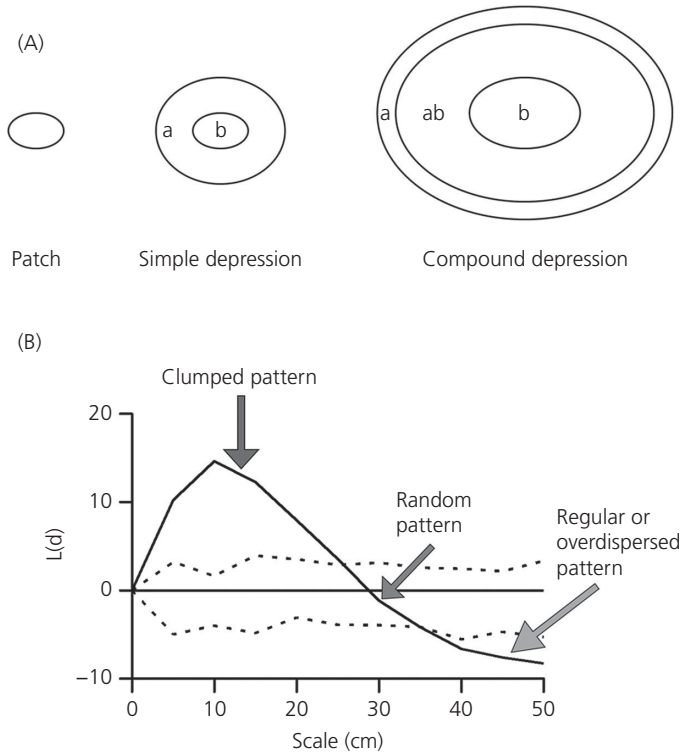



**Figure 8.3** (A) Patch and depression habitats of *Anastatica hierochuntica*; a = outer zone, ab = intermediate zone, and b = core zone. (B) L-function tests the spatial pattern by indicating the degree of clumping or overdispersion. Values of L (d) > 0 indicate a clumped pattern; values of L (d) < 0 indicate an over-dispersed pattern, and values between the dashed lines delimit the 95% confidence regions for the random distribution.

of individuals is clumped in different microhabitat types, with several scales of aggregation. The microhabitats—runnels and patches, simple- and compound depressions—at two sites (gravel and sand) had clumped patterns in nearly all the study microsites (see Figure 8.5). Presumably larger plants exude more inhibitor than smaller ones and so larger individuals differentially suppress smaller neighbors. Small individuals on the other hand release less inhibitor, so nearby small individuals can continue to coexist in a clumped pattern. This may explain why smaller individuals in the population are clumped but larger ones are more likely to be distributed randomly or over-dispersed. The size-class structure and their spatial interrelationships depend on the interaction between dispersal mode, amount of rainfall, and microhabitat type.

### 8.6.2 *Chenopodium* species

*Chenopodium murale* (Chenopodiaceae) is a fast-growing annual species, widespread in an array of habitats in Egypt. It was introduced from Europe and grows best in moist soil. It is abundant in winter-to-early-summer, and is considered a pest in agroecosystems, roadsides, and waste places. Previous studies (Kosinova 1975; Shaltout et al. 1992) showed a significant negative association with many weeds and cultivars.

El-Khatib et al. (2004) studied the effect of soils mulched with powdered *C. murale* on seedling emergence and growth in five crop species, *Trifolium alexandrinum*, *Triticum aestivum*, *Melilotus indicus*, *Lycopersicon esculentum*, and *Cucumus sativus*. Treated soils produced allelopathic effects on seedling emergence and growth in test species. Rates of emergence, dry matter production, and levels of chlorophyll and carotenoid pigments, carbohydrates, and proteins were significantly lower in plants raised in soil treated with *C. murale*. Separately, soil treated with powdered shoot tissue had greater inhibitory effects than soil with powdered roots.

*Chenopodium ambrosioides* is an annual or short-lived perennial herb from which a variety of

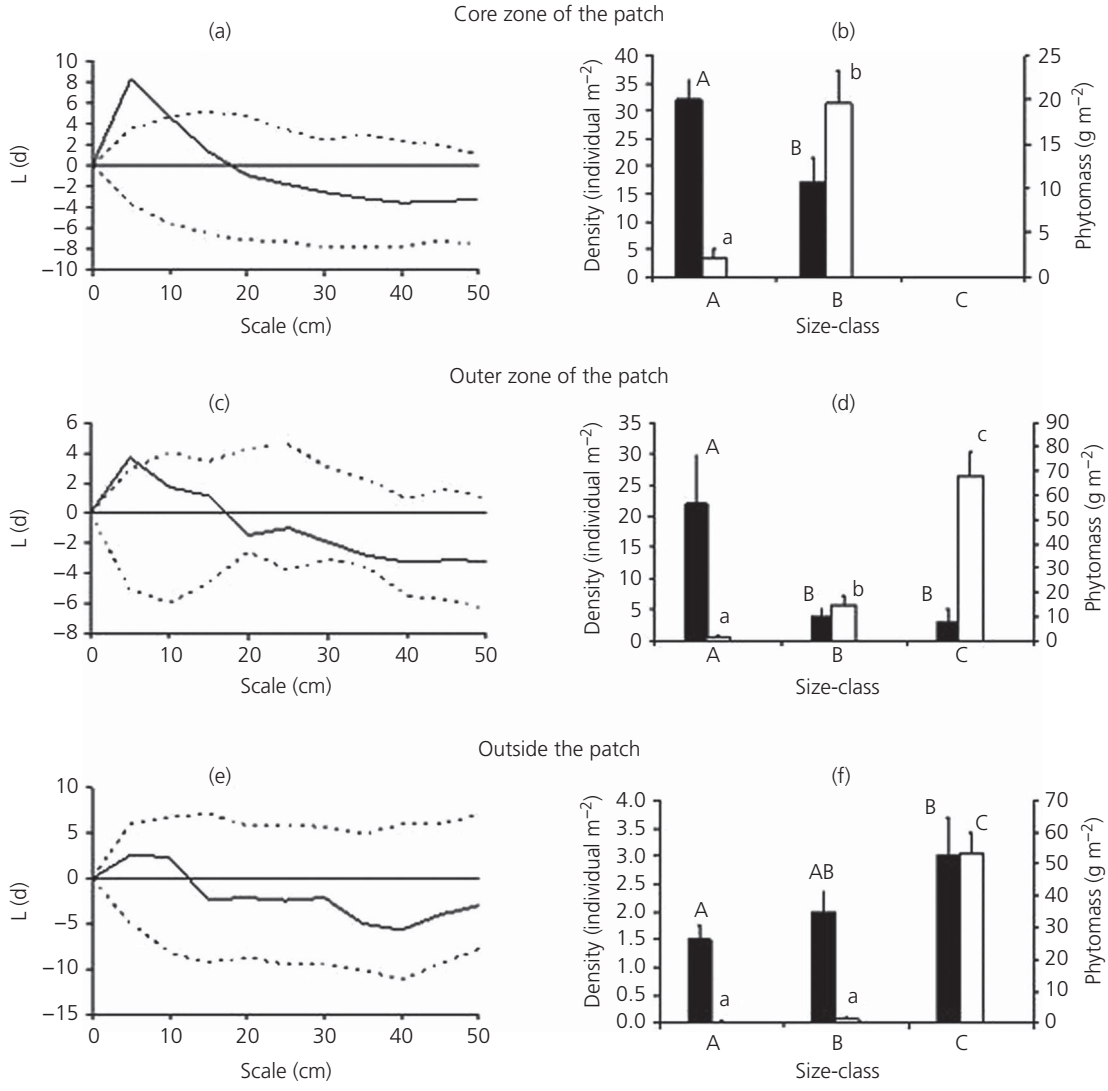



**Figure 8.4** Testing the spatial pattern in *Anastatica hierochuntica* in different microhabitats (a, c, e). Solid lines are values of the L (d) statistic; dotted lines delimit 95% confidence regions for the random model. Bars show density (closed bars) and phytomass (open bars) of *A. hierochuntica* size-classes in different microhabitats (b, d, f). The volume range of size-classes is: A < 1 $cm^3$; B = 1.1–5 $cm^3$; C = 5.1–20 $cm^3$. Bars topped by the same letter are not significantly different ($P < 0.05$) within the same series; upper case letters show significance of difference for the density and lower case for phytomass. (After Hegazy et al. 2005.)

secondary metabolites have been isolated. These include different monoterpenes, alkaloids, saponins, and flavonol glycosides (Hegazy and Farrag 2007). The broad spectrum biological activity of *C. ambrosioides* suggests allelopathic interference likely occurs (Jiménez-Osornio et al. 1996) and that it could play a significant role in community structure (Hegazy et al. 2008b).

A bioassay by Hegazy and Farrag (2007) showed that allelopathic substances from *C. ambrosioides* caused inhibition of both germination and seedling growth in two cultivated species, *Lycopersicon*

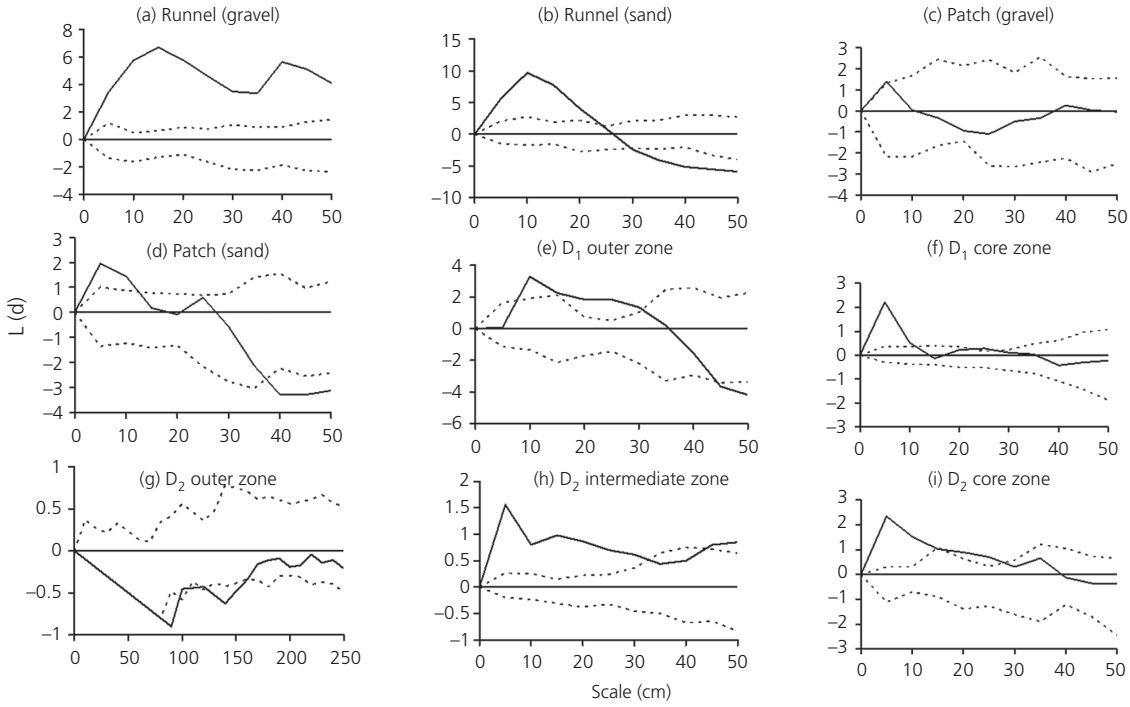



**Figure 8.5** Values of the L (d) statistic in different microhabitats testing spatial pattern in *Anastatica hierochuntic*a. D1, simple depression; D2, compound depression. Solid lines are the calculated values of the statistic, dotted lines delimit the 95% confidence regions for the random model. Note the scale is up to 250 cm in the outer zone of the compound depression (D2) (after Hegazy and Kabiel 2007, used with permission).

*esculentum, Beta vulgaris*, and two weeds, *Melilotus indicus* and *Sonchus oleraceus*. An oxygenated monoterpene, ascaridole, is the major oil component of *C. ambrosioides* and the compound most likely causing this effect.

There is evidence that terpenes influence certain semi-arid vegetation patterns (e.g., Muller 1986). It is also likely that plants producing monoterpenes (including *C. ambrosioides*) may have been deliberately included in early agricultural systems as a means of biological pest and weed control. This could explain the strong effects of three invasive species *Heliotropium curassavicum, Bassia indica*, and *Chenopodium ambrosioides* in Egyptian agroecosystems (Hegazy et al. 2008c).

### 8.6.3 *Prosopis juliflora*

El-Keblawy and Al-Rawai (2007) studied effects of the invasive exotic shrub, *Prosopis juliflora*, on native plant communities and soil chemistry in the UAE. As noted elsewhere, annuals were significantly more inhibited by this species than perennials. The number of annuals showing significant reductions in density and/or abundance under *P. juliflora* canopies was much greater than the number of perennials. Over time *P. juliflora* ameliorates certain soil characters, reducing pH and increasing levels of N, P, K, and organic matter.

*P. juliflora* reduced species richness and evenness values, population densities and the frequencies of associated native species. Several studies showed significant inhibition of seed germination and seedling growth by *P. juliflora* in many different test species (Al-Humaid and Warrag 1998; Chellamuthu et al. 1997; Noor et al. 1995). Others showed extracts of *P. juliflora* inhibited mycelial growth and spore germination in several pathogenic fungi (Gomathi and Kannabiran 2000; Kamalakannan et al. 2001). Investigations on auto-toxicity in Saudi Arabia

(Warrag 1994) suggested the presence of secondary compounds in the fruit pericarp, which inhibited seed germination and seedling growth (presumably functioning as a germination inhibitor that would be leached in the presence of sufficient moisture and rainfall, and would then allow seed germination to proceed).

### 8.6.4 *Coffea arabica*

Allelopathic effects in an important beverage plant, *Coffea arabica*, have been studied by several authors (e.g., Chou and Waller 1980a, b; Waller et al. 1986; see, too, Box 9.1). Coffee plantations are managed in different ways, ranging from intensive cultivation to natural forest ecosystems, but little attention has been given to management in relation to allelopathic effects.

Many compounds have been isolated and identified from coffee plants (Chou and Waller 1980a, b). These include caffeine, theobromine, theophylline, paraxanthine, and scopoletin, as well as an array of chlorogenic, ferulic, *p*-comaric, *p*-hydroxybenzoic, caffeic, and vanillic acids. Most of these compounds are water soluble and may be leached out of plant tissue and accumulate in the soil. Compounds have been detected in various concentrations in adult root, stem, leaf, and fruit tissues, as well as in seedlings and young plants.

Allelopathic effects have been reported from plantations where weeds were found to be suppressed, while it has been proposed that auto-toxicity may be causing the widely observed degradation of coffee plantations (see Waller et al. 1986). This is believed to be due to the large amounts of caffeine accumulated in topsoil from the litter of coffee trees (Waller et al. 1982). The challenge is that we have selected for higher content of these various stimulants, and plants are simply responding to the higher concentrations of these substances in the soil. Caffeine remains stable for relatively long periods in soil,[2] and has proved to be highly toxic when it reaches the roots of coffee plants, as well as having many adverse effects on soil microflora.

[2] Caffeine has been used as an indicator of human sewage inputs to drinking water, due to its persistence (Sauvé et al. 2011).

The dispersal unit and seeds of *Coffea arabica* (and of *Zygophyllum dumosum* and *Trigonella arabica*) were found to contain germination inhibitors which, in combination with external environmental conditions has significant seed germination effects (Friedman and Waller 1983). They may prevent premature germination, for example when seeds are still on the parent plant, or may extend germination over a longer time or allow germination only after sufficient rainfall, etc., thereby improving the chances of seedling establishment.

### 8.6.5 *Artemisia* species

In the Negev, Friedman et al. (1977) demonstrated that shoots of *Artemisia herba-alba* release both volatile and water soluble substances that strongly inhibited seed germination in *Helianthemum ledifolium* and *Stipa capensis*. These two target species were rare annuals in communities where *A. herba-alba* is present, but common in adjacent communities. Friedman and Orshan (1975) reported that *A. herba-alba*'s own seedlings were only rarely found under the parent plant, and more often were widely scattered at great distances from the parent. They suggested auto-toxic effects were acting either through inhibition of germination or death of seedlings at an early stage. Many different volatiles and water soluble compounds are produced by Artemesia plants. Studies by Carmeli et al. (1991) on *Artemisia judaica* chemotypes from Libya, Egypt, and Israel showed different chemotypes with different effects.

### 8.6.6 Host–parasite allelopathy

Hegazy and Fahmy (1999) found evidence for some reciprocal host-parasite chemical communication in perennial angiosperm root parasites and some of their hosts. The parasite *Cistanche phelypaea* was tested against two hosts, *Atriplex leucoclada* and *Zygophyllum album*, and a second parasite, *Cynomorium coccineum*, was tested against two other hosts, *Arthrocnemum macrostachyum* and *Limonium raddianum*.

Laboratory tests showed that not only was the presence of the host plants indispensable for establishment of the parasite but, reciprocally, that the parasites may stimulate seed germination and

seedling growth of host individuals. Germination and growth of the parasitic species were promoted at low concentrations (up to 1%) of their host extracts, and reduced at higher concentrations. Host shoot tissue was more sensitive to the parasite stressor than were roots. Allelopathic effects of the parasite on host seedlings included decreased chlorophyll and increased carotenoid content.

### 8.6.7 Other species

Chemical effects of the aerial cushion plant, *Cleome droserifolia*, were tested by Hegazy and Fadl Allah (1995) in Egypt. Bioassays showed reduced rates of seed germination, with inhibition ranging from 35 to 95% at extract concentrations of 4 to 10%. These concentrations of *C. droserifolia* extract caused 50 to 100% suppression in the growth of its own seedlings (i.e., an auto-toxic effect).

*Acacia tortilis* is a common desert tree in the Middle East that has been introduced to India as an exotic. Investigations by Sundaramoorthy et al. (1992) showed that these common understory plants have lower biomass and higher mineral content than the same species in otherwise comparable, surrounding areas. Tests on various other legume species indicated that both soil leachate and tissue extracts of *A. tortilis* had both inhibitory and stimulatory effects, depending on concentration.

## 8.7 Summary

This chapter explores something of the nature of plant "intelligence" as they integrate different stimuli to manage their growth and "make decisions" about development. This chapter emphasizes the role of plant chemistry, including volatiles and allelopathy for communication in the desert. Chemical communication can involve both competitive and auto-toxic effects, as well as having certain facilitative elements. Many examples are given including those in *Anastatica hierochuntica, Prosopis juliflora, Coffea arabica*, and *Artemisia* species.

CHAPTER 9

# Agriculture and plant ecology

## 9.1 Gardening, win–win, and the evolution of cultures

Agriculture has surely played a pivotal role in the emergence and development of human cultures. By one account of our origin we *began* in a garden. But before we became gardeners, the earliest people lived by hunting, fishing, trapping, and gathering what they could from the wild. According to the botanists Otto and Dorothy Solbrig (1994), for more than a hundred thousand years prior to the emergence of agriculture, human beings much like ourselves ate mostly fruits and seeds, leaves, roots and tubers, as well as birds, snakes and lizards, frogs and snails, plus maggots and other insects. Tracking the seasonal abundance of these foods, small tribal bands likely consumed well over a hundred different kinds of plant and animal.

Our diets would have differed from place to place and season to season; in some cases, such as the rare event of bringing down a large mammal, social co-operation was essential. Like the wildebeest we probably cycled through the best sites every year or two. We were vagile food gatherers for far longer than we have been settled farmers and gardeners. People first began systematically to cultivate plants and domesticate animals only some seven to eleven thousand years ago, during the Neolithic, and we did so in some very specific regions of the world, which not coincidentally today are recognized as biodiversity hotspots.

Human genes are still essentially Pleistocene, having spent comparatively so much of our evolutionary history there. And yet, there have also been huge effects from those ten Holocene millennia of cultural developments, representing the difference between, say, space travel and walking (or closer to home, between, say, the magnificent Garden of Versailles and an untended patch of harsh desert). What makes us distinctively human is our great capacity for communication, and our civilization, and most of *that* has come together over the past ten thousand years or so. Our genetic nature provides a deep Pleistocene backdrop to a far greater force, namely an overlay of human cultural evolution. Nearly all our cultural evolution sprang from agriculture.

With agriculture came the capacity to store dried food, especially grains, to enjoy and share surplus food supplies, and to have stored resources to tide us over in lean times. Only after the emergence of agriculture and its settled lifestyle could new social classes of specialists arise—artisans, clerks, defenders, priests, teachers, even kings and dictators. Living standards and cultural progress increased following advances in agricultural technology.

According to the framework of game theory, which is sometimes applied to analyses of evolutionary processes and complex interactions, "non-zero-sum games" are those in which one player's gain is not necessarily bad news for the other players, since it allows for "win–win" situations (see, e.g., Wright 2000). Indeed, in highly non-zero-sum games the players' interests overlap nearly entirely, making a strong case for co-operation. In contrast, in a zero-sum game the fortunes of the players are inversely related. In football or hockey games, for instance, one team's win is the other's loss. Political scientists and economists sometimes break down human interactions into zero-sum and non-zero-sum components. On occasion evolutionary biologists do the same in considering how living systems

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work. Non-zero-sum models underpin much of human social cooperation, providing potential synergy and mutual benefit between individuals.

Agriculture and gardening are non-zero-sum activities (Wright 2000). The development of crafts, including metallurgy, smithing, brewing, baking, etc., and of art, religion, science, transportation, and architecture—indeed the richness and complexity of all human activities that are hallmarks of civilization—could not have happened without the emergence of the garden culture, the gardening meme.

Cities first arose in those parts of the world where people adopted gardening and agriculture, and the first cities grew out of successful agricultural villages. In the Middle East—in Mesopotamia—this included Babylon, Ur, and Ninevah, later Cairo and elsewhere. The change from farming at a subsistence level to producing a surplus for sale, barter, or tribute, represents a change in the social organization of farming communities that is almost as profound as the adoption of farming itself.

Hunter-gatherers take and consume (and to a limited degree stockpile) what their environment offers. By contrast farmers seek to influence a particular piece of the environment, to manipulate it so as to increase the amount of product—food, fiber, fuel, pharmaceuticals—that becomes available and consumable. More recently we have created decorative gardens that make social statements rather than necessarily yielding product.

In Diamond's (1997) analysis of the forces underpinning broad patterns of human history, he suggests the adoption of agriculture was both "evolutionary" and "revolutionary." It did not happen overnight, but it does seem to have crystallized, about ten thousand years ago, in seven or eight different regions of the world including the "Fertile Crescent" of land around Anatolia and the edges of the Arabian Peninsula.

According to Diamond the areas where agriculture first arose were Southwest Asia, also known as the Near East or Fertile Crescent; Southeastern Asia; Mesoamerica (the term applied to central and southern Mexico and adjacent areas of Central America); the Andes of South America and possibly the adjacent Amazon Basin, as well; and the eastern United States.

The ecologist Colin Tudge (1998) provocatively extended the above, general thesis, arguing that agriculture in *some* form existed in the behavioral repertoire of our ancestors, thousands of years before the Neolithic farming revolution. The "revolution" was not so much the *beginning* of agriculture as it was the beginning of agriculture *on a large scale*, in one place, using refined tools. Tudge takes this line of thinking much further back in time, to some forty thousand years ago in the late Paleolithic, and argues that people were already managing their environments to such an extent that they might properly be called "proto-farmers." The idea would be that certain patches of the natural habitat might be home to desired food species, and the proto-farmers might augment resources there in terms of bringing water, or mulch and organic wastes, to enhance production and yield of the desired species. Many plants, particularly clonal grasses and allelopathic species, will tend to form monocultures, which makes harvesting of their seeds or fruits a little easier.

While we do not have any accurate account of precisely when primitive people *first* began the domestication of plants and animals, we do know that latterly quite sophisticated "pleasure-gardens" existed—in Egypt and Mesopotamia for example—long before the Christian era (see Figure 9.1). Indeed the English word *paradise* derives from an ancient Persian term meaning garden[1] (Lovett-Doust 2003). And if Eden is the most famous garden of ancient times, the Babylonian "Hanging Gardens" of Nebuchadnezzar are surely next (and one of the Seven Wonders of the Ancient World). They are of course largely legend, in that accounts were passed along through oral tradition and only written down long after they were gone, but the city of Babylon, which dates to at least five thousand years ago, is believed to have included a terraced hill adjacent to the royal palace, planted with numerous horticultural specimens and rare plants. These terraced gardens, when observed from a distance, would have appeared to be floating in space[2] . . .

[1] Other words we have borrowed from Old Persian include peach, lemon and orange, cummerbund, kaftan, pajama, and assassin . . .

[2] And see the Assyriologist Stephanie Dalley's fascinating *Mystery of the Hanging Garden of Babylon* (2015), which argues convincingly that the famous Hanging Garden was in fact built at Ninevah, not Babylon, by Sennacherib, not Nebuchadnezzar.

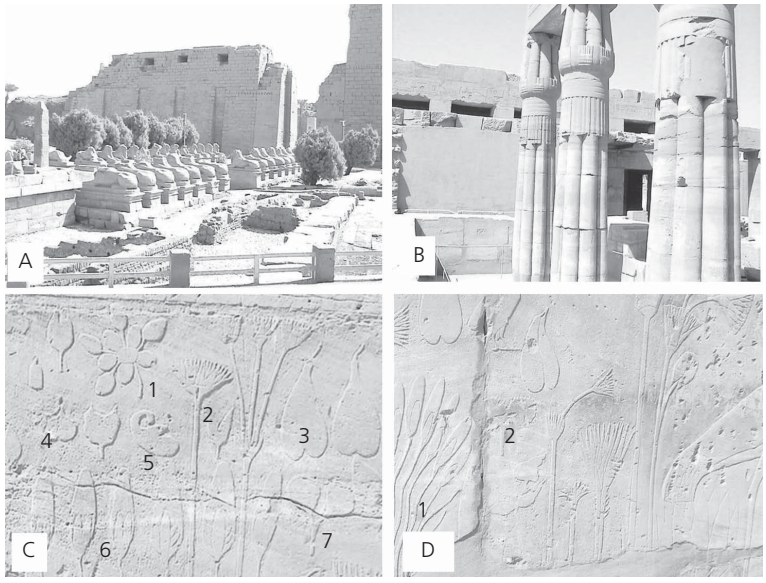



**Figure 9.1** (A) Entrance of Karnak temple in Luxor, Egypt. Note *Tamarix nilotica* trees at the entrance; (B) Botanical Garden of Thutmose III at the Karnak temple; (C) Plant and animal reliefs carved on the walls of the Botanical Garden: 1 = *Laurus nobilis*, 2 = *Nymphaea caerulea* var. nouchali, 3 = *Luffa aegyptiaca* (= *L. cylindrica*), 4 = *Orhis* sp./*Ophrys* sp., 5 = *Cucumis melo*, 6 = *Hordeum vulgare*, and 7 = *Pistacia eurycarpa*; and (D) 1 = *Potomogeton nodosus* and 2 = *Vitis vinifera* (plants identified by Prof. W. M. Amer). [For a color version of this figure, see the color plate section, Plate 12]

In many ways a flower garden is an early display of "conspicuous consumption" in that it suggests the gardener is so well off in terms of food supply that he or she can afford the "indulgence" of simply growing things for their intrinsic beauty or exoticism.

## 9.2 The plant's-eye-view

Michael Pollan's bestselling book, *The Botany of Desire: A Plant's Eye View of the World* (2001) engagingly discusses the process of domestication from the special perspective of the plant. Pollan's title phrase, "plant's eye view" was first used by the population biologist John L. Harper (1977). The term appropriately distinguishes the individual plant (or animal) as an evolutionary *player*, where every organism defines the scale of its own environment. A plant exerts an influence as far as its products are dispersed. However, a plant community that may appear diverse to a human observer may actually be quite monotonous from the perspective of an organism within it.

Just as, say, a gazelle samples the diversity of a desert quite differently from a lizard, so too a clonal plant with long rhizome internodes "samples" or experiences the surrounding vegetation in a very different way from a tufted, tussock-forming plant. Lesley Lovett-Doust (1981a, b) represented these alternatives of plant clonal morphology as *guerrilla* and *phalanx* growth strategies, respectively, and described the different consequences in terms of plant competition. In*ter*-specific competition is significantly more likely with the guerrilla form of growth—as in, e.g., some of the herbaceous *Launaea* species. In contrast intra-specific and even intra-genotypic competition is more likely with the phalanx strategy—as in perennial grasses like *Lasiospermum brachyglossum* and *Pennisetum divisum*. Some forms of the perennial grass, *Panicum turgidum*, produce both phalanx (via ramets from underground rhizome growth) and guerrilla growth (ramets sprouting from culm nodes) (see Figure 9.2). Tussock grasses with a phalanx-type growth, and the resulting more monocultural stands, may be more likely recruits to agriculture.

As Pollan pointed out, we tend to think of domestication as something *we* do to other species, but it is entertaining to turn this idea on its head and look at domestication as something certain plants and animals have done to *us*—a subtle strategy for advancing their own interests, as it were.

The species that have spent the last ten thousand years or so "figuring out" how best to feed, heal, clothe, intoxicate, and otherwise serve humans have

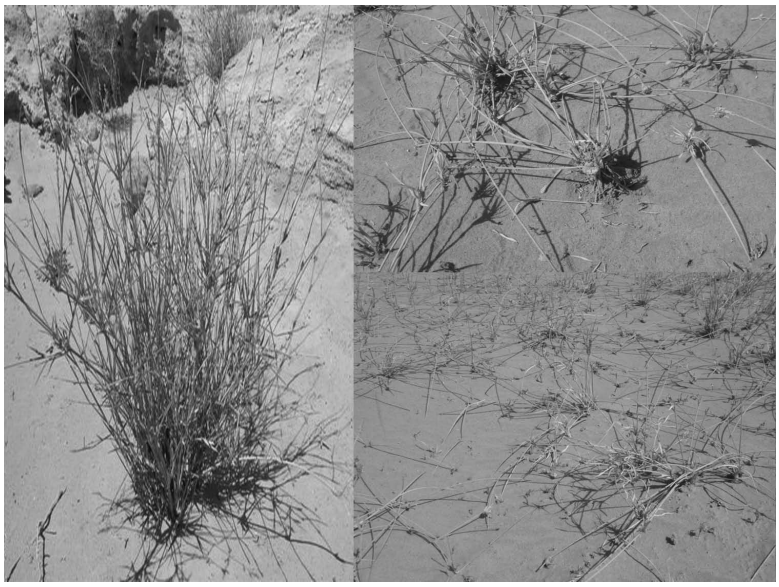


**Figure 9.2** Phalanx and guerrilla growth forms of *Panicum turgidum* in Thumamah sand dunes west of Riyadh, Saudi Arabia. Individual genet of *P. turgidum* with vertical culms producing dwarf sprouts at various heights produced from phalanx growth on underground rhizomes (left side). Long vegetative shoots (ramets) developed either from aerial culms, or underground rhizomes spreading on the ground surface with the guerrilla growth form (right bottom). Enlarged shoot and roots developed on the running stolon nodes (upper right). Photos provided by S. L. Al-Rowaily and M. I. El-Bana.

made themselves some of nature's greatest "success stories." Pollan's domesticated exemplars nicely illustrate this, including for example the apple, tulip, potato, and marijuana plants. Pollan develops the obvious point that, precisely *because* domesticated species have satisfied our most basic desires, they have thrived. These days we have started to use genetic modification and refined culturing techniques (rather than simply cultivating the most desirable variants arising from centuries of directional selection) to get what we want from plants—potatoes that fry well, tulips that flower out of season or with striking black-purple blooms, or pot plants that produce 22% tetra-hydrocannabinol levels.

As far as plants are concerned, we are simply one of thousands of animal species that more or less unconsciously "domesticate" plants. In this co-evolutionary dance (and in common with all animal species including humans), plants must spread their offspring to areas where they can thrive and so pass on *their* genes. In the game of evolution for crop and garden-ornamental species, humans have selected and bred plants for their desired attributes—including size, sweetness, color, scent, fleshiness, oiliness, fiber content, and drug concentration.

Beginning in pre-history, by choosing to harvest those particular wild plants which possessed these qualities to an exceptional degree, ancient people unconsciously dispersed individuals differentially and set them on the road to domestication. At the same time we often bred out or reduced any secondary chemicals we found distasteful, and that may have previously protected the plants from herbivores (e.g., bitter mustard oils in *Brassica oleracea*, whose different cultivated varieties include cauliflower, cabbage, broccoli, Brussels sprouts, and kohl rabi). Of course today, since these varieties are no longer so well protected, we have to deal with pests which, like us, find the (now vulnerable) crop very attractive. In that sense we have also revised the role of opportunist organisms—we have aided and abetted the species we see as pests—weeds and herbivores that infest crops and are essentially competitors for resources we view as "ours." These ecological specialists now undergo population boom cycles when they settle on vulnerable host individuals –which we experience as pest/disease outbreaks in our farms and gardens.

## 9.3 Early agricultural societies

Mainstream agriculture in the Middle East originated in Mesopotamia ("the country between the

rivers")—i.e., the western steppes and foothills of the Zagros, the Fertile Crescent, and the Nile Valley. The region of the Fertile Crescent encompasses territories of modern-day Iraq, Jordan, Lebanon, Israel, Palestine, Syria, western Iran, and southeastern Turkey (see Figure 9.3). The favorable environment, diverse habitat, and particular plants all combined to launch the Neolithic Age in the Fertile Crescent (see, e.g., Jaradat 2007).

The ancient cultures of Mesopotamia—Sumerian, Babylonian, Assyrian, and Chaldean—developed an integrated agricultural system including irrigated terraces, parks, and ornamental gardens. Ancient Egyptian civilization also flourished through agricultural development, made possible by regular renewal of soil fertility, following annual cycles of overflow of the Nile's banks. Ancient Egyptians developed various agricultural technologies (see Figure 9.4A–F), developing tools and techniques of cropping, irrigation, and drainage that are still used today (Rindos 1984).

Following early Levantine–Mesopotamian and Old Egyptian agricultural innovations, came Greek and Roman contributions. Theophrastus—known as the "Father of Botany"—helped shape botanical thinking until at least the seventeenth century. He described the botany of more than 500 species, both cultivated and wild, and discussed "dusting" of the fruit-forming female date palm with flowers of the male trees to increase fruiting quality and quantity (Janick et al. 1981). The Romans improved and built upon previous developments. The earliest agricultural writing in Latin is the "*Terse De Agri Cultura*" of Marcus Porcius Cato (2163–2248 B.P.), which described practical aspects of crop and livestock management.

The early rise of Islam, *c*. 1400 B.P., partially subsumed but also gathered together the remnant

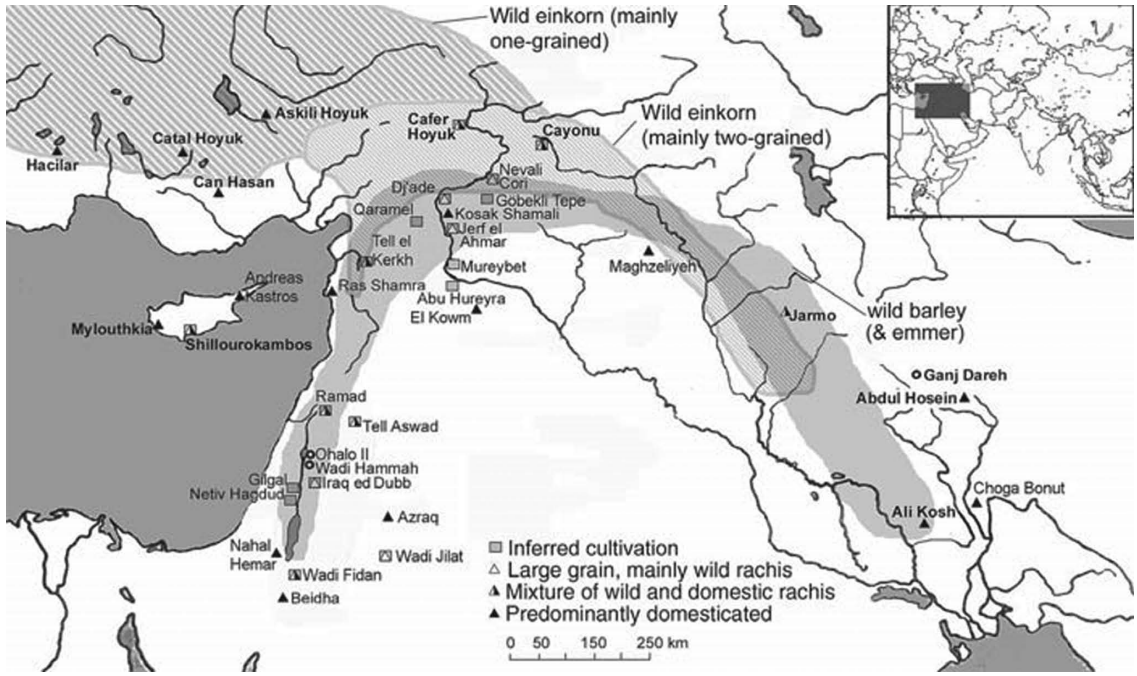



**Figure 9.3** Map of southwestern Asia, showing the locations of Fertile Crescent sites containing evidence that contributes to understanding the origins and spread of agriculture. Sites are differentiated on the basis of whether they provide evidence for pre-domestication cultivation, enlarged grains, mixed, or predominantly domestic-type rachis data. Note that these sites represent a range of periods, and many sites have multiple phases of use, in which case the earliest phase with significant archaeobotanical data is represented. Shaded areas indicate the general distribution of wild progenitors. Note that wild emmer wheat (*Triticum turgidum* subsp. *diococcoides*) occurs over a subset of the wild barley zone, and mainly in the western part of the crescent (after Fuller and Allaby 2009, used with permission).

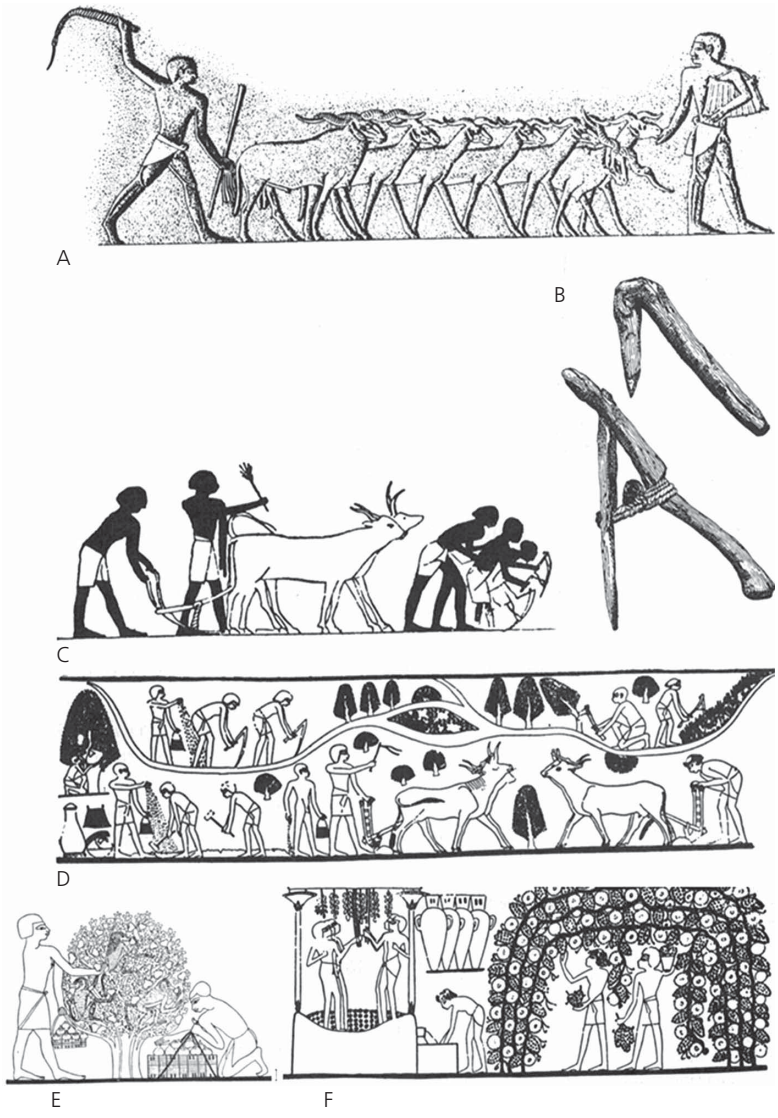



**Figure 9.4** Development of agricultural technology in ancient Egypt (A–F). (A) Using sheep to "tread in" seed (*c.* 4500 B.P.). (B) A primitive hoe (top) made from a forked branch and a more developed form (below) with hafted wooden blade (Middle Kingdom, *c.* 4490–3915 B.P.). (C) Plowing and hoeing (*c.* 4015 B.P.). (D) Agricultural implements and land reclamation (*c.* 3535 B.P.). (E) Picking figs (*c.* 3915 B.P.). (F) Collecting grapes from a round vine arbor and treading the fruits to express the juice (*c.* 4015 B.P.) (after Janick et al. 1981).

cultures and helped preserve the agricultural heritage of antiquity. During Europe's Dark Ages, medieval technologies and products were passed from East to West via the Byzantine Empire. For example the peach, *Prunus persica*, was known to the Chinese by at least 4000 B.P. and was later introduced to the Mediterranean region. Sugar cane, soybean, and bananas are among many other crops introduced from East Asia (Janick et al. 1981).

