Chapter 3
The Evolution of North American Deserts and the Uniqueness of Cuatro Ciénegas

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Abstract With an area of less than 600 km^2, the Cuatro Ciénegas Basin harbors one of the most diverse desert landscapes in Mexico. On the general aridity pattern of the Chihuahuan Desert, limited by a very short season of scant summer rain, a unique geology of gypsum soils is superimposed, dotted by montane sky islands where relicts of temperate vegetation that occupied the Mexican Plateau still survive. Plants here show remarkable adaptations to this unique desert environment, including tolerance to gypsum and salinity, seed retention (serotiny) during the dry season, thick, isolateral leaves, and a panoply of different life-forms, including desert annuals, stem- and leaf-succulents, microphyllous shrubs, desert perennial with photosynthetic stems, and drought-deciduous trees, and phreatophytes, tapping the deep with powerful pivot roots. This chapter analyzes the evolution of this diversity of life-forms in the heart of the Chihuahuan Deserts, and discusses the challenges and opportunities it offers for conservation and sustainable resource use.

Keywords Gypsophily · Sky islands · Relictual vegetation · Desert annuals · Serotiny · Leaf isolaterality · Nurse plants

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Introduction

With an area of less than 600 km^2, the Cuatro Ciénegas Basin harbors one of the most diverse landscapes in Mexico, including (a) aquatic habitats maintained by the basin's lowland *pozas* (artesian pools); (b) desert plains; (c) gypsum dunes and flats; (d) basin grasslands; (e) montane chaparral; (f) oak and oak-pine woodlands, and (g) montane conifer forests. Plants here have to deal with a panoply of environmental factors limiting their growth, including aridity in the desert plains, seasonal flooding around the *pozas*, salinity in the lower playas, shifting substrates in the dunes, gypsum soils, and freezing conditions in the mountains. This heterogeneity has been the driving factor of the region's remarkable biodiversity: With a flora of 860 vascular plants, the valley contains 49 species whose type specimens were found in the valley, and 23 species that are fully endemic to the basin. Endemism is particularly high in the lower parts of the basin, where extreme conditions have forced desert species to develop unique adaptations (Pinkava 1984).

Thus, the taxonomic diversity of the area is complemented by an extraordinary array of morphologies and life histories. Psammophily, the adaptation to dune substrates, is combined here with gypsophily, the ability to grow on gypsum soils saturated by calcium sulfate. Desert plants show a remarkable array of drought-evading strategies such as deep taproots, microphylls with exceptionally small leaves, water-storing succulents, and short-lived ephemerals that retain seeds in their dead tissues until the next rains arrive, among many others. The Cuatro Ciénegas Basin (henceforward, CCB) provides a deep insight into the evolution of desert plants.

Geologic Origin

During the middle of the Cretaceous Period, some 100 million years ago, North America was a set of two major land masses called by geologists Laramidia (the western section) and Appalachia (the eastern one). The central part of what is now North America was part of a gigantic depression where the Arctic Ocean and the Gulf of Mexico met to form a large seaway—the Western Interior Seaway—800 m deep, 1000 km wide, and over 3000 km long. Different sediments accumulated in the floor of this ancient sea—in some parts, organic debris and mud, in others, sand or the remains of the calcareous exoskeletons and shells of algae, diatoms, crinoids, foraminifera, corals, bryozoans, and mollusks (Cochran et al. 2003).

The tectonic forces pushing the North American Plate produced the uplift of the Cretaceous Seaway and folded the coast of Mexico into the Eastern Sierra Madre, around 65 million years ago at the end of the Cretaceous. The old ocean floors were raised and the ancient marine sediments were hoisted into layers of shale, sandstone, and limestone that can be seen today from the Great Plains along

