Environmental biology deals with how organisms respond to their environment. This includes responses to physical factors such as air temperature, relative humidity, precipitation, wind speed, and solar radiation – factors generally familiar from weather reports. It also encompasses these factors in very local regions, or microhabitats (Fig. 1.1), where a seed may chance to fall and hence seeding establishment ensue. Seeds of Agave deserti or Ferocactus acanthodes* can germinate in late summer in the Sonoran Desert, when the maximum air temperature reported by the regional weather bureau or registered on the digital electric sign of a local bank may be 35°C. But this is of little consolation to a small seeding in bare ground where the soil surface temperature can exceed 70°C (158°F)! The environment represents all the external conditions that can affect the growth and survival of an organism. Thus, we will also consider the edaphic or soil factors, ranging from nutrients to water. It is not sufficient to know how much rainfall there is; we must also know how a particular precipitation event affects the energy of the soil water in the vicinity of a root. Water moves energetically downhill,

* The full, unambiguous, scientific name of an organism is an italicized Latin binomial, indicating genus and species, followed by the authority (usually abbreviated), which indicates the person who first applied the current binomial. The complete names, including authorities for all the species mentioned in this book, are collected together in the section Taxonomy and Morphology (Table 1.1 for agaves and Table 1.2 for cacti).

so the water potential must be lower in the root than in the adjacent soil for water uptake to occur. We will also consider why a succulent agave or cactus filled with water does not lose this precious commodity back to a drying soil and thus become desiccated to the point of death. The topic of water relations, including water uptake by roots, requires a detailed consideration of the components that contribute to water potential together with the observed
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root properties, such as the rehydration of existing roots and the induction of new lateral roots after rain.

Understanding the consequences for water uptake of the observed root distribution in the soil can be aided by sets of equations that are combined into a model to describe plant behavior. We will find that models help interpret the shapes of agaves and cacti with respect to the interception of solar radiation; models can indicate the influences of spines on stem temperatures, which affect the ranges over which cacti can occur naturally. Another objective in our consideration of the environmental biology of agaves and cacti will be to integrate all the physical factors so that we can predict productivity in different regions – after all, a plant will not be successful in a particular environment if it does not have a net positive uptake of carbon dioxide (CO₂) from the atmosphere and the incorporation of the carbon from such CO₂ into organic compounds. As is already apparent, we are building up a specialized vocabulary in this chapter, some terms of which have rather specific definitions. For example, desert is an anthropocentric term; referring to dry places that are often generally hot for part of the year, arid refers to regions with less than 250 mm of annual rainfall (ignoring certain complications between the timing of rainfall and the ambient air temperature), and semiarid generally refers to regions with 250 to 450 mm of annual rainfall (250 mm = 0.25 m = 10 inches).

There are many reasons for choosing agaves and cacti for our study, not the least of which is their intriguing shapes. Indeed, many people are attracted to them because of their morphology, or external form and structure (Fig. 1.2). The often spectacular and bizarre morphology of these desert succulents can also lead to interesting effects on their distribution. Other people are attracted by the frequently severe nature of their habitats. Survival of agaves and cacti in such regions is often related to their fleshy massiveness, or succulence. We shall see that such water storage capability also occurs on a cellular level and is related to the photosynthetic pathway used by most of them, known as Crassulacean acid metabolism, or CAM for short. Plants exhibiting CAM open their stomata (surface pores) and have a net uptake of CO₂ mainly at night, when the lower tissue temperatures and higher ambient relative humidity lead to less water loss than for daytime stomatal opening. Thus, CAM can be crucial for growth and survival in arid habitats and has evolved many times in diverse taxa (groups of related plants). Indeed, another reason for studying agaves and cacti together is that these unrelated taxa have evolved remarkably similar responses to a particular set of environmental conditions, as we shall see when individual physical factors are considered. Over the years many different species of agaves and cacti have been used for food, fodder, fiber, fences, fuel, medicinal purposes, and ornamental horticulture, and many agaves and cacti are currently cultivated over wide areas in arid and semiarid regions of the world. As more marginal lands in arid and semiarid regions are, of necessity, brought into cultivation in the future, these species will assume even greater economic importance.

