

Annuals and perennials of warm deserts

JAMES EHLERINGER

7.1 Introduction

Warm deserts have held a certain attraction and fascination for plant ecologists and physiologists for many decades. The reasons for this interest lie in the different types of plant assemblages, the large diversity of life forms, and the remarkable plant adaptations which have arisen in response to the environmental extremes of high air and soil temperatures, high solar radiation levels, low relative humidities, low precipitation levels, and extended drought periods. Substantial progress has been made in understanding the ecology of some of the dominant plant species, including the relationships between form and function, adaptation at morphological, physiological, and biochemical levels, and factors affecting distributional ranges.

This chapter deals with the physiological ecology of both perennials and annuals of warm deserts, but excludes cacti and other succulents which are discussed in Chapter 8. The Sonoran Desert and its various sub-divisions and the low elevation regions of the Mohave Desert such as Death Valley are included in this discussion, but the Chihuahuan Desert of northern Mexico is not. Together these regions comprise the warm deserts; the higher elevation cold deserts will be covered in Chapter 9. The location of warm and cold deserts is indicated in Fig. 8.1.

7.2. The physical environment

Before discussing the ways in which plants have adapted to warm deserts, it is essential to have an

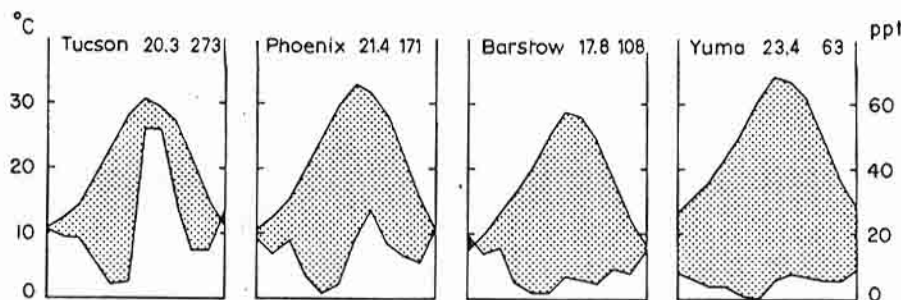


Figure 7.1 Climate diagrams for representative sites within warm deserts. Sites were chosen to represent a range of precipitation levels, both in amount and seasonality (from Sellers and Hill, 1974, and US Weather Bureau Records). Left hand axis is mean monthly temperature and right hand axis is mean monthly precipitation

understanding of the physical environment and the constraints it imposes on plant activity. High temperatures and drought are two factors which severely limit plant growth, and are evident in representative climate diagrams of desert sites (Fig. 7.1). Precipitation varies between sites in both amount and seasonality, and all locations have drought periods ranging from 5 to 12 months. Both the length and magnitude of the drought (difference between precipitation and temperature curves) are greatest at the driest sites. These data suggest that at the drier sites, potential evapotranspiration always exceeds precipitation and that plants are continuously exposed to drought conditions.

Although the climate diagrams indicate high mean monthly temperatures throughout the year, they underestimate the actual potential for stress during growth periods in winter and early spring. Mean maximum daily air temperatures range from 15 to 20 °C in winter, from 25 to 35 °C in spring, and 38 to 43 °C in the summer, depending on location

(Ives, 1949; Sellers and Hill, 1974; US Weather Bureau records). Thus, daily air temperature fluctuations may be quite high and plants can be exposed to temperatures in excess of 30 °C for most of the growth periods. Since these are weather screen data (usually measured at ~ 1.5 m), plants growing near the surface (0–30 cm) will be exposed to much higher temperatures. Soil surface temperatures greater than 60 °C are common during summer months (Ehleringer *et al.*, unpublished; Sellers and Hill, 1974; Terjung *et al.*, 1970). This would imply that plants growing close to the surface in the summer would be exposed to air temperatures of 45–55 °C.

Skies are often clear and levels of solar radiation are generally higher than in other ecosystems (Sellers and Hill, 1974; Thekaekara, 1976). The greater incident solar radiation should enhance plant productivity during periods of available soil moisture. However, clear nighttime skies and low relative humidities result in high net radiation loss

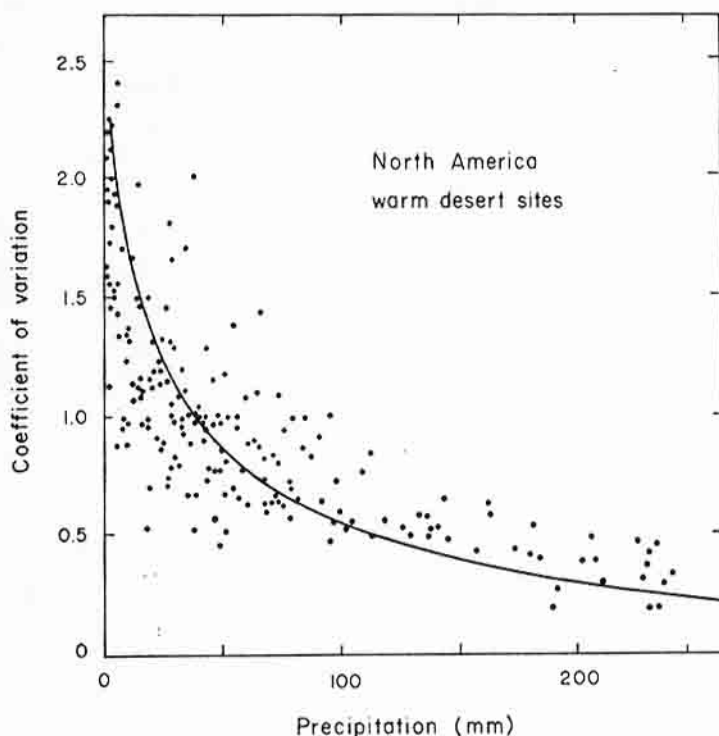


Figure 7.2 The coefficient of variation of precipitation plotted as a function of mean precipitation for warm desert sites (modified from Ehleringer and Mooney, 1983).

and large daily fluctuations in air temperatures.

Equally important as the range of mean annual precipitation is the variability or predictability of that rain. Between one season and the next, precipitation is often highly predictable (Pianka, 1967). However, from year to year the coefficient of variation increases asymptotically as mean precipitation decreases (Fig. 7.2). This is also the case for precipitation falling within individual seasons. Consequently, precipitation is highly unpredictable at low precipitation sites. In fact, the mean annual precipitation exceeds the mode in desert locations so that most years are drier than the average (McDonald, 1956).

An important but neglected component in considerations of the desert physical environment is the soil. Typical desert soils, termed aridisols, are clearly distinguishable from soils of other regions by their lack of development (Steila, 1976). Low precipitation results in reduced weathering, shallow soil depths, low concentration of organic matter and low cation exchange capacity. Soils on slopes and bajadas (alluvial fans) tend to be rocky, while those on flat plains are high in clay particles and often have caliche layers 1–2 m from the surface. Desert pavement, a surface of finely packed rocks in a swelling clay matrix, has a very low infiltration rate, and is common in many of the drier areas. Unlike most ecosystems, not all drainage basins empty into the oceans. Those that do not, create highly alkaline regions at their termini, many of which are ancient lake beds. This combination of soil characteristics tends to accentuate the arid conditions already imposed on the vegetation by the climate.

7.3 Phenology and life cycle adaptations

7.3.1 OPPORTUNISTIC RESPONSE

The feature which most generally characterizes warm desert plants is their opportunistic response to water availability. Water is the cue for plants to commence vegetative growth (Beatley, 1974; Ehleringer and Björkman, 1978a). Most perennial shrubs, irrespective of whether they have deciduous or evergreen leaves, are capable of vegetative growth and reproductive activity in either winter

(November–April) or summer (July–October) seasons. A critical minimum amount of rainfall, usually in the form of a large storm, is necessary to trigger vegetative growth in perennials. This minimum precipitation is thought to be approximately 25 mm (Beatley, 1974). Because of the pronounced geographical gradient in seasonality of precipitation, most of the annual growth in the northern and western portions of warm deserts occurs in winter and spring. Only in the southern and eastern portions is vegetative growth predominantly in summer.

Germination of annuals is also triggered by a critical minimal rainfall (Beatley, 1974; Juhren *et al.*, 1956; Went 1948, 1949). For winter annuals, 10–15 mm is necessary to induce germination. Higher germination percentages and more vegetative growth occur with greater rainfall amounts (Beatley, 1969; Went and Westergaard, 1949). Specific temperature requirements for germination for winter and summer annual floras prevent germination during the wrong season (Koller, 1972).

The timing of the initial heavy rainstorms is variable. Based on weather records it appears that late November to early December is the most likely period for the start of the winter precipitation season in northern portions of the warm deserts. About one year in four, these rains will not come until January or later (Beatley, 1974). Summer rainfall is just as variable (McDonald, 1956), and usually begins in late July. The effects of precipitation timing and amounts on the germination of particular annual or perennial species are not known.

7.3.2. LIFE FORMS

One result of the large spatial and temporal variability in the physical environment of warm deserts is a high diversity of plant life forms (Fig. 7.3). Warm deserts stand out from adjacent vegetation types (chaparral, cold desert, pinyon – juniper woodland, thorn forest and grassland) by the differences in physiognomy of its dominant plants. Shreve (1951) describes 25 major life forms for the Sonoran Desert. These include the dominants of the Raunkiaer life form system, but also forms varying in leaf duration, character of stem, degree of succulence, and seasonality.