## 9.4 Omani oasis agriculture

Oman is well known as the origin of, or trading base for, much of the world's best frankincense, as well as being a significant copper source. The country maintained trade relations with major countries for millennia. Frankincense and other valuable plant products were transported by camel-train from production areas in southern Oman through

Yemen, passing Mecca and Medina along the ancient "Frankincense Road" to markets in Mesopotamia and the Mediterranean.

Despite a shortage of fresh water, annual and perennial crops have been cultivated in Oman since ancient times, using rain-fed conditions in Musandam and Dhofar, and ingenious, irrigated "oasis agriculture" in other parts of the country. Due to their spectacular slopes, the terraces on the Al Jabal al Akhdar massif long ago became famous as "Hanging Gardens," far beyond the borders of Oman (Buerkert and Schlecht 2010). Oman's different geographic regions are characterized by a wide range of climate. It is hot-dry in the interior, hot-humid in the coastal area, and humid in the south where monsoon rains provide ample moisture in summer.

Much of Oman's cultural identity today continues to depend on oasis agriculture, in which the maintenance of agro-biodiversity is an essential component. Northern Oman contains more than 2000 oases of some six distinct types.[3] Unfortunately, during recent decades, hundreds of Omani agricultural oases have been abandoned and fallen into ruin.

The single most important component of Oman's irrigated oasis agriculture is the innovative *falaj* system, known locally as *Aflaj*, which allows the tapping of water resources that are otherwise hard to access in the difficult terrain. Networks of man-made channels and aqueducts have been used for millennia to collect a combination of groundwater, spring water, and surface water, transporting it by gravity to areas of high demand such as homes and plantations (Al Suleimani et al. 2007).

One of these agricultural oases, Biladsayt, in the upper part of the Wadi Bani Awf, probably owes its 3000 years of continued existence to the stable flow of twelve springs originating from a 1000 m thick Hajar limestone formation above the settlement. According to Buerkert and Schlecht (2010) its agricultural area is now covered by *c*. 2800 date palms comprising fourteen varieties on 8.8 ha of terraced land, to which some 385 fields totaling 4.6 ha have to be added. These are planted with ancient varieties of wheat, alfalfa, barley, onion, garlic, banana, grape, and other species.

These ancient agricultural systems in northern Oman offer outstanding examples of ecological sustainability. They are complex, intensively irrigated desert oasis systems with terraced fields consisting of small man-made, silt and manure-filled stone structures, built over many centuries on often very steep slopes (Patzelt 2010). Typical terrace sizes range from 2 to 100 $m^2$ and fields carry a broad range of annual and perennial crop and tree species, often species that are particularly good at using scarce water efficiently.

Hammer et al. (2008) reported on Oman's cultivated resources, documenting the history of many Omani crop plants, and listing some 194 species from 133 genera and 53 families. Most of the agricultural species are introduced, while real indigenous elements such as *Boswellia sacra* and *Prunus arabica* are rare. In terms of present-day Omani crops, about a fifth came from southern and southeastern Asia, at least another fifth from the Near East and eastern Mediterranean and 15% from Central and South America.

Approximately 200 indigenous weed species are known from the Omani oasis systems, representing *c*. 17% of the national flora. These include a number of pan-tropical, multi-regional, and cosmopolitan species. Pan-tropical species such as *Achyranthes aspera* and *Ammi majus* reflect the former land connections of Arabia with Africa and Asia. Patzelt (2010) pointed out that multi-regional species (e.g., *Andrachne elephioides, Apium graveolens, Brachypodium distachyum*, and *Eragrostis papposa*), and cosmopolitan species such as *Anagallis arvensis* and *Euphorbia helioscopia* are all weedy and ruderal here, reflecting significant long-term human influence.

Several species endemic to northern Oman are found in oasis vegetation, including *Campanula akhdarensis, Orobanche perangustata*, and *Verbascum akhdarense* (Patzelt 2010). The fragile *Campanula akhdarensis* occurs on old stone walls in mountain villages much more frequently than in natural *Olea-Juniperus* woodland, and to conserve them these old structures should be maintained (Patzelt 2010).

[3] According to Luedeling and Buerkert (2010), "Plain Oases" and "Urban Oases" are non-traditional oases that can only be irrigated using modern techniques. "Foothill Oases" and "Drainage Oases" lie along the main wadi courses and rely on water accumulation in sediments. "Mountain Oases" and "Kawr Oases" lie at the bottom of extensive water-bearing limestone formations that give rise to natural springs.

The vegetation here also includes species that are threatened on a national scale, such as *Epipactis veratrifolia, Gladiolus italicus, Gynandiris sisyrinchium, Ixiolirion tataricum, Muscari longipes, Pycnocycla caespitosa*, and *Scandix pecten-veneris* (Patzelt 2010).

## 9.5 Domestication and selection

The challenges of farming and gardening are of course rooted in botanical and ecological factors. The plant, the target of all horticultural activities, is first and foremost a living organism that exists as a member of a population and that will undergo a natural life cycle including stages of germination, growth, reproduction, and sooner or later, death. Charles Darwin (1859) famously took his inspiration for evolution through natural selection from the analogous world of animal and plant husbandry—from domesticated species and the everyday products of human gardening. The *Origin of Species* begins with a long chapter on a special case of natural selection that Darwin called "artificial selection"—his term for the process by which domesticated species and varieties come into being.

The selection process, which Darwin presciently saw as the *engine* driving evolutionary change in all living organisms (and including various processes which he distinguished as "natural," "artificial," and "sexual" selection) acts ultimately through the differential reproductive success of individuals in a population—i.e., through differential rates of sex and death among neighbors, and more importantly, differential numbers of descendants in future generations.

In the *Origin* Darwin begins by discussing how farmers develop varieties of gooseberries—less hairy fruits being more desirable than their hirsute ancestors; he writes also about hybrid roses and cultivated pears, and about varieties of cattle, goats, and pigeons, among others—and shows that domesticated species contain great reservoirs of genetic variation from which humans select the particular variants, or traits, that they wish to see passed down to the next generation.

Darwin explained how in the special case of domestication, human preferences play the same role that otherwise "blind nature" does everywhere else, determining over time what constitutes suitability to prevailing conditions, or evolutionary fitness, and thereby leading to the emergence of new forms of life. Darwin subsequently explored this idea in depth in the richly detailed and popular *Variation of Animals and Plants under Domestication* (1868).

Domestication includes a genetic transformation of wild forms into improved, cultivated forms, adapted to human need (Harlan 1992). These changes would have first appeared during a period of "pre-domestication" cultivation. Weiss et al. (2006) and others have suggested the multiple processes of plant domestication can be divided into several stages. These include the gathering of annual wild plants and/or the tending/pruning of fruit trees; also cultivation (by which wild individuals/genotypes are systematically accumulated through repeated sowing); and domestication, in which cultivars with desirable traits are raised. One might also add the activities that have been so important in the Middle East, namely provision of a reliable supply of water and augmentation of nutrients in the soil.

Various suites of traits have been called, collectively, indicators of the "domestication syndrome" (Prakash 2001). Desirable traits include a synchronized phenology (plants flower and fruit at the same time, which enhances pollination rates and makes harvesting easier); the loss of natural dispersal mechanisms (e.g., elimination of pod/grain shattering[4]) and seed dormancy; synchronous ripening and shorter maturation period; reduction of any bitter compounds and harmful toxins (herbivore deterrents); greater productivity, including larger individual seeds and fruits—often associated with polyploidy: e.g., wheat (hexaploid), strawberry (octaploid), and sometimes parthenocarpy (and elimination of seed formation, as in banana and seedless varieties of citrus and grape).

[4] Several agricultural advances have involved mutations in a crop plant that reduced "shattering"—i.e., instead of seeds being dispersed as soon as they were ripe, mutant plants retained the seeds longer, which made harvesting more successful. One mutation removed the "brittle rachis" problem from wheat (Fuller and Allaby 2009). A ripe head of wild-type wheat is easily shattered into dispersal units when touched, or blown by the wind, because during ripening a series of abscission layers form, dividing the rachis into short segments, each attached to a single spikelet (containing two to three seeds). A different kind of shattering mechanism involves dehiscence of the mature fruit, which releases the seeds.

By *c*. 8000 years ago, agricultural societies had developed settlements from the Eastern Mediterranean across Turkey to Iran, and into Southeastern Europe and the islands of Cyprus, Crete, Sardinia, and Corsica (Hole 2007). Some eight "founder crops" characterized most diets in the Middle East, and their descendants continue to predominate in much of the world today. These include Emmer wheat, *Triticum dicoccoides*; Einkorn wheat, *Triticum monococcum*; Barley, *Hordeum distichum*; Lentil, *Lens culinaris*; Pea, *Pisum sativum*; Chickpea, *Cicer arietinum*; Flax, *Linum usitatissimum*; and Bitter vetch, *Vicia sativa*.

The individual plants that are most closely related to modern crop varieties and cultivars are known as "*landraces*."[5] They are domesticated, regional ecotypes that have developed over time. All the crop plants we grow today have their origins in the wild. The "crop wild relative" is a wild plant taxon closely related to a domesticated crop taxon, whose geographic origins can often be traced to regions known as Vavilov Centers.[6] It is estimated that *c*. 300 species of crop wild relatives still occur in the Middle East (Harlan 1995; Zohary and Hopf 2000).

Vavilov is an important figure in our understanding of the relatively small selection of "staple" crops we continue to farm today. The son of a wealthy Moscow merchant, he had grown up in Imperial Russia seeing frequent crop failures and food rationing; his great passion was to end famine in Russia and around the world.[7]

Vavilov's eight major centers for crop wild relatives are: (1) South Mexican and Central American Center; (2) South American Center (Peru, Ecuador, Bolivia and Chile); (3) Mediterranean Center (countries bordering the Mediterranean Sea); (4) Middle East; (5) Abyssinian Center (Ethiopia); (6) Central Asiatic Center; (7) Tropical Centre (South China, India, and Southeast Asia—Indo–Burma and Siam–Malaya–Java sub-centers); and (8) East Asiatic Center (Central and West China, Korea, Japan, and Taiwan) (see Figure 9.5). The majority of the crops

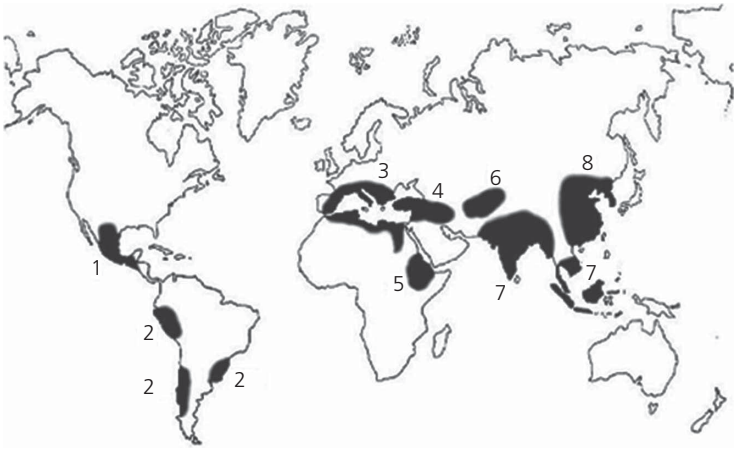



**Figure 9.5** Vavilov's centers of crop wild relatives, and origins of major modern crops. (1) South Mexican and Central American Center, (2) South American Center, (3) Mediterranean Center, (4) Middle East, (5) Ethiopia, (6) Central Asiatic Center, (7) Indian Center—Indo–Burma and Siam–Malaya–Java subcenters, and (8) Chinese Center. Source: ICEM 2014.

[5] Farmers have traditionally held back part of the seed from their crops to sow in a subsequent year (often called "seed crop"). The seed was usually selected on the basis of particular traits, resulting in the development of distinct, local crop varieties, so-called landraces analogous to ecotypes for wild species. Similar terms include "primitive"- cultivars, varieties and forms; farmers' varieties, traditional varieties, local varieties, folk varieties, ecotypes, heirloom varieties, heritage varieties, and conservation varieties. There has been little consistency and plenty of confusion in the use of these terms (Camacho Villa et al. 2005; Vincent et al. 2013; Zeven 1998).

[6] Named after Dr. Nikolai Vavilov, who first developed the theory of centers of origin of domesticated plants (and see Crow 2001; Harlan 1992). A Vavilov Center is a region of the world considered to be an original center for the domestication of various plant crops. The plants may be wild ancestors of the same species as the domesticated variety, or other closely related taxa.

[7] Unfortunately Vavilov ran afoul of Joseph Stalin because he was a strong critic of Trofim Lysenko, a favorite of Stalin. Vavilov was imprisoned and sentenced to death in 1941; although his sentence was commuted to 20 years, he died two years later in prison, of starvation (Harland 1954).

domesticated in the Fertile Crescent region of the Middle East, as well as their wild ancestors are of worldwide importance today. Table 9.1 provides a short list of the globally important crops for which the center of origin and diversity lies around the Fertile Crescent (Harlan 1992; Jaradat 2007).

Although crop wild relatives and landraces were not the product of modern techniques for genetic improvement, they do share certain ecological characteristics, including high genetic diversity, local adaptation, recognizable phenotypic features, and a long-standing association with particular localities. It is now well understood that the wild relatives of crops are a critically important source of new alleles of genes for crop improvement, particularly for traits that confer resistance to pathogens,

**Table 9.1** Globally important crops having their centers of origin and diversity in the Fertile Crescent region and thereabouts (Source: Harlan 1992; Jaradat 2007).

- **Cereals**: *Avena* spp. (wild oats); *Hordeum* spp. (wild and cultivated barley); *Secale cereale* (wild rye)
- ***Triticum* species**: (wild and cultivated wheat); *Aegilops* spp. (Goat grass)
- **Pulses/legumes**: *Cicer* spp. (wild and cultivated chickpea); *Lens* spp. (wild and cultivated lentils); *Pisum* spp. (wild and cultivated peas); *Vicia faba* (cultivated faba beans)
- **Vegetables**: *Lactuca sativa* (lettuce); *Brassica* spp. (turnip, cabbage and their wild relatives); *Raphanus sativus* (radish); *Allium* spp. (wild and cultivated onions and garlic); *Daucus* spp. (carrot and wild relatives); *Cynara scolymus* (artichoke); *Sinapis alba* (mustards)
- **Spices**: *Cumminum cyminum* (cumin); *Mentha piperita* (peppermint); *Foeniculum vulgare* (fennel); *Sesamum indicum* (Sesame)
- **Essential oils and herbs**: *Achillea* spp., *Artemisia* spp., *Origanum spp., Thymus* spp.
- **Fiber/jute crops**: *Linum usitatissimum* (flax, linseed)
- **Forages**: *Medicago* spp. (medics and wild relatives); *Vicia sativa* (vetch and wild relatives)
- **Fruit and nut trees**: *Olea europea* (olives and wild relatives); *Ficus carica* (figs and wild relatives); *Phoenix dactylifera* (date palm); *Vitis vinifera* (grapes); *Punica granatum* (pomegranates); *Pistacia* spp. (pistachio and wild relatives); *Prunus* spp. (plum, pear, apricot, etc); *Amygdalus* spp. (almonds and wild relatives)
- **Timber trees**: *Abies* spp., *Acacia* spp., *Castanea sativa, Cedrus* spp., *Fagus orientalis, Juglans regia, Pinus* spp.
- **Dyes**: *Alkanna tinctoria, Anchus italica, Indegofera* spp., *Rubia tinctoria*
- **Plants of horticultural value**: *Allium* spp., *Asparagus* spp., *Colchicum* spp., *Crocus* spp., *Lilium* spp., *Rosa persica, Tulipa* spp.

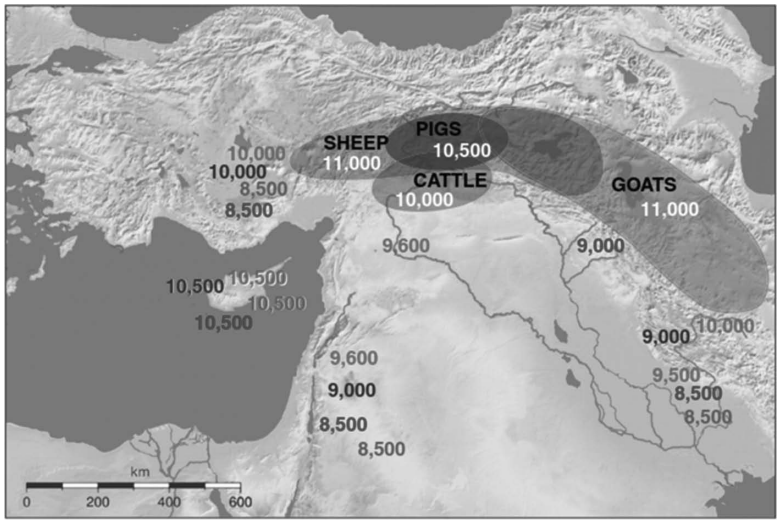



**Figure 9.6** The origin and dispersal of domestic livestock in the Fertile Crescent. Shaded areas show the general region and approximate dates in terms of years B.P. in which initial domestication is thought to have occurred. Dates outside the shaded areas show the approximate date when a particular domesticate first appears in a region: Goats (*Capra hircus*), sheep (*Ovis aries*), cattle (*Bos taurus*), pigs (*Sus scrofa*) (after Zeder 2008, used with permission). Copyright (2008) National Academy of Sciences, U.S.A. [For a color version of this figure, see the color plate section, Plate 13]

or characteristics that we now value, like drought tolerance (Hunter et al. 2012; Maxted et al. 2006).

Plants in the Middle East have experienced browsing and grazing by various domesticated herbivores for a *very* long time. Four of the earliest animals domesticated in the region were goats, *Capra aegagrus*; sheep, *Ovis orientalis*; pigs, *Sus scrofa*; and cattle, *Bos primigenius* (Zeder 2008). Domestication of sheep and goats is associated with the earliest transitions from hunting to herding, *c.* 10 000–9500 B.P., and occurred at least a thousand years after the domestication of crop plants in the Levant region (Bar-Yosef and Meadows 1995). Both goats and sheep were domesticated across the region from the northern Zagros to southeastern Anatolia (see Figure 9.6).

As for pigs and cattle, they were first domesticated in southeastern Anatolia and the upper Euphrates Valley by *c*. 10 500–10 000 B.P. The timing of their expansion as domesticates was similar to, if somewhat slower than, that of sheep (Zeder 2008). Other species such as gazelle, which are behaviorally unsuited to domestication, may have been unsuccessfully considered as farm animals in both the southern and northern Levant, where they were the most abundant wild ungulates (Zeder 2008).

## 9.6 Humans, horses, and camels

Historically the greatest changes brought about by farming were surely social changes. The invention of agricultural tools and the development of agriculture itself transformed humans from being a species living in small, nomadic bands of related individuals whose activities had a small ecological "footprint" into one living in highly complex and interrelated societies engaged in industrial activities that now affect all life on the planet. Consider one example: plowing technology and the relatively slow, gradual incorporation of first oxen, around 4000 B.P. in Europe and the Middle East, and later the horse, followed much later by its rapid replacement by the internal combustion engine. Until relatively recently, horses were responsible for nearly all the hauling and heavy work of agriculture (and of course we still measure the power of our tractors and other machines in terms of horse-power).

As Smil (2000) has pointed out, horses are biomechanically superior to cattle, which had preceded them as domesticated draft animals. Unlike cattle, horses' front ends are heavier than their rear ends, giving them an advantage in overcoming inertia through forward motion. Moreover they can stand without using muscle energy simply by locking their leg joints. Horses can also grow larger and live longer than cattle, and have greater physical endurance. A little more than a thousand years ago, medieval Europe began to adopt fitted and padded collar harnesses and iron horseshoes. Older throat and girth harnesses had choked the animals, and breast-band harnesses were even less efficient. With the "new" harness technology horses were mechanically primed to play a bigger role in medieval society, yet it still took them several centuries in Europe to displace oxen as the principal draft animals.

According to Smil, the size of the animals, their nutrition, and the plows they pulled explain why this happened. The body weight (and power) of draft horses began to rise only after several centuries of selective breeding for the heavy war-horses needed in Europe to carry armored knights. But even larger, well-fed horses had a tough time with wooden plows. The plow's heavy points of contact[8] generated enormous friction, particularly in wet soils. Without a smooth, curved fitting between the plowshare and the flat mold-board, they were constantly becoming clogged with soil and weeds. Iron mold-boards crossed from China to Europe only in the seventeenth century, and it was not until the rise of the modern steel fabricating industry in the mid-nineteenth century that smooth, curved, steel plowshares replaced heavy, cast-iron implements.

The heaviest nineteenth-century horse breeds—French Percherons, English Shires, and German Rhinelanders—worked in teams of more than

[8] A plowshare is one component of a plow. It is the cutting or leading edge of a moldboard, which closely follows the coulter (one or more ground-breaking spikes) when plowing. The plowshare itself is often a hardened blade formed by the blacksmith into a unified combination of plowshare and moldboard, the whole unit being responsible for entering the cleft in the earth (made by the coulter's first cutting through) and turning the earth over. In well-tilled terrain the plowshare may work without a preceding coulter. In modern plows, both coulter and plowshare are readily detachable.

thirty animals, and pulled the first grain combines. But such large numbers of animals needed abundant farmland to provide their food. According to Smil, for example, when the number of farm horses in the United States peaked at twenty-one million animals, in 1919, at least 20% of the country's farmland was required merely to cultivate their feed! By that time, in industrial countries, the internal combustion engine had almost totally displaced draft animals for transportation. Their eventual replacement in Western farming was inevitable, as even the small engines mounted on the first tractors could replace at least ten horses—and needed no oats or pasture.

While camels provided meat, milk, leather, and transport for desert peoples in the Middle East, horses were faster and more maneuverable. The original purpose of the specialized "Arabian" horse was as a desert warhorse, selected for the ability to launch the rapid surprise raids that were a hallmark of desert warfare. Horses also played a significant role in the spread of the Islamic religion. By 1385 B.P., Islam had expanded across the Middle East and North Africa, and after another hundred years or so it reached Spain and most of the Iberian Peninsula.

Horses were introduced early into Egypt (from the Caucasus) and were used along with donkeys by the military elite and ruling class. In general Egyptians did not so much ride on horses but used them for pulling chariots and other wagons. King Tutankhamen is thought to have enjoyed riding on horseback because a riding crop, found in his tomb, bears the inscription that he "*came on his horse like the shining Ra*."

Horse-drawn chariots were a crucial tool of early warfare. Tomb paintings and various carved inscriptions show Egyptians used horses in this role at least as early as 3700 B.P. (see Figure 9.7), while large-scale military use of horses began soon after, under the reign of Pharaoh Thutmose III (3619–3565 B.P.).

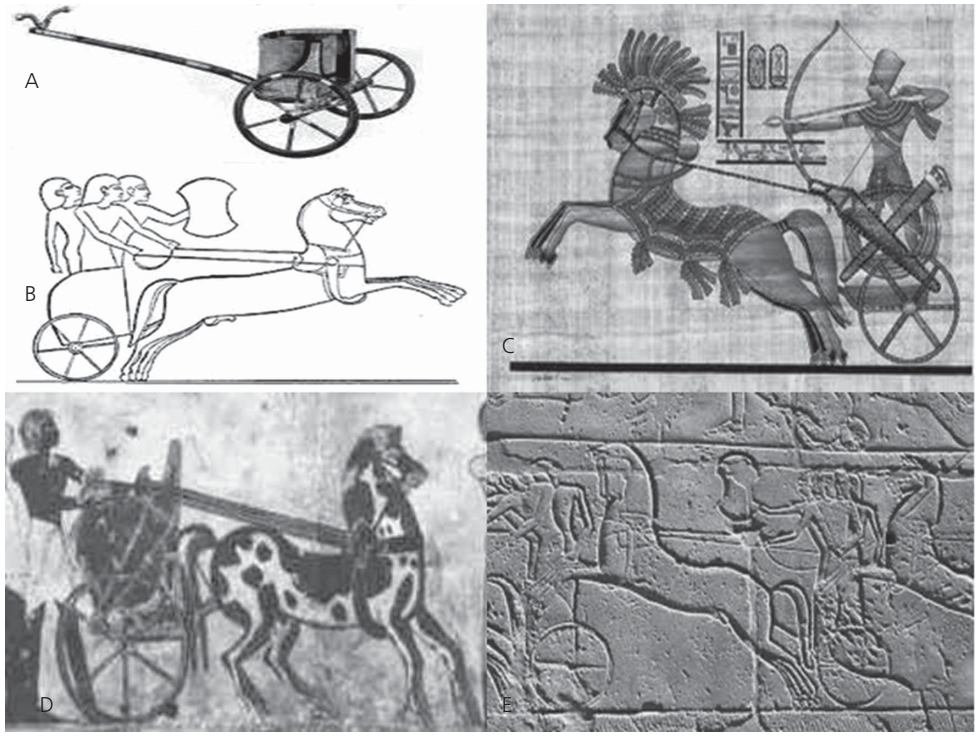



**Figure 9.7** Two-wheeled chariot (A), three warriors on a horse-pulled chariot (B), warrior armed with bow and arrow on a chariot, drawn on papyrus (C), and painted and inscribed horse-pulled chariots on a Pharaoh's tomb walls (D & E). Sources: downloaded from internet sites.

## 9.7 Fruit trees and early fruit cultures

During the late Neolithic and Bronze Ages, between *c*. 8000 and 2500 B.P., the major ancient Mediterranean fruits—dates, olives, grapes, figs, and pomegranates—were all domesticated (see Table 9.2). Other fruits including citrus, banana, various pome fruits (apple, pear, quince, and medlar), and stone fruits (almond, apricot, cherry, peach, and plum) were all first domesticated in central, eastern, and southeastern Asia but still reached the West in antiquity. Some additional fruits and nuts (blueberry, blackberry, pecan, and kiwifruit) were domesticated elsewhere and introduced only more recently in the nineteenth and twentieth centuries (Janick 2005; Zohary and Hopf 2000). During the period known as the Age of Exploration, some 600 years ago, various American fruits (including pineapple, cacao, new species of strawberry, papaya, tomato, potato, avocado, pepper, and squash) all reached Europe, Asia, and Africa while, reciprocally, southeastern Asian fruits like banana, mango, and persimmon reached the Americas (Janick 2005).

The establishment of urban centers in the Middle East is frequently associated with the development of settled agriculture, coinciding with the beginning of fruit cultivation. Mesopotamian and Old Egyptian cultures both produced a rich art in which fruits were a major motif (Janick et al. 1981; Zohary and Spiegel-Roy 1975). Paintings and sculptures from Egyptian tombs and monuments that include fruits and fruit trees are well known. Sumerian writings *c*. 2400 B.P., and earlier Egyptian writings on papyrus and stone have all documented early agricultural traditions that continue today.

Fruit-tree culture involves a more complicated gardening than the cultivation of herbaceous annuals such as cereals and legumes (pulse crops). Tree crops require a long-term series of horticultural manipulations and year-round activities including pruning, pollinating, and harvesting, activities that need to be more or less customized to each species.

**Table 9.2** Evidence for fruit crops in Egypt (Source: Janick 2002).

| Fruit crop | Binomial | Earliest record (dynasty or period) | Evidence |
|---|---|---|---|
| Date palm | *Phoenix dactylifera* | Pre-dynastic (6000 years B.P.) | Archeological |
| Doum palm | *Hyphaene thebaica* | Pre-dynastic | Archeological |
| Sycomore fig | *Ficus sycomorus* | Pre-dynastic | Archeological |
| Jujube (Christ's thorn) | *Ziziphus spina-Christi* | I (Old Kingdom)—4700 years B.P. | Archeological |
| Common fig | *Ficus carica* | II (Old Kingdom) | Artistic |
| Grape | *Vitis vinifera* | II (Old Kingdom) | Archeological |
| Hegelig | *Balanites aegyptiaca* | III (Old Kingdom) | Archeological |
| Persea (lebakh) | *Mimusops shimperi* | III (Old Kingdom) | Archeological |
| Argun palm | *Medemia argun* | V (Old Kingdom) | Archeological |
| Carob | *Ceratonia siliqua* | XII (Middle Kingdom) | Archeological |
| Pomegranate | *Punica granatum* | XII (Middle Kingdom) | Archeological |
| Egyptian plum | *Cordia myxa* | XVIII (New Kingdom)—3650 years B.P. | Archeological |
| Olive | *Olea europea* | XVIII (New Kingdom) | Archeological |
| Apple | *Malus* × *domestica* | XVIIII (New Kingdom) | Literary |
| Peach | *Prunus persica* | Graeco-Roman | Archeological |
| Pear | *Pyrus communis* | Graeco-Roman | Archeological |
| Cherry | *Prunus avium;P. cerasus* | About 2120 years B.P. | Literary |
| Citron | *Citrus medica* | About 2120 years B.P. | Literary |

The development of fruit cultivation in the Middle East began first in Mesopotamia and the Nile Valley, and later additional species and technologies came from Greece, Persia (modern Iran), Turkey, India, and China (Janick 2005).

Most fruit trees have out-crossing breeding systems, maintained by an array of mechanisms that avoid self-fertilization (Janick 2005). These include dioecy and herkogamy[9] (carob, date palm, grape, fig, strawberry, kiwifruit, and papaya); physiological/biochemical self-incompatibility (pome and stone fruits); and dichogamy[10] (avocado and lychee). In some fruits, promotion of cross-pollination is achieved through co-evolution with insect pollinators (e.g., common fig and sycomore fig) or birds (e.g., pineapple).

The date palm (*Phoenix dactylifera*, Arecaceae) (Table 9.2) is regarded as indigenous from northern Africa through the Arabian Peninsula to northern India (Smartt and Simmonds 1995). It may have been the first cultivated fruit and was certainly well established in the Middle East during the Bronze Age. A big part of cultivation involves the selective cultivation of female individuals of this dioecious species (sometimes from cuttings of known females), and the use of pollen from only a few male plants. To ensure full pollination and fruit set, hand-pollination of the females is carried out using ladders or strapping, to safely dust female flowers with the male inflorescences. More than 3000 cultivars are known, of which some 60 are still widely grown (and some cultivars have been grown for a thousand years or more). Wild date palms often produce small and unpalatable fruits, while those of domesticated cultivars are significantly larger and have abundant sweet pulpy tissue.

The sycomore fig (*Ficus sycomorus,* Moraceae) originated in the savannas of eastern Africa and was introduced to Egypt in pre-dynastic times, becoming an important cultivated plant in the Early and Middle Kingdoms about 4000 B.P. The tree was highly prized and considered as sacred; representations of both the fruit and tree are found on bas-reliefs and commemorated in Pharaonic songs (Janick 2005). The tree was widely introduced in the eastern Mediterranean and Cyprus.

The common fig (*Ficus carica*) is considered one of the classic fruits of the Mediterranean basin and fig cultivation has been recorded at many Neolithic and late Neolithic sites (Zohary and Spiegel-Roy 1975). Egyptian records indicate its cultivation since *c.* 2500 B.P. Through domestication, figs have developed larger fruits with higher sugar content, and lost the need for pollination (through apomixis) (Storey 1975). Other fruit variation includes the color of the skin and flesh (white, amber, red, and purple), and resistance to splitting when mature.

Pomegranate (*Punica granatum,* Punicaceae),[11] native to the southern Caspian region in Iran and northeastern Turkey, is a Bronze Age fruit that has been cultivated in the Middle East for at least 5000 years (Zohary and Spiegel-Roy 1975). The pomegranate was introduced to Egypt and is commonly illustrated in Egyptian art from the New Kingdom. Through domestication, pomegranate fruits became larger and sweeter and there was a shift to clonal propagation through cuttings. In Egypt juice from the pomegranate has been consumed and also fermented, for wine. The rind was used as a medicine and the flowers can be crushed to make a red dye.

Wild grapes of the Old World (*Vitis sylvestris*, Vitaceae) are indigenous to the southern Caspian belt,

[9] Dioecy is complete sexual separation into male and female individuals (see Chapter 6). Herkogamy is a spatial separation of the anthers and stigma in hermaphrodite individuals. Two forms of herkogamy are most common:

1. Approach herkogamy (presentation of the stigma above the level of the anthers). This arrangement causes floral visitors to first contact the stigma, before removing pollen from the anthers; it is considered to be common, and is associated with a large, diverse fauna of floral visitors/pollinators.

2. Reverse herkogamy (when the stigma is recessed below the level of the anthers). This causes floral visitors to first contact the anthers before the stigma. For this reason reverse herkogamy is believed to facilitate greater pollen export than approach herkogamy. This type of arrangement is typically associated with Lepidopteran (moth or butterfly) pollination.

[10] Sequential hermaphroditism in a plant—the maturation of male and female reproductive organs at different times (either female-first protogyny, or male-first protandry), ensuring cross-fertilization.

[11] The Latin name *Punica* refers to Carthage, and the fruit was once known as the apple of Carthage (today Tunis, in modern Tunisia).

Turkey, and the Balkans, and were widely distributed in the northern Mediterranean region to the Black and Caspian Seas (Reisch and Pratt 1996). Cultivation of the wine grape in the Near East was evident as early as 3000 B.P. and *V. vinifera*, the domesticated wine grape, had spread from Anatolia to the Levant, Mesopotamia, and Egypt *c*. 7000 B.P. (Reisch and Pratt 1996).[12] The culture of grapes (viticulture) and the technology of wine making (enology) were both common practices in ancient Egypt, and wine was the beverage of choice, there and in ancient Greece and Rome. With the advent of Islam, wine became prohibited in many parts of the Middle East but grapes and raisins remain highly prized.

The cultivated olive (*Olea europea*, Oleaceae), characterized by large, fleshy fruits and high oil content, originated about 6000 years ago in the Levant, around the frontier between Turkey and Syria. The olive has long been known in Mesopotamia and was introduced to Egypt. Early records (Blazquez 1996; Smartt and Simmonds 1995) suggest olives were cultivated in Anatolia and imported to Egypt from about the time of Ramses II (*c*. 3279–3213 B.P.). The olive spread from Egypt and then to Carthage in North Africa, reaching Italy *c*. 2700 to 2600 B.P.

## 9.8 Plant resins

Southern Arabia was an early nexus of trade—an "*entrepôt*" for goods from all over Eurasia and Africa. In southern Arabia *c*. 3000 B.P., spices and textiles arrived in transit from India, silk from China, and gold and ostrich feathers from Ethiopia. These goods were then packed off to Egypt and Persia, to Palmyra in Syria, and on to Rome and elsewhere. However nothing in the shipments was more prized than the two locally grown, gum-resin products, frankincense (*Boswellia sacra*) and myrrh (*Commiphora myrrha*). These were a longstanding source of wealth for the region as, for about a thousand years (*c*. 2500 to 1500 B.P.) frankincense and myrrh served to fuel a major global economy. *Boswellia* and *Commiphora* grow in Oman, Yemen, parts of Ethiopia, the Horn of Africa, and the Red Sea coast of Sudan. Both trees "weep" resins through cracks and cuts in the bark. The resins are exuded and harden upon exposure to the air, typically forming tear-shaped lumps.

Frankincense is known locally as "*Olibanum*" from the Arabic for "milk" and a reference to the milky sap tapped from *Boswellia* trees. This has been used for many centuries as incense in religious rituals, on funeral pyres, as offerings to the gods, and mostly, perhaps, to ameliorate the odor of decay and burning bodies.[13] Myrrh was also used in incense, and as an ingredient in medicines, perfumes, and cosmetics.

The decline of the ancient southern mercantile civilization of *Arabia felix* began about 1600 years ago, with the collapse of the frankincense market in Europe and development of trade routes directly across the Indian Ocean, without stopping in Aden or other Yemeni ports. Following the proclamation of Christianity as the state religion of the Roman Empire, simple burials replaced cremation and the elimination of funeral pyres reduced the demand for frankincense. The Romans had also come to appreciate that most of the luxury goods aside from incense and myrrh were actually coming from further east; as they and others learned to navigate the monsoon winds, they were able to bypass Arabian middlemen.

## 9.9 Eco-crises and water shortages

Following World War II, new agricultural technologies created new environmental problems. The

[12] A number of grape species were also domesticated in the New World. These new species, including *V. labrusca* (fox grape), were rapidly domesticated while others were hybridized with *V. vinifera* to develop *Phylloxera*-resistant rootstocks.

[13] Nero, famous for his inattention to a fire sweeping through Rome, also once used a massive amount of frankincense (reported as ten times the annual total output of all Arabia) for the funeral of his wife, Poppaea. The cost and use of frankincense was so great that Pliny expressed concern about this level of consumption as a lead-in to collapse (others argue Rome's decline was because it was not a producer of any particular goods, only an importer of many, costly goods). Ancient Egyptians and later others used frankincense in embalming; the pharaohs believed burning it allowed them to commune with the gods.

"Green Revolution" of the 1970s brought increased crop yields through the introduction of new seed varieties, greatly increased inputs of inorganic fertilizer (>9-fold increase since 1950), extensive use of pesticides (32-fold increase since 1950), and increased water consumption (Edwards 1994, 2001; Pimentel and Lehman 1993). Unfortunately there has also been ongoing soil erosion, progressive loss of fertile cropland, and a significant decline in how much water is available for irrigation.

Soil erosion is a major cause of soil degradation and loss of fertility, in particular in the Middle East. According to Gardner (1996), the annual rate of worldwide soil erosion in cropland averages *c.* 30 tons per hectare, which is about 30 times faster than the rate of topsoil renewal. Over recent decades rates of soil loss in Africa have increased *c.* 20-fold. In 1989, more than 11% of the world's cropland was identified as "severely eroded." Gardner estimated that by 2020 effects of agricultural land degradation will depress food production by 15–30%. Soil erosion hurts productivity by destroying soil structure, reducing rooting depth for crops, and losing soil organic matter; this in turn reduces soil water-holding capacity, lowering water availability and nutrient levels. Because of the slow rate of topsoil renewal under agriculture, it takes several centuries to produce just a couple of centimeters of topsoil.

Rapid human population growth and increased consumption are seriously depleting available water resources. Between 1960 and 1997, per capita availability of potable freshwater worldwide declined by 60%; a further 50% decrease is projected by 2025 (Pimentel and Edwards 2000). According to Pimentel and Edwards, *c.* 93% of the water removed from all sources worldwide is used solely for crop irrigation. Water demand already far exceeds supply in nearly 80 nations of the world. In the Middle East and parts of North Africa, shortages of water are already critical. Because of low rainfall and absence of year-round water, the future of agricultural production there is grim and getting more so as human populations increase (see Box 9.1). Political conflicts over water (hydro-politics) in some parts of the region have already strained relations between severely water-starved nations seeking to draw from the same watercourse or groundwater reserves.

River discharge is highly variable and difficult to manage; drainage basins often span several countries. Major watersheds include the Jordan, Nile, and Euphrates/Tigris, all of which are subject to contention. Large subterranean aquifers underlie North Africa and the Arabian Peninsula but are costly to access and pose many potential problems; they are already being mined (Section 10.8) but recharge is not keeping up with consumption (Edwards 2001).

Deteriorating water *quality* is also an increasingly serious issue in almost all the region's rivers, due to a combination of low flow, inadequate wastewater treatment, agricultural runoff, and uncontrolled effluent from industry. In many locations seawater intrusion (and related saltwater wedge effects) is impacting coastal aquifers and salinity issues are affecting several major irrigated areas (World Bank 1995).

The use of traditional irrigation methods, some established thousands of years ago, may increase crop yield but this has also lowered water tables and left large deposits of salt residue. As a result—and since most wild and cultivated plants are glycophytes, intolerant of salt—much of the landscape has become bare and vulnerable to soil loss. Any gains from the Green Revolution have been more than offset by losses due to salinization and soil depletion, as well as effective mining of groundwater reserves.

The balance between water supply and demand differs among countries in the region, ranging from relatively water-rich countries like Turkey, to virtually dry states like Jordan. Table 9.3 gives estimates of population size, growth rates, and water supply per capita for some Middle Eastern states for 2007 and 2025.