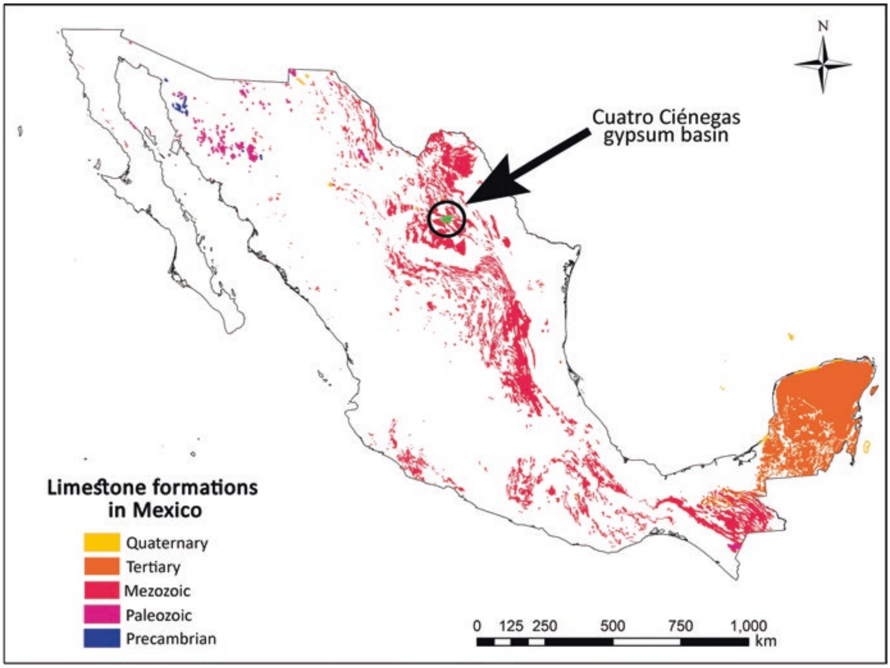

Fig. 3.1 Distribution of limestone substrates in Mexico (modified from INEGI's Geologic chart of Mexico, available at https://www.inegi.org.mx/temas/mapas/geologia/). Note the large corridor of Mezozoic rocks (66–251 My BP) of marine origin that form the Eastern Sierra Madre, and the location of the Cuatro Ciénegas gypsum basin in a closed watershed, or "bolsón," in the arid north of the calcareous ranges

Mexico's Sierra Madre all the way to the Guatemalan border (Cochran et al. 2003). As a consequence, the system of mountains and ranges that form Mexico's Eastern Sierra Madre are rich in calcareous sediments transformed into limestone rocks (Fig. 3.1).

In some closed valleys within these massive calcareous sierras gypsum deposits have been formed over the years by solubilization of calcium salts and their re-deposition combined with sulfate solutions from hydrothermal veins. The closed basins allow waters high in calcium and sulfate content to slowly evaporate and be regularly replenished with new sources of water. The result is the accumulation of large beds of sedimentary gypsum, and Cuatro Ciénegas Basin (CCB) is one of the most spectacular examples of this process in the world. Furthermore, because gypsum dissolves over time in water, gypsum sand dunes are only found in extremely dry environments such as Cuatro Ciénegas in México (Ochoterena et al. 2020, this volume) and White Sands in the US State of New Mexico, both within the northern Chihuahuan Desert.

The Causes of Aridity

Two large deserts occupy the northern states of Mexico: (a) the Sonoran Desert, which runs along the coastal states of Mexico's Pacific Northwest (Sinaloa, Sonora, Baja California, and Baja California Sur), and (b) the Chihuahuan Desert, which occupies the Mexican northern *Altiplano*, i.e., the highland plateau that stretches between Mexico's two large range systems, the Eastern and the Western Sierra Madre. Together with the Mojave Desert in the USA, they form the large subtropical deserts of North America, lying at 25–35° latitude and some 2000 km away from the tropical rainforests of southern Mexico and Central America (Ezcurra et al. 2006; Ezcurra and Mellink 2013).

Deserts in North America occur in these precise latitudes because of the general thermodynamics of our planet: Solar radiation hits the Earth with highest intensity near the equator. Because the Earth's axis is tilted 23.5° with respect to the plane of its orbit, during a part of the year, the zone of maximum solar interception shifts northwards, towards the Tropic of Cancer, and during the other part it moves southwards, towards the Tropic of Capricorn. Thus, the warm tropics form a belt around the equator from latitude 23°N to latitude 23°S, where the tropical heat generates rising, unstable air. As the rising air cools in its ascent, it condenses the moisture evaporated from the warm tropical seas and forests producing the heavy downpours that characterize the wet tropics. Having lost its moisture, the air moves in the upper atmosphere away from the tropical belt, and starts to descend around 25–30° latitude. This stable, dry air forms the mid-latitude arid fringes that run north and south of the tropical belt, forming corridors of stable atmosphere—known as the "horse" latitudes—where calm air dominates. The closed circulation of air, ascending in the tropics into the upper atmosphere to descend in the subtropical latitudes and moving again towards the tropics, is known as the "Hadley Cells" (in honor of the British climatologist George Hadley). Hadley Cells, the low-latitude overturning circulations that have air rising at the equator and sinking at 30° latitude, are responsible for the trade winds in the Tropics and control low-latitude weather patterns. Because of the stable atmosphere in the polar-ward side of the cells not only winds are slack but also rainstorms seldom develop; and this is the reason why most of the world's large deserts occur at these latitudes both in the northern and southern hemisphere (Goudie and Wilkinson 1977; McGinnies et al. 1977).