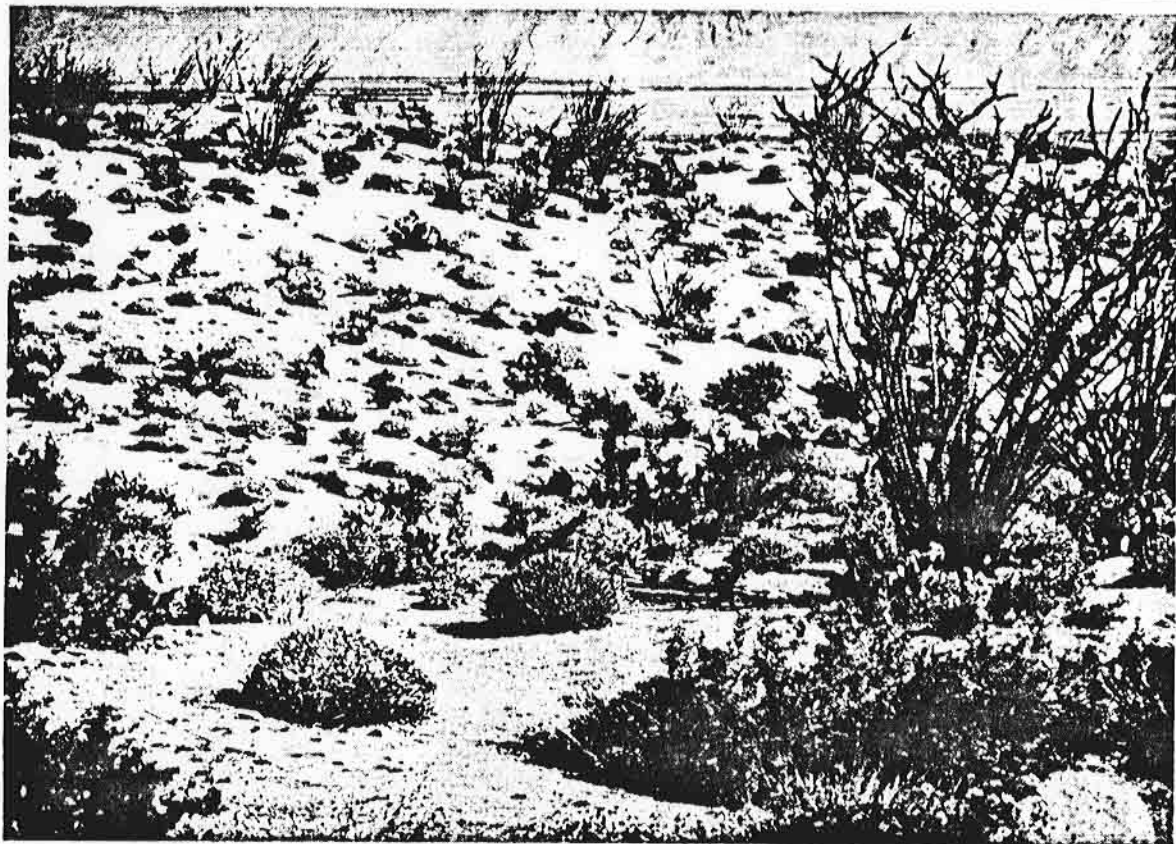


Figure 7.3 The variety of plant life forms present in warm deserts is evident in this photograph of the Anzo-Borrego desert in Southern California.

The distribution of life forms is not uniform, suggesting adaptive and competitive limitations of specific life forms. Some desert regions are characterized by complex communities, whereas other have near monospecific stands. Evergreen and deciduous-leaved shrubs dominate bajadas as well as the plains. Trees are for the most part phreatophytic or restricted to water courses. Succulents of various types are much more common on well-drained rocky slopes than the silty plains. As a class winter ephemerals do not appear to be restricted to certain microsites, although particular species may be (Forseth *et al.*, 1983). Summer ephemerals appear most abundant along water courses and plains, and facultative perennials are most common on disturbed sites.

While annuals occur in virtually all warm desert sites, their abundance as an adaptive life form is very much affected by the variability in precipitation. Schaffer and Gadgil (1975) have shown that as the variability in precipitation from year to year increases, so does the percentage of annuals that comprise the flora. It appears that in low precipitation sites, the probability of surviving extended drought periods becomes so low that perennial life forms be they shrubs, succulents or root perennials, are selected against. It should be noted, however, that while the diversity of perennial forms declines with precipitation levels, certain perennials such as *Larrea divaricata* may predominate even at the driest locations.

7.3.3 VEGETATIVE AND REPRODUCTIVE GROWTH

Several contrasting adaptations occur in the vegetative and reproductive features of annuals and perennials. In perennials, vegetative growth occurs rapidly following the 'triggering' rain storm. Presumably carbohydrate reserves from the previous year are the source of carbon. Following this initial development, vegetative growth occurs at a reduced rate and ceases at flowering in zoophilous species. In anemophilous perennials, vegetative growth may continue after flowering, since flowering occurs so early in the growing season. More data on specific dominant perennials are needed to verify the generality of this pattern. In contrast, winter annuals exhibit slow vegetative growth until the onset of warmer spring temperatures (Beatley, 1974). Also unlike perennials, these same winter annuals will add vegetative growth following late season precipitation (Beatley, 1974; Clark and Burk, 1980). Death in annuals appears to be caused by a shortage of water. In years with above normal and late season precipitation, many annuals are able to persist and become facultative perennials (Beatley, 1967, 1969, 1970).

Sexual reproduction occurs by either zoophily or anemophily in perennials. Flowering appears cued by photoperiod in anemophilous species and occurs in late winter. Developing fruits often have large green (presumably photosynthetic) bracts and mature over the remainder of the growing season (~4 mon). In contrast, zoophilous perennials flower late in the growing season, and reproduction is presumably induced by water stress or high carbohydrate levels. Fruits of these species are also green, have photosynthetic activity (Werk and Ehleringer, 1983), and mature in a relatively short period (~1 mon). For the most part, vegetative growth and reproductive activity are distinct in these perennials. This is not the case for most winter and summer annuals.

In most annuals reproductive activity begins after plants have attained some minimal size, and then both vegetative growth and reproductive activity progress simultaneously until the plant dies. This continued flowering can be either determinate (as in the axillary flowering of *Mohavea*) or indeterminate

(as in terminal spikes of *Lupinus*). In indeterminate flowering species, new vegetative growth is axillary. Early and continuous flowering of annuals is presumably an adaptive feature in desert habitats, where the rainfall and the end of the growing season are both unpredictable. Reproductive output (number of seeds produced) appears to be directly related to both plant size and carbon balance (Ehleringer *et al.*, unpublished data). Therefore, small differences in water availability and slope geometry affecting solar radiation levels between microsites will have a large impact on reproductive output.

Environmental gradients also affect aspects of the reproductive biology of perennials. Dioecy is common in many desert plants (Freeman *et al.*, 1976; Simpson, 1977), including representatives of the genera *Atriplex*, *Ephedra*, *Jatropha*, and *Simmondsia*. As sexes within a single population segregate along microenvironmental gradients (Freeman *et al.*, 1976), dioecy can be considered as an adaptation to stressful conditions. Male plants tend to be more common in microsites where high salinity, high radiation, or low soil moisture increase drought stress, while female plants are overrepresented on mesic microsites. Since there is a differential cost to the production of male versus female reproductive structures, the plant carbon balance is likely to be a key factor in these sex ratio clines. The observed distributions are consistent with the notion that female reproduction is more costly in terms of carbon and should therefore be more common on microsites where the carbon gaining capacity of the plant is greater. Also consistent with this notion is the observation that sex expression in *Atriplex canescens* is a function of annual environmental conditions (McArthur, 1977). In mild wet years, the sex ratio is female biased, while in cold dry years it is male biased.

7.3.4 COMPETITION

When nondesert plant communities are compared, one common feature is the high degree of life form similarity in the dominant species, irrespective of differences in phylogenetic relationships. In these situations it might be concluded that strong competition has produced this uniformity. In warm deserts

though, the distances between plants are great, and under only the rarest of situations do canopies of neighboring plants overlap. As a consequence, Shreve (1951) concludes... 'there has been much less competition. The greatest "struggle" of the plants has not been with one another, but with the environment. Therefore the conditions tending toward the elimination of certain types and the survival and dominance of a relatively uniform one have not been operative'. For perennial and annual warm desert plant species this is probably the case for aboveground competitive interactions, with the possible exceptions of the establishment phase in some species and high density situations in micro-depressions. However, there is evidence for below-ground competition in several perennial species.