As of 2007, most countries in the region are either "*water stressed*" or already suffering from "*water scarcity*." Assuming a relatively stable supply, and based on the human population projections, by 2025 most Middle East countries will be suffering extreme shortages. The region has high population growth rates, an inadequate food supply, large income gaps both within and between countries, and

**Table 9.3** Annual population growth rates and water supply per capita per year for some Middle Eastern countries. *Italics* indicate that a country is water-stressed. Bold indicates that a country is water supply scarce. Population source: The *CIA World Factbook*, http://www.cia.gov. Population is expressed in millions of persons. ? = data not available. Estimated populations are based on a continuation of present growth rates.

| Country | Population (Millions) (2007) | Water supply per capita ($m^3$) | Population growth rate (%) | Projected population (2025) | Projected water supply per capita ($m^3$) (2025) |
|---|---|---|---|---|---|
| Libya | 6.0 | **99.9** | 2.27 | 9.0 | **66.7** |
| Egypt | 80.3 | **732.8** | 1.72 | 109.2 | **538.9** |
| Sudan | 39.4 | 1843.5 | 2.08 | 57.1 | *1272.0* |
| Ethiopia | ? | ? | ? | ? | ? |
| Eritrea | ? | ? | ? | ? | ? |
| Djibouti | ? | ? | ? | ? | ? |
| Somalia | 9.1 | *1494.2* | 2.83 | 15.0 | **906.5** |
| Saudi Arabia | 27.6 | **165.1** | 2.06 | 39.8 | **114.5** |
| Yemen | 22.2 | **233.8** | 3.46 | 41.0 | **126.6** |
| Oman | 3.2 | **600.9** | 3.23 | 5.7 | **337.3** |
| Emirates | 4.4 | **451.1** | 4.0 | 8.9 | **223.0** |
| Qatar | 0.9 | **49.8** | 2.39 | 1.4 | **32.0** |
| Bahrain | ? | ? | ? | ? | ? |
| Kuwait | 2.5 | **64.6** | 3.56 | 4.7 | **34.4** |
| Jordan | 6.0 | **344.7** | 2.41 | 9.2 | **224.8** |
| Syria | 19.3 | **288.3** | 2.24 | 28.8 | **193.2** |
| Israel (incl. Gaza & West Bank) | 6.4 | **334.3** | 1.15 | 8.4 | **254.7** |
| Lebanon | 3.9 | *1426.2* | 1.12 | 4.8 | *1158.8* |
| Iraq | 27.5 | 3781.1 | 2.62 | 43.8 | 2374.0 |
| Turkey | 71.1 | 1760.9 | 1.04 | 85.7 | *1460.9* |
| Iran | 65.4 | 1795.7 | 0.66 | 73.6 | *1595.6* |
| Cyprus | ? | ? | ? | ? | ? |
| Armenia | ? | **?** | ? | ? | **?** |
| Azerbaijan | ? | ? | ? | ? | ? |

limited arable land and water resources. Most of the region, where 60% of the total population lives, falls within the arid to semi-arid rainfall zones. According to Table 9.3, 10 of the 17 countries listed will have less, and often *much* less than 500 $m^3$ of water per person per year by 2025 (Yetim 2003, Yoffe et al. 2003, Shetty 2006).

Agriculture is the dominant user of water in the region. At the same time, the relative contribution of agriculture to overall Gross Domestic Product (GDP) in most of these countries is low and declining. For example in countries like Iran, Syria, Saudi Arabia, Yemen, and Egypt, agriculture consumes more than 90% of all the available water resources. Yet the share of agriculture as a contribution to GDP in these countries is only *c*. 19% in Iran, 24% in Syria, 7% in Saudi Arabia, 15% in Yemen (see Box 9.1), and 14% in Egypt. In Jordan, agriculture consumes 75% of the water resources while contributing a mere 2% of GDP (Shetty 2006).

## Box 9.1 Coffee and qat in Yemen

### Coffee

Coffee trees and shrubs belong to the large, mostly tropical family Rubiaceae, and there are approximately 100 species in the genus. The subgenus *Coffea* contains a single tetraploid species and about 80 diploid species (2n = 22) (Moncada and McCouch 2004). The two main cultivated species are *Coffea arabica* (the tetraploid, which provides 75–80% of world production) and *Coffea canephora* which has higher caffeine content, but less of the typical coffee flavor, and is much used to manufacture instant coffee (Geletu 2006; Wellman 1961). A third species that is cultivated less extensively is *C. liberica* (Van der Vossen 1985).

*Coffea arabica* is native to the highlands of the African Horn, particularly southwestern Ethiopia and northern Kenya. It is a segmental allo-tetraploid (Meyer 1969), arising from the hybridization of two diploid species. All cultivated and wild tetraploids are believed to have originated from the same two diploid progenitors, *Coffea eugenioides* and *C. canephora* (Lashermes et al. 1999). *C. arabica* is autogamous (self-pollinating) and shows relatively low phenotypic variation.

At some point *C. arabica* made its way from its place of origin to Yemen. Various accounts have been proposed but none is conclusive. What is certain is that the first record of coffee as a beverage occurred in Yemen (i.e., southwestern Arabian Peninsula), and by *c.* 700 BP it was widely consumed in the Islamic world (Grigg 2002). Coffee cultivation was limited to Arabia before its introduction to the new world (Smith 1985; Wrigley 1988). Coffee's popularity spread from Mocha, in Yemen, to Egypt and North Africa and by 500 BP had reached the rest of the Middle East, resulting in emergence of the coffee house, where klatches ever since have met to discuss news and debate ideas and politics.

Historical evidence suggests all *C. arabica* varieties in the Americas descended from a small number of trees which survived a series of efforts during the early part of the eighteenth century to introduce *C. arabica* from Yemen (Van der Vossen 1985). These few introductions have given rise to multiple varieties, regional types, and cultivars, all reflecting the influence of artificial selection despite a very limited starting gene pool.

As mentioned *Coffea canephora* has been widely used for manufacturing instant coffee. It is an open-pollinated species, showing significant variation among forms and ecotypes (Van der Vossen 1985). This has allowed selective breeding for certain traits, including resistance to coffee leaf rust, caused by *Hemileia vastatrix* (Wellman 1961).

Moncada and McCouch (2004) used fluorescently labeled microsatellite markers to compare genetic diversity in a set of 30 wild *Coffea* accessions. They found over half (*c.* 55%) of the alleles present in the wild tetraploids were not shared with cultivated *C. arabica* genotypes. Clearly wild tetraploid ancestors from Ethiopia could be a useful source of novel variation, expanding the gene pool of the relatively limited *C. arabica* genome, possibly generating novel flavors or increased resistance to pests and pathogens. In 2014 the coffee genome was sequenced, with more than 25 000 genes identified. An interesting finding was that coffee plants synthesize caffeine using a different set of genes from those used by tea, cacao, and other caffeine-producing plants (Denoeud et al. 2014).

Cultivation of arabica coffee provides an unfortunate example of the problems associated with agricultural *intensification* that are common to most crops. Because higher yields increase household income, farmers are incentivized to convert adjacent natural areas to cropland; in so doing they negatively impact local biodiversity and ecosystem services.

Wild *Coffea arabica* is a small shrubby tree native to the understory of the moist evergreen Afromontane forests. According to Aerts et al. (2015), arabica coffee was originally harvested directly from wild populations, but over time, shade trees and coffee shrubs have been increasingly managed to increase yields. These practices improve local livelihoods but unfortunately also degrade natural forests and cause severe biodiversity losses (Hundera et al. 2013a, b). More importantly this intensive management and the use of locally improved cultivars are threatening the diversity and genetic resources of wild *C. arabic*a. Natural-forest conversion to heavily managed forest plantations has resulted in significant habitat loss, with more limited pollen dispersal and increased self-pollination in wild arabica stands. Other evidence suggests the indigenous coffee gene pool already shows signs of admixture with cultivars through pollen dispersal from plantations (Aerts et al. 2013; Berecha et al. 2014).

Aerts et al. (2015) argued that if the global coffee industry plans to tap the genetic diversity of Ethiopian wild coffee to adapt arabica coffee to climate change and emerging pests and disease, significantly greater conservation efforts are needed in the indigenous Ethiopian coffee forests.

### . . . and what about Qat?

For a long time coffee cultivation represented the backbone of Yemen's economy, with much of the crop yield getting

**Box 9.1** *Continued*

exported. In contrast today qat[14] (*Catha edulis*: Celastraceae) and its cultivation and domestic consumption are dominant ecological factors, in particular in the mountains of Sana'a and Taiz. The dark green leaves of qat are chewed by a significant fraction of Yemeni people.

Qat is a crop that provides a high-cash income to the people involved in its production and sale. Chewing it is a socially accepted custom in East Africa and Yemen. The psychological experience associated with qat chewing is a complex mix of positive and negative effects. Desirable effects include a sense of increased energy and alertness, improved self-esteem and increased libido. Habitual use or overuse may produce anxiety, restlessness, hallucinations, hypomania, and even psychosis (Pantelis et al. 1989).

Like coffee, qat came first from Ethiopia, probably *c.* 1500–1800 years ago and then spread widely, eventually (but only recently) replacing the cultivation of coffee trees. Getahun and Krikorian (1973) and Hill (1965) described many differences in the morphology and chemical constituents of qat grown in different areas. In Yemen there is only one species but more than 40 named varieties, many corresponding to sources grown at different altitudes. "Red" and "white/yellow" varieties are widespread, as are general patterns of variability. It is unclear the extent to which any morphological and chemical variation is based on genetic diversity versus phenotypic plasticity, however reciprocal transplant–replant studies with cloned varieties could address this. Zahran et al. (2013) reported on ecological features of qat farms in twelve sites in the mountains of Taiz and Sana'a. Some seven environmental variables were shown to have significant effects on plant performance.

Qat cultivation reportedly accounts for up to 40% of the water drawn from the Sana'a Basin each year, and that figure is rising (Heffez 2013). That is because qat takes a lot of water to farm (much more than coffee) and also because its cultivation is increasing by around 12% each year, according to Yemen's Ministry of Agriculture and Water Resources (see Filkins 2011; Heffez 2013). Not only is the crop drying up the Sana'a Basin, it has displaced tens of thousands of hectares of more vital crops—fruits, vegetables, and cash crops like coffee—which in turn has caused food prices to rise.

## 9.10 Summary

This chapter reviews the profound effects of agriculture on the region's plant ecology, and the early role of plant and animal domestication in developing human societies. Most of the countries of this region are either "*water stressed*" or already suffering from "*water scarcity*." The region is characterized by high human population growth rates, an inadequate food supply, large income gaps both within and between countries, and limited arable land and water resources. Most of the region (where 60% of the total population lives) falls within the arid to semi-arid rainfall zones. Many aspects of modern crop varieties are described, including the value of "landraces" or domesticated, regional ecotypes for many crop species including the resin plants, frankincense and myrrh. The effects of horses, camels, and other domesticated grazers are reviewed, and Omani oasis agriculture is described as an instance of sustainable agriculture. Coffee and qat are compared as major Yemeni crops.

[14] A "mild narcotic" plant that releases a stimulant when chewed. Known variously as qat, khat, gat, chat, and Abyssinian-, Arabian- or Somali tea, Flower of Paradise, etc. In 1980, the World Health Organization classified it as a drug of abuse that can produce mild-to-moderate psychological dependence (though less than tobacco or alcohol).

CHAPTER 10

# Human impacts and plant conservation

## 10.1 Introduction

For everything on Earth especially including the plants, *here* and *now* represent notions which may be defined in some ongoing way by astronomy and geology. We live on a planet orbiting a star, embedded in one of the spiral arms of the Milky Way, etc. And in terms of geology: the 10 000-year-old Holocene Epoch, which has been a stable and warm part of the Quaternary Period, has otherwise been distinguished by fairly regular shifts in and out of ice ages. Recently, however, Crutzen and Stoermer (2000) have argued the explanatory baseline has radically shifted, and we are today in a *post*-Holocene time they have called the Anthropocene: the "Recent Age of Man."

Crutzen and Stoermer's argument is that today humans are *central* to, and highly influential in, the workings of the natural world, rather than being mere participants like all other organisms. In some of the more dismal scenarios of the future, whole cities are seen as becoming "cultural fossils," in particular cities located on fast-sinking river deltas. Such deltas, further undermined by the pumping of groundwater and starved of sediment by the interception of upstream dams, are becoming increasingly common (Section 10.7). Other markers of the Anthropocene include the increasing abundance of organisms that humans *use* (our crops, food animals, and pets), or that have adapted to life in a human-dominated world (pests, pathogens, and weeds). And there will be other fossils harder to find—species driven to extinction through habitat loss, aggravated by the ongoing effects of climate change. It is clear we are in a time of major species extinction—some call it the sixth global mass extinction—as natural habitat becomes increasingly degraded and lost.[1]

The Middle East has a timeline reaching back to the Neolithic, capturing the emergence of agriculture, the development of numeracy, construction of the Pyramids, and other great artifacts and, more recently, it has been the source of the hydrocarbon energy that has fueled innovation and growth in the twentieth century. These days, unfortunately, the Middle East seems to be experiencing an environmental catastrophe, with politics and human wellbeing in a state of near chaos, various wrecked nations following upon failed states. At the same time there is ever-increasing desertification resulting from increasing global climate change, superimposed on individual and multiple effects of humans and their activities.

There are interesting and worrisome parallels with earlier periods of history in the region.

[1] The argument about the Anthropocene has been extended to a strong conclusion that humans are changing the way the planet *works*—for example, altering the size of compartments in Earth's biogeochemical recycling systems. Over the past couple of centuries, people have released into the atmosphere quantities of fossil carbon that took hundreds of millions of years to accumulate. One relatively rapid effect has been a warmer climate; other effects include melting Arctic and Antarctic regions, higher sea levels, and improvements in the photosynthetic efficiency of many plants, intensification of the hydrologic cycle of evaporation and precipitation, and changed ocean chemistry.

The nitrogen cycle is being particularly affected by human actions. By adding industrial activity (and the Haber process) to the activity of nitrogen-fixing bacteria and other microbes, humans have greatly increased the total amount of nitrogen fixed on land (industrially-fixed nitrogen is largely used only for fertilizers, and explosives).

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Dasmann (1984) identified the main cause of the downfall of early civilizations in the Middle East (in particular in the Nile Valley and Mesopotamia) to environmental collapse brought on by human pressures on natural resources, and repeated wars and invasions.

The surface area of Middle Eastern and other drylands having hyper-arid, arid, and semi-arid climates is shown in Table 10.1. Taken together they represent about a third of the Earth's surface. Soil surfaces not protected by permanent vegetation are subject to erosion by water and wind, to salinization by evaporation, trampling by animals, and water-logging and anoxia in places. Taken together these effects all lead to desertification and arid-land degradation.

Tables 10.2 and 10.3 summarize the major causes of desertification in global drylands. Wood collection is very important in many parts of Asia and Africa, where fuel-wood often represents the bulk of family energy use among rural populations. In Arabia, Iran, Iraq, and Afghanistan the pattern is similar to that of North Africa and the Near East, while northwestern India resembles more the conditions of the

**Table 10.1** Size and distribution of the world's arid lands. Modified after Le Houérou (1996), used with permission.

| Regions and countries | Geographical surface area ($km^2 \times 10^3$) | Bioclimatic zone | | | | | |
|---|---|---|---|---|---|---|---|
| | | Eremitic | Hyperarid | Arid | Semi-arid | Total | % |
| Aridity index (I) (P/PET × 100) | | I < 3 | 3 < I < 6 | 6 < I < 30 | 30 < I < 50 | | |
| P (Approx. mm) | | P < 50 | 50–100 | 100–400 | 400–600 | | |
| **Africa (total)** | 30 312 | 6232 | 3017 | 3570 | 2951 | 15770 | 52 |
| North Africa (total) | 6019 | 3952 | 1137 | 505 | 248 | 5842 | 97 |
| Egypt | 1001 | 685 | 286 | 30 | – | 1001 | 100 |
| Libya | 1760 | 1435 | 230 | 90 | 2 | 1757 | 99 |
| West Africa (total) | 8772 | 2120 | 1475 | 1250 | 955 | 8500 | 67 |
| Sudan (incl. So. Sudan) | 2505 | 560 | 190 | 375 | 250 | 1375 | 55 |
| Sahara | 8684 | 6010 | 2612 | 62 | – | 8684 | 100 |
| East Africa (total) | 3641 | 40 | 215 | 898 | 622 | 1775 | 49 |
| Ethiopia | 1222 | 25 | 35 | 310 | 250 | 620 | 51 |
| Djibouti | 22 | 5 | 10 | 5 | 2 | 22 | 100 |
| Somalia | 638 | 10 | 170 | 393 | 65 | 638 | 100 |
| Southern Africa (total) | 5428 | 120 | 190 | 900 | 1095 | 2305 | 43 |
| **North and South America** | | | | | | | |
| Canada | 9976 | – | – | – | 30 | 30 | 0.3 |
| Mexico | 1973 | 5 | 75 | 570 | 230 | 880 | 45 |
| U.S.A. | 9373 | 5 | 15 | 455 | 1675 | 2150 | 23 |
| Argentina | 2777 | – | 11 | 720 | 720 | 1451 | 52 |
| Bolivia | 1099 | – | – | 53 | 42 | 95 | 9 |
| Brazil | 8512 | – | – | 120 | 330 | 450 | 5 |
| Chile | 757 | 185 | 75 | 40 | 12 | 312 | 41 |
| Columbia | 1139 | – | – | 1 | 9 | 10 | 1 |

*continued*

**Table 10.1** *Continued*

| Regions and countries | Geographical surface area ($km^2 \times 10^3$) | Bioclimatic zone | | | | | |
|---|---|---|---|---|---|---|---|
| | | Eremitic | Hyperarid | Arid | Semi-arid | Total | % |
| Equador | 285 | – | – | 3 | 15 | 18 | 6 |
| Paraguay | 407 | – | – | – | 50 | 50 | 12 |
| Peru | 1285 | 90 | 30 | 25 | 65 | 210 | 16 |
| Venezuela | 912 | – | – | 5 | 25 | 30 | 3 |
| **Asia (total)** | 43 770 | 1595 | 3225 | 5415 | 4817 | 1502 | 34 |
| China | 9305 | 656 | 776 | 1375 | 1293 | 4100 | 44 |
| Egypt (Sinai) | 60 | 20 | 35 | 5 | - | 60 | 100 |
| Iran | 1636 | 20 | 306 | 685 | 375 | 1386 | 85 |
| Iraq | 435 | – | 96 | 291 | 48 | 435 | 100 |
| Israel | 21 | 4 | 3 | 5 | 9 | 21 | 100 |
| Jordan | 98 | 18 | 25 | 40 | 15 | 98 | 100 |
| Kuwait | 18 | – | – | 18 | - | 18 | 100 |
| Oman | 212 | 107 | 91 | 12 | 2 | 212 | 100 |
| Qatar | 22 | | 22 | – | – | 22 | 100 |
| Saudi Arabia | 2150 | 700 | 1250 | 200 | 10 | 2150 | 100 |
| Syria | 185 | – | 10 | 157 | 18 | 185 | 100 |
| Turkey | 781 | – | – | 50 | 130 | 180 | 23 |
| UAE | 84 | – | 84 | – | – | 84 | 100 |
| Yemen | 527 | 70 | 257 | 160 | 40 | 527 | 100 |
| **Australia** | 7618 | – | – | 3250 | 1375 | 4625 | 61 |
| **Europe** | | | | | | | |
| (Spain, Greece, and Italy) | 500 | – | – | 100 | 300 | 400 | 80 |
| **World (totals)** | 130 737 | 7500 | 7059 | 14 330 | 12 651 | 41 540 | 32 |

**Table 10.2** Causes of desertification in percentage of desertified land (after Le Houerou 1996, used with permission).

| Regions and countries | Over-cultivation | Over-stocking | Fuel-wood collection | Salinization | Urbanization | Other |
|---|---|---|---|---|---|---|
| NW China | 45 | 16 | 18 | 2 | 3 | 14 |
| N Africa and Near East | 50 | 26 | 21 | 2 | 1 | – |
| Sahel and East Africa | 25 | 65 | 10 | – | – | – |
| Middle Asia | 10 | 62 | – | 9 | 10 | 9 |
| U.S.A. | 22 | 73 | – | 5 | ? | – |
| Australia | 20 | 75 | – | 2 | 1 | – |

**Table 10.3** Extent and severity of desertification ($10^3$ km$^2$) (after Le Houerou 1996, used with permission).

| | Light* | | Moderate | | Strong | | Severe | | Total** | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Region** | **S** | **%** | **S** | **%** | **S** | **%** | **S** | **%** | **S** | **%** |
| Africa | 1180 | 9 | 1272 | 10 | 707 | 5 | 35 | 0 | 12 860 | 56 |
| Asia | 1567 | 9 | 1701 | 10 | 430 | 3 | 5 | 0 | 16 718 | 42 |
| Australasia | 836 | 13 | 24 | 4 | 11 | 0 | 4 | 0 | 6633 | 32 |
| North America | 134 | 2 | 588 | 8 | 73 | 0 | — | — | 7324 | 50 |
| South America | 418 | 8 | 311 | 6 | 62 | 1 | — | — | 5160 | 29 |
| Total | 4273 | 8 | 4703 | 9 | 1301 | 3 | 75 | 0 | 51 691 | 40 |

*S = Area desertified in $10^3$ km$^2$; % = area desertified in percentage of total dry lands (dry lands = arid + semi-arid + dry)

**S = Total dry lands; % = percentage of desertified areas in the non-hyperarid dry lands, i.e., excluding the true climatic deserts, below 50 mm/year of mean annual rainfall.

Sahel and East Africa (Le Houérou (1996). Three causes—overstocking of grazers, deforestation/wood collection, and over-cultivation underpin some 90% of both land degradation (Table 10.2) and desertification (Table 10.3).

## 10.2 Deforestation and wood collection

Deforestation and wood-cutting activities have been practiced for millennia in the Mediterranean and Levant countries (in Egypt, Israel, and the Palestinian territories, Lebanon and Syria, for at least 5000 years) (Thirgood 1981). In Egypt important woody species that have been used extensively but manage to persist include various *Acacia* species, *Balanites aegyptiaca, Ziziphus spina-christi, Tamarix nilotica*, and *Moringa peregrina* (Thirgood 1981). Wood-cutting for cooking and fuel is still widely practiced by small populations of nomads living in Middle Eastern deserts (Figure 10.1).

In Saudi Arabia natural vegetation in the Nafud basin has also been cut intensively. Half a century ago it was estimated that about 40 000 hectares were subject to woodcutting each year by Bedouins (see Batanouny 1983). Vast areas—in particular surrounding settlements—have become completely bereft of trees and shrubs as modern four-wheel-drive vehicles have opened up previously inaccessible areas. Batanouny (1979) reported that cleared communities once dominated by *Acacia* were being replaced by populations of the more weedy *Calitropus procera* (Apocynaceae, according to APG III (2009); formerly Asclepiadaceae).[2] Woodcutting continues today for camping and leisure activities, and many species are becoming seriously degraded, including *Acacia, Juniperus*, and *Olea* species.

Likewise in Israel, sclerophyllous trees such as *Quercus calliprinos, Q. ithaburensis, Olea europea, Pinus halepensis*, and *Pistacia* species have long been major sources of wood for local use and export. They are now nearly all gone and today large parts of a region once covered with trees and shrubs have more open vegetation with very few trees.

Much of present-day Lebanon was also once forested. Over millennia of human occupation, deforestation and woodcutting have been intense and now only scattered remnants survive of what were once extensive forests dominated by *Cedrus libani, Pinus halepensis, Abies cilicia*, and *Juniperus excelsa*. Syria and the northern part of the Fertile Crescent

[2] Commonly called apple of Sodom. Lives as a perennial, often annual in colder zones; grows up to 3–4 m, with a long flowering season and produces a toxic milky sap. Recently Al-Yemni et al. (2011) described bioaccumulation of heavy metals in these plants, and their potential use as indicators of site contamination.

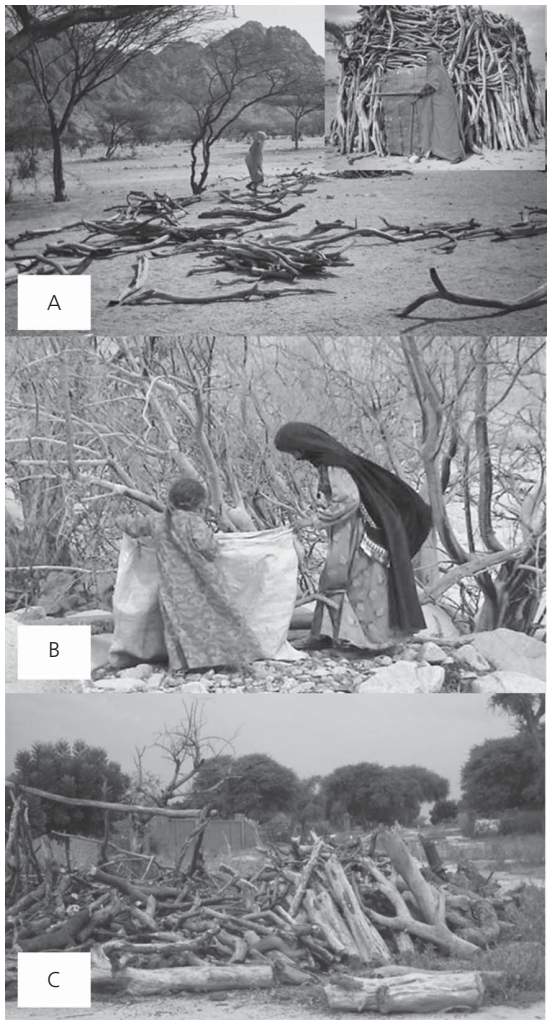



**Figure 10.1** Wood cutting in arid lands of the Middle East. (A) Cutting of *Acacia tortilis* by locals for firewood and housing material (top right) in Gebel Elba, south west Egypt [Photo from Mr. Khalid Mubarak, Al Ahram newspaper]. (B) Collection of *Moringa peregrina* by local Maaza Bedouin girls in Eastern Desert, Egypt. (C) Wood cutting for various purposes in Sudan and Horn of Africa countries; a pile of cut and stored wood of *Acacia tortilis, Balanites aegyptiaca, Faidherbia albida*, and *Albizia amara* in Wadi Saliah, Darfur, Sudan.

were once highly productive lands that also had a rich forest component. Over-exploitation of woodland there has left only scattered patches today. Among the most preferred trees for cutting are *Quercus coccifera, Q. cerris, Pinus halepensis, P. nigra, Cedrus libani, Juniperus excelsa*, and *Abies cilicia.* The pistachio, *Pistacia vera* (Anacardiaceae)[3] is an important Syrian Desert tree, distributed across the country.

Turkish forests extend through the more remote portions of the mountains running parallel to the Aegean, Mediterranean, and Black Seas. People in the coastal towns and villages there have long relied on forest clearing for agriculture, firewood cutting, and forest grazing by sheep and other livestock.

In the Horn of Africa effects of forest loss are today starkly evident, though there are no reliable records of the original extent of woodlands in the region. It is estimated that about 40% of Ethiopia was covered with forest in 1900; this had already been reduced to 16% by 1995. The same is true in Eritrea, where 30–40% of the land area was classified as forested in 1900 (Nyssena et al. 2004). Trees and shrubs steadily declined due to grazing, woodcutting, and land conversion for agriculture (Kebrom and Hedlund 2000). Most of the forested areas became shrubland, and today much of that shrubland has become open steppes. In arid zones of North Africa the minimum daily consumption of firewood is about one kg per person (Le Houérou 1974); as a result harvesting of firewood will, inexorably, completely clear these woody steppes.

## 10.3 Overgrazing

In their introduction to the *Flora of the Arabian Peninsula and Socotra*, Miller and Cope (1996) suggested that the single greatest problem affecting the natural vegetation of Saudi Arabia, and perhaps of the Peninsula as a whole, has been the cumulative effect of several thousand years of animal husbandry, and in particular, overstocking of grazed areas. Historically a kind of rangeland management known as *Hema*—Arabic for "protection"—was long practiced in the Peninsula and Fertile Crescent region. This involved a system of designated grazing rotations, a series of regionally managed "commons," where both grazing and woodcutting were regulated and cycled over long periods (see Draz 1972).

[3] Pistachio is a small, dioecious desert tree, highly tolerant of saline soil. It is originally from the Middle East and central Asia and trees can be found in regions of Egypt, Iran, Syria, Lebanon, Turkey, Greece, Turkmenistan, India, Pakistan, and Afghanistan.

Today the practice of *Hema* has been largely abandoned and as a result of human population growth and concomitant growth in the number of grazing animals, large areas of dryland are suffering significant overgrazing. If management of these grazing lands is not significantly improved, the deterioration of natural vegetation will only accelerate. Going hand-in-hand with significant loss of biodiversity has been an increase in unpalatable, poisonous species, as well as invasive alien weeds.

Al-Rowaily et al. (2015) studied the effects on plants of 35 years of exclusion of large-animal grazing at the National Wildlife Research Center, near Taif, in Saudi Arabia. Various vegetation features including plant palatability were compared across 30 stands of grazed and ungrazed sites. Results showed that livestock exclusion significantly increased plant cover, density, and species richness among annuals, grasses, perennial forbs, shrubs, and trees. Exclosure enhanced the abundance and richness of palatable and rare species (e.g., *Boerhavia repens, Maurea crassifolia, Otostegia fruticosa, Pulicaria crispa, Psiadia punctulata*, and *Stipagrostis plumosa*) and depressed the development of weedy species. Nearly two-thirds of the species recorded at exclosure sites were classified as highly palatable (vs. one-third at grazed sites). These results clearly demonstrate that livestock exclusion could be an effective and useful management tool for vegetation restoration and conservation of plant diversity in degraded arid rangelands.

Overgrazing and trampling degrades the soil in many ways—through increased compaction and bulk density; decreased organic matter; decreased moisture-holding and hydraulic conductivity. All these contribute to reduced water infiltration, increased runoff, and increased flushing of fine suspended particles (e.g., Mwendera and Mohamed 1997; Mwendera et al. 1997).

In desert regions an *open* system of grazing is typically practiced where a variety of herbivores range for forage (Figure 10.2A–E). According to

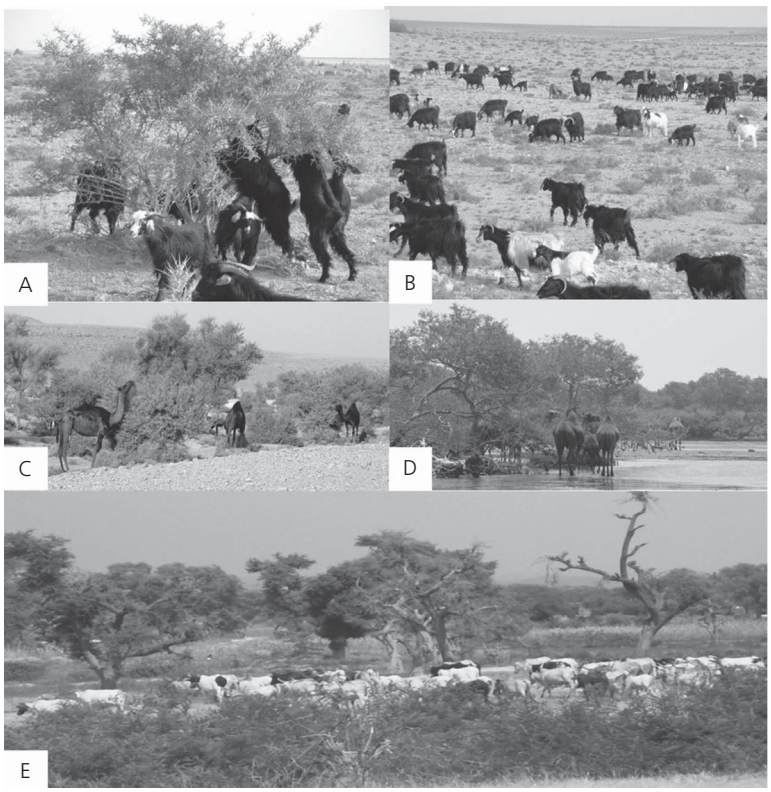



**Figure 10.2** (A and B) Open grazing of goats on a shrub of *Lycium shawii* and annual and perennial herbs near Kiklah at 760 m, Nafusa Mountains in western Libya. (C and D) Camel browsing of *Acacia gerrardii* in Wadi Huraimla, Central Saudi Arabia, and of *Avicennia marina* mangrove in Herida, Red Sea coast, southwestern Saudi Arabia. (E) Livestock grazing in Sudan and Horn of Africa countries, photo from Darfur, Sudan. [For a color version of this figure, see the color plate section, Plate 14]

Batanouny (1983), camels graze a wider array of plant growth forms, ranging from trees to ephemerals. Sheep and goats will browse on thorn bushes, but prefer the more attractive annual and perennial herbs. Cattle and donkeys are less agile and mostly limited to valley bottoms and depressions, eating mixed herbaceous grasses and forbs. Goats are the most destructive grazers, given their ability to access almost any site and browse on a wide array of trees and shrubs, at all altitudes from valley bottoms to peaks. As shown in Figure 10.3 (A–F), plants can become very deformed, with unusual shapes produced by the overgrazing and trampling.

### 10.3.1 Camel grazing

Dromedary camels (*Camelus dromedarius*) have been a significant driver of Middle Eastern plant ecology for ages, at least since the Bedouin camel-herding lifestyle emerged thousands of years ago. Camel grazing is estimated to affect about 90% of the Arabian Peninsula, of which some 44% is categorized as either severely or very severely degraded (Ferguson et al. 1998).

As mentioned, camels graze a wide range of fodder plants (Figure 10.2C and D) including thorny bushes, halophytes, and aromatic species usually avoided by other domesticated herbivores (Iqbal and Khan 2001). El-Keblawy (2003) showed that overgrazing by camels in the UAE had resulted in a significant reduction in the palatable plants *Crotalaria aegyptiaca, Indigofera articulata, Pennisetum divisum, Stipagrostis plumosa*, and *Panicum turgidum*, showing that these species are all preferred items in the diet of camels there. Ghazanfar (2004) suggested overstocking had increased the proportion

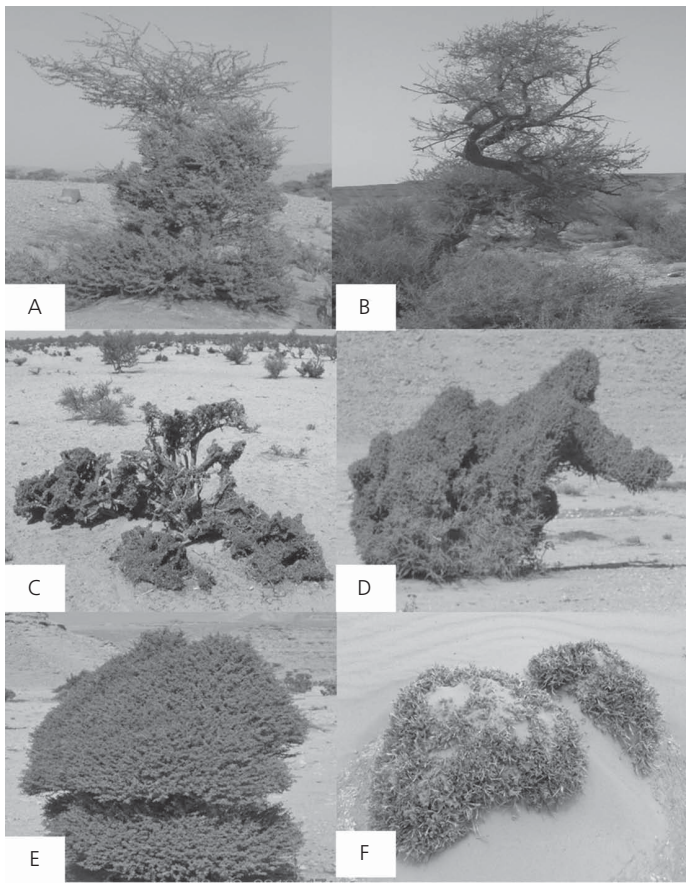



**Figure 10.3** Deformation of overgrazed plant shoots in arid land of central Saudi Arabia. (A and B) Mild grazing of *Acacia gerrardii* trees result in stratified crowns, the upper stratum is ungrazed, the middle is browsed by camels, and lower stratum by goats and sheep as well as camels. (C) *Acacia tortilis* subsp. *tortilis* tree subjected to overgrazing and trampling resulting in extreme shoot deformations. (D) Overgrazing of *Lycium shawii* resulted in an oddly shaped shoot. (E) an overgrazed *Acacia tortilis* subsp. *raddiana* shrub with shoot shaped like mace or scepter. (F) Overgrazed *Panicum turgidum* in the Saudi Nefud Desert resulting in dome-shape or cushion-like shoots. [For a color version of this figure, see the color plate section, Plate 15]

of unpalatable shrubs and dwarf-shrubs throughout central Oman. In northern Kuwait, Brown and Porembski (1998) suggested the current "dwarf shrub" ecosystems there likely arose as a result of overgrazing, replacing the earlier savanna of *Acacia* trees and perennial grasses.

Until perhaps 60 years ago, the inland desert of the UAE was grazed by oryx (*Oryx leucoryx*), now extinct in the wild there; it was also grazed by gazelles (*Gazella* spp.), whose numbers have dropped drastically; and the Arabian ostrich (*Struthio camelus syriacus*), which also went extinct (Gross and Jongbloed 1996). Grazing by smaller species, including rodents, lizards, and hares continues, and fluctuates with season.

In a grazing regeneration experiment, Gallacher and Hill (2006a, b) studied perennial species on several different substrates, on either side of a fence at Al Maha, UAE. The fence separated land that had been continuously grazed by camels from other land in which—for five years—camels had been replaced by oryx and gazelle. Plots were sampled in 43 pairs, one on each side of the fence, at intervals of 300–600 m. Within the Al Maha "camel-free zone," plots contained almost three times the median plant cover and 33% more small, perennial species compared to camel-grazed areas. Areas that were free of camels also showed slightly higher species richness (Gallacher and Hill 2006b).

Most of the plant biomass within the camel-free zone was in the form of large shrubs. Indeed a single species, *Leptadenia pyrotechnica*, made up *c*. 90% of all the large shrubs growing near the Al Maha fence. Its palatability was categorized as moderate (despite production of a milky latex), since camels, oryx, and gazelles all grazed it. *Calotropis procera, Calligonum comosum*, and *Lycium schawii* were the next most common species.

Gallacher and Hill concluded that large shrubs have been differentially impacted by camel grazing. On camel-grazed areas *Calligonum comosum* has been devastated while *Leptadenia pyrotechnica* and *Lycium schawii* have been substantially reduced. Heavy grazing has reduced the cover of small perennials, but the large shrub *Calotropis procera* and sedge *Cyperus conglomeratus* appeared to have benefited from heavy grazing, along with the desert squash, *Citrullus colocynthis*, which was particularly successful in areas of high camel traffic and defecation.

In the inland desert of the UAE, overgrazing is the norm (see El-Keblawy et al. 2009). The Emirates is a rapidly developing country with equally rapid changing patterns of land-use, largely as a result of development of open desert, but in some places, such as Dubai, through extensive coastline engineering and development.

Following unification, the government of the UAE initiated policies to increase agricultural production and establish permanent settlements for the nomadic people whose lives had been built primarily around seasonal migrations involved in camel herding. A cultural reverence for camels has so far minimized restrictions on their movement. Among domesticated animals only camels are permitted to graze open desert throughout the Emirates. At nearly three camels per $km^2$ the density in the UAE is second only to Qatar, and higher than that of Saudi Arabia (3.36 and 0.12 per $km^2$, respectively) (Gallacher and Hill 2006 a).

Total numbers were estimated in 2004 at *c*. 250 000—domestic camel production in the UAE is mostly for racing and there were *c*. 14 000 actively racing camels competing on 15 tracks throughout the UAE, with females comprising nearly three quarters of that herd (Gallacher and Hill 2006a). Gallacher and Hill suggested other livestock industries have increased even faster since national unification, notably goats (125 000 to 1.45M) and dairy cattle (5000 to 115 000).

## 10.4 Effects of grazing on Omani juniper forest decline

Forest decline in general and juniper decline in particular have been tied to acid rain, climate change, deforestation, overgrazing, and more. Sometimes the cause is obvious, as with *Juniperus thurifera* in Morocco, where visible and unsustainable cutting for firewood occurred (Fromard and Gauquelin 1993). But in other cases, like that of red spruce in the eastern United States (Eagar and Adams 1992) and sugar maple in Quebec (Payette et al. 1996), direct causes of the forest decline are less apparent.

For the most part forest decline appears to be mostly of this latter, less obvious type. According to Fisher (1997), a good example occurs at the lower elevations of montane *Juniperus* woodland in Arabia. There *Juniperus excelsa* ssp. *polycarpos* has been experiencing widespread decline, for example in the mountains of Oman. At the same time in the western highlands of Saudi Arabia, *J. phoenicea* and *J. procera* are also in decline, e.g., on the Taif escarpment; *J. procera* has also declined over the Al-Sodah heights and at the Raidah Cliff Protected Area and other parts of the 'Asir Highlands. Fisher concluded that all these juniper forest declines were related in significant ways to climate, but in conjunction with other factors, especially overgrazing.

As in many dryland regions, rangeland and woodland in rural Oman still represent the major source of feed for livestock and contribute a large portion of community resources and income (Brinkmann et al. 2009). In more traditional, tribal times, the practice of *hema* meant that grazed areas were rested in a cyclical way, allowing the vegetation to regenerate. Certain areas had restricted access and it was only when grazing conditions were particularly poor elsewhere that plants from an otherwise closed area would be cut to provide supplemental fodder (Lancaster and Lancaster 1990).

According to Brinkmann and colleagues the traditional *Hema* conservation practices have been largely abandoned in Omani rangelands. Together with the increase in domestic livestock, the rangelands there are now being seriously overgrazed. Large numbers of feral donkeys have added greatly to the problem.

Following introduction during the 1970s of a network of regional roads there, donkeys—that had formerly been used to move merchandise across the mountains—were released into northern Oman and have been multiplying ever since, grazing in large uncontrolled herds. In a detailed survey Brinkmann and co-workers determined that overall more than a quarter of all plant species observed showed significant damage attributable to grazing.

