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Abstract

- There is no single definition of “desert,” but it is widely agreed that deserts are arid because they receive little precipitation and experience high evaporation annually. These factors result in low soil water availability that severely limits plant productivity. Thus, another feature of deserts is low vegetation cover.
- Although all deserts are dry, there is extreme abiotic and biotic variability among the world’s deserts – perhaps more so than for any other biome. This arises in part from the varied causes of desert formation, their disjunct distributions, and their independent floral histories.

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- High spatial and temporal variability of the abiotic environment present challenges to desert life that has important implications at both the ecological and evolutionary scales. Besides limited water, other abiotic factors play important roles in desert ecosystems. Temperatures can be extremely high, but in some deserts low temperatures also constrain productivity. Resources, such as nitrogen, are also generally low in deserts, so that even when water is available, plant productivity may be relatively constrained.
- Most if not all life forms are present in desert ecosystems, regardless of the classification scheme used. Perennial shrubs dominate most desert landscapes, but in any single habitat trees, grasses, annuals, stem succulents, or leaf succulents may be the dominant form.
- From studies of desert plants, researchers have identified many adaptive functions at the ecophysiological level. These emerge from a plant's need to grow and survive through extreme drought, high solar radiation, and high temperatures, as well as through wide fluctuations in all of these abiotic factors.
- Plants exhibiting the succulent syndrome (which includes water storage, extensive surficial roots, and often CAM photosynthesis) are well adapted for life in warm arid ecosystems. Succulent plants are key components of many desert communities but they are rarely the dominant life form and are entirely absent from some deserts.
- Nutrients usually limit desert productivity during periods when water is available. Low external nutrient input results in decomposition by both abiotic and biotic processes playing a major role in nutrient availability. Other biotic-mediated processes, such as microbial nitrogen fixation and fungal root associations, are critical to maintaining favorable nutrient balance in desert plants.
- In spite of low productivity, deserts have surprisingly high biodiversity and endemism. Climate variability, geographic isolation, geologic history, and edaphic anomalies are among the primary drivers for greater-than-expected plant biodiversity.
- Biotic interactions were once thought to be rare in deserts and thus not important in desert community dynamics. In recent decades however, intra- and interspecific competition and facilitation have been clearly identified as important drivers in shaping desert plant communities. Arid and semiarid ecosystems are now widely used to test theories about the interplay between competition and facilitation.
- Deserts have always been susceptible to soil disturbances by nonnative ungulates and human activities. The profound effects on soil and nutrient losses are difficult to restore. In contrast, deserts were once considered relatively resistant to alien plant invasion, but recent spread of nonnatives has led to altered biogeochemical cycles and increased fire disturbances. In some cases, the changes have led to type conversion of vegetation. New pressures, such as renewable energy development, underscore the need for a solid scientific understanding of plant functions and ecosystem processes in arid and semiarid ecosystems.

Introduction

Desert is the biome classification for terrestrial regions of Earth that are climatically arid and have low vegetation cover. Additionally, the climate of such regions is often highly variable across seasons and years. While there is no single index that is used universally to define deserts, a simple one, proposed by Meigs (1953), is based only on precipitation, whereby extremely arid regions experience at least 12 months without rainfall, arid regions receive <250 mm rainfall annually, and semiarid regions receive 250–500 mm rainfall annually (Fig. 1). Boundaries based on this index do a good job delimiting deserts across the globe and correspond closely to boundaries used in other classification systems (e.g., Ezcurra 2006). But aridity is not simply based on the amount of water derived from precipitation; it also depends on the loss of that water, which affects its availability for plant productivity. A more inclusive definition of aridity comes from the comparison of water loss via evapotranspiration (ET) versus water input from precipitation (P). The ratio P/ET is a commonly used index of aridity (e.g., UNESCO 1977) defining hyperarid zones as having $P/ET < 0.03$ and arid zones having P/ET of 0.03–0.20. Although this definition does not significantly change the global boundaries of deserts as compared to other indices, such as Meigs', it does provide a more biologically relevant measure of aridity in terms of water availability for plant use.

Other environmental parameters, such as timing and intensity of rainfall, seasonal temperatures, and soil texture, to name a few, can also play a role in affecting the aridity of deserts, albeit at smaller spatial and temporal scales. These additional factors affect the abiotic heterogeneity within deserts that contributes to the surprising functional diversity of plants found in desert ecosystems. This chapter explores the diversity of desert plants from an ecological context. It begins with a short review of desert formation and abiotic variability as a foundation for understanding the causes of biotic diversity among and within deserts. Then, the diversity of desert vegetation is explored from a functional context through the community level.

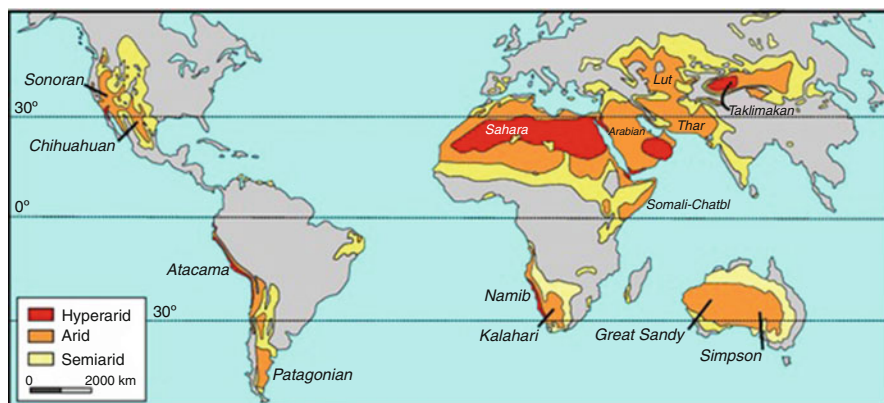


Fig. 1 Global distribution of nonpolar arid lands based on Meigs' (1953) classifications

It ends with some considerations of how the desert biome has changed due to human activities and how it may change with future global changes.

Desert Formation Affects Desert Diversity

Approximately one-third of the terrestrial biosphere can be classified as desert (Fig. 1), but beyond the common feature of being arid, there is extreme variability among and within deserts in terms of abiotic properties and thus biotic composition. One reason for this variability is that desert formation varies across global, regional, and local scales. With the exception of polar deserts, most large deserts are found in the horse latitudes, near 30°N and 30°S (e.g., Sahara desert; Fig. 1). This is the result of global atmospheric circulation patterns known as *Hadley cells*. These cells are fluid masses of circulating air driven by energy from the absorption of solar radiation near the equator (where solar radiation is greatest on average). This radiation generates masses of rising warm air that are moist with water from evaporation, but as an air mass rises, it expands and cools, and the water vapor within it condenses to form clouds and rain. Most of the water is lost from this air mass as it reaches higher altitudes. The now cool and dry air mass cannot sink back to the Earth at the equator owing to the continual convection of warm air. Instead, it is deflected to the north and south, where it begins to sink near the 30°N and 30°S latitudes. As the cool dry air mass sinks, it is compressed and warms, which allows it to absorb additional moisture that it may encounter. This contributes to a reduction of cloudiness in the latitudes around 30°N and 30°S and increases penetration of solar radiation to the land surface. The combination of dry air and high radiation results in low precipitation and high evaporation in these high-pressure *subtropical latitude deserts*. Most of the deserts on our planet are influenced in part by this global pattern of air circulation.

Hadley cell circulation predisposes the latitudes around 30°N and 30°S to being arid, but processes at regional and local scales may also contribute to, or even be fully responsible for, the formation of deserts. At a regional scale, some deserts form in the interior of continents – commonly called *mid-continent deserts* (e.g., Taklimakan desert of central Asia). These exist because they are far from the ocean, which is the primary source of moisture for rainfall. As an air mass containing water evaporated from the ocean moves across land, rain falls more or less continuously; thus, by the time the air mass reaches the most interior region of a continent, most of the moisture has already precipitated. The result is a vast area of arid land within the interior of the continent.

Other major causes of desert formation occur on more localized scales. The most common are *rain-shadow deserts*, which form on the leeward side of high mountain ranges (e.g., Great Basin Desert leeward of the Sierra Nevada and Cascade mountains). These mountains force moisture-rich air masses upward, thereby decreasing the pressure and temperature of the air mass moving across the land. Water vapor within the air condenses causing rainfall on the windward mountain slopes, but as these air masses move over the range and descend to lower elevation on the

opposite side, the air pressure and temperature rise (similar to Hadley cells). The limited moisture left in the descending air mass is prevented from precipitating because of the increasing pressure and temperature. Low rainfall, warm air, and high solar radiation resulting from the presence of a mountain range result in arid areas in the mountain's "shadow."

Coastal deserts form where very cold ocean waters occur at the surface and adjacent to a relatively warm continental margin (e.g., the Namib Desert occurs where upwelling brings cold water to the surface along the western coast of Africa). The interaction of the ocean, air, and land is complex in these systems, but in general the cold surface waters cause air masses that overlie them to cool. This decreases evaporation and reduces the capacity of the overlying air to hold water vapor, causing condensation and offshore precipitation. Sometimes the condensation forms fog, which may be drawn onto land, but as the fog blankets the land, it too warms and evaporates back into vapor. Because of this phenomenon, coastal deserts may also be known as *fog deserts*. Coastal deserts are among the driest in the world sometimes experiencing years without measurable rainfall (e.g., Namib and Atacama). In fact, fog is typically the most reliable source of water for productivity in these deserts, and many plants of these deserts show adaptations for capturing and taking up fog-derived water (e.g., *Nolana mollis*).