Vast areas of the desert consist of a two species community, *Larrea divaricata* (= *L. tridentata*) and *Ambrosia dumosa* (= *Franseria dumosa*). The horizontal spatial dispersion patterns of the long-lived evergreen shrub *Larrea* are often regular and for the short-lived drought deciduous shrub *Ambrosia* are contagious (Fonteyn and Maball 1978; Woodell *et al.*, 1969). In an elegant experiment, Fonteyn and Mahall (1978) followed the development of leaf water stress of single individuals in which there had been differential and/or total removal of the other neighboring plants (Table 7.1). Their results imply that:

1. competition is not occurring between *Larrea* individuals;
2. competition is occurring between *Ambrosia* individuals; and
3. competition is occurring between *Larrea* and *Ambrosia* individuals. Presumably the distribution of

Larrea was originally contagious, but as a result of competition for water and the resultant elimination of individuals, the plants now occupy a regular distribution in which competition no longer occurs. Competition occurs among *Ambrosia* individuals, because they are short lived and have higher recruitment rates.

7.4 Leaf and canopy adaptations

7.4.1 LEAF ENERGY BALANCE

One result of the large spacing between plants is that leaves are potentially exposed to high radiation loads in this high temperature environment. The consequence can be seen in the broad array of adaptations found in leaves of warm desert plants. The relevance of different morphological features is made quantitatively clear through an analysis of leaf energy budgets as developed by Gates (1980). As a review of this topic will not be provided here, the reader is referred to the work by Gates for an introduction and the specific equations. The leaf energy budget is a balance of energy inputs (absorbed solar and infrared radiation) and losses (reradiation, convection, and transpiration) which determines the physiologically important parameters of tissue temperature and water loss.

The preponderance of small, highly dissected, or compound leaves as in *Acacia*, *Ambrosia*, *Larrea*, *Pectis* and *Prosopis* has been considered an adaptation to warm desert environments (Schimper, 1903; Warming, 1909). The smaller leaf size (1–10 mm width) results in a higher heat transfer coefficient, and consequently leaf temperature will remain close to or slightly above air temperatures (Gates, 1980; Smith and Geller, 1980). This will be of particular value to plants experiencing high solar radiation loads and high air temperatures, especially when wind speed and transpiration rates may be low.

Not all desert plants are characterized by small leaf size, however. A number of drought-deciduous perennials such as *Datura*, *Encelia*, and *Hyptis* as well as annuals such as *Amaranthus*, *Atrichoseris*, and *Proboscidea* have leaf widths in the 30–200 mm range. Smith (1978) and Smith and Geller (1980)

Table 7.1 Effects of differentially removing plant species surrounding a central individual in a *Larrea divaricata*–*Ambrosia dumosa* community on its leaf water potential (from Fonteyn and Mahall, 1978). Values are means \pm 1 s.d. Units are MPa

Treatment	<i>Larrea</i>	<i>Ambrosia</i>
Control	-3.90 ± 0.13	-4.42 ± 0.32
Total removal	-3.37 ± 0.16	-3.05 ± 0.34
<i>Larrea</i> removal	-3.93 ± 0.23	-4.46 ± 0.39
<i>Ambrosia</i> removal	-3.46 ± 0.27	-3.65 ± 0.28

have pointed out that large leaf size can be beneficial and result in significant leaf undertemperatures (leaf temperature lower than air temperature) if sufficient soil moisture is present to allow the maintenance of high transpiration rates. Additionally, a low leaf absorptance to solar radiation will enhance this advantage. Many of these large-leaved species are restricted to microhabitats having greater soil moisture contents. In response to decreases in water availability or to increases in air temperatures, large-leaved species show substantial decreases in leaf size (Cunningham and Strain, 1969; Mooney *et al.*, 1977b; Smith and Nobel, 1977).

Two principal adaptations exist to reduce the amount of solar radiation absorbed by the leaf under stress conditions. First is a steep leaf inclination, and second, a decrease in leaf absorptance to solar irradiance. Leaves with inclinations greater than 70° occur in a number of evergreen perennial shrubs, including *Atriplex hymenelytra* and *Simmondsia chinensis* (Mooney *et al.*, 1977b). Steep leaf angles result in decreased energy loads, and thus lowered leaf temperatures during stressful midday conditions of the late spring and summer months. During winter and early spring, steep leaf angles result in a more constant solar radiation load incident on the leaf than is the case with more horizontal orientations.

Leaf absorptance may be reduced by increasing surface reflectance through epidermal modifications including hairs (*Brickelia*, *Encelia*), salt glands (*Atriplex*), and waxes and spines (*Opuntia*) (Ehleringer, 1981) (Fig. 7.4). Over the 400–700 nm waveband (photosynthetically useful wavelengths), green leaves such as those of *Prosopis juliflora* typically absorb 85% of the incident solar radiation. In contrast, species with well-developed epidermal modifications may have leaf absorptances as low as 30–40% (Ehleringer and Björkman, 1978a; Ehleringer *et al.*, 1976; Mooney *et al.*, 1977b). Changes in leaf absorptance are reversible within the same leaf in species utilizing salt glands to reflect light (Mooney *et al.*, 1977b) and probably also in species using waxes. However, reversible changes in the same leaf do not occur in species utilizing hairs (Ehleringer, 1982; Ehleringer and Björkman, 1978a). In those situations, older leaves are ab-

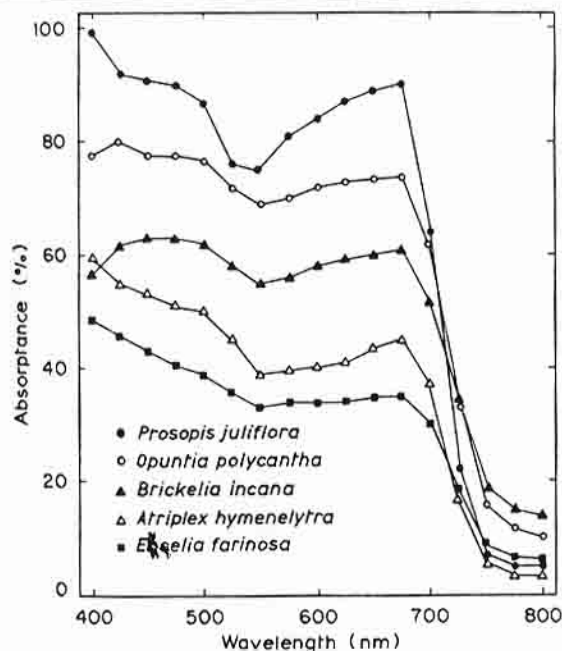


Figure 7.4 Leaf absorptances over the 400–800 nm waveband for a number of warm desert species (from Ehleringer, 1981).

scised and new leaves with different spectral characteristics are produced.

Leaf temperature and energy balance depend on the leaf absorptance over the entire solar spectrum, not just over the 400–700 nm waveband. However, as one might expect, the two are very tightly correlated (Ehleringer, 1981). For example, leaf absorptances in the 400–700 nm band of 85% (green leaf) and 40% (white leaf) correspond to 50% and 17% absorptances over the entire solar band, respectively. As a consequence of this three-fold difference in leaf absorptance to total solar radiation, there are substantial decreases in both leaf temperature and transpiration (a result of decreased leaf water-vapor pressure). Decreases in leaf temperature of 5–10°C as a result of decreased leaf absorptance are common (Ehleringer and Mooney, 1978; Smith, 1978; Smith and Geller, 1980). Just exactly what this means to the plant in terms of competition or extending growth activity into the drought period is not known.

Reduction of leaf absorptance as an adaptation to hot, arid conditions is best developed in shrubs,

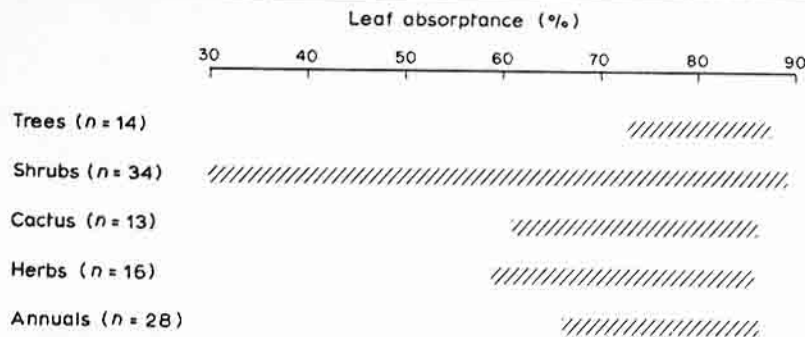


Figure 7.5 Leaf absorptances to solar radiation in the 400–700 nm waveband for the dominant life forms in the Mohave and Sonoran Deserts (from Ehleringer, 1981).

occurs to a lesser extent in cacti and perennial herbs, and is rare or absent in trees and annuals (Fig. 7.5). Within the shrub life form, several dominant species are capable of varying leaf absorptance from 50% to 85% (400–700 nm) depending on environmental conditions, and a few such as *Encelia farinosa* produce leaves whose absorptance will vary from 30% to 85% (Ehleringer, 1981; Ehleringer and Björkman, 1978a; Mooney *et al.*, 1977b). As a rule, herbaceous and shrub species with reduced leaf absorptances occur on drier, exposed bajadas and rocky slopes and not in ravine bottoms or along water courses where glabrate-leaved species predominate. Within the trees and annuals, most of the variation in leaf absorptances are the result of differences in leaf thickness (transmittance) and not surface reflectance. The absence of reduced leaf absorptances in these two groups is not surprising, since trees occur primarily along water courses and annuals have an ephemeral life history. One notable exception to this trend is *Dicoria canescens*, which is a pubescent leaved, spring and summer active annual of sand dune habitats, and has a late season leaf absorptance of 66% (Ehleringer, 1981).

