Ernst-Detlef Schulze
Martyn M. Caldwell (Eds.)

Ecophysiology of Photosynthesis

With 163 Figures

Professor Dr. Ernst-Detlef Schulze
Lehrstuhl für Pflanzenökologie
Universität Bayreuth
Postfach 101251
D-95447 Bayreuth
Germany

Professor Dr. Martyn M. Caldwell
Department of Range Science and Ecology Center
Utah State University
Logan, UT 84322-5230
USA

Design of the cover illustration by Roswitha Asche

18 Variation in Gas Exchange Characteristics Among Desert Plants

J.R. Ehleringer

18.1 Introduction

Professor Otto Lange and colleagues have made significant contributions to our understanding of ecophysiological aspects of plant performance under arid land conditions. It was their pioneering field research in the Negev Desert during the 1960s and 1970s that firmly established our understanding of the impacts of drought and high temperature on photosynthetic gas exchange, respiration, and transpiration in extreme environments. These field studies described the mechanistic bases for photosynthetic adjustment to desert habitats and evaluated the carbon gain significance of different acclimation patterns. During the past decade, Lange and colleagues have extended this research by examination of plant performance in sclerophyllous shrub and tree species in the arid mediterranean climate zones of Portugal, and these studies have provided further insights into the cellular adjustments of plants to arid conditions.

In this chapter, I would like to build on the foundation laid down by Lange and colleagues and to examine a question related to the physiological and evolutionary ecology of plants in arid zones. Namely, given the spatial and temporal diversity of deserts: what kinds of photosynthetic gas exchange characteristics are expected under different selective regimes? In particular, what patterns are expected within different life forms and how do life-form-related physiological characters relate to species composition in different desert locations? Are the known gas exchange patterns from field studies consistent with these relationships? The primary focus of this chapter will be the deserts of North America with special emphasis on the Sonoran Desert, since it is the most diverse of the North American deserts (Shreve and Wiggins 1964). However, the patterns that emerge should be applicable to other desert regions of the world.

18.2 Species Distribution Gradients in the Desert

The deserts of western North America (Chihuahuan, Colorado Plateau, Great Basin, Mojave, and Sonoran) are defined by a limited-precipitation

regime, but differ quite substantially in biological, climatic, and geomorphic aspects (Brown 1968; Bender 1982; MacMahon 1985; Osmond et al. 1990). Plant growth and activity are, of course, constrained by limited soil moisture availability in each of these deserts. In the northerly and higher elevation Colorado Plateau and Great Basin Deserts, cold winter temperatures further restrict activity to the spring and early summer months (Caldwell 1985; Comstock and Ehleringer 1992). Seasonal precipitation patterns further differentiate these deserts, with the Mojave Desert being primarily a winter-precipitation desert and the Chihuahuan Desert a summer-precipitation desert. The Sonoran Desert, geographically at the center of the deserts,
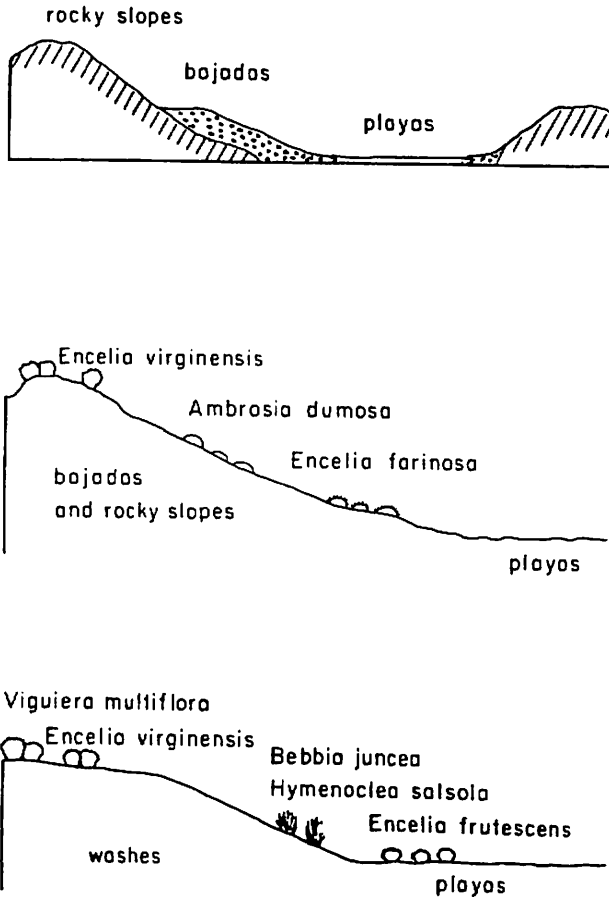
Fig. 18.1. *Top* Cross section of elevational transect in the Sonoran Desert showing the three dominant macrohabitats – rocky slopes, bajadas (coarse alluvium), and playas (fine alluvium). With the bajadas and rocky slopes are washes of varying size and dimension. *Middle* Distribution of common drought-deciduous shrubs along elevational transect on bajadas and rocky slopes near Needles, California. *Bottom* Distribution of common drought-deciduous shrubs along elevational transect in washes near Needles, California

experiences both winter and summer precipitation regimes; since the Sonoran Desert is a low-elevation desert, plants may be active at any time of the year when precipitation is received.

Species and life-form abundance vary substantially along elevation clines (Hastings and Turner 1965b), reflecting both changes in precipitation and temperature. Whittaker and Niering (1965) described a progression from predominance of trees to increased abundance of suffrutescent shrubs as precipitation decreases. In particular, they noted a higher species diversity and greater life-form diversity in the kinds of leaf and stem morphologies of plants in drier desert locations. Similar trends in the Sonoran Desert vegetation have also been described by Phillips and MacMahon (1978) and Bowers and Lowe (1985). As first discussed by Schulze (1982), these patterns relate to variation in gas exchange characteristics in terms of both photosynthetic pathways and seasonality of carbon gain activities.

Within the Sonoran Desert, elevation-related transects are usually also related to substrate variation (Fig. 18.1). Upper elevations of a range typically have shallow, coarse soils; the gradient from upper rocky slopes along a bajada and ending up at a playa is associated with an increase in the fine particle structure of soils. At various places along a bajada, washes erode through the alluvium, creating microhabitats that are coarser in structure and typically have greater soil moisture availability.

Of interest to this discussion is that a dominant life form will often persist over this entire transect, including wash and slope microhabitats. One species is typically dominant at a site and there is usually a single-species replacement pattern along these elevation gradients. For instance, drought-deciduous shrubs are a key component of virtually all Sonoran Desert plant communities. In most situations, there is just one dominant species at a location (Table 18.1), but in both wash and bajada slope microhabitats, there is a continual replacement of species with elevation. *Encelia virginensis* may dominate slope bajada sites at upper elevations, but it is replaced first by *Ambrosia dumosa*, and then by *E. farinosa* at lower elevation sites (Fig. 18.1). Similarly, while *Viguiera multiflora* predominates at upper elevation wash sites, *E. frutescens* dominates the lower elevation sites.

18.3 Variation in Moisture and Temperature as Selective Forces for Photosynthetic Variation

Availability of moisture is the primary feature influencing plant productivity and overall performance. To better understand the possible benefits and disadvantages of different gas exchange characteristics, it is useful to know the absolute moisture inputs and the variability of those inputs. The predictability of moisture inputs on both a seasonal and an interannual basis is

Table 18.1. Percentage abundance of shrub species on slope and in wash microhabitats along an elevational gradient in the Sonoran Desert near Needles, California

	Elevation (m)				
	180	365	615	715	975
Slope					
Encelia farinosa	–	89	93	0	0
Ambrosia dumosa	–	6	4	88	0
Krameria parviflora	–	6	2	12	55
Encelia virginensis	–	0	0	0	29
Viguiera multiflora	–	0	0	0	16
Wash					
Encelia frutescens	80	0	0	0	0
Hymenoclea salsola	20	96	78	37	3
Bebbia juncea	0	4	14	58	14
Chrysothamnus paniculatus	0	0	6	5	0
Encelia virginensis	0	0	0	0	41
Viguiera multiflora	0	0	0	0	24
Krameria parviflora	0	0	0	0	14

key to understanding aspects of plant carbon gain such as whether or not annual versus perennial life forms are favored, whether or not acclimation to drought or drought avoidance will lead to higher rates of carbon gain, and whether or not conditions are sufficiently predictable to favor the emergence of one particular set of photosynthetic characteristics over another in a particular habitat.

18.3.1   Predictability of Precipitation

Rainfall is the life's blood of deserts, yet precipitation amounts are usually sufficiently low that primary productivity and precipitation are linearly related (Noy-Meir 1973; Evanari et al. 1976; Ehleringer and Mooney 1983; Le Houérou 1984). Plants of arid regions not only face low annual amounts of precipitation, but the interannual variation in that precipitation is high, resulting in a variability of primary production that exceeds the variability in precipitation input (Le Houérou et al. 1988). The distribution of mean annual precipitation in deserts can be approximated by a negative binomial or gamma distribution (Thom 1958; Hershfield 1962; Hastings 1965; Nicholson 1980). What this indicates is that the coefficient of variation increases as the mean precipitation decreases (Fig. 18.2). As a consequence, the interannual variation in precipitation becomes progressively greater at drier sites. Total precipitation in most years then becomes progressively lower than the arithmetic mean precipitation values.
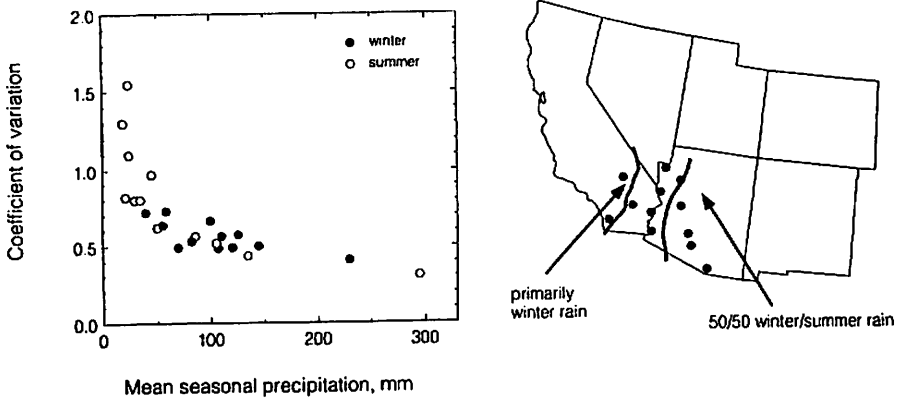
Fig. 18.2. *Left* The relationship between the coefficient of variation of precipitation and mean seasonal precipitation for selected sites in the arid regions of the southwestern United States. Sites are those indicated on *right*. Precipitation data are presented for winter (November–May) and summer (June–October) seasons. Calculations are based on data from the US Weather Bureau records (NOAA) during the period 1929–1979. *Right* Approximate geographic boundaries of predominant winter and summer rain environments in the arid regions of the southwestern United States. Shown also are the sites used for meteorological analyses in Figs. 18.3–18.7

Of particular interest is that front-related winter storms do not generate a significantly different relationship between mean and coefficient of variation from those of convectional summer storms (Fig. 18.2). Contrary to the popular belief that summer rainfall is more variable, that applies only to short-term spatial variability (McDonald 1956). In the long term, the year-to-year variability for summer and winter rains is the same for a given mean; it is only the long-term precipitation values that are needed to generate information on the interannual predictability of that precipitation.

