Water Deficits

plant responses from cell to community

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Gas-exchange implications of isotopic variation in arid-land plants

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17.1 Introduction

At some time during their life cycle, virtually all terrestrial plants are exposed to periods of water deficit that have an impact on leaf gas exchange and possibly also on plant growth. Plants in arid-land ecosystems experience frequent water deficits brought about by extremely low soil water content and high water stress. Deserts, perhaps more than any other ecosystem, are characterized by large shifts in soil moisture availability, ranging from saturating, flood-like conditions after intense rains to extreme soil water deficit during prolonged droughts.

Deserts can be defined as having an average annual precipitation of 250 mm or less, and as regions in which the potential evapotranspiration rate exceeds precipitation input. In the driest deserts, plants are not only exposed to very dry soils, but the duration of this drought is variable, because the predictability of precipitation is low. That is, the coefficient of variation of annual precipitation increases as average annual precipitation decreases. This pattern holds whether the precipitation is considered on an annual (Ehleringer and Mooney, 1983) or on a seasonal (Figure 17.1) basis. The coefficient of variation is a measure of unpredictability, indicating that as annual precipitation decreases along an environmental gradient, the probability of extremes increases, such as long drought lasting more than a year or more, only commonly exposed to droughted conditions in which evapotranspiration rates exceed precipitation, but the repeatability of these average environmental conditions from year to year is low, reducing the likelihood that a single adaptive pattern will be optimal. High variability in life-history, interrupted by unusually wet periods. Plants occurring in arid lands are not
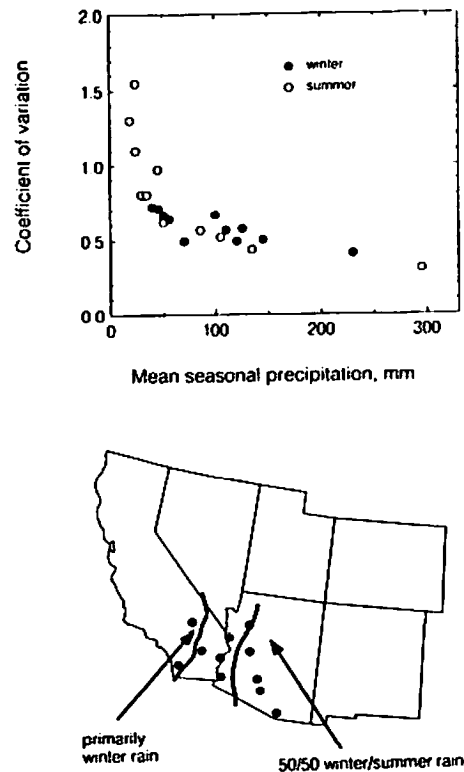
Figure 17.1. The relationship between mean seasonal precipitation and the coefficient of variation for 10 locations in the arid regions of the south-western United States. Precipitation is divided in two seasons: winter (November–April) and summer (May–October) and is based on US Weather Bureau Records between 1929 and 1979. Shown on the right are the specific locations sampled.

life-form and physiological parameters characterize many of the world's desert plant communities, and this variation may be an evolutionary response to temporal variation in water availability. It is beyond the scope of this chapter to evaluate plant performance from all deserts throughout the world, and so an effort is made to concentrate on the arid-land plants of western North America, although it is likely that the patterns discussed are applicable to all deserts.

Given the environmental constraints imposed by both low amounts of precipitation and the high interannual variability in that precipitation, how should plants respond? This chapter focuses on one particular aspect of that response, photosynthetic gas-exchange. It will become clear as this chapter develops that variation in particular gas-exchange characteristics are associated with a broader syndrome of metabolic and structural characteristics, and as a result, investigation of gas-exchange patterns can provide information on adaptive variation in life-history patterns in response to fluctuating and diverse arid-land environments. The overall theme is in understanding those key aspects of gas-exchange activity that are important determinates of plant fitness.