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Research on agaves and cacti prior to the twentieth century did not employ the equipment currently considered indispensable for environmental biology. Nevertheless, certain agronomic principles were clearly recognized by native Indians in what is now North America, especially Mexico. Such Indians supplemented their diets with the raw fruits from many species of cacti and the roasted inflorescences, stems, and folded leaves of agaves (Sauer, 1965); roasting broke down the glucans (polymers of glucose, such as the common glukan starch) and other hexose polymers into digestible sugars (e.g., glucose and fructose).

Based on evidence from fossilized human feces, Callen (1965) has shown that both agaves and cacti were consumed by humans at least 9,000 years ago (Fig. 1.3). The characteristic stomata and druses (aggregate crystals of calcium oxalate radiating from a central point) of cacti helped identify the consumed cacti as a Stenocereus (organ-pipe cactus) and an Opuntia (termed “prickly-pear”) cactus based on fruit shape for those opuntias with characteristically flattened pads known as platyopuntias). The Agave was identified
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Figure 1.2. Variation in stem morphology of four species of cacti occurring sympatrically (meaning, at the same site): (A) *Ferocactus acanthodes* (a barrel cactus), (B) *Opuntia acanthocarpa* (deerhorn cholla; note the red diamond rattlesnake (*Crotalus ruber*) near the center of the picture), (C) *Mammillaria dioica* (known as the fishhook cactus because of the shape of its spines), and (D) *Opuntia basilaris* (beaver-tail cactus). The site is the same as for Figure 1.1.

Figure 1.3. Percentage of fossilized human feces that contained material identified as coming from an agave or a cactus. Samples were collected from caves in Tamaulipas, a state in northwestern Mexico, and Tehuacán, a state in southern Mexico. Modified from Callen (1985).
based on the pattern of epidermal (outermost) leaf cells around its stomata. On average, about half of the human feces contained cactus stem material, and nearly as much contained agave leaf material, throughout the entire period studied of nearly 9,000 years (Fig. 1.3), indicating the occurrence of desert succulents in the diet of prehistoric Indians from Mexico for an extremely long period. Archeological evidence also indicates that artifacts made from agave fibers and tools from agave leaf tips have been in use from 9,000 years before the present onward (Gentry, 1982). For instance, the hard fiber from Agave lechuguilla was used over 8,000 years ago for sandals (Crane and Griffin, 1958). Use of agaves and cacti undoubtedly led to their cultivation, beginning at least 6,000 years before the present (Sánchez-Mejorada R., 1982). For instance, cacti were apparently vegetatively propagated by prehistoric people in the Caribbean by inserting stem segments into specially raised soil mounds, which provided locally well-drained soil suitable for these desert succulents. Agaves were cultivated in the southwestern United States about 1,000 years ago by the Hohokam, who apparently used rocks as a mulch to prevent loss of soil water from around the plants (Fish et al., 1985).

Beginning in the fifteenth century, many of the ancient agronomic practices and uses of these plants were described by the invading Europeans, who disseminated agaves and cacti worldwide. In this section we will summarize some of these uses of agaves and cacti. In the next section we consider certain early research that helps illustrate the environmental “strategies” used by desert succulents.

**AGAVES**

**Beverages**

In the late fifteenth and early sixteenth centuries, the cultivation of agaves became widespread (Sanchez Marroquin, 1979; Gentry, 1982). As the Spaniards colonized regions in the northcentral part of present-day Mexico, they forced the Nahua Indian Indians to move with them and to cultivate Agave salmiana (Fig. 1.4A) and a few other species (commonly called “maguey”) in warm and arid climates for pulque (Fig. 1.4B), a fermented beverage produced from the sap that collects near the top of the stem after the central spike of folded leaves is excised from the larger plants (Fig. 1.4C). Actually, the sweetish sap is often consumed directly as the beverage aquaamiet (“honey water”). These two beverages presumably were drunk in prehistoric times. Indeed, the Aztecs discovered the use of pulque during their migration to the Valley of Mexico at the end of the twelfth century (Gentry, 1982).

