

Carbon and Water Relations in Desert Plants: An Isotopic Perspective

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Deserts have fascinated ecologists for many decades, not only because of the extremes in abiotic conditions and the harshness of the environmental conditions to which plants must be adapted, but also because of the diversity of physiological and morphological patterns evolved by plants that persist in such regions. Water and the discussions of water use have been pervasive in our thinking about desert plants and of how they have adapted to the overall low precipitation amounts and prolonged soil moisture deficits that characterize these environments (Walter and Stadelmann, 1974; MacMahon and Schimpf, 1981). The historical view was that the primary selective force in plant adaptation to deserts was abiotic extremes of high temperature and low precipitation; competitive interactions were thought to be essentially nonexistent (Shreve and Wiggins, 1964). This view has given way to a broader view that competitive interactions (especially for water) may be as important in structuring desert communities (Fonteyn and Mahall, 1978; Fowler, 1986) as the adaptations that allow plants to persist through environmental extremes. In this paper, the role that stable isotopes have played in increasing our understanding of the water and carbon relations of desert plants is examined from both abiotic and biotic interaction perspectives.

I. Desert Climate and Life Form Variation

On a global basis, deserts share one feature in common: limited precipitation. Long-term average precipitation in deserts is less than 250 mm annually. Most years are below average (arithmetic mean), since annual precipitation amounts in deserts are not normally distributed, but instead follow a

gamma distribution (McDonald, 1956). The coefficient of variation of annual precipitation is a measure of the unpredictability of that precipitation; it increases exponentially with decreases in mean annual precipitation (Fig. 1). What this means for plant performance in aridlands is that perennial plants must not only be adapted to low precipitation amounts, but also, as average precipitation decreases, they must be able to tolerate droughts of increasing frequency and duration.

Under such water-limited conditions, we might expect selection for tolerance of water deficits, perhaps efficiency in water use, or drought escape by completion of the growth cycle before onset of drought. Vegetation com-

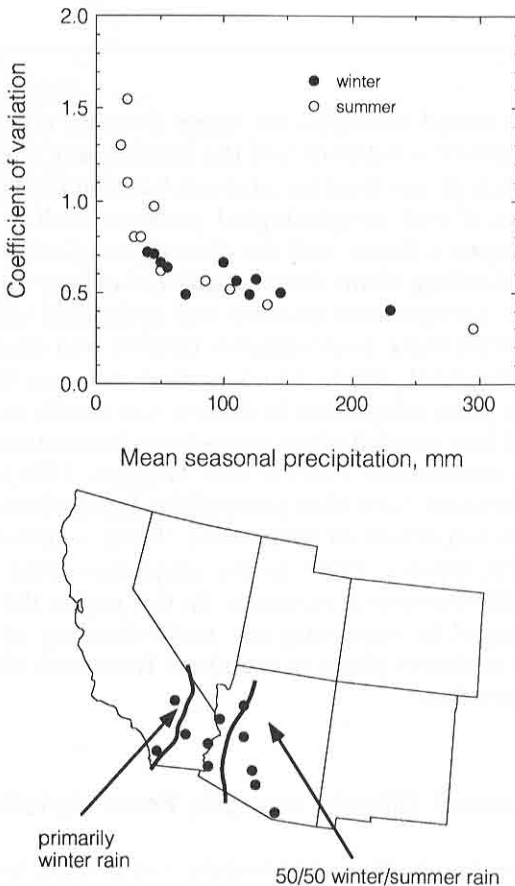


Figure 1. Coefficients of variation of summer precipitation and winter precipitation as a function of long-term mean values (1929–1988) for different aridland locations in the southwestern United States. Based on data from U.S. Weather Bureau records.

position and the morphological or physiological characteristics of these species that allow them to persist in arid climates vary from strongly convergent to highly variable between desert locations, reflecting both abiotic and edaphic constraints (Walter and Stadelmann, 1974; MacMahon and Schimpf, 1981; Smith and Nowak, 1990). While much of the metabolic activity of desert plants is driven by the availability of soil moisture, it is to a large extent the seasonality, duration, and predictability of that precipitation that influences variation in species composition and physiological diversity.

II. Carbon Isotope Composition as a Measure of the Set Point for Gas Exchange Activity

Gas exchange metabolism at the leaf level can be considered as consisting of a number of trade-offs. As stomata open to allow increased CO_2 diffusion rates, outgoing H_2O diffusion rates are also increased. Where a specific plant operates in this continuum between maximizing photosynthetic rate and minimizing transpiration will depend on both environmental conditions and genetic constraints. At either of the extremes, two alternative patterns of water use exist for desert plants (Mulroy and Rundel, 1977; Mooney and Gulmon, 1982). In the first, plants possess a rapid growth rate and high rates of gas exchange during moist periods of the year and complete seasonal growth before the onset of drought. These plants tend to have limited tolerance to water deficits. In contrast, the second category of plants have a prolonged period of growth and lower rates of gas exchange, and maintain activity longer into the drought period. These plants tend to be tolerant of water deficit. Perhaps an oversimplification, but examples of these contrasting patterns would be annuals versus perennials or drought-deciduous versus evergreen perennials. There is no *a priori* reason why these contrasting patterns, albeit perhaps of less magnitude, cannot occur intraspecifically or even within a single breeding population. In this chapter, I first consider interspecific aspects of variation and then consider intraspecific aspects of variation and their natural selection consequences.