The proportion of species that was heavily grazed decreased with distance from settlements, but there was only a weak correlation between plant species richness and animal grazing damage (expressed as the proportion of species heavily grazed). The interaction between species richness and grazing pressure seemed to depend on palatability and the relation between palatability and competitive ability. It also varied along gradients of soil fertility and precipitation. Brinkmann concluded an altitudinal gradient modifies the heavy grazing effects of goats and feral donkeys on plant diversity.

All-in-all it is worth appreciating the wisdom of the traditional practice of *Hema* as a mechanism for balancing grazing and periods of "rest," or regeneration of rangeland vegetation. Unfortunately with the policies of settling previously nomadic people in permanent villages, the practice is likely to die out entirely. This parallels the loss of other traditional practices elsewhere, including crop rotation and fallow-year cycling in which leguminous crops like clover and alfalfa are part of the cycle; and other measures such as "no-till" cropping, and mulching of dead plant skeletons, all intended to restore the structure and health of soils and vegetation. In place of these, solutions have been largely technological involving addition of industrially produced nutrients, and other manipulations.

## 10.5 Collection of plant materials

In many parts of the Middle East the gathering of medicinal plants—"wildcrafting"—remains a common practice. Some plants have been gathered to the point of local extirpation as collectors take plants for both personal use and commerce (Batanouny 1983; Hegazy et al. 2013a, b).

Among species most collected as medicinals and sold locally are *Hyoscyamus muticus, Urginea maritime, Cassia acutifolia, Anastatica hierochuntica, Citrullus colocynthus, Artemisia judiaca, Tecrum pollium*, and *Mimosopus laurifolius*. Various edible wild fruits (Figure 10.4) are also collected, including *Arbutus pavarii* in Libya; *Nitraria retusa* and *Ficus palmata* in Egypt; *Coccinea grandis, Olea europaea* ssp. *Africana, Cissus rotundifolius, Ephedra foeminea*, and *Diospyros mespiliformis* in Saudi Arabia; and *Glossonema edule* in Qatar. Other plants are collected for use as fiber for ropes and mat-weaving (e.g., stems of *Thymelaea* and leaves of *Dracaena ombet*). *Commiphora myrrah* and *Acacia* species are gathered for their gum and wood (Hegazy et al. 2013a).

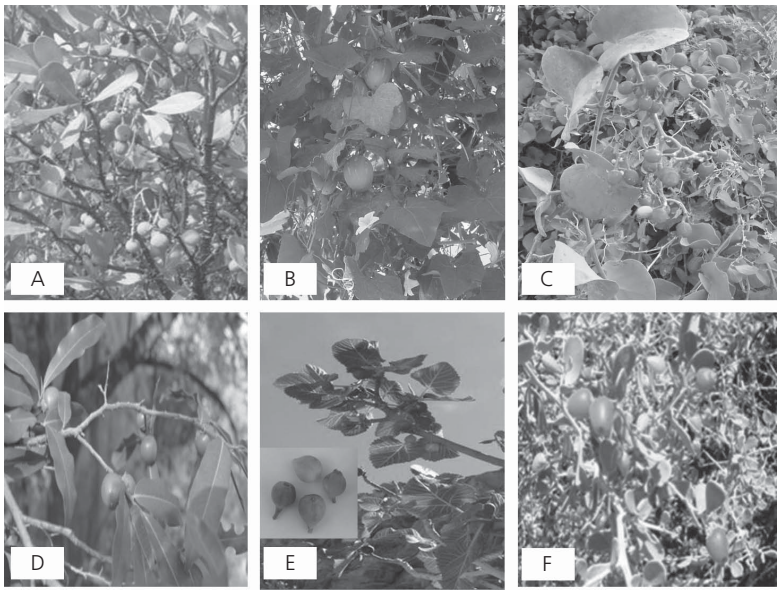



**Figure 10.4** Edible wild fruits collected by local dwellers. (A) *Arbutus pavarii* in Mount Al Akhdar of Libya. (B) *Coccinea grandis* in Taif, western mountains of Saudi Arabia. (C) *Cissus rotundifolius* in Abha, Saudi Arabia. (D) *Diospyros mespiliformis* in Mount Shada, southwest Saudi Arabia. (E) *Ficus palmata* in Mount Qutar, Eastern Desert of Egypt. (F) *Nitraria retusa* in Wadi Al Reshrash, Eastern Desert of Egypt. [For a color version of this figure, see the color plate section, Plate 16]

## 10.6 Land conversion and shifting agriculture

Agriculture in the desert involves conversion of dryland to cropland, typically accompanied by new settlements and supported by irrigation. Many expensive projects have been implemented, moving and managing people according to water availability.

Conversion to agriculture has become more widespread in response to national strategies for food security. Large areas are being converted toward cultivation, which in the first instance results in loss of natural vegetation. These "reclaimed" areas get further degraded through heavy cropping and, usually, little crop rotation with brief or no fallow periods. In much of Libya, Egypt, and the Arabian Peninsula, after soil salinity increases and yields fall, or competition from weeds becomes too intense, reclaimed lands are often abandoned.

In many areas with scanty and irregular rainfall—less than 200 mm a year—an "ephemeral cultivation" is practiced. Grains such as barley, wheat, or sorghum are cultivated opportunistically, relying only on rainfall. Such rain-fed cultivation gets carried out in gullies and slight depressions scattered about in plots across the region. The soil is ploughed and seeds are sown, then left in the hope that rain will fall and accumulate in the depressions. Successful harvests occur only one in every three or more years (Batanouny 1983). In dry years the failure of this cultivation accelerates aeolian (wind driven) erosion and the loosened sandy soil becomes increasingly vulnerable to deflation.[4] Such shifting, ephemeral cultivation is especially common in the Mediterranean belt of the Middle East and many parts of the Arabian Peninsula; it is a powerful factor accelerating the loss of natural vegetation (Batanouny 1983; Le Houérou 1974).

In the southwestern mountainous parts of the Peninsula—including large parts of Yemen and Saudi Arabia—*terraced* cultivation occurs in many small, scattered areas (Figure 10.5). There, as in Omani terraces, garden vegetables, barley, sorghum, medicago, and fruit trees (including apricot, apples, bananas, and pomegranate) are all grown. Terracing changes the landscape in significant ways. It protects the hillside against sliding and soil erosion; and perpendicular, dry stone walls separate

[4] This is the *removal*, or loss of loose rock material and sand by the wind.

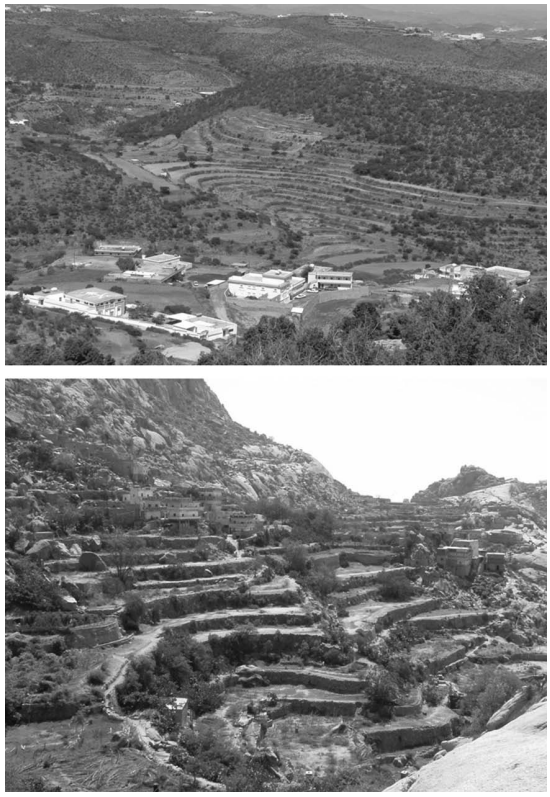


**Figure 10.5** Terraced agriculture in El-Sodah (upper) and Shada Mountains (bottom), southwestern Saudi Arabia.

individual terraces. If the slope is gentle each terrace can be relatively wide, but terraces become smaller and narrower as slopes get steeper.

Many of these terraced lands have been abandoned and, in turn, colonized by surrounding vegetation and grazed by domestic animals. Since the stone walls are no longer being maintained such sites fall into decay and erode, losing much of their productive capacity along with their soils. Varisco (1991) has argued this traditional practice is sustainable and should be supported and reinstated, with traditional knowledge being grafted onto modern methods and technology.

Vegetation in reclaimed agricultural lands appears to include both the weedy flora of the formerly cultivated land, and new weeds, recruited from the flora of the surrounding desert, as well as exotic weeds introduced with new seedstock, agricultural equipment, etc. Hegazy et al. (2004) studied the vegetation of natural and agricultural lands in the Beni Suif governate, in middle Egypt. There the weedy flora in reclaimed lands included both weedy species typical of the old cultivated land and also newly recruited desert annuals, such as *Senecio glaucus, Reichardia tingitana*, and *Launaea nudicaulis.* Clearly any r-selected traits such as short life cycle and opportunistic growth and reproduction that are valuable to annuals in arid lands are similar to the traits contributing to success as a "weed."

## 10.7 Damming of rivers and wadis

Water *harvesting* involves the capture, diversion, and storage of rainwater for various uses (Abdo and Eldaw 2004). Harvesting of episodic torrential downpours is a key element in spreading that resource over time and alleviating water scarcity, and involves dam building. The damming of wadis has been widely practiced for millennia. Dams have been built both at the headwaters of catchments in mountainous regions and in the downstream parts of wadi catchments.

Water politics—often called *hydro*politics—is basically ordinary human politics inflected by the availability of water and water resources, a necessity for all life and essential for human development. The concept includes systematic study of conflict and cooperation between states over water resources which transcend international borders (see, e.g., Elhance 1999; Waterbury 1979). For example, damming of the Nile River in its upstream source countries is currently creating significant political tension among countries downstream in the Nile basin.

Egypt depends on the Nile for its freshwater needs and is vulnerable to any decrease in flow. The reservoir behind the Aswan High Dam (created 1964–1968) is the second largest in the world (total length *c.* 500 km). Most of the lake lies in Egypt (350 km) and is known as Lake Nasser, while on the Sudanese side of the cataract, at Dal, it is referred to as Lake Nubia. Water level varies between 152 and 182 m above sea level, and the storage capacity is 162 billion $m^3$ (Mousa 2013). Typically water levels increase in July and reach a maximum in November

and December due to summer rainfall on the Ethiopian Plateau.

The Nile has been the major source of sediment to the eastern Mediterranean from late Miocene times until quite recently (Ross and Uchupi 1977). Today much of the Nile delta is being lost to erosion; there is no longer an actively building delta but rather an eroding coastal plain (Stanley and Warne 1993).

While the delta is eroding at the coast the sediment load of the Nile is now building up between the Dal Cataract and Abu Simbel, in southern Egypt. This deposit is about 200 km long and for the most part underwater (Eldardir 1994; Stanley and Wingerath 1996). Deposition is occurring due to reduced flow as the Nile enters the reservoir behind the dam (Figure 10.6A); nearly all of the silt load which once flowed through the Nile to the delta and sea is now being dropped in the southern section of this dammed reservoir.

In some contrast to Egypt, Saudi Arabia is the largest country in the world that lacks a permanent river and in light of the highly arid climate has invested heavily in harvesting seasonal rainfall. Many dams have been constructed to hold and accumulate any torrential runoffs and floods. According to the international registry of dams, Saudi Arabia ranks fourth in the Middle East (after Turkey, Iran, and Syria) in terms of the number of large dams. By the year 2000 there were some 220 in different regions of Saudi Arabia; the collective capacity exceeded 833 million $m^3$ (Al Hamid 2004). The huge King Fahd dam on Wadi Bishah (Figure 10.6B) is the largest in the country at 103 m high and 325 million $m^3$ of potential storage capacity. Meantime the Diraih dam, in Riyadh, like nearly all the dams in Saudi Arabia is mainly intended to recharge the reserves of underground water (Figure 10.6C and D). Water stored behind recharge dams usually dries up after 4–8 weeks as it seeps into the soil. According to Al Hamid (2004), the annual volume of surface water runoff for Saudi Arabia as a whole was about 3000 million $m^3$ per year.

In Turkey Şekercioğlu et al. (2011) surveyed what is known about that country's biodiversity in order to identify the major conservation challenges. As it happens, immediate action is necessary, along with international attention and greater support for conservation in Turkey; these authors drew particular attention to river damming as a major ongoing problem.

Increasing urban development in Turkey threatens to eliminate much of the remaining biodiversity,

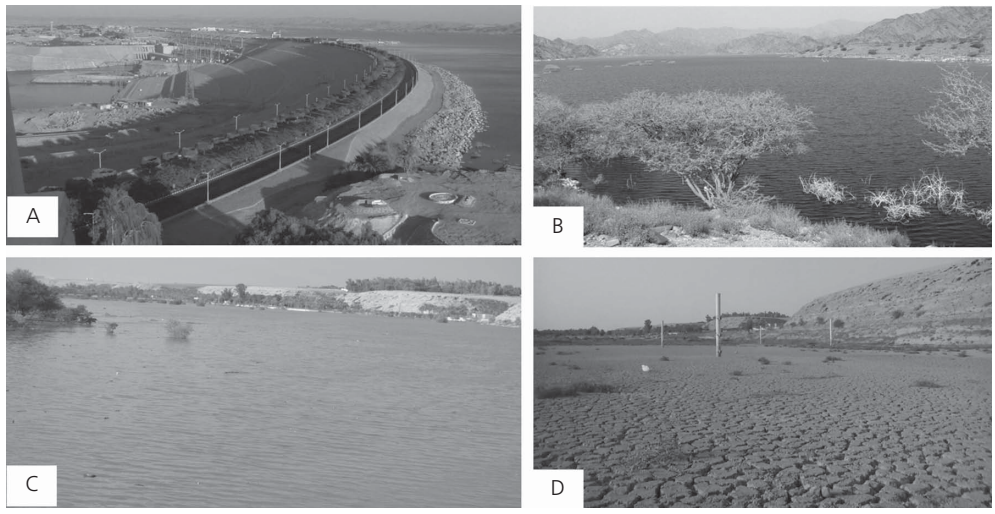



**Figure 10.6** Damming of rivers. (A) Aswan High dam for water storage with the lake at the right and electricity power station at the left. (B) Lake King Fahd dam of Bishah dam complex located at elevation 350 m, southwestern Saudi Arabia with *Acacia tortilis* subsp. *tortilis* at the lake shore and the flooded (dead) trees in the lake. (C and D) Diraih dam for recharge of underground water, (C) is the lake filled with water after torrential rainstorm in November, 2013 and (D) is the dry lake where the recharge wells appear at the back.

and is driving large-scale migration from rural areas to the cities. By 2023 Turkey's rivers and streams will be nearly completely dammed, with almost 4000 dams, diversions, and hydroelectric plants for power, irrigation, and drinking water (Şekercioğlu et al. 2011). Unchecked urbanization, dam construction, draining of wetlands, and intensive irrigation appear to be the most widespread threats in Turkey, as they are elsewhere in the Middle East. The damming of the Tigris and Euphrates by Turkey has also led to increased international tension, as these activities significantly affect water availability downstream in Syria and Iraq.

Finally consider Lake Urmia, located in Iran's northwestern corner, and fast shrinking away. Once it was the world's sixth largest salt lake (at *c*. 5200 km$^2$ it was a little larger than the Great Salt Lake in Utah), but these days its extent is barely 10% of its previous maximum (Stone 2015). As it dries away a salty desert surface is left, generating a noxious dust which threatens crops and people, even as the local wildlife gets extinguished (including the endemic brine shrimp, and rare halophytes such as *Microcnemum coralloides*).

While the weather –droughts and rising temperatures –may be a partial cause, national policy regarding water management has also been a major driver. The three rivers that supply nearly 90% of the water flowing into Urmia have all been dammed for irrigation and hydropower. Moreover groundwater recharge to those rivers has been reduced by *c*. 40 000 illegal wells, all significantly lowering the water table (Stone 2015). Conservationists in Iran are also concerned by progress there toward construction of two large new dams: Shafarud Dam in Gilan province, which would flood vast swathes of Hyrcanian relict forest; and the Khersan 3 Dam in Chaharmahal and Bakhtiari province, which would submerge 2400 hectares of Zagros oaks (see Stone 2015).

## 10.8 Water recharge wells

Most pooled runoff from rain events in flat, arid regions evaporates, and little moves into the soil or deeper aquifers. Groundwater recharge wells have been established in many places to create detention basins, e.g., throughout much of Saudi Arabia, Bahrain, Kuwait, and Qatar (Abdulrazzak 2003; Abdo and Eldaw 2004).

A system of groundwater recharge can serve many needs. The temperature underground is significantly lower so less water is lost through evaporation. The wells increase the reliable supply of water and improve groundwater quality through dilution of salts, and reduce the energy needed to lift water to the surface (especially where the extra water significantly raises the groundwater table).

In the undulating topography of Qatar, groundwater supports up to 93% of the nation's irrigation needs. Many depression areas of various sizes and catchment volumes exist; these collect surface runoff and accumulate any suspended sediments of silt and clay. Unfortunately demand for irrigation exceeds the natural rate of recharge (Hersh and Al-Mahmoud 1991). To increase the availability of groundwater, artificial recharge wells have been established in all the major depressions (Figures 10.7 and 10.8). These accumulate considerable volumes of water during scattered torrential rainstorms, diverting excess runoff and surface drainage into the underlying karst formations (limestone caverns) (Al-Hagari 1991).

The extent of natural aquifer recharge in Qatar was estimated at about 15% of torrential storm volumes (Hersh and Al-Mahmoud 1991). After the installation of recharge wells in all the major depression sites, the extent of aquifer recharge improved to 47.3% to 86.4% of torrential rainfall events (Table 10.4). Volume of pooled runoff in these sites, monitored during 90 minutes of torrential storm, ranged from 4327 to 172 800 m$^3$, in the Um-Alamad and Al-Faras sites, respectively. These two depressions have catchment areas (watersheds) of 0.36 km$^2$ and 10.4 km$^2$, respectively (see Table 10.4).

Field observations carried out 20 years after establishment of the Qatari recharge wells suggested over 70% mortality in the dominant perennial, *Ziziphus numularia*, and co-dominant *Acacia* and *Lycium* species. The richness of ephemeral species in these arid depressions also dropped significantly (A. K. Hegazy, unpublished data). Increased mortality was due to the increased rates of seepage (within a few weeks rather than months, as before). This left insufficient water to support much vegetation under the highly arid conditions in Qatar.

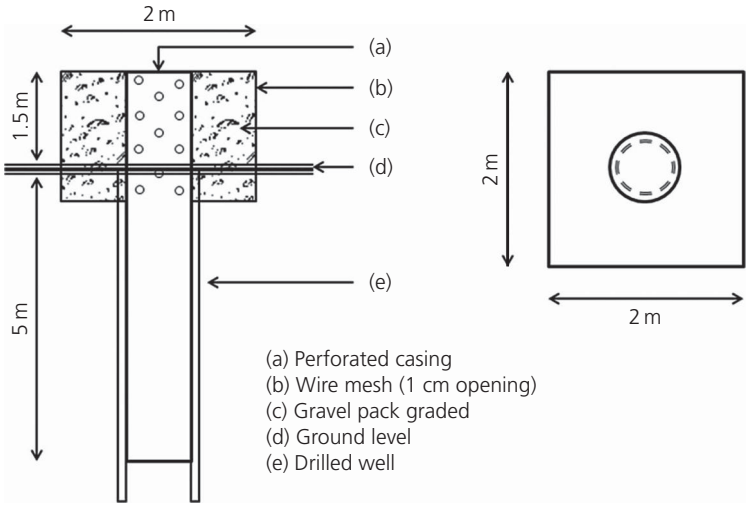



**Figure 10.7** Elements of a recharge well as used in depression sites in Qatar.



**Figure 10.8** Recharge wells: Upper (left side) recharge well in Rodaht Al Magda, Qatar, after heavy rain storm in October 1994, and after water drainage about three weeks later (right side). At lower left, the lake behind Al Deraih dam in Wadi Hanifa in Riyadh full of water after heavy rain storm during November 2013, and after water drainage about eight weeks later.

**Table 10.4** Examples of torrential rainfall events of different duration and catchment areas, indicating the amount of pooled runoff water and the aquifer recharge. Results were collected following the establishment of water recharge wells in Qatar (data from Hersh and Al-Mahmoud 1991).

| Site | Rainfall (mm) | Rainfall duration (min) | Catchment area ($km^2$) | Volume of pooled runoff water ($m^3$) | Aquifer recharge ($m^3$) | Percentage aquifer recharge |
|---|---|---|---|---|---|---|
| Al-Faras | 76.6 | 90 | 10.4 | 200 000 | 172 800 | 86.4 |
| Al-Dawdaiya | 31.0 | 120 | 1.9 | 17 335 | 9941 | 57.3 |
| Al-Ghuwairiyah | 10.0 | 30 | 28.75 | 50 801 | 43 534 | 85.7 |
| Al-Attoriyah | 38.4 | 90 | 1.75 | 14 960 | 9096 | 60.8 |
| Um-Alafae | 73.5 | 415 | 0.375 | 6843 | 4564 | 66.7 |
| Um-Firn | 91.5 | 90 | 0.99 | 20 536 | 12 835 | 62.6 |
| Um-Alamad | 91.5 | 90 | 0.36 | 6344 | 4327 | 68.2 |
| Al-Majdah | 68.2 | 160 | 15.3 | 22 372 | 15 419 | 68.9 |
| Wadi Al-Wasaa | 91.5 | 90 | 1.08 | 15 619 | 7288 | 47.3 |

## 10.9 Sediment removal

Most desert reclamation involves some soil amendment, minimally the addition of a top-dressing of topsoil. Excavation and removal of the alluvial deposits from valley fill and depression sites to provide topsoil has destroyed many once-fertile sites. Subsequent erosion has caused further deterioration in what were once diverse and productive sites in the drylands of the Arabian Peninsula. Native trees and shrubs that once grew in the eroded sites, including *Acacia, Ziziphus, Maerua*, and *Lycium* species are being replaced by ephemeral and herbaceous species including *Aizoon canariense, Boerhavia diffusa, Glinus lotoides, Corchorus depressa*, and *Aerva javani*ca.

## 10.10 Mining, quarrying, and petroleum-related activities

Over the past three-quarters of a century an array of mining, quarrying, and petroleum-related activities have disrupted Middle Eastern ecosystems. Exploration and development operations, drilling, road construction, pipeline installation, and the inevitable leakage of oil, all negatively impact the underlying desert pavement and surface drainage, often destroying extensive areas of vegetation.

Similarly, except over millennia, quarrying for road stone and raw materials to manufacture cement (including abundant limestone) has destroyed many limestone outcrops and their associated flora. Examples include the ridges and vegetation at Borg Al-Arab, and the outcrops in Egypt's Suez Gulf, which have all been severely impacted by quarrying.

Cement factories have been estimated to account for some 5% of global emissions of carbon dioxide; first it is produced when calcium carbonate is thermally decomposed, producing lime and carbon dioxide; and second a great deal of energy from combusted fossil fuels is used in making cement. Dust fallout in the vicinity of cement plants is a further problem. Hegazy (1996) classified common desert species in the area surrounding the cement factories in Ain Sokhna, in the Suez Gulf, into four groups according to their response to cement dust fallout:

1. "Tolerant" species present in the most polluted sites, e.g., *Iphiona mucronata, Pituranthos tortuosus, Tamarix nilotica*, and *Fagonia buveana*.
2. Non-tolerant species present in the least polluted sites, e.g., *Lycium shawii, Trichodesma africanum, Kickxia aegyptiaca, Artemisia judaica*, and *Cleome droserifolia*.
3. Species showing intermediate tolerance, e.g., *Farsetia aegyptia, Scrophularia deserti, Lasiurus scindicus, Salvia aegyptiaca, Retama raetam, Acacia raddiana*, and *Francoeuria crispa*.
4. Indifferent species, which were recorded at all sites surrounding the cement dust sources, e.g., *Haloxylon scoparium, Zygophyllum coccinium*, and *Zilla spinosa*.

Within a radius of at least 5 km, vegetation cover and plant density, seed production and size of the seed bank, germination and seedling establishment were all significantly reduced at all the sites surrounding cement works (Hegazy 1996). Similar impacts occur at Wadi Al-Shams in Merrat, about 120 km west of Riyadh, Saudi Arabia. The cement works and related quarrying there have destroyed the nearby vegetation of the wadi (Figure 10.9A–C). Populations of the dominant woody species in the vicinity of the cement works, *Acacia gerrardii* and *A. tortilis*, and the perennial herb *Rhazya stricta* have all almost completely disappeared, compared to populations at least 5 km away (A. K. Hegazy, personal observations).

During the First Gulf War of the 1990s, the unique sand-sheet vegetation of the Al-Huwaimliyah plain, in south central Kuwait, was destroyed due to oil seepage and accumulation in low areas that were once rich in plants. The resulting "lakes" of oil left significant regional soil pollution. A study of tar-polluted coastal areas in Qatar (Hegazy 1997a) reported reduced abundance in *Atriplex leucoclada, Cressa critica, Launaea nudicaulis, Oligomeris linifolia*, and *Richardia tingitania*, compared to uncontaminated areas (see Figure 10.9D).

## 10.11 Road construction

The trend of increased mobility and development has produced a growing network of paved highways and other roads. Road construction involves bulldozing vegetation and replacement by gravel and other construction materials. In many cases roads get built in vegetation-rich wadis, disrupting drainage; sometimes due to poor engineering—culverts and bridges are badly placed and drainage

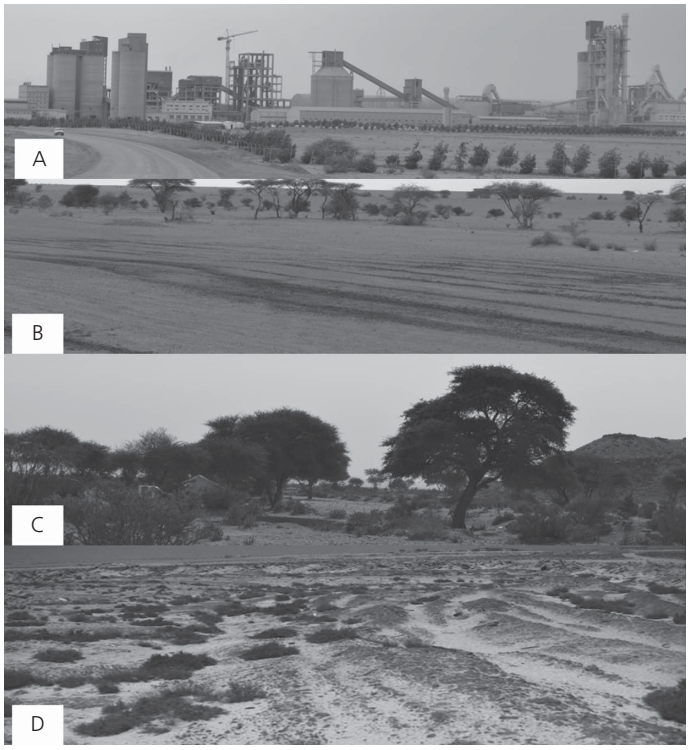



**Figure 10.9** Impact of cement works and tar pollution on vegetation. (A) Cement works and related quarrying activities in Wadi Al-Shams about 120 km west of Riyadh, Saudi Arabia. (B) Destroyed vegetation in the area surrounding the cement works. (C) Natural vegetation in the wadi at distance from the cement works, dominated by *Acacia gerrardii*, *A. tortilis*, and *Rhazya stricta*. (D) Tar-polluted coastal areas in north Qatar and severely affected coastal vegetation.

may be insufficient to prevent ponding and washouts, further eroding the vegetation.

Regionally the landscape as a whole is disturbed and fragmented by roads. Vegetation can be impacted for at least 100 m on each side. In parts of Saudi Arabia and the Emirates, roads are fenced to separate the large grazing animals (camels, sheep, and goats) from traffic. Roadsides are often seeded or planted with introduced trees and shrubs, particularly near settlements and airports. In Gulf countries planted *Prosopis juliflora* has escaped and invaded many regions, often replacing native *Acacia* and *Lycium* species.

The use of off-road vehicles rather than traditional horses and camels is increasingly common around settled areas and results in significant surface disturbance, soil erosion, and loss of vegetation cover.

## 10.12 Warfare

Thirgood (1981) considered in some detail the ever-increasing impact of humans on Mediterranean forests, stating ". . . throughout the ages, the Middle East has been subject to incoming waves of invasion, including Seljuks, Turkomans, Othomans, Afjars, Mongols, Uzbeks, Qazars, Baluchies, Persians, Assyrians, Dorian Greeks, Hebrews, Tartars, Goths, Vandals and Arabs. All contributed to the depletion of desert vegetation and Mediterranean forests." To this list we can surely add the more recent impacts of the French, Germans, Italians, British, and Americans. More recently, the revolutionary wave and subsequent tribal and sectarian wars continue in some countries including Sudan, Libya, Syria, Iraq, and Yemen which are expected to cause severe impacts on both terrestrial and marine ecosystems. In Somalia continuing tribal wars are impacting vegetation over extended areas.

The major environmental effects of warfare are summarized in several reviews (Austin and Bruch 2000; Gleditsch 1998; Hanson et al. 2009; Jarrett 2003; Machlis and Hanson 2008). Wars in the Middle East have had profound consequences, including many direct and secondary effects on the

plant ecology. From the earliest times, large areas of Mediterranean forest have been cleared to meet the needs of armies for fuel and passage (Thirgood 1981). During World War I construction of the Hedjaz railway from Turkey to Saudi Arabia resulted in depletion there of major forest resources. Meantime Allied forces depleted forests in Cyprus during that war. The Balkan Wars, the Turkish-Greek War, the two World Wars, Israeli–Arab wars, Iran–Iraq War, and the American Iraq-based war and its sequelae have all had hugely significant destructive effects on the vegetation.

El-Baz (2004) reported on environmental impacts of the Gulf War. There was severe disruption of the desert pavement (the layer of pebbles and gravel that protects the more fine-grained soils underneath). The digging of trenches and pits, construction of large berms and sand walls, and continuous heavy traffic of tanks and military vehicles all significantly impacted local vegetation. Exposure of fine-grained soil beneath the pavement promoted dust storms and numerous shifting sand dunes. Most significantly the explosions and burning of some 600 oil wells had major impacts, including the formation of *c*. 240 oil "lakes" in low-lying areas. Plumes from well-fires deposited huge volumes of oil droplets and soot which hardened on the desert surface as a crust of "tarcrete," coating the natural vegetation. El-Baz estimated nearly a third of the total land surface of Kuwait was damaged by that war.

Omar et al. (2005) considered the impact of the Gulf War at sites in Kuwait including the Sabah Al-Ahmad Nature Reserve. There, munitions disposal pits accounted for more than a tenth of the 12 ha study site, and compacted areas including pits and road tracks covered 36.4% and 3.6%, respectively, of Reserve area. Less than half the original protected area was left undisturbed.

War-related activities in Kuwait caused significant soil compaction, disturbing soil horizons and adversely affecting the standing vegetation, species composition, and overall plant productivity (Omar et al. 1998). Prior to the invasion the Reserve had four major plant communities. Three were dominated by one of the following: *Rhanterium epapposum* (*c*. 60% cover); *Haloxylon salicornicum* (*c*. 30%); or a mix of *Nitraria retusa* and *Zygophyllum qatarense* (*c*. 10% cover); and salt marsh vegetation along the coast. Total cover averaged 25% during the pre-invasion period but had dropped to 7.3% afterward. Some communities have since become rare or threatened.

Mangroves have been especially hard hit by the massive oil spills following the first American Gulf War. Spalding et al. (2010) reported that 50% of the mangroves and adjacent salt marsh in the complex embayment to the north of Jubail, in eastern Saudi Arabia, were severely damaged by the spill.[5]

## 10.13 Invasive species

Because of the "crossroads" nature of their location, Middle Eastern countries have experienced many successive waves of plant and animal migration, following climatic shifts associated with glacial and interglacial periods. The problems of invasive plants have been widely reported, but detailed, quantitative assessments of their abundance and impact are rare (Pyšek and Richardson 2010; Murphy et al. 2006 b). In the Middle East most invasives begin as ruderals along roadsides and in urban landscapes, altering community structure and sometimes displacing native species.[6]

Shmida and Whittaker (1979) noted the significance of certain New World plant introductions, such as *Opuntia* into the Old World (and Australia), and reciprocally *Salsola, Halogeton*, and the annual grass *Bromus* to the New World as highly successful immigrants. They suggested such plants have been "over-successful" as immigrants because they represent major adaptive types that are either absent, or limited by history, in the arid regions of one or the other continent.

The leguminous mesquite, *Prosopis juliflora*, is native to North and South America. It is a rapidly growing, salt- and drought-tolerant tree, able to grow in areas that receive as little as 50 mm of rainfall per

[5] Aquatic macrophytes have proved highly effective as biomonitors and bioaccumulators of various aquatic pollutants including PCBs and heavy metals (Biernacki and Lovett-Doust 1997; Lovett-Doust et al. 1993, 1994a, b), and possibly oil (see Moubasher et al. 2015).

[6] At least two Caspian/Black Sea animal natives, the zebra mussel and the common carp, have reversed this trend and become important alien invasives in North America.

year. When left unmanaged it colonizes disturbed, eroded, and over-grazed lands, often forming impenetrable thickets (Gardner and Howarth 2009). The dense shade and allelopathic chemicals it produces (Section 8.6.3) appear to inhibit germination and growth of other species.

*Prosopis juliflora* has been introduced to most Middle Eastern countries and is cultivated for shade, timber, forage, food, and medicine (LeHouérou 1980). It has become well established in many habitats (e.g., El-Keblawy and Al-Rawai 2005, 2007; Pasiecznik et al. 2001); control has proved difficult and eradication seems impossible (Shiferaw et al. 2004).

The success of *P. juliflora* stems from a suite of traits associated with rapid invasion. They include production of large numbers of seeds and nutritious fruits attractive to animals; accumulation of a long-lived seed bank; production of some readily germinable and other dormant seeds; and the ability to form basal buds that produce multiple stems (and regrowth in cut or damaged trees). Mainly because of the high seed output and regrowth capacity, mesquite outcompetes most native vegetation (El-Keblawy and Al-Rawai 2005, 2006; Shiferaw et al. 2004).

The invasive herb *Bassia indica* (= *Kochia indica*, Chenopodiaceae) was accidentally introduced to Egypt with military supplies during World War II. First recorded in 1946 around an old military camp (Drar 1952), the species lives in a wide range of soil types. It has become widespread in fallow and agricultural lands, along canals, field banks, and roadsides, and in many water catchment areas, replacing the native species and dominating some communities.

Another major invasive is the water hyacinth (*Eichhornia crassipes*, Pontederiaceae), generally considered the most noxious of all aquatic weeds and ranked number eight among the world's worst weeds overall, but also one which has helped elucidate our understanding of the evolutionary ecology of floral heterostyly (e.g., Barrett 1989). The species is native to tropical America and introduced to many other parts of the world.

In Egypt water hyacinth was introduced as an ornamental in the 1880s (see Hegazy et al. 1999). By the 1930s it had become a serious pest in the canals near Cairo, Alexandria, and Damietta. Simpson (1932) reported the plant's distribution in Egypt at that time was localized and could be contained by manual removal and strict legislation. Unfortunately by the 1990s it was hardly possible to find a canal or ditch, including the main Nile system, which was not overrun (Hegazy et al. 1999). As a result of blocked throughflow there were increased outbreaks of water-borne disease and interference with fishing and agriculture. Obeid (1975a) compared evaporation patterns in open water and *E. crassipes*-infested areas, in Sudan, and showed that water loss in hyacinth infested areas of the Nile was 1.8 times that from open surfaces. Kassas (1972) pointed out the loss of primary production by phytoplankton and benthic algae due to lower light penetration, and the loss of diversity in the aquatic food web.

Another water-plant—the annual free-floating fern *Azolla*—was recently (*c.* 1990) introduced to Egypt, put into rice fields as a green manure. The symbiotic filamentous cyanobacterium *Anabaena*, which is usually found in ovoid cavities inside the leaves of the fern, carries out nitrogen fixation within specialized "oxygen-free" cells (Hegazy et al. 1999). Plants soon escaped from the rice fields to irrigation canals and in less than ten years extended from the Nile delta to Middle Egypt. Five species are reported (Boulos 2009): *Azolla caroliniana*, *A. filiculoides*, *A. rubra*, *A. mexicana*, and *A. microphylla*.

The rapid expansion of *Azolla* is likely due to its wide environmental tolerance. It survives at pH 3.5–10; it can survive in temperatures from 5 to 45°C; and tolerates salinity of up to 1 g/L (Hegazy et al. 1999). Azolla also grows in nutrient-poor habitats as their cyanobacterial symbiont supplies extra nitrate that can support plant growth.

Another Egyptian invasive, *Heliotropium curassavicum* (Boraginaceae), has become one of the most common perennial weeds of the newly reclaimed agricultural lands in the middle of the Nile delta. Because of its vigorous rapid growth and ability to colonize disturbed sand flats, the species spreads quickly. The invasiveness and rapid spread come from a combination of opportunistic traits (including high seed germination and seedling establishment in open areas), along with an ability to

produce adventitious root buds, enabling both perennation and clonal growth (Hegazy 1994; Hegazy et al. 1994). *H. curassavicum* has displaced many native weeds in local environments including *Aeluropus lagopoides, Polygonum equisetiforme, Sporobolus spicatus, Cynodon dactylon, Lotus halophilus, Chenopodium ambrosioides*, and *Bassia muricata*.

El-Bana (2008) evaluated effects of invasive *Acacia saligna*, a native of Australia, on floristic diversity at the Zaranik and Ahrash sand dunes on the Mediterranean coast of Sinai. El-Bana measured and compared attributes of the native community in both invaded and uninvaded patches. Species richness, evenness, and dominance–diversity patterns were all significantly lower in invaded patches. Dominance–diversity curves showed invaded patches had significantly lower species richness, even in the cases of certain mono-specific communities. Severity was significantly dependent on the size of *A. saligna* canopy, and extent of aridity. Larger canopies and more arid conditions had greater detrimental effects on native species.

Plants typical of uninvaded but not invaded patches (hence species that appear competitively excluded by *A. saligna)* included shrubs and undershrubs such as *Thymelaea hirsuta, Retama raetam, Calligonum polygonoides, Moltkiopsis ciliata, Helianthemum stipulatum, Artemisia monosperma, Convolvulus lanatus, Asparagus stipularis*, and *Cornulaca monacantha*.

## 10.14 Coastal development and recreation

Intensive coastal developments in many countries of the Middle East have led to much destruction and loss of natural habitat. This has led to extensive environmental changes in land use, urban growth, the health of marine and coastal ecosystems, and altered hydrology, all compounded by the impacts of global climate change (Picow 2013).

The countries surrounding the Gulf have all established extensive seaside resorts and artificial land reclamation using dredging and infilling. More than 40% of the coastline has been developed since 1970, and the emergence of oil-based economies (Hamza and Munawar 2009). The many threats to coastal environments come from dredge and infill operations in shallow areas, power and desalination plants, oil bunkering and refineries, recreation and tourism, solid and liquid waste dumping, mining and quarrying activities (Sheppard et al. 1992; UNEP/PERSGA 1997).

Coastal engineering and land reclamation has led directly to the loss of sandy embayments, wetlands, and mangroves, and many habitats have been lost due to dredging and infilling (Gladstone et al. 2013). The best-known coastal development is the artificial archipelago including the "Palm" and "World" islands, in the UAE, which has caused significant habitat change. Meantime, pressures from associated activities have caused further damage to surrounding areas.

UAE species already recognized as of national concern and threatened by development include the ghaf tree (*Prosopis cineraria*) as well as a number of animals—the free-ranging mountain gazelle (*Gazella gazella cora*), the cream-colored courser (*Cursor cursorius*), the Pharaoh eagle owl (*Bubo ascalaphus*), the Persian wonder gecko (*Teratoscincus keyserlingii*), and Leptien's spiny-tailed lizards (*Uromastyx aegyptia leptieni*).

Likewise, on the Red Sea, all countries have extensive coastal developments. In Egypt most of the Red Sea and Mediterranean coastal zones include development for seaside tourism. Similar development has taken place in Israel, Lebanon, Syria, and Turkey. Further damage occurs from alteration of regional floodways. At Neimah Bay in south Sinai, for example, a large diversion of local floodways was constructed to avoid flooding of the established resorts during torrential rainstorms.

Large scale development has occurred in coastal regions including around Yanbu, Jeddah, Qatif and the Tarut Islands (in Saudi Arabia), Mesaieed Industrial City (Qatar), and Aden (in Yemen). Tourism has been developed in many Red Sea and Mediterranean coastal locations, including several urban centers at Suez, Hurghada, Taba, Nuweiba, and Sharm el Sheikh (in Egypt); and the artificial archipelagos of the Emirates. Concentrated coastal developments in the Gulf of Aqaba (Jordan and Israel) have transformed coastal and marine environments there. Evidence of coral reef and coastal degradation due to tourism and development is

clear in all these areas (Abdel-Latif et al. 2012). In addition, large recreation centers have been developed along the Jeddah coastline and other coastal cities in Saudi Arabia without adequate evaluation of potential environmental impacts which resulted in deterioration of mangroves, seagrass beds, and coral reefs, and decreased productivity of fisheries (UNEP/PERSGA 1997).