17.2 Intercellular CO_2 concentration as a set point for gas-exchange metabolism

17.2.1 Flux versus set point

Gas-exchange responses at the leaf level can be viewed from two perspectives: what changes absolute flux rates and what controls flux rates. Changes in maximum photosynthesis (A) and transpiration (E) rates in response to maximum photosynthesis (A) and transpiration (E) rates in response to soil moisture availability (or any other measures of plant water status for that matter) have been described in numerous studies (Ehleringer and Mooney, 1983; Lange, et al., 1976; Smith and Nobel, 1986; Smith and Nowak, 1990). While absolute photosynthesis and transpiration rates among species may exhibit substantial variation, these flux rates decrease as water stress increases. Variation in maximum flux capacities is loosely associated with life form, with annuals often having higher rates than perennials (Mooney and Gulmon, 1982; Mooney et al., 1976). 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, 1978) that generalities of this type cannot be drawn with a high degree of certainty. 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 ultimate plant fitness, although the parameters are ultimately linked with each other (Figure 17.2). Continuous monitoring of photosynthetic activity would, of course, provide a stronger correlation with productivity, but is impractical on more than a few individuals. In order to view gas-exchange processes over a broader range of individuals and species, other measures are needed that can be more easily obtained on a wide range of individuals and which encompass an extended period of time.

An alternative approach to examining absolute flux rates and their impact on gas-exchange performance is to examine control points or set points in gas-exchange activity. Set points may be more stable than absolute flux rates, thereby providing more information in response to stress. That is, whereas flux rates will vary greatly in response to resource levels on the short term or to stress levels on the long term, changes in the set point may be substantially less. 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 Figure 17.2 is the intercellular CO_2 concentration (c_i), which represents a balance between rates of inward CO_2 diffusion (controlled by stomatal conductance) and CO_2 assimilation (controlled by photosynthetic light/dark reactions). In principle, there is no expected relationship between flux rate and reactions.
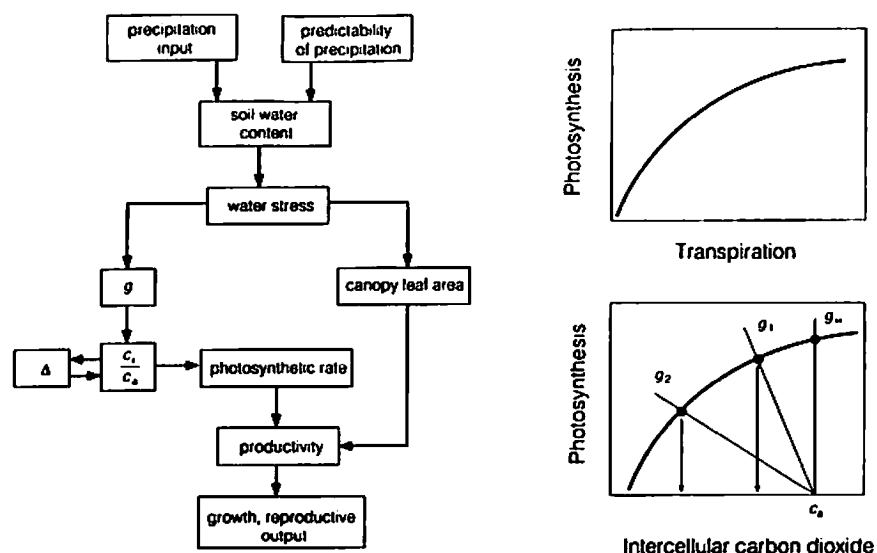
Figure 17.2. *A conceptual model of plant productivity; ultimately growth, reproductive output and plant fitness are influenced by water stress and several of the gas-exchange characters that influence photosynthetic rate.* Δ, *Carbon isotope discrimination;* c, *and* c_a *are the intercellular and ambient* CO_2 *concentrations, respectively;* V, *is the transpiration rate; and* g *is the leaf conductance to water vapour.*

and set point. A primary advantage of set point analysis over flux rate would arise if set points remained relatively fixed among plants under non-stressed conditions, and if, in response to abiotic stresses, there were no changes in the relative rankings of plants. A second advantage would be if there were methods for directly assessing this set point that were more easily measured than continuously monitoring absolute flux rates.