7.4.2 CANOPY MORPHOLOGY

The air temperatures, humidities, wind speeds, and consequently leaf temperatures to which a plant canopy is exposed are very much dependent on where the canopy is within the microclimatic profile. Soil surfaces are heated quickly because of high incident solar radiation and low soil evapora-

tion. Microclimatic profiles are steep (Fig. 7.6), and there may be significant temperature (and thus metabolic) differences between leaves at different heights.

During the cool winter and early spring periods, annuals take advantage of this microclimatic profile by growing as rosettes just above the soil surface (Ehleringer *et al.*, 1979; Mulroy and Rundel, 1977). Winter annuals often have highly dissected leaves (Mulroy and Rundel, 1977). Since wind speeds are low near the soil surface, leaf dissection may be of advantage in keeping leaf boundary layer small. Notable exceptions include *Atrichoseris platyphylla*, a species with orbicular leaves up to 8 cm diameter and closely appressed to the ground surface.

As air temperatures increase rapidly in the spring, many winter ephemerals simply lengthen internodes (e.g. *Geraea canescens*, *Lupinus arizonicus*, *Malvastrum rotundifolium*, and *Phacelia calthafolia*) so that leaves are raised above the hot surface into a cooler part of the microclimatic profile. When temperatures get hot, other plants, including *Atrichoseris platyphylla* and *Eriogonum rexfordii*, bolt and allow the basal leaves to wither away. Still other prostrate annuals such as *Astragalus lentiginosus*, *Coldenia nuttallii*, and *Polygonum aviculare* raise and lower their branches diurnally apparently to avoid high soil surface temperatures (Ehleringer *et al.*, unpublished).

Leaf canopies of perennial herbs and shrubs fit either of two qualitatively distinct morphologies. They are tightly packed and hemispherical (*Ambrosia dumosa*, *Encelia farinosa* and *Hymenoclea*

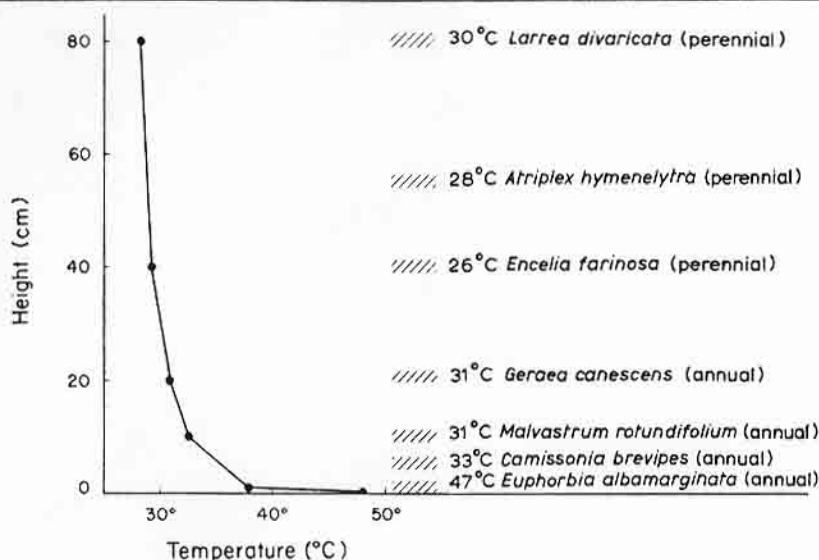


Figure 7.6 Left: microclimatic profile of air temperature as a function of height above the soil surface at midday in late March on a bajada in Death Valley, California. Right: representative leaf temperatures measured on the dominant plant species at approximately mid-canopy height.

salsola) or loosely arranged and amorphous (*Hyptis emoryi*, *Larrea divaricata*, and *Simmondsia chinensis*). The functional significance of either of the two canopy types is not understood.

7.5 Photosynthetic and water relations adaptations

7.5.1 ADAPTATION MODEL

Throughout this discussion, the assumption is made that natural selection favors plants whose form (physiology, morphology, physiognomy) maximizes net carbon gain, since such plants should have the greatest resources for (a) reproduction, (b) survival during drought periods (perennials only), and (c) competition with other plants for additional water and nutrients.

A model which relates net carbon gain to increases in environmental stress in desert plants is given in Fig. 7.7. Available data for photosynthetic and water relations adaptations in warm desert plants are consistent with this model. In this model a genotype is thought to be capable

of expressing multiple phenotypes in response to changes in the physical environment. For each plant species, and specifically each genotype, there is a combination of environmental parameters that is optimal in the sense of producing the highest net carbon gain. Deviations in the environment from these optimal conditions (e.g. increases or decreases in solar radiation, temperature, humidity, available soil moisture) will decrease net carbon gain. As the environmental stress increases, the plant may acclimate to express a new phenotype, a different combination of physiological, morphological, and physiognomic characteristics, which enhances net carbon gain. However, this form of adaptation has an associated cost. A measure of this cost is that while net carbon gain of the acclimated phenotype under the environmental stress will be greater than for the previous phenotype, it will be less should the environment return to its previous state. The transition in expression of one phenotype to another is gradual and continuous as the environmental stress increases, but may be abrupt when the environmental stress is removed (such as when rainfall removes long-term drought).

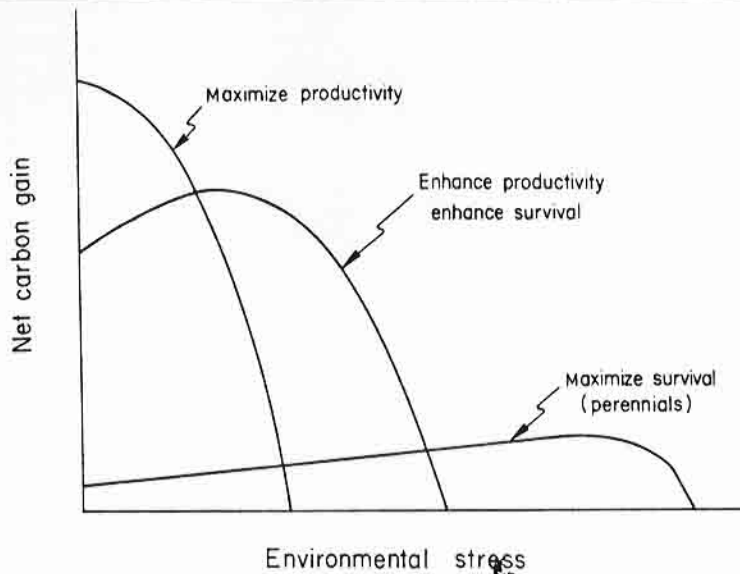


Figure 7.7 Adaptation model relating net carbon gain of a plant with environmental stress. Each curve represents a specific and different phenotypic expression (combination of physiology, morphology, and physiognomy) by a single genotype. See text for further details.

7.5.2 MECHANISMS TO MAXIMIZE NET CARBON GAIN

How net carbon gain is maximized depends on a balance of the photosynthetic capacities of leaves and other structures, on allocation patterns and phenology, and on carbon losses (maintenance respiration, predator defense, and leaching by the various plant parts). As yet there have been no complete and detailed studies of carbon balance in any warm desert species. Essentially all of the information available relates to the photosynthetic characteristics of different plants. While these data are by no means complete, distinct patterns are emerging.

Both C_3 and C_4 photosynthetic pathways are present in the annual and perennial floras (Eickmeier, 1978; Mooney *et al.*, 1974; Mulroy and Rundel, 1977; Stowe and Teeri, 1978; Syvertsen *et al.*, 1976; Teeri and Stowe, 1976). Annuals and grasses of the winter flora utilize the C_3 pathway exclusively, whereas C_4 is predominant in the summer flora. This trend is consistent with the notion that C_4 photosynthesis is a necessary component for achieving high photosynthetic rates in hot

temperature environments. Within the perennials, the C_4 pathway is rare except for

1. halophytic species, where it is common, and
2. short-lived summer active perennials, where it occurs infrequently. The latter category includes *Boerhaavia coccinea* and *Tidestromia oblongifolia*, and in both cases all closely related species are annuals. In northern warm desert sites, the low percentage of C_4 perennials is perhaps explained by the fact that most of the rains and the growth of perennials occurs during the cooler winter–spring periods. However, this does not explain the absence of C_4 photosynthesis among perennials of southern warm desert locations, where precipitation occurs primarily during the summer.

The C_4 photosynthetic pathway is generally considered to be more productive, but is not a consistent predictor of maximum photosynthetic capacity in warm desert plants. Whereas C_4 photosynthetic capacities of $82 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Amaranthus palmeri* (Ehleringer, 1983b), $67 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Hilaria rigida* (Nobel, 1980), and $56 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Tidestromia oblongifolia* (Björkman *et al.*, 1980) have been measured, other species such as *Atriplex*

hymenelytra and *A. lentiformis* have maximum rates of $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ or less (Mooney *et al.*, 1977b; Pearcy, 1977). Several C_3 species including *Camissonia claviformis* (Mooney *et al.*, 1976), *Encelia californica* (Ehleringer and Björkman, 1978b), and *Malvastrum rotundifolium* (Forseth and Ehleringer, 1982; Mooney and Ehleringer, 1978) have photosynthetic capacities equivalent to the higher rates in C_4 species.