This leads to two patterns. First, drier sites will be characterized by drought of increased length. Second, single-storm events will have a greater impact on plants growing in the driest regions. Goude and Wilkinson (1980) have shown that the maximum daily rainfalls in South African deserts constitute a much larger percentage of the annual precipitation than in wetter regions. In other words, episodic large-storm events would be expected to have a much greater impact on the dynamics of arid zones than in semi-arid or mesic regions.

When evaluating the impact of storms on the annual precipitation, it appears that the frequency distribution of storm sizes is the same for sites differing widely in total annual precipitation. Phoenix, Arizona, receives 185 mm precipitation annually, whereas Indio, California, receives only 80 mm. However, the frequency distributions of storms sizes have similar shapes (Fig. 18.3). Needles, California, is intermediate at 110 mm, but still has a distribution curve similar to those at Phoenix and Indio. The same conclusion is reached if the data are evaluated on a seasonal basis instead of
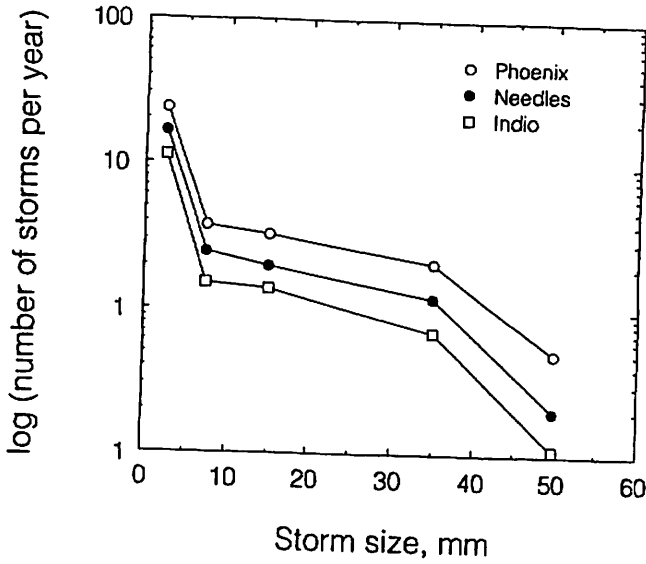
Fig. 18.3. The frequency distribution of storm sizes for sites receiving different average amounts of precipitation in either winter (November–May) or summer (June–October) seasons. Calculations are based on data from the US Weather Bureau records (NOAA) during the period 1929–1979. A storm is defined as the total cumulative precipitation at a site in a contiguous time period (typically 1–3 days)
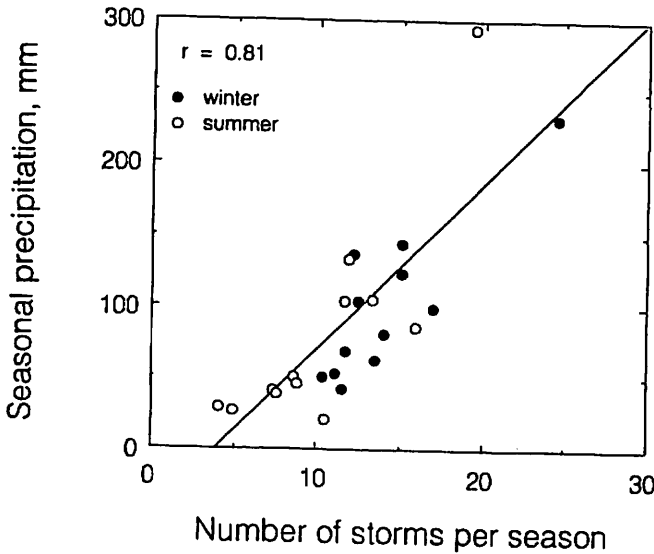
Fig. 18.4. The correlation between mean precipitation in either winter (November–May) or summer (June–October) seasons at a location and the number of storms. Calculations are based on data from the US Weather Bureau records (NOAA) during the period 1929–1979. The combined correlation is significant at the $P < 0.01$ level

an annual basis (data not presented). The vast majority of storm events result in less than 10 mm precipitation, and it may be questionable as to just how useful this input is to increasing soil moisture at soil depths where plants can effectively use the precipitation input. Sala and Lauenroth (1982) examined the impact of small precipitation events (~5 mm) on plant water relations in a semi-arid glassland. They concluded that for shallow-rooted grasses these small precipitation events could significantly improve gas exchange for 1–2 days following the storm.

Given the frequency distributions in Fig. 18.13, total annual precipitation and the number of storm events should be tightly correlated. Figure 18.4 shows that not only is there indeed a significant linear relationship between

Fig. 18.5. The frequency distribution of the date of the first winter rains for three sites differing in the predictability of that winter precipitation. The first winter storm is defined as the first storm after October 1 that was ≥10 mm. Calculations are based on data from the US Weather Bureau records (NOAA) during the period 1929–1979. The three figures are arranged in a west-to-east transect from *top to bottom*

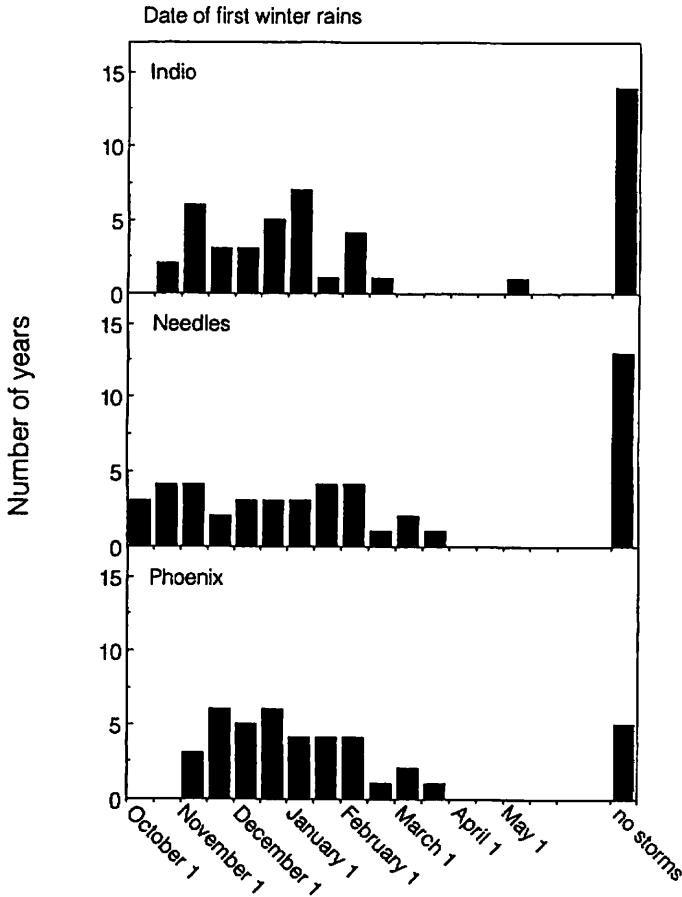these two parameters, but that the relationships for both summer and winter storms are the same.

18.3.2   Drought Duration

Of importance in trying to understand the constraints imposed on plant performance by drought is length or duration of the drought period. One way of examining this character is to examine how long it takes, after the "winter season" or "summer season" begins, before significant precipitation occurs. A 10-mm event is often considered a minimal trigger for plant growth activities in the desert (Beatley, 1974a,b). Winter precipitation is driven by frontal storms coming off the Pacific Ocean. If we examine the date of occurrence of the first 10-mm precipitation for the winter season at sites differing in the mean annual precipitation, we see that this date is highly variable (Fig. 18.5). The "beginning" of the winter season may be essentially any date between October 1 and May 15 in the Sonoran Desert; the frequency distribution is flat enough that there is little tendency for the winter growing period to begin during any specific window. Moreover, at the two driest sites (Indio and Needles), there was not a single storm large enough to trigger growth according to the criteria of Beatley (1974b) in almost one-third of the years. As such, we would obviously expect that perennial plants at the driest sites would require features to insure persistence throughout an entire year without precipitation.

The entry of moist tropical air into the Sonoran Desert is more reliable. In the more southerly sites, the dates of the first summer monsoonal rains are predictable (Fig. 18.6). The date of the first summer rains is, however, very much dependent on the average amount of summer rains received. In the regions receiving less summer precipitation, the date of these first rains is less predictable, such that at the drier sites this summer moisture (if any) could come at virtually any time during the summer.

Once the first rains have arrived, just how good is early season moisture as a predictor of the overall quality of the growing season? If the first rains events portend a generally wet and favorable season, then plants should respond (break dormancy, germinate) shortly after these rains events to capitalize on the available soil moisture and to be positioned to effectively use later moisture inputs. However, if the first rains of the season do not provide qualitative information about the remainder of the season, then perhaps responding to those early rains is a chance event. For 10 of the 12 stations listed in Fig. 18.2, there is a highly significant, positive correlation ($P < 0.01$) between the amount of winter precipitation falling in the first 30 days of the growing season and the total amount for that growing season. For 7 of 12 stations, there was an equivalently positive and significant correlation for summer rains as well. Thus, early season precipitation is statistically a reliable indicator of future moisture inputs. Pianka (1967) ex-