Strong trade-offs will exist between photosynthesis (A) and transpiration (E) of the dominant desert landscape species as stomata open and close. Perhaps contrary to popular perception, the preponderance of desert species have C_3 photosynthesis, not C_4 or CAM photosynthesis (Stowe and Teeri, 1978; Teeri *et al.*, 1978; Winter and Troughton, 1978; Winter, 1981). The C_4 photosynthetic pathway is common only in those perennials of saline habitats (especially in the Chenopodiaceae) and in summer-active herbaceous species (grasses, annuals) in areas receiving reliable summer monsoonal rains.

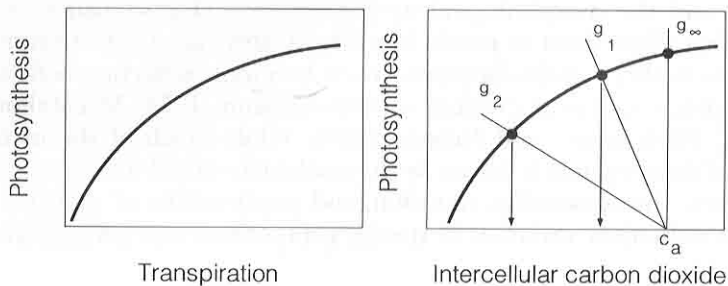


Figure 2. (Left) The expected relationships between photosynthetic rate (A) and transpiration (E) of C_3 photosynthetic leaves as stomata open or close under high light. (Right) The dependence of photosynthesis on intercellular CO_2 (c_i) in a C_3 plant and its relationship to stomatal conductance. The slope of the line emerging from the ambient CO_2 concentration (c_a) and intersecting the $A - c_i$ response curve is the stomatal conductance. The point of intersection of the two curves is the operational c_i value and photosynthetic rate. The extent of photosynthetic stomatal limitation is the reduction in photosynthesis from that occurring with infinite stomatal conductance ($c_i = c_a$) to the observed photosynthetic rate.

Associated with differences in photosynthetic rate of C_3 species will be differences in instantaneous water-use efficiency (A/E), depending on where individual leaves are operating on the photosynthesis versus transpiration curve (Fig. 2). Just where a leaf is operating on this curve also defines $\partial A/\partial E$ (Cowan and Farquhar, 1977); A/E is also closely related to the extent of stomatal limitation of photosynthetic rate (Sharkey, 1985). Thus, while many of the contributions to this volume have focused on carbon isotope composition (especially carbon isotope discrimination, Δ) and its exclusive application to water-use efficiency, the other water-related gas exchange parameters should not be ignored. If natural selection favors some parameter related to long-term intercellular CO_2 concentration (as measured by carbon isotope composition), it will be difficult to distinguish among the above, closely related characters, a point worth keeping in mind when interpreting the carbon isotope composition data that follow.

A more productive approach might be to consider long-term intercellular CO_2 concentration as being an indicator of the set point for gas exchange metabolism, reflecting overall trade-offs between carbon gain and water loss and associated characters that go along with having either a higher or lower rate of gas exchange activity. The Δ value then becomes a convenient measure of long-term intercellular CO_2 . Many features other than simply leaf-level physiology may show strong correlations with the Δ value, including aspects of water-conducting capacity, root/shoot surface areas, and mineral nutrition. As seen below, plants with lower Δ values not only tend to have higher water-use efficiencies, but also lower photosynthetic rates, longer life expectancies, and greater survival under long-term stress conditions. On the other hand, plants with higher Δ values tend to possess an opposite set of metabolic and life-history characteristics.

III. Δ as a Reliable Indicator of Intercellular CO_2 Concentration and Water-Use Efficiency

In C_3 desert plants (Fig. 3), carbon isotope discrimination (Δ) is related to intercellular CO_2 concentration (c_i) as predicted by a model developed by Farquhar *et al.* (1982). These on-line gas exchange data suggest that there is no reason to suspect that desert species behave any different from theoretically expected relationships for C_3 species and, therefore, that it is possible from field observations of Δ in leaves to infer long-term c_i/c_a values.