To help conserve the coastal and marine ecosystems in the Red Sea and Arabian Gulf, protected areas have been established (Section 10.16) including Ras Mohammed Marine National Park, the Eilat coral reserve, the marine nature reserve in Jordan, and various coral reef marine protected areas in Bahrain, Iran, Oman, Saudi Arabia, Djibouti, Egypt, Israel, Sudan, and the planned coral reef Peace Park for the Gulf of Aqaba as part of one Middle East Peace Initiative.

## 10.15 Biodiversity hotspots

The concept of biodiversity and conservation "hotspots," widely promoted by the NGO Conservation International, is useful, highlighting areas of the world that contain significant concentrations of endemic species and where regional biodiversity may be at particular risk of extinction. The hotspot approach provides a focal point for our discussion of conservation in the Middle East, but it does not adequately address some of the most pressing concerns, especially for desert and saline environments.

Hotspots were first defined as areas home to at least 1500 endemic species of vascular plant (i.e. >0.5% of the global total) and which had also lost 70% or more of their original vegetative cover (Mittermeier et al. 1999; Myers 1988, 2003). The initial analysis, though based only on plant diversity and habitat loss, was supported by analyses of vertebrate biodiversity. Mittermeier et al. (2004) later added to their original list and identified some 34 global hotspots, which include about half of the world's plant species and 42% of the vertebrates—yet cover only 2.3% of the total land surface.

Individual global hotspots differ widely in size—three identified by Mittermeier et al. (2004) exceed two million km$^2$, while the smallest one covers less than 20 000 km$^2$. Two of the 34 hotspots, namely the "Horn of Africa" and the "Eastern Afromontane," include major parts of the Arabian Peninsula.

The Horn of Africa Hotspot extends across the arid and semi-arid zones of Ethiopia, Eritrea, Somalia, Djibouti, northeastern Kenya, southeast Sudan, and across the straits of Bab-el-Mandeb to southwestern Arabia. The Arabian sector comprises the lower mountains and coasts of Saudi Arabia, Yemen (including Socotra) and Oman. The Eastern Afromontane Hotspot includes the isolated mountains of the Afrotropical region extending from Zimbabwe, Tanzania, Kenya, and Uganda, to Ethiopia and the high elevation zone of the southwest Arabian mountains, in Saudi Arabia and Yemen (Figure 10.10).

In fact the Arabian segments of these two biological hotspots are contiguous. Together they encompass the mountains and coastal regions of the southwestern and southern rim of the entire Peninsula. The combined area is also referred to as the Arabian Hotspot Area (Mallon 2011) (Figure 10.10).

Three other major hotspots that relate to the Middle East include the Eastern Mediterranean Basin, or Levant, which, like the others in the region has been under heavy human influence for millennia, and also harbors valuable genetic resources for many crop species (e.g., Nadel et al. 2012) (Section 9.5). It is also one of the few regions for which climate models all agree in their predictions . . . that there will be "more of the same," namely a decrease in precipitation, increase in temperature and increase in temporal variation (Tielborger et al. 2014) (see, too, Section 11.5). The Eastern Mediterranean basin contains thousands of endemic plant species—possibly more than the number of endemics found in the rest of Europe.

Another hotspot is the Irano–Anatolian region, the great plateau that forms a natural barrier between the Mediterranean basin and dry plateaux of western Asia; it contains many centers of local endemism. The region includes the forestland south of the Caspian. As described in Section 2.26, these "Hyrcanian" forests arc along the southern shore of the Caspian, in a region bounded to the south by the Elburz mountain range. At lower altitudes the flora includes a large number of relict

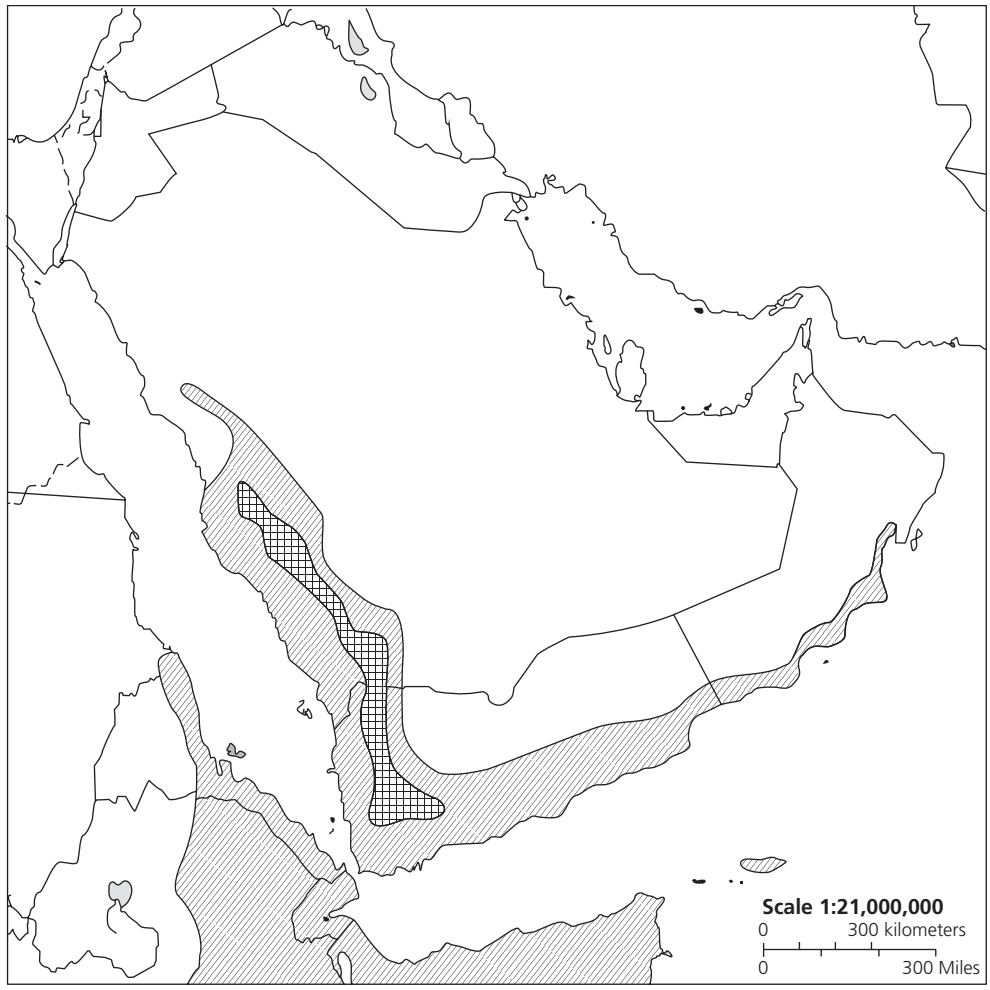



**Figure 10.10** The Arabian Hotspot Area. Pale grey = Horn of Africa Hotspot, hatched = Eastern Afromontane Hotspot (after Mallon 2011). Reproduced with permission from Taylor and Francis.

Arcto-Tertiary[7] thermophilous species, including *Parrotia persica*, *Gleditsia caspica*, *Zelkova carpinifolia*, and *Pterocarya fraxinifolia* (Akhani et al. 2010).

[7] The Arcto-Tertiary geoflora is the floral assemblage envisioned as once covering the Northern Hemisphere, from roughly late Mesozoic to mid Cenozoic eras. It helps explain the disjunct distribution of identical or closely related plant species (e.g., magnolia species and tulip trees, native to both the southeast United States and southern China and Indochina). The Arcto-Tertiary flora likely had wider distribution when the global climate was warmer than currently, when the continents were closer together in late Mesozoic to early Cenozoic times. With the onset of global cooling and the Ice Ages, these tropical to subtropical species were left in isolated pockets where the climate was warmer.

Akhani et al. showed that these Caspian forests are among the most seriously threatened ecosystems in Iran for reasons that parallel our concerns about conservation across the Middle East. They are worth summarizing here.

1. Because of the mild climate and very fertile soil, the area is heavily populated (*c.* 7 million people or 10% of the Iranian population).
2. The area provides a large part of the country's timber needs.
3. The Caspian forest, like other parts of Iran, suffers from severe pressures of overgrazing.

4. Transportation, roadways, etc., have degraded and fragmented the forest.
5. The pleasant climate, beautiful landscape, and Caspian Sea coasts attract millions of tourists during holiday periods, which further degrades the local environment.
6. The forest area is very sensitive to fire and each year large tracts of the Caspian forests are damaged by anthropogenic fires.
7. There has been too much dam construction.
8. There have been serious invasions of exotic plants and over-exploitation and collection of medicinal and ornamental wild plants.

The final hotspot is the Caucasus, where extensive mountainous barriers contribute to a warm and humid climate. This has been present in the region since the late Tertiary and is the main reason the Caucasus—like the Caspian—could serve as a shelter for humid- and warm-requiring (hygrothermophilous) relicts during the previous ice ages. This makes the Colchic and Hyrcan forests there and others in the Hyrcanian region of Iran the oldest forests in Western Eurasia in terms of their origin and evolutionary history, as well as the most diverse in terms of relictual and endemic woody species and tree diversity, and the most "natural" (in terms of least inferred change from its historic structure).

There are at least 17 endemic genera in the Caucasus of which nine are associated with the high mountains. About a quarter of all the endemics there are believed to have originated in the Greater Caucasus range; these include many high mountain and xeric mountain forms, as well as those growing on rock and scree. In addition to many "young" endemics in the region, there are also many distinctly old species. According to Zazanashvili (2009), the following genera are rich in Caucasian endemics: *Saxifraga, Draba, Delphinium, Astragalus, Rosa, Pyrus, Onobrychis, Scutellaria, Campanula, Pyrethrum, Primula, Heracleum*, and *Cirsium*. Caucasian plants are significantly under-represented in the IUCN Red List. To fill that gap the status of endemic species of the Caucasus requires further assessment and relevant recommendations implemented (e.g., Schatz et al. 2009).

Even taken together, these five biodiversity hotspots do not adequately characterize the complexity of the conservation challenges facing the nations of the Middle East. For one thing, deserts exist as so-called coldspots of global biodiversity, biomes where the species list may not always be long, but nevertheless important endemics and rare communities and ecological functional groups may be present (Karieva and Marvier 2003). Deserts and other species-poor biomes—including all of the polar tundra—clearly do support abundant endemic species and unique communities. But they do not fit in the traditional hotspot category because of their low primary productivity and low diversity. This is especially true in Arabia as arid, semi-arid, and hyper-arid deserts cover much of the Peninsula. Characteristic regional habitats such as sand dunes and sabkhat are under-represented or even unrecognized in the Arabian Hotspot area (Mallon 2011).

Mallon has usefully assessed the effectiveness and utility of the Arabian Hotspot designation in the context of regional strategies to conserve biodiversity in the Peninsula (Socotra was excluded from these studies). Rates of vertebrate endemism in the region ranged from 6 to 75%. Some 58% of the Peninsula's endemic vertebrates have distributions restricted to the Arabian Hotspot area. Moreover, the western mountains are important refugia as well as being home to several endemic trees; they call out for urgent conservation care (Hall and Miller 2011).

Mallon argued that in principle the original Horn of Africa Hotspot should be extended continuously eastward to include the Hajar range of Oman and the UAE. He described a smaller concentration of vertebrate endemics there including the Arabian Tahr, endemic to southeastern Arabia, also three species of endemic fish, several lizards, and one snake. The Hajar range was also recognized as one of five centers of endemism for Arabian reptiles. Such an expanded hotspot area corresponds closely to the WWF Global 200 Ecoregion, the Arabian Highlands, Woodlands, and Shrublands, which includes the Hajar range (Olson and Dinerstein 1998).

An extended Arabian Hotspot area would include more of the region's endemic species but would still cover only the mountainous rim of the west and south. This covers only a small proportion of the Peninsula and omits the central and northern deserts of the interior. As regards the effectiveness of regional conservation strategies, Mallon concluded

that the "global biodiversity hotspots" approach is insufficient, and that additional approaches are needed for a fully representative and comprehensive conservation strategy.

## 10.16 *In situ* and *ex situ* conservation

It is a long-standing discussion in conservation science as to whether we should base an argument on any inherent "rights" of other species to exist . . . the celebration of nature for its own intrinsic value or, in order to bring along more supporters, to explain in terms of money or financial value the many "services" provided by other living organisms—that is, emphasizing the *instrumental* value of nature—and what nature does *for* us in terms of protecting and building healthy soils, cleaning water, providing pollinators for crops, etc. (see Costanza et al. 1997; Daily et al. 1997). We would argue that the best hope of protection for Earth's biodiversity lies in education and building community support, since at the end of the day we cannot afford to fail; death is real and extinction is forever.

Preservation of species in their natural environment, sometimes called *in situ* or "on site" conservation is one way of protecting natural habitat, and usually works best in the context of nature reserves. However, natural populations need to be able to share gene pools with neighboring populations, and in some cases we are at the stage where habitat loss and landscape fragmentation have undermined the ability of many wild species to maintain self-sustaining populations. The widespread failure of many endangered species to recruit juveniles to their populations shows that the "regeneration niche" may simply no longer be available, and such species will not survive without active initiatives including assisted propagation. As a last resort, maintenance of species off site (or *ex situ*) conservation can be used. Initiatives involve development of "gene banks," seed banks, and cryogenic storage, as well as cultivation in botanic gardens (Box 10.1). Since most wild species are difficult to regenerate *ex situ*, on site conservation is often undertaken in parallel (Heywood 1990, 1992).

Protected natural areas are specifically dedicated to protection of biological diversity, ecological function, and associated natural and cultural resources, through management. According to the IUCN categories of protected areas there are about 800

**Box 10.1 Techniques for *ex situ* plant conservation or preserving germplasm off site (adapted from Hamilton and Hamilton 2006)**

| Technique | Definition |
|---|---|
| Botanical gardens/ Arboreta | These are primary repositories for living taxa that may have little commercial significance, or special characteristics. They play a role in public education. |
| Field gene bank | This is suitable for species having short-lived seeds or those that do not readily produce seeds. Accessions are preserved as vegetative plants in field conditions or controlled greenhouse environments. Important in re-introductions and enrichment planting. |
| Seed bank | Suitable for many long-lived seeds; storage in a gene bank at sub-zero temperatures. Seed longevity depends on seed moisture content, storage temperature and environment, and genetic composition of the seeds. This technique may give viability to some seeds for c. 100 years if seed moisture content is 5–8% and storage temperature from –10 to –20° C. Requires regular viability testing and regeneration. |
| Cryogenic storage | Most seeds can be stored at –150 to –180°C for more than 100 years. Reduces the need for viability testing and regeneration. |
| Pollen and DNA storage | Pollen grains and isolated DNA are stored in appropriately refrigerated conditions. |
| In vitro storage | Plant materials—cells, tissues, organs, or plantlets—are maintained in culture under sterile conditions. Materials are made to produce plantlets to be transferred to field conditions. |

**Box 10.2 Definitions of the IUCN protected area management categories (data available from the websites of IUCN)**

The protected area categories systems advocated by IUCN since 1994 are:

**Category Ia**—Strict Nature Reserve: protected area is managed mainly for science. The area possesses some outstanding or representative ecosystems, geological or physiological features and/or species, available primarily for scientific research and/or environmental monitoring.

**Category Ib**—Wilderness Area: protected area is managed mainly for wilderness protection. The area is unmodified or slightly modified, retaining its natural character, without permanent or significant habitation, which is protected and managed to preserve its natural condition.

**Category II** Ecosystem Conservation and Protection: protected area is managed mainly for ecosystem protection and recreation. The area is designated to (a) protect the ecological integrity of one or more ecosystems for present and future generations, (b) exclude exploitation or occupation inimical to the purposes of designation of the area, and (c) provide a foundation for spiritual, scientific, educational, and recreational and visitor opportunities, all of which must be environmentally and culturally compatible.

**Category III** Natural Monument: protected area is managed mainly for conservation of specific natural features. The area contains one or more specific natural or cultural feature which is of outstanding or unique value because of its inherent rarity, representative or aesthetic qualities, or cultural significance.

**Category IV** Habitat/Species Management Area: protected area is managed mainly for conservation through management intervention. The area is subject to active intervention for management purposes so as to ensure the maintenance of habitats and/or to meet the requirements of specific species.

**Category V** Protected Landscape/Seascape: protected area is managed mainly for landscape/ seascape conservation and recreation. The area of land, with coast and sea as appropriate, where the interaction of people and nature over time has produced an area of distinct character with significant aesthetic, ecological, and/or cultural value, and often with high biological diversity. Safeguarding the integrity of this traditional interaction is vital to the protection, maintenance and evolution of such an area.

**Category VI** Managed Resource Protected Area: protected area is managed mainly for the sustainable use of natural ecosystems. The area contains predominantly unmodified natural systems, managed to ensure long-term protection and maintenance of biological diversity, while providing at the same time a sustainable flow of natural products and services to meet community needs.

protected areas (categories I–VI) across the Middle East (IUCN 1994). These are often arranged as a series of protected area networks to bring connectivity between areas of suitable habitat, and in order to share resources and approaches (Box 10.2 and Table 10.5).

The major objectives of a protected areas network include the following:

1. To conserve representative examples of a nation's natural habitats and physiographic regions
2. To help maintain the nation's biodiversity
3. To help maintain the nation's ecological viability
4. To optimize economic and social return from the nation's natural systems, in a manner ensuring their long-term sustainability
5. To maintain options and choices for future generations.

Table 10.5 shows that nearly all countries in the Middle East have begun to develop networks of protected areas. For example, in Egypt the network includes some 30 protected areas covering almost 10% of the country's land and marine areas. It includes representatives of habitats and physiographic regions along with important biodiversity hotspots, cultural heritage sites, geological formations, and landscapes of outstanding natural beauty.

Egyptian protected areas include a range of sizes, from the largest, Elba, at about 35 000 $km^2$, to Saluga and the Ghazal Islands, at 0.5 $km^2$. The stated intention is that protected areas will eventually comprise *c*. 18% of Egypt's total land area; this is a little more than the minimum target recommended by the IUCN. The larger protected areas are intended

**Table 10.5** Protected areas in the Middle East countries and their IUCN categories. Data based on different sources: Groombridge (1992), Website of World Database on Protected Areas, and some country national reports. Numbers in some countries may exceed the reported figures in the table but are unclassified or not applicable to IUCN categories I–VI.

| Country | IUCN category of protected areas | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | Ia | Ib | II | III | IV | V | VI | |
| Libya | | | | | 3 | | | 3 |
| Egypt | 7 | 2 | 2 | 3 | 3 | 4 | 9 | 30 |
| Sudan | | | 8 | | 3 | | 11 | 22 |
| Ethiopia | | | 15 | | 8 | | 19 | |
| Eritrea | | | | | 3 | | | 3 |
| Djibouti | 1 | | | | | | 1 | 2 |
| Somalia | | | | | 1 | | 3 | 4 |
| Saudi Arabia | | | 6 | 1 | 6 | 7 | 8 | 28 |
| Yemen | | | | | | | | 5 |
| Oman | | | 3 | | 2 | 1 | 1 | 7 |
| Emirates | | | 2 | | | | | 2 |
| Qatar | | | | | 1 | | | 1 |
| Bahrain | 1 | | 1 | | 1 | | | 3 |
| Kuwait | | | 1 | | 9 | 11 | | 21 |
| Jordan | 1 | 1 | | 2 | 10 | 6 | | 20 |
| Syria | 2 | 2 | 13 | 1 | 4 | 2 | | 24 |
| Israel (incl. Gaza & West Bank) | | | 1 | 3 | 115 | 8 | | 127 |
| Lebanon | 1 | 1 | 1 | 1 | 1 | 3 | | 8 |
| Iraq | | | 2 | 2 | | 3 | | 7 |
| Turkey | 8 | 1 | 18 | 3 | 25 | 19 | 8 | 82 |
| Iran | | | 10 | 3 | 19 | 29 | | 61 |
| Cyprus | 1 | | 14 | 1 | 6 | 1 | | 23 |
| Armenia | 3 | | 2 | 230 | 25 | | | 260 |
| Azerbaijan | 14 | | | | 20 | | | 34 |
| Total | | | | | | | | 777 |

to take account of the fact that plants in desert and semi-arid areas grow at relatively lower densities and depend on long-range dispersal of pollen and propagules to carry out reproduction and colonize microsites that may be far from the parent plant and that may be suitable for only a short time.

Turkey has three major phytogeographic regions: Euro-Siberian, Mediterranean, and Irano–Turanian. The country has a wide range of ecosystems, reflected in its high floral diversity and endemism. The main threats in Turkey are further loss and degradation of habitats, over-exploitation of natural resources, pollution, and climate change. Kucuk and Erturk (2013) report there are 40 national parks, 31 nature conservation areas, 107 natural monuments, 184 nature parks, 81 wildlife reserves, 58 conservation forests, 239 genetic conservation areas, 373 seed stands, 15 "specially" protected areas, 1273 natural sites, 14 Ramsar sites, and one biosphere reserve. Out of all these areas, 82 of the national protected areas come under the terms of the IUCN categories (Table 10.5).

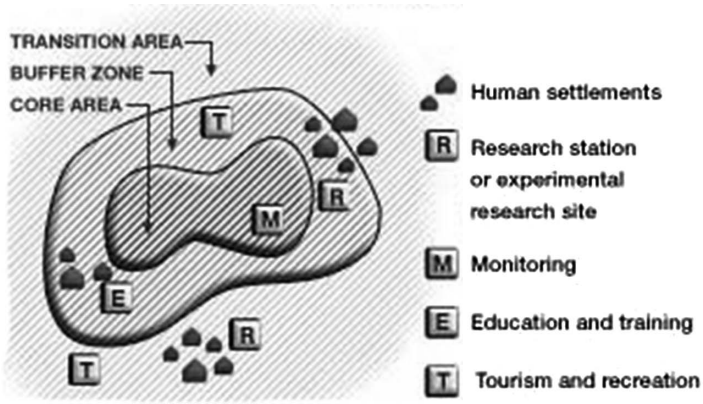



**Figure 10.11** Elemental zonation of the UNESCO biosphere reserve design. The core area is for strict conservation and environmental monitoring; buffer zone for sustainable use in controlled human settlements, research and education, training, tourism, and recreation; and transitional area for planned human settlements, research, tourism, and recreation.

Iran includes three phytogeographic regions. The Hyrcanian in the north; the Nubo-Sindian in the south; and the Irano-Turanian in the rest of the country (and occupying more than two-thirds of the total). Most protected areas lie in the Irano–Turanian region, though Zehzad et al. (2002) pointed out that there are still representative landscapes there where new sites need to be set aside to complete a representative network in Iran. Out of these protected areas there are 61 national protected areas covered by IUCN categories (Table 10.5).

Various international reserves have been established under the auspices of the United Nations Educational, Scientific and Cultural Organization (UNESCO) Program on Man and the Biosphere (MAB). These were created with the goals of protecting biological and cultural diversity in world regions while promoting sustainable economic development. A major strategy has involved collaboration among stakeholders, sharing research data to better understand human impacts on nature.

The "biosphere reserve" concept assigns different zones for different activities (Figure 10.11). The "core zone" represents the ecosystem that is being protected, where biological communities and their environment are strictly protected. In many cases more than one core zone is designated. Then there is a "buffer zone," surrounding or adjoining the core and protecting it from any destructive human activities. The projected ecosystem services offered by the biosphere reserves come through integrated conservation, development, scientific research, education, and capacity building by training, tourism, and recreation. To date, some 621 biosphere reserves in 117 countries constitute the World Network of Biosphere Reserves. A total of 27 biosphere reserves are currently located in Middle Eastern countries. Iran has the most (ten), followed by Ethiopia, Lebanon, and Egypt (each has two). The Emirates, Qatar, Jordan, Syria, Israel, and Turkey all have one each.

## 10.17 Populations and the "abundant-center" model

At one level environmental conservation is rooted in geography—*this* region, this *place*, indeed this *biosphere reserve* . . . but in another sense it is largely about genetics and evolution—*this* lineage, *these* organisms, this *provenance*. Over the long term a particular spot on the planet may simply no longer provide the habitat, substrate, climate, or other conditions necessary for a species to continue to live there . . . and with some luck, another site may become more suitable. There is therefore a certain danger to looking at conservation in terms of specific parks and protected areas where rare species may be carefully guarded and protected, rather than thinking in terms of populations and their requirements, and more importantly considering protection of the functioning ecosystem of which that rare species is a part.

This all surely reflects the importance to conservation of a population approach, as it is of course *populations* which evolve over time. Plant ecology,

and evolutionary ecology at its core, is essentially an attempt to understand the distribution and abundance of organisms. *Where* are organisms found? How many are there, and why? This understanding should lie at the heart of a conservation argument, especially if we intend to protect self-sustaining populations, rather than simply gardens where specimens representative of our lost vegetation may be viewed.

Building on this, species and their populations are being identified and assessed by global non-government organizations, including the International Union for Conservation of Nature (IUCN), and Regional Red Lists are being produced by individual countries or organizations. Evaluations and designations such as "endangered" or "critically endangered," or "vulnerable," etc. (Box 10.3) are based upon the population biology of species across their geographic ranges. Populations are assessed as increasing over time, being stable, or decreasing.

The widely used "abundant center" model in ecology and biogeography is based on the assumption that species abundances should be greater toward the center of the geographic range, and lower around the edges. Related major predictions are that species should occupy more sites toward the center of the range, and abundance and occupancy should decline linearly toward the edge of the range. This reflects a mindset largely driven by consideration of abiotic influences on plant distribution and the assumption that these same factors determine population size. We have some evidence that this approach is too simplistic, and that a blend of biotic and abiotic factors better determines where populations will be larger, or plants growing at higher densities.

Murphy et al. (2006 a) used a large USDA Forest Service database for 134 eastern North American tree species, and extracted estimates of the range size and spatial locations of abundance, relative to position in the range, for each species. Results suggested that for most species the common assumption that species show an "abundant-center" distribution was not well supported. At the same time, most species (85%) *were* abundant somewhere in their geographical range. In common with observations of other biota, tree species that have relatively high abundances tended also to have larger range sizes. Competitive relationships may be involved in the distribution of abundance across tree ranges, and species with larger ranges (and therefore possibly broader niches) may be more affected by biotic interactions than are smaller-ranging species.

Murphy et al. (2006 a) did provide a certain level of support for abundant-center hypotheses. Species were never *more* abundant at edges, and the proportion of potential sites that were occupied was nearly always higher in central parts of the range. (Though it was also clear that areas closest to the center were not always the areas where the species was *most* abundant, within the range.

**Box 10. 3 The IUCN Red List Categories**

**Extinct** (EX) A taxon is extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, and annual), and throughout its historic range, have failed to record an individual.

**Extinct in the Wild** (EW) A taxon is extinct in the wild when it is known only to survive in cultivation/domestication or as a naturalized population(s) outside the past range.

**Critically Endangered** (CR) A taxon is critically endangered when facing an extremely high risk of extinction in the wild.

**Endangered** (EN) A taxon is endangered when considered to be facing a very high risk of extinction in the wild.

**Vulnerable** (VU) A taxon is vulnerable when considered to be facing a high risk of extinction in the wild.

**Near Threatened** (NT) A taxon is near threatened when is close to qualifying for or is likely to qualify for a threatened category in the near future.

**Least Concern** (LC) A taxon is least concern when it does not qualify for critically endangered, endangered, vulnerable, or near threatened. Widespread and abundant taxa are included in this category.

**Data Deficient** (DD) A taxon is data deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status.

**Not Evaluated** (NE) A taxon is not evaluated when it is has not yet been evaluated against the criteria.

Instead, peaks of abundance often occurred at intermediate areas between the center and edge of range.) Moreover, many species reached relatively high abundances at peripheral parts of the range, though their occurrence there was less frequent than elsewhere. Species with large ranges were more likely to show an abundant-core distribution; abundance in such species may be more affected by factors *other* than abiotic gradients, though they still experience reduced abundance toward the edges of their range.

## 10.18 "Rear-edge" populations and opportunities for conservation

There is a long ecological tradition of comparing behaviors of local populations across a species range (see Brown et al. 1996; Murphy et al. 2006a, 2010a). A major prediction of the abundant center model mentioned in Section 10.17 is that marginal populations are more prone to extinction and will be genetically less diverse than those from the center, at least in part because they tend to occur in less favorable habitats and are present at lower and more variable densities, so are vulnerable to the effects of genetic drift (Lawton 1994). Although the utility of this paradigm at local to regional scales is generally accepted, recent empirical work has challenged its significance at broad geographical scales (see, e.g., Murphy et al. 2006a, 2010a; Sagarin and Gaines 2002).

Hampe and Petit (2005) have urged a more ecologically dynamic view of present-day distributions, one used increasingly in recent studies of phylogeography, invasion biology, and the biology of global climate change. Such a perspective emphasizes the demographic and evolutionary processes that accompany species expansions (see Petit et al. 2004; Sakai et al. 2001; Thomas et al. 2001). The "leading edge" hypothesis of colonization has become central in phylogeography, helping to explain the commonly observed poleward decrease of genetic diversity, both within and among populations (Hewitt 1993, 2000). The leading edge model interprets range expansions as involving mostly populations from the colonization front, and controlled largely by rare long-distance dispersal events, followed by local, exponential population growth.

In contrast to models of range expansion, few studies have investigated the behavior of populations located at eroding margins of a species' range (but see Murphy et al. 2010a). Hampe and Petit (2005) reviewed findings from fossils, phylogeography, and ecology to illustrate that rear-edge populations are often disproportionately important in survival and evolution of biota. Their ecological features, dynamics, and conservation requirements differ significantly from those of populations in other parts of the range.

Hampe and Petit argued that such rear-edge populations—including species in the Middle East living at the low-latitude margins of their range of distribution—are disproportionately important for the long-term conservation of genetic diversity, phylogenetic history, and evolutionary potential of species, and that as such their investigation and conservation deserve especially high priority. Rear edge populations are typically small and so isolated that regional population dynamics cannot easily compensate for local extinction events.

Hampe and Petit (2005) described results of various studies on plant recruitment. These have typically observed that water stress during summer reduces seedling survival to nearly zero in the most peripheral populations (which appear to be essentially remnant under current conditions). Unfortunately in long-lived species like trees, the demographic trends of rear-edge populations cannot simply be inferred from their current recruitment rates. Changes in adult mortality would be a better indicator, but mortality of "elderly" adult individuals has rarely been monitored. Hampe and Petit suggest the existence of stable rear edges could be common in those plants or animals whose populations are able to endure long periods without recruitment (for example, by virtue of having a long life span, clonal growth, or long-lived, persistent seed banks, etc.). Unfortunately few studies exist to test this.

According to Hu et al. (2009), at higher latitudes postglacial range expansions often occurred in various directions, and lineages originating from different refugia may have converged and mixed extensively (and see Petit et al. 2003). Such a "melting pot" effect would explain the higher intrapopulation genetic diversity seen in several woody

species in central Europe compared to levels of diversity seen in populations further south.

There is a strong argument to give special attention to populations in the Middle East as they may contain critical genetic diversity, representing the rear-edge of species that have expanded their range to the Mediterranean and beyond. Also the terrain of the Middle East includes several regions that have acted as important refugia, often because they have remained moist (like the mountains of Oman) or have experienced strong selection for traits like salt tolerance or have been isolated (as in the case of Socotra).

## 10.19 Summary

This chapter considers the multiple challenges faced by plant conservation in the Middle East and outlines what is needed for successful conservation. It describes how humans are exacerbating the ongoing effects of desertification. This includes deforestation and other forms of wood collection, road construction, and extractive petroleum-related technologies. Meanwhile, massive coastal developments are degrading some of the most diverse and productive marine ecosystems.

Agriculture continues to stress the regional ecology through overstocking of livestock, land conversion, and the effects of ephemeral agriculture. Negative consequences of wadi-damming and water recharge wells all create additional challenges and the hydro-politics are a major source of conflict.

The region's major biodiversity hotspots are described including the Horn of Africa and Eastern Afromontane regions, Eastern Mediterranean basin, the Irano–Anatolian region with its ancient "Hyrcanian" forestland south of the Caspian, and the Caucasus mountain refugia of Arcto–Tertiary relicts (the Colchic and Hyrcan forests there and in Hyrcanian Iran being among the oldest forests remaining in Western Eurasia).

CHAPTER 11

# Conclusions

## 11.1 Introduction

Today, much of the Middle East is a seriously parched part of the world. The region suffers from chronic political instability, yet it offers a timeless fascination. Incomparable as an historical part of the world, full of many, truly ancient cities, some famous as seats of some of the world's greatest empires, others, like Damascus, that have been continuously inhabited for at least 9000 years—and of course the Middle East is the incubator of *three* of the world's major religions that today, taken together, represent 55% of humanity.

These lands provide the setting for some of the earliest history of *Homo sapiens*. Most significantly from our plant ecology perspective, the Middle East experienced the emergence of that signal human achievement whereby we became so closely intertwined with a select few members of the plant kingdom, and their useful, humanity-sustaining biology. This was the early discovery of *agriculture*—farming, and the *domestication* of plants and animals—arguably these inventions have given us the opportunity to have ample, and indeed surplus, resources which in turn opened humanity to further cultural and social opportunities. The Middle East has also long been a nexus for widespread trade over land and sea and many domesticated species have been introduced to the region, over a very long time.

The Middle East convenes the floras of several distinct and biodiverse regions; there is a great deal of endemism, and high biodiversity, as well as significant loss of natural habitat. All of this contributes to the fact that the Middle East is home to all or parts of five of the world's 34 recognized "biodiversity hotspots." The great tragedy is that this hotspot of the human imagination is today severely over-populated and unfortunately the theatre of some of the most destructive and tragic forms of human disagreement. The region—like the Earth's endangered species—needs our special appreciation, protection, and conservation efforts. This can be achieved through peace and stewardship—both ironically explicit goals of the religions that are currently tearing the region apart.

To illustrate the complexity of the problem and conflicting needs of nature and humans, consider the damming of rivers. River damming represents our best attempt to extract electrical energy out of an accumulated volume of water and its natural tendency to move due to gravity. Of course in doing so dams *change* rivers dramatically. Upstream they create a reservoir with "hard" edges and little natural coastal vegetation along with the destruction of the reservoir's valley, which has become flooded. Downstream they alter fluxes of water, sediment, and nutrients, modify water temperatures, and block the upstream and downstream dispersal of aquatic and water-dependent species. Dams are not a new phenomenon—they have been used for millennia, and they are everywhere.

In the United States, for example, there are 75 000 dams exceeding 2 m in height, one for every 50 km along mid-sized rivers (Poff 2014). Globally over 40 000 large dams (>15 m in height) have been built and thousands more proposed, chiefly in developing countries to produce so-called green energy. In the Middle East there are particular difficulties associated with damming rivers with their headwaters in one country (e.g., Ethiopia and Turkey), and that then run through the lowlands of others (e.g.,

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the Sudan, Egypt, and Iraq). Hydro-politics and the management and prioritization of increasingly limited supplies of fresh water are fast generating further conflicts in this dry part of the planet. It is important to identify, analyze, and address these issues because the Middle East is in many ways a crucible for our encounter with global climate change. The Middle East could lead the world in developing solutions and strategies to counter and survive the ongoing climate change.

## 11.2 Desert "stress" and the plants that live there

Deserts represent a distinct set of environmental conditions, but many people have an overly simplistic idea of the nature of plant and animal existence there. Thus, just as the desert world tends to be seen simply as very hot and very dry, so too it is typically regarded as especially *stressful* for the organisms that live there. Yet as Mangel (2009) aptly put it, "deserts are not places where organisms die; rather, they are places where organisms succeed with less." That is, the species that are present have *adapted*—and continue to adapt. There is much to be learned from desert ecosystems and the desert offers many excellent demonstrations of "evolution in action." These products of natural selection and differential survival are, in Darwin's sense the most "fit" or suitable solutions for particular local environments, constraints, and patterns of availability of critical resources, most especially water.

For plants in the desert, this is their home and evolutionary arena; by definition, their ancestors had what it took to persist and reproduce. Of the most important desert perennials, many occur in just a few families. These include the Chenopodiaceae,[1] perhaps most significant of all the desert families (and today assimilated and subsumed by an enlarged Amaranthaceae), also the Zygophyllaceae, Aizoaceae, Polygonaceae, and Asteraceae (many of which appear *not* to be associated with mycorrhizae—see Box 11.1). Other major perennial families are the grasses (Poaceae), sedges (Cyperaceae), and euphorbs (Euphorbiaceae), and also members of the Brassicaceae, Burseraceae, Boraginaceae, and Capparaceae. Major families among the many ephemeral annuals are the Fabaceae, Asteraceae, Brassicaceae, and Plantaginaceae. Other families containing iconic (often endangered) species include the Asparagaceae, Sapotaceae, and others . . .

These relatively few families (among the approximately 400 total Angiosperm families) tend to dominate the region's major plant communities, at least in desert regions. Many desert species are *succulent*—the ice plants, chenopods and amaranths, brassicas and crucifers, caryophs and euphorbs in particular, and they achieve succulence through a variety of morphological adaptations. Different tissues may be differentially succulent and the degree varies greatly among species. The phenomenon is seen in its most spectacular form in the famous caudiciform and pachycaul succulents. These include the rotund bottle trees, *Adenium socotranum* and *A. obesum* (Apocynaceae), *Adansonia digitata* (Malvaceae), and the cucumber tree, *Dendrosicyos socotrana* (Cucurbitaceae), all spectacular and striking Middle Eastern icons on the way out (e.g., Figure 2.11).

Old World euphorbias mostly exploit what is known as the "cactus niche" in the New World. The prevalence of succulent growth forms suggests the management of water relations is a more significant limiting factor to survival and reproduction than simple carbon gain through photosynthesis.

The "dirty secret" of the Middle East is the hidden bounty of plant diversity there. The chenopods, euphorbs, ice plants, and other dryland specialists that make do with less, getting by in a largely hot and dry desert world, where mountains make for durable and persistent refugia against both global warming and periodic glaciations. According to Shmida (1985), legumes are the most important group of trees and shrubs in the world's subtropical deserts. *Acacia, Cassia*, and *Prosopis* are dominant leguminous genera in many of the semi-desert savannas, and extend to the true desert in wadis, sometimes creating a gallery forest. Both *Acacia* and *Prosopis* are mostly thorny, microphyllous, multi-stemmed trees, with leaves that are often facultatively drought deciduous (Shmida 1985). *Juniperus* species

[1] In extent it is the most widespread family within the large Irano–Turanian phytogeographic region; it is very important in the Sahara, as well as in the deserts of North America, Australia, and South America.

**Box 11.1 Plants and their fungal friends**

Most (>90%) of the plant species on Earth benefit from symbiotic relationships—mutualisms—with mycorrhizae. The association is of mutual benefit because the fungus receives a host individual as well as complex carbon compounds from the plant, while the plant effectively increases its rooting surface area more than a hundred-fold by virtue of its intimate connections to the fungal hyphae.

The "functionalist" argument for hosting mycorrhizae runs along the following lines: If a soil is low in nutrients, particularly nitrogen and phosphorus, it is likely that a mycorrhizal relationship will occur and a plant is more likely to allocate its carbon to roots (producing more root growth for foraging further afield in the soil, and/or carbohydrates for symbiotic mycorrhizae). Similarly, a plant should develop mycorrhizal associations in areas where there is a low water supply. In contrast, environments with ample nutrients and water should be less likely to favor a symbiotic relationship between plants and mycorrhizae, as the fungus would benefit more than the plant. In a sense this is widely demonstrated in agriculture where the application of luxury supplies of fertilizer and irrigation reduces the role and benefits of association with mycorrhizae, and the level of mycorrhizal infection drops correspondingly.

On the basis of this intuitive argument one might argue, then, that in the harsh desert environment plants would benefit from having mycorrhizal associates in order to capture more water and nutrients (but see later). Brundrett (2009) carried out a wide-ranging survey and analysis of mycorrhizal associations, focusing on why some species *lack* them. Non-mycorrhizal (NM) species are by far the minority of angiosperms (at about 6%). The obvious question to ask next is whether these species represent particular branches of plant evolution, . . . or live in particular habitats, . . . or have particular life history strategies?

It turns out that being NM is not a simple matter of phylogenetics. Brundrett reported that there are some 90 families of NM or flexible arbuscular mycorrhizal–NM plants scattered across at least 30 clades, with the NM strategy often arising more than once in some clades. It seems there have been multiple different reasons for "becoming" non-mycorrhizal. Generally mycorrhizae are dropped when other forms of nutrient uptake become more important. Examples include many or most of the "parasitic" plants, which attach to host plants via haustoria; also carnivorous plants that supplement their nitrogen supply by digesting animal protein, specialized hydrophytes (aquatic plants), and plants that produce various forms of root "clusters" (including dense tufts of long, thin root hairs) (Brundrett 2009).

It is interesting that of the 90 NM families listed by Brundrett, 12 occur in arid and arid-saline habitats. These include many families that are common in the Middle East, such as the Amaranthaceae, Chenopodiaceae, Cleomaceae, Frankeniaceae, Plumbaginaceae, Tamaricaceae, and Zygophyllaceae.

Selivanov and Eleusenova (1974, cited in Brundrett 2009) assessed some 234 desert plants in northern Kazakhstan and determined that a high proportion (35%) were NM. Families such as the Brassicaceae, Caryophyllaceae, Frankeniaceae, Juncaceae, and Polygonaceae were fully NM while the Chenopodiaceae, Cyperaceae, Plumbaginaceae, and Papaveraceae had mostly NM plants.