Besides the different formation processes, highly varied ages among the world's deserts also contribute to the diversity among them. Some deserts appear to be extremely old (e.g., Namib Desert >55 myo) giving rise to high diversity and endemism through many generations of evolution. Other deserts are very young (e.g., Mojave Desert ~11,000) and are strongly impacted by migration processes from regional biota. This can also lead to high diversity, especially if the desert forms at the intersection of multiple ecological regions. Biodiversity among deserts is also a result of their disjunct distribution. That is, deserts of the world are largely separated from each other compared to other biomes. As such, evolutionary processes within them have taken place largely in isolation from each other.

The Abiotic Environment Underlying Desert Productivity

As already noted, there is extreme abiotic and biotic variability among the Earth's deserts. Polar deserts are at one extreme of this variability. Although they are arid, the reason they sustain little life is mostly due to very low temperatures and a limited growing season. (Polar desert plants are reviewed in the Chap. 13, ► "[Plants in Arctic Environments](#)" of this volume and are not further included herein.) For the rest of the world's deserts, plant production is limited by a general lack of resources. The most ubiquitous, of course, is the lack of water, but other resources (e.g., mineral nutrients) may also be limiting, especially during periods when water is abundant. Other abiotic factors also have important impacts on desert plants and their function. Intense solar radiation, high and low air temperatures, saline soils, and strong winds are but a few of the abiotic stresses that regularly impact desert plants. Furthermore, in desert environments some of the highest

spatial and temporal variability of these abiotic factors is found as compared to anywhere globally. Biotic interactions and their affect to desert plant communities have historically been considered less important than abiotic factors; however there are many examples of important biotic interactions, both plant-plant and plant-animal, that influence desert vegetation, especially in terms of community structure, pollination, and plant recruitment.

Precipitation and Drought

All discussions of desert abiotic factors begin with precipitation and for obvious reasons. Water is the most limiting resource for productivity in deserts. But the amount of water is only one of the many water-related factors affecting plant function in deserts. The precipitation form (rain, snow, fog), intensity, and timing all affect its ultimate availability and use by plants. Furthermore, the absence of water and duration of that absence (i.e., drought) have substantial effects on desert plant ecological functions and evolutionary responses. Because water limits lifetime growth and reproduction in desert plants, all face the challenge of balancing carbon gain against water loss. This trade-off results, for the most part, because the primary path for carbon uptake is the same as for water loss – both flux through the stomata. This trade-off appears to have driven many of the adaptive changes in physiology, morphology, and behavior seen in desert plants.

Functional Diversity and Responses to the Environment

Ecological Groupings of Desert Plants

Desert plant activity is limited first and foremost by low water availability, but more specifically it is the pulsed nature of water availability and periods of severe water limitation between these pulses that have most strongly impacted the evolution and ecology of desert biota. Not surprisingly, many classifications of desert plants focus on patterns of activity through rain and drought cycles. The simplest of this function-based classification scheme is to group plants along a continuum from drought avoiding to drought tolerating. Avoiders do not experience the stress of drought because either they have mechanisms that circumvent it or they become inactive (including dying, as in the case of annuals). Tolerators maintain activity through the drought albeit at a substantially reduced level.

This simplified scheme is sometimes difficult to use across the broad range of desert species with highly varied adaptive responses to drought, and a number of related classification systems persist in the literature. In an early and still widely used scheme proposed by Kearney and Shantz (1912) and later modified by Shantz (1927), annuals are considered *drought escaping* because they are active only during favorable conditions and absent during drought. *Drought-enduring* plants are present during drought, but become inactive usually during the early stages of

water stress. Drought-deciduous shrubs (plants that do not die, but do lose their leaves during drought) are drought enduring. There is overlap in Shantz' (1927) definitions of *drought evading* and *drought resisting*, which appears to have generated some confusion in the literature. Both types are active during drought, but *drought-evading* plants typically have higher growth per unit water used (i.e., higher water-use efficiency) due to adaptive traits that reduce water loss and prolong the growing period. Reduced transpiration due to stomatal regulation coupled with morphological features such as stomatal pits, leaf hairs or waxes, and small leaf sizes is often found in drought evaders. Kearney and Shantz (1912) also classified plants with extensive root systems into the drought-evading category. *Drought-resisting* plants have persistently low-to-moderate levels of activity through periods of low water availability as well as during more favorable periods. Reduced transpiration is the norm for drought resisters, but they can tolerate very low water potentials, often via osmotic regulation. Succulent plants and some of the most successful desert perennial shrubs (e.g., creosote bush) fall into this category.

Categorizing plants in terms of their functional attribute is useful only to a limited extent, and there are many examples of taxa that exhibit properties of more than one category. For example, one could argue that creosote bush exhibits both drought-resisting and drought-enduring characteristics (small leaves with resinous excretions to reduce transpiration). For this reason, a popular alternative is to group desert plants based on life forms. These forms usually include annuals, perennial grasses, deciduous shrubs, evergreen shrubs, CAM succulents, and deep-rooted trees (phreatophytes). Smith et al. (1997) took this approach in their summary of North American desert plant ecophysiology, and many others have applied it as a way to simplify the presentation of the complex diversity of form and function found in desert species. Interestingly, these diverse life forms are present in a broad cross section of desert taxa suggesting that the mechanisms for dealing with aridity and heat, or the ability to form them through natural selection, are fundamental to many lineages.

Photosynthesis in a Water-Limited Environment

The Desert Plant Dilemma: Balancing Carbon Gain and Water Loss. There is a long history of research on the ecophysiology of desert plants and a number of valuable reviews of such studies. Smith et al. (1997), for example, provide a comprehensive review of plant ecophysiology in North American deserts, and many studies from the Namib Desert are present in von Willert et al. (1992). Most ecophysiological investigations of desert plants emphasize photosynthetic gas exchange, plant water relations, and the link between them, but these emphases are reasonable given that maximizing carbon gain and minimizing water loss are the prevailing challenges in desert systems.

In arid ecosystems any extraneous plant water loss has the consequence of reduced production and, in extreme circumstances, potentially plant death. Photosynthesis relies on CO₂ uptake through stomata, but this process incurs the unavoidable loss of water via the reverse path (transpiration), thus resulting in a trade-off that forms the

foundation for many of the adaptive characteristics seen in desert (and other) plants. In deserts, plant water loss from leaves is exacerbated by high water vapor pressure differences (VPD) between the leaf and the air. When water is abundant, as during the growing period for annuals, the water lost via transpiration may be inconsequential, especially compared to its role in reducing leaf temperatures. For plants that remain active during the drought period, mechanisms that help reduce water loss should be favored. The most straightforward mechanism for reduction of water loss during periods of drought is to reduce the size of the stomatal opening, thereby decreasing conductance of water from the leaf. But this comes at a cost; it reduces uptake of CO_2 . In addition, for most desert plants, a reduction in transpiration results in a potentially dangerous increase of leaf temperature (see discussion of energy balance in chapter ► “Plants in Alpine Environments”). Over the years, myriad fascinating examples of morphological, physiological, and behavioral mechanisms have been identified that help desert plants avoid the full consequences of these trade-offs. In general these can be grouped into ways of improving photosynthesis relative to water loss, decrease dependence on transpiration for energy balance, and ways to take up or save more water.

Photosynthetic Pathways

Pick up almost any book about photosynthesis and entire chapters can be found about C₃, C₄, and CAM photosynthesis. Indeed, the ecology and biochemistry of these three photosynthetic pathways differ so greatly that they warrant entire volumes. Rather than review the three photosynthetic pathways in detail, the attributes of each that are important for their presence in deserts are highlighted; then their distribution and how the different pathways correspond to variability among these arid ecosystems are explored. All three pathways are present across the deserts of Earth, but as might be expected, their abundances differ in relationship to the environments of each desert.

Of the three pathways, C₃ photosynthesis is the most widespread globally, and the same is true across deserts. However, net carbon gain of C₃ plants is negatively affected by photorespiration, which goes up with increasing temperatures. This is one reason C₄ and CAM plants may have a competitive advantage over C₃ plants in hot deserts (Ehleringer and Monson 1993). In deserts with cooler temperatures during the growing season, the disadvantage of photorespiration is significantly lower, thereby reducing the relative benefit of the C₄ pathway. The C₄ pathway also requires two additional ATP to fix CO_2 (compared to C₃), making it best suited to high-light environments. As expected from these fundamental differences, the greatest abundance of C₄ plants in deserts is where temperatures and light are high and water is available during warm periods.

C₄ plants have high water-use efficiency (carbon gain vs. water loss) because the CO_2 -concentrating mechanism of the C₄ pathway maintains higher internal CO_2 concentrations relative to stomatal conductance and thus transpiration. However, the need for water during the warm growing season prevents most C₄ plants from being well adapted to drought conditions. In contrast, CAM plants have extremely high water-use efficiency. They benefit from the same CO_2 -concentrating

mechanism found in C4 plants, but additionally keep their stomata closed during the day when evaporative demand (i.e., VPD) is high, and then open them for CO₂ exchange during the lower-VPD hours of darkness.