Direct extrapolation of carbon isotope discrimination data to water-use efficiency among plants assumes that leaf temperatures are equal. Rarely is this exactly satisfied; more typically, leaf temperatures are within several degrees of each other, depending on leaf size, thermal load, and transpiration rate. Ehleringer *et al.* (1992) evaluated the consequence of leaf temperature differences between plants and how this might affect interpretation of rankings of water-use efficiency based on Δ values alone. They calculated a near-linear relationship between leaf temperature differential and the difference in isotopic composition necessary to distinguish differences in water-use efficiency. When leaf temperature differentials between plants were $\leq 2.5^\circ\text{C}$, a 1‰ difference in Δ was sufficient to correctly and unambiguously rank plants with respect to water-use efficiency, indicating the extent to which changes in intercellular CO_2 can offset possible differences in the evaporative gradient among plants when calculating water-use efficiencies. As leaf Δ values among different species often range 4‰ on a

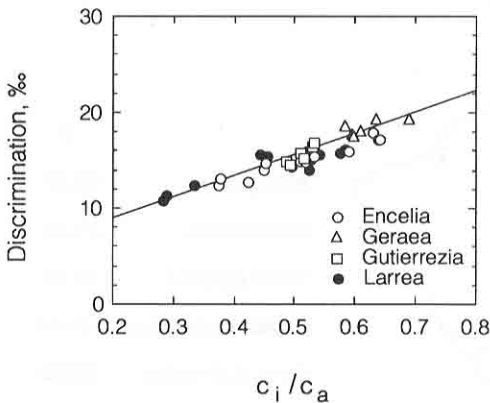


Figure 3. Observed carbon isotope discrimination values from on-line gas exchange measurements as a function of the simultaneously measured ratio of intercellular to ambient CO_2 concentrations for *Encelia farinosa* (drought-deciduous shrub), *Gerarea canescens* (annual), *Gutierrezia sarothrae* (winter-deciduous shrub), and *Larrea tridentata* (evergreen shrub). Line through the data represents the C_3 carbon isotope discrimination model, $\Delta = a + (b - a) c_i/c_a$, where a is 4.4‰ and b is 27‰. From Ehleringer *et al.* (1992).

given sampling date, Ehleringer *et al.* (1992) concluded that Δ values appeared to be a feasible approach for ranking relative short- or long-term water-use efficiency differences among aridland plants.

IV. Desert Environments Are Characterized by Low Δ Values

Surveys of the carbon isotope composition of aridland plants have indicated that most are C_3 species and are usually characterized by low c_i values (reviewed in Ehleringer, 1989); absolute Δ values appear related to individual species longevity (Ehleringer and Cooper, 1988; Ehleringer and Cook, 1991). 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 $125 \mu\text{l liter}^{-1}$ (Fig. 4). 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 now been found in a large number of species from deserts throughout the world (see Rundel, Chapter 12, this volume; Winter and Troughton, 1978; Winter, 1981; Ehleringer, 1989; Ehleringer *et al.*, 1992).

The Δ values of perennial plants from the Sonoran Desert of North America are generally not as low as those observed in plants from the Atacama Desert, likely reflecting the shorter drought duration that plants experience in the Sonoran Desert. Whereas precipitation in the Atacama Desert comes primarily during the winter and plants experience frequent extended interannual droughts, most parts of the Sonoran Desert are less arid and plants there experience drought periods that typically last less than a single year.

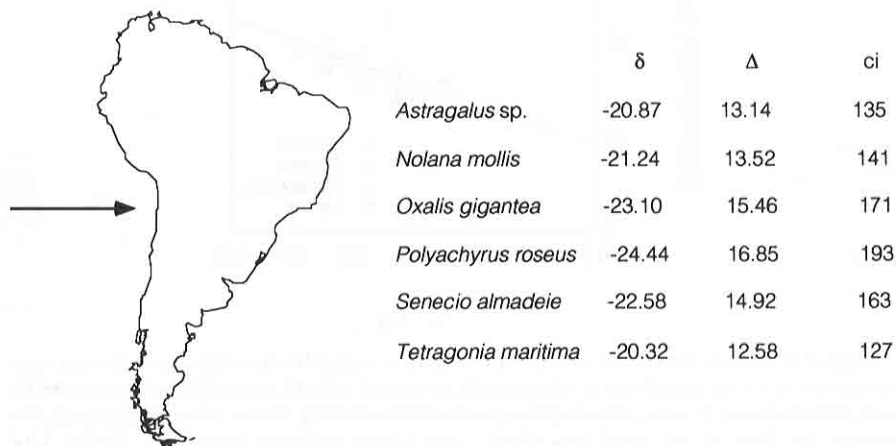


Figure 4. Carbon isotope discrimination values and corresponding calculated intercellular carbon dioxide concentrations for several species common to the Atacama Desert of northern Chile. Based on data from Ehleringer *et al.* (1993).

One pattern that emerges from studies of Sonoran Desert plant species is that carbon isotope discrimination at the species level is inversely related to life expectancy. Ehleringer and Cooper (1988) observed that longer-lived species (>50 years) had the lowest Δ values among species within the community, irrespective of the plant age when measurements were made. Short-lived perennial species (2–5 years) had carbon isotope values that were 3–5‰ lighter. Species with intermediate life expectancies (10–40 years) were intermediate in Δ value. Recently Ehleringer *et al.* (1993b) extended this observation by evaluating Δ values in five different communities across the Colorado Plateau, Mojave, and Sonoran Deserts. These observations confirmed the earlier pattern; while there is overlap among categories, there remains a clear pattern with Δ values of long-lived species being lowest and short-lived highest (Fig. 5). All of these observations represent mean Δ values ($n = 5–10$ individuals per species) for mature individuals of a species. It is worth noting that seedlings and young juveniles often do have higher carbon isotope discrimination values than adults, although relative ranking among species remains consistent (Sandquist *et al.*, in press).