Rates of photosynthesis in desert plants are higher than those in plants from other ecosystems. Annuals have greater photosynthetic capacities than do perennial species, and among perennials, rates are higher in deciduous-leaved species than in evergreen-leaved species (Ehleringer and Mooney, 1983). Taken as a whole, there appears to be a strong negative correlation between maximum leaf photosynthetic rate and life expectancy.

One characteristic typical of desert plants is that the leaf photosynthetic rates are not saturated by midday irradiances (Fig. 7.8). High stomatal conductances, high enzyme contents, and high meso-

phyll surface volume ratios are necessary to achieve these high photosynthetic rates (Armond and Mooney, 1978; Ehleringer, 1983b; Ehleringer and Björkman, 1978b; Longstreth *et al.*, 1980; Mooney *et al.*, 1976, 1977a). The quantum yield of desert plants appears not to be different from that of other species (Ehleringer and Björkman, 1977) and, thus, high photosynthetic rates occur because leaves are able to utilize the higher irradiances.

In many warm desert species, a leaf adaptation called diheliotropism or solar tracking occurs, potentially resulting in high photosynthetic rates throughout the day (Ehleringer and Forseth, 1980). Solar-tracking leaves move during the day so that they remain perpendicular to the sun's direct rays at all times. This results in a 38% or higher daily quantum flux on solar tracking leaves over those with fixed orientations (Fig. 7.9). Given the capacity to utilize high irradiances, species with solar tracking leaves should have greater rates of daily net carbon gain and be at a competitive advantage.

Solar tracking leaves occur in both winter and

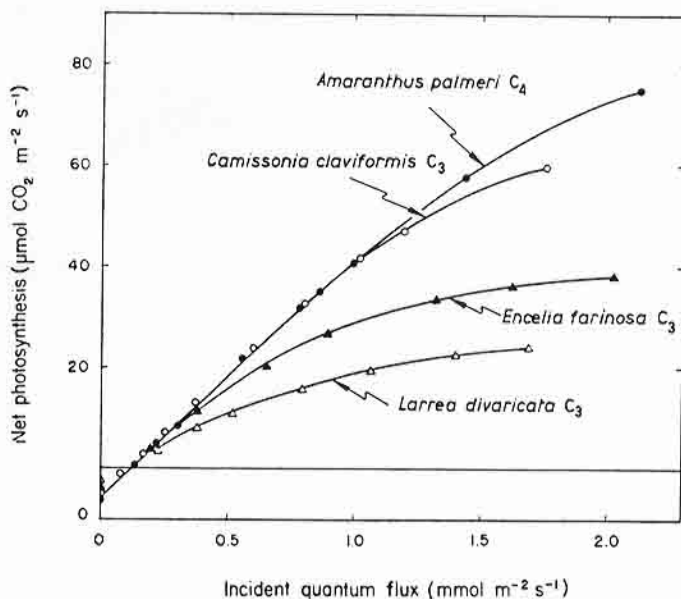


Figure 7.8 Response of photosynthesis to changes in quantum flux (400–700 nm) for *Amaranthus palmeri* (a summer annual), *Camissonia claviformis* (a winter annual), *Encelia farinosa* (a drought deciduous perennial), and *Larrea divaricata* (an evergreen perennial). Measurements were made under normal atmospheric conditions and at a leaf temperature of 30°C , except for *Amaranthus palmeri* which was measured at 40°C (from Ehleringer, 1983b; Ehleringer and Björkman, 1978b; Mooney, unpublished data; Mooney *et al.*, 1976).

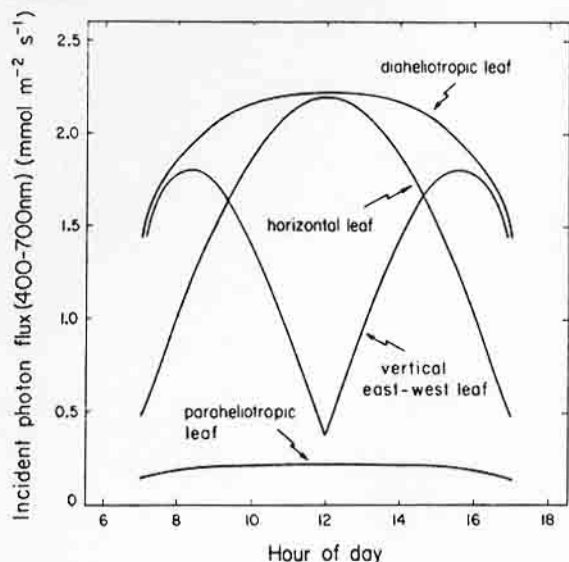


Figure 7.9 Photosynthetically active radiation incident on three leaf types over the course of a midsummer day: a diheliotropic leaf (cosine of incidence = 1.0); a fixed leaf angle of 0° , the horizontal leaf, and a paraheliotropic leaf (cosine of incidence = 0.1) (from Ehleringer and Forseth, 1980).

summer annuals as well as in many perennials (Table 7.2). The ability to solar track is independent of plant family and photosynthetic pathway. The percentage of the flora that has solar trackers increases as the length of the growing season decreases (Ehleringer and Forseth, 1980). Many solar trackers also exhibit paraheliotropic or leaf cupping movements. This results in leaf orientation parallel to the sun's rays and reduces incident solar radiation (Fig. 7.8); this will be considered later as an adaptation to drought.

7.5.3 PHOTOSYNTHETIC ADAPTATION TO TEMPERATURE

Three possibilities exist for adapting to the seasonally fluctuating thermal environments of warm deserts (Fig. 7.10). These are a short leaf duration, metabolic adjustment, and morphological adjustment. All three possibilities have been found in warm desert species, and the adaptation employed by a particular species appears independent of

Table 7.2 Photosynthetic pathway and families of common solar tracking species in warm deserts (from Ehleringer and Forseth, 1980)

Species	Photosynthetic pathway	Family
Winter ephemerals		
<i>Abronia villosa</i>	C ₃	Nyctaginaceae
<i>Astragalus lentiginosus</i>	C ₃	Fabaceae
<i>Coldenia nuttallii</i>	C ₃	Boraginaceae
<i>Lotus saluginosus</i>	C ₃	Fabaceae
<i>Lupinus arizonicus</i>	C ₃	Fabaceae
<i>Malvastrum rotundifolium</i>	C ₃	Malvaceae
<i>Oxystylis lutea</i>	C ₃	Capparidaceae
<i>Palafoxia linearis</i>	C ₃	Asteraceae
<i>Sphaeralcea coulteri</i>	C ₃	Malvaceae
Summer ephemerals		
<i>Allionia incarnata</i>	C ₄	Nyctaginaceae
<i>Amaranthus palmeri</i>	C ₄	Amaranthaceae
<i>Boerhaavia wrightii</i>	C ₄	Nyctaginaceae
<i>Cleome subulata</i>	C ₃	Capparidaceae
<i>Dicoria canescens</i>	C ₃	Asteraceae
<i>Eriogonum deflexum</i>	C ₃	Polygonaceae
<i>Euphorbia abramsiana</i>	C ₄	Euphorbiaceae
<i>Helianthus annuus</i>	C ₃	Asteraceae
<i>Hymenoxys wislizenii</i>	C ₃	Asteraceae
<i>Kallstroemia grandiflora</i>	C ₄	Zygophyllaceae
<i>Portulaca oleracea</i>	C ₄	Portulacaceae
<i>Proboscidea parviflora</i>	C ₃	Martyniaceae
<i>Solanum rostratum</i>	C ₃	Solanaceae
<i>Tidestromia lanuginosa</i>	C ₄	Amaranthaceae
<i>Trianthema portulacastrum</i>	C ₄	Aizoaceae
<i>Tribulus terrestris</i>	C ₄	Zygophyllaceae
Perennials		
<i>Abutilon parvulum</i>	C ₃	Malvaceae
<i>Acacia angustissima</i>	C ₃	Mimosaceae
<i>Boerhaavia annulata</i>	C ₃	Nyctaginaceae
<i>Boerhaavia coccinea</i>	C ₄	Nyctaginaceae
<i>Cassia bauhinioides</i>	C ₃	Caesalpinaceae
<i>Cercidium microphyllum</i>	C ₃	Caesalpinaceae
<i>Croton californica</i>	C ₃	Euphorbiaceae
<i>Dalea emoryi</i>	C ₃	Fabaceae
<i>Marina divaricata</i>	C ₃	Fabaceae
<i>Prosopis juliflora</i>	C ₃	Mimosaceae
<i>Sida lepidota</i>	C ₃	Malvaceae
<i>Sphaeralcea abbigua</i>	C ₃	Malvaceae
<i>Stylosanthes viscosa</i>	C ₃	Fabaceae

taxonomic association and photosynthetic pathway.