17.2.2 Carbon isotope discrimination as a measure of intercellular carbon dioxide concentration

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 (Farquhar *et al.*, 1982; Farquhar and Richards, 1984; Farquhar *et al.*, 1989; see Chapter 12). 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:

$$\Delta = a + (b - a)\frac{c_i}{c_a} \qquad 17.1$$

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.

The leaf carbon isotopic composition has been used to estimate water-use efficiency (ratio of photosynthesis to transpiration) in C_3 plants (Farquhar *et al.*, 1989). To associate the Δ value only with water-use efficiency is a mistake, since other water relations parameters are also directly related to the c_i value. For instance, both λ, a set point describing the optimal pattern of stomatal behaviour that maximizes carbon gain for a given amount of water loss (Cowan and Farquhar, 1977), and l_s, the extent of stomatal limitation on photosynthesis (Farquhar and Sharkey, 1982; Jones, 1985; see Chapter 12), are directly related to the c_i value of a leaf. Moreover, it is not clear just what water-use efficiency means to plant performance outside of an agronomic context. A more productive approach might be to consider c_i as a measure of the metabolic set point for gas exchange, providing an integrated measure of the multitude of factors that relate both CO_2 uptake and water loss in plants.

17.3 Field observations of carbon isotope discrimination

Is there any evidence to indicate that analysis of c_i values provides new information on gas-exchange metabolism of desert plants; in particular, information suggesting that c_i values are in some way measures of a metabolic set point and associated with specific life-history patterns or a syndrome of morphological and physiological characters?

### 17.3.1 Community-level patterns

In arid-land community-level analyses, carbon isotope discrimination values were related to life expectancy of that species. Ehleringer and Cooper (1988) observed that Δ values were inversely correlated with longevity for Sonoran Desert species. Carbon isotope discrimination values varied by more than 5‰ among different longevity groups (Figure 17.3). Smedley *et al.* (1991) observed a similar pattern between annuals and herbaceous perennials in a Great Basin grassland; similar trends can be extracted from the shrub-tree species data of
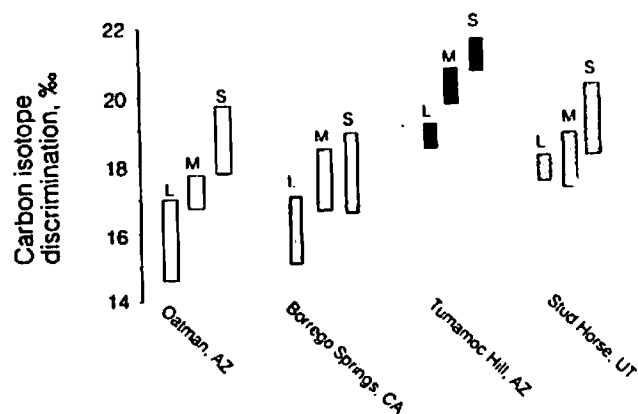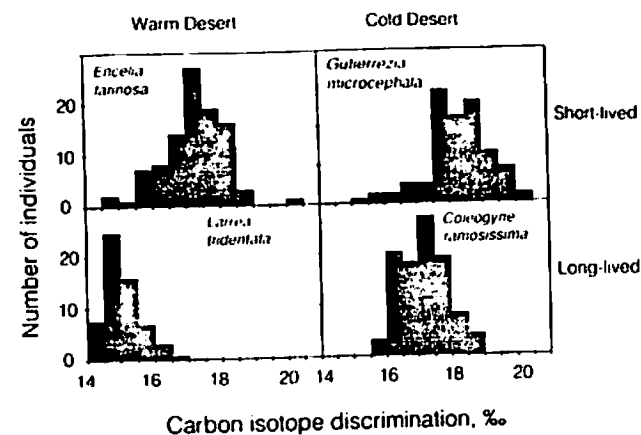
Figure 17.3. Ranges of carbon isotope discrimination (Δ) values of short-lived (2–5 years), medium-lived (10–40 years) and long-lived (> 50 years) species at four different sites in the deserts of western North America. (Data are from Ehleringer and Cooper, 1988, and Ehleringer, unpublished.)