Mexico's topographic heterogeneity also contributes to the formation of drylands, especially within the country's tropical belt. When the moisture-laden tropical trade winds reach continental mountain ranges they cool as they ascend, condensing as fog and drizzle that feed montane cloud forests. Once the winds pass the mountain divide, they start compressing and warming-up again in their descent, but, having left behind their original moisture, they become hot and dry. Thus, while the windward slopes of most tropical mountain ranges are covered by cloud forests, the leeward part, also known as the "rain shadow" of the mountains, is covered by arid scrubs. The rain shadow effect is largely responsible for the intriguing occurrence of tropical drylands in areas where one would expect tropical forests, such as the Tehuacán Valley desert in the states of Puebla and Oaxaca, Mexico, a hotspot for cactus biodiversity. Because the Chihuahuan Desert lies between the two Sierra Madre ranges, potential sources of precipitation are also trapped in the rain shadow of these mountains.

Desert Sky Islands and Climates of the Past

At a very large scale, two very distinct types of desert geomorphologies can be recognized: large, mostly flat "shield" deserts, and highly folded, topographically heterogeneous "basin-and-mountain" deserts (Cooke et al. 1993). Shield deserts have developed on ancient crystalline bedrocks and are mainly composed of very old land systems unearthed and leveled by erosion forming relatively flat landscapes with continuous desert vegetation, such as the Sahara or the Arabian deserts. Basin-and-mountain deserts are formed by recent and present-day tectonic forces and are largely composed of tall mountain ranges or *sierras* that emerge from alluvial plains. The deserts in North America are mostly of this type. In basin-and-mountain deserts the desert sierras form islands of moister, colder ecosystems with temperate vegetation, and conifer forests surrounded by continuous plains of alluvial sediments covered by true desert vegetation. Alluvial fans are common at the point where sediment-laden streams leave the mountain front and spread out over the plain or *bajada* zone (Flores-Vázquez et al. 2020, this volume). Many of these desert basins do not drain onto larger rivers but have a closed drainage system, forming a geomorphologic landscape known as a *bolsón*, with salty playas at their bottom. CCB is one of the most outstanding of these bolsones in the Chihuahuan Desert.

This landscape of temperate mountains, or "sky islands," surrounded by hot subtropical desert vegetation is an evolutionary witness of past climate changes. During the last 2 million years (the Pleistocene period) the Earth underwent a series of alternating cycles of cooling and warming, induced by variations in the planet's orbit and in the inclination of its axis. During the colder periods—known as the "Ice Ages"—most of the high-latitude regions of the world became covered by massive glaciers and temperate ecosystems such as cold grasslands and conifer forests moved southwards. During these glacial periods the tropical belt narrowed and the mid-latitude hot deserts shrunk, replaced by grasslands, semiarid scrubs, and open woodlands. The desert biota found refuge in dry subtropical valleys where arid conditions persisted under the rain shadow of large mountain ranges. The last glaciation ended around 15,000 years ago, and we are still living in the warm interglacial period that followed—the Holocene (Betancourt et al. 1990).

When, 20,000 years ago, the ice sheets started to retreat, most of the temperate flora and fauna started to move back into higher latitudes. A subset of those species, however, managed to survive in the mid-latitude regions by climbing up the rugged and cool mountain ranges that emerge like islands from the desert plains. Establishing higher-up with each passing generation as the climate warmed, the ice-age organisms were able to persist in the cool mountain environments where they found a climate similar to the one they had enjoyed in the lower plains during the ice ages. As they ascended into the isolated desert mountains, the communities of the desert "sky islands" became separated from other mountains by a sea of harsh desert plains. Like antediluvian castaways, the ice-age species now survive high-up in the cool refuges of the sky islands. The temperate forests and scrubs that prosper in the mountains that dapple the Chihuahuan Desert in North America are a magnificent example of these relictual ecosystems; a biological memory of bygone evolutionary history surviving high-up in the mountains like a ghost of climates past (Dimmit 2000), covering the slopes with pinyon, juniper, and oaks, and the wetter and colder canyons with majestic conifers such as *Pinus strobiformis* and *Abies coahuilensis* (Pinkava 1984).