Date of first summer rains
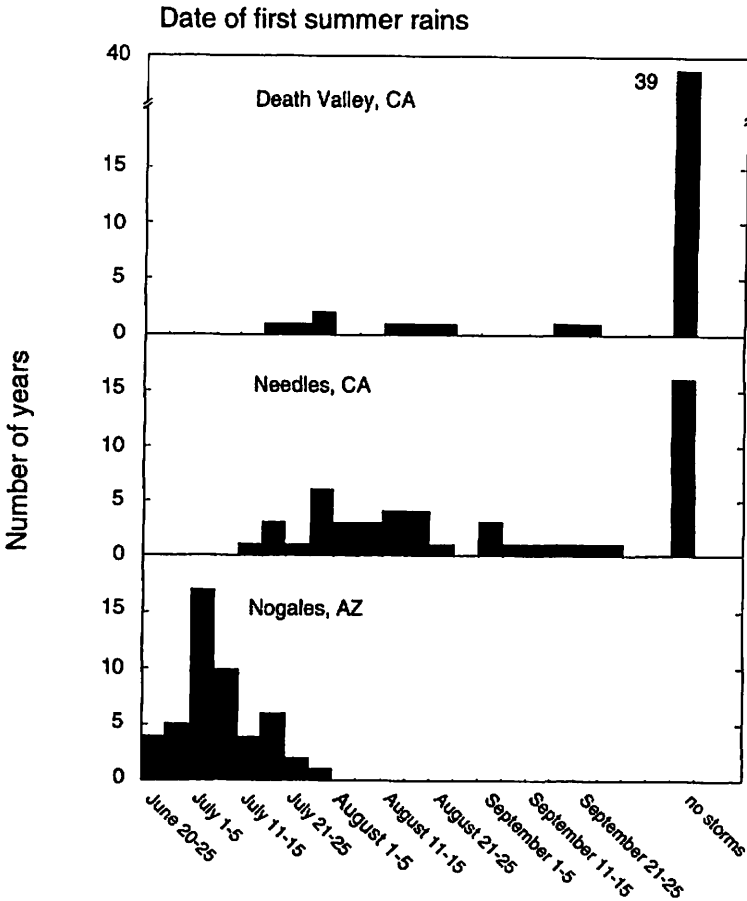
Fig. 18.6. The frequency distribution of the date of the first summer rains for three sites differing in the predictability of that summer precipitation. The first summer storm is defined as the first storm after June 1 that was ≥10mm. Calculations are based on data from the US Weather Bureau records (NOAA) during the period 1941–1989. The three figures are arranged in a north-to-south transect from *top to bottom*

amined autocorrelations of monthly precipitation for different sites throughout the Great Basin, Mojave, and Sonoran Deserts. As in the previous analysis, he noted a strong autocorrelation for up to 2–3-month periods in the Mojave and Sonoran Deserts. However, for the Great Basin, Pianka (1967) found no autocorrelation between months and concluded that precipitation had little predictability from month to month.

18.3.3 Predictability of Temperature

Air temperatures exhibit less variance than precipitation (Fig. 18.7). However, there is a strong tendency for temperatures in the cooler months of the
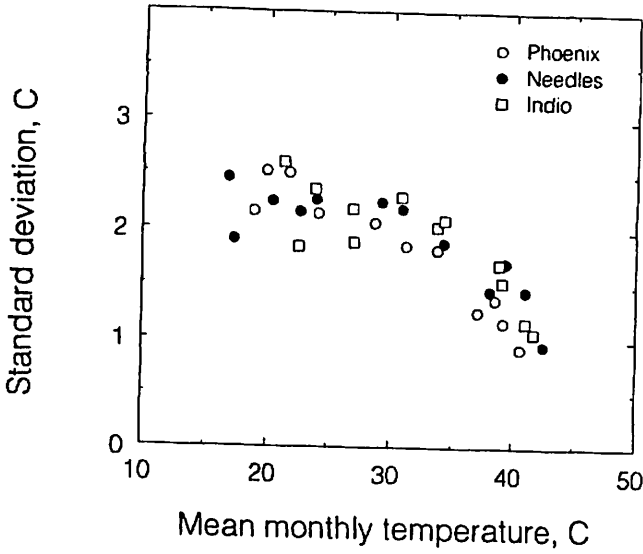
Fig. 18.7. The relationship between the mean monthly temperature and the standard deviation of values about the mean for different locations in arid regions of the western United States. Calculations are based on data from the US Weather Bureau records (NOAA) during the period 1929–1979

year to be more variable than those in the hotter months (Hinds and Rotenberry 1979). Variability of air temperatures during the winter months in the Sonoran Desert is almost twice that in summer months. One possible interpretation of these data is that drier winters are warmer and have a greater impact on absolute temperatures than do differences in temperature arising from changes in the number of convection storms that occur during summer months. An alternative explanation is that infrequently during the winter months Arctic air moves into the southern desert regions for a brief period of time. These episodic events would influence calculations of temperature variability, and would undoubtedly have a significant impact on freezing and plant distribution. In probably the best known example, Shreve (1911) showed that exposure to freezing temperatures for only a day was sufficient to kill the giant saguaro cactus. Episodic low-temperature events are known to play a major role in defining the distribution limits of saguaro and other cacti (Nobel 1980).

18.4 Gas Exchange Patterns Among Life-Forms

18.4.1 Photosynthetic Pathway Distribution Among Life-Forms

Deserts contain a much larger range of life-forms than are found in more mesic regions, particularly in those deserts that receive bimodal precipitation

(Shreve 1942; Werger 1986; Shmida and Burgess 1988). Shreve and Wiggins (1964) described 25 categories of life forms within the Sonoran Desert. While many of the different life-forms relate to overall physiognomy (tree, subtree, shrub, annual, etc.), 19 relate to succulence and to the high diversity associated with shrubs as a life-form. For photosynthetic purposes, we will examine the diversity of life-forms related to leaf types and succulence differences, because these are of particular importance to understanding the distribution patterns of photosynthetic pathways.

Within the C_3 photosynthetic pathway, there is wide variation in photosynthetic tissue types in that leaves, twigs, stems, or any combinations of these serve as the photosynthetic surface. Green-stem or green-photosynthetic nonleaf tissues are perhaps the most frequent variant (Ehleringer et al. 1987; Osmond et al. 1987; Smith and Osmond 1987; Comstock and Ehleringer 1988, 1990). Species exhibiting photosynthesis by nonleaf tissues increase both as precipitation decreases and as the fraction of summer precipitation increases (Shmida and Burgess 1988; Cody 1989). Twig and stem photosynthesis contribute significantly to the overall carbon balance of these species, and in some cases, leaves no longer serve a significant role in the plant's carbon balance (Comstock et al. 1988). In all instances, the intercellular CO_2 concentrations of twigs are lower than those of leaves and the twig tissues are more drought-tolerant than leaf tissues. As elaborated in Section 18.5.4, leaves of C_3 species in the desert exhibit over a $100\,\mu l\,l^{-1}$ variation in intercellular CO_2 concentrations, which will have significant bearing on both the extent to which stomata limit photosynthesis and on water-use efficiency.

In terms of carbon gain, advantages and disadvantages can be associated with each of the three photosynthetic pathways depending on environmental conditions. Under today's CO_2 environment, the C_4 photosynthetic pathway offers little or no intrinsic advantage over C_3 under cool temperatures ($\leqslant 25\,°C$). In fact, the increases in quantum yield and reductions in photorespiration associated with C_3 photosynthesis under cooler temperatures suggest an advantage to plants possessing that pathway in cooler environments (Ehleringer 1978; Osmond et al. 1982). While C_4 photosynthesis may not have originally evolved under hot, arid conditions (Ehleringer et al. 1991b), C_4 photosynthesis does result in a reduced photorespiration rate and increased quantum efficiency at high temperatures ($\geqslant 35\,°C$). Thus, we should expect C_4 photosynthesis to predominate in hot temperature environments and C_3 photosynthesis in cool temperature environments, provided that adequate moisture for growth is available. There is no evidence that intrinsic aspects of each photosynthetic pathway should confer any competitive advantage with respect to drought tolerance. However, because of the higher water-use efficiency of C_4 photosynthesis, these plants are expected to be at a competitive advantage in saline environments (Pearcy and Ehleringer 1984).

CAM photosynthesis provides a mechanism for a potential advantage over C_3 and C_4 plants under limited moisture conditions (Lange et al. 1974,

1975, 1978; Smith and Nobel 1986). The extremely high water-use efficiency of the CAM pathway may be of advantage during drought periods, when carbon gain by other pathways approaches zero. However, it is unclear whether or not the low photosynthetic-capacity constraints of CAM plants during wetter periods of the year offsets its advantage during drought. It may be that CAM plants exhibit an advantage only if competition for light is insufficient to exclude these plants during the wetter periods. Consistent with this is the observation of an increase in the frequency of CAM plants along gradients of decreasing precipitation in coastal regions of southern California and northern Chile (Mooney et al. 1974).

Following the initial observations by Bender (1968) that photosynthetic pathways could be distinguished on the basis of their carbon isotope ratio (δ^{13}C), there was an extensive attempt to survey the world's flora to determine the ecological and taxonomic distribution of photosynthetic pathway types. Over the past 20 years, these efforts resulted in the development of a relatively complete picture of the distribution of photosynthetic pathway types in arid zones (summarized in Ehleringer 1989, and Ehleringer and Monson 1993). Life-form related aspects of these patterns are summarized

Table 18.2. Taxonomic distribution of photosynthetic pathway types according to life form. Abundance estimates are for floristic abundance (not ecological abundance). Abundance estimates are $+$ = infrequent occurrences known, $++$ = occasionally, $+++$ = common, and $++++$ = essentially exclusive

	C_3	C_4	C_3-CAM	CAM
Annuals				
Winter anual	$++++$			
Summer annual	$++$	$+++$		
Perennial succulents				
Leaf deciduous	$++$		$+++$	
Leaf succulent	$++$		$+++$	
Stem succulent				$++++$
Perennial arborescents				
Subtree	$++++$	$+$		
Tree	$++++$			
Perennial shrubs				
Evergreen-leaved	$+++$	$++$		
Drought-deciduous	$+++$			
Winter-deciduous	$++++$			
Photosynthetic twigs				
Twigs only	$+++$			$+++$
Leaves and twigs	$++++$			
Perennial herbs				
Graminoid	$+++$	$+++$		
Geophytes	$++++$			

in Table 18.2. From this table it is evident that C_4 plants are not so taxonomically common in deserts. The C_4 pathway is essentially found in only three life-forms: graminoids, evergreen shrubs, and summer annuals. The distribution of C_4 photosynthesis among evergreen perennials is essentially restricted to halophytic plants (e.g., *Atriplex*). When the distribution of photosynthetic pathway types is analyzed with respect to the different North American deserts, C_4 photosynthesis is rare in deserts that do not receive significant amounts of summer rain (Teeri and Stowe 1976; Stowe and Teeri 1978), except in the case of halophytes (Caldwell et al. 1977; Pearcy and Ehleringer 1984). The distribution of CAM plants closely parallels that of C_4 species (Teeri et al. 1978). CAM plants are most frequent in habitats receiving summer rains and those regions without cold winter temperatures.