Between slope and wash microhabitats, Ehleringer and Cooper (1988) observed gradients in Δ values for a species, suggesting higher Δ values for individuals occupying the wettest microhabitats (wash). These patterns were initially attributed to acclimation to soil moisture variability. However, recently Schuster *et al.* (unpublished data) have shown that there is significant local genetic differentiation across microhabitats in the desert, specifi-

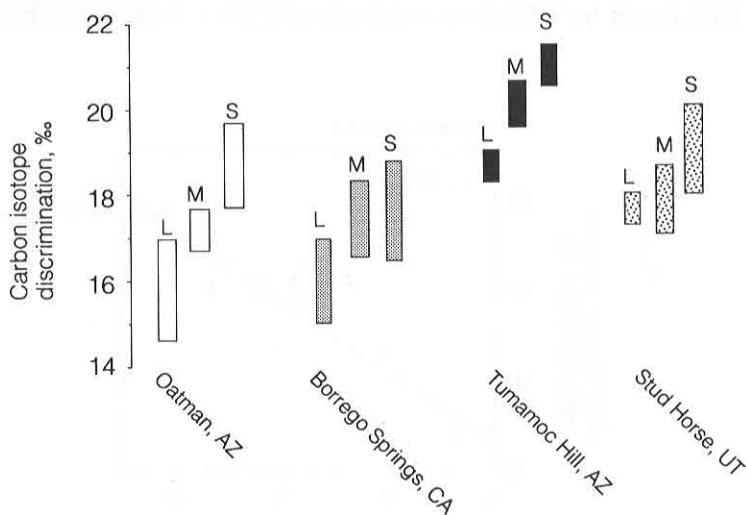


Figure 5. Ranges of carbon isotope discrimination (Δ) values of short-lived (2–5 years), medium-lived (10–40 years), and long-lived (>50 years) species at four different sites in the deserts of western North America. Data are from Ehleringer and Cooper (1988) and Ehleringer *et al.* (1993b).

cally between a wash and adjacent slope microhabitats. Carbon isotope discrimination is a highly heritable character in desert plants (Schuster *et al.*, 1992a) and the higher Δ values of wash plants likely represent local adaptation, although the significance of these Δ value differences is not yet well established.

The Δ surveys described above represent a snapshot picture in time, but these observations are consistent with longer-term observations. Ehleringer and Cook (1991) analyzed Δ values of species across years at the same site and observed a significant, consistent ranking of differences among species (Fig. 6). The slope of the relationship was not 1:1, likely reflecting an acclimation by the species to site water deficits in the different years. Likewise, the Δ values of individuals are not constant through the season, but vary with soil moisture deficit (Smith and Osmond, 1987; DeLucia and Heckathorn, 1989; Ehleringer *et al.*, 1992).

The absolute water-use efficiency through the growing season is very much influenced by both changes in c_i (measured by Δ) and by temperature changes, which influences the leaf-to-air water vapor gradient. Changes in the evaporative gradient in deserts are sufficiently large that plants are not able to maintain a constant water-use efficiency throughout the year (Ehleringer *et al.*, 1992). Instead, absolute water-use efficiency fluctuates substantially in response to seasonal temperature changes between winter, spring, and summer months. However, it is doubtful that there is any substantive advantage to the plant to maintain a constant water-use efficiency. What is likely to be of greater importance to plant fitness is its performance relative to others in the community. Thus, it is the relative ranking of Δ values that provides greater insight into any fitness component that might be related to water-use efficiency. Generally, the relative

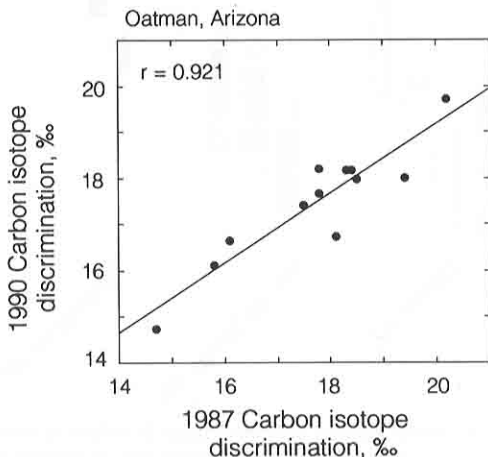


Figure 6. Mean carbon isotope discrimination (Δ) values for several species in 1987 and 1990 at a desert site near Oatman, Arizona. From Ehleringer and Cook (1991).

ranking among plants remain constant over time (Johnson *et al.*, 1990; Ehleringer and Cook, 1991; Ehleringer, 1993).