Cycles of Abundance and Scarcity

Three climatic signals bring precipitation to Mexican deserts: (a) Convective winds coming across the Pacific from the northwest bring winter rains to Baja California and the northern Sonoran Desert. (b) Thunderstorms driven by low-pressure centers that develop in summer when the continent becomes hot bring monsoon-type rainfall to the southern Sonoran and the Chihuahuan deserts, including CCB. (c) Lastly, hurricanes and tropical storms that develop in fall (September–November) over the tropical Pacific Ocean may bring autumnal downpours to southern Sonora and Baja California's Cape Region. While the Sonoran Desert receives mostly winter rains in its northwestern reaches, near the Mojave, and is fed by the Mexican summer monsoon in its tropical southern reaches (Robichaux 1999), the Chihuahuan Desert, in contrast, is almost entirely driven by summer rains (Caso et al. 2007).

The intensity of the atmospheric and oceanic signals that drive these patterns may vary significantly from year to year, driven by oscillations in the intensity of the Hadley cells and semi-cyclical changes in oceanic water temperature. When the temperature of the California current increases, winter precipitation in Mexican deserts increases in what we call "El Niño" seasons. Similarly, when water temperatures decrease in the tropical Pacific Ocean, the Mexican monsoon increases in strength and the likelihood of strong downpours in CCB increases (Caso et al. 2007).

These pulses of abundance and scarcity of resources are a major force in the ecological organization of deserts. During pulses of bounty, the fragile seedlings of desert plants can germinate, establish, and prepare for long droughts burying their roots deep into the desert soils. Ephemerals can replenish their seed banks, desert toads can reproduce in extraordinary numbers before entering again into their waterless torpor, and granivorous rodents, such as the kangaroo rats (*Dipodomys* spp.) and the pocket mice (*Chaetodipus* spp.), can stock up their underground caches. The desert becomes renewed, and ready to face again years, or even decades, of extreme hardship.

Annual plants—often called ephemerals for their short and opportunistic life cycle—survive the long drought periods in the form of seeds, bulbs, or tubers, and

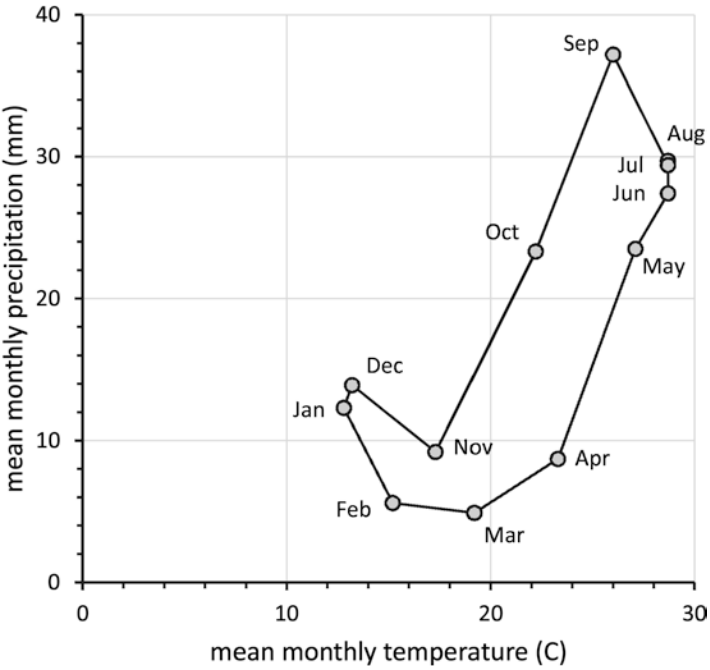

Fig. 3.2 Climatic diagram for Cuatro Ciénegas (data from the Servicio Meteorológico Nacional online database, available at http://smn.cna.gob.mx/es/climatologia/informacion-climatologica/normales-climatologicas-por-estado). Note the monsoon-type weather pattern driven by summer rainfall, revealed by the positive correlation between monthly mean precipitation and temperature

quickly sprout during the narrow window of opportunity that the desert rains provide. Perennial plants often show extensive networks of shallow roots, as many plants compete to extract water from the soil immediately after the rain has fallen. In monsoon deserts, like Cuatro Ciénegas, rainfall pulses coincide with adequate temperatures for plant growth (Fig. 3.2). Plants with succulent, water-storing tissues, like cacti and agaves, are well adapted to accumulate water and are common in CCB.