The arid zone succulent species in the Aizoaceae, Crassulaceae, Mesembranthaceae, Portulacaceae, and Molluginaceae have NM–AM or NM roots, but clearly there is no one unitary strategy among succulent species, as many other succulents—such as members of the Agavaceae, Cactaceae, and Euphorbiaceae—have AM roots (Bethlenfalvay et al. 1984; Camargo-Ricalde et al. 2003; Carrillo-Garcia et al. 1999).

Brundrett (2009) took a perspective shaped by studies in the ancient landscape and infertile soils of the Australian Western Desert. His view counters the "common wisdom" that plants lacking water and nutrients should have mycorrhizae, outlined earlier. Instead he argued that in arid habitats mycorrhizae may be less beneficial than elsewhere because plant productivity is very low and periods of root activity brief.

So what is happening in the case of Middle Eastern plants? This is an area that calls for concerted, rigorous study as very little indeed is known about the occurrence of NM and facultative mycorrhizal associations with plants in the region. It is possible that inoculation of areas with mycorrhizal spores could boost plant growth by making them more efficient at gathering sparse and sporadic supplies of nutrients and water; on the other hand it may make little difference. Further work could make a tremendous difference to primary productivity in the Middle East.

(with scaly micro-leaves) are common in temperate semi-deserts, and also form a huge steppe forest of open woodland in the cold semi-deserts of the Middle East (at elevations above 1000 m), as well as in Central Asia and North America (Shmida 1985).

Generally speaking, as conditions get drier the dominant plants become smaller. Dwarf shrubs (= suffrutescent chamaephytes), semi-shrubs, and low shrubs (chamaephytes and some nanophanerophytes) are the most *conspicuous* growth form in the arid environment (Shmida 1985). Under semi-arid conditions dominant shrub genera include *Artemisia, Atriplex, Cassia, Ephedra, Larrea*, and *Retama*.

In areas with < 120 mm annual rainfall (i.e., true and extreme deserts) dwarf-shrub communities predominate where vegetation occurs. These plants have a small, perennial arborescent form and each year part of their canopy is shed. Genera such as *Anabasis, Hammada, Salsola*, and *Suaeda* (all Chenopodiaceae), *Fagonia*, and *Zygophyllum* (Zygophyllaceae) are very abundant in the extreme deserts of the Middle East and elsewhere. *Astragalus* (Fabaceae) and Asteraceae (e.g., *Achillea, Anvillea, Anastatica*, and *Asteriscus*) are also important in the region.

Many of these drought- and salt-resistant species have Crassulacean Acid Metabolism (CAM photosynthesis; Section 5.5), or are physiologically flexible and able to switch to CAM. The ice plants and other specialists all successfully manage the suite of desert selection pressures . . . low and sporadic rainfall, intense solar irradiation, and high temperature, high salinity, and much windy sand-blasting. Low temperatures appear to limit the distribution of mesembs, but most of the other succulent lineages—certainly those from mountain regions in the Middle East—have become cold adapted, too.

The development of a large, central vacuole, capable of storing water and solutes, was an early and important event in the evolution of eukaryote plants, facilitating homeostasis and buffering the plant from an unpredictable external water supply (see Becker 2007; Larcher 2006). The cells of highly succulent tissues have taken this water-storing capacity to an extreme, developing greatly enlarged vacuoles that come to occupy 90% or more of the cell volume (Gibson 1982; von Willert et al. 1992). In many taxa, e.g., *Aloe vera*, extracellular mucilage (Nobel et al. 1992) or pectic compounds having a high affinity for water, provide additional capacity for water storage. Succulence at the cellular level typically "scales up" to a succulent appearance at the tissue, organ, or whole organism level, though this is not always the case.

Succulence, sclerophylly, metabolic flexibility and ways of dealing with excess salt are all parts of a successful suite of strategies allowing desert specialists to deal with uncertain water supplies and effects of high rates of evaporation in soils. Various life history strategies help the individual (and species) to "avoid" the worst effects of aridity. However, there are often distinctive demographic consequences for the different life forms (Section 5.9).

## 11.3 Biodiversity hotspots

The Middle East includes five of the 34 recognized global biodiversity hotspots (Mittermeier et al. 1999, 2004; Myers et al. 2000). Of course to "qualify" as a biodiversity hotspot a region must contain at least 1500 endemic species of vascular plants, and it needs to have already lost at least 70% of its original habitat. Such areas are often, not coincidentally, hotspots of human conflict (Hanson et al. 2009), which places additional pressures and constraints on conservation.

First, the arid and semi-arid "Horn of Africa," which include parts of Ethiopia, Eritrea, Somalia, Djibouti, southeast Sudan, and crosses the straits of Bab-el-Mandeb to the southwestern part of the Arabian Peninsula. Second, the "Eastern Afromontane" region, which includes chains of isolated mountains from Zimbabwe, Tanzania, Kenya, and Uganda, to Ethiopia and across to the southwestern Arabian mountains that run parallel to the coast of the Red Sea in Saudi Arabia and Yemen. The Arabian segments of these two hotspots are in fact contiguous and together represent the mountains and coastal regions of the southwestern and southern rim of the Arabian Peninsula. The combined area is sometimes referred to as the Arabian Hotspot area (e.g., see Mallon 2011).

A third hotspot is the Irano–Anatolian area, which represents a natural barrier between the Mediterranean basin and the dry plateaux of western Asia.

Much of this region is one enormous endorheic region, made up of many adjacent, closed drainage basins including the Caspian Sea and a large part of Eastern Europe (drained by the Volga River). Other salty basins include Lake Urmia in northwestern Iran (the largest lake in the Middle East and third largest salt water lake on Earth, with a surface area *c*. 5200 km$^2$); the Aral Sea; the Dead Sea (lowest surface point on Earth and one of its saltiest bodies); Lakes Van and Tuz, both in Turkey and both among the world's largest endorheic lakes; Sabkhat al-Jabbul's extensive salt flats, that include a 100 km$^2$ lake in Syria; and Solar Lake, Sinai, near the Israeli–Egyptian border.

Salt is obviously a major fact of life in many Middle Eastern regional habitats, the Irano–Anatolian hotspot in particular. In these endorheic basins evaporation exceeds precipitation; this creates large salty areas (*sabkhas*), where only salt-tolerant plants can survive. Table 11.1 summarizes many of the adaptive mechanisms that plants have evolved to cope with salinity stress.

**Table 11.1** Adaptive mechanisms of plants for coping with salinity stress (after Batanouny 2001, used with permission)

| |
|---|
| Avoidance mechanisms |
| Growth only during seasons of favorable low salinity |
| such plants have short life cycles |
| Growth only on favorable sites with low salinity |
| Limitation of root growth and absorption to distinct soil horizons |
| Evasion mechanisms |
| Selectivity against $Na^+$ and $Cl^-$ |
| Separation of salts from the assimilating tissue |
| Compartmentalization of salt within plant organs, tissues, and cells |
| Retranslocation of salts to roots and its excretion by the roots |
| Leaching of salt out of the shoot |
| Shedding of salt-loaded tissues and organs |
| Secretion of salts by salt glands or bladders |
| Production of adventitious roots and mound building |
| Tolerance mechanisms |
| Increasing the salt resistance of tissues, cells, and organelles |
| Production of protectants (proline and other organic metabolites) |
| Osmotic adjustment |
| Ion-specific adaptation of the cytoplasm |
| Increase of halo-succulence; leaf and stem succulence |

Water-storing succulents make up much of the vegetation, along with various other halophytes. All of these plants have evolved to live with salt through elaborate processes of excretion, accumulation, and dilution. For example, many species of *Aeluropus, Limoniastrum, Sporobolus*, and *Tamarix* excrete salt crystals extra-cellularly. A smaller group of water-storing succulents, like *Arthrocnemum macrostachyum, Halocnemum strobilaceum, Zygophyllum album*, and *Suaeda* species deal with it more metabolically, including simply diluting the salt by storing more water in their tissues. There are also important biochemical and metabolic associations between coping with drought, and the particular photosynthetic pathway used by a plant (C3, C4, or Crassulacean acid metabolism, and combinations of these systems).

The other two major hotspots are the Eastern Mediterranean basin, or Levant, and the Caucasus region. Even taken together these five variously assembled biodiversity hotspots do not adequately characterize the complexity of the conservation challenges facing the nations of the Middle East. For one thing, it is arguable that deserts exist as so-called coldspots (see Kareiva and Marvier 2003) of global biodiversity, as they are biomes where the species list may not be long enough to "qualify," but nevertheless important endemics, rare communities, and ecological functional groups exist there.

Deserts and other species-poor biomes—including all the polar tundra—clearly do support abundant endemic species and unique communities. They do not fit in the traditional hotspot category because of their low biodiversity and the fact that they may not show severe habitat loss. However, they may well have suffered habitat degradation and other indirect effects of human activities. This is especially true in Arabia, as arid, semi-arid, and hyper-arid deserts cover much of the Peninsula. Characteristic regional habitats such as sand dunes and sabkhas are underrepresented or even unrecognized in the Arabian Hotspot area (Mallon 2011).

Mountain ranges provide important opportunities for processes such as speciation resulting from reproductive isolation, which in turn generates

more endemism, etc. In the Caucasus, for example, extensive mountainous barriers have helped maintain a warm and humid climate that has been fairly consistent since the late Tertiary. This is why the Caucasus has been able to serve as a shelter for humid- and warm-requiring relicts during the previous ice ages (Miller 1994b). As a result, some of these and the Colchic and Hyrcan forests of Iran and Azerbaijan are the most diverse in terms of relictual and endemic woody species and tree diversity, and also the most "natural" (in terms of least amount of inferred change from its historic structure). They are the oldest forests in Western Eurasia in terms of their origins and evolutionary history.

## 11.4 Desert selections: cooperation and plants helping plants, dispersal and "bet-hedging" strategies, and absent tree regeneration

Plant competition in deserts would seem to be quite secondary to their struggle for existence in the harsh and unpredictable physical environment (e.g., Noy-Meir 1979). For a plant, life consists of typically very low and highly sporadic rainfall, and usually very intense solar irradiation and high daytime temperatures; there is often very high salinity, poor soil, and a need to tolerate a great deal of sandy wind-blasting. It is a very high stakes poker game where the antes are high, the bets are no-limit, it is outdoors in the baking sun, and very few snacks and drinks are provided. Yet, as indicated, these desert pressures have selected for many resilient players that are members of a variety of plant lineages.

In terms of the several kinds of ecological interactions possible between and among living organisms, plants in desert habitats are found frequently to be acting *facilitatively*. The dominant shrubs in these Arabian desert communities often effectively modify the habitat for annual plants, primarily through soil-stabilizing effects, but also by creating a dome of enhanced humidity, a moister microclimate under their canopy. According to many authors annual species often congregate around and under woody plants, simply because these readily trap wind-driven seeds and propagules, collect rain, and provide shelter from the wind and direct sunlight (e.g., Hunter and Aarssen 1988; and see Sections 1.7 and 4.7). If the beneficiary of facilitation were a perennial plant that continued to grow and ultimately compete with the "facilitator," the interaction will transition to a simple competitive interaction (-/-).

There are numerous examples of inter-specific facilitative interactions in desert organisms, whereby one species provides a protected and often moist microhabitat enabling germination and regeneration of another species. Such examples occur with high frequency in arid lands (Section 4.7). This happens in the Middle East just as it does in the Sonoran and deserts elsewhere and is well exemplified by species of long-lived trees such as ironwood (*Olneya tesota*), palo verde (*Cercidium* spp.), and mesquite (*Prosopis* spp.), as well as *Acacia* species and *Ochradenus* and other Middle Eastern cases.

We have shown how in dryland systems plants may often facilitate neighbors in various ways, for example by acting as a surface for nocturnal condensation and increasing water infiltration while competing for water with distant individuals. Overall, this tends to produce a characteristic, large-scale, and spatially periodic "clustering" in vegetation. We find this in the phytogenic hillocks, or nabkhas, for example, as well as in mangrove systems, and in African savanna and grassland systems. Vegetation patterns such as these have been usefully described using models of scale-dependent feedback, coupling short-range activation with long-range inhibition. Thus, for example, vegetation in a dry place will tend to arrange itself in fairly regularly spaced clumps, rather than forming a uniform lawn as may happen in wetter places.

Because each plant's roots modify the soil to help concentrate water and slow its loss, plants in dry places "prefer" to grow close to other plants—or more accurately they survive better when they are close to other plants. There are many benefits. Emergent clumps may have extensive lateral root systems that sequester water from more distant surrounding soil, making the space in between more inhospitable to plants. This in addition to the benefits just covered, such as physical protection and microclimate enhancement as well as ducting of condensed water and nutrient resources as organic matter accumulates. Nevertheless, as the

environment dries through increasingly erratic and low rainfall, the space between clumps should expand. As a result, in a savanna or grassland, when water becomes *too* low, there can be an essentially irreversible shift in vegetation, overall, back to desert.

The extent of association between annual species and woody shrubs/trees in semi-arid and arid areas depends, ultimately, on the balance between various negative and positive effects on these contrasting plant life forms. The balance will range between the effects of interference and facilitation, an interplay of costs and benefits that has become an important theme in community ecology (e.g., Bruno et al. 2003). Various workers have predicted that positive interactions among plants will be stronger in more stressful sites, while negative interactions, or interference and competition, will dominate in less stressful situations (Bertness and Callaway 1994; Callaway and Walker 1997).

Nabkhas represent significant ecological opportunity for these complex interspecific interactions. They are islands of organic matter in an otherwise infertile sea, representing pockets of potential resources for many lowland desert species. These in turn influence longer-term, local vegetation dynamics and ecosystem processes (Danin 1996) (and see Section 2.19). El-Bana et al. (2002, 2003) and Quets et al. (2013) showed how particular host species—including *Nitraria retusa, Zygophyllum qatarense, Haloxylon salicornicum*, and *Panicum turgidum* are all especially adept at forming nabkhas because of their ability to produce *adventitious* roots from buried vegetative organs, letting new shoots replace those buried by accumulating sand. They also possess a highly branched shoot system. *Haloxylon salicornicum* is so effective at recovering from sand burial and providing microhabitat for other species that Brown and Porembski (2000) described them as "ecosystem engineers."

Nabkha plants create, modify, and maintain desert micro-habitats by improving and conserving soil water and nutrients in the patches where they are growing; they also promote biodiversity (El-Bana et al. 2002; Lawton, 1994). In essence they are fertile microhabitats created by certain host plants enabling many other plants to persist there too. Nabkhas influence not only the community dynamics and survival of species but also prevent soil degradation and erosion (Danin 1996). Brown and Porembski showed that nabkhas also provide elevated "safe sites" for plants in the oil-contaminated areas of northern Kuwait where oil spills accumulate and are most concentrated in the depressions between nabkhas.

In contrast to the larger (>1 m high), more stable dunes formed around perennials such as *Nitraria retusa* (Brown 2003)—many smaller, less stratified, and less nutrient-rich "micro-nabkhas" also exist. An array of similar communities characterize the desert plain that occupies most of Kuwait (Figure 2.19). Elsewhere, date palm trees (*Phoenix dactylifera*) also appear to act like giant nabkhas. Date palms are typically restricted to sites with a high water table and are often associated with *Nitraria retusa, Juncus arabicus, Phragmites australis*, and *Cressa cretic*a.

We have noted that many of the adult perennials present in populations today germinated hundreds of years ago. Since then the human population has grown, demanding an ever-increasing "share" of space and resources. It is becoming clear the entire region is losing its "regeneration niche." That is, many populations of numerous tree species—often climate relicts—are made up of mostly *older* individuals. The once abundant juvenile stages, growing their way up through the ranks, are simply absent. As a result the populations have a highly unstable age- and size-structure, and when these older individuals senesce and die, they will not be replaced.

With regard to these populations of aging trees, the world into which they germinated long ago has changed dramatically. We see tragic evidence of this in the elderly stands of Socotran dragon's-blood trees, and in populations of *Moringa peregrina* in Egypt, Saudi Arabia, and the Emirates, the Bankoualé Palm, *Livistona carinensis* in Djibouti and Yemen, Phoenician Junipers (*Juniperus phoenicea*) and the endemic shrub *Arbutus pavarii* in the coastal mountains of Libya, and many others. It is important not to be lulled into complacency simply because stands of these species may still exist. We need to look at population age structure in more species and assess whether the age structure is stable, showing successful juvenile recruitment.

A short-term solution may be to establish seedling nurseries from which to re-stock natural populations, but the absence of intermediate age classes as well as juveniles suggests this problem has existed for a long time, so at a minimum fairly large, well-developed transplants may be necessary, and the challenges of survival in situ and re-establishing self-sustaining populations may be insurmountable.

Populations of the Bankoualé Palm, *Livistona carinensis*, are also clearly "over-mature," consisting of adults and older individuals but few young trees and rosettes, although many plants continue to flower and set fruit. This is reminiscent of the Socotran *Dracaena cinnabari* and many other ancient Middle Eastern tree species. Some of the demographic variation in *L. carinensis* may be due to differences in the timing of observations, as it is clear seedlings and other juvenile stages are highly vulnerable to grazing and may be missed altogether by field researchers. This susceptibility of seedlings to grazing may account for the frequent association of *L. carinensis* with *Phoenix reclinata*, as this latter palm forms fairly dense thickets, often impenetrable to the dominant grazers—fat-tailed sheep, goats, cattle, camels, and donkeys. As a result, *P. reclinata* may be credited with providing shelter for *L. carinensis* seedlings from herbivores, especially during susceptible, early stages of growth.

The parameters of the regeneration niche are probably more relevant for assessing the *long-term* viability of populations living at the edge of their climatic tolerance, than are the niche requirements of current adult individuals (e.g., Jackson et al. 2009). This argues for the importance of looking at the age structure of relict populations in general, and in particular assessing whether the age structure is stable, with successful juvenile recruitment, in order to evaluate the potential of any given population for long-term sustainability.

In the uncertain dryness of a desert the overriding importance of the *timing* of major life-events in relation to highly unpredictable externalities like moisture availability or rainfall is obvious—along with selection for ecological *opportunism*. Thus, for example, there has been strong selection for flexibility in the timing of seed germination, a certain agility in terms of life history, and the temporal safety of seed dormancy. Many studies have shown the benefits of an evolutionary "bet hedging" strategy favoring seed dormancy. Several different kinds of seed dormancy and physiological triggers for seed germination exist; however, this great diversity falls into a fairly ordered set of patterns (see Chapter 7).

Ellner and Shmida (1981) take the "pause" of dormancy a step further back, strategically, interpreting adaptations that act to *hinder* dispersal (technically "anti-telechory")—as one part of a complex portfolio of traits for individual plant success in the desert. The syndrome—essentially, "it may be better to move in time than space"—is related to both dispersal *and* germination control and functions to regulate the timing of seed dispersal and germination within a given year, *and* to spread germination of one year's seed cohort over several years. This desert strategy, too, has been usefully regarded as a kind of evolutionary "bet-hedging" for progeny, following the death of the mother plant.

In the evolutionary balancing act involving transpiration and photosynthesis, molecules of water lost by the plant may be offset against other molecular currencies (for instance, carbon dioxide gas units gained). Collectively these act as the limiting factors behind environmental selection pressures. There is always a delicate balance between adaptations that facilitate nutrient and water uptake, and photosynthesis, which requires access to atmospheric $CO_2$ and water. Careful comparisons have illustrated this balance in many different situations. It has even been shown to drive aspects of sexual specialization, including the rather different cost-benefit "decisions" that distinguish male and female reproductive physiology.

Reproductively, Middle Eastern plants show an impressive array of evolved structures and behaviors that all facilitate production and establishment of progeny. Dioecy (complete separation of the sexes as male and female individuals) is rare in the desert, though floral unisexuality (separating regions of production of male and female flowers on the same plant) and sequential hermaphroditism or monoecy is not uncommon (where individuals reproduce first as males and later, when they are larger and have more resources, as females).

It is interesting that Raunkiaer life forms are still used extensively by plant ecologists in the Middle East, though both Zohary (1962) and Kassas (1966)

early on argued they were of limited utility as a basis for the description of vegetation or analysis in arid regions. Raunkiaer's life forms were initially designed to characterize the strategies plants used in cold temperate regions to survive the adverse season of winter. However, when one considers the period of most extreme drought as the adverse season in deserts, the life form categories are useful as they describe the various resting bud positions seen in desert perennials. This can be related to certain facultative responses such as forming smaller leaves at some times of year (microphylly), and complete leaf shedding. A Raunkiaer-based life form summary can be informative as a starting point for plant description. However, further investigation of population ecology is needed, along with identification of the potential drivers of population and community change. Characterization of population age and size structure, and tracking of individuals and their individual progeny fates, would be the most useful focus at this point.

## 11.5 Global climate change and possible shifts in vegetation

Physically and climatically this vast region is mostly desert,[2] and fast becoming more so as a consequence of global climate change in conjunction with increasingly intense human activities (Chapters 3, 9, and 10). Still despite—or perhaps *because*—of the history of the place, many plants in this dryland region continue to adapt, and certainly their evolutionary ecology continues to fascinate. They are plant water resource conservationists par excellence.

According to Tolba (1997) global dryland—including arid, semi-arid, and dry sub-humid areas—is vast, covering nearly half the land surface of the Earth (and some 62% of the world's irrigated land, 36% of rain-fed cropland, and 68% of rangelands). Land degradation, caused mainly by human activities in any of these areas, is known as *desertification*. Chapter 10 considers the array of factors *accelerating* desertification in the Middle East, including global climate change. Desertification due to climate warming is an ongoing challenge in the region. This is doubly a problem in that many additional drivers are also ongoing and intense. These anthropogenic effects include extensive overgrazing by domestic livestock, general agricultural intensification, surface water diversion, and the "overmining" of groundwater—that is the extraction of artesian and other groundwater reserves at rates that are not matched by the rate of replenishment.

Because semi-arid and Mediterranean ecosystems are so highly water-limited and also under such intense pressure, many theoretical studies have regarded them as among the *most* vulnerable to global climate change (e.g., Loarie et al., 2009; Sala et al. 2000) although empirical evidence for the proposition is scarce. "Long term" experiments (>5 years) manipulating precipitation in drylands are rare, and when they have been carried out they usually characterize a single site which limits the generalizations that can be drawn from the study. Moreover, such studies when examining multiple-year effects mostly only investigate perennial species. This may not be very informative as perennials are less likely to respond within a short time period; by definition they are already "amortizing" their resources over an extended lifespan.

Tielborger et al. (2014) recently used a multi-site approach across Israel to test experimentally the major prediction of popular "non-mechanistic" models—i.e., bioclimatic envelope models (e.g., Bellard et al. 2012)—which map future ecosystem properties onto their current climatic niche. These models typically assume that community shifts are largely a consequence of the migration of species—moving to "catch up" to their climatic niche—but studies often tend to assume unrealistically high dispersal abilities for the plants. The question remains whether in situ decreasing precipitation leads to an in situ increase in dry adapted species.

Over a period of nine years Tielborger et al. (2014) examined the prediction that there would be a changed community structure in terms of resident annual plant species. Water availability was modified experimentally through providing irrigation and imposing drought on dryland communities situated along a steep climatic gradient. Four sites in Israel, sharing many environmental characteristics but with an eight-fold difference in

[2] But of course not *all* of it is so dry. Consider the great Sudd region of southern Sudan, a hot, perspiring wetland which is as big as the United Kingdom of Great Britain (Section 2.8.1).

annual rainfall between the driest and wettest sites, were located in arid, semi-arid, Mediterranean, and mesic-Mediterranean climates. Rainfall was experimentally reduced or supplemented by 30% in semi-arid and Mediterranean sites using rainout shelters (clear structures that allow light penetration but reduce rainfall) and irrigation systems, respectively. Community response was monitored annually in both open areas and areas underneath targeted shrubs. Moreover the authors compared treatment responses to two different sets of controls, in situ control plots and regional control sites with rainfall similar to the manipulations. This enabled tests of predictions of correlative models based on geographic gradients, as well as generating mechanistic response data for communities and comparisons within sites.

The approach (multi-year experimental manipulation at multiple sites) is rooted in an assumption that under climate change the structure and function of plant communities—i.e., the community ecology taking place in a particular location—will move away from the currently no-longer-suitable site toward those locations that offer more suitable climatic conditions to which they are better adapted.

Despite the considerable scope of the study by Tielborger et al., spanning nine plant generations and including many different species, very few differences between treatments were observed in terms of variables related to the response of vegetation to different moisture availability. That is there were few differences in terms of biomass, species composition, species richness, and density. There was no response in terms of overall species composition, and only three significant changes were observed among some 36 pairwise comparisons of community structure. Those were a significant increase in biomass under irrigation; a subtle increase in species richness; and a decrease in plant density under drought. Tielborger et al. concluded the Mediterranean and semi-arid annual communities they investigated would actually be relatively *little* affected by future climate change, at least in the short-to-medium term.

The absence of any clear drought effect in this experiment challenges the widespread assumption that dryland systems will be most vulnerable to global climate change. Tielborger et al. attributed this resistance (the property of communities to remain essentially unchanged when subjected to "disturbance") to the tremendous temporal and spatial heterogeneity of the habitats themselves in which the plants evolved. Also, only annual species were considered; these were species that had successfully evolved the annual habit, with its many advantages in terms of opportunism and flexibility of response that have proved so valuable in the desert. A combination of adaptations to climatic variation in subtropical drylands may delay species responses to climate change, at least among the annuals and short-lived ephemerals. The pre-existing high drought resistance and significant phenotypic plasticity enable reproduction in annuals even under conditions of limited rainfall (e.g., Petru et al. 2006). Moreover various "bet-hedging" mechanisms, in particular patterns of seed dormancy and persistent seed banks, act highly effectively to buffer catastrophic years and detrimental effects of environmental variation on population growth, at least for a time (see Sections 6.4, 7.2, and 7.3).

Tielborger et al. (2014) pointed out that the species they studied included some that have clear risk-spreading strategies, such as large seed size, promoting higher seedling survival despite strong environmental selection pressures. Large-seeded species were described as abundant in their study system; indeed several of these—such as wild barley, oats, and chickpea—are progenitors of important modern crops.

In models of scale-dependent feedback in dryland systems, reducing rainfall produces a predictable sequence of patterns—decreasing overall biomass, over-dispersed gaps in vegetation, more "spotty" plant distribution and, finally, transitions from savanna and grassland to barren desert. This last transition is known as a "catastrophic shift," or sudden collapse to an unvegetated state (Rietkerk et al. 2004).

The relative resistance of drylands to such catastrophic shifts is an urgent matter, given that drylands cover so much of Earth's land surface and are home to >38% of the human population (Reynolds et al. 2007), combined with the increased frequency and intensity of drought predicted under climate change (Diffenbaugh and Field 2013). Increasingly

"spotty" vegetation patterns in savanna and grasslands are often a warning sign of imminent desertification. It should be noted, however, that other influences, such as the presence of termites, can also produce increased "spottiness" and other overdispersed patterns in dryland vegetation. In other words, the presence of spotty vegetation, per se, is not sufficient to infer desertification is intensifying, as several biotic patterns such as facilitation and substrate heterogeneity due to structures like termite mounds, can generate patchy vegetation.

## 11.6 "Keystone" species as a source of stability and ecological resistance

Termite mounds play a key role in arid landscapes, especially in Africa. Like the Arabian nabkhas, these create nutrient islands that sustain many different plants and animals besides the termites themselves. In the savannas of Africa, associated animals include zebra, buffalo, eland, and other large herbivores. Foraging termites actively concentrate plant material in mounds where fungi process it, releasing nitrogen, phosphorus, and essential minerals, which in turn foster more plant and animal growth.[3] Mounds also retain water better than the surrounding soil (Bonachela et al. 2015).

In many arid ecosystems termite nests amplify substrate heterogeneity by altering soil properties, thereby enhancing plant growth. Bonachela et al. (2015) recently showed in a theoretical study, confirmed by field data from Kenya, that termite-induced heterogeneity interacts with scale-dependent feedbacks to produce discernible vegetation patterns at different spatial scales. Although the coarse-grained patterning they observed does resemble that created by scale-dependent feedback alone, Bonachela et al. concluded that for their study location in Kenya the patterns did not indicate imminent desertification.

Rather, they showed that mound-field landscapes were significantly more *robust* (i.e., more ecologically resistant) to aridity, suggesting that termites in the long run may help to stabilize dryland ecosystems in the face of global change. By creating refugia for plants and nuclei for revegetation, the termites enhance dryland resistance to, and recovery from, environmental drought. By such soil stabilization, termites and other such "ecosystem engineers" may buffer the effects of anthropogenic global change in some of the most environmentally sensitive regions (Bonachela et al. 2015).

It is clear *frugivory* plays an important role in the ecology of deserts, helping generate contagious spatial structure, a phenomenon that is frequently observed in populations of fleshy-fruited species. Bronstein et al. (2007) suggest this effect in fleshy-fruited species may itself be part of a larger, emergent property of dryland systems, exerting a strong influence on frugivore behavior, and creating positive feedbacks through resource-aggregating effects. Bronstein et al. suggest that, at least in desert environments, the few, highly abundant fleshy-fruited species—such as *Ochradenus baccatus*—should also be regarded as "keystone" species, and are therefore particularly urgent, individual targets for conservation.

Another keystone group are the Acacias (Sections 6.8 and 7.8.1); these trees often have specialized seed adaptations for dispersal by birds and ants (O'Dowd and Gill 1986), though passive dispersal by water and wind is also common. Biotic dispersal falls into two broad categories based on whether seeds have arils (edible outgrowths at the funiculus, the attachment site of the seed) or *elaiosomes* (fleshy structures at the seed attachment that are rich in lipids and proteins). Arillate appendages in the bird-dispersed seeds, and an elaiosome in ant-dispersed seeds, attach the seed to the lining of the seed pod and make them attractive to various bird and ant species respectively.

Typically ants remove and fairly rapidly bury *Acacia* seeds with their elaiosomes in underground nests, and so transport them on a local scale. Gibson et al. (2011) noted that species described as having a "bird-dispersal syndrome" are often likely to be also dispersed vertically by ants, as myrmecochory, or seed dispersal by ants occurs even when elaiosomes are absent and accounts for much of the movement of seeds from the litter layer into the deeper seed bank.

[3] "Harvester termites" retrieve vegetation from the local environment and use it to fertilize "gardens" of microbes and fungi in the mound, concentrating nitrogen, phosphorus, and organic matter around the mound.

Ants appear to be the main drivers of the maintenance and persistence of *Acacia* seed banks; gravity and water play a role when ants are absent. Once seeds have dropped to the ground, ants bury many of them in their nests while they exploit the elaiosome (Milton and Hall 1981). Such seeds benefit from protection from above-ground seed predators and also from fire, besides being moved into the substrate in a location that is locally enriched in terms of nutrients and organic matter within the underground nest (Holmes 1990).

In considering the keystone roles of ants and acacias in allowing the growth of "islands" of vegetation, Rohner and Ward (1999) predicted that the loss of Acacia trees in the Middle East would lead to a significant loss of biodiversity in the region. They also pointed out that large mammalian herbivores are essential components of arid Acacia savannas and that wild and domestic ungulates should be included in conservation plans.

## 11.7 Overgrazing and the acceleration of desertification

Throughout the Middle East there is extensive overgrazing by livestock, and many of the ecosystems are clearly experiencing ongoing desertification. Grassland and savanna have farther to go to reach desert than many other semi-arid and aridland communities; however, overgrazing is a constant challenge.

In the midlands of Socotra are the mountain cliff regions with fog- and mist-trapping microhabitats. There frankincense trees *are* able to regenerate, probably because, like the *Dracaena* on these cliffs, they are protected from goat grazing as much as they are protected from drought. These protected mountain cliff sites—like others everywhere: Israel, Turkey, Iran, Oman, and elsewhere—have continued to serve as refugia during times of aridification up to the present.

As the weather has gradually changed to its presently hotter, drier conditions, Mediterranean plant communities have become more restricted to areas that were more suitable. Such ecological refugia of cooler, moister conditions were typically at higher elevations, usually separated by warmer, drier valleys. The gaps between such refugia are becoming larger. Today many Mediterranean genera such as honeysuckle and pistacia are no longer found in the hotter, drier lowlands—between Taif, in Saudi Arabia, and Israel for example. Similarly the Arabian juniper *Juniperus procera* now has distinct, reproductively isolated regional populations—for example in the 'Asir Highands of Saudi Arabia, in the highlands of northern Oman, and in the mountains of Somalia and Ethiopia.

The ameliorating effects of oceans and seas are especially evident in the 'Asir, as the highland juniper forest is rarely more than a few km wide at any point in Saudi Arabia, nor is it ever far from the sea. In the 'Asir it is supported by a long summer rainy season. Moisture-laden southwesterly winds, sweeping in from the Red Sea, produce orographic rain as they meet the steep escarpment. Thunderclouds formed during April and May result in occasional intense storms. Although some rain percolates into the rocky terrain, most runs off as flash flood events. Fortunately, significant government conservation initiatives and interventions are protecting this unique forest ecosystem before complete degradation takes place. The 'Asir National Park near Abha, in Saudi Arabia, preserves some of the finest stands of juniper (and once had some of the last remaining Arabian leopards).

## 11.8 Priorities and areas for further research

Many areas are underworked in the region and need attention. Some is urgent given the ongoing, often extensive loss of habitat. Kassas (2002) reviewed the literature and suggested seven broad foci needed for a fuller understanding of the plant ecology of the region as a whole. Thus he urged the following as priority challenges.

1. First of all any "Vulnerable" species (*sensu* IUCN Red List), which are at risk of extinction in the wild (see Box 10.3).
2. The relatively small number of ecologically highly significant "keystone" species, upon which much community diversity and ecosystem stability depends.

3. Regionally representative, classic Middle Eastern "umbrella" species, which cover large areas and have a wide range of distribution.
4. The small number of regionally iconic "flagship" species, which have disproportionately valuable socioeconomic and charismatic value.
5. Any ecological "indicator" species, which act as signals of major anthropogenic effects.
6. "Endemic" species –a rough estimate suggests there are at least some 8800 endemic species in the Middle East, yet we know the ecological details of only a relative few.
7. Research about "wild plant crop relatives" will expand the applications of plant ecology into the development of genetically selected and/or modified crops for food, fodder, and medicine.

From a practical point of view, a working flora that brings together the species of the entire Middle Eastern region is urgently needed. Collaborative effort is required, possibly building upon the already excellent flora of Israel. An up-to-date, integrated electronic flora embracing all the countries included here would be a very valuable resource, serving as a foundation for more detailed studies. We would advocate a modern approach that includes, or is followed up by, genetic surveys as well as field identification in order to quantify the endemism and clarify the degree to which regional populations represent distinct varieties or species.

The region contains fascinating disjunct distributions of e.g., *Euphorbia* and *Dracaena* species involving Macaronesian, Socotran, Arabian, and African locations. These should be special priorities for further study. Mies (1998) for example speculates that because there are so many relict species in the Atlantic region with a probable eastern origin, there may have existed a "southern Tethys trail" or dispersal corridor along the shores of the ancient Tethys Ocean for these species (Figure 7.6). Many Socotran and Macaronesian species occur, either in South Africa or along the East African rift valley and mountain-range system. Mies has proposed that previous connecting sites linking the eastern and western islands of Africa, presumably along the shores of the former Tethys Ocean, have been lost.

Recent Holocene relicts are often found in small, environmentally uniform areas such as mires, talus slopes, or canyons. In contrast those that have survived at least one complete glacial oscillation essentially in situ—sometimes referred to as pre-Last-Glacial-Maximum (pre-LGM) relicts—are almost exclusively found in patchy, heterogeneous landscapes that allow persistence under very different regional climates (Hampe and Jump 2011). Pre-LGM relicts have survived through changes in altitude, or slope orientation, etc., and it is unclear the extent to which the success of these species should be attributed to having broader ecological tolerance (i.e., sufficient phenotypic plasticity to allow acclimation), and/or some greater genetic capacity to evolve and adapt to the new conditions. Further work testing phenotypic plasticity using clonal ramets and comparing genetic individuals or genets, and using transplants and "replants" would be useful (see Lovett-Doust 1981b).

Freckleton and Watkinson (2002) have shown that, at the regional scale, some species do appear to exist as metapopulations (in the classic sense), where regional persistence is governed by the recursive processes of patch colonization, extinction, and recolonization by external "source" populations. However, many other species exist as *regional ensembles*, or systems of essentially unconnected local populations, persisting in an ill-defined mosaic of suitable and unsuitable habitat patches, as for example the tree *Moringa peregrina* (Hegazy et al. 2008a). Still other species exist as spatially extensive populations, essentially a single, large population occupying large tracts of suitable habitat, but whose regional dynamics represent simple extensions of local dynamics. Many desert perennials—including the various saltbushes—appear to fit this category and merit further study in this larger, landscape ecological regard.

## 11.9 Ongoing challenges

As of 2007, most of the countries of this region are either "water stressed" or already further along the pathway to aridity and suffering from "water scarcity" (Chapter 10). Assuming a relatively stable water supply, and based on human population projections, by 2025 most countries will be suffering extreme shortages. The region is characterized by high population growth rates, an inadequate

food supply, large income gaps within and between countries, and limited arable land and water resources. Most of the region, at least the parts where 60–70% of the population lives, falls within the arid to semi-arid rainfall zones. According to Table 10.3, ten of the 17 countries listed will have less, and often *much* less than 500 $m^3$ of water per person per year by 2025 (Shetty 2006; Yetim 2003; Yoffe et al. 2003). This extreme scarcity of a reliable freshwater supply is going to need greater collective attention.

The waters of the Arabian Gulf, in the middle of the Middle East, exist ecologically as a nearly land-locked "sink" environment, rather than a gateway or portal to the Indian Ocean. In particular, the high rate of evaporation and low discharge of rivers into the Gulf make the net flow across the Strait of Hormuz a distinctly *westward* flow, into the Gulf. This produces an inverse estuarine circulation and an overall counterclockwise circulation in the Gulf where surface waters flow *into* the Gulf in the northern part of the Strait of Hormuz as a wedge of less saline water from the Gulf of Oman entering at the surface. This later penetrates deeper into the Gulf along the Iranian coast. This water warms and increases in salinity and exits the Arabian Gulf at depth, through the Strait of Hormuz. The net flow in is problematic, given the input of pollutants from coastal communities. In addition, since the vast petroleum resources of the region are shipped mostly through and around the Gulf, there are serious risks of leakage and oil spills, in addition to the extensive pollution that has followed regional warfare.

The Gulf is home to a major fishery, which benefits from the coral encrustations on the pre-Pleistocene limestone deposits there, supporting rich communities of commercial fisheries. According to Sale et al. (2011) these fisheries represent the second most important natural resource in the region after oil. Unfortunately the coral communities, reef resources, and their rich biota are being degraded and lost to shoreline mega-developments. Another large development is an Egyptian project involving a nearly complete side-by-side doubling of the Suez Canal, which is in early stages; it will be important to monitor and track the consequences of this major change at the northern end of the Red Sea . . .

In his "Essay on the Customs and Character of Nations," Voltaire identified a moment around 1650 as a particular high point of political unrest in the world,[4] amounting to a "perfect storm" that fueled the French and arguably the American revolutions. A case can be made that Middle Eastern instability is now at an all-time high. Many countries in the region are young, while some of the local cultures are very old. Many national borders are artifacts of colonialism, breaking up ancient cultures in an arbitrary and destructive manner. Some of these new nations have, in turn, often endured a subsequent despotism and/or "benevolent" dictatorship. A gulf exists in the region between rulers and ruled, with a succession of popular revolts toppling leaders and often ending in conflict and further turmoil. Iraq and Syria remain unstable, especially in regard to the future of Kurdish people and their land. Libya, Sudan, Somalia, and Yemen are all under severe stress as nation states. The ingrained regional tribalism and the emergence of jihadism suggests further uncertainty and regional instability. All of this in turn makes it all the more challenging to do something that is at the same time as mundane, and as critical for the future of the region, as to survey and monitor the surviving plant life of the region.

## 11.10 Summary

In the uncertain dryness of this desert region only a special subset of plants has survived. Moreover the over-riding importance of the *timing* of major life-events in relation to highly unpredictable moisture availability is obvious—along with selection for ecological *opportunism*. Thus there has been strong selection for flexibility in the timing of seed germination, a certain agility in terms of life history, and the temporal safety of seed dormancy.

The chapter describes how in dryland systems plants *facilitate* neighbors in various ways. Overall this tends to produce a characteristic, large-scale "clustering" in vegetation. Various "keystone"

[4] The phenomenon of so many contemporaneous revolutions for Voltaire included the deposition of the Ottoman Sultan Ibrahim, the destabilizing of the Holy Roman Emperor, the flight of the young Louis XIV from Paris in the face of popular revolt, and others (see e.g., Parrott 2015).

species are highlighted as major sources of stability and ecological facilitation (e.g., fleshy-fruited shrubs like *Ochradenus baccatus*, various Acacias, and a number of species forming nabkhas). At the same time, many populations of numerous tree species—often climate relicts—have lost their regeneration niche and consist of mostly *older* adult individuals. The once-abundant juvenile stages are missing and populations are doomed to extinction.