DeLucia et al. (1988). More recently, Ehleringer (unpublished) extended his earlier observations, demonstrating that similar Δ-value rankings were maintained among different life-history groups across a broad range of desert communities throughout the Mojave and Sonoran Deserts.

Variations in leaf carbon isotope discrimination among species arise because of both genetic and environmental factors (Ehleringer et al., 1993; Farquhar et al., 1989) and it is not clear from Figure 17.3 just how large differences might be in the two components. Although the previous observations represented single snapshots-in-time of the distribution of Δ values within a community, variation in the rankings of species through time appears to be minimal. Ehleringer and Cook (1991) examined 12 species at the same site in the Sonoran Desert 3 years apart; they observed virtually no difference in the rankings among species over that period (Figure 17.4). From other studies with agricultural and rangeland species, carbon isotope discrimination measured over different time intervals within a single season or across seasons has shown interseasonal variation. This variation in the absolute Δ values has
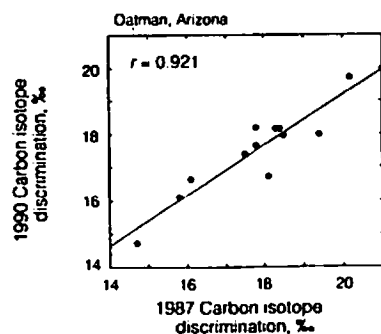
Figure 17.4. Mean carbon isotope discrimination (Δ) values for different species in 1987 and 1990 at a Sonoran Desert site near Oatman, Arizona. (From Ehleringer and Cook, 1991.)


Carbon isotope discrimination, ‰

Figure 17.5. 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., 1992.)

been attributed to abiotic acclimation, but there were no significant changes in the relative rankings of different plants (Ehleringer, 1990; Ehleringer et al., 1990; Farquhar et al., 1989; Johnson et al., 1990). Thus, if Δ values are used as an indication of a photosynthetic gas-exchange set point, then the set point appears to be relatively stable over time in terms of differences that are maintained between species and/or cultivars within species.

17.3.2 Intraspecific variation

A greater understanding of the potential significance of Δ might come from looking at variation among individual plants. Evaluating interplant variation in gas-exchange characteristics has had limited success in the past, mostly because variations in characteristics, such as photosynthesis, are usually so small that it is difficult to detect individual differences and because equipment limitations restrict the number of simultaneous measures that can be obtained. However, stable isotopes offer an approach to overcome those limitations, because of the integrating nature of the measurement. Dawson and Ehleringer (1993), Geber and Dawson (1990) and Schuster et al. (1992) all observed significant intrapopulation variation in Δ values. In a study of the extent of population-level variance in Δ values of warm and cold desert ecosystems, Schuster et al. (1992) observed that variance was greater in populations of the shorter-lived species than in the longer-lived species (Figure 17.5). If there is a relationship between longevity and Δ value as implied in Figure 17.3, then lower Δ values would be expected in that longer-lived population. Over time, natural selection may favour genotypes with specific Δ values, which would then result in a narrower variance in the longer-lived species. Both trends
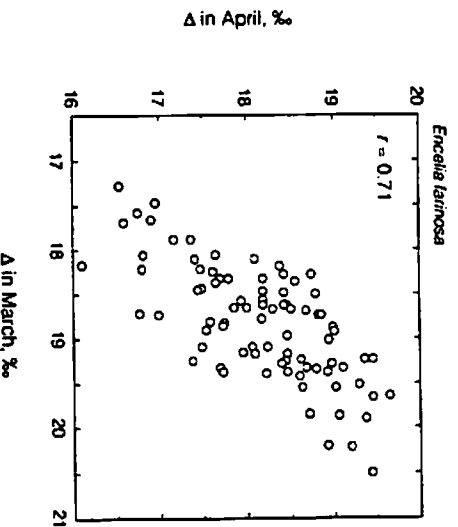
are observed in the species comparisons, where variances in Δ values were 0.82 vs. 0.28 and 0.92 vs. 0.47 for the shorter- vs. longer-lived species, respectively, and population mean values were 1.1 and 2.2‰ higher than that of the longer-lived species in the cold- and warm-desert habitats, respectively.