Life-Forms and Adaptations

In its origins, life on Earth evolved in water, and water is the most crucial element for the survival of all organisms (Souza et al. 2018). Thus, it is no surprise that some of the most remarkable adaptations for survival are found in deserts, i.e. in the environments where water is most scarce (Louw and Seely 1982). The short pulses of abundance that contrast sharply with the background condition of aridity and scarcity are the major force that has driven evolution, natural selection, and adaptation in desert biota. Plants and animals are adapted to these seasonal strokes. Natural selection and evolution have molded in very precise ways the life-forms of desert organisms to their harsh and unpredictable environment. Furthermore, because most deserts of the world have evolved recently and in relative isolation from each other, many of their constituent species have evolved from different ancestors (Morton 1979). Thus, deserts are prime ecosystems to study and understand the phenomenon of convergent evolution—the development of similar growth forms and adaptations derived from different ancestors.

Adaptations of Plants to Aridity

Most desert species have found remarkable ways to survive by evading drought. Desert succulents, such as cacti or agaves (century plants), can evade dry spells by accumulating moisture in their fleshy tissues. They have an extensive system of shallow roots that allows them to capture soil water only a few hours after it has rained. Their photosynthesis is modified to exchange gases and fix carbon dioxide (CO_2) during the night, when evaporative demand is low, and to accumulate the fixed carbon in the form of malic acid, which is later used by the plant as the building blocks of more complex organic molecules (this photosynthetic pathway is called "Crassulacean Acid Metabolism" or CAM). Additionally, cacti are leafless and commonly have vertically erect, green trunks that maximize light interception during the early and late hours of the day, but avoid the midday sun, when excessive heat may damage, or even kill, the plant tissues. Vertically-oriented photosynthetic tissues are noticeable, for example, in the columnar *Grusonia bradtiana* (Plascencia-López et al. 2020, this volume) in barrel cacti such as *Echinocereus freudenbergeri*, or in flat or cylindrical-stemmed prickly pears and chollas such as *Opuntia anteojoensis* (=*Cylindropuntia anteojoensis*). A similar behavior is observed in the central leaves of agave rosettes, such as *Agave lecheguilla*, which have a predominantly vertical orientation.

Woody desert trees, such as acacias, cannot store much water in their trunks, but many of them evade drought by shedding their leaves as the dry season sets in, entering into a sort of drought-induced latency. Many of these desert species, such as the mesquite *Prosopis glandulosa*, also have deep pivotal roots that allow them to tap into the desert's aquifer, the underground water layer accumulated deep beneath the soil. Some of these deep-tapping, deciduous trees also possess green stems, such as the Texas paloverde *Parkinsonia texana*. Green stems allow these trees to maintain a low level of photosynthesis during long periods of drought, recycling the CO_2 produced by respiration and maintaining the plant alive without the need to risk water loss through the exchange of gases (Ávila-Lovera and Ezcurra 2016).

Other group of trees, called pachycauls, have convergently evolved a mixture of these strategies: they can store water in gigantic trunks and have a smooth bark that can do some cactus-like photosynthesis during dry periods. When it rains, however, they produce abundant green leaves and shift their metabolism towards that of normal-leaved plants. This group is formed by trees with famously "bizarre" trunks, such as the Baja-Californian cirio or Boojum-tree (*Fouquieria columnaris*) and elephant-trees (*Bursera* and *Pachycormus*). Pachycauls, however, dominate in hot tropical deserts and are not present in CCB, but some taxonomically-related species can be found, such as the highly-ramified Shreve's ocotillo *Fouquieria shrevei*, with deciduous leaves and photosynthetic stems that can burst with new leaves only hours after heavy rains, and it is endemic to CCB (Nova et al. 2020, this volume).

A third group of plants, the "true xerophytes" or true drought-tolerant plants, have simply adapted their morphology and their metabolism to survive extremely long droughts. These species have remarkably low osmotic potentials in their tissue, which means that they can still extract moisture from the soil when most other plants cannot do so. True xerophytes, such as the creosote bush (*Larrea tridentata*) (Fig. 3.3), are mostly shrubs with small, leathery leaves that are protected from excessive evaporation by a dense cover of hairs or a thick varnish of epidermal resin (Ezcurra et al. 1991). Their adaptive advantage lies in their capacity to extract a fraction of soil water that is not available to other life-forms. However, because their leaves are so small and protected from transpiration by a thick layer of resin, their gas-exchange metabolism is comparatively inefficient after rain pulses when moisture is abundant. In consequence, these species are extremely slow growers but very hardy plants that can bear always a green foliage.