Other attributes of CAM species benefit their tolerance of drought. As previously described, many CAM plants are succulent, having tissues that store water for use during drought, but CAM is not restricted to succulent plants. Likewise, not all succulents are CAM (e.g., many leaf-succulent shrubs of the Succulent Karoo are C3). Some CAM species can switch to C3 photosynthesis when environmental conditions are favorable, especially when water availability is high, and many can use C3 photosynthesis during a small fraction of the regular daily CAM cycle.

CAM plants increase in abundance in hot deserts that have some degree of water limitation during the warm season. This limitation may stem from an absence of precipitation or from an ephemeral and unpredictable precipitation regime. But, most CAM species are sensitive to freezing temperatures and thus absent from cold (high-elevation or high-latitude) deserts.

In North American deserts, the relative abundances of C3, C4, and CAM along a north-to-south gradient of increasing temperature and summer rainfall reflect the typical pattern among global deserts. In the winter-rain-dominated Great Basin cold desert, CAM and C4 plants are largely absent except in saline habitats (see “Desert Halophytes”). The proportion of CAM and C4 species increases slightly in the Mojave Desert to the south, where annual temperatures are warmer but winter rains still dominate. In both of these deserts, C3 species greatly outnumber C4 and CAM species. Even further south, and at overall lower elevations, CAM species become an important part of the Sonoran Desert flora, with some taxa (e.g., Cactaceae) showing remarkable morphological as well as taxonomic diversity. Summer rains are abundant here but spatially and temporally variable. C4 species, especially grasses, also become a more integral part of the flora in the Sonoran Desert but normally in the higher elevations where rainfall is more abundant and predictable. The southernmost North American desert, the Chihuahuan, has an abundance of CAM and C4 species related to the higher annual temperatures and summer rainfall of this desert. CAM agaves and cacti are more speciose here and can be the dominant taxa of some Chihuahuan communities. C4 grasses can likewise dominate vast areas of the Chihuahuan, especially where rainfall is relatively plentiful. But, both C4 grasses and CAM species are often not the dominant plants on heavily calcareous soils that occupy many parts of the Chihuahuan. Here they are replaced by C3 shrubs (primarily creosote bush and tarbush) – a shift that probably reflects poor retention of shallow water on such substrates. This pattern illustrates the potential for local edaphic effects to modify climate patterns that would otherwise favor certain ecophysiological syndromes over others.

Leaf Energy Balance

Many adaptive traits at the leaf level are related to energy balance because (1) maintaining a favorable leaf temperature is important for photosynthesis and (2) the most efficient means of heat dissipation is by *latent heat transfer* which is due to transpiration. When moisture is abundant, the consumption of water for

latent heat transfer poses few, if any, problems. But when water is limited, which often corresponds to the warmer periods of the year, reliance on latent heat transfer presents a challenge. This challenge appears to have driven functional diversification and adaptation at the leaf level among many desert plants, as well as in other ecosystems. (For a more detailed review of energy balance, see the chapter ► “Plants in Alpine Environments”.)

Small Leaves Decrease Leaf Temperature and Transpiration

Reduced leaf size is one of the most widespread morphological adaptive features seen in desert plants. It seems intuitive that because there is less surface area on smaller leaves, water loss will be lower, but this is not necessarily true. Water loss from a leaf is dependent on transpiration rate, which is an area-standardized measurement (e.g., $\text{mmol H}_2\text{O m}^{-2} \text{ leaf s}^{-1}$). A priori, small and large leaves can have the same transpiration rate, in which case a canopy of many small leaves will lose the same amount of water as one with fewer large leaves (i.e., the total surface area is the same). For small leaves to be adaptive in terms of water loss, they must instead have a lower transpiration rate, which, as explained below, they usually do. Small leaves also do not heat up to the same extent as larger leaves. These two properties go hand-in-hand, and since heat and water limitations are two of the greatest challenges for desert life, it is not surprising that small leaves are common in the desert flora.

The primary reason smaller leaves stay cooler, and subsequently have lower transpiration than larger leaves, is that they have a reduced boundary layer for heat transfer. A smaller boundary layer means that heat transfer from the leaf to the surrounding air (i.e., *convective heat transfer*) is more rapid. Thus, as the leaf heats up from absorption of radiation from the sun and surrounding objects, higher convective heat loss keeps the leaf temperature closer to the air temperature (ΔT). Convective heat loss means that the plant is less dependent on *latent heat transfer*, via transpiration, for maintaining a favorable leaf temperature. But additionally, a lower ΔT also reduces the vapor pressure difference (VPD) between the leaf and air, which also lowers transpiration.

Lower leaf temperature may also benefit the leaf in terms of photosynthetic rate since the lower temperature is likely closer to the thermal optimum for photosynthesis. Recall also that lower temperatures reduce photorespiration in C3 plants.

For many species, leaf sizes can vary across seasons and years, with smaller leaves produced during warmer periods or during drought. Such adjustment are crucial in plants that persist through periods of water shortage and high temperatures, underscoring the importance of another adaptive function in desert plants – acclimation.

Leaf Angles and Leaf Movement Affect Light Interception

Another beautiful example of acclimation in desert plants is leaf movement known as *heliotropism* (meaning sun orienting). Some desert species, mainly annuals, display *diaheliotropic* leaf movement (orientation perpendicular to sun rays) and *paraheliotropic* leaf movement (orientation parallel to sun rays), although not all species do both. The former maximizes interception of solar radiation whereas in

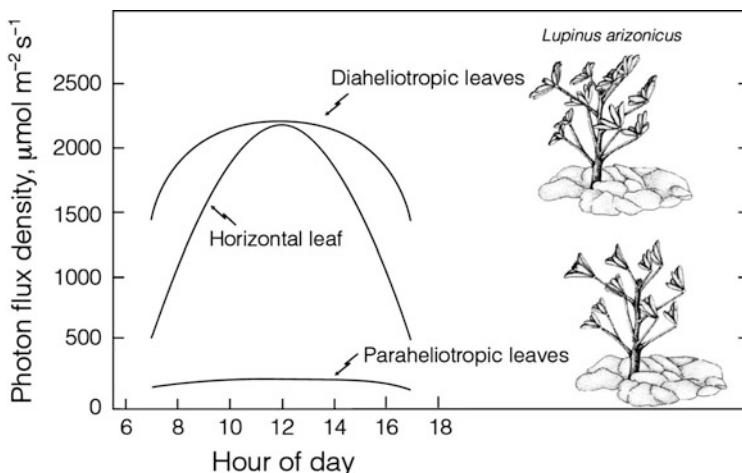


Fig. 2 Interception of solar radiation (measured as photon flux density) by diaheliotropic and paraheliotropic leaves during daylight hours. Arizona lupine (*Lupinus arizonicus*) of the Mojave and Sonoran Deserts can switch from fully diaheliotropic during periods of favorable soil moisture to fully paraheliotropic during water-stressed periods – or combine both dia- and paraheliotropism during a single day. For comparison, interception by a non-heliotropic horizontal leaf is also shown. A vertical leaf (not shown) would have an inverted curve from the horizontal leaf (Redrawn with permission from J. R. Ehleringer)

the latter minimizes it (Fig. 2). Diheliotropism ensures that photosynthesis is rarely, if ever, light limited, which is beneficial over the short growing season of desert annual plants. The increased heat load owing to high incident solar radiation is balanced by high transpiration, which may explain why diaheliotropism is largely limited to annuals.

An interesting example of heliotropism is found in Arizona lupine (*Lupinus arizonicus*), an annual of the legume family (Fabaceae) that displays both dia- and paraheliotropism. During the warm and dry late-growing season, Arizona lupine displays diaheliotropism during the early morning hours, but as soil water declines and temperatures increase later into the day, leaves switch to being paraheliotropic (Fig. 2). This switch substantially reduces interception of direct solar radiation, which reduces photosynthesis but also decreases leaf heat load and transpiration.

Heliotropism is not restricted to annuals but is much less common in other life forms. One woody genus in which it appears is *Prosopis* – also a member of the legume family. Although the heliotropic species of *Prosopis* have extensive root systems, some being phreatophytic (described below), they may still experience daily cycles of water stress especially in non-riparian habitats (e.g., sand dunes). These daily cycles of water stress result in switches between dia- and paraheliotropic leaf movements, as seen in Arizona lupine.