In plants characterized by short leaf duration, leaves are present only during a narrow air temper-

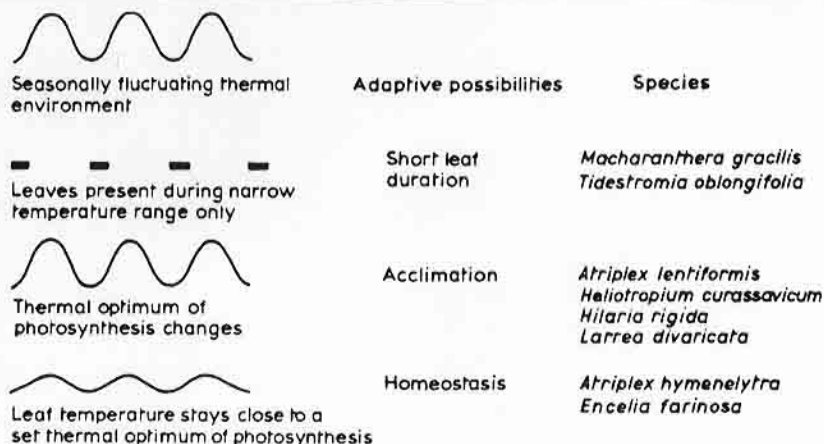


Figure 7.10 Three possibilities for photosynthetic adaptation to a seasonally fluctuating thermal environment and examples of species utilizing each possibility (after Mooney, 1980a).

ature range, that includes either hot summer or cool winter temperatures. Ephemerals and seasonal, short-lived herbaceous perennials appear to use this adaptive possibility. The temperature response curves for photosynthesis are vastly different for annuals depending on the season in which the species normally grow (Fig. 7.11). The temperature

optima for photosynthesis of winter active *Camissonia claviformis* and summer active *Amaranthus palmeri* are 23°C and 42°C, respectively, reflecting the differences in leaf temperatures found during these seasons. Studies of thermal acclimation potential in the annual, *Machraeranthera gracilis*, have shown that acclimation does not occur (Monson

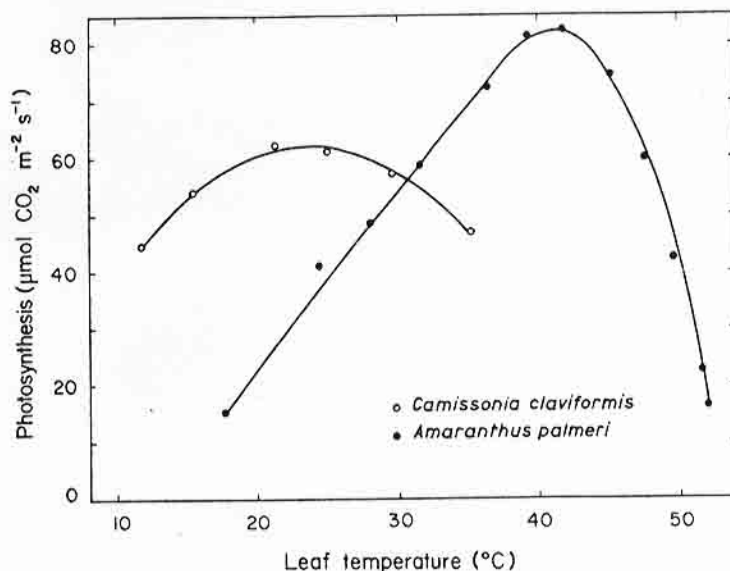


Figure 7.11 Response of photosynthesis to changes in leaf temperature for *Camissonia claviformis*, a winter annual, and *Amaranthus palmeri*, a summer annual. Measurements were made on outdoor grown plants under normal atmospheric conditions and midday irradiance levels (from Ehleringer, 1983b and Ehleringer et al., 1979).

and Szarek, 1979). Thermal acclimation also does not occur in the summer active herbaceous perennial *Tidestromia oblongifolia* (Björkman *et al.*, 1980). While data for other annuals and herbaceous perennials are unavailable, Seemann *et al.* (1979) have reported as much as 8°C shifts in the fluorescence-temperature curves of several winter annuals. These shifts imply increased thermal stability of the photosynthetic apparatus when plants are exposed to higher temperatures, although there may be no change in the photosynthetic temperature optimum.

Adaptations involving metabolic adjustment entail biochemical and physiological changes within a leaf (often an evergreen leaf) so that the temperature optimum for photosynthesis as well as the thermal stability at both ends of the curve changes in concert with changes in air temperature (Björkman *et al.*, 1980; Raison *et al.*, 1980). Temperature acclima-

tion results in a higher photosynthetic rate under the new environmental conditions, but the maximum rate is often less than that observed under optimal temperatures (see *Larrea* in Fig. 7.12), suggesting a cost associated with acclimation to stress conditions. Species which adjust metabolically to changes in the thermal environment tend to be perennials capable of growing during both winter and summer seasons. These encompass a diversity of forms including evergreen shrubs such as *Atriplex lentiformis* (Percy, 1977) and *Larrea divaricata* (Mooney *et al.*, 1977a), the prostrate herb *Heliotropium curassavicum* (Mooney, 1980b), the grass *Hilaria rigida* (Nobel, 1980), the fern *Notholaena parryi* (Nobel, 1978), and the tree *Chilopsis linearis* (Strain and Chase, 1966).

The third adaptive possibility, a homeostatic response, involves changes in leaf spectral characteristics and/or stomatal conductances so that mid-day leaf temperatures remain fairly constant through the season, even though there may be large fluctuations in air temperatures. Species utilizing this adaptation are similar to those characterized by short leaf duration in that the photosynthetic temperature response is fixed and does not show acclimation (see *Encelia farinosa* in Fig. 7.12). To maintain constant leaf temperatures, leaf absorptance may fluctuate from 30% to 85% (400–700 nm) (Ehleringer, 1981; Ehleringer and Björkman, 1978a; Mooney *et al.*, 1977b). Species in this category would include shrubs such as *Atriplex hymenelytra* and *Encelia farinosa*. Shrub species that use transpiration to regulate temperature are restricted to washes and include *Encelia frutescens* (Ehleringer and Cook, unpublished) and *Hymenoclea salsola* (Strain and Chase, 1966).

That physiological adjustment and homeostatic response are of adaptive value has been shown by calculations of the net carbon gain under different environmental conditions. Mooney (1980a) has shown for *Larrea divaricata* (physiological adjustment) and Ehleringer (1980) has shown for *Encelia farinosa* (homeostatic response) that the daily net carbon gain is greater under suboptimal environmental conditions when the species adjust (express new phenotype) than if no adjustment were to occur.

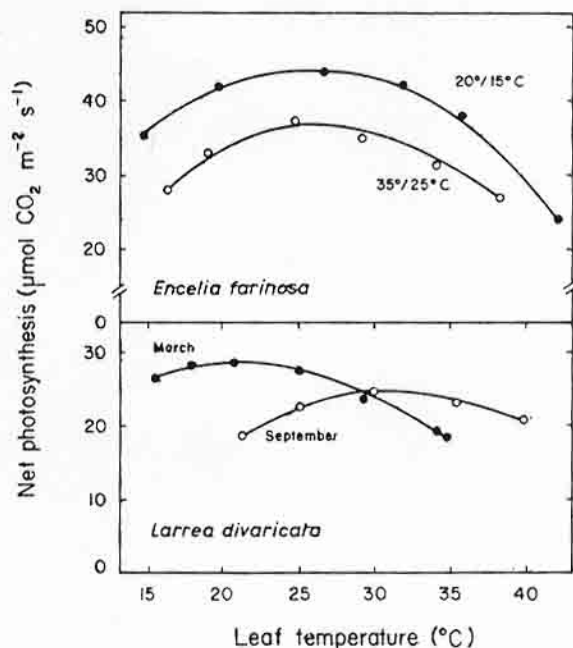


Figure 7.12 Response of photosynthesis to changes in leaf temperature for *Encelia farinosa* and *Larrea divaricata* under contrasting growth conditions. Measurements were made under normal atmospheric conditions and midday irradiance levels (from Ehleringer and Björkman, 1978b; Mooney *et al.*, 1977a).

7.5.4 ADAPTATION TO DROUGHT

Warm deserts are well known for their extended droughts. Plant adaptations to drought fall into two categories: mechanisms to survive through extended drought periods and mechanisms to enhance productivity under drought conditions. Along warm desert gradients of increasing drought, several trends are evident within the vegetation: a decrease in both leaf and canopy size, an increase in drought-deciduousness, and an increase in drought and desiccation tolerance. Additionally, within a site shrub density is correlated with soil water potential and shrub height is negatively correlated with soil water potential (Balding and Cunningham, 1974).

While there has been substantial progress in understanding how plants grow and cope with increasing drought or temperature stress under desert conditions, very little information is available on the mechanisms of adaptation to long periods of inactivity (Levitt, 1980). The picture emerging suggests that most perennial plants are capable of withstanding desiccation to leaf water potentials far below those water potentials at which stomates close and growth ceases.

In addition to the temperature adaptations, that is, the ability for leaf tolerance characteristics to change as the environment changes (discussed in previous section), osmotic adjustment is a principal means of enhancing photosynthetic activity into drought periods. Osmotic adjustment involves an active increase in solute concentrations (osmotic component of water potential) as leaf water potentials decline so that positive turgor pressure is maintained, and therefore stomates can remain open. The ranges of osmotic adjustment that occur in warm desert plants are largely unknown. While osmotic pressure data from Walter and Stadelmann (1974) suggest that osmotic adjustment is high in summer ephemerals, shrubs, and trees, and low in winter ephemerals, ferns, and rain phanerophytes, our knowledge is sufficiently sparse as to be inconclusive. From their data, it is not possible to distinguish between the ranges over which a plant can remain photosynthetically active, and the ranges of water potentials over which the plant is simply able to survive.