Internationally, agaves are better known for the distilled beverages mescal (also spelled mezcal), produced from A. salmiana and at least eight other species (e.g., A. angustifolia in Oaxaca), and tequila, produced primarily from A. tequilana (Fig. 1.5). These beverages were developed after Europeans introduced distillation into North America in the sixteenth century. A mescal factory tends to be a cottage (even bootleg) industry, where the piñas or cabezas (Fig. 1.5B), generally weighing 25–50 kg (but which can be up to 170 kg), are traditionally crushed by a large millstone turned by a burro, oxen, or, more recently, a tractor. The resulting mash is fermented and then distilled in small stills, sometimes with a second distillation (Bahre and Bradbury, 1980; Tello Balderas, 1983; Tello Balderas and García-Moya, 1985). Tequila, which is generally double distilled, tends to be produced in large, modern factories near its namesake town of Tequila, Jalisco, where its manufacture began in 1621. Its production is more formal than that of mescal; in addition, the better grades of tequila are aged for various periods before distribution (Valenzuela, 1985).

**Fiber**

Beginning in the nineteenth century, fiber-bearing agaves, mainly Agave sisalana (sisal; Fig. 1.6), were exported from Mexico, forming the basis of major industries in Indonesia and the Philippines in the nineteenth century and in East Africa in the twentieth century. To protect its fiber industry, Mexico had prohibited the export of its native A. sisalana, but some plants were available from Florida. In 1893, 1,000 bulbls (plantlets produced on the inflorescence of certain agaves and which are suitable for vegetative reproduction) of such A. sisalana were sent to Germany; about 200 survived this trip and 62 sur-
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![Image of agave plants](image)

Figure 1.4. (A) *Agave salmiana*, which is used for both pulque and mescal, growing near Salinas de Hidalgo, San Luis Potosí, Mexico. The leaves and inflorescences have been cut on the large plants, which leads to the accumulation of more organic compounds such as sugars in the stem. (B) A “pulquero” using a gourd to remove aguamiel from a large agave near Tijuana, Jalisco, Mexico (photographed by Ana G. Valenzuela). (C) The sap collects in a basin atop the stem formed by cutting through many leaves.

vived the ensuing trip to German East Africa, now Tanzania (Lock, 1962). Within five years, these plants had multiplied into 63,000 plants, which laid the foundation for what was to become one of the most widespread cultivations of any CAM plant. Indeed, plantations of *A. sisalana* currently occupy much of Tanzania and part of Angola, Kenya, Mozambique, and Uganda. These African countries supply about half of the world’s hard fiber, another 20% or
so coming from *A. sisalana* grown in Brazil (Gentry, 1982). By the early twentieth century, *A. sisalana* was also successfully cultivated in India, Southeast Asia, many Pacific islands, and Australia in regions of sufficient rainfall and well-drained soils (Smith, 1929). Besides commercial uses as a hard fiber, primarily as a twine for bales of hay, for rope, and for sacks, a large handicraft industry has arisen around *A. sisalana*, ranging from baskets to upholstery to dart boards (Kenya Sisal Board, 1984; Baker, 1985).