Most desert plants do not have heliotropic leaf movement, but leaf angles can still play an important role in light interception and energy balance. Many desert species have vertically biased, nonrandom leaf angles. Although fixed, these leaf



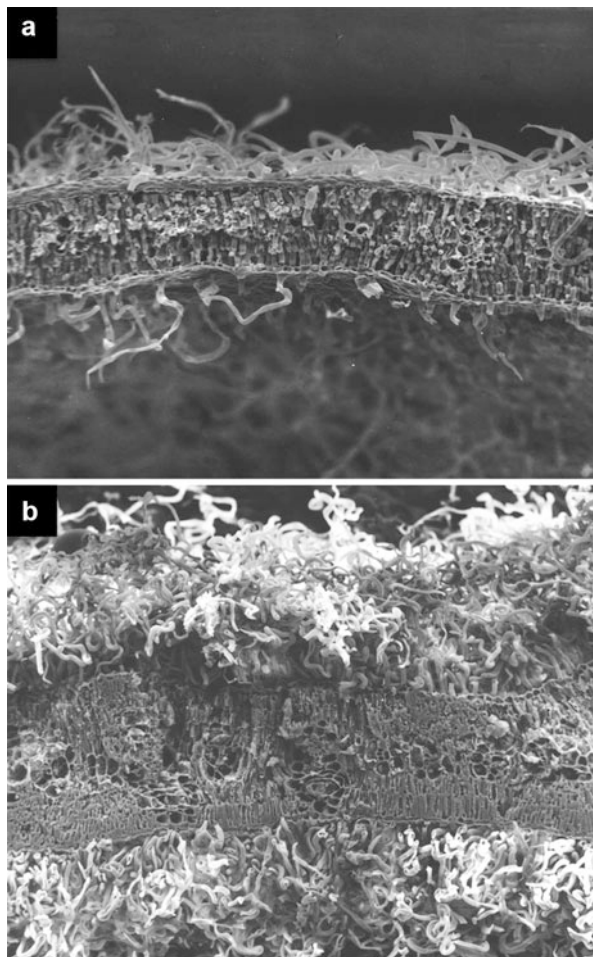
Fig. 3 *Copiapoa cinerea* ssp. *columna-alba* of the Atacama Desert, Chile, grow with a northward orientation that helps maintain warm temperatures on the apical meristem during the cool period of the year but reduces heat load during the hot season (Photo: D. R. Sandquist)

angles function much the same as switching between dia- and paraheliotropism (Fig. 2). That is, they maximize light capture in early morning and late afternoon hours, when air temperature and VPD are lower, but avoid direct solar radiation in the more severe midday hours. Nonrandom leaf orientations may also reduce self-shading, with the angles being specific not just to daily radiation changes but also to seasonal changes. Such orientation benefits are also found in photosynthetic stems, including those of succulent species. An example of this is seen in the cactus *Copiapoa cinerea* ssp. *columna-alba* from the Atacama Desert of Chile. The succulent stems of these plants orient due-north giving the comical appearance of a small cactus army marching towards the equator (Fig. 3). Ehleringer et al. (1980) showed that this orientation facilitates apical warming for growth during the cool/wet parts of the year and reduces radiation (thus heat load) during the driest part of the year.

Reflective Leaf Surfaces Decrease Absorption of Solar Radiation

The multiple benefits of reducing direct solar radiation suggest that other leaf properties should serve this function in desert plants. Indeed, there are a number of traits that do so at the leaf surface, reflective waxes and leaf hairs being among the most common. A well-studied example of this is found in brittlebush (*Encelia farinosa*, Asteraceae), a drought-deciduous shrub of the Mojave and Sonoran Deserts. Leaves produced by this species can have a thick layer of trichomes (leaf hairs) that strongly reflects solar radiation. Notably, the thickness of the trichomes, and thus the amount of reflectance, depends on the level of water stress experienced by the plant. Leaves produced early in the rainy season are generally large and have

Fig. 4 Micrographs of brittlebush (*Encelia farinosa*) leaves from the Mojave Desert. (a) Leaves produced early in the growing season when soil water availability is favorable have low trichome densities. (b) Leaves produced later in the season, when water stress has increased, have a dense trichome layer (Photos: J. R. Ehleringer)



few trichomes (Fig. 4a). These leaves absorb ~80 % of the solar radiation incident on their surface, but the heat load resulting from this radiation is easily balanced by transpiration during this wet period of the year. As the season progresses, and soil water decreases, new cohorts of leaves are produced which have increasing trichome densities (Fig. 4b). The higher densities lower radiation absorption to as little as 40 %, which attenuates excessive heat load and, importantly, reduces dependence on transpiration as the plants enter the drought period. As one would expect, the lower light absorption also decreases photosynthesis, but acclimation through increased trichome development allows plants to remain active much longer into drought, thereby compensating for the decrease of photosynthesis.

Biochemical Acclimation Changes Thermal Optimum of Photosynthesis

Rather than maintaining a narrow range of leaf temperatures for optimal photosynthesis, an alternative is to change the optimum temperature. (One might call this,

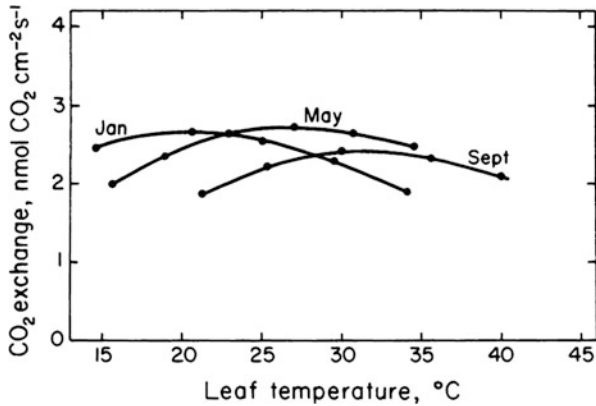


Fig. 5 Temperature acclimation of photosynthesis (measured as CO₂ exchange) by creosote bush (*Larrea tridentata*) in Death Valley, California. Regardless of season, leaf photosynthesis spanned a broad range of temperatures, but the photosynthetic optimum temperature changed from ~20 °C in January to ~32 °C in September, reflecting temperature changes of the environment (Mooney et al. 1978, reproduced with permission of American Society of Plant Biologists)

“if you can’t beat them, join them.”) In a number of desert species, biochemical adjustments do just this. Such physiological acclimation results in changes of the optimum temperature for photosynthesis that closely match seasonal differences in ambient temperatures (Fig. 5). *Thermal acclimation of photosynthesis* is found primarily in evergreen plants across many forms (e.g., shrubs, grasses, succulents, and ferns) and appears to be uncommon in annuals and drought-deciduous perennials, presumably because these two growth forms do not experience the breadth of leaf temperatures that evergreen species do.

Creosote bush (*Larrea tridentata*, Zygophyllaceae) is often cited as the quintessential thermal acclimating desert species, showing temperature optima changes in the field from 20 °C in January to 32 °C in September. Importantly, these changes could be replicated in reciprocal transplant and controlled temperature experiments, thereby confirming the response to be acclimation based specifically on temperature.

Non-leaf Photosynthetic Structures

Photosynthetic stems and twigs are present in plant species throughout the world, but this trait is of special interest in deserts where highly modified green stems are found in a number of drought-deciduous, microphyllous, and aphyllous woody species. Furthermore, unlike most species from other biomes, stem photosynthesis in these desert plants often contributes significantly to net carbon gain. The syndrome is most well studied in the deserts of North America, especially for the microphyllous tree species of the Sonoran, and although the ultimate cause of stem photosynthesis may be debated, most studies have demonstrated that stem photosynthesis confers a number of ecophysiological benefits for growth in arid and hot conditions.

When water is abundant, the majority of plants with photosynthetic stems flush a cohort of small leaves that have high transpiration and photosynthetic rates. As drought ensues leaves are abscised but carbon gain continues in the photosynthetic stems. These stems usually have lower net photosynthetic rates but greater water-use efficiency than leaves. Some studies have also shown stems to have higher temperature optima for photosynthesis than leaves. These trends suggest that these highly modified photosynthetic stems are well adapted for operation during dry and potentially hot conditions of deserts, enabling year-round carbon gain for many species and potentially facilitating more rapid responses to pulses of water availability.

The costs associated with stem photosynthesis (e.g., construction costs and lower carbon assimilation) may be high compared to photosynthetic leaves, but those costs appear to be outweighed by the benefits. For some species the contribution of photosynthetic stems and twigs to annual plant carbon gain is important, as it can exceed 70 % (Szarek and Woodhouse 1978) and extend carbon uptake by 7 months (Tinoco-Ojanguren 2008). Furthermore, stems play other structural roles that should also be considered in the benefits, as not all plants with green photosynthetic stems engage in exogenous gas exchange. Instead, these species benefit from stem photosynthesis through the re-fixation of respired CO₂, which may help maintain reserves of stored carbohydrates.

Adaptive Forms and Functions Related to Desert-Plant Water Relations

Roots that Increase Water Uptake

Maintaining a favorable water balance is a clearly one of the primary challenges to living in water-scarce desert environments. Thus, it is not surprising to find a number of adaptive traits related to increased water uptake and the prevention of water loss. One of the simplest solutions for achieving greater uptake is to have a large rooting system, but this is not as common as one might expect in desert plants, probably because the rooting zone eventually dries and the maintenance costs of a large root area would be unsustainable. More effective strategies present in desert plants include rapid production of new roots in response to rainfall (described below for cacti) and development of roots that exploit more favorable microhabitats in the soil. One example of the latter are plants that produce long roots capable of accessing the more permanent water supply found in the saturated soil zone (i.e., permanent water table). These deeply rooted species are called *phreatophytes*, and many of the most deeply rooted plants in the world are phreatophytes from arid or semiarid regions. For example, *Boscia albitrunca* (shepherd's tree) of the Kalahari semidesert in Africa has the deepest roots ever measured, at 68 m.

Phreatophytes are found in most deserts, possibly because water tables tend to be deeper in deserts than other ecosystems and the phreatophytic habit confers such a significant fitness advantage. In North American deserts, phreatophytic species have the highest primary production and standing biomass of these ecosystems.