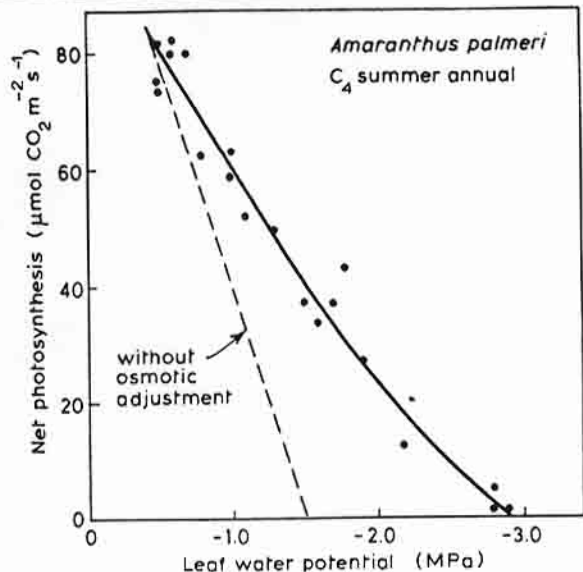


Figure 7.13 Net photosynthesis as a function of leaf water potential in *Amaranthus palmeri*. Measurements were made under normal atmospheric conditions, midday irradiances, and 40 °C leaf temperature. The dashed line is based on pressure-volume water relations curves and indicates the expected response if no osmotic adjustment were to occur in leaves of this species (from Ehleringer, 1983b).

In terms of net carbon gain, the advantages of osmotic adjustment are evident in the net photosynthesis – leaf water potential response curve for *Amaranthus palmeri* (Fig. 7.13). Without osmotic adjustment, leaves would wilt, and net photosynthesis would reach zero at leaf water potentials below –1.55 MPa (Ehleringer, 1983b). However, because of the osmotic adjustment that occurs, *A. palmeri* is able to grow with enhanced productivity under mild drought conditions and have positive photosynthetic rates down to leaf water potentials of –3 MPa. Although osmotic adjustment results in a higher rate of net photosynthesis than would have occurred without the adjustment the photosynthetic rate is never as high as it was under high water potentials, again suggesting a cost associated with the new phenotypic expression under stress conditions.

Photosynthetic rates decline in response to de-

creased leaf water potentials (Ehleringer 1983b; Forseth and Ehleringer, 1982; Mooney, 1980a; Odensing *et al.*, 1974). The decline in photosynthesis in a long-term drought cycle is associated with decreases in both leaf conductance and intrinsic photosynthetic capacity. As a result, the stomatal diffusion limitations to photosynthesis are constant or increase only slightly as leaf water potentials decrease. In those species in which stomatal diffusion limitation does not increase with decreasing leaf water potential (e.g. *Amaranthus palmeri* and *Malvastrum rotundifolium*, water use efficiency (photosynthesis/transpiration ratio under a constant vapor-pressure deficit gradient) also remains constant. In contrast, the stomatal diffusion limitations on photosynthesis increase in *Lupinus arizonicus* as leaf water potentials decrease, resulting in a higher water use efficiency under low leaf water potentials. However, the adaptive value of an increased water use efficiency is as yet not demonstrated for desert plants.

As the drought period develops, some species can switch from leaf to stem photosynthesis. In a number of trees such as *Cercidium microphyllum* and in rain phanerophytes such as *Fouquieria splendens* and *Idria columnaris*, leaves abscise at relatively high leaf water potentials, and the plants rely on bark photosynthesis. For those cases studied, photosynthetic activity of stems can result in substantial carbon gain to the plant (Adams and Strain, 1968; Mooney and Strain, 1964; Szarek and Woodhouse, 1978). Presumably, stem photosynthesis also gives the plant a higher water use efficiency during drought periods, although the overall photosynthetic rate is reduced.

For those species which use leaf reflectance as a morphological adjustment in photosynthetic adaptation, the percentage reflectance by the leaf de-

pends on the extent of drought development. Ehleringer *et al.* (1976) found that leaf reflectance decreased linearly with increases in precipitation in *Encelia farinosa*. Similar patterns can be seen for other species with pubescent leaves (Ehleringer, 1983a). The drought stress cue to which *E. farinosa* responds by producing differentially pubescent leaves (thus varying in leaf absorptance) is leaf water potential (Ehleringer, 1982).

A number of solar tracking annuals with compound leaves show an interesting adaptation to brief drought periods. This involves paraheliotropism or leaf cupping and serves to reduce the amount of solar radiation striking the leaf by reducing the cosine of the angle of incidence (Forseth and Ehleringer, 1982). Consequently, paraheliotropic leaves have reduced temperatures and rates of water loss when compared to strictly diaheliotropic leaves with similar leaf conductances, and can therefore survive brief drought periods without developing low leaf water potentials (Forseth and Ehleringer, 1980). In rainy periods after an intermittent drought, paraheliotropic leaves resume diaheliotropic leaf movements.

7.6 Summary

Water is the environmental parameter most affecting plant life in warm deserts. Growth, productivity, and phenological activity are tightly linked to the brief periods in which adequate soil moisture is available. In response to these selective pressures, warm desert plants have evolved a diversity of physiological, morphological and life cycle adaptations that allow plants to maximize net carbon gain during periods of high soil moisture availability, to enhance carbon gain during early drought, and to maximize survival through extended drought periods.

References

- Adams, M.S. and Strain, B.R. (1968) Photosynthesis in stems and leaves of *Cercidium floridum*: spring and summer diurnal field response and relation to temperature. *Oecologia Plantarum*, 3, 285-97.
- Armond, P.A. and Mooney, H.A. (1978) Correlation of photosynthetic unit size and density with photosynthetic capacity. *Carnegie Institution Washington Yearbook*, 77, 234-7.
- Balding, F.R. and Cunningham, G.L. (1974) The influence of soil water potential on the perennial vegetation of a desert arroyo. *Southwest Naturalist* 19, 241-8.
- Beatley, J.C. (1967) Survival of winter annuals in the

- northern Mojave Desert. *Ecology*, 48, 745-50.
- Beatley, J.C. (1969) Biomass of desert winter annual plant populations in southern Nevada. *Oikos*, 20, 261-73.
- Beatley, J.C. (1970) Perennation in *Astragalus lentiginosus* and *Tridens pulchellus* in relation to rainfall. *Madroño*, 20, 326-32.
- Beatley, J.C. (1974) Phenological events and their environmental triggers in Mohave Desert ecosystems. *Ecology*, 55, 856-63.
- Björkman, O., Badger, M.R. and Armond, P.A. (1980) Response and adaptation of photosynthesis to high temperatures, in *Adaptations of Plants to Water and High Temperature Stress* (eds N.C. Turner and P.J. Kramer). Wiley-Interscience, New York, pp. 233-49.
- Clark, D.D. and Burk, J.H. (1980) Resource allocation patterns of two California Sonoran Desert ephemerals. *Oecologia*, 46, 86-91.
- Cunningham, G.L. and Strain, B.R. (1969) Ecological significance of seasonal leaf variability in a desert shrub. *Ecology*, 50, 400-8.
- Ehleringer, J. (1980) Leaf morphology and reflectance in relation to water and temperature stress, in *Adaptations of Plants to Water and High Temperature Stress* (eds N.C. Turner and P.J. Kramer). Wiley-Interscience, New York, pp. 295-308.
- Ehleringer, J. (1981) Leaf absorptances and Mohave and Sonoran Desert plants. *Oecologia*, 49, 366-70.
- Ehleringer, J. (1982) The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *American Journal of Botany*, 69, 670-5.
- Ehleringer, J. (1983a) Ecology and ecophysiology of leaf pubescence in North American desert plants, in *Biology and Chemistry of Plant Trichomes* (eds E. Rodriguez, P. Heley and I. Mehta). Plenum Press, New York, pp. 113-132.
- Ehleringer, J. (1983b) Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer ephemeral. *Oecologia*, 57, 107-12.
- Ehleringer, J. and Björkman, O. (1977) Quantum yields for CO₂ uptake in C₃ and C₄ plants: dependence on temperature, CO₂, and O₂ concentration. *Plant Physiology*, 59, 86-90.
- Ehleringer, J. and Björkman, O. (1978a) Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa*. *Oecologia*, 36, 151-62.
- Ehleringer, J. and Björkman, O. (1978b) A comparison of photosynthetic characteristics of *Encelia* species possessing glabrous and pubescent leaves. *Plant Physiology*, 62, 185-90.
- Ehleringer, J. and Forseth, I. (1980) Solar tracking by plants. *Science*, 210, 1094-8.
- Ehleringer, J. and Mooney, H.A. (1978) Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. *Oecologia*, 37, 183-200.
- Ehleringer, J. and Mooney, H.A. (1983) Photosynthesis and productivity of desert and mediterranean-climate plants. *Encyclopedia of Plant Physiology*, Vol. 12D, Springer-Verlag, New York, pp. 205-31.
- Ehleringer, J., Björkman, O. and Mooney, H.A. (1976) Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. *Science*, 192, 376-7.
- Ehleringer, J., Mooney, H.A. and Berry, J.A. (1979) Photosynthesis and microclimate of a desert winter annual. *Ecology*, 60, 280-6.
- Eickmeier, W.G. (1978) Photosynthetic pathway distributions along an aridity gradient in Big Bend National Park, and implications to enhanced resource partitioning. *Photosynthetica*, 12, 290-7.
- Fonteyn, P.J. and Mahall, B.E. (1978) Competition among desert perennials. *Nature*, 275, 544-5.
- Forseth, I. and Ehleringer, J. (1980) Solar tracking response to drought in a desert annual. *Oecologia*, 44, 159-63.
- Forseth, I.N. and Ehleringer, J. (1982) Ecophysiology of two solar tracking desert water annuals. II. Leaf movements, water relations, and microclimate. *Oecologia*, 54, 41-9.
- Forseth, I.N., Ehleringer, J., Werk, K.S. and Cook, C.S. (1983) Field water relations of Sonoran Desert annuals. *Ecology*, 65, 1436-45.
- Freeman, D.C., Klikoff, L.G. and Harper, K.T. (1976) Differential resource utilization by the sexes of dioecious plants. *Science*, 193, 597-9.
- Gates, D.M. (1980) *Biophysical Ecology*. Springer-Verlag, New York.
- Ives, R.L. (1949) Climate of the Sonoran Desert region. *Annals Association of American Geographers*, 39, 143-87.
- Juhren, M., Went, F.W. and Phillips, E. (1956) Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology*, 37, 318-30.
- Koller, D. (1972) Environmental control of seed germination, in *Seed Biology*, Vol. 2 (ed. T.T. Kozlowski). Academic Press, New York, pp. 1-101.
- Levitt, J. (1980) *Responses of Plants to Environmental Stresses*. Academic Press, New York.
- Longstreth, D.J., Hartsock, T.L. and Nobel, P.S. (1980) Mesophyll cell properties for some C₃ and C₄ species with high photosynthetic rates. *Physiologia Plantarum*, 48, 494-8.
- McArthur, E.D. (1977) Environmentally induced changes of sex expression in *Atriplex canescens*. *Heredity*, 38, 97-103.