Climate change and desertification influence plant ecology in terms of growing seasons, the use of marginal lands, crop yields, and agricultural diversity. Drought fosters food instability and famine; banditry and civil war can sometimes follow. Much work remains, including basic sampling and demographic study. What better collective goal for the people of the Middle East than to restore the promise of the Promised Land?

APPENDIX 1

# What's in a (plant) name?

It is well known that in the Linnaean system of Latinized binomials, the genus—or generic—name of a species gets further refined and delimited at the level of species, often using some appropriately inflected adjective. In linguistics, "declension" involves the grammatical inflection of nouns and pronouns and the adjectives that describe them, to indicate number (singular or plural), gender, and case (nominative, genitive, dative, accusative, vocative, and ablative). A Latin noun belongs to one of five declensions, each with distinctive endings for each case.[1]

In terms of the specifics of a name, most often the second part—or *species epithet*—of the binomial is an adjective, and so must agree in gender and number with the noun that names the genus. Sometimes commemorative credit goes to the person who found the species, often some far-traveled field botanist. In such cases the species name is usually a second noun, used in the genitive, or *possessive* case (the species *of* so-and-so). The genitive case may also be used to indicate *where* a plant came from, or the kind of habitat it lives in (*of* such-and-such a place). In other cases the second name is simply another noun, but this time used in the nominative case, in apposition to the genus name. That second noun may happen to be of a different gender from the first . . . but two *nouns* need not necessarily agree, when they are both sitting in apposition! So we see names like *Lythrum salicaria*, the purple loosestrife or "Lythrum that looks like a willow," where the endings of the genus and species name are different; all the more intriguing from a gender perspective since there are three distinct floral morphs in this tristylous species!

This all begins to beg the question: Who decided anyway that a particular plant species should be considered masculine, feminine, or indeed neuter? After all, all *plantae* at the Kingdom level at least, are plural and feminine!

[1] Old Latin teachers never die, they just decline . . .

## 1 Many names reflect their most prominent feature

In the Middle East whole plant families, a great many genera, and a host of individual species have been named for their tolerance of salt, in a world where salt build-up on land is a frequent fact of life. This is especially true where temperatures get very high, rainfall is sparse, and surface drainage is low. A small number of flowering plants live in the sea. In all of these plants their taste for salt is flagged with the prefix "halo-" (Greek for salt) or "hali-" at the beginning of their family, genus, or species name. Consider the following "salt lovers": The Haloragaceae; *Halocnemum* spp.; *Halopeplis* spp.; *Haloxylon* spp.; *Halimione* spp.; *Halopyrum* spp.; *Halophila* spp.; *Halogeton* spp.; *Halodule* spp.; *Atriplex halimus*, *Lotus halophilus*, etc.

Many plant species names signal their bearers' sharp and prickly defenses against animal herbivores—the grazers and browsers that can seriously cut into a plant's biomass and reproduction. Consider *Echinops spinosissimus*. This species is not simply "regular" spiny, but spiny expressed to the superlative degree—the *most* spiny of the spiny globe thistles! Or *Ziziphus spina-christi* (the Christ's thorn jujube, alluding to the story of its prickly stems being woven into the famous "crown of thorns"). There is also *Astragalus spinosus, Capparis spinosa, Salsola spinescens, Zilla spinosa, Sarcopoterium spinosum, Emex spinosa, Indigofera spinosa, Xanthium spinosum*, etc. The "*spin-*" prefix suggests the general prickliness of the situation! In the Middle East many plants are to varying degrees hairy, woolly, furry, or otherwise floccose, often as part of an efficient water-trapping mechanism, providing a large surface area where water can condense at night, combined with the sensory stimulation that can act as a herbivore repellent. Consider *Aristida plumosa, Frankenia hirsuta, Lithospermum hispidulum, Arnebia hispidissima,* and *Solanum villosum*—with the adjectives corresponding to different words all describing feathery or hairy surfaces.

Many species are edible and some are named for this feature. Consider the tomato, *Lycopersicon esculentum* or buckwheat, *Fagopyrum esculentum*, and *Catha edulis*

(chewed as qat)—all essentially described in their specific name as "tasty." For species that have become cultivated crops, whether for eating or other uses, the word *sativus/sativa/sativum* describes the particular family member that has been put under the plow. Examples include cultivated wheat, *Triticum sativum*; hemp, *Cannabis sativa*; onion, *Allium sativum*; coriander, *Coriandrum sativum; Crocus sativus*, source of saffron; and many others. Some species are really, *really* useful to us, like the superlative *Linum usitatissimum*. This species has been a source of fiber for textiles over some tens of thousands of years. Its oil is also highly valued as a protective treatment for wood. No other species has the superlative second name "*usitatissimum*" so flax certainly holds the record in terms of recognition of its value. Take that, *Gossypium herbaceum* (cotton)!

In dryland habitats many plants are succulent, *holding onto* water in swollen leaves or stems, e.g., *Silene succulentum, Polycarpon succulentum, Pachypodium succulentum*, etc. Others go so far as to shed their leaves (reducing the surface area being desiccated) and rely on the stem for photosynthesis: e.g., *Anabasis aphylla*, or *Cissus subaphylla* (a species on the evolutionary pathway to losing its leaves, but not quite there yet), and *Cercidium microphyllum*, distinguished by its tiny leaves.

## 2 Location. Location. Location. Plants are often named based on where they live—or where they came from

In the Middle East, where deserts are a dominant fact of life, many species have been named as the "desert form" of their genus. Where they are simply regarded as "of the desert," the singular, genitive-cased noun is used—e.g., *Scrophularia deserti, Capparis deserti, Salvia deserti, Nigella deserti, Brassica deserti, Convolvulus deserti*—but if the more sweeping description "of the deserts" is assigned, the second part of the species name becomes the genitive plural "*desertorum*," as in *Filago desertorum, Pulicaria desertorum, Allium desertorum, Carex desertorum, Bellevalia desertorum, Alyssum desertorum*, and *Zygophyllum desertorum*.

Some names use a different Latin word for desert: *eremeus*, seen in *Eremobium aegyptiacum*, or the "desert-loving" *Astragalus eremophilus*. Some live in the Sahara (a term that is simply Arabic for desert), e.g., *Diceratella sahariana, Argyrolobium saharae*, and *Daucus sahariensis*; others live in the Sinai Desert, e.g., *Caralluma sinaica, Fagonia sinaica, Poa sinaica, Galium sinaicum, Hypericum sinaicum, Micromeria sinaica, Verbascum sinaiticum, Solanum sinaicum, Ferula sinaica, Centaurea sinaica, Phagnalon sinaicus, Plantago sinaica*, and *Volutaria sinaica*; or in the Negev Desert, *Reaumuria negevensis*; the Nubian Desert, *Lotus nubicus, Acacia nubica, Viola nubica*; the Galala Desert in Egypt, *Echinops galalensis*; or the salty Iranian Kavir Desert, *Astragalus kavirense*.

Some plants have been named for the Mediterranean region, and others for their coastal or "littoral" habitats. These include *Minuartia mediterranea, Moraea mediterranea*; and *Schoenoplectus littoralis, Daucus littoralis, Aeluropus littoralis, Juncus littoralis*, and *Atriplex littoralis*. Many species are maritime in their habitat (living by the sea): *Sonchus maritimus, Urginea maritima, Hordium marinum, Otanthus maritimus, Peplidium maritimum, Crucianella maritima, Silybium marianum, Centaurium maritimum, Trigonella maritima*, and *Spergularia marina*.

The centrality of the Arabian Peninsula is mirrored in the many species named for it. Some of these are Arabian specialists within otherwise large, widespread genera: *Tamarix arabica, Cleome arabica, Cakile arabica, Gypsophila arabica, Schismus arabicus, Rosa arabica, Medicago arabica, Amygdalus arabicus, Bassia arabica, Fagonia arabica, Fumana arabica, Silene arabica, Limeum arabicum, Reseda arabica, Salsola arabica, Tribulus arabicus, Lycium arabicum, Pancratium arabicum, Lobularia arabica, Cornulaca arabica*, and *Sporobolus arabicus*. Some describe the local variant of an otherwise more wide-ranging species, e.g., *Calligonum crinitum* ssp. *arabicum*, and *Hildebrandtia africana* ssp. *arabi*ca. For all of these the place has been turned into an adjective . . . which agrees in its ending with the gender of its genus . . . they are the Arabian representatives of their genera, or in the case of the two subspecies, they are distinctive subspecies of their species, found in Arabia.

Next most frequent has been Egypt, likely a consequence of its great antiquity and location, as well as the extent of scholarly attention. Consider *Shanginia aegyptiaca, Stachys aegyptiaca, Suaeda aegyptiaca, Orobanche aegyptiaca, Balanites aegyptiaca, Salvia aegyptiaca, Farsetia aegyptiaca, Kickxia aegyptiaca, Taverniera aegyptiaca, Zygophyllum aegyptium*, etc. Or perhaps it is localized to the River Nile, *Tamarix nilotica, Coronopus niloticus, Acacia nilotica, Cyperus niloticus*, and *Deckera nilotica* . . .

Also consider Palestine and thereabouts: *Pistacia palaestina, Suaeda palaestina, Rhamnus palaestinus, Scabiosa palestina, Ammochloa palaestina, Astragalus palaestinus, Vicia palaestina, Cuscuta palaestina, Lupinus palaestinus*, and *Suaeda palaestina*; also *Verbascum transjordannicum, Astragalus bethlehemiticus*, and *Commiphora gileadensis* (a shrubby myrrh species which "bleeds" the famous Balsam of Mecca). Again, for all these species the place became an adjective describing and agreeing with the gender of the genus. So as a general rule, the place in question is used as an adjective, modified in the nominative case to agree with the gender of its genus, whether masculine ending in *–us*, feminine ending in *–a*, or neuter, ending in *–um*.

But sometimes place names are not massaged into adjectives that agree with the genus/noun. Thus species may, for example, be described as *from* Yemen, or *from* Oman's southern Dhofari highland, in which cases the genitive

case of the noun may be used to denote *of* Yemen or *of* Dhofar: e.g., *Blepharispermum yemense, Centaurea yemense, Anogeissus dhofarica, Blepharis dhofarica*, and *Aloe dhofarensis*. In this last example, the suffix "*–ensis*" to the adjective means "pertaining to" or "originating in," so this particular Aloe came from Dhofar. (There is also an entire genus, *Dhofaria*). Yemen's exotic island archipelago, Socotra, with its greater than 30% endemism, is reflected in such names as *Croton socotranus, Boswellia socotrana, Commiphora socotrana, Caralluma socotrana, Adenium socotranum, Dendrosicyos socotrana, Euphorbia socotrana, Ficus socotrana, Gnidia socotrana, Lycium socotranum*, and many others.

*Juniperus phoenicea* commemorates Phoenicia, an ancient maritime network of merchant cities, centered on the coastline of modern-day Lebanon. Phoenicians used the galley, a human-powered sailing vessel, to trade far and wide, and are credited with invention of the bireme. In this plant name there is a surprise . . . *Juniperus* would seem to be masculine, with the "*–us*" ending, but in fact the noun is feminine . . . a fourth declension noun! So the species name, in this case *phoenicia*, meaning the adjective Phoenician, ends in an "*–a*"!

Lebanon proper is also commemorated, both as a noun in the genitive case as in *Quercus libani* and *Cedrus libani*, and adjectivally, in *Minuartia libanotica, Marrubium libanoticum, Scrophularia libanotica*, and *Anthemis libanotic*a. Also Libya and Syria: *Lobularia libyca*; and *Scrophularia syriaca, Alkanna syriaca, Majorana syriaca, Anabasis syriaca*, and *Pyrus syric*a. Or Qatar, *Zygophyllum qatarense*; and Ethiopia (also formerly known as Abyssinia): *Pistacia aethiopica, Sansevieria abyssinica, Rhus abyssinica, Artemisia abyssinica*, and *Rosa abyssinica* (which as Shakespeare said, would by any other name, smell as sweet).

Then there's Persia (now Iran): *Persea indica, Parrotia persica, Salvadora persica, Lycium persicum, Veronica persica, Melica persica, Enneapogon persicum*, etc.; and Mesopotamia: *Thymelaea mesopotamica, Centaurea mesopotamica*; and the plant-rich Caspian and Hyrcanian regions: *Gleditsia caspica, Zelkova hyrkana, Acer hyrcana, Buxus hyrkana, Ruscus hyrkanus*, etc. Or the mountains of the Caucasus, *Orobanche caucasia*, or of the Asir region in Saudi Arabia: *Rubus asirensis*, or of the Pontic range along the Black Sea coast of northern Turkey: *Quercus pontic*a. Plants of the Azore Islands, the Canaries (and Macaronesia), include *Erica azorica, Laurus azorica*, and *Aizoon canariense* . . .

Sometimes plant names refer to a particular city or place within a country, for example, *Atriplex alexandrina, Trifolium alexandrinum*, or *Silene apetala* var. *alexandrina* (all named for Alexandria, in Egypt); or *Astragalus kahiricus*, and *Euphorbia kahirensis* (named for Cairo); *Astragalus mareoticus, Carthamus mareoticus, Filago mareotica* (the Mareot region in Egypt); *Senecio belbeysius* (the city of Belbeys in Egypt); *Allium tel-avivense* (Tel Aviv, in Israel); *Sorghum halepense* (Aleppo city, in Syria); *Fagonia elba* (Gebel Elba in Egypt).

## 3 And then there are the people . . .

Another group of Middle Eastern plants have names which recognize famous botanists, often those responsible for collecting and identifying plants in the region. Sometimes again the name becomes a simple adjective, agreeing with the gender of the genus, and sometimes the genitive case of a noun is used in the name.

Professor M. Zohary (an early authority on the Biblical flora, pioneering phytogeographer and giant of Israeli botany) is recognized in, for example, *Anthemis zohariana*; the Scottish botanist Ian Hedge (specializing in the floras of Iran, Iraq, Turkey, and Afghanistan) is commemorated in *Erysimum hedgeanum*; Vivi Taeckholm, a Swedish botanist who taught several generations of students at the Botany Department of Cairo University and wrote the first book—*Students' Flora of Egypt*—on the Egyptian flora, is commemorated in *Echinops taeckholmiana* and *Fagonia taeckholmiana*.

Also from Cairo's Botany Department were, for example, M. Drar, with *Scorzonera drarii* and *Stipagrostis drarii*; M. Kassas, with *Fagonia kassasii* and *Tephrosia kassasii*; and A. Migahid, with *Zygophyllum migahidii. Atractylis boulosii* and *Fagonia boulosii* honor Loutfy Boulos the Egyptian taxonomist who worked at a number of Middle Eastern universities and authored the multi-volume *Flora of Egypt*.

Other examples include James P. Mandaville, who produced the very useful *Flora of Eastern Saudi Arabia: Zygophyllum mandavillei*. And Sheila Collenette, whose *Illustrated Guide to the Flowers of Saudi Arab*ia has helped so many: *Aloe collenettae, Aloe sheilae, Trianthema sheilae*, and *Rhytidocaulon sheilae*. Or Karl Rechinger (the editor of *Flora Iranica*): *Rosularia rechingeri*.

Or consider the early, ill-fated explorer Peter Forsskaol: *Forsskaolea tenacissima, Forsskaolea griersonii, Centropodia forsskalii, Mesembryanthemum forsskaolii, Commelina forsskaolii*, and *Asthenatherum forsskaolii*; and Isaac Bayley Balfour, who early on studied Socotra's plants: *Adiantum balfourii*. Also Georg Schweinfurth: *Schweinfurthia latifolia, Potamogeton schweinfurthii*, and *Salsola schweinfurthii*; Georg Wilhelm Schimper: e.g., *Schimpera arabica, Dregea schimperi, Silene schimperiana*, and *Astragalus schimperi*; and P. E. Boissier: e.g., *Boissiera squarrosa, Pyrus boissieriana*, and *Sorbus boissieri.*

Going back in time, *Avicennia marina* honors the Persian physician-polymath Avicenna, in Arabic known as "*Ibn Sina*" (who lived from 980–1037), and going back even further, the ancient Greek, Pedanius Dioscorides, whose book in Latin *De Materia Medica* was, for over 1500 years, the principal reference work on pharmacology across the Middle East and Europe, is celebrated in the genus *Dioscorea*, and the species *Pluchea dioscoridis*.

APPENDIX 2

# Species list

Checklist of plant and animal species cited in the text. Taxa are arranged alphabetically. The accepted names of plant species are provided with synonyms given in parentheses after the full scientific name.

## Plant species

*Abies cilicia* (Antoine & Kotschy) Carrière [= *Pinus cilicia* Antoine & Kotschy]

*Abutilon fruticosum* Guill. & Perr.

*Acacia baileyana* F.Muell.

*Acacia constricta* A.Gray

*Acacia cyclops* G.Don

*Acacia ehrenbergiana* Hayne

*Acacia gerrardii* Benth.

*Acacia johnwoodii* Boulos [= *Vachellia johnwoodii* (Boulos) Ragup]

*Acacia longifolia* (Andrews) Willd. [= *Mimosa longifolia* Andrews]

*Acacia mearnsii* De Wild.

*Acacia mellifera* (M.Vahl) Benth.

*Acacia nilotica* (L.) Delile [= *Mimosa nilotica* L.]

*Acacia nubica* Benth.

*Acacia pachyceras* O.Schwartz

*Acacia papyrocarpa* Benth.

*Acacia raddiana* Savi [= *Acacia tortilis* subsp. *raddiana* (Savi) Brena]

*Acacia saligna* (Labill.) Wendl. [= *Mimosa saligna* Labill.]

*Acacia senegal* (L.) Willd.

*Acacia seyal* Delile

*Acacia sieberiana* DC.

*Acacia tortilis* subsp. *raddiana* (Savi) Brena [= *Acacia raddiana* Savi]

*Acacia tortilis* (Forssk.) Hayne subsp. tortilis

*Acacia yemenensis* Boulos [= *Vachellia yemenensis* (Boulos) Ragup.]

*Acanthocardamum*

*Acantholimon armenum* Boiss. & A.Huet

*Acer cinerascens* Boiss. [= *Acer monspessulanum* subsp. *cinerascens* (Boiss.) Yalt.]

*Acer grandidentatum* Nutt. [= *Acer saccharum* subsp. *grandidentatum* (Torr. & A.Gray) Desmarais]

*Acer hyrcanum* Fisch. & C.A.Mey.

*Acer insigne* Boiss. & Buhse [= *Acer velutinum* Boiss.]

*Acer microphyllum* (Boiss.) Dinsm. [= *Acer monspessulanum* subsp. *microphyllum*(Boiss.) Bornm.]

*Acer negundo* L.

*Acer obtusifolium* Sm. [= *Acer orientale* var. *obtusifolium* (Sm.) Pax]

*Achillea conferta* DC.

*Achillea fragrantissima* (Forssk.) Sch.Bip. [= *Santolina fragrantissima* Forssk.]

*Achyranthes aspera* L.

*Adansonia digitata* L.

*Adenia venenata* Forssk.

*Adenium obesum* (Forssk.) Roem. & Schult.

*Adenium socotranum* Vierh. [= *Adenium obesum* (Forssk.) Roem. & Schult. Subsp. *socotranum* (Vierh.) Lavranos]

*Adiantum balfourii* Bak.in Hk.

*Adiantum capillus-veneris* L.

*Adonis dentata* Delile

*Aegilops geniculata* Roth [= *Aegilops ovata* L.]

*Aegilops kotschyi* Boiss. [= *Aegilops triuncialis* var. *kotschyi* (Boiss.) Boiss.] [=*Aegilops kotschyi* var. *palaestina* Eig]

*Aeluropus lagopoides* (L.) Trin. ex Thwaites [= *Dactylis lagopoides* L.]

*Aeluropus littoralis* (Gouan) Parl. [= *Poa littoralis* Gouan]

*Aeonium leucoblepharum* Webb ex A.Rich. [=*Sempervivum leucoblepharum* (Webb ex A.Rich.) Hutch. & E.A.Bruce]

*Aerva javanica* (Burm.f.) Juss. ex Schult. [= *Iresine javanica* Burm.f.]

*Afrocarpus* sp.

*Afzelia africana* Pers

*Agave deserti* Engelm.

*Agave macroacantha* Zucc.

*Aizoon canariense* L.

*Albizia julibrissin* Durazz. [= *Acacia julibrissin* (Durazz.) Willd.] [=*Mimosa julibrissin* (Durazz.) Scop.]

*Albizia zygia* (DC.) J.F.Macbr. [= *Inga zygia* DC.] [=*Feuilleea zygia* (DC.) Kuntze]

*Alcea* sp.

*Alkanna syriaca* (Boiss. & Hohen.) Boiss.

*Alkanna tinctoria* (L.) Tausch [= *Alkanna tinctoria* subsp. *lehmanii* (Tineo) Nyman] [= *Lithospermum tinctorium* L.]

*Allium calyptratum* Boiss.

*Allium desertorum* Forssk.

*Allium sativum* L.

*Allium tel-avivense* Eig

*Alnus subcordata* C.A.Mey.

*Aloe asperifolia* A.Berger

*Aloe collenetteae* Lavranos

*Aloe dhufarensis* Lavranos

*Aloe dichotoma* Masson

*Aloe greatheadii* Schönland

*Aloe mahraensis* Lavranos & T.A.McCoy

*Aloe rubroviolacea* Schweinf.

*Aloe sheilae* Lavranos

*Aloe yemenica* J.R.I.Wood

*Alyssum desertorum* Stapf

*Ambrosia deltoidea* (Torr.) W.W.Payne [= *Franseria deltoidea* Torr.]

*Ambrosia dumosa* (A.Gray) W.W.Payne [= *Franseria dumosa* A.Gray]

*Ammi majus* L.

*Ammochloa palaestina* Boiss.

*Ammophila arenaria* (L.) Link [= *Arundo arenaria* L.] [= *Psamma arenaria* (L.) Roem. & Schult.]

*Amygdalus arabica* Olivier [= *Prunus arabica* (Olivier) Meikle]

*Amygdalus communis* L. [= *Prunus dulcis* (Mill.) D.A.Webb.]

*Amygdalus communis* Bunge [= *Prunus davidiana* (CarriŠre) Franch.]

*Amygdalus scoparia* Spach [= *Prunus scoparia* (Spach) C.K.Schneid.]

*Anabaena* sp.

*Anabasis aphylla* L.

*Anabasis articulata* (Forssk.) Moq. [= *Salsola articulata* Forssk.]

*Anabasis calcarea* (Charif & Aellen) Bokhari & Wendelbo [= *Esfandiari calcarea* Charif & Aellen]

*Anabasis setifera* Moq.

*Anabasis syriaca* Iljin [= *Anabasis syriaca* var. *zoharyi* (Iljin) Zohary]

*Anagallis arvensis* L.

*Anastatica hierochuntica* L.

*Andrachne telephioides* L.

*Anemone* sp.

*Anogeissus bentii* Baker

*Anogeissus dhofarica* A.J.Scott

*Anogeissus leiocarpa* (DC.) Guill. & Perr. [= *Anogeissus leiocarpus* (DC.) Guill. & Perr.] [= *Conocarpus leiocarpus* DC. ]

*Anogramma leptophylla* (L.) Link [= *Polypodium leptophyllum* L.]

*Anthemis cassia* Boiss. [= *Anthemis cretica* subsp. *cassia* (Boiss.) Grierson.]

*Anthemis libanotica* DC.

*Anthemis odontostephana* Boiss.

*Anthemis zoharyana* Eig

*Anvillea* sp.

*Apium graveolens* L.

*Arabidopsis thaliana* (L.) Heynh. [= *Arabis thaliana* L.]

*Arbutus andrachne* L.

*Arbutus paravii* Pamp. [= *Arbutus unedo* L.]

*Argania spinosa* (L.) Skeels [= *Sideroxylon spinosum* L.]

*Argyrolobium saharae* Pomel

*Arisaema triphyllum* (L.) Schott [= *Arum triphyllum* L.]

*Arisarum vulgare* O.Targ.Tozz.

*Aristida plumosa* L. [= *Stipagrostis plumosa* Munro ex T.Anderson.]

*Arnebia hispidissima* (Lehm.) A.DC.

*Artemisia abyssinica* Sch.Bip. ex A.Rich.

*Artemisia fragrans* Willd.

*Artemisia herba-alba* Asso [= *Seriphidium herba-alba* (Asso) Soják]

*Artemisia judaica* L.

*Artemisia monosperma* Delile

*Artemisia sieberi* Besser

*Arthrocnemum indicum* (Willd.) Moq. [= *Halosarcia indica* (Willd.) Paul G.Wilson.] [=*Salicornia indica* Willd.

*Arthrocnemum macrostachyum* (Moric.) K.Koch. [= *Salicornia macrostachya* Moric.] [= *Arthrocnemum glaucum* (Moq.) Ung.-Sternb.]

*Arundo donax* L.

*Asparagus aphyllus* L.

*Asparagus stipularis* Forssk. [= *Asparagus horridus* L.]; [=*Asparagus stipularis* var. *brachyclados* Boiss.]

*Asphodelus fistulosus* L.

*Asphodelus microcarpus* Viv.

*Asphodelus ramosus* L. [= *Asphodelus microcarpus* Viv.]

*Aspidosperma quebracho-blanco* Schltdl.

*Asteriscus graveolens* (Forssk.) Less. [= *Buphthalmum graveolens* Forssk.] [= *Nauplius graveolens* (Forssk.) Wiklund]

*Asteriscus hierochunticus* (Michon) Wiklund [= *Saulcya hierochuntica* Michon] [= *Pallenis hierochuntica* (Michon) Greuter.]

*Asteriscus pygmaeus* (DC.) Coss. & Durieu [= *Asteriscus aquaticus* var. *pygmaeus* DC.] [= *Pallenis hierochuntica* (Michon) Greuter.]

*Asthenatherum forskalii* (Vahl) Nevski

*Astoma* sp.

*Astragalus adscendens* Boiss. [= *Astracantha adscendens* (Boiss. & Hausskn.) Podlech.]

*Astragalus bethlehemiticus* Boiss. [= *Astracantha bethlehemitica* (Boiss.) Podl.]

*Astragalus brachycalyx* Fisch. ex Boiss. [= *Astracantha brachycalyx* (Fisch. ex Boiss.) Podl.]

*Astragalus echinus* DC. [= *Astracantha echinus* (DC.) Podlech]

*Astragalus eremophilus* Boiss.

*Astragalus fasciculifolius* Boiss. [= *Tragacantha fasciculifolia* (Boiss.) Kuntze]

*Astragalus gummifer* Labill. [= *Astracantha gummifera* (Labill.) Podlech.]

*Astragalus kahiricus* DC.

*Astragalus kavirensis* Freitag

*Astragalus mareoticus* Delile

*Astragalus mossulensis* Bunge

*Astragalus palaestinus* Eig

*Astragalus schimperi* Boiss.

*Astragalus spinosus* (Forssk.) Muschl. [= *Colutea spinosa* Forssk.]

*Astragalus tragacantha* L. [= *Astragalus tragacanthus* Lam.]

*Atractylis boulosii* Täckh.

*Atraphaxis spinosa* L.

*Atriplex alexandrina* Boiss.

*Atriplex canescens* (Pursh) Nutt. [= *Calligonum canescens* Pursh]

*Atriplex farinosa* Forssk.

*Atriplex glauca* L. [= *Atriplex stylosa* Viv.]

*Atriplex halimus* L.

*Atriplex leucoclada* Boiss. [= *Atriplex leucoclada* var. *inamoena* (Aellen) Zohary][= *Atriplex leucoclada* var. *mandavillea* Al-Turki, & S.Omer & A.Ghafoor][= *Atriplex leucoclada* subsp. *turcomanica* (Moq.) Aellen]

*Atriplex littoralis* L.

*Avena sterilis* L.

*Avicennia marina* (Forssk.) Vierh.

*Azanza garckeana* (F.Hoffm.) Exell & Hillc. [= *Thespesia garckeana* F.Hoffm.]

*Azolla caroliniana* Willd.

*Azolla filiculoides* Lam.

*Azolla mexicana* C. Presl

*Azolla microphylla* Kaulf.

*Azolla nilotica* Dcne.

*Azolla rubra* R. Br. [= *Azolla filiculoides* var. *rubra* (R. Br.) Strasb.]

*Bacopa monnieri* (L. ) Wettst. [= *Lysimachia monnieri* L.]

*Balanites aegyptiaca* (L.) Delile [= *Ximenia aegyptiaca* L.]

*Balthasaria* sp.

*Barleria* sp.

*Bassia arabica* (Boiss.) Maire & Weiller [= *Chenolea arabica* Boiss.]

*Bassia indica* (Wight ) A.J.Scott [= *Kochia indica* Wight]

*Bassia muricata* (L.) Asch. [= *Salsola muricata* L.]

*Bellevalia desertorum* Eig & Feinbrun

*Bellevalia zoharyi* Feinbrun

*Beta vulgaris* L.

*Betula medwediewii* Regel

*Biarum olivieri* Blume

*Bienertia cycloptera* Bunge

*Blepharis ciliaris* (L.) B.L.Burtt [= *Ruellia ciliaris* L., *Acanthus edulis* Forssk.]

*Blepharis dhofarensis* A.G.Mill.

*Blepharis permum yemense*

*Boerhavia diffusa* L.

*Boerhavia repens* L.

*Boissiera squarrosa* (Sol.) Nevski

*Bomeria* sp.

*Boscia senegalensis* Lam.

*Boswellia frereana* Birdw.

*Boswellia papyrifera* (Caill. ex Delile) Hochst. [= *Amyris papyrifera* Caill. ex Delile]

*Boswellia sacra* Flueck.

*Boswellia socotrana* Balf.f.

*Bothrodendron* sp.

*Brachiaria* sp.

*Brachypodium distachyon* (L.) P.Beauv. [= *Bromus distachyos* L.]

*Brassica aucheri* Boiss.

*Brassica deserti* Danin & Hedge

*Brassica oleracea* L.

*Breonadia salicina* (Vahl) Hepper & J.R.I.Wood [= *Nerium salicinum* Vahl]

*Bromus fasciculatus* C.Presl

*Bruguiera gymnorhiza* (L.) Lam. [= *Rhizophora gymnorrhiza* L.]

*Bursera microphylla* A.Gray

*Buxus hildebrandtii* Baill. [= *Buxanthus hildebrantii* (Baill.) Tiegh.]

*Buxus hyrcana* Pojark. [= Buxus sempervirens subsp. hyrcana (Pojark.) Takht]

*Cadaba farinosa* Forssk.

*Cakile arabica* Velen.

*Cakile maritima* Scop.

*Calotropis procera* (Aiton) Dryand. [= *Asclepias procera* Aiton]

*Calligonum comosum* L'Hér. [= *Calligonum polygonoides* subsp. *comosus* (L'Hér.) Soskov]

*Calligonum crinitum* Boiss. subsp. *arabicum* (Soskov) Soskov [= *Calligonum arabicum* Soskov]

*Calligonum tetrapterum* (Meisn. ex DC.) Jaub. & Spach [= *Pterococcus tetrapterus* Meisn.]

*Campanula akhdarensis* A.G.Mill. & Whitc.

*Campanula edulis* Forssk.

*Campylosporus* sp.

*Cannabis sativa* L.

*Capparis aegyptia* Lam.

*Capparis decidua* (Forssk.) Edgew.

*Capparis deserti* (Zohary) Täckh. & Boulos

*Capparis spinosa* L.

*Caralluma cicatricosa* (Deflers) N.E.Br. [= *Boucerosia cicatricosa* Deflers]

*Caralluma deflersiana* Lavranos [= *Pachycymbium deflersianum* (Lavranos) M.G. Gilbert] [= *Angolluma deflersiana* (Lavranos) Plowes]

*Caralluma penicillata* (Deflers) N.E.Br. [= *Boucerosia penicillata* Deflers]

*Caralluma shadhbana* Lavranos [= *Caralluma hexagona* Lavranos]

*Caralluma sinaica* (Decne.) A.Berger [= *Boucerosia sinaica* Decne.]

*Caralluma socotrana* (Balf.f.) N.E.Br. [= *Boucerosia socotrana* Balf.f.]

*Caralluma wissmannii* Schwartz [= *Angolluma wissmannii* (O. Schwartz) Plowes] [= *Pachycymbium wissmannii* (O. Schwartz) M.G. Gilbert]

*Carex stenophylla* Wahlenb.

*Carissa spinarum* L.

*Carnegiea gigantea* (Engelm.) Britton & Rose [= *Cereus giganteus* Engelm.]

*Carpinus betulus* L.

*Carrichtera annua* (L.) DC. [= *Vella annua* L.]

*Carthamus mareoticus* Delile

*Cassia acutifolia* Delile [= *Senna alexandrina* Mill.]

*Catha edulis* (Vahl) Endl. [= *Celastrus edulis* Vahl]

*Ceanothus* sp.

*Cedrus libani* A.Rich.

*Cedrus libani* var. *brevifolia* Hook.f.

*Cenchrus echinatus* L.

*Centaurea aegyptiaca* L.

*Centaurea balsamitoidea* Post [= *Stizolophus balsamitoides* (Post) Soják]

*Centaurea mesopotamica* Bornm.

*Centaurea scoparia* Sieber ex Spreng.

*Centaurea sinaica* DC.

*Centaurea wendelboi* Wagenitz

*Centaurea yemensis* Wagenitz

*Centaurium maritimum* (L.) Fritsch

*Centaurium pulchellum* (Sw.) Druce [= *Gentiana pulchella* Sw.]

*Centropodia forsskalii* (Vahl) Cope

*Cephalocrotonopsis socotranus* (Balf.f.) Pax [= *Cephalocroton socotranus* Balf.f.]

*Cerasus* sp.

*Ceratonia oreothauma* Hillc. & *al.*

*Ceratonia siliqua* L.

*Ceratophyllum* sp.

*Cercidium microphyllum* (Torr.) Rose & I.M.Johnst. [= *Parkinsonia microphylla* Torr.]

*Cercidium* sp.

*Ceriops tagal* (Perr.) C.B.Rob. [= *Rhizophora tagal* Perr.]

*Ceropegia* sp.

*Chaetosciadium* sp.

*Chamaephyton supinum* (L.) Fourr. [= *Potentilla supina* L.?]

*Cheilanthes* sp.

*Chenopodium ambrosioides* L.

*Chenopodium hastatum* St.-Lag. [= *Chenopodium bonus-henricus* L.]

*Chenopodium murale* L. [*Chenopodium nutans*?]

*Cichorium bottae* Deflers

*Chiliadenus montanus* (Vahl) Brullo [= *Chrysocoma montana* Vahl.] [= *Varthemia montana* (Vahl) Boiss.]

*Chrysopogon aucheri* (Boiss.) Stapf [= *Andropogon aucheri* Boiss.]

*Cibirhiza* sp.

*Cicer arietinum* L.

*Cinnamomum* sp.

*Cirsium* sp.

*Cissus hamaderohensis* Radcl.-Sm.

*Cissus rotundifolia* Vahl

*Cissus subaphylla* (Balf.f.) Planch. [= *Vitis subaphylla* Balf. f.]

*Cistanche phelypaea* (L.) Cout. [= *Lathraea phelypaea* L.]

*Cistanche tubulosa* (Schenk) Wight [= *Phelipaea tubulosa* Schenk]

*Cistus* sp.

*Citrullus colocynthis* (L.) Schrad. [= *Cucumis colocynthis* L.]

*Clematis flammula* L.

*Cleome arabica* L.

*Cleome droserifolia* (Forssk.) Delile [= *Roridula droserifolia* Forssk.]

*Coccinia grandis* (L.) Voigt [= *Bryonia grandis* L.]

*Cocculus balfourii* Schweinf. ex Balf.f.

*Cocculus pendulus* (J.R.Forst. & G.Forst.) Diels [= *Epibaterium pendulum*J.R.Forst. & G.Forst.]

*Coffea arabica* L.

*Coffea canephora* Pierre ex A.Froehner

*Coffea eugenioides* S.Moore

*Combretum cordofanum* Engl. & Diels

*Combretum hartmannianum* Schweinf.

*Combretum molle* R.Br. ex G.Don

*Commelina forskaolii* Vahl

*Commicarpus* sp.

*Commiphora africana* (A.Rich.) Endl. [= *Heudelotia africana* A.Rich.]

*Commiphora myrrha* (Nees) Engl. [= *Balsamodendrum myrrha* T.Nees]

*Commiphora socotrana* (Balf.f.) Engl.

*Convolvulus acanthocladus* Boiss. & Kotschy

*Convolvulus deserti* Hochst. & Steud. ex Steud.

*Convolvulus lanatus* Vahl

*Corchorus depressus* (L.) Stocks [= *Antichorus depressus* L.]

*Coriandrum sativum* L.

*Cornulaca arabica* Botsch. [= *Cornulaca monacantha* Delile]

*Cornulaca monacantha* Delile [= *Cornulaca arabica* Botsch.]

*Cornulaca setifera* (DC.) Moq. [= *Astragalus setiferus* DC.]

*Corydalis rutifolia* (Sm.) DC. [= *Fumaria rutifolia* Sm.]

*Cotoneaster nummularius* Fisch. & C.A.Mey.

*Cotoneaster racemiflorus* (Desf.) K.Koch [= *Mespilus racemiflora* Desf.]

*Cousinia chaborasica* Bornm. & Hand.-Mazz. [= *Cousinia wesheni* Post]

*Cousinia stenocephala* Boiss.

*Crassula* sp.

*Crataegus azarolus* L.

*Crataegus monogyna* Jacq.

*Crataegus pentagyna* Waldst. & Kit. ex Willd.

*Cressa cretica* L.

*Crocus sativus* L.

*Coronopus niloticus* (Delile) Spreng.

*Crotalaria burhia* Benth.

*Crotalaria persica* (Burm.f.) Merr. [= *Cytisus persicus* Burm.f.]

*Crotalaria squamigera* Deflers

*Crotalaria aegyptiaca* Benth.

*Croton confertus* Baker

*Croton pachyclados* Radcl.-Sm. [= *Croton socotranus* var. *pachyclados* (Radcl.-Sm.)Radcl.-Sm.]

*Croton socotranus* Balf.f.

*Crucianella platyphylla* Ehrend. & Schönb.-Tem.

*Crucianella maritima* L.

*Cocculus balfourii* Schweinf. ex Balf.f.

*Cucumis canoxyi* Thulin & Al-Gifri

*Cucumis sativus* L.

*Cupressus sempervirens* L.

*Curtisia* sp.

*Cuscuta palaestina* Boiss.

*Cussonia arborea* Hochst. ex A.Rich.

*Cutandia memphitica* (Spreng.) Benth. [= *Dactylis memphitica* Spreng.]

*Cymbopogon jwarancusa* (Jones) Schult. [= *Andropogon jwarancusa* Jones]

*Cymbopogon parkery* Stapf [= *Cymopogon commutatus* (Steud.) Stapf]

*Cynara cornigera* Lindl.

*Cynodon dactylon* (L.) Pers. [= *Panicum dactylon* L.]

*Cynomorium coccineum* L.

*Cyperus conglomeratus* Rottb.

*Cyperus niloticus* Forssk. [= *Cyperus articulatus* L.]

*Cyperus papyrus* L.

*Cystostemon kissenioides* (Deflers) A.G.Mill. & Riedl [= *Trichodesma kissenioides* Deflers]

Dalbergia melanoxylon Guill. & Perr.

*Danae racemosa* (L.) Moench [= *Ruscus racemosus* L.]

*Dasylirion* sp.

*Datura innoxia* Mill.

*Datura socotranum* ?

*Datura stramonium* L.

*Daucus littoralis* Sm.

*Daucus sahariensis* Murb.

*Deckera nilotica* (Steud.) Sch.Bip. [= *Picris sulphurea* Delile]

*Delonix elata* (L.) Gamble [= *Poinciana elata* L].

*Delphinium* sp.

*Dendrosicyos socotrana* Balf.f.

*Desmidorchis penicillata* (Deflers) Plowes [= *Caralluma penicillata* (Deflers) N.E.Br.]

*Desmidorchis retrospeciens* Ehrenb. [= *Caralluma retrospeciens* (Ehrenb.) N.E.Br.]

*Desmodium hirtum* Guill. & Perr.

*Deverra tortuosa* (Desf.) DC. [= *Bubon tortuosum* Desf.]

*Deverra triradiata* Hochst. ex Boiss.

*Dhofaria* sp.

*Diacanthium* sp.

*Diceratella sahariana* Corti [= *Morettia philaeana* DC.]

*Dianthus crinitus* Sm.

*Dionysia mira* Wendelbo

*Diospyros lotus* L.

*Diospyros mespiliformis* Hochst. ex A.DC.

*Diplotaxis acris* (Forssk.) Boiss. [= *Hesperis acris* Forssk.]

*Diplotaxis harra* (Forssk.) Boiss. [= *Sinapis harra* Forssk.]

*Dirachma socotrana* Schweinf. ex Balf.f.

*Dirachma somalensis* D.A.Link

*Dodonaea angustifolia* L.f. [= *Dodonaea viscosa* subsp. *angustifolia* (L.f.) J.G.West]

*Dodonaea viscosa* (L.) Jacq.

*Dorstenia gigas* Schweinf. ex Balf.f.

*Dorstenia gypsophila* Lavranos

*Draba* sp.

*Dracaena cinnabari* Balf.f.

*Dracaena draco* (L.) L. [= *Asparagus draco* L.]

*Dracaena ombet* Heuglin ex Kotschy & Peyr.