A particular group of desert plants, linked to the true xerophytes, is found in some mosses, ferns, and fern allies, which have the ability to completely desiccate and lose all their moisture without facing the death of the cell, and to recover their cellular activity and re-sprout within a few hours of receiving moisture. The phenomenon, known as *revivescence*, is typically found in desert mosses, in some ferns, and in the "resurrection plants" of the genus *Selaginella* (a fern-ally within the *Licopodium* group), such as *Selaginella lepidophylla*, frequent in the rocky desert scrubs of CCB that looks dry and dead during times of drought but can open their rosette-arranged fronds, and turn bright green and photosynthetically active in a few hours after a good rain.

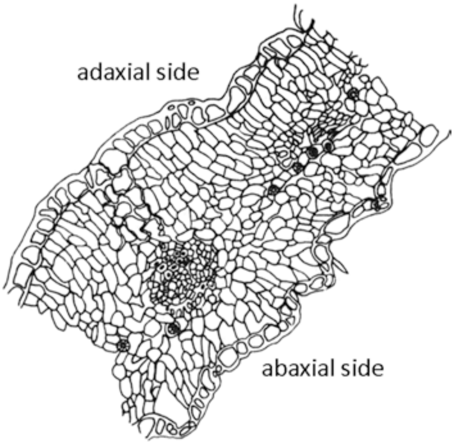

Fig. 3.3 Leaf xeromorphism in *Larrea*. A leaf transversal section of creosote bush or gobernadora (*Larrea tridentata*) leaves shows palisade tissue on both sides of the leaf (isolaterality) as well as the presence of stomata on both the adaxial and the abaxial sides (amphistomaty). Redrawn from Pyykkö (1966)

Finally, one of the most effective drought-survival adaptations for many species is the evolution of an ephemeral life cycle. Selection for a short life and for the capacity to leave behind resistant forms of propagation is perhaps one of the most important evolutionary drivers in most deserts, found not only in plants but also in many invertebrates. Desert ephemerals are extraordinarily rapid growers capable of reproducing at a remarkably high rate during good seasons, leaving behind myriad resistance forms that persist during adverse periods. In CCB, short-lived desert plants in the genus *Gilia* (Polemoniaceae), and various genera in the family Boraginaceae (e.g., *Nama*, *Phacelia*, *Tiquilia*) embellish the desert plains with their showy flowers after a good rainy season. Their population numbers simply track environmental bonanzas: Their way to evade critical periods is to die-off, leaving behind immense numbers of propagules (seeds or bulbs in the case of plants, eggs in the case of insects) that will restart the life cycle when conditions ameliorate. These opportunistic species play an immensely important role in the ecological web of deserts: A myriad organisms, like ants, rodents, and birds, survive the dry spells by harvesting and consuming the seeds left behind by the short-lived ephemeral and other perennial plants. Granivory (the consumption of seeds) and not herbivory (the consumption of leaves) is at the base of the food chain in most deserts, as those few plants that maintain leaves during dry spells usually endow them with toxic compounds or protect them with spines. The onset of rainy periods brings to the desert a reproduction frenzy of desert annuals, and a subsequent seed-pulse that drives the entire food web for years (Brown 1979).

Coping with Unpredictability: The Evolution of Serotiny in Deserts

In most deserts rainfall is not only scarce but also highly unpredictable (Noy-Meir 1973). Desert annuals have developed precise evolutionary responses to cope with environmental unpredictability by avoiding taking excessive risk when a single rain falls. These ephemeral plants spend most of their life cycle as seeds, and germinate and grow only when there is available moisture. But a false signal, like a single rain not followed by additional moisture, can drive all the seeds that germinate following that false queue to die before reaching reproductive age. In order to avoid this risk, most desert annuals have evolved fractioned germination, where not all the seeds of a cohort will germinate following a water queue. Some will germinate easily with the first rain, and, if more rains continue, they will have a competitive edge of having taken early advantage of available water. Others will not germinate with a single rain, but may require successive rains to accumulate enough moisture in the environment. These more prudent germinators will not have the adaptive advantage of early sprouters, but will face none of the risks of a false rain cue. For a single plant, producing highly variable seeds, ranging from quick sprouters to extremely cautious germinators will increase its chances of survival in extremely unpredictable deserts (Gutterman 1993; Mulroy and Rundel 1977).

Timing of seed dispersal also allows desert annuals to cope with environmental variability. Many desert plants retain the seeds within the maternal tissue in capsules or dry fruits, and release them gradually into the risky desert environment only when enough moisture softens the seed-retaining structure. Serotiny—the ability to retain seeds in the mother plant—allows plants to reduce risk by retaining seed safely within protected maternal structures and releasing them gradually into the environment as rains arrive (Martínez-Berdeja et al. 2015).