Predictability and patterning of precipitation provide a basis for understanding the distribution of C_3 and C_4 photosynthesis in perennials. Throughout much of the Sonoran Desert, the most effective precipitation comes during the winter periods when temperatures are cooler and evaporative gradients are lower (see Sect. 18.5). If winter and spring are the primary periods of active growth, then C_3 photosynthesis may have an advantage over C_4 photosynthesis in perennial species. Under the moderate temperatures prevailing at that time, photorespiration rates would be expected to be reduced in C_3 plants and quantum yields higher in C_3 relative to C_4

Carbon isotope ratio, ‰

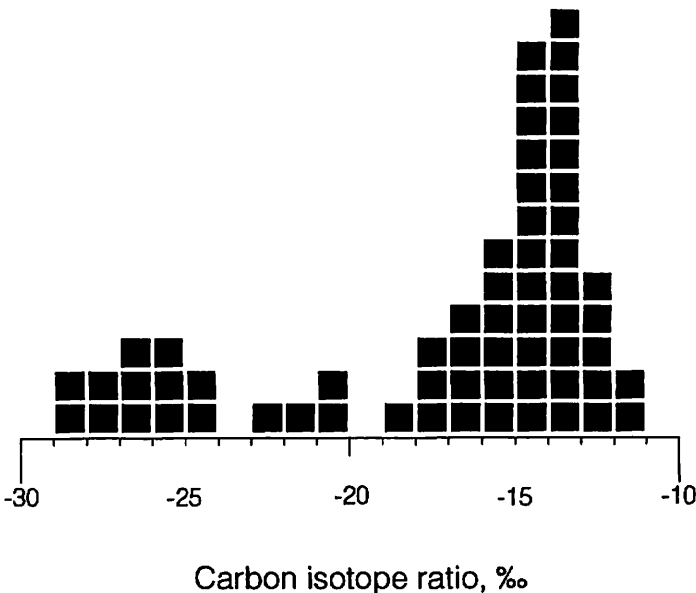**Fig. 18.8.** Variation in the carbon isotope ratio ($\delta^{13}C$) of *Aloe* species from South Africa. The $\delta^{13}C$ values approaching -10% indicate a species that uses only CAM photosynthesis; values approaching -30% indicate a species using only C_3 photosynthesis. Intermediate $\delta^{13}C$ values indicate a species using both C_3 and CAM photosynthesis (After Vogel 1980)

plants (Ehleringer and Björkman 1977; Ehleringer and Pearcy 1983; Pearcy and Ehleringer 1984). While such an explanation may be satisfactory for the northern and central portions of the Sonoran Desert, it falls short on explaining the lack of C_4 photosynthesis in perennials from the southern desert regions where precipitation comes primarily during the summer months and where temperatures are high. At present, there is no satisfactory explanation (other than historical) as to why C_4 photosynthesis is not so taxonomically common in the southern Sonoran Desert.

Two interesting patterns emerge with respect to shifts in photosynthetic pathway within a plant in response to increased soil moisture deficit. The first is tissue-dependent differentiation of photosynthetic pathway. Lange and Zuber (1977) were the first to note this with *Frerea indica*, a south African perennial having a succulent stem with CAM photosynthesis and drought-deciduous C_3 leaves. Presumably, by such a mechanism, the plants is able to gain carbon longer into the drought period than were it to have only C_3 metabolism. More common, though, is a second pattern in which the same leaf tissue switches from C_3 to CAM photosynthesis depending on the external soil moisture stress (Troughton et al. 1977; Winter et al. 1978; Bloom and Troughton 1979). Perhaps nowhere is this better developed than in the south African genus *Aloe*, whose members span the entire range from 100% C_3 to 100% CAM photosynthesis (Fig. 18.8).

18.4.2 Environment and Life-Form Distribution

It is difficult to evaluate or predict leaf-level gas exchange characteristics of different life-forms in the absence of information about other possible constraints within the plant that influence overall carbon gain. For photosynthetic gas exchange, two of the most critical aspects will be factors related to mineral nutrition and to water acquisition and transport. Mineral nutrition (particularly nitrogen) limits those aspects of gas exchange most closely associated with capacity (Field and Mooney 1986; Evans 1989). Models exist to predict the optimal allocation of nitrogen to maximize carbon gain (Field 1983). Photosynthetic capacity in desert species is linearly related to leaf nitrogen contents (Mooney et al. 1981; Field and Mooney 1986). A priori, there is no reason to expect that life form should impose constraints on the maximum photosynthetic capacity of leaves in desert plants, although field observations indicate distinct trends (Mooney and Gulmon 1982; Smith and Nobel 1986). Stomatal and biochemical aspects of gas exchange are known to be closely integrated (Wong et al. 1979; Woodrow and Berry 1988), suggesting that water-related aspects of gas exchange may account for the life-form-dependent patterns recognized by Mooney and Gulmon (1982).

There are reasons to expect that life-form characters should impose constraints on actual photosynthetic rates, particularly in perennial plants
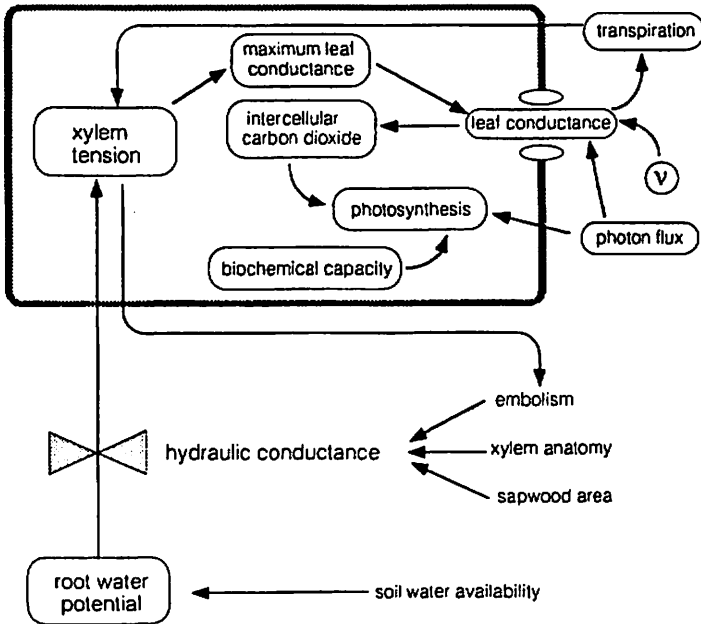
Fig. 18.9. A conceptual model of how higher intercellular CO_2 concentrations driven by increased stomatal conductances may contribute to enhanced xylem embolism rates, particularly under conditions of low root water potentials as would be expected during periods of extreme soil water deficit. (After Ehleringer 1993b)

which must persist through repeated drought periods. Tyree and Sperry (1989) have shown that under low water potentials cavitation events within the xylem increased, leading to a reduced capacity to conduct water. Structural adaptations exist which permit tolerance of reduced water potentials, but appear to come at the expense of a reduced capacity to conduct water. Given equal stem hydraulic conductances between two species, a relatively higher stomatal conductance by one species should result in an increased transpiration rate and a decreased leaf water potential (Fig. 18.9). As soil moisture availability decreases during the season, the water potential gradient between leaf and root should increase and ultimately under extreme or prolonged drought stress, water potentials may reach the point at which cavitation events occur with high frequency. In theory, progressive accumulation of these cavitation events could restrict water flow sufficiently to reduce transpiration and result in stem death if drought persisted over an extended period.

If drought-induced cavitation events are irreversible or mostly irreversible, then persistence through time and stem hydraulic conductivity should be inversely related. That is, perennials would be expected to have lower

hydraulic conductances than annuals. Long-lived perennials, which must persist through repeated droughts of varying duration, would be expected to have lower hydraulic conductances than short-lived perennials in order to avoid extensive xylem cavitation. With respect to perennial life forms accessing the same limited soil moisture, trees would be at a significant disadvantage to shrubs (an overall shorter conducting system). On this point Balding and Cunningham (1974) showed that plant height became progressively shorter in *Acacia constricta* (tree) and *Larrea tridentata* (shrub) as drought severity increased along an aridity gradient. Stem xylem cavitation events would be expected to proceed from the stem tip where transpiration is occurring toward basal regions, creating progressive stem dieback under conditions of increasing drought duration. This may in part be the explanation for why suffrutescent growth (many stems emerging from a common root base) is so common among aridland shrubs.

Life-form diversity of perennial species is positively related to climatic diversity. Cody (1989) showed that life-form diversity among Sonoran Desert sites increased under extreme conditions – conditions likely to reflect both extremes in drought and a high year-to-year variability in precipitation. Shmida and Burgess (1988) found that biseasonality of precipitation was the major driving factor accounting for the increased growth-form diversity in the Sonoran Desert. Biseasonal precipitation was also correlated with these same life-form patterns within the Great Basin and Colorado Plateau (Comstock and Ehleringer 1992). Together, these data suggest that in North American deserts it is the diversity of incoming moisture sources that drives the evolution of differences in life-form.

The coefficient of variation is a measure of unpredictability (Sect. 18.2.1) and an unpredictable environment will preclude the evolution of perennial plants dependent on frequent rainfall episodes or not capable of persisting through extended drought periods. The loss of constancy (the degree to which conditions are similar from year to year) in drier sites should have a direct impact on the distribution of life-forms along an aridity gradient. Hastings and Turner (1965a) examined the amounts and variability of winter and summer precipitation in Baja California. They noted that the variability in precipitation corresponded to the distribution of vegetation types described by Shreve (1934) and Shreve and Wiggins (1964). After Colwell (1974) showed that predictability and constancy were mathematically related, Schaffer and Gadgil (1975) then followed with a prediction of the distribution abundances of annual versus perennial life-forms as predictability of rainfall decreased. The data of Harper (unpubl. data cited in Schaffer and Gadgil 1975) supported the prediction that annuals become an increasing fraction of the total flora as predictability of that precipitation decreases. What these data sets did not reveal was any information on the distribution of photosynthetic pathways among these annuals. Such information can be extracted from Shreve and Wiggins (1964), who noted that there were distinct winter- and summer-annual floras, even within a particular region. It turns out that winter annuals have C_3 photosynthesis exclusively, while summer annuals

are primarily C_4 plants (Mulroy and Rundel 1977). Such a distribution pattern is consistent with the observation that C_4 photosynthesis, through its effects on reduced photorespiration and increased quantum yields at high temperature, provides a significant potential carbon gain advantage over the C_3 pathway under hot summer conditions if soil moisture is adequate.

18.5   Longevity and Gas Exchange

While absolute photosynthesis and transpiration rates among species may exhibit substantial variation, these flux rates decrease as water stress increases (Smith and Nobel 1986; Smith and Nowak 1990). Variation in maximum flux capacities is loosely associated with life-form, with annuals typically having higher rates than perennials (Mooney and Gulmon 1982; Smith and Nobel 1986). However, there are enough counter-examples of annuals having low photosynthetic capacities (Seeman et al. 1980; Werk et al. 1983) and perennials having high photosynthetic capacities (Ehleringer and Björkman 1977) that generalities of this type cannot be drawn with a high degree of certainty. An alternative approach to understanding life-history variation in gas exchange parameters is to evaluate ratios of activity (such as water-use efficiency) or possible set points in photosynthetic gas exchange.

18.5.1   Water Use in Relation To Carbon Gain

Gas-exchange responses at the leaf level can be viewed from two perspectives: what causes changes in absolute flux rates and what controls changes in flux rates. Changes in maximum photosynthesis (A) and transpiration (E) rates of desert plants in response to soil moisture availability (or any other measures of plant water status for that matter) have been described in numerous studies (Lange et al. 1976; Ehleringer and Mooney 1983; Smith and Nobel 1986; Smith and Nowak 1990). Changes in flux rates and canopy photosynthetic area almost always show a linear response to plant stress (e.g., water potential), and species vary widely in their capacity to maintain photosynthetic activity under water stress. As a consequence, instantaneous measures of gas exchange activity at a single point in time may provide limited insight into primary productivity and plant fitness, although the parameters are ultimately linked with each other (Fig. 18.10).