V. Interpopulation-Level Variation in Carbon Isotope Discrimination

As clearly described in many chapters within this volume, cultivar-level variation in carbon isotopic composition is known to exist within crop species. While such variation may represent the product of agricultural breeding efforts, the variation is no doubt reflective of the level of variation to be

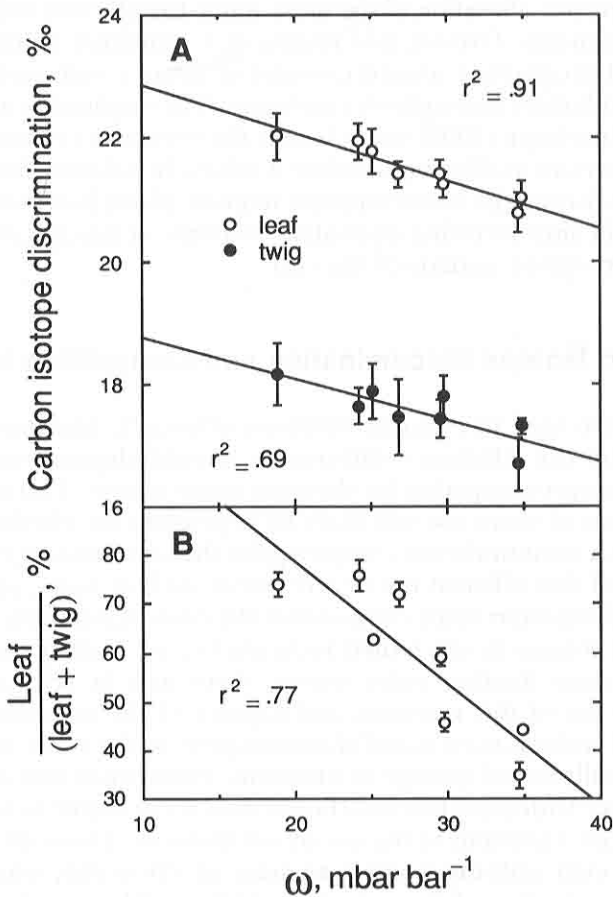


Figure 7. (A) Leaf and twig carbon isotope discrimination values for different ecotypes of *Hymenoclea salsola* field grown under uniform conditions plotted as a function of ω , the average leaf-to-air water vapor gradient weighted for those times of the year when soil moisture is available. (B) Leaf photosynthetic area as a fraction of total photosynthetic area (leaf and twig) plotted against ω . Data are from Comstock and Ehleringer (1992).

expected in native species. Interpopulation variability (i.e., ecotypic) has been examined in a limited number of species and is thought to reflect differences in environmental conditions to which plants are adapted. Comstock and Ehleringer (1992) have shown ecotypic variation in *Hymenoclea salsola*, a common shrub in the Mojave and Sonoran Deserts.

Under common garden conditions, the isotopic variation was greater than 2‰ and was negatively related to ω (Comstock and Ehleringer, 1992), the average leaf-to-air water vapor gradient weighted for periods when soil moisture was available (Fig. 7). *H. salsola* has both photosynthetic twigs and leaves, with twigs always having 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 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 toward canopies of greater water-use efficiency in climates with drier atmospheric conditions. 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 habitats where precipitation occurs during the hotter summer months, plants had lower Δ values than plants in sites receiving equivalent amounts of precipitation during cooler winter-spring periods of the year.

VI. Carbon Isotope Discrimination and Competition for Water

If Δ values are used to evaluate water-use efficiency, any significance of possible water-use efficiency differences should depend on knowing whether plants are competing for the same water source. That is, variation in the patterns of water use will likely be dependent on whether adjacent plants within a community are competing for the same limiting resource. It can be argued that efficient use of a resource, such as water, may only be adaptive if plants exert some control over the rates of soil water extraction from the soil volume in which their roots are located. If plants are competing for the same limiting water source, there may be selection against conservative use of this resource, and capture of the resource as fast as possible and perhaps even wasteful consumption of the water since it cannot be internally stored (except in succulent crassulacean acid metabolism (CAM) plants). Unfortunately insufficient data are available to assess possible intraspecific variations in the use of soil moisture. However, a number of data sets exist utilizing isotopic analyses of xylem sap, which allow a quantitative evaluation of the extent to which neighboring plants use the same or different soil moisture sources (see Dawson, Chapter 30, and Thorburn, Chapter 32, in this volume). When δD xylem sap analyses are combined with water-stress estimates, they provide a quantitative measure

of both water used by neighboring species and of the water-stress impact on plant performance due to the presence of that neighbor.

In the Colorado Plateau Desert of southern Utah, there appears to be life-form-dependent variation in sources of moisture used during the summer months (Fig. 8). Annual and herbaceous perennial vegetation appear to use the moisture from summer convection storms, whereas woody perennial species either use none or only a limited fraction of the summer-input moisture (Ehleringer *et al.*, 1991). One possible conclusion from these data is that woody and herbaceous perennials (as functional groups) were not in direct competition with each other. However, during the spring growing season and during stress periods of the year (late spring and fall), the hydrogen isotope ratios of xylem sap of woody and herbaceous perennials were similar, suggesting use of the same general water source (Ehleringer *et al.*, 1991). This does not demonstrate that they are competing for the same water on a microscale, it simply says that they are exploiting the same general moisture stratum in the soil. Yet plants in these arid zones are thought to compete for limited soil moisture (Fowler, 1986); it may be that there is competition for soil moisture among species within a life form during the summer and among species across all life forms at