Much hard fiber is also produced from agaves in Mexico (about 20% of the world’s supply). This fiber comes mainly from *A. fourcroydes* (benequén, Fig. 1.7) grown in plantations in the Yucatán peninsula of eastern Mexico and secondarily from *A. lechuguilla* (Fig. 1.8), which has been collected from the wild in at least seven states in northeastern Mexico on more than 130,000 km² at some time during the last 200 years (Taylor, 1966; Sheldon, 1980; García de Fuentes and de Sicilia, 1984; Ramírez, 1985). The older unfolded leaves of *A. fourcroydes* are harvested one or two times per year; for *A. lechuguilla* the young leaves still folded about the central spike are harvested for fiber, and new central spikes are then produced so that the same plants can be harvested every one to five years. These species occur in quite different habitats: *A. fourcroydes* is grown in the unique, shallow limestone soils of Yucatán, which has no surface streams or rivers, although the mean annual temperature is mild (27°C) and annual precipitation regularly exceeds 1,000 mm (Smith and Cameron, 1977); *A. lechuguilla* is exposed to the rainfall vagaries of the Chihuahuan Desert.

Over twenty specific commercial uses

Figure 1.5. (A) Fields of *Agave tequilana* growing near Tequila, Jalisco, Mexico. Plants in the foreground are five years old. (B) The author holding the stem and attached leaf bases, which is called a *pilán* because it resembles a pineapple (or a “cabeza,” meaning head). This *pilán* was harvested from an eight-year-old plant and will be taken to a local factory for roasting for 24–36 h followed by shredding and then fermenting of the mash for 36–48 h as a prelude to distillation to obtain tequila.
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Figure 1.6. *Agave sisalana*, which has been cultivated worldwide for the hard fiber in its leaves known as "sisal" or "sisal hemp": (A) Abandoned sisal plantation near Thika, Kenya; (B) Mature plants from which lower leaves have been harvested; and (C) Empty, rusty carts for hauling sisal from field near Nairobi, Kenya.

exist for the fibers of agave from Mexico, primarily for woven objects, ropes, or as stuffing (Gentry, 1982). The fiber has been used for paper and, more recently, in construction material (Belmares, Castillo, and Barrera, 1979; Cruz-Ramos, Orellana, and Robert, 1985; Padilla R. and Fuentes R., 1985). *Agave four-roydes* began to dominate the economy of the Yucatán peninsula in the mid-nineteenth century and became the main export crop of Mex-
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Figure 1.7. (A) Agave fourcroydes growing near Mérida, Yucatán, Mexico. The six-year-old plants are growing at the experimental plots of Centro de Investigaciones Agrícolas de la Península de Yucatán (CIAPy). Measurements are being made by Carlos Oropeza. (B) Woodcut of a fiber plantation of A. fourcroydes in Yucatán (adapted from Royal Gardens, Kew, 1898). (C) Fiber drying in sun near Mérida (photographed by Luis del Castillo).

ico near the turn of the century (Camp, 1980). Also, at least some annual income for up to 500,000 people in northeastern Mexico can come from A. lechuguilla (Sheldon, 1980). However, the advent of synthetic fibers in the 1920s and 1930s has led to the worldwide economic demise of fibers from agaves (Smith and Cameron, 1977; Sprague, Hanna, and Chappell, 1978).

Additional uses

Although agaves have chiefly been used for the production of fiber and alcoholic beverages, they have served man in many other ways. Other food uses include the eating of flowers after boiling or scrambling them with eggs and peeling off the cuticle (waxy layer on the epidermis) of Agave atrovirens for use as a translucent wrapper for tortilla sandwiches and of A. salmiana to wrap meat. The Seri Indians, who inhabit the state of Sonora in northwestern Mexico, currently consume parts of nine different species of agaves; the most common food is prepared from the leaf bases, stem, or inflorescence after roasting (Felger and Moser, 1985). Acanthium has also


Uses

Figure 1.8. (A) Agave lechuguilla, which apparently has more rosettes under natural conditions than any other agave, growing near Saltillo, Coahuila, Mexico. Leaves of the plants were marked and examined monthly as part of a productivity study with Edgar Quero. (B) Fibers of the harvested central spike of A. lechuguilla drying in the sun prior to commercial use for burlap sacks and pillow filling.

served as uncontaminated drinking water for thirsty desert travelers. Agaves were exported from Mexico to Europe as ornamentals, mainly A. americana (Fig. 1.9). By the eighteenth century it was established in both private and public gardens along the Mediterranean Sea and the warmer parts of Europe – the cold winters prevented the growth of A. americana outdoors in northern and central Europe. Indeed, A. americana and various other species are now horticulturally used worldwide.