18.5.2   Gas Exchange Flux Versus Set Point

An alternative approach to examining absolute flux rates and their impact on gas exchange performance is to examine control points or set points in
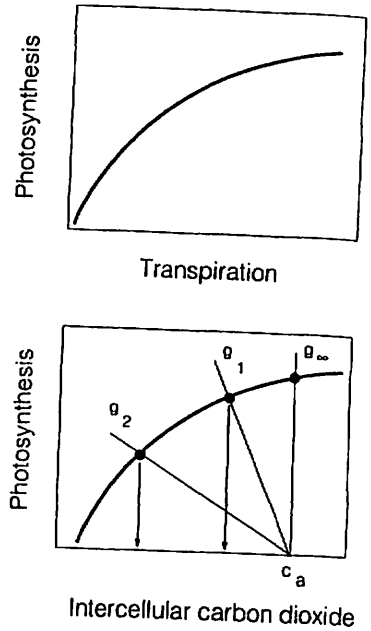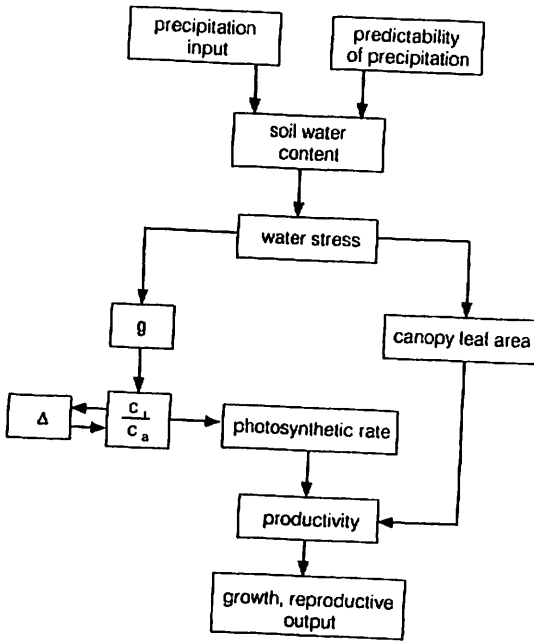
Fig. 18.10. A conceptual model of how plant productivity and ultimately growth, reproductive output, and plant fitness are influenced by water stress and several of the gas exchange characters that influence photosynthetic rate. Δ = carbon isotope discrimination, c_i and c_a are the intercellular and ambient CO_2 concentrations, respectively, and g is the leaf conductance to water vapor. (After Ehleringer 1993b)

gas exchange activity. Set points may be more stable than absolute flux rates, thereby providing a better indicator of whole-plant constraints. That is, whereas absolute flux rates will vary greatly in response to resource levels over the short term or to stress levels over the long term, changes in the set point may be substantially less. The intercellular CO_2 concentration will be considered as a set point for photosynthetic activity, providing integrated information about photosynthesis without providing information on the absolute fluxes. In this manner, the intercellular CO_2 concentration is analogous to body temperature in warm-blooded animals, providing a system-level measure of metabolic activity.

Photosynthesis requires the simultaneous inward diffusion of carbon dioxide from outside the leaf and its fixation into organic compounds by light and dark reactions within the chloroplast. One set point illustrated in Fig. 18.10 is the intercellular CO_2 concentration (c_i), which represents a balance between rates of inward CO_2 diffusion (controlled by stomatal conductance, g) and CO_2 assimilation (controlled by photosynthetic light/dark reactions). In principle, there is no expected relationship between flux rate and set point. A primary advantage of set point analysis over flux rate would arise if set points remained relatively fixed among plants under

nonstressed conditions, and, if in response to abiotic stresses, any changes in the absolute value of a set point resulted in the relative rankings of plants remaining constant.

Using long-term estimates of the c_i value as a measure of the set point for gas exchange metabolism provides a comparative estimate of the extent to which stomatal conductance and water-related process limit photosynthesis instead of photosynthetic capacity and mineral-nutrition-related processes under a specific set of climatic conditions. This is exactly analogous to previous indications of tradeoffs between water-use efficiency and nitrogen-use efficiency (Field et al. 1983). Both parameters cannot be simultaneously increased and the operational point represents a relative difference in the extent to which gas exchange is controlled by mineral-related components versus water-related components. Annuals and perennials would be expected to represent two ends of this spectrum, with limitations in the gas exchange of perennial plants largely controlled by water-related components (e.g., leaf conductance, hydraulic conductance).

18.5.3 Carbon Isotope Discrimination as a Measure
of Intercellular Carbon Dioxide Concentration

18.5.3.1 C_3 Plants

Over extended time periods, the intercellular CO_2 concentration can be estimated through measurement of the carbon isotopic composition of plant material (Farquhar et al. 1989). Carbon isotope discrimination (Δ) in C_3 plants is related to photosynthetic gas exchange; because Δ is in part determined by c_i/c_a, the ratio of CO_2 concentrations in the leaf intercellular spaces to that in the atmosphere. This ratio, c_i/c_a, differs among plants because of variation in stomatal opening (affecting the supply rate of CO_2), and because of variation in the chloroplast demand for CO_2. Of the models linking C_3 photosynthesis and $^{13}C/^{12}C$ composition, the one developed by Farquhar et al. (1982) has been the most extensively tested. In its simplest form, their expression for discrimination in leaves of C_3 plants is

$$\Delta = a + (b - a)\frac{c_i}{c_a},$$

where a is the fractionation occurring due to diffusion in air (4.4‰), and b is the net fractionation caused by carboxylation (mainly discrimination by RuBP carboxylase, approximately 27‰). The result of these constant fractionation processes during photosynthesis is that the leaf carbon isotopic composition represents the assimilation-weighted intercellular CO_2 concentration during the lifetime of that tissue. Farquhar et al. (1989) and Ehleringer et al. (1992) summarize the data showing that Δ values of leaf material are a reliable estimate of c_i/c_a during the lifetime of that leaf for C_3 species.

18.5.3.2 C_4 Plants

Farquhar (1983) developed an expression for carbon isotope discrimination in C_4 plants,

$$\Delta = a + (b_4 + b_3\phi - a)\frac{c_i}{c_a},$$

where b_3 and b_4 are the fractionation of gaseous CO_2 by Rubisco and the fixation of bicarbonate by PEP carboxylase, respectively, and ϕ is the leakage of CO_2 from the bundle sheath cells. Depending on the value of ϕ, the relationship with c_i/c_a could be positive, negative, or zero. The value of ϕ cannot be measured directly, but only indirectly estimated by biochemical or gas-exchange techniques. Early gas-exchange studies suggested that the value of ϕ was close to 0.34, resulting in a zero slope between Δ and c_i/c_a for C_4 plants (Evans et al. 1986). Alternative biochemical calculations suggested that ϕ should be in the range of 0.1–0.13 (Hatch and Osmond 1976; Jenkins et al. 1989). The most recent estimates of ϕ for a broad range of C_4 species are 0.21 (Henderson et al. 1992), resulting in a negative relation between Δ and c_i/c_a.

There is limited information on variation in Δ of C_4 species. O'Leary (1988) and Hubick et al. (1989) report variation on the order of 1–1.5‰ for two crop species. While this may appear to be a small amount of variation, at $\phi = 0.21$, it does represent significant variation in c_i/c_a (Henderson et al. 1992). Bowman et al. (1989) reported that salt stress would induce an equivalent change in online Δ values and attributed increased Δ values to an increased bundle sheath leakage during stress. More recently, Walker and Sinclair (1992) have reported changes in Δ of *Atriplex* along salinity gradients in Australian deserts. The extent to which the changes in Δ values in the field represent genetic differences and/or environmental acclimation is unclear at this time. Should the differences in Δ of native C_4 species represent genetic differences, then it is possible that c_i values and life-history patterns may vary in a manner analogous to that of C_3 plants, but opposite in sign since Δ and c_i are negatively related at $\phi = 0.21$.

18.5.4 Intercellular CO_2 and Life History in C_3 Plants

The Δ values vary among C_3 species in the Sonoran Desert (Fig. 18.11). Carbon isotope discrimination was positively correlated with expected soil moisture availability, suggesting that species in wetter habitats had higher c_i values. Of ecological interest, Δ values of species within a microbabitat were inversely related to the life expectancy of the shrub. Longer-lived species has lower c_i values than shorter-lived species, indicating a more conservative efficiency of water use than in shorter-lived species. Similar negative correlations between life expectancy and Δ have also been observed among
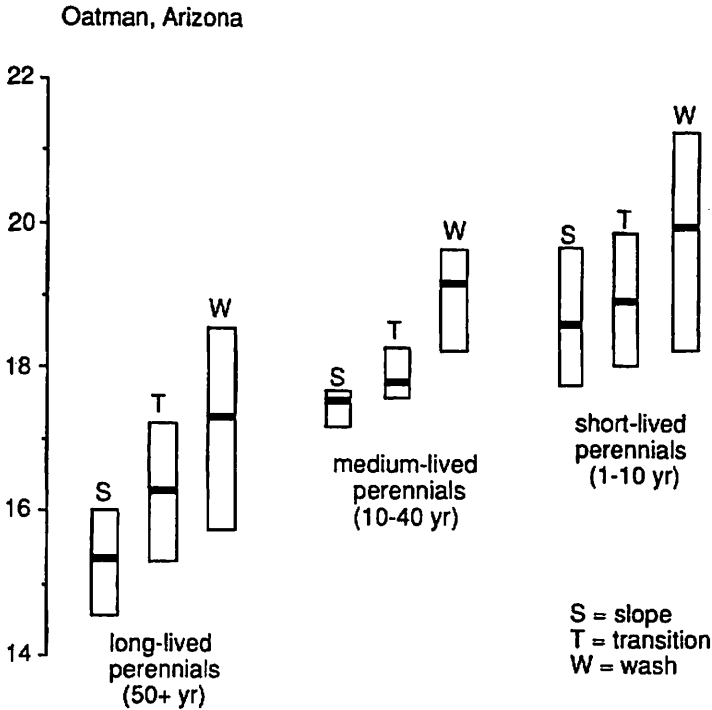
Fig. 18.11. Ranges of carbon isotope discrimination (Δ) values of short-lived (1–10 years), medium-lived (10–40 years), and long-lived (>50 years) species growing in different microhabitats at a Sonoran Desert site. (After Ehleringer and Cooper 1988)

species in grassland communities (Smedley et al. 1991) and between bean cultivars (Ehleringer et al. 1990) and wheat cultivars (Richards and Condon 1993) with respect to date of flowering. This pattern of Δ values among desert species is maintained through time, indicating a high degree of stability in this parameter (Ehleringer and Cook 1991). The slope of the correlation of isotope observations at the two time intervals was less than 1, indicating plasticity or acclimation potential in Δ in response to seasonal environmental fluctuations. From other data sets on agricultural and range species, there is strong evidence that Δ is a stable character and that differences in Δ among genotypes are maintained through time and across sites (see references in Farquhar et al. 1989) so that time-series analyses in individual plants (such as for tree rings) does provide meaningful valuable information of the long-term responses of the genotype to environmental fluctuation.