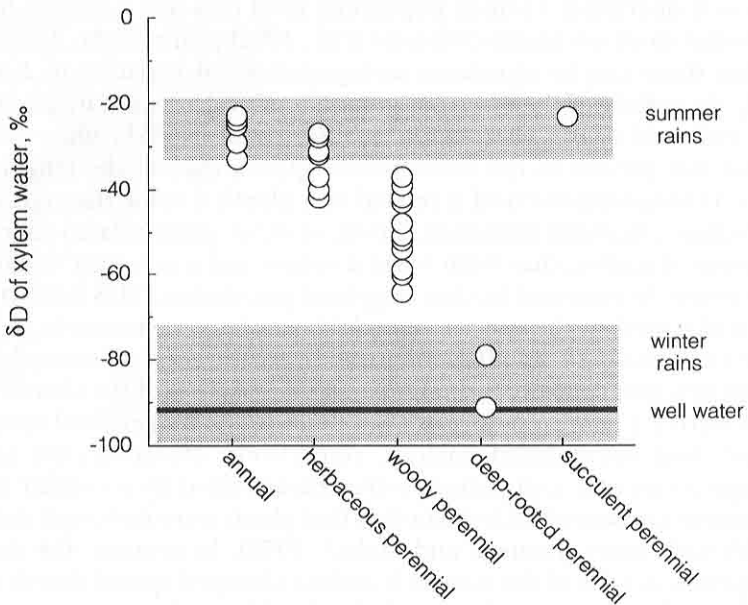


Figure 8. Hydrogen isotope ratios of xylem sap in mid-summer of different species co-occurring at Stud Horse Point, Utah, a Colorado Plateau desert site. Species are functionally grouped according to life form. Also shown are the range of summer and winter rain hydrogen isotope ratio values as well as the value for groundwater at this site. Based on data in Ehleringer *et al.* (1991).

other times of the year. As of yet, however, there is no direct experimental evidence to support these anticipated competitive patterns. High water-use efficiency (such as associated with a reduced rate of water use) might not have high survival value in such competitive environments, unless there were other overriding factors selecting for high water-use efficiency (or something else related to low Δ values). Long-term survival through extended drought periods is one such consideration and is discussed in the following section. During summer months, when herbaceous perennials have access to surface moisture minimally used by woody perennials, it is interesting to note that the Δ values of species within the community were positively associated with the utilization of summer moisture inputs. This is the water-use pattern expected if herbaceous plants were not competing with woody perennials, but with the main loss of surface moisture due to abiotic physical factors.

VII. Selection for Variation in Carbon Isotope Discrimination Values

To better understand the possible significance of Δ , it is necessary to focus on the extent of the variation found at the individual level, where natural selection is operating. Limited population level data are available, but recent studies in desert plants (Schuster *et al.*, 1992b; Ehleringer, 1992) indicate that there can be significant intrapopulation variation in Δ values (Fig. 9). In a study of the extent of population-level variance in Δ values of warm and cold desert ecosystems, Schuster *et al.* (1992b) observed that variance was greater in the shorter-lived species than in the longer-lived species. If long-term survival is related to a plant's Δ value through water-use efficiency, stomatal limitation, $\partial A/\partial E$, or other water-related characters as mentioned earlier, then both lower Δ values and a narrower variance in values would be expected in that long-lived population. This is exactly the pattern observed in the species comparisons, where variances in Δ values were 0.82 versus 0.28, and 0.92 versus 0.47 for the shorter- versus longer-lived species, respectively, and population mean values of the shorter-lived species were 1.1 and 2.2‰ higher than those of the longer-lived species in the cold- and warm-desert habitats, respectively. Moreover, the longer-lived species in each comparison were characterized by a regular spatial distribution, consistent with the notion that plants were no longer competing with each other (Fonteyn and Mahall, 1978). In contrast, the shorter-lived species in each of the comparisons had clumped spatial distributions.

Variation in Δ values at the population level is consistent over time (Fig. 10). Leaf Δ values from *Encelia farinosa* shrubs in the Sonoran Desert changed between successive sampling periods during the spring, but there was a high degree of uniformity in the relative rankings of those Δ values through time. Johnson *et al.* (1990) showed that cloned grasses also maintained the same relative rankings of Δ values when grown under contrast-

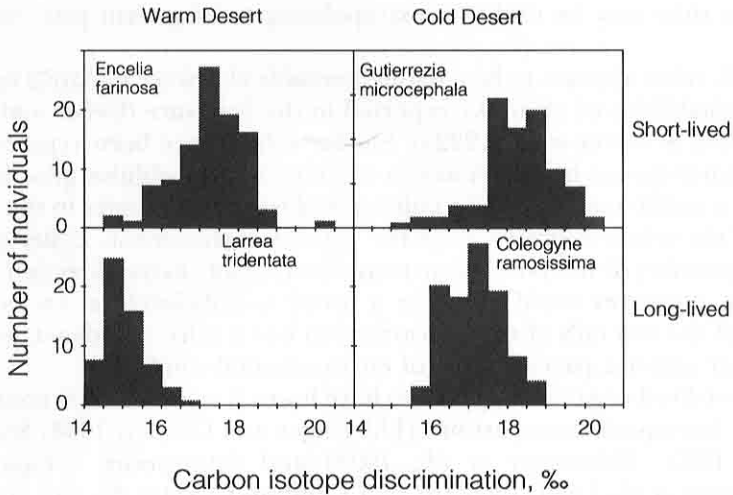


Figure 9. Frequency distribution of carbon isotope discrimination values of subpopulations of species occurring in the Colorado Plateau (cold desert) and Sonoran Desert (warm desert) that differ in their life expectancy. Data are from Schuster *et al.* (1992b).