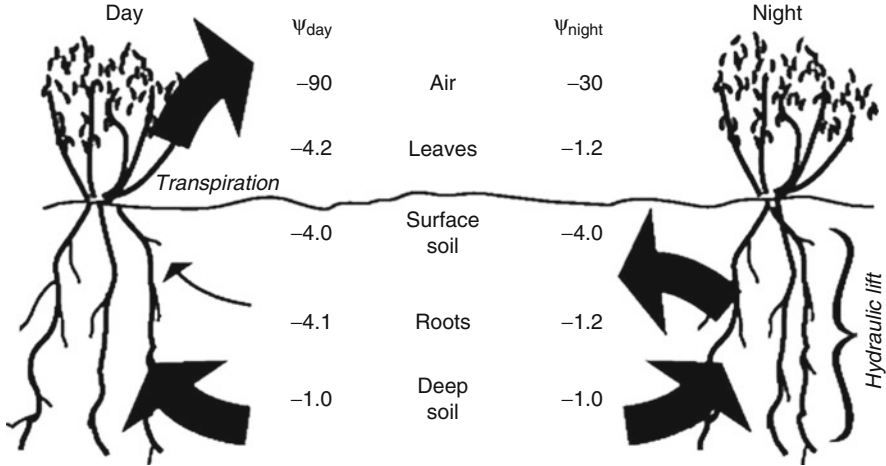


Fig. 6 Hydraulic lift is the process of water being moved from areas in the soil with high water potential to areas with low water potential via plant roots. This occurs at nighttime when stomata are closed and transpiration of water from the leaves is shut down. The translocated soil water may serve as a reserve for plant uptake the next day when transpiration resumes

Such high productivity is partly due to phreatophytes being largely decoupled from surface drought conditions. Such decoupling allows phreatophytes to be productive throughout rainless periods, even when those rainless periods extend for years – as for *Prosopis tamarugo*, a deeply rooted species of the hyper-arid Atacama Desert of Northern Chile.

Deep roots are also commonly found in plants that display a functional process described as *hydraulic lift* (or *hydraulic redistribution*). Popular accounts of this process describe it as “self-watering” by plants, whereby water from zones of high water potential (usually deep soil) is nocturnally redistributed through roots to zones of low water potential (i.e., shallow soils) and stored there until daytime when the plant takes up the stored shallow water for transpiration. This phenomenon was first quantified in the ubiquitous Great Basin Desert shrub *Artemisia tridentata* (big sagebrush) and coined “hydraulic lift” because water movement was in an upward direction. It has since been found in other desert species with roots that experience a hydraulically heterogeneous soil profile. In spite of the apparent fitness value of hydraulic lift, its presence has not been widely examined in most ecosystems, including deserts.

Hydraulic lift (Fig. 6) is driven by water potential differences that develop in the soil profile during the day. Root densities are typically greatest in shallow soil and decrease with depth, as such transpiration depletes water in the shallow layers to a greater extent than that at depth (especially if the deep roots are near saturated soils). Evaporation also contributes to a higher loss of water from shallow soils. The result is a water potential gradient in the soil profile that is bridged by the roots of the plant. At night, when stomata close and transpiration is greatly reduced, water continues to move within the plant along the residual water potential gradient.

Movement continues from the roots to the shoots until the shoot water potential comes to equilibrium with the root water potential. Below ground, in a similar manner, water fluxes from the deep roots in moist soil (high water potential) to the shallow roots in soil that has dried through the day (low water potential). The surprising aspect of this process is that the water “leaks” out of the shallow roots and into the surrounding dry soil, meaning that water movement in these shallow roots reverses. The hydraulically lifted water accumulates in the shallow root zone overnight, where it is then available for uptake by the plant the next day – when transpiration resumes and the shallow root flux again reverses.

As might be expected, water redistribution by roots can also occur in the opposite direction – inverse hydraulic lift. The movement of water from wet upper soil layers (such as after a monsoon rain) into dryer deep layers may benefit root growth into deep soil and can redistribute water away from access by shallow-rooted competitors. Inverse hydraulic lift has been demonstrated for a number of desert plants and across life forms, including Kalahari dune grasses and a Chihuahuan tree (Arizona walnut). The facultative phreatophyte, *Prosopis velutina* (velvet mesquite) of the Sonoran Desert has even been shown to engage in both hydraulic lift and inverse hydraulic lift.

Recently, hydraulic lift was shown to facilitate greater nutrient availability to plants. This results from microbial activity in shallow root zones being stimulated by hydraulically lifted water exuded by the plant. This important discovery adds another dimension (“self-fertilization”) to the value of hydraulic lift.

Preventing Loss of Water Transport

Water for transpiration is moved by negative pressure (i.e., tension) from the roots to stems and leaves via the xylem. (Imagine the xylem as a straw, through which water is sucked from soil to air.) When soil water is abundant, little tension is required to move the water through this transpiration stream, but during drought, greater and greater tensions are needed to pull water up this transpiration column. Higher tensions increase the probability of breaking the water column due to *cavitation*, the change of water in a xylem conduit from liquid to vapor. Water-stress-induced cavitation occurs when xylem tensions becoming so great that they exceed the capillary forces that sustain water-filled conduits in the xylem. Once a conduit fills with vapor, it can no longer transport water. Cavitation is normal in most plants, and refilling of the conduit is possible in some species, but when cavitation is rampant throughout the xylem, water transport is substantially reduced. Because desert plants typically operate under conditions of low soil water availability, they regularly face high xylem tensions. For this reason, desert plants would be expected to have adaptive anatomical features that help resist cavitation to a greater degree than plants from more mesic habitats, and this appears to be the case.

Broad surveys indicate that plants of from arid and semiarid regions are less susceptible to water-stress-induced cavitation than those from more mesic habitats. One mechanism for this greater resistance is smaller pit pores, but this pattern is only strong for perennial evergreens – the group of plants that typically remain active during the drought period. For other life forms, short-term reductions of



Fig. 7 Leaf and stem succulent species dominate the vegetation of the Vizcaíno region of the Sonoran Desert. Centered in this photo is the elephant-stemmed *Pachycormus discolor*. The large columnar cactus to the left is Cardón, *Pachycereus pringlei*, and the tall slender plant to the right is Boojum tree (*Fouquieria columnaris*). A number of other succulents from the Agavaceae and Cactaceae families are also present in this scene (Photo: D. R. Sandquist)

transpiration by stomatal closure help to prevent cavitation. Alternatively, some life forms are only active when cavitation is not likely (e.g., annuals, drought-deciduous perennials). In fact, resistance to water-stress-induced cavitation is not strongly associated with mean annual precipitation (MAP) within deserts and may actually increase at the lower end of MAP owing to greater reliance pulsed water availability and the high water fluxes needed for growth during the ephemeral periods of water availability.

Storing Water: Succulent Plants

To many, succulent plants, especially cacti, are synonymous with desert life, even though these “denizens of the desert” are actually absent or rare in the most arid deserts. They are also rare in high-elevation and high-latitude deserts because succulent plants have a low tolerance for freezing temperatures. Nonetheless, succulence is a successful syndrome for desert survival that nicely illustrates the coupling of morphological and physiological functions. It is also hard to deny that desert regions favorable to abundant succulent plant growth create some of the most intriguing landscapes on the planet (e.g., Vizcaíno region of the Sonoran Desert Fig. 7, Karoo region of South Africa).

Succulence refers to the fleshy and relatively thickened tissues of a plant that store water which can be used during periods of water stress (Von Willert et al 1992; Egli and Nyffeler 2009). The requirement of being able to store water is important to this definition because there are plants that appear succulent but wilt or die when exposed to drought. These are not succulent in spite of being water rich and fleshy.

For truly succulent plants, the degree of succulence varies greatly across species, but overall it is adaptive because it allows a plant to become temporarily decoupled

from unfavorable environmental conditions (e.g., low soil water, high soil salinity) and facilitates growth and survival through such periods. Cacti are arguably the most recognizable of the succulent species with their fattened stems and spiny armor, but succulence is present in 30 of 50 plant orders (Eggle and Nyffeler 2009), most of which are represented in arid and semiarid habitats. These taxa show great diversity of form and physiology in spite of having the similar ultimate function of attenuating water stress.

In places, succulents may dominate the biomass or diversity of a desert. The arid and semiarid regions of southern Africa that include the Namib Desert and Succulent Karoo harbor the highest diversity of succulents – equaling approximately 1/3 of the estimated ~10,000 succulent species globally. Parts of the Sonoran Desert are so influenced by the presence of succulent species that Forrest Shreve relied heavily on them for delineating four of six vegetational subdivisions (Shreve and Wiggins 1964). The Arizona Upland is *crassicaulescent* (succulent stem cacti), the Central Gulf Coast is *sarcocaulous* (fleshy stem trees), the Vizcaíno region is *sarcophyllous* (succulent leaf), and the Magdalena region is *arbocrassicaulescent* (tree and stem succulent). These divisions also highlight the most common groupings of succulence among species: *leaf succulents* (e.g., aloe and yucca), *stem succulents* (e.g., most cacti), and *caudiciform succulents*, whose succulent parts may include non-photosynthetic portions of the stem, the upper part of the root and the root proper (e.g., many *Euphorbia* sp.).

Given the pulsed nature of rainfall in most arid ecosystems, rapid uptake of large quantities of water is important for succulent species. To accomplish this, many succulents have extensive root systems that are often only a few centimeters below the soil surface (e.g., cholla and barrel cacti). Another adaptive feature of the roots of some succulent species is the very rapid formation of new roots when water is present. These *rain roots* form within a couple days of wetting and die once the soil is again dry. Thereafter the main root system is impermeable to water uptake and water loss throughout the dry period, which can last for many months. Both shallow roots and rain roots provide a mechanism for succulent plants to rapidly take advantage of ephemeral water availability and small rain events that wet just the upper soil layer.