In the driest desert environments, such as the Atacama Desert of northern Chile, Δ values are quite low with effective c_i values as low as $125 \mu l\, l^{-1}$ (Ehleringer et al. 1993). Such low c_i values might once have been thought to occur only in C_4 species, and they indicate that stomata are very nearly closed during the main periods of carbon gain. Such low Δ values have been

found in a large number of species from deserts throughout the world (Winter and Troughton 1978; Winter 1981; Rundel and Sharifi 1993), suggesting that long-lived species are very conservative in their set point.

Within populations, there can be variation in Δ values corresponding to c_i value differences of $30 \mu l l^{-1}$ (Schuster et al. 1992), suggesting life-history variation not only at the species level but also variation within a species. Ehleringer (1993a) examined variation in Δ values among adjacent *Encelia farinosa* shrubs and showed that high-Δ genotypes grew faster than low-Δ genotypes, but were also more sensitive to drought. In response to the extremes in precipitation patterns that characterize the desert, there appeared to be tradeoffs, with one end of the temporal water-availability spectrum favoring high-Δ genotypes and the other favoring low-Δ genotypes. Thus, variation at the population level in this case mirrored patterns also seen at the community level in terms of variation in c_i.

18.6 Integrating Gas Exchange Across Complex Environmental Gradients

18.6.1 Evaporative Gradients

A common observation is that in response to a decreased humidity level, stomata partially or completely close (Lange et al. 1971), resulting in a reduced c_i value. When plants are grown under reduced humidity levels, c_i values are reduced, as indicated by heavier $\delta^{13}C$ values (Winter et al. 1982). If plants show this environmental plasticity, it seems reasonable to expect that populations adapted to different climatic regimes should show corresponding differences. On an instantaneous basis, transpiration (E) is the product of leaf conductance (g) and the leaf-to-air water vapor gradient divided by total atmospheric pressure (v). Temporal variations in the growing season among sites can be incorporated without bias by averaging the saturation vapor pressure expressed as a mole fraction ($e_{a,sat}/P_{total}$) over each month of the year, using the monthly ratio of precipitation (P) to potential evapotranspiration (E_p) as a weighting factor (Comstock and Ehleringer 1992). The effective seasonal leaf-to-air water vapor gradient (ω) is then calculated as

$$\omega = \frac{\dfrac{1}{P_{total}} \sum_{Jan}^{Dec} \left(e_{a,sat} \dfrac{P}{E_p} \right)}{\sum_{Jan}^{Dec} \dfrac{P}{E_p}}.$$

ω is an index which can be used to rank sites according to the mean evaporative demand expected during the most likely growing seasons throughout the year and has the same units as v (mbar bar^{-1}). In the low humidity

environments that characterize aridlands, the value of ω converges on the actual mean growing-season value of v (Comstock and Ehleringer 1992). ω is but one way of characterizing the evaporative gradient in leaves, but provides a means for predicting plant gas exchange parameters for plants that would be active at different seasons through the year. Habitats in which the evaporative gradients are higher during the growing season are characterized by higher ω values. As such, ω appears to be a useful means for differentiating habitats and seasonal variation in the evaporative gradient across sites in a way that encompassed both the driving potential for transpiration as well as moisture input into the soil.

At the ecotypic level, Comstock and Ehleringer (1992) have shown that variation in Δ values reflected shifts in habitat quality in *Hymenoclea salsola*, a common shrub in the Mojave and Sonoran Deserts. The carbon isotope discrimination values in *H. salsola* can vary by >2‰ in the field, suggesting that c_i values among populations differ by more than $30 \, \mu l \, l^{-1}$. Under common garden conditions, the isotopic variation was greater than 2‰ and was negatively related to the ω (the average leaf-to-air water vapor gradient weighted for periods when soil moisture was available) values for the habitats from which the plants originated (Fig. 18.12). *Hymenoclea salsola* has both photosynthetic twigs and leaves, with twigs always having lower c_i and Δ values. Since leaves and twigs both have small diameters, resulting in strong convective exchange and equivalent tissue temperatures, twigs also always have a greater water-use efficiency (Comstock and Ehleringer 1988). The fraction of leaf to twig photosynthetic areas is also negatively related to ω, resulting in plants from drier habitats (atmospheric drought) having both lower Δ values (higher water-use efficiencies) at the leaf level as well as a greater allocation to the more water-use efficient twig tissues in these environments. Overall, this results in a combined morphological-physiological progression towards canopies of greater water-use efficiency in climates with drier atmospheric conditions. This pattern of decreasing Δ values in plants from drier environments and an increased allocation to photosynthetic twigs is consistent with possible tradeoffs between Δ, as a set point for gas exchange, and drought stress.

The implication of the Comstock and Ehleringer (1992) study is that the seasonality of soil moisture inputs is important in affecting absolute Δ values; in desert habitats where precipitation occurred during the hotter summer months, plants had lower Δ values than from sites receiving equivalent amounts of precipitation during cooler winter-spring periods of the year. Implicit in this interpretation is that those ecotypes growing in summer-wet habitats have the capacity to utilize summer precipitation. For *H. salsola*, this is the case (Ehleringer and Cook 1991). In broader terms, it is expected that along a north-to-south transect through the Sonoran Desert, which is a gradient of increasing summer precipitation, intraspecific c_i values of leaves of plants should decrease even though there might be more summer moisture inputs at those locations.
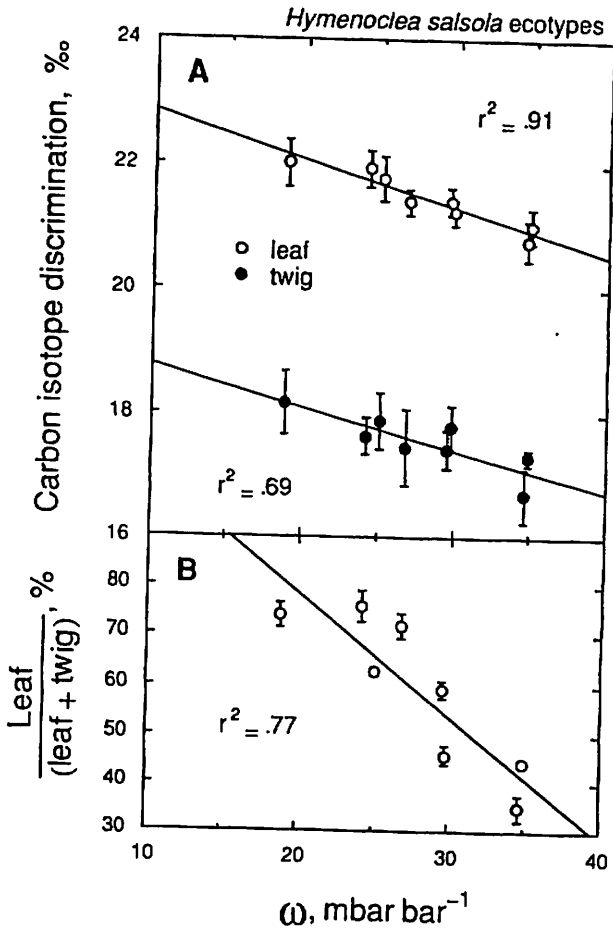
Fig. 18.12. A Carbon isotope discrimination of leaves and twigs from different ecotypes of *Hymenoclea salsola* grown under common garden conditions as a function of ω the leaf-to-air evaporative gradient weighted for seasonal precipitation input. B The ratio of leaf area as a proportion of total photosynthetic area plotted as a function of ω. (Comstock and Ehleringer 1992)

18.6.2 Utilization of Summer Moisture Inputs

The evolution of greater life-form diversity in desert regions with bimodal precipitation patterns may relate niche differentiation to the use of moisture resources. Cannon (1911) and Cody (1986) both noted striking differences in the root distributions of desert plants, suggesting that plants were using different moisture resources. From illustrations provided in those studies, it is evident that there can be substantial root overlap and thus it is unclear that plants have nonoverlapping soil moisture sources. The water resource

used by plants can be distinguished by examining the hydrogen isotope ratio (δD) of water in xylem sap of stems and quantitative estimates of the uptake of different moisture sources can be determined (White et al. 1985).

In desert ecosystems, Ehleringer and Cook (1991) used δD observations of xylem sap to analyze the extent to which Sonoran Desert perennials near Needles, California, utilized summer precipitation. They observed that in moderately dry summers, long-lived species (includes both trees such as *Acacia greggii*, *Carcidium floridum*, and *Chilopsis linearis* as well as shrubs such as *Ephedra viridis*) did not utilize summer rain, but instead relied on moisture from deeper soil layers. In contrast, shorter-lived perennials (such as *Ambrosia dumosa* and *Encelia farinosa*) used moisture from those summer rains whenever it was available. It was only during years of above-average summer rains, when moisture penetrated to greater depths, that long-lived species increasingly utilized summer rains.

Winter rains come as slow-moving frontal systems, and if they are of sufficient magnitude, saturate the soil profile. In contrast, summer rains occur as shorter, more intense convectional storms, often saturating only the upper soil layers. As shown earlier, the frequency distributions of summer and winter storms are not different at sites receiving the same average amount of precipitation. Thus, it would appear that because of the short intense duration of summer rains, the depth of penetration for storms of equivalent rainfall would be less. For plant water use in the desert, the situation is further compounded by the greater ω values for plants growing in summer-wet habitats. Thus, we might expect that Δ values to be lower for plants using summer moisture.

Parts of southern Utah receive 30% or more of the annual precipitation during the summer months. Ehleringer et al. (1991a) studied desert species near Wahweap (Utah) over a 2-year period and observed that following the onset of summer rains (δD value of approximately -25‰), annuals, herbaceous perennials and CAM perennials used water from the upper soil layers wetted by summer rains (Fig. 18.13). A fraction of the woody perennials had δD values intermediate between the summer rains and the deeper soil layers (which were approximately -80‰), implying that both water sources were being utilized in equal proportion. On the other hand, the δD values in a second group of woody perennials did not use any moisture from the summer rains. Similar apparent niche separations for summer what use by perennial shrubs have been described by Donovan and Ehleringer (1992) in the Great Basin and Valentini et al. (1992) in the macchia of Italy.