Cortez in the early sixteenth century complained about the deterrent influence of agave spines on the advance of his army (Sprague et al., 1978). Indeed, agave spines were used for punishing juvenile delinquents and runaway slaves (Gentry, 1982). The stalks of the inflorescences have been used for fencing and construction. From a more industrial point of view, agaves have been used in the manufacture of paper, including that for currency, and the production of soaps, shampoos, and medicines (Gentry, 1982). Indeed, many species of agaves contain by dry weight over 2% sapogenins, which are soapy compounds, widely used as shampoos, from which cortisone and sex hormones like estrogen can be synthesized (dry weight is the mass of a plant or plant part after drying to remove water, such as in an oven at 80°C). For instance, A. schottii can contain 2% sapogenins by dry weight and was used as a cleaning agent by Indians, and A. vilmoriniana can contain over 4% sapogenins (Gentry, 1982). About 6% of the world’s supply of precursors for corticosteroid synthesis has come from agaves, indicating their pharmacological importance (Blunden, Culling, and Jewers, 1975; Herz, 1985). Fermentable sugars can be 50% of the dry weight of the leaves, so agaves can also be used to produce ethanol for industrial purposes and for gasohol (McDaniel, 1985; but see de Menezes and Azzini, 1985). Leaves of agaves such as A. salmiana have been used as cattle fodder in Mexico. The pulp of leaves of A. fourcroydes, a waste product of the fiber
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Figure 1.9. Agave americana, the first-named member of the genus, used as a fence in the jungle region of northern Thailand near the border with Burma. It occurs worldwide as an ornamental plant and is used in certain parts of Mexico for the production of pulque.

industry, has been used as a source for bacterial fermentation, which can increase the protein content of the resulting meal, making it more useful as a livestock feed (Sanchez Marroquin, 1979; Blancas et al., 1982). The list of uses for agaves is indeed quite long.

CACTI

Because of their unusual stem morphology and their attractive flowers, cacti became very popular in European gardens and households beginning in the sixteenth century. Indeed, collectors, hobbyists, and landscape designers have exerted a major influence on the commercialization of hundreds of cactus species and the establishment of major cactus societies in Canada, the United States, Mexico, Great Britain, Belgium, the Netherlands, France, West Germany, Switzerland, East Germany, Czechoslovakia, Japan, Taiwan, New Zealand, Australia, Zimbabwe, South Africa, and many other countries. A cactus figures in the Aztec legend of the founding of what is now Mexico City and consequently is recognized in the national flag of Mexico, which is embellished with an eagle perched on an opuntia, a rendition of the vision seen by the Aztecs in 1325 as a divine sign that they had reached the promised land (Sánchez-Mejorada R., 1982).

Specialized uses

Besides their worldwide use as ornamental plants, cacti became widely propagated as host plants for the cochineal scale insect (previously, Coccus cacti; now Dactylopius coccus). The Aztecs prized the rich red color of carminic acid (termed carminate for the disassociated acid) extracted from the dried bodies of the female insects, which were raised on cladodes of many species of prickly-pear cacti, including Opuntia ficus-indica, O. littoralis, O. phaeacantha, and O. stricta, among others (Evans, 1967; Donkin, 1977; Benson, 1982). Indeed, the white, cottonlike, fibrous cocoon material secreted by the female insects is still a common sight on the cladodes of platypuntias, generally near the arrocles (auxillary buds that produce a cluster of spine primordia and which are found only on the stems of cacti).