In leaf and stem succulent plants, water is typically stored in the vacuoles. Thus, another feature of succulent plants is the presence of very large vacuoles in the succulent tissues, occupying up to 90 % of the cell volume. These vacuoles also serve another purpose in many succulent species, storage of organic acids associated with CAM photosynthesis. Most succulent species display some degree of CAM photosynthesis (although there are many without any CAM activity). The combination of CAM and succulence represents a structure-function relationship that is remarkably well suited for life in warm and arid environments.

Desert Halophytes Face Two Challenges: Water and Salt Stress

Plants growing near the base of a watershed or drainage basin would normally be expected to have higher water availability, but in deserts, such basins typically also have highly saline soils. High soil salinity is common throughout arid regions due to

high evaporation rates that exceed precipitation input. Dissolved solutes are not leached from these soils; instead, they are concentrated near the soil surface as water evaporates. In low-lying basins, salts are transported with rain runoff from the surrounding elevations and then further concentrated by evaporation. Over many years, this process results in extremely saline “playas” or salt basins. The center of most basins has such high salinity and fine soil particles that no vegetation can establish or survive, but along the margins where particle sizes are larger and salinity is not as extreme, the plant community is usually unique, composed of species that can survive relatively high salinity. Such salt-adapted plants are known as *halophytes*, meaning “salt plants.”

Plants that live in saline habitats but have mechanisms to prevent uptake of salts through the roots are called salt avoiders or excluders. These are not true halophytes because they always grow best in the absence of salinity. In general, salt excluders are not particularly common in deserts because the process of salt exclusion leads to increasingly greater soil salinity in the rooting zone.

True halophytes take up salt minerals (primarily Na^+ , K^+ , and Cl^-) through the roots and into the plant tissues; thus they face the challenge of preventing physiological dysfunction and possible cell death caused by the toxicity of high salt concentrations. Controlled balance of cell ionic concentrations through rapid growth and synthesis of compatible organic solutes (i.e., osmotic adjustment), coupled with compartmentalization of the salt ions are keys to salt tolerance in halophytes. Another challenge to growth in saline soils is that salinity causes soil water potential to be lower, making it more difficult for plants to take up water. For halophytes, however, the uptake of salts into the roots facilitates water uptake by lowering the root water potential, thereby counteracting the problem of lower soil water potential.

Some halophytes actually have lower growth in nonsaline soils than in those with modest levels of salinity (i.e., 50–250 mM NaCl) (Flowers and Colmer 2008). All, however, must have mechanisms to prevent the toxic ramifications of high salt concentrations in living tissues. *Salt accumulators* prevent these negative effects by sequestering salts in the vacuoles or other cell structures, thus eliminating interactions between the salts and cytoplasmic components and membranes. Many salt accumulators are succulent because they rely on large vacuoles for this purpose. Examples of succulent salt accumulators are common in the Chenopodiaceae family (e.g., *Salicornia*, *Suaeda*, and *Allenrolfea*), but also from this family are species in the genus *Atriplex* that sequester salts in modified epidermal hairs (salt bladders). Interestingly, the salt bladder can serve an additional beneficial function. As water evaporates from the bladder, the salts precipitate from solution and become white. This increases the albedo of the leaf, which, like the leaf hairs of *Encelia farinosa*, increases leaf reflectance of solar radiation, attenuates heat load, and reduces transpiration (Mooney et al. 1977).

Another mechanism to avoid the toxic effects of high salinity is to excrete the cellular salts onto the outer leaf or stem surface. *Salt excretors* are found across plant functional groups and taxa (e.g., salt cedar tree, *Tamarix*, and salt grass, *Distichlis*). Many rely on specialized salt glands to excrete the cellular salts, where once on the surface, the salt is either washed or blown off or eliminated when the leaf abscises.

Biotic-Mediated Processes Are Critical for Nutrient Balance in Deserts Plants

Although water is the resource that most limits desert plant productivity, nutrients have often been shown to constrain productivity when water is not limiting, even over short periods of time (e.g., during annual plant growth). Nutrient limitations have been documented in many deserts through experimental supplements of water and nutrients (especially nitrogen); however, not all species within a desert respond equally to nutrient supplements – and some do not respond at all (e.g., perennial grasses in Chihuahuan). Owing to such differential responses, the interplay of water and nutrient limitations can have a distinct impact on community composition in deserts.

Nutrient availability in desert soils is typically low and both spatially and temporally heterogeneous. As in many systems with low nutrient availability, plant tissues in deserts have high retention of nutrients, and although resorption of some nutrients can be much higher in desert plants than is typical, plant litter nonetheless returns more nutrients to the soil than any other input. As such decomposition plays a critical role in desert nutrient availability and cycling. In contrast to more mesic ecosystems, decomposition of surface biomass in deserts is dominated by abiotic processes, namely, photodegradation by UV light followed by physical fragmentation by wind or rain. Subsequent burial of degraded tissues completes decomposition via biological processes. Subsurface decomposition is almost entirely biological and can proceed at rates comparable to those in mesic ecosystems. However, the majority of biotic decomposition is controlled by moisture and is therefore episodic (pulse driven) in most desert systems.

Spatial variability of nutrients is also characteristic of desert ecosystems. In most deserts, *islands of fertility* form around the base of shrubs and trees owing to the accumulation of nutrients and its feed-forward effect. Litter that falls from the plant, as well as capture of litter and dust blown across the landscape, contributes to the buildup of nutrients at the base of the plant. (In some cases a coppice mound will also develop from particle accumulation below the plant and erosion around the plant.) Higher nutrient presence, as well as the shading effect of the plant, usually facilitates growth of annuals around the plant base. When these annuals die, their litter will further add to the nutrient island. Burrowing animals are also common at the base of such plants due to the cover provided by the plant, the friability of soils, and the food sources present within the island (e.g., herbaceous plants, seeds, and insects). The burrows influence water infiltration that can improve growth of the shrub or tree, while animal waste and decomposition may further contribute to the nutrients beneath the plant. Another place where nutrients commonly accumulate is surface depressions. Here, litter and soil accumulate due to particulate transport in runoff water and blowing wind.

As in other ecosystems where nutrients may limit primary productivity, biotic fixation of atmospheric nitrogen represents an important nutrient input in deserts. As such, it is not surprising that a few plant taxa having symbiotic relationships with nitrogen-fixing bacteria are common and widespread in arid and semiarid systems.

Among the most widespread are trees in the legume family (Fabaceae), which form nitrogen-fixing associations with *Rhizobium* and *Bradyrhizobium* bacteria. These trees, and the input of nitrogen due to their presence, are important components of desert communities across both the western and eastern hemispheres (e.g., *Acacia* in African and Middle East deserts; *Prosopis* in North and South American deserts). Nitrogen-fixing associations may also be formed between actinomycetes and plants and between free-living bacteria and plants that release root secretions into the rhizosphere surrounding roots. The latter is often accompanied by a rhizosheath, an anatomical specialization of the root that facilitates development of the bacterial association. The importance of these alternative nitrogen-fixing associations in deserts is poorly understood at present.

Biological soil crusts play many important roles in arid and semiarid ecosystems, including nitrogen input through nitrogen fixation. Biological soil crusts are an autotrophic microbiotic community composed of cyanobacteria (and other bacteria), green algae, lichens, mosses, and microfungi. Organisms in these microcommunities grow together as a mat or mound that integrates with particles in the top few millimeters of the soil via a network of cyanobacteria and fungal filaments. All arid and semiarid regions of the world have biological soil crusts, and in some places they occupy up to 70 % of the surface cover. In places where such crusts are present, plants often have greater overall biomass and higher tissue nitrogen concentrations (e.g., tissue nitrogen is 9–31 % higher for plants growing among biological soil crust in the Great Basin Desert).

One function of biological soil crusts that contributes to plant nutrition is fixation of atmospheric nitrogen by cyanobacteria and lichens of these microcommunities. This nitrogen is made available to plants through both decomposition of dead biomass and leaking of nitrogen from the cyanobacteria and lichen. For example, the cyanobacteria *Nostoc* has been shown to lose up to 80 % of its fixed nitrogen. This nitrogen enters the soil mostly as NO_3^- and is readily available for plant uptake. However, fixation and release of nitrogen are highly variable within and between deserts depending on the species composition of the crust, the soil moisture levels, and the soil temperatures. Biological soil crusts also contribute carbon to the soil microbial communities of deserts, thereby benefiting decomposition and other microbial-mediated processes that impact plant nutrition.

Biological soil crusts may also affect desert plant communities because of their impact on soil water availability, seed germination, and plant establishment. Soil water is typically greater in the presence of biotic crust because it slows the surface movement of water, which allows greater time for infiltration and may reduce evaporation from the subsurface. These benefits are best realized after large or prolonged precipitation events. Small pulses of rain may only wet the biotic crust without ever percolating into the subcrust soil. A number of studies have also shown biological soil crusts to improve or, at worst, not affect germination and establishment of native plants. In contrast, many alien species have reduced germination and establishment on biotic crusts. Such findings imply an evolutionary response of native desert plants to the presence of biological soil crust, but few hypotheses based on this context have been tested.