Taken together, these data suggest that some perennial species may have rooting patterns allowing them to utilize both summer and winter rains, whereas other perennial species have effective rooting patterns restricted to deeper soil layers and thus the plants are unable to utilize summer rains. Functionally dimorphic root systems for water uptake are a possibility, but since the carbon cost of root turnover is high, this should only occur if the
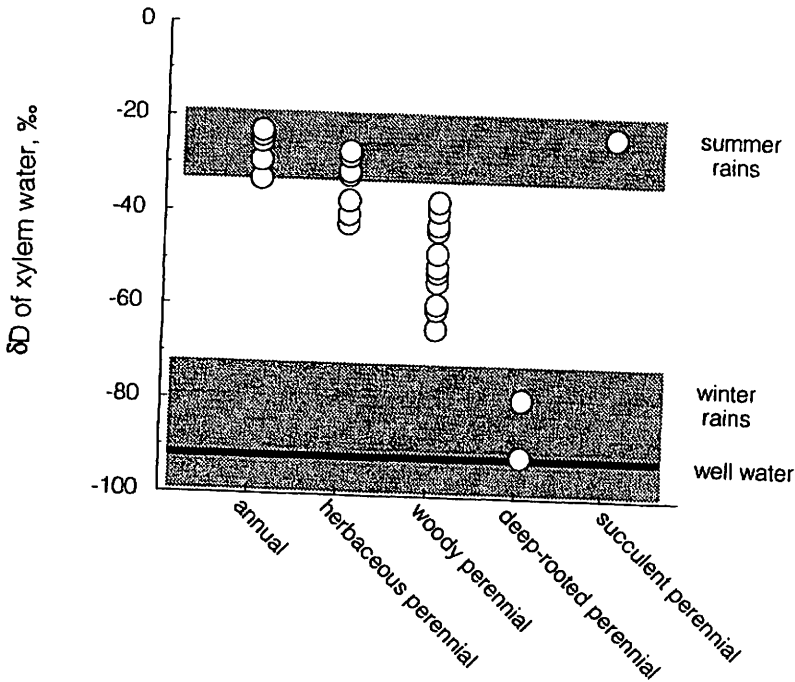
Fig. 18.13. The hydrogen isotope ratio of xylem sap for different species (categorized by life form) at a desert site in southern Utah following summer rains. The *gray areas* represent the range of hydrogen isotope ratios for both summer and winter rain events. The *solid line* represents the hydrogen isotope ratio of goundwater at this site. (Based on a figure and data in Ehleringer et al. 1991a)

summer surface moisture input is reliable (Ehleringer 1993b). In regions characterized by both heavy winter and summer rains, plants would be expected to have summer-active roots in the upper layers to capture summer rains and also a deeper root system to capture water from the deeper perco- lating winter storms. In regions characterized by less predictable summer rains, some species may be adapted to use that summer surface moisture, whereas other species do not, opening the possibility of increased life-form diversity in less predictable environments. The gain to be derived from being able to capitalize on surface moisture in unpredictable environments is that a greater fraction of the total annual precipitation comes from these infrequent storm events. In terms of understanding water dynamics within an ecosystem or possible competitive interactions between plants in an ecosystem, it is critical to know to what extent plants are capable of utilizing different moisture sources.

18.7   Conclusions

Desert environments are characterized by both low precipitation inputs and high year-to-year variability in soil moisture inputs. In response to this environmental variation, there is significant variation in plant gas exchange characteristics. While C_4 and CAM photosynthesis are associated with deserts, they do not constitute the dominant photosynthetic pathways and most of the gas-exchange variation occurs in C_3 photosynthesis. These patterns include substantial variations in the intercellular CO_2 concentrations of leaves and in the photosynthetic tissue type (leaves, twigs, and stems). Variation in the fractions of winter versus summer precipitation and of a species' ability to use summer moisture are also associated with variations in the intercellular CO_2 concentrations of C_3 plants. These environmental constraints and unpredictability of year-to-year precipitation may be the major selective force for the high life-form diversity that characterizes desert vegetation.

References

Balding FR, Cunningham GL (1974) The influence of soil water potential on the perennial vegetation of a desert arroyo. Southwest Nat 19: 241–248

Beatley JC (1974a) Effects of rainfall and temperature on the distribution and behavior of *Larrea tridentata* (creosote-bush) in the Mojave Desert of Nevada. Ecology 52: 245–261

Beatley JC (1974b) Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55: 856–863

Bender GL (ed) (1982) Reference handbook on the deserts of North America. Greenwood Press, Westport, Connecticut

Bender MM (1968) Mass spectrometric studies of carbon 13 variations in corn and other grasses. Radiocarbon 10: 468–472

Bloom AJ, Troughton JH (1979) High productivity and photosynthetic flexibility in a CAM plant. Oecologia 38: 35–43

Bowers MA, Lowe CH (1985) Plant-form gradients on Sonoran Desert bajadas. Oikos 46: 284–291

Bowman WD, Hubick KT, von Caemmerer S, Farquhar GD (1989) Short-term changes in leaf carbon isotope discrimination in salt- and water-stressed C_4 grasses. Plant Physiol 90: 162–166

Brown GW Jr (ed) (1968) Desert biology, vol 1. Academic Press, New York

Caldwell MM (1985) Cold desert. In: Chabot BF, Mooney HA (eds) Physiological ecology of north American plant communities. Chapman and Hall, New York, pp 198–212

Caldwell MM, White, RS, Moore RT, Camp LB (1977) Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. Oecologia 29: 275–300

Cannon WA (1911) The root habits of desert plants. Carnegie Inst Wash Year Book 131: 7–96

Cody ML (1986) Structural niches in plant communities. In: Diamond J, Case TJ (eds) Community Ecology. Harper and Row, New York, pp 381–405

Cody ML (1989) Growth-form diversity and community structure in desert plants. J Arid Environ 17: 199–209

Colwell RK (1974) Predictability, constancy and contingency of periodic phenomena. Ecology 55: 1148–1153

Comstock JP, Ehleringer JR (1984) Photosynthetic responses to slowly decreasing leaf water potentials in *Encelia frutescens*. Oecologia 61: 241–248

Comstock JP, Ehleringer JR (1986) Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. Oecologia 68: 271–278

Comstock JP, Ehleringer JR (1988) Contrasting photosynthetic behavior in leaves and twigs of *Hymenoclea salsola*, a green-twigged, warm desert shrub. Am J Bot 75: 1360–1370

Comstock JP, Ehleringer JR (1990) Effect of variations in leaf size on morphology and photosynthetic rate of twigs. Funct Ecol 4: 209–221

Comstock JP, Ehleringer JR (1992) Plant adaptation in the Great Basin and Colorado Plateau. Great Basin Nat 52: 195–215

Comstock JP, Cooper TA, Ehleringer JR (1988) Seasonal patterns of canopy development and carbon gain in nineteen warm desert shrub species. Oecologia 75: 327–335

Donovan LA, Ehleringer JR (1993) Water sources and use of summer precipitation in a Great Basin shrub community. Funct Ecol (in press)

Ehleringer JR (1978) Implications of quantum yield differences on the distribution of C_3 and C_4 grasses. Oecologia 31: 255–267

Ehleringer JR (1989) Carbon isotope ratios and physiological processes in aridland plants. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Ecological Studies Series. Springer, Berlin Heidelberg New York, pp 41–54

Ehleringer JR (1993a) Variation in leaf carbon isotope discrimination in *Encelia farinosa*: implications for growth, competition, and drought survival. Oecologia (in press)

Ehleringer JR (1993b) Gas exchange implications of isotopic variation in aridland plants. In: Griffiths H, Smith J (eds) Plant responses to water deficit. Environmental Plant Biology Series. BIOS Scientific Publ, London (in press)

Ehleringer J, Björkman O (1977) Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, carbon dioxide, and oxygen concentration. Plant Physiol 59: 86–90

Ehleringer JR, Cook CS (1991) Carbon isotope discrimination and xylem D/H ratios in desert plants. Stable isotopes in plant nutrition, soil fertility, and environmental studies. IAEA, Vienna, pp 489–497

Ehleringer JR, Cooper T (1988) Correlations between carbon isotope ratio and micro-habitat in desert plants. Oecologia 76: 562–566

Ehleringer JR, Monson RK (1993) Ecology and evolution of photosynthetic pathway types. Annu Rev Ecol Syst 24: 411–439

Ehleringer JR, Mooney HA (1983) Photosynthesis and productivity of desert and Medi-terranean climate plants, p. 205–231. In: Encyclopedia of plant physiology, New Series, vol 12D. Springer, Berlin Heidelberg New York

Ehleringer JR, Pearcy RW (1983) Variation in quantum yields for CO_2 uptake in C_3 and C_4 plants. Plant Physiol 73: 555–559

Ehleringer JR, Comstock JP, Cooper TA (1987) Leaf-twig carbon isotope ratio differences in photosynthetic-twig desert shrubs. Oecologia 71: 318–320

Ehleringer JR, White JW, Johnson DA, Brick M (1990) Carbon isotope discrimination, photosynthetic gas exchange, and water-use efficiency in common bean and range grasses. Acta Oecol 11: 611–625

Ehleringer JR, Phillips SL, Schuster WFS, Sandquist DR (1991a) Differential utilization of summer rains by desert plants: implications for competition and climate change. Oecologia 88: 430–434

Ehleringer JR, Sage RF, Flanagan LB, Pearcy RW (1991b) Climate change and the evolution of C_4 photosynthesis. Trends Ecol Evol 6: 95–99

Ehleringer JR, Phillips SL, Comstock JP (1992) Seasonal variation in the carbon isotopic composition of desert plants. Funct Ecol 6: 396–404

Ehleringer JR, Hall AE, Farquhar GD (eds) (1993) Stable isotopes and plant carbon/water relations. Academic Press, San Diego

Evanari M, Schulze E-D, Lange OL, Kappen L, Buschbom U (1976) Plant production in arid and semi-arid areas. In: Lange OL, Kappen L, Schulze E-D (eds) Water and plant life. Ecological Studies Series. Springer Berling Heidelberg New York, pp 439–451

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78: 9–19

Evans JR, Sharkey TD, Berry JA, Farquhar GD (1986) Carbon isotope discrimination measured concurrently with gas-exchange to investigate CO_2 diffusion in leaves of higher plants. Aust J Plant Physiol 13: 281–292

Farquhar GD (1983) On the nature of carbon isotope discrimination in C_4 species. Aust J Plant Physiol 10: 205–226

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. Aust J Plant Physiol 9: 121–137

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol 40: 503–537

Field CB (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia 56: 341–347

Field CB, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 25–55

Field CB, Merino J, Mooney HA (1983) Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60: 384–389

Flanagan LB, Ehleringer, JR, Marshall JD (1992) Differential uptake of summer precipitation and groundwater among co-occurring trees and shrubs in the southwestern United States. Plant Cell Environ 15: 831–836

Goudie A, Wilkinson J (1980) The warm desert environment. Cambridge University Press, Cambridge