ing soil moisture regimes in a rain-out shelter. Furthermore, many studies have reported significant correlations in the rankings of Δ values between years (Johnson *et al.*, 1990; Ehleringer and Cook, 1991). The importance of these observations is that snapshot evaluations of Δ values at a particular

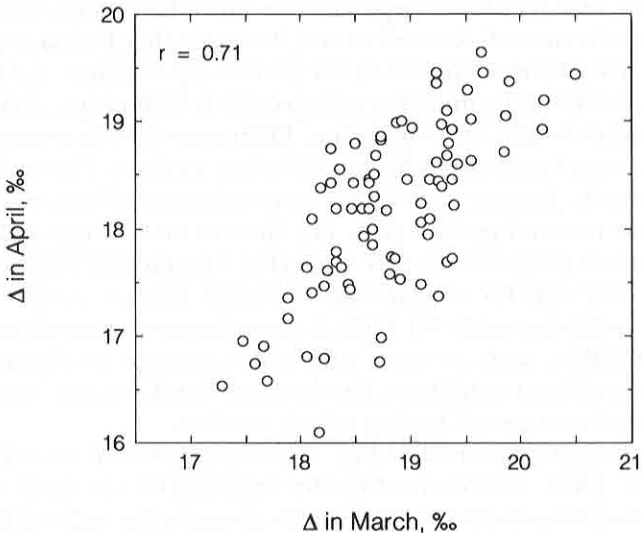


Figure 10. Carbon isotope discrimination values for individuals of *Encelia farinosa* measured under natural conditions in early March and again on newly produced leaves in late April. Data are from Ehleringer (1993).

point in time may be useful in extrapolating to long-term patterns in Δ values.

The Δ value appears to be a highly heritable character in native species, with heritabilities of up to 0.7 reported in the literature (Geber and Dawson, 1990; Schuster *et al.*, 1992a). Similar values have been reported for agricultural species by others in this volume. A large additive genetic variance in a native species may be indicative of frequent changes in the direction of the selective pressures in the natural environment. Either spatial (e.g., microsite) or temporal (year-to-year) variability in the direction of the selective pressures could result in a broad population-level variance, if either of the two tails of the Δ distribution had a selective advantage over the other under a particular set of environmental conditions.

Longer-lived organisms appear to have lower Δ values. This is consistent in both interspecies comparisons (Ehleringer and Cooper, 1988; Smedley *et al.*, 1991; Ehleringer *et al.*, 1992) and intraspecies comparisons (Ehleringer *et al.*, 1990; Richards and Condon, Chapter 29, this volume; Hall *et al.*, Chapter 23, this volume). Within *E. farinosa* populations, there is a weak but significant correlation with plant size (Ehleringer, 1993). Since reproductive output is also correlated with plant size (Ehleringer and Clark, 1988), it would appear that either low Δ results in larger plants or some critical factor eliminates high Δ value plants from the population over extended time periods. Long-term drought may be such a selective pressure.

Under natural field conditions, *E. farinosa* plants compete for water (Ehleringer, 1984). Plants with neighbors had greater water deficits (as measured by plant-water potential), maintained lower leaf areas and growth rates, and had lower reproductive rates than plants whose neighbors had been removed. Related to this, it may be that high Δ plants in the population are poorer competitors for limited soil moisture. In an experiment to evaluate the competitive and growth relationships of different Δ value genotypes within the population, Ehleringer (1993) removed neighbors from around individuals having differing Δ values. The rankings of Δ values among *E. farinosa* individuals were maintained between pre- and postneighbor-removal periods (Fig. 11). Growth rate in response to neighbor removal was proportional to Δ value (Fig. 12); no differences in growth rates were observed for similar control plants. Such a positive response suggests an adaptive value for high Δ plants in environments of high resource availability, such as years with above-average precipitation or in microhabitats without neighbors. On the other hand, it is not clear whether there are disadvantages to having a high Δ value.