Finally, while plants in more predictable environments have well-defined life history phases (seedling, sapling, vegetative, and reproductive phases), many desert plants start producing flowers shortly after germination and keep on flowering as they grow, until the resumption of dry conditions ends their ephemeral life. If the rainy season is short, they will have produced at least a few fruits, and if the rainy season continues they will opportunistically keep on producing seeds to replenish their seed banks and reinitiate their ephemeral life cycle when future rains arrive.

In Cuatro Ciénegas, plants with woody, gradually-opening capsules, such as agaves and yuccas, a number of species in the Onagraceae (*Calylophus*, *Gaura*, *Oenothera*), or the jimsonweed (*Datura wrightii*, Solanaceae) typically retain seeds in the dry flowering scape for more than one season, and shed them gradually into the environment as the suture of the carpels in the dry capsule become weathered (Fig. 3.4). Similarly, desert families endowed with many-carpelled schizocarps—or

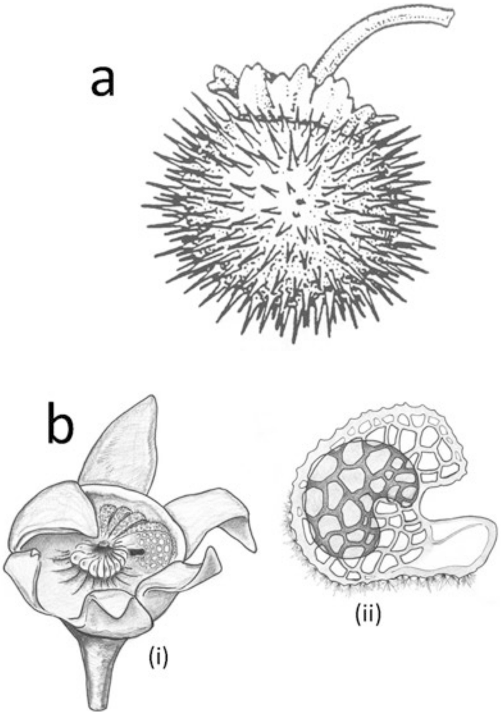

Fig. 3.4 Delayed dispersal (serotiny) in desert plants. (**a**) The lignified capsules of the jimson weed or toloache (*Datura wrightii*) stay attached to the dry mother plant for months, or even years, gradually opening along their carpel sutures and slowly releasing their seeds into the environment. (**b**) The schizocarps (i) of the desert mallows (*Spheralcea* sp.) can gradually release some of their carpels while retaining other carpels attached to the mother plant. Each detached carpel, called a mericarp (ii), contains a single seed inside and functions as the basic dispersal unit. Redrawn from Martínez-Berdeja et al. (2015)

"divided fruits," as in the Malvaceae (*Spheralcea*) and Zygophyllaceae (*Larrea*)—also have fruits that become lignified and gradually detach in parts from the mother plant, shedding seeds continuously for many months or even years. The mechanism of serotinous fruit retention also occurs in some cacti, such as *Grusonia bradtiana* (Rosas Barrera et al. 2020, this volume) and the sunken fruits of the nipple-cacti *Mammillaria* (Peters et al. 2011).

Leaf Xeromorphism: Shifting Photosynthesis to Favorable Hours

Most angiosperms possess leaves with a bifacial or dorsiventral structure. The upper (adaxial) side normally harbors a layer of palisade tissue, formed by a chloroplast-rich parenchyma of tightly-packed columnar cells under the upper epidermis. Between the palisade tissue and the lower (abaxial) epidermis there is a spongy mesophyll, with cells widely separated from each other so that the circulation of CO_2 entering the leaf through the abaxial stomata and diffusing on to the palisade tissue above, is enhanced. In short, most angiosperms show some level of functional specialization in their leaf sides, the upper surface being specialized in the capture of light, and the lower one being specialized in the exchange of gases with the surrounding atmosphere (Smith et al. 1998).

In arid environments, however, it is common to observe plants that have lost the dorsiventral specialization showing instead isolateral leaves with palisade tissue on both sides. Isolaterality in dryland plants is often accompanied by amphistomaty (the presence of stomata in roughly equal density in both sides of the leaf), as well as by a vertical orientation of the leaf laminae and increased leaf thickness (Smith et al. 1998). Vertically-oriented leaves allow desert plants to shift photosynthesis to the early hours of the morning and the late hours of the afternoon, when temperatures are lower and water vapor pressure is higher, allowing the plants to photosynthesize with less water loss and, hence, with a higher water-use efficiency.