Hastings JR (1965) On some uses of non-normal coefficients of variation. J Appl Meteorol 4: 475–478

Hastings JR, Turner RM (1965a) Seasonal precipitation regimes in Baja California, Mexico. Geog Ann 47: 204–223

Hastings JR, Turner RM (1965b) the changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. University of Arizona Press, Tucson

Hatch MD, Osmond CB (1976) Compartmentation and transport in C_4 photosynthesis. In: Stocking CR, Heber U (eds) Encyclopedia of plant physiology New Series, vol 3. Springer, Berlin Heidelberg New York, pp 144–184

Henderson SA, von Caemmerer S, Farquhar GD (1992) Short-term measurements of carbon isotope discrimination in several C_4 species. Aust J Plant physiol 19: 263–285

Hershfield DM (1962) A note on the variability of annual precipitation. J Appl Meteorol 1: 575–578

Hinds WT, Rotenberry J (1979) Relationship between mean and extreme temperatures in diverse microclimates. Ecology 60: 1073–1075

Hubick KT, Hammer GL, Farquhar GD, Wade LJ, von Caemmerer S, Henderson SA (1989) Carbon isotope discrimination varies genetically in C_4 species. Plant Physiol 91: 534–537

Jenkins CLD, Furbank RT, Hatch MD (1989) Mechanism of C_4 photosynthesis – a model describing the inorganic carbon pool in bundle-sheath cells. Plant Physiol 91: 1372–1381

Lange OL, Zuber M (1977) *Frerea indica*, a stem succulent CAM plant with deciduous C_3 leaves. Oecologia 31: 67–72

Lange OL, Lösch R, Schulze E-D, Kappen L (1971) Responses of stomata to changes in humidity. Planta 100: 76–86

Lange OL, Schulze ED, Evenari M, Kappen L, Buschbom U (1974) The temperature-related photosynthetic capacity of plants under desert conditions I. Seasonal changes of the photosynthetic response to temperature. Oecologia 17: 97–110

Lange OL, Schulze ED, Kappen L, Evenari M, Buschbom U (1975) CO_2 exchange pattern under natural conditions of *Caralluma negevensis*, a CAM plant of the Negev Desert. Photosynthetica 9: 318–326

Lange OL, Kappen L, Schulze E-D (1976) Water and plant life: problems and modern approaches. Ecological Studies 19. Springer Berlin Heidelberg New York, 536 pp

Lange OL, Schulze ED, Evenari M, Kappen L, Buschbom U (1978) The temperature-related photosynthetic capacity of plants under desert conditions. Oecologia 34: 89–100

Le Houérou HN (1984) Rain-use efficiency: a unifying concept in arid land ecology. J Arid Environ 7: 1–35

Le Houérou HN, Bingham RL, Skerbek W (1988) Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. J Arid Environ 15: 1–18

MacMahon JA (1985) Deserts. Chanticleer Press, New York

McDonald JE (1956) Variability of precipitation in an arid region: a survey of character-istics for Arizona. Technical reports on the meteorology and climatology of arid regions, University of Arizona, Tucson

Mooney HA, Gulmon SL (1982) Constraints on leaf structure and function in reference to herbivory. BioScience 32: 198–206

Mooney HA, Troughton JH, Berry JA (1974) Arid climates and photosynthetic systems. Carnegie Inst Wash Yearb 73: 793–805

Mooney HA, Ehleringer J, Berry JA (1976) High photosynthetic capacity of a winter annual in Death Valley. Science 194: 322–324

Mooney HA, Field C, Gulmon SL, Bazzaz FA (1981) Photosynthetic capacity in relation to leaf positions in desert versus old-field annuals. Oecologia 50: 109–112

Mulroy TW, Rundel PW (1977) Annual plants: adaptations to desert environments. BioScience 27: 109–114

Nicholson SE (1980) The nature of rainfall fluctuations in subtropical West-Africa. Monthly Weather Rev 108: 473–487

Nobel PS (1980) Morphology, surface temperature, and the northern limits of columnar cacti in the Sonoran Desert. Ecology 61: 1–7

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4: 25–51

O'Leary MH (1988) Carbon isotopes in photosynthesis: fractionation techniques may reveal new aspects of carbon dynamics in plants. BioScience 38: 328–336

Osmond CB, Winter K, Ziegler H (1982) Functional significance of different pathways of CO_2 fixation in photosynthesis. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Plant physiological ecology II: Encyclopaedia of plant physiology New Series, vol 12B. Springer, Berlin Heidelberg New York, pp 479–547

Osmond CB, Smith SD, Gui-Ying B, Sharkey TD (1987) Stem photosynthesis in a desert ephemeral, *Eriogonum inflatum*: characterization of leaf and stem CO_2 fixation and H_2O vapor exchange under controlled conditions. Oecologia 72: 542–549

Osmond CB, Pitelka LF, Hidy GM (eds) (1990) Plant biology of the basin and range. Springer, Berlin Heidelberg New York

Pearcy RW, Ehleringer J (1984) Ecophysiology of C_3 and C_4 plants. Plant Cell Environ 7: 1–13

Phillips DL, MacMahon JA (1978) Gradient analysis of a Sonoran Desert bajada. South-west Nat 23: 669–680

Pianka ER (1967) On lizard species diversity: North American flatland deserts. Ecology 48: 333–351

Richards RA, Condon AG (1993) Challenges ahead using carbon isotope discrimination in plant breeding programs. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon water relations. Academic Press, San Diego (in press)

Rundel PW, Sharifi MR (1993) Carbon isotope discrimination and resource availability in the desert shrub, *Larrea tridentata*. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon/water relations. Academic Press, San Diego (in press)

Sala OE, Lauenroth WK (1982) Small rainfall events: an ecological role in semiarid regions. Oecologia 53: 301–304

Schaffer WM, Gadgil MD (1975) Selection for optimal life histories in plants. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, pp 142–157

Schulze E-D (1982) Plant life forms and their carbon, water, and nutirent relations. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Plant physiological ecology II: Encyclopaedia of plant physiology New Series, vol 12B. Springer, Berlin Heidelberg New York, pp 615–676

Schuster WSF, Sandquist DR, Phillips SL, Ehleringer JR (1992) Comparisons of carbon isotope discrimination in populations of aridland plant species differing in lifespan. Oecologia 91: 332–337

Seemann JR, Field CB, Berry JA (1980) Photosynthetic capacity of desert winter annuals measured in situ. Carnegie Inst Wash Year Book: 146–147

Shmida A, Burgess TL (1988) Plant growth-form strategies and vegetation types in arid environments. In: Werger MJA (ed) Vegetation structure. SPB Academic Publ, The Hague, pp 1–31

Shreve F (1911) The influence of low temperature on the distribution of giant cactus. Plant World 14: 136–146

Shreve FS (1934) Vegetation of the northwestern coast of Mexico. Bull Torrey Bot Club 61: 373–380

Shreve F (1942) The desert vegetation of North America: the Bot Rev 8: 195–246

Shreve F, Wiggins I (1964) Vegetation and flora of the Sonoran Desert. Stanford University Press, Stanford

Smedley MP, Dawson TE, Comstock JP, Donovan LA, Sherrill DE, Cook CS, Ehleringer JR (1991) Seasonal carbon isotopic discrimination in a grassland community. Oecologia 85: 314–320

Smith SD, Nobel PS (1986) Deserts. In: Baker NR, Long SP (eds) Photosynthesis in contrasting environments. Elsevier, Amsterdam, pp 13–62

Smith SD, Nowak RS (1990) Ecophysiology of plants in the intermountain lowlands. In: Osmond CB, Pitelka LF, Hidy GM (eds) Plant biology of the basin and range. Ecological studies series 80. Springer, Berlin Heidelberg New York, pp 179–241

Smith SD, Osmond CB (1987) Stem photosynthesis in a desert ephemeral, Eriogonum inflatum: morphology, stomatal conductance and water-use efficiency in field populations. Oecologia 72: 533–541

Stowe LG, Teeri JA (1978) The geographic distribution of C_4 species of the Dicotyledonae in relation to climate. Am Nat 112: 609–623

Teeri JA, Stowe LG (1976) Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23: 1–12

Teeri JA, Stowe LG, Murawski DA (1978) The climatology of two succulent plant families: Cactaceae and Crassulaceae. Can J Bot 56: 1750–1758

Thom HCS (1958) A note on the gamma distribution. Monthly Weather Rev 86: 117–122

Troughton JH, Mooney HA, Berry JA, Verity D (1977) Variable carbon isotope ratios of *Dudleya* species growing in natural environments. Oecologia 30: 307–311

Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. Annu Rev Plant Physiol Mol Biol 40: 19–38

Valentini R, Scarascia Mugnozza GE, Ehleringer JR (1992) Hydrogen and carbon isotope ratios of selected species of a mediterranean macchia ecosystem. Funct Ecol 6: 627–631

Vogel JC (1980) Fractionation of the carbon isotopes during photosynthesis. In: Sitzungsberichte der Heidelberger Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Klass Jahrang 1980, 3. Abhandlung. Springer, Berlin Heidelberg New York, pp 111–135

Walker CD, Sinclair R (1992) Soil salinity is correlated with a decline in ^{13}C discrimination in leaves of *Atriplex* species. Aust J Ecol 17: 83–88

Werger MJA (1986) The Karoo and southern Kalahari. In: Evanari M, Noy-Meir I, Goodall DW (eds) Hot deserts and arid shrublands. Ecosystems of the World vol 12B. Elsevier, Amsterdam, pp 283–359

Werk KS, Ehleringer J, Forseth IN, Cook CS (1983) Photosynthetic characteristics of Sonoran Desert winter annuals. Oecologia 59: 101–105

White JWC, Cook ER, Lawrence JR, Broecker WS (1985) The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. Geochim Cosmochim Acta 49: 237–246

Whittaker RH, Niering WA (1965) Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology 46: 429–452

Winter K (1981) C_4 plants of high biomass in arid regions of Asia – occurrence of C_4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR. Oecologia 48: 100–106

Winter K, Troughton JH (1978) Photosynthetic pathways in plants of coastal and inland habitats of Israel and the Sinai. Flora 167: 1–34

Winter K, Luttge U, Winter ETJH (1978) Seasonal shift from C_3 photosynthesis in Crassulacean acid metabolism in *Mesembryanthemum crystallinum* growing in its natural environment. Oecologia 34: 225–237

Winter K, Holtum JAM, Edwards GE, O'Leary MH (1982) Effect of low relative humidity on $\delta^{13}C$ value in two C_3 grasses and in *Panicum milioides*, a C_3–C_4 inter-mediate species. J Exp Bot 33: 88–91

Woodrow IE, Berry JA (1988) Enzymatic regulation of photosynthetic CO_2 fixation in C_3 plants. Annu Rev Plant Physiol 39: 533–594

Wong SC, Cowan IR, Farquhar GD (1979) Stomatal conductance correlates with photo-synthetic capacity. Nature 282: 424–426