- McDonald, J.E. (1956) *Variability of precipitation in an arid region: a survey of characteristics for Arizona*. University of Arizona Institute of Atmospheric Physics Technical Report No. 1.
- Monson, R.K. and Szarek, S.R. (1979) Ecophysiological studies of Sonoran Desert plants. V. Photosynthetic adaptations of *Machaeranthera gracilis*, a winter annual. *Oecologia*, 41, 317-27.
- Mooney, H.A. (1980a) Seasonality and gradients in the study of stress adaptations, in *Adaptations of Plants to Water and High Temperature Stress* (eds N.C. Turner and P.J. Kramer) Wiley-Interscience, New York, pp. 279-94.
- Mooney, H.A. (1980b) Photosynthetic plasticity of populations of *Heliotropium curassavicum* L. originating from differing thermal regimes. *Oecologia*, 45, 372-6.
- Mooney, H.A. and Ehleringer, J. (1978) The carbon gain benefits of solar tracking in a desert annual. *Plant, Cell, Environment*, 1, 307-11.
- Mooney, H.A. and Strain, B.R. (1964) Bark photosynthesis in ocotillo, *Madroño*, 17, 230-3.
- Mooney, H.J., Troughton, J.H. and Berry, J.A. (1974) Arid climates and photosynthetic systems. *Carnegie Institution Washington Yearbook*, 73, 793-805.
- Mooney, H.A., Ehleringer, J. and Berry, J.A. (1976) High photosynthetic capacity of a winter desert annual in Death Valley. *Science*, 194, 322-4.
- Mooney, H.A., Björkman, O. and Collatz, G.J. (1977a) Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. I. Carbon dioxide exchange characteristics of intact leaves. *Plant Physiology*, 61, 406-10.
- Mooney, H.A., Ehleringer, J. and Björkman, O. (1977b) The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra*. *Oecologia*, 29, 301-10.
- Mulroy, T.W. and Rundel, P.W. (1977) Annual plants: adaptations to desert environments. *Bioscience*, 27, 109-14.
- Nobel, P.S. (1978) Microhabitat, water relations and photosynthesis of a desert fern, *Notholaena parryi*. *Oecologia*, 31, 293-309.
- Nobel, P.S. (1980) Water vapor conductance and CO₂ uptake for leaves of a C₄ desert grass, *Hilaria rigida*. *Ecology*, 61, 252-8.
- Odening, W.R., Strain, B.R. and Oechel, W.C. (1974) The effect of decreasing water potential on net CO₂ exchange of intact desert shrubs. *Ecology*, 55, 1086-95.
- Pearcy, R.W. (1977) Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. *Plant Physiology*, 59, 795-9.
- Pianka, E.R. (1967) On lizard species diversity: North American flatland deserts. *Ecology*, 48, 333-51.
- Raison, J.K., Berry, J.A., Armond, P.A. and Pike, C.S. (1980) Membrane properties in relation to the adaptation of plants to temperature stress. in *Adaptations of Plants to Water and High Temperature Stress* (eds N.C. Turner and P.J. Kramer) Wiley-Interscience, New York, pp. 261-73.
- Schaffer, W.M. and Gadgil, M.D. (1975) Selection for optimal life histories in plants, in *Ecology and Evolution of Communities* (eds M.L. Cody and J.M. Diamond), Belknap Press, Cambridge, MA, pp. 142-57.
- Schimper, A.F.W. (1903) *Plant Geography Upon a Physiological Basis*, Clarendon Press, Oxford.
- Seemann, J.R., Downton, W.J.S. and Berry, J.A. (1979) Field studies of acclimation to high temperature: winter ephemerals in Death Valley. *Carnegie Inst. Wash. Yb.*, 78, 157-62.
- Sellers, W.D. and Hill, R. (1974) *Arizona Climate 1931-1972*, University of Arizona Press, Tucson.
- Shreve, F. (1951) *Vegetation of the Sonoran Desert*, Carnegie Institute Washington Publication No. 591.
- Simpson, B.B. (1977) Breeding systems of dominant perennial plants of two disjunct warm desert ecosystems. *Oecologia*, 27, 203-26.
- Smith, W.K. (1978) Temperatures of desert plants: another perspective on the adaptability of leaf size. *Science*, 201, 614-16.
- Smith, W.K. and Geller, G.N. (1980) Leaf and environmental parameters influencing transpiration: theory and field measurements. *Oecologia*, 46, 308-13.
- Smith, W.K. and Nobel, P.S. (1977) Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. *Ecology*, 58, 1033-43.
- Steila, D. (1976) *The Geography of Soils*, Prentice Hall, Englewood Cliffs, New Jersey.
- Stowe, L.G. and Teeri, J.A. (1978) The geographic distribution of C₄ species of the Dicotyledonae in relation to climate. *Amer. Nat.*, 112, 609-23.
- Strain, B.R. and Chase, V.C. (1966) Effect of past and prevailing temperatures on the carbon dioxide exchange capacities of some woody desert perennials. *Ecology*, 47, 1043-5.
- Syvertsen, J.P., Nickell, G.L., Spellenberg, R.W. and Cunningham, G.L. (1976) Carbon reduction pathways and standing crop in three Chihuahuan Desert plant communities. *Southwest. Nat.*, 21, 311-20.
- Szarek, S.R. and Woodhouse, R.M. (1978) Ecophysiological studies of Sonoran Desert plants. IV. Seasonal photosynthetic capacities of *Acacia greggii* and *Cercidium microphyllum*. *Oecologia*, 37, 221-9.
- Teeri, J.A. and Stowe, L.G. (1976) Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia*, 23, 1-12.

- Terjung, W.H., Ojo, S.O. and Swarts, S.W. (1970) A nighttime energy and moisture budget in Death Valley, California, in mid-August. *Geog. Ann.*, 52A, 160-73.
- Thekaekara, M.P. (1976) Solar radiation measurement: techniques and instrumentation. *Solar Energy*, 18, 309-25.
- Walter, H. and Stadelmann, E. (1974) A new approach to the water relations of desert plants. in *Desert Biology*, Vol. 2 (ed. G. Brown), Academic Press, New York, pp. 213-310.
- Warming, E. (1909) *Oecology of Plants: An Introduction to the Study of Plant Communities*, Oxford University Press, London, UK.
- Went, F.W. (1948) Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology*, 29, 242-53.
- Went, F.W. (1949) Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology*, 30, 1-13.
- Went, F.W. and Westergaard, M. (1949) Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. *Ecology*, 30, 26-38.
- Werk, K.S. and Ehleringer, J. (1983) Photosynthesis by flowers of two shrubs. *Encelia farinosa* and *Encelia californica*. *Oecologia*, 57, 311-15.
- Woodell, S.R.J., Mooney, H.A. and Hill, A.J. (1969) The behavior of *Larrea divaricata* (creosote bush) in response to rainfall in California. *Journal of Ecology*, 57, 37-44.