Mycorrhizal fungi facilitate uptake of water and nutrients of desert plants in the same manner as they do for other species, and they appear to be as widespread among desert plant families as for those of other ecosystems. Most desert mycorrhizae are of the arbuscular type. They improve uptake of water and nutrients because the extensive network of fungal hyphae greatly increases the functional surface area for uptake while exploiting a greater soil volume than do roots alone. *Dark septate endophytic fungi* is another group of fungi that form associations with desert plants. This group appears to be equally wide spread in deserts as mycorrhizae, perhaps more so. Their prevalence has led most authors to conclude that they play an important role in desert ecosystems and for desert plants (including for water or carbohydrate storage) yet their exact role has been difficult to elucidate.

Desert Biodiversity and Community Composition

Species Diversity Can Be Surprisingly High in Deserts

On a global scale, species diversity generally correlates with ecosystem productivity; thus deserts would be expected to have very low biodiversity, limited by scarce resources and severe climate conditions. In contrast to these constraints, however, deserts have high spatial variability of the physical environment, which generally facilitates increased species diversity and endemism. Indeed, with the exception of hyper-arid deserts, plant diversity and endemism in the world's deserts are surprisingly high. Species diversity on a local scale (alpha-diversity) can be remarkably high, as in the Negev desert where over 100 species per 0.1 ha can be found in places. In many deserts, annual plant species contribute greatly to this diversity. This is partly due to the greater number of annual individuals that can be supported in any given area compared to perennial plants but also because annuals can escape (as seeds) the constraints of resource limitations and severe climate and then grow and reproduce during periods of high resource availability and low stress.

A number of deserts have notably high biodiversity and endemism. The Chihuahuan desert of North America has nearly 3,500 plant species, including many *edaphic endemics* – species that are restricted to specific substrate types (in this case unusually widespread gypsum soils). Endemism can also result from evolution under unique climate conditions, such as that related to fog in the central Namib Desert.

The Succulent Karoo desert stands out as one of the world's most speciose regions, with over 5,000 plant species and nearly 2,000 endemics. But unlike other deserts, annual species do not dominate the biodiversity of this desert. Instead, the Succulent Karoo, as the name suggests, is home to the world's greatest diversity of succulent species (Fig. 8), including over 1,700 leaf succulents. The region also harbors a great diversity of bulb and bulb-like *geophyte* species (~600). In contrast, there are only 35 tree species. Both alpha-(local)diversity (74 species per 0.1 ha) and beta-(species turnover)diversity (1.5 per 100 m) are high in the Succulent Karoo. The relatively mild climate of the Succulent Karoo region may contribute



Fig. 8 The Succulent Karoo is considered a global biodiversity hot spot. It harbors over 5,000 plant species including about one-third of the world's succulent species (Photo courtesy of A. G. West)

to its high biodiversity. Winter low temperatures are not extreme and neither are summer high temperatures; the latter are often buffered by cool coastal fogs and dew, which also serve to reduce drought severity and duration. Rainfall, though low (150 mm on average), comes in winter, and unlike many other deserts, it is relatively predictable.

Vegetation of Unique Habitats Increases Local and Regional Biodiversity

There are many unique habitats in deserts that increase plant biodiversity owing to properties quite different from usual desert environments. Some, such as riparian corridors and oases, are anomalous water-rich havens in a sea of drought. Others, like *sky islands*, harbor biota that are not typical desert dwellers, but nonetheless interact with and influence desert plant communities. The concept of a sky island is not restricted to desert systems, but it was first applied to the Madrean sky island mountains found in the Sonoran and Chihuahuan deserts of southwestern North America. Sky island vegetation is composed of taxa that are not desert specific, although desert taxa are often present. Instead, sky island communities are a complex mix of remnant species from the past when the region was less arid, species that have migrated to the mountains in spite of the surrounding desert barrier, and species that have evolved in situ as a result of the isolation. Not surprisingly, biodiversity on sky islands tends to be greater than the lowlands of the surrounding desert. The Madrean sky islands, in fact, are part of the Madrean pine-oak woodland global biodiversity hot spot. Elsewhere, sky islands may not receive enough rainfall to support vast assemblages of vegetation, but nonetheless form plant communities that are distinct from those of lower elevations.

The central Sahara massifs, for example, receive enough water to form shrubland and grassland communities that are different from the surrounding desert and often contain endemic taxa – and where water persists for long periods of time, unique montane wadis communities form.

Population and Community Dynamics Are More Complex than Expected

Plant communities of arid and semiarid ecosystems have often been used as a canvas for examining species coexistence and community dynamics. This may not seem surprising given that such systems usually have relatively few dominant species of only two or three functional types and a strongly limiting resource (water). But this simplicity is misleading, as in recent decades the role of biotic interactions has been more carefully scrutinized in arid and semiarid environments, with both theoretical and empirical evidence growing for its importance.

Perhaps understandably, early studies of desert plant communities placed most emphasis on abiotic controls. In contrast to more mesic systems, deserts have very low biomass and plants are usually so widely spaced that competition seems of relatively little importance to vegetation composition and structure. Furthermore, prominent desert ecologist, such as Forest Shreve working in the Sonoran Desert during the first half of the twentieth century, were immersed in the debate of succession theory, dominated at the time by Frederic Clements. Biotic interactions (i.e., competition) are implicit to the Clementsian theory of succession – yet to workers like Shreve, desert communities appeared to have little species succession, if any. The alternative explanation for succession, raised by Henry Gleason and later Robert Whittaker, of individualistic responses by species to environmental factors seemed more tenable for arid systems. Thus, abiotic controls were widely embraced in the desert literature, while biotic interactions were largely dismissed.

The Role of Competition in Shaping Desert Communities

Over the past few decades, a number of experimental and observational studies have brought biotic interactions to the forefront of desert community ecology. Abiotic factors still play a dominant role in broad-scale patterns of diversity, but increasingly biotic factors are being identified as drivers of community- and population-level dynamics. Competition has been implicated as a driver of plant spatial patterns in deserts, in that observations of *regular* (equal) spacing of plants across a landscape are interpreted as a result of strong competition that minimizes interactions. Although disputed, this interpretation has been reported for both intra- and interspecific plant patterns. But just as often, desert plant patterns are *random*, an indication of neutral overall interactions, or *clumped* (also called contagious) indicating potential facilitation between plants or clustering of plants within favorable microhabitats. (Although the latter implies an absence of competition, seasonal changes in resource availability can result in temporal variability of competition.)

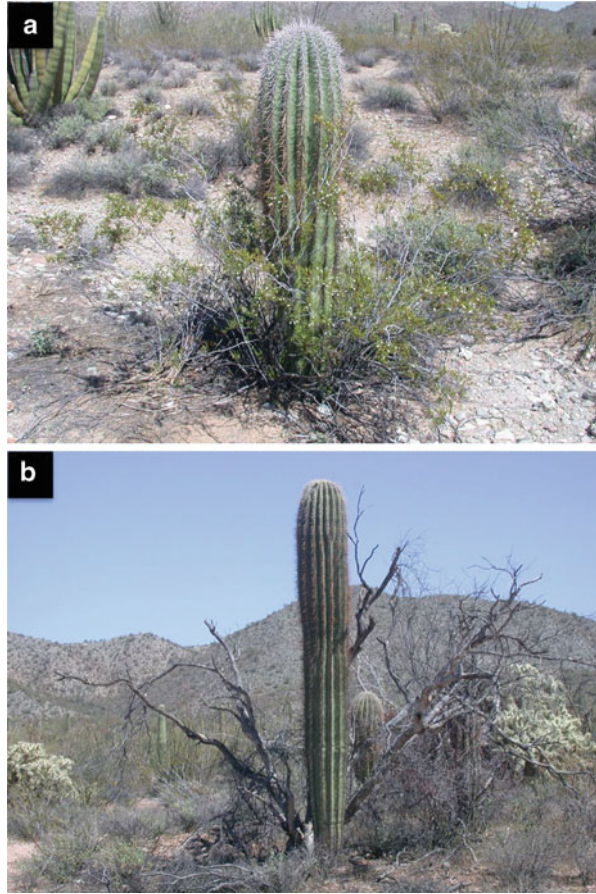
More direct evidence of competition has been elucidated from field manipulations of plants and plant resources. One early and widely cited example includes *Larrea tridentata* (creosote bush) and *Ambrosia dumosa* (white bursage), two of the most ubiquitous species of North American deserts. Widespread coexistence of these two species led to questions about belowground resource competition. In a series of studies, Fonteyn and Mahall (1978, 1981) used different combinations of plant removals (e.g., removal of *Larrea* only, *Ambrosia* only, neither, or both) to demonstrate both the presence of interspecific competition for water and that intraspecific competition was weaker than interspecific competition. Later studies by this group identified two mechanisms for these outcomes: inhibition of root growth mediated by an apparent exudate from *Larrea* roots (*allelopathy*) and avoidance of overlapping growth due to physical contact between roots of *Ambrosia*. Since these studies, a number of other neighbor-removal experiments in deserts have confirmed that competition, especially for water, is common both within and among species and for plants showing regular, clumped, and even random distributions.

Interspecific competition is one mechanism expected to lead to *resource (or niche) partitioning* between species. Studies on coexistence among desert plants have been instrumental in testing and, in many cases, verifying this concept, and although resource partitioning may not lead to full elimination of competition, it helps to minimize it. One widely used framework for such investigations is the “Walter two-layer hypothesis” attributed to German ecologist Heinrich Walter (1939, reviewed in Ward et al. 2013). The two-layer hypothesis predicts that species may coexist by partitioning belowground water resources such that one species relies primarily on shallow soil water and the other on deeper soil water. Originally proposed to explain coexistence of savanna grasses (shallow rooted) and trees (deeper rooted), this model has proved robust in deserts (reviewed by Ward et al. 2013). Coupled with an understanding of phenological differences among species, the Walter two-layer model has also proved valuable for understanding different interspecific responses to amount and seasonality of precipitation in deserts.