Leaf xeromorphism (joint amphistomaty and isolaterality, coupled with thick, resinous or waxy leaves) is very strikingly visible in many dominant desert plants such as desert legumes in the genera *Senna*, *Parkinsonia*, *Hoffmanseggia*, and *Dalea*, or the creosote bush dominant in all North and South American deserts (Pyykkö 1966; Gibson 1998). Indeed, many studies suggest that the xeromorphic leaf anatomy (isolateral, amphistomatic leaves, often thick and mostly vertically-oriented) might be dominant in most drylands (Wood 1932; Mott et al. 1982; Arambarri et al. 2011).

Species Interactions

The harsh conditions of desert ecosystems have promoted the evolution of a complex set of relations among desert organisms, a surprising number of which are positive interactions. Desert shrubs in general and woody legumes in particular, create microhabitats that are critical for the survival of other species. Small animals seek the shade of desert trees and shrubs, birds find refuge and nesting sites in their canopies and many small plants recruit their juveniles under the nitrogen-rich canopy of desert legumes such as acacias, carobs, and mesquites. Because of their CAM metabolism, desert succulents such as agaves and cacti are poor thermoregulators as young seedlings, and cannot survive the harsh ground-level midday temperatures (Martorell and Portilla-Alonso 2020, this volume). For this reason, they can germinate and establish only under the protective shade of shrubby “nurse plants” that act as true cornerstone species in desert conservation (Franco and Nobel 1989). If the desert trees and shrubs are cut, all the accompanying biota soon disappears (Callaway 1995).

Additionally, many desert plants have very specific requirements in terms of their pollinators and seed dispersers. Although some desert ephemerals are truly unspecific in their requirements and produce thousands of seeds, the slow-growing desert perennials are frequently highly specialized in their reproductive habits, and depend strictly on co-evolved animals to help them out in their sexual and reproductive processes. Many cacti and agaves produce sugar-rich nocturnal flowers that engage the pollinating services of nectar-eating bats. Red tubular flowers attract hummingbirds and giant sphinx-moths. The sweet pulp of prickly pears (*Opuntia* spp.) lures birds to disperse their seeds miles away (Mandujano et al. 2010).

Deserts and Agriculture

Because desert ephemerals grow so fast and produce so much seeds in just a few weeks, it comes as no surprise that the earliest archeological records of agriculture come from dryland regions and that the first domesticated crops evolved from desert annuals. Indeed, the first records of cultivated wheat and barley (two dryland ephemerals) come from the Fertile Crescent of the Middle-East some 7000–9000 years ago. In the American Continent, the first agricultural records come from the Tehuacán Valley in southern Mexico, a hot tropical dryland where corn and squash (two annual, drought-tolerant fast growers) were first domesticated. To a large extent deserts have been the cradle of agriculture, and humans have been using desert environments for thousands of years (Cloudsley-Thompson 1979, 1996).

Concluding Remarks

For the untrained eye, deserts look scrubby and poor in biological richness, especially during dry periods. However, because of their evolution in relative geographic isolation, most deserts of the world are rich in rare and endemic species, and are hence highly vulnerable to biological extinction and environmental degradation. In spite of their remarkable convergence in adaptation, all deserts are different in their origin and their evolutionary history (Pipes 1998; Ricciuti 1996).

The incredible variation of the world's deserts in rainfall patterns, continentality, temperature regime, and evolutionary history have all contributed not only to their biological uniqueness, but also to their wondrous wealth of life-forms and adaptations. This adaptive diversity—what Darwin, strongly influenced by deserts himself, called "forms most beautiful and most wonderful"—is what makes deserts so unique. In the hot deserts, we may find giant cacti and trees with mammoth fleshy stems coexisting with some of the toughest hardwoods; ground-creeping succulents side by side with fog-harvesting rosettes, incredibly fast-growing annuals together with some of the hardiest drought-resistant perennials ever known; aromatic shrubs of enticing odors with some of the nastiest, spiniest plants ever. Very few places on Earth contain a richer collection of natural adaptations and such a unique array of evolutionary histories that deserts possess (Davis 1998), and, of these, few are as diverse and rich as Cuatro Ciénegas.

The fragmented evolutionary history of the deserts of the world has been the driving force of their biological rarity, of adaptation to local conditions, of specialization to isolated environments. After millions of years in isolation, the forces of evolution and fragmentation have yielded unique life-forms in each desert, strangely shaped desert plants and extraordinary animals. The world's deserts have been indeed almost biological and cultural islands, lands of fantasy and adventure, habitats of surprising, often bizarre growth forms, and territories of immense natural beauty.

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