The experiment presented in Fig. 12 was repeated on an adjacent hillside in 1987–1991. However, after the experiment was underway there was a period of unusually long and severe drought throughout the deserts of the western United States (1988–1990). Mortality in *E. farinosa* populations that had been monitored since the early 1980s was 50–80%. Ehleringer (1993) noted that mortality was dependent on the presence of

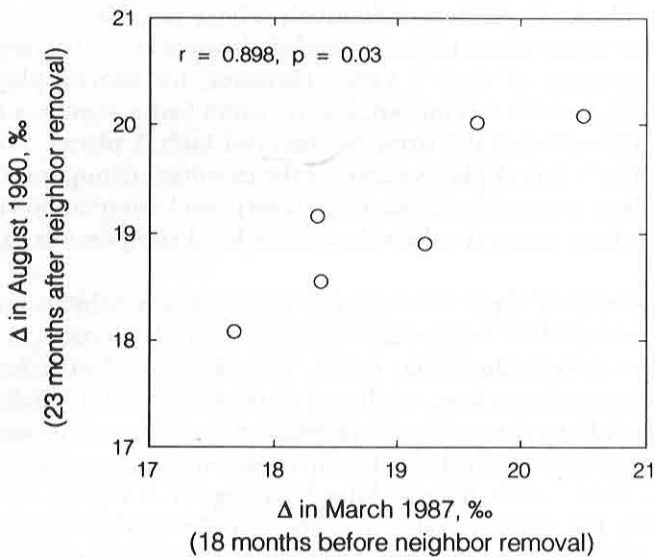


Figure 11. A comparison of carbon isotope discrimination values measured on *Encelia farinosa* individuals in the field 18 months before neighbors had been removed and 23 months following neighbor removal. Data are from Ehleringer (1993).

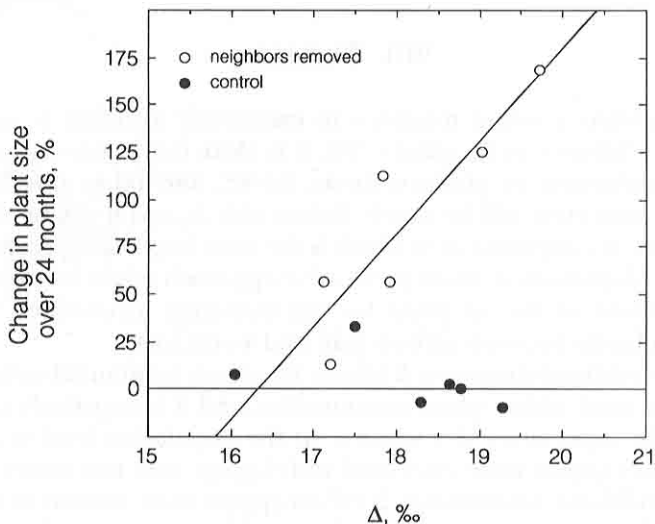


Figure 12. Growth rates of *Encelia farinosa* individuals following neighbor removal and of control plants whose neighbors were not removed as a function of the carbon isotope discrimination value of the plant. Data are from Ehleringer (1993).

neighbors. Those *E. farinosa* individuals whose neighbors had been removed (prior to the onset of the extended drought) survived the drought period, irrespective of their Δ value. However, for control plants whose neighbors had not been removed, low Δ plants had a significantly higher probability of surviving the drought than did high Δ plants. The mechanism whereby the low Δ plants survived the extended drought is unknown, but this pattern is consistent with community-level observations that long-lived species have lower Δ values than short-lived components of the community.

An implication of these results is that where desert habitats are spatially heterogeneous and/or temporally variable, natural selection against both high and low Δ individuals may occur. The deserts of North America are spatially heterogeneous (e.g., wash and slope microhabitats). Schuster *et al.* (unpublished) have shown that *E. farinosa* individuals occupying wash microhabitats are genetically distinct from those on adjacent slope microhabitats. Plants in the wash microhabitat have higher Δ values, but this may reflect either the greater water availability in this microhabitat (possible acclimation response) or the decreased life expectancy of plants occupying areas subject to frequent flash flood events (possible genetic response). The temporal variability of soil moisture availability and the likelihood for extended drought periods may select against high Δ individuals. It is possible that field observations indicating a tendency for low Δ values to be associated with the larger individuals in a population may reflect drought-induced loss of high Δ individuals over time. Long-term observations and experimental manipulations are necessary to evaluate this hypothesis.

VIII. Summary

There has been a recent tendency to exclusively associate Δ values with water-use efficiency in C_3 plants. Yet it is clear that water-use efficiency, stomatal limitations to photosynthesis, $\partial A/\partial E$, and other possible water-relations parameters will be closely linked with Δ , and it will be difficult to differentiate among these as to which is the most important parameter with respect to adaptation. A more productive approach might be to consider Δ as an indicator of the set point for gas exchange metabolism, reflecting overall tradeoffs between carbon gain and water loss.

Plants in aridlands have low Δ values. However, substantial variation in Δ values does exist within plant communities, and it is negatively correlated with the life expectancy of a species. At the population level of a species, high Δ values appear to be associated with high growth rate under noncompetitive conditions, whereas low Δ values appear to be related to the ability to persist through long-term drought conditions. Variation in Δ within a population may be related to selection for either tail of the distribution, driven by both spatial and temporal variability in habitat quality and water availability. In the future, greater emphasis should be placed on under-

standing the dynamics of populations in desert environments, where episodic events play a major role in structuring populations and landscapes.

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