*Dracaena schizantha* Baker [= *Dracaena ombet* subsp. *schizantha* (Baker) Bos]

*Dracaena serrulata* Baker

*Dracaena tamaranae* Marrero Rodr., R.S.Almeira & M.Gonzales-Martin

*Dregea schimperi* (Decne.) Bullock

*Duvalia* sp.

*Ebenus armitagei* Schweinf. & Taub.

*Ebenus pinnata* Aiton

*Echidnopsis globosa* Thulin & Hjertson

*Echidnopsis cereiformis* Hook.f.

*Echidnopsis nubica* N.E.Br. [= *Echidnopsis cereiformis* Hook.f.]

*Echidnopsis scutellata* (Deflers) A.Berger

*Echidnopsis socotrana* Lavranos

*Echinochloa haploclada* (Stapf) Stapf [= *Panicum haplocladum* Stapf]

*Echinochloa pyramidalis* (Lam.) Hitchc. & Chase [= *Panicum pyramidale* Lam.]

*Echinops galalensis* Schweinf.

*Echinops spinosissimus* Turra

*Echinops taekholmiana* Amin

*Echium hispidum* Burm.f.

*Ehretia cymosa* Thonn.

*Ehretia obtusifolia* Hochst. ex A.DC.

*Eichhornia crassipes* (Mart.) Solms [= *Pontederia crassipes* Mart.]

*Emex spinosa* (L.) Campd.

*Encelia farinosa* A.Gray ex Torr.

*Enneapogon persicus* Boiss.

*Ephedra alata* Decne.

*Ephedra aphylla* Forssk.

*Ephedra foeminea* Forssk.

*Ephedra foliata* Boiss. ex C.A.Mey.

*Ephedra pachyclada* Boiss.

*Ephedra transitoria* Riedl

*Epigaea gaultherioides* (Boiss. & Balansa) Takht.

*Epipactis veratrifolia* Boiss. & Hohen.

*Equisetum ramosissimum* Desf.

*Eragrostis papposa* (Desf. ex Roem. & Schult.) Steud. [= *Megastachya papposa* Roem. & Schult.]

*Eragrostis* sp.

*Eremobium aegyptiacum* (Spreng.) Asch. ex Boiss. [= *Malcolmia aegyptiaca* Spreng.]

*Erica azorica* Hochst. ex Seub.

*Eriogonum* sp.

*Eriolobus trilobatus* (Labill. ex Poir.) M. Roem. [= *Crataegus trilobata* Labill. ex Poir.]

*Erodium bryoniifolium* Boiss. [= *Erodium oxyrhinchum* subsp. *bryoniifolium* (Boiss.) Schönb.-Tem.]

*Erodium glaucophyllum* (L.) L'Hér. [= *Geranium glaucophyllum L.*]

*Eruca sativa* Mill.

*Erucaria hispanica* (L.) Druce [= *Sinapis hispanica* L.]

*Erysimum hedgeanum* Al-Shehbaz

*Euclea schimperi* (A.DC.) Dandy [= *Euclea racemosa* subsp. *schimperi* (A.DC.) F.White]

*Euphorbia abdelkuri* Balf.f.

*Euphorbia ammak* Schweinf.

*Euphorbia aphylla* Brouss. ex Willd.

*Euphorbia applanata* Thulin & Al-Gifri

*Euphorbia arbuscula* Balf.f.

*Euphorbia balsamifera* subsp. *adenensis* (Deflers) P.R.O.Bally [= *Euphorbia adenensis* Deflers]

*Euphorbia bottae* Boiss.

*Euphorbia cactus* Ehrenb. ex Boiss.

*Euphorbia caducifolia* Haines

*Euphorbia canariensis* L.

*Euphorbia decorsei* Drake

*Euphorbia fruticosa* Forssk.

*Euphorbia gracilipes* Baill. [= *Euphorbia pyrifolia* Lam.]

*Euphorbia handiensis* Burchard

*Euphorbia helioscopia* L.

*Euphorbia inarticulata* Schweinf.

*Euphorbia kahirensis* Raeusch. [= *Euphorbia retusa* Forssk.]

*Euphorbia larica* Boiss.

*Euphorbia latifolia* C.A.Mey. ex Ledeb.

*Euphorbia nicaeensis* All.

*Euphorbia obcordata* Balf.f.

*Euphorbia oblanceolata* Balf.f.

*Euphorbia parciramulosa* Schweinf.

*Euphorbia pulcherrima* Willd. ex Klotzsch

*Euphorbia retusa* Forssk.

*Euphorbia schimperi* C.Presl

*Euphorbia* sect. *Euphorbia*

*Euphorbia* sect. *Monadenium*

*Euphorbia septemsulcata* Vierh.

*Euphorbia socotrana* Balf.f.

*Euphorbia spiralis* Balf.f.

*Euphorbia stenoclada* Baill.

*Euphorbia* subg. *Chamaesyce*

*Euphorbia* subg. *Esula*

*Euphorbia* subg. *Esula* sect. *Paralias*

*Euphorbia* subg. *Esula* section *Aphyllis*

*Euphorbia* subg. *Euphorbia*

*Euphorbia* subg. *Rhizanthium* (=*Athymalus*

*Euphorbia tirucalli* L.

*Euphorbia uzmuk* S.Carter & J.R.I.Wood

*Exacum affine* Balf.f. ex Regel [= *Exacum socotranum* Vierh].

*Fagonia arabica* L.

*Fagonia boulosii* Hadidi

*Fagonia boveana* (Hadidi) Hadidi & El Garf

*Fagonia cretica* L.

*Fagonia elba* Hadidi

*Fagonia indica* Burm. f.

*Fagonia kahirina* Boiss. [= *Fagonia scabra* Forssk.]

*Fagonia kassasii* Hadidi

*Fagonia mollis* Delile

*Fagonia sinaica* Boiss.

*Fagonia taeckholmiana* Hadidi

*Fagus orientalis* Lipsky

*Fagus sylvatica* L.

*Faidherbia albida* (Delile) A.Chev. [= *Acacia albida* Delile]

*Farsetia aegyptia* Turra

*Farsetia hamiltonii* Royle [= *Farsetia stylosa* R.Br.]

*Ferocactus acanthodes* (Lim.) Britton Rose [= *Ferocactus cylindraceus* (Engelm.) Orcutt]

*Ferula glaucopruinosa* (Rech.f.) Akhani [= *Peucedanum glaucopruinosum* Rech.f.]

*Ferula gummosa* Boiss.

*Ferula laseroides* (Akhani) Spalik & S.R.Downie [= *Leutea laseroides* Akhani]

*Ferula sinaica* Boiss.

*Festuca pinifolia* (Hack. ex Boiss.) Bornm. [= *Festuca ovina* subsp. *pinifolia* Hack. ex Boiss.]

*Ficalhoa* sp.

*Ficus carica* L.

*Ficus cordata* Thunb.

*Ficus ingens* Miq.

*Ficus palmata* Forssk.

*Ficus socotrana* Balf.f. [= *Ficus vasta* Forssk.]

*Ficus sur* Forssk.

*Ficus sycomorus* L.

*Ficus vasta* Forssk. [= *Ficus socotrana* Balf.f.]

*Filago desertorum* Pomel

*Forsskaolea griersonii* A.G.Mill. & J.A.Nyberg

*Forsskaolea tenacissima* L.

*Fouquieria splendens* Engelm.

*Francoeuria crispa* (Forssk.) Cass. [= *Pulicaria undulata* (L.) C.A.Mey.]

*Frangula alnus* Mill.

*Frankenia hirsuta* L.

*Fraxinus excelsior* L.

*Fraxinus ornus* L.

*Fraxinus rotundifolia* Mill. [= *Fraxinus angustifolia* Vahl]

*Fumana arabica* (L.) Spach [= *Cistus arabicus* L.]

*Galium setaceum* Lam.

*Galium sinaicum* (Delile ex Decne.) Boiss.

*Genista sphacelata* Spach [= *Genista fasselata* Decne.]

*Gladiolus italicus* Mill.

*Gleditsia caspia* Desf.

*Glinus lotoides* L.

*Globularia arabica* Jaub. & Spach

*Glossonema edule* N.E.Br. [= *Glossonema varians* (Stocks) Benth. ex Hook.f.]

*Glossonema boveanum* (Decne.) Decne.

*Gnidia socotrana* (Balf.f.) Gilg [= *Lasiosiphon socotranus* Balf.f.]

*Gossypium herbaceum* L.

*Grewia* (Tiliaceae)

*Grewia schweinfurthii* Burret

*Grewia tembensis* Fresen.

*Grewia villosa* Willd.

*Gundelia tournefortii* L.

*Gymnocarpos decander* Forssk.

*Gymnocarpos dhofarensis* Petruss. & Thulin

*Gynandriris sisyrinchium* (L.) Parl. [= *Moraea sisyrinchium* (L.) Ker Gawl.]

*Gypsophila arabica* Barkoudak

*Hagenia abyssinica* (Bruce ex Steud.) J.F.Gmel. [= *Banksia abyssinica* Bruce ex Steud.]

*Halimione* sp.

*Halocnemum strobilaceum* (Pall.) M.Bieb. [= *Salicornia strobilacea* Pall.]

*Halodule uninervis* (Forssk.) Boiss.

*Halogeton alopecuroides* (Delile) Moq. [= *Agathophora alopecuroides* (Delile) Fenzl ex Bunge]

*Halopeplis perfoliata* (Forssk.) Bunge ex Ung.-Sternb. [= *Salicornia perfoliata* Forssk.]

*Halophila ovalis* (R.Br.) Hook.f. [= *Caulinia ovalis* R.Br.]

*Halophila stipulacea* (Forssk.) Asch. [= *Zostera stipulacea* Forssk.]

*Halophyllum salicornicum*?

*Halopyrum mucronatum* (L.) Stapf [= *Uniola mucronata* L.]

*Haloxylon aphyllum* (Minkw.) Iljin [= *Haloxylon ammodendron* (C.A.Mey.) Bunge ex Fenzl]

*Haloxylon articulatum* (Moq.) Bunge [= *Haloxylon salicornicum* (Moq.) Bunge ex Boiss.]

*Haloxylon persicum* Bunge

*Haloxylon scoparium* Pomel [= *Hammada scoparia* (Pomel) Iljin

*Haloxylon stocksii* (Boiss.) Benth. & Hook. f. [= *Salsola stocksii* Boiss.

*Hammada elegans* (Bunge) Botsch. [= *Haloxylon articulatum* (Moq.) Bunge] [=*Haloxylon salicornicum* (Moq.) Bunge ex Boiss.]

*Hammada scoparia* (Pomel) Iljin [= *Haloxylon scoparium* Pomel]

*Hedera helix* L.

*Hedysarum boveanum* Basiner

*Helianthemum kahiricum* Delile

*Helianthemum ledifolium* (L.) Mill [= *Cistus ledifolius* L.]

*Helianthemum lippii* (L.) Dum.Cours. [= *Cistus lippii* L.]

*Helianthemum stipulatum* (Forssk.) C.Chr. [= Cistus *stipulatus Forssk*.]

*Helianthemum vesicarium* Boiss.

*Helichysum* (Asteraceae)

*Heliotropium bacciferum* Forssk.

*Heliotropium curassavicum* L.

*Heracleum humile* Sm.

*Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg. [= *Siphonia brasiliensis* Willd. ex A.Juss.]

*Hildebrandtia africana* Vatke

*Hordeum distichon* L.

*Hordeum marinum* Huds.

*Hordeum spontaneum* K.Koch

*Huernia hadramautica* Lavranos

*Hyoscyamus boveanus* (Dunal) Asch. & Schweinf.

*Hyoscyamus muticus* L.

*Hyoscyamus pusillus* L.

*Hyoscyamus gallagheri* A.G.Mill. & Biagi

*Hyparrhenia rufa* (Nees) Stapf [= *Trachypogon rufus* Nees]

*Hypericum balfourii* N.Robson

*Hypericum perforatum* L.

*Hypericum sinaicum* Hochst. ex Boiss.

*Hypericum socotranum* R.D.Good

*Hyparrhenia hirta* (L.) Stapf

*Ifloga spicata* (Forssk.) Sch.Bip. [= *Chrysocoma spicata* Forssk.]

*Imperata cylindrica* (L.) Raeusch. [= *Lagurus cylindricus* L.]

*Indigofera bracteolata* DC.

*Indigofera spinosa* Forssk.

*Iphiona mucronata* (Forssk.) Asch. & Schweinf. [= *Chrysocoma mucronata* Forssk.]

*Iris* sp.

*Isatis* sp.

*Isoleucus* sp.

*Ixiolirion tataricum* (Pall.) Schult. & Schult.f. [= *Amaryllis tatarica* Pall.]

*Jatropha unicostata* Balf.f.

*Juglans regia* L.

*Juncus arabicus* (Asch. & Buchenau) Adamson [= *Juncus rigidus* Desf.]

*Juncus littoralis* C.A.Mey.

*Juncus maritimus* Lam.

*Juniperus brevifolia* (Seub.) Antoine [= *Juniperus oxycedrus* var. *brevifolia* Seub.]

*Juniperus drupacea* Labill.

*Juniperus excelsa* M.Bieb.

*Juniperus excelsa* subsp. *polycarpos* (K.Koch) Takht.

*Juniperus foetidissima* Willd.

*Juniperus oxycedrus* L.

*Juniperus phoenicea* L.

*Juniperus procera* Hochst. ex Endl.

*Juniperus thurifera* L.

*Kalidiopsis wagenitzii* Aellen [= *Kalidium wagenitzii* (Aellen) Freitag & G.Kadereit]

*Khaya senegalensis* (Desv.) A.Juss. [= *Swietenia senegalensis* Desv.]

*Kickxia aegyptiaca* (L.) Nábělek [= *Antirrhinum aegyptiacum* L.]

*Kickxia woodii* D.A.Sutton

*Kleinia deflersii* (O.Schwartz) P.Halliday [= *Senecio deflersii* Schwartz]

*Kleinia scottii* (Balf.f.) P.Halliday [= *Senecio scottii* Balf.f.]

*Kochia indica* Wight [= *Bassia indica* (Wight) A.J.Scott]

*Lactuca orientalis* (Boiss.) Boiss. [= *Phaenopus orientalis* Boiss.]

*Larrea tridentata* (Sessé & Moc. ex DC.) Coville [= *Zygophyllum tridentatum* Sessé & Moc. ex DC.]

*Lasiospermum brachyglossum* DC.

*Lasiurus scindicus* Henrard [= *Lasiurus hirsutus* (Vahl) Boiss.]

*Lathyrus* sp.

*Launaea nudicaulis* (L.) Hook.f. [= *Chondrilla nudicaulis* L.]

*Launaea* sp.

*Launaea spinosa* (Forssk.) Kuntze [= *Prenanthes spinosa* Forssk.]

*Laurus azorica* (Seub.) Franco [= *Persea azorica* Seub.]

*Laurus nobilis* L.

*Lavandula subnuda* Benth.

*Lemna gibba* L.

*Lens culinaris* Medik.

*Leontice leontopetalum* L.

*Lepidodendron* sp.

*Leptadenia pyrotechnica* (Forssk.) Decne. [= *Cynanchum pyrotechnicum* Forssk.]

*Leucaena leucocephala* (Lam.) de Wit [= *Mimosa leucocephala* Lam.]

*Leucosidea* sp.

*Limeum arabicum* Friedrich

*Limonium axillare* (Forssk.) Kuntze [= *Statice axillaris* Forssk.

*Limonium narbonense* Mill. [= *Limonium globuliferum* Kuntze]

*Limonium meyeri* (Boiss.) Kuntze [= *Limonium gmelinii* (Willd.) Kuntze]

*Limonium iconium* (Boiss. & Heldr.) Kuntze [= *Statice iconia* Boiss. & Heldr]

*Limonium raddianum* (Boiss.) Pignatti ex Brullo

*Lindbergella sintenisii* (H.Lindb.) Bor [= *Poa sintenisii* H.Lindb.]

*Linum usitatissimum* L.

*Lippia nodiflora* (L.) Michx. [= *Phyla nodiflora* (L.) Greene] [= *Verbena nodiflora* L.]

*Lithospermum hispidulum* Sm. [= *Lithodora hispidula* (Sm.) Griseb.]

*Livistona carinensis* (Chiov.) J.Dransf. & N.W.Uhl [= *Hyphaene carinensis* Chiov.]

*Lobularia arabica* (Boiss.) Muschl.

*Londesia eriantha* Fisch. & C.A.Mey. [= *Bassia eriophora* (Schrad.) Asch.]

*Lonicera etrusca* Santi

*Lonicera nummulariifolia* Jaub. & Spach

*Lotus halophilus* Boiss. & Spruner

*Lotus nubicus* Baker

*Lupinus palaestinus* Boiss.

*Lycium arabicum* Schweinf. ex Boiss. [= *Lycium shawii* Roem. & Schult.]

*Lycium persicum* Miers

*Lycium shawii* Roem. & Schult.

*Lycochloa* (Poaceae)

*Lycopersicon esculentum* Mill.

*Maerua crassifolia* Forssk.

*Majorana syriaca* (L.) Raf. [= *Origanum syriacum* L.]

*Malus* sp.

*Marrubium libanoticum* Boiss. [= *Marrubium globosum* subsp. *libanoticum* (Boiss.) P.H.Davis]

*Marsilea minuta* L.

*Matricaria aurea* (Loefl.) Sch.Bip. [= *Cotula aurea* Loefl.]

*Maytenus* sp.

*Medicago arabica* (L.) Huds.

*Melanocenchris abyssinica* (R.Br. ex Fresen.) Hochst.

*Melica persica* Kunth

*Melilotus indicus* (L.) All. [= *Trifolium indicum* L.]

*Mesembryanthemum crystallinum* L.

*Mesembryanthemum forskahlii* Hochst. ex Boiss.

*Mesembryanthemum nodiflorum* L.

*Micromeria sinaica* Benth.

*Mimosa pigra* L.

*Mimusops laurifolia* (Forssk.) Friis.

*Minuartia libanotica* Bornm.

*Minuartia mediterranea* (Ledeb. ex Link) K.Malý

*Moltkiopsis ciliata* (Forssk.) I.M.Johnst. [= *Lithospermum ciliatum* Forssk.]

*Monsonia nivea* (Decne.) Webb [= *Erodium niveum* Decne.]

*Moraea mediterranea* Goldblatt

*Moricandia nitens* (Viv.) E.A.Durand & Barratte [= *Hesperis nitens* Viv.]

*Moringa peregrina* (Forssk.) Fiori [= *Hyperanthera peregrina* Forssk.]

*Mosbeovia* sp.

*Malva parviflora* L.

*Muscari longipes* Boiss. [= *Leopoldia longipes* (Boiss.) Losinsk.]

*Myrica faya* Dryand.

*Myriophyllum spicatum* L.

*Myrtus communis* L.

*Neobuxbaumia mezcalaensis* Bravo

*Nerium mascatense* A.DC.

*Nerium oleander* L. [= *Nerium mascatense* A.DC.]

*Neurada procumbens* L.

*Nicotiana glauca* Graham

*Nigella deserti* Boiss.

*Nitraria retusa* (Forssk.) Asch. [= *Peganum retusum* Forssk.]

*Noaea mucronata* (Forssk.) Asch. & Schweinf. [= *Salsola mucronata* Forssk.]

*Nolina* sp.

*Notholaena* sp.

*Notoceras bicorne* (Aiton) Amo [= *Erysimum bicorne* Aiton]

*Nymphaea lotus* L.

*Ochradenus baccatus* Delile

*Ochradenus harsusiticus* A.G.Mill.

*Ocotea foetens* (Aiton) Baill. [= *Laurus foetens* Aiton]

*Olea europaea* subsp. *cuspidata* (Wall. & G.Don) Cif. [= *Olea europaea* subsp. *africana* (Mill.) P.S.Green]

*Olea europaea* L.

*Oligomeris linifolia* (Vahl ex Hornem.) J.F.Macbr. [= *Reseda linifolia* Vahl ex Hornem.]

*Oliveria decumbens* Vent.

*Oliveria orientalis* DC.

*Olneya tesota* A.Gray

*Onobrychis* sp

*Ononis natrix* L.

*Ophioglossum polyphyllum* A. Braun ex Schub.

*Opuntia ficus-indica* (L.) Mill. [= *Cactus ficus-indica* L.]

*Origanum syriacum* L.

*Orobanche aegyptiaca* Pers.

*Orobanche caucasica* Beck

*Orobanche cernua* Loefl.

*Orobanche hypertomentosa* M.J.Y.Foley [= *Phelipanche hypertomentosa* (M.J.Y.Foley) M.J.Y.Foley]

*Orobanche perangustata* M.J.Y.Foley [= *Phelipanche perangustata* (M.J.Y.Foley) M.J.Y.Foley]

*Orobanche pubescens* d'Urv.

*Oryza barthii* A.Chev.

*Oryza longistaminata* A.Chev.& Roehr.

*Oryza sativa* L.

*Ossaea cuspidata* Poepp. ex Triana

*Ostrya carpinifolia* Scop.

*Otanthus maritimus* (L.) Hoffmanns. & Link

*Oxalis dillenii* subsp. *filipes* (Small) G.Eiten [= *Oxalis florida* Salisb.]

*Oxydendrum arboreum* (L.) DC. [= *Andromeda arborea* L.]

*Oxyria digyna* (L.) Hill [= *Rumex digynus* L.]

*Pachypodium succulentum* (L.f.) Sweet

*Paliurus spina-christi* Mill.

*Pancratium arabicum* Sickenb.

*Pancratium sickenbergeri* Asch. & Schweinf.

*Pandanus odorifer* (Forssk.) Kuntze [= *Keura odorifera* Forssk.]

*Panicum turgidum* Forssk.

*Parrotia persica* C.A.Mey.

*Pectocarya recurvata* I.M. Johnst.

*Peganum harmala* L.

*Pennisetum divisum* (Forssk. ex J.F.Gmel.) Henrard [= *Panicum divisum* Forssk. ex J.F.Gmel.]

*Pennisetum glaucum* (L.) R.Br. [= *Panicum glaucum* L.]

*Pennisetum pedicellatum* Trin.

*Pennisetum polystachion* (L.) Schult. [= *Panicum polystachion* L.]

*Peplidium maritimum* (L.f.) Asch.

*Periploca laevigata* Aiton

*Persea indica* (L.) Spreng. *Laurus indica* L.

*Petrorhagia cretica* (L.) P.W.Ball & Heywood [= *Saponaria cretica* L.]

*Petrosimonia brachiata* Bunge

*Phagnalon sinaicum* Bornm. & Kneuck.

*Phagnalon viridifolium* var. *omanense* Qaiser [= *Phagnalon schweinfurthii* Sch.Bip. ex Schweinf. & Lack]

*Phlomis bruguieri* Desf.

*Phoenix caespitosa* Chiov.

*Phoenix dactylifera* L.

*Phoenix reclinata* Jacq.

*Phragmites australis* (Cav.) Trin. ex Steud. [= *Arundo australis* Cav.] [= *Phragmites communis* Trin.]

*Phragmites karka* (Retz.) Trin. ex Steud. [= *Arundo karka* Retz].

*Picris babylonica* Hand.-Mazz.

*Pilgerochloa* sp.

*Pinus pinaster* Aiton

*Pinus brutia* Ten.

*Pinus halepensis* Mill.

*Pinus nigra* J.F.Arnold

*Pinus nigra* subsp. *pallasiana* (Lamb.) Holmboe [= *Pinus pallasiana* Lamb.]

*Pistacia atlantica* Desf.

*Pistacia khinjuk* Stocks

*Pistacia lentiscus* L.

*Pistacia palaestina* Boiss.

*Pistacia terebinthus* L.

*Pistacia vera* L.

*Pisum sativum* L.

*Pituranthos tortuosus* (Desf.) Benth. & Hook.f. ex Asch. & Schweinf. [= *Deverra tortuosa* (Desf.) DC.]

*Pityrogramma* sp.

*Plantago boissieri* Hausskn. & Bornm.

*Plantago ciliata* Desf.

*Plantago ovata* Forssk.

*Plantago phaeostoma* Boiss. & Heldr.

*Plantago psammophila* Agnew & Chal.-Kabi

*Plantago sinaica* Decne.

*Platypterocarpus* sp.

*Pluchea dioscoridis* (L.) DC.

*Poa sinaica* Steud.

*Podocarpus gracilior* Pilg. [= *Afrocarpus gracilior* (Pilg.) C.N.Page]

*Podonosma galalense* Schweinf. ex Boiss.

*Polycarpaea repens* (Forssk.) Asch. & Schweinf. [= *Corrigiola repens* Forssk.]

*Polycarpon succulentum* (Delile) J.Gay

*Polygala abyssinica* R.Br. ex Fresen.

*Polygonum equisetiforme* Sm.

*Populus* × *canescens* (Aiton) Sm. [= *Populus alba* var. *canescens* Aiton]

*Populus deltoides* Marshall

*Portulaca* sp.

*Postia* sp.

*Potamogeton schweinfurthii* A.Benn.

*Potentilla geranioides* Willd.

*Premna resinosa* (Hochst.) Schauer [= *Holochiloma resinosum* Hochst.]

*Primula boveana* Decne. ex Duby

*Prosopis cineraria* (L.) Druce [= *Mimosa cineraria* L.]

*Prosopis glandulosa* Torr.

*Prosopis juliflora* (Sw.) DC. [= *Mimosa juliflora* Sw.]

*Prunus africana* (Hook.f.) Kalkman [= *Pygeum africanum* Hook.f.]

*Prunus arabica* (Olivier) Meikle [= *Amygdalus arabica* Olivier]

*Prunus lusitanica* L.

*Prunus persica* (L.) Batsch [= *Amygdalus persica* L.]

*Pseudofortuynia* sp.

*Psiadia punctulata* (DC.) Vatke [= *Nidorella punctulata* DC.]

*Pteranthus dichotomus* Forssk.

*Pteris vittata* L.

*Pterocarya fraxinifolia* (Poir.) Spach

*Puccinellia distans* (Jacq.) Parl. [= *Poa distans* Jacq.]

*Pulicaria crispa* Sch.Bip.

*Pulicaria desertorum* DC. ex Decne.

*Pulicaria nobilis* E.Gamal-Eldin

*Punica protopunica* Balf. f.

*Punica granatum* L.

*Pycnocycla cespitosa* Boiss. & Hausskn.

*Pyrethrum cassium* Boiss. [= *Tanacetum poteriifolium* Grierson]

*Pyrus boissieriana* Buhse

*Pyrus syriaca* Boiss.

*Quercus alnifolia* Poech

*Quercus boissieri* Reut. [= *Quercus infectoria* subsp. *veneris* (A.Kern.) Meikle]

*Quercus brantii* Lindl.

*Quercus calliprinos* Webb [= *Quercus coccifera* L.]

*Quercus castaneifolia* C.A.Mey.

*Quercus cerris* L.

*Quercus coccifera* L.

*Quercus ilex* L.

*Quercus ilex* L. subsp. *ilex*

*Quercus infectoria* G.Olivier

*Quercus ithaburensis* Decne.

*Quercus libani* G.Olivier

*Quercus macranthera* Fisch. & C.A.Mey. ex Hohen.

*Quercus mediterranea* Gand. [= *Quercus pubescens* Willd.]

*Quercus petraea* (Matt.) Liebl. [= *Quercus robur* L. var. *petraea* Matt.]

*Quercus pontica* K.Koch

*Quercus praeco* Trel.

*Quercus robur* L.

*Ranunculus* sp.

*Reaumuria hirtella* Jaub. & Spach

*Reaumuria negevensis* Zohary & Danin

*Reichardia tingitana* (L.) Roth [= *Scorzonera tingitana* L.]

*Reseda arabica* Boiss.

*Reseda muricata* C.Presl

*Retama raetam* (Forssk.) Webb [= *Genista raetam* Forssk.]

*Rhamnus alaternus* L.

*Rhamnus lycioides* subsp. *graeca* (Boiss. & Reut.) Tutin [= *Rhamnus graeca* Boiss. & Reut.]

*Rhamnus palaestina* Boiss.

*Rhamnus punctata* Boiss.

*Rhanterium epapposum* Oliv.

*Rhazya stricta* Decne.

*Rhipsalis* sp.

*Rhizophora mucronata* Lam.

*Rhodiola* sp.

*Rhododendron ponticum* L.

*Rhododendron ungerni* Trautv. ex Regel

*Rhus abyssinica* Hochst. ex Oliv. [= *Searsia glutinosa* subsp. *abyssinica* (Hochst. ex Oliv.) Moffett]

*Rhus natalensis* Bernh. ex C.Krauss [= *Searsia natalensis* (Bernh. ex C.Krauss) F.A.Barkley]

*Rhus thyrsiflora* Balf.f. [= *Searsia thyrsiflora* (Balf.f. ) Moffett]

*Rhus tripartita* (Ucria) Grande [= *Searsia tripartita* (Ucria) Moffett]

*Rhytidocaulon* sp.

*Rhytidocaulon macrolobum* Lavranos

*Rhytidocaulon sheilae* D.V.Field

*Reichardia tingitana* (L.) Roth [= *Scorzonera orientalis* L].

*Ricinus communis* L.

*Rosa abyssinica* R.Br.

*Rosa arabica* Crép.

*Rosularia rechingeri* C.-A. Jansson

*Rubia tenuifolia* d'Urv.

*Rubus asirensis* D.F.Chamb.

*Rubus fruticosus* L. ex Dierb. [= *Rubus vulgaris* Weihe & Nees]

*Rumex cyprius* Murb.

*Rumex nervosus* Vahl

*Rumex vesicarius* L.

*Ruppia maritima* L.

*Ruscus hyrcanus* Woronow

*Salicornia europaea* L. [= *Salicornia herbacea* L].

*Salicornia* sp.

*Salix* sp.

*Salsola abarghuensis* Assadi

*Salsola arabica* Ehrenb. ex Boiss.

*Salsola canescens* (Moq.) Boiss. [= *Noaea canescens* Moq.]

*Salsola dendroides* Pall.

*Salsola gossypina* Bunge ex Boiss. [= *Kaviria gossypina* (Bunge ex Boiss.) Akhani]

*Salsola imbricata* Forssk.

*Salsola inermis* Forssk.

*Salsola spinescens* Moq.

*Salsola spinosa* Lam.

*Salsola schweinfurthii* Solms

*Salsola tragus* L. [= *Salsola kali* subsp. tragus (L.) Čelak.]

*Salsola vermiculata* L.

*Salsola volkensii* Schweinf. & Asch. [= *Caroxylon volkensii* (Schweinf. & Asch.) Akhani & Roalson]

*Salvadora oleoides* Decne.

*Salvadora persica* L.

*Salvia aegyptiaca* L.

*Salvia areysiana* Deflers

*Salvia deserti* Decne.

*Salvia mirzayanii* Rech.f. & Esfand.

*Sansevieria abyssinica* N.E.Br. [= *Sansevieria forskaliana* (Schult. & Schult.f.) Hepper & J.R.I.Wood]

*Sansevieria ehrenbergii* Schweinf. ex Baker

*Sarcobatus vermiculatus* (Hook.) Torr. [= *Batis vermiculata* Hook.]

*Sarcopoterium spinosum* (L.) Spach [= *Poterium spinosum* L.]

*Sarcostemma forskaolianum* Schult. [= *Cynanchum forskaolianum* (Schult. ) Meve & Liede]

*Sarcostemma socotranum* Lavranos

*Savignya parviflora* (Delile) Webb [= *Lunaria parviflora* Delile]

*Saxifraga* sp.

*Scabiosa leucactis* Patzak [= *Lomelosia leucactis* (Patzak) Soják]

*Scabiosa olivieri* Coult. [= *Lomelosia olivieri* (Coult.) Greuter & Burdet]

*Scabiosa palaestina* L. [= *Lomelosia palaestina* (L.) Raf.]

*Scandix pecten-veneris* L.

*Schanginia aegyptiaca* (Hasselq. ) Aellen [= *Suaeda aegyptiaca* (Hasselq.) Zohary]

*Schimpera arabica* Hochst. & Steud.

*Schismus arabicus* Nees

*Schismus barbatus* (L.) Thell. [= *Festuca barbata* L.]

*Schoenoplectus litoralis* (Schrad.) Palla

*Schweinfurthia latifolia* Baker

*Schweinfurthia pedicellata* Benth. & Hook.f.

*Sclerocarya birrea* (A.Rich.) Hochst. [= *Spondias birrea* A.Rich.]

*Scorzonera alpina* Hoppe [= *Scorzonera aristata* Ramond ex DC.]

*Scorzonera drarii* Täckh.

*Scrophularia deserti* Delile

*Scrophularia libanotica* Boiss.

*Scrophularia syriaca* Benth.

*Scutellaria* sp.

*Sedum* sp.

*Seidlitzia rosmarinus* Bunge ex Boiss.

*Selaginella* sp.

*Senecio belbeusius* Delile

*Senecio glaucus* L.

*Seriphidium herba-alba* (Asso) Soják [= *Artemisia herba-alba* Asso]

*Sesbania rostrata* Bremek. & Oberm.

*Sida urens* L.

*Sigillaria* sp.

*Silene arabica* Boiss.

*Silene apetala* var. *alexandrina* Asch. [= *Silene apetala* Willd.]

*Silene succulenta* Forssk.

*Silybum marianum* (L.) Gaertn. [= *Carduus marianus* L.]

*Sisymbrium erysimoides* Desf.

*Solanum sinaicum* Boiss.

*Solanum villosum* Mill.

*Sonchus maritimus* L.

*Sonchus oleraceus* L.

*Sorbus boissieri* C.K.Schneid. [= *Sorbus aucuparia* L].

*Sorbus umbellata* (Desf.) Fritsch [= *Crataegus umbellata* Desf.]

*Sorghum halepense* (L.) Pers.

*Spergula fallax* (Lowe) E.H.L.Krause [= *Spergularia fallax* Lowe ]

*Spergularia marina* (L.) Besser

*Sporobolus arabicus* Boiss. [= *Sporobolus ioclados* Nees]

*Sporobolus pyramidalis* P.Beauv.

*Sporobolus spicatus* (Vahl) Kunth [= *Agrostis spicata* Vahl

*Stachys aegyptiaca* Pers.

*Sterculia africana* (Lour.) Fiori [= *Triphaca africana* Lour.

*Sterculia rivae* Chiov.

*Sterculia setigera* Delile

*Stipa capensis* Thunb.

*Stipa parviflora* Desf.

*Stipagrostis ciliata* (Desf.) De Winter [= *Aristida ciliata* Desf.

*Stipagrostis drarii* (Täckh.) De Winter [= *Aristida drarii* Täckh.

*Stipagrostis plumosa* Munro ex T.Anderson

*Straussiella* sp.

*Styrax officinalis* L.

*Suaeda aegyptiaca* (Hasselq.) Zohary

*Suaeda fruticosa* Forssk. ex J.F.Gmel. [= *Suaeda vermiculata* Forssk. ex J.F.Gmel.]

*Suaeda monoica* Forssk. ex J.F.Gmel.

*Suaeda palaestina* Eig & Zohary

*Swertia abyssinica* Hochst.

*Synelcosciadium* sp.

*Syringodium isoetifolium* (Asch.) Dandy [= *Cymodocea isoetifolia* Asch.]

*Talinum calycinum* Engelm.

*Tamarindus indica* L.

*Tamarix aphylla* (L.) H.Karst. [= *Thuja aphylla* L.]

*Tamarix arabica* Bunge [= *Tamarix senegalensis* DC.]

*Tamarix nilotica* (Ehrenb.) Bunge [=*Tamarix senegalensis* DC.]

*Tamarix passerinoides* Delile

*Taverniera aegyptiaca* Boiss.

*Taverniera spartea* (Burm.f.) DC. [= *Hedysarum spartium* Burm.f.]

*Teclea nobilis* Delile [= *Vepris nobilis* (Delile) Mziray

*Tephrosia apollinea* (Delile) DC. [=*Galega apollinea* Delile]

*Tephrosia kassasii* Boulos

*Terminalia brownii* Fresen.

*Teucrium polium* L.

*Teucrium stocksianum* Boiss.

*Thymelaea hirsuta* (L.) Endl. [= *Passerina hirsuta* L.]

*Thymelaea mesopotamica* (C.Jeffrey) B.Peterson [= *Ligia mesopotamica* C.Jeffrey]

*Tilia rubra* DC.

*Tirucalli* sp.

*Tithymalus* sp.

*Trianthema sheilae* A.G.Mill. & J.Nyberg

*Tribulus arabicus* Hosni

*Trichilia emetica* Vahl

*Trichocalyx* sp.

*Trichocladus* sp.

*Trichodesma africanum* (L.) Sm. [= *Borago africana* L.]

*Trifolium alexandrinum* L.

*Trifolium patens* Schreb.

*Trifolium repens* L.

*Trigonella arabica* Delile

*Trigonella maritima* Poir.

*Trigonella stellata* Forssk.

*Trisetaria chaudharyana* H.Scholz

*Tristicha trifaria* (Bory ex Willd.) Spreng. [= *Dufourea trifaria* Bory ex Willd.]

*Triticum aestivum* L.

*Triticum dicoccoides* (Körn. ex Asch. & Graebn.) Schweinf. [= *Triticum dicoccon* var. *dicoccoides* Asch. & Graebn.]

*Triticum monococcum* L.

*Tulipa* sp.

*Typha domingensis* Pers.

*Ulmus glabra* Huds.

*Urginea maritima* (L.) Baker [= *Drimia maritima* (L.) Stearn]

*Valerianella oxyrhyncha* Fisch. & C.A.Mey.

*Valerianella sclerocarpa* Fisch. & C.A.Mey.

*Verbascum akdarense* (Murb.) Hub.-Mor. [= *Celsia akdarensis* Murb.]

*Verbascum sinaiticum* Benth.

*Verbascum transjordanicum* Murb.

*Veronica persica* Poir.

*Vicia palaestina* Boiss.

*Vicia sativa* L.

*Vicoa pentanema* Aitch. & Hemsl. [= *Pentanema divaricatum* Cass.]

*Viola nubica* Hutch. ex Broun & Massey

*Viola spathulata* Willd. ex Schult.

*Vitex doniana* Sweet

*Vitis labrusca* L.

*Vitis sylvestris* C.C.Gmel. [= *Vitis vinifera* L.]

*Volutaria sinaica* (DC.) Wagenitz

*Vulpia muralis* (Kunth) Nees [= *Festuca muralis* Kunth]

*Wellstedia laciniata* Thulin & A.Johanss.

*Wellstedia socotrana* Balf.f.

*Wellstedia somalensis* Thulin & A.Johanss.

*Xanthium spinosum* L.

*Yucca* sp.

*Zelkova carpinifolia* (Pall.) K. Koch [= *Rhamnus carpinifolia* Pall.]

*Zelkova hyrcana* Grossh. & Jarm. [= *Zelkova carpinifolia* (Pall.) K. Koch]

*Zerdana* sp.

*Zilla spinosa* (L.) Prantl [= *Bunias spinosa* L.]

*Ziziphus mauritiana* Lam. [= *Ziziphus jujuba* Mill.]

*Ziziphus nummularia* (Burm.f.) Wight & Arn. [= *Rhamnus nummularia* Burm.f.]

*Ziziphus spina-christi* (L.) Desf. [= *Rhamnus spina-christi* L.]

*Ziziphus lotus* (L.) Lam. [= *Rhamnus lotus* L.]

*Zygophyllum aegyptium* Hosny

*Zygophyllum album* L.f.

*Zygophyllum coccineum* L.

*Zygophyllum decumbens* Delile

*Zygophyllum desertorum* Forssk.

*Zygophyllum dumosum* Boiss.

*Zygophyllum mandavillei* Hadidi

*Zygophyllum migahidii* Hadidi

*Zygophyllum qatarense* Hadidi

*Zygophyllum simplex* L.

## Animal species

*Aepyceros melampus* Lichtenstein

*Arabitragus jayakari* Thomas

*Bos primigenius* Bojanus [= *Bos primigenius africanus* Thomas]

*Bubo ascalaphus* Savigny

*Camelus dromedaries* L.

*Capra aegagrus* Erxleben

*Capra ibex* L.

*Caracal caracal schmitzi* Schreber

*Ceratotherium simum* Burchell

*Chelonia mydas* L.

*Cursorius cursor* Latham

*Dugong dugong* Muller

*Felis silvestris* lybica Forster

*Francolinus ochropectus* Dorst & Jouanin

*Gazella dorcas* L.

*Gazella gazella* cora Pallas

*Giraffa camelopardalis* L.

*Loxodonta Africana* Blumenbach

*Onychognathus tristramii* Sclater

*Oryx leucoryx* Pallas

*Ovis orientalis* Gmelin

*Panthera pardus nimr* Hemprich & Ehrenberg

*Pinctada radiata* Leach

*Pycnonotus xanthopygos* Hemprich & Ehrenberg,

*Raphicerus campestris* Thunberg

*Sousa chinensis* Osbeck

*Struthio camelus* L. [= *Struthio camelus syriacus* Rothschild]

*Sus scrofa* L. [= *Sus scrofa domestica* Erxleben]

*Sylvicapra grimmia* L.

*Taurotragus oryx* Pallas

*Teratoscincus keyserlingii* Strauch

*Tragelaphus strepsiceros* Pallas

*Tursiops truncatus* S.Str.

*Uromastyx aegyptia* leptieni

*Vulpes cana* Blanford

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