Other Species Interactions in Desert Plant Communities

Seedling establishment in deserts is generally rare and sporadic owing mostly to the great spatial and temporal variability of favorable soil water conditions. When establishment does occur, seedlings of some species are found under the canopy of mature plants more often than expected (i.e., nonrandomly). This plant-plant interaction is called a *nurse plant* or *nurse-protégé* association. The reasons for this pattern can vary among species and may also change through time, but at the establishment stage, this association is one of *commensalism*, whereby the nurse plant facilitates establishment of the protégé, but is not affected by its presence. Nurse plant associations are more often reported in arid and semiarid environments than elsewhere, supporting the tenet that facilitation is most common in stressful environments. However, the relationship often changes as the protégé grows out of the difficult establishment period and eventually becomes a competitor with the nurse plant.

Fig. 9 (a) A young saguaro (*Carnegiea gigantea*) growing from within the canopy of its nurse plant, creosote (*Larrea tridentata*). (b) Facilitation by the nurse plant may change to competition as the protégé saguaro matures, potentially leading to death of the nurse plant. The nurse tree here is palo verde (*Cercidium microphyllum*) (Photos: D. R. Sandquist)



Nurse plant associations are found among many plant families and thus do not appear to be phylogenetically restricted; however, in deserts the association strongly benefits establishment of CAM succulent species of the Cactaceae family. In the establishment period, tender CAM seedlings are sensitive to many environmental and biotic forces that are ameliorated by the presence of the nurse plant. The nurse canopy reduces direct solar radiation and high temperatures by shading and attenuates low overnight and winter temperatures. Surface water availability may also be greater beneath a nurse canopy due to shading or from water supplemented by hydraulic redistribution. Nurse plants also offer physical protection from herbivory and strong winds, the latter of which may also cause desiccation of young seedling plants. It is likely that a combination of these factors results in the nurse-protégé relationships found among desert cacti and other species.

The saguaro cactus (*Carnegiea gigantea*) of North America's Sonoran Desert is one of the most well-studied protégé species of the nurse-protégé syndrome (Fig. 9). Saguaro has multiple nurse species, but the palo verde tree (*Cercidium*

microphyllum) appears to be most common. Saguaro is protected from herbivores by palo verde, but studies have also demonstrated the importance of the microclimate under palo verde for facilitating saguaro establishment. For example, by decreasing nighttime loss of longwave radiation, temperatures above small saguaros under palo verde canopies are up to 10 °C greater. This appears to contribute to a more northerly distribution of saguaro than would be expected in the absence of a nurse plant association.

Disturbance, Global Changes, and Future Challenges

Disturbances Pose Significant Challenges in Low Productivity Ecosystems

Any ecosystem with low productivity and episodic recruitment will be slow to recover from disturbance. Deserts are no exception and in fact represent an extreme example of this tenet. For that reason, studies of responses to disturbance and recovery in arid and semiarid regions provide critical information about human impacts on ecosystem processes. Among the many types of anthropogenic disturbances that occur in desert systems, grazing of domesticated animals is one of the oldest. An obvious link exists between livestock presence and biomass decline due to herbivory, but grazing also causes soil disturbances that can reduce nutrients, increase erosion, and destroy beneficial biotic crusts. Such disturbances can also lead to loss of biodiversity and increased invasion by nonnative plant species. On a more positive note, much attention is now being given to determining sustainable practices of grazing in arid and semiarid systems.

Nonnative Species Are a Major Threat to Desert Communities

Owing to the harsh growing conditions of deserts, they are considered relatively resistant to invasion by nonnative species; however there are numerous examples of successful and widespread invasion in arid and semiarid ecosystems. One of the most troubling consequences of nonnative spread in desert ecosystems is the increase of fire where alien grasses invade desert shrubland. Low biomass and relatively large bare spaces between plants in a natural desert shrublands mean that fires rarely spread if started. Invasive grasses add a fine-textured fuel to the system that often occupies the shrub interspaces and once ignited easily carries fire from shrub to shrub (i.e., artificially increasing fire spread). Furthermore, because many grasses are adapted to recovering from fire and desert shrubs are not, grass cover increases at a much greater rate following fire than that of shrubs. Subsequent fires may eliminate shrubs altogether, resulting in an *ecosystem-type conversion* from native shrubland to alien grassland. Such conversion has pronounced impacts on biogeochemical cycles that are very difficult to return to preinvasion levels, even with intensive restoration efforts.

Other Global Changes also Threaten Desert Regions

Many other impacts of human activities affect deserts, including global warming, elevated CO₂, altered rainfall patterns, air and soil pollution, and habitat fragmentation. Owing to the underlying complexity inherent to arid and semiarid ecosystems (e.g., high spatial and temporal climate variability), ecologists are just beginning to understand the long-term consequences of these impacts. The stochastic nature of plant recruitment and mortality in deserts also hinders our ability to understand effects that are small or gradual through time (e.g., increases in temperature). Only through very long-term observations or detailed modeling efforts can one begin to understand the future of desert vegetation in the changing climate on Earth. Nonetheless, important information is beginning to emerge. For example, in a 10-year study of elevated CO₂ in the Mojave Desert, no changes were seen for plant cover, diversity, or richness; however using remotely sensed data over a longer time frame and larger area, the effects of increased atmospheric CO₂ appear to have caused a modest increase in arid-land plant cover.

Human pressures on deserts are as great as ever. Ironically, these problems are increasingly at-odds with other environmentally favorable activities, such as the growing demand for lands with high solar radiation or strong winds for development of renewable energy projects. Such conflicts mean that high-quality, scientific understanding of these landscapes is more important than ever. This understanding will enable intelligent management decisions that allow sustainable use but minimize inevitable losses of desert biota and mitigate impacts on important ecosystem processes.

References

- Eggle U, Nyffeler R. Living under temporarily arid conditions – succulence as an adaptive strategy. *Bradleya*. 2009;27:13–36.
- Ehleringer JR, Monson RK. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annu Rev Ecol Syst*. 1993;24:411–39.
- Ehleringer J, Mooney HA, Gulmon SL, Rundel P. Orientation and its consequences for *Copiapoa* Cactaceae in the Atacama Desert, Chile. *Oecologia*. 1980;46:63–7.
- Ezcurra E, United Nations Environment Programme. Division of Early Warning and Assessment. Global deserts outlook. Nairobi: United Nations Environment Programme; 2006.
- Flowers TJ, Colmer TD. Salinity tolerance in halophytes. *New Phytol*. 2008;179:945–63.
- Fonteyn PJ, Mahall BE. Competition among desert perennials. *Nature*. 1978;275:544–5.
- Fonteyn PJ, Mahall BE. An experimental analysis of structure in a desert plant community. *J Ecol*. 1981;69:883–96.
- Kearney TH, Shantz HL. The water economy of dry-land crops, Yearbook of the United States Department of Agriculture 1911. Washington, DC: Government Printing Office; 1912.
- Meigs P. World distribution of arid and semi-arid homoclimates. In: UNESCO, editor. Reviews of research on arid zone hydrology. Paris: United Nations; 1953.
- Mooney HA, Ehleringer J, Björkman O. The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra*. *Oecologia*. 1977;29:301–10.
- Mooney HA, Björkman O, Collatz, GJ. Photosynthetic acclimation to temperature in the desert shrub *Larrea divaricata*. *Plant Physiology*. 1978;61:406–10.

- Shantz HL. Drought resistance and soil moisture. *Ecology*. 1927;8:145–57.
- Shreve F, Wiggins IL. *Vegetation and flora of the Sonoran Desert*. Stanford: Stanford University Press; 1964.
- Smith SD, Monson RK, Anderson JE. *Physiological ecology of North American desert plants*. Berlin: Springer; 1997.
- Szarek SR, Woodhouse RM. Ecophysiological studies of Sonoran Desert plants 4. Seasonal photosynthetic capacities of *Acacia greggii* and *Cercidium microphyllum*. *Oecologia*. 1978;37:221–30.
- Tinoco-Ojanguren C. Diurnal and seasonal patterns of gas exchange and carbon gain contribution of leaves and stems of *Justicia californica* in the Sonoran Desert. *J Arid Environ*. 2008;72:127–40.
- UNESCO. *Map of the world distribution of arid regions: explanatory note*. Paris: UNESCO; 1977.
- von Willert DJ, Eller BM, Werger MJA, Brinckmann E, Ihlenfeldt H-D. *Life strategies of succulents in deserts: with special reference to the Namib Desert*. New York: Cambridge University Press; 1992.
- Ward D, Wiegand K, Getzin S. Walter's two-layer hypothesis revisited: back to the roots! *Oecologia*. 2013;172:617–30.

Further Reading

- Evenari M, Noy-Meir I, Goodall DW. *Hot deserts and Arid Shrublands*. New York: Elsevier; 1985.
- Ward D. *The biology of deserts*. Oxford/New York: Oxford University Press; 2009.
- Whitford WG. *Ecology of desert systems*. San Diego: Academic; 2002.

Web Resources

- <http://worldwildlife.org/biomes/deserts-and-xeric-shrublands>
- <http://www.eoearth.org/view/article/168410>