As plants acclimate to variations in soil water availability, there can be changes in Δ values (Ehleringer et al., 1993; Guy et al., 1980; Smedley et al., 1991). When newly produced leaves were sampled at two time intervals in spring on neighbouring plants within a community, Ehleringer (1993) noted that all individuals had somewhat lower Δ values on the second sample date (Figure 17.6). This response is likely to represent an acclimation to drought, as has been noted by others (Farquhar et al., 1989; Guy et al., 1980). With respect to genotype rankings, they remained essentially constant throughout the season. There was a strong, significant correlation between Δ values at the two sampling periods. Again this indicates that at both the intraspecific and interspecific levels (as shown in Figure 17.4), differences in Δ values among different individuals are maintained over time. One possible complication when interpreting these data is that seasonal variations in Δ values could be determined by either abiotic factors (acclimation in response to soil water stress development) or biotic factors (presence of neighbouring plants influencing local soil water conditions). Ehleringer (1993) examined long-term variations in Δ values in a monospecific stand of Encelia farinosa before and after neighbour removal (Figure 17.7). The rankings among plants remained constant, reinforcing the notion that Δ is a measure of the relative metabolic set point largely independent of neighbour effects.

The notion of Δ as a measure of set point and an indication of life-history patterns is further supported by studies within different agronomic species. Maturity date among cultivars under uniform garden conditions has been shown to be inversely related to Δ value for several crop species (Ehleringer et al., 1990; Richards and Condon, 1993; White, 1993). Variation in flowering

Figure 17.6. *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 at a Sonoran Desert site near Oatman, Arizona. (Data are from Ehleringer, 1993.)*
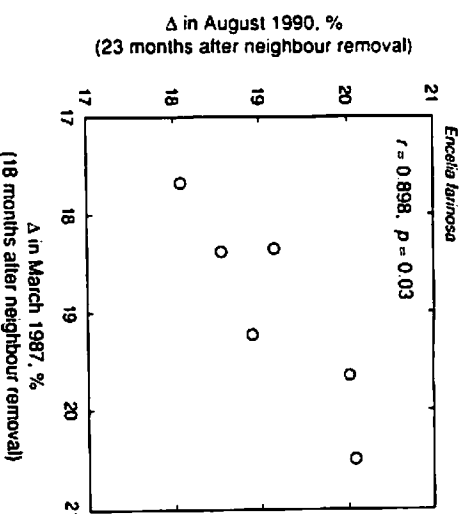
Encelia farinosa
r = 0.71
Δ in April, ‰
Δ in March, ‰

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date likely reflects carbon gain, allocation and developmental rate differences among genotypes. Since the rankings of Δ values of different genotypes within a crop species remained constant through development within a growing season, the constant Δ rankings among genotypes suggest that the relative set point has remained fixed and would therefore be a useful comparative parameter when examining metabolic differences within a species. That Δ values are tightly correlated with small differences in flowering dates may be coincidental or, more likely, may be indicative of an overall metabolic and morphological syndrome, in which the characters associated with rapid growth and early maturity allow plants to complete their life cycle before the onset of stress.

17.4 Consequences of carbon isotope discrimination differences among neighbours

17.4.1 Carbon isotope discrimination and growth

Substantial variation in Δ values of plants within a natural population would arise if

(1) there are substantial differences in Δ values among populations and significant gene flow between populations, even if Δ values are unimportant to overall plant performance and not under any strong selective pressure; or

(2) there is either spatial or temporal variation in environmental characteristics within a small location that selects for divergent Δ values.

In the first possibility, genetic drift would be expected ultimately to fix Δ values within an isolated population, and variance within a population would

Figure 17.7. *A comparison of carbon isotope discrimination values measured on Encelia farinosa individuals in the field 18 months before neighbours had been removed and 23 months following neighbour removal at a Sonoran Desert site near Oatman, Arizona. (Data are from Ehleringer, 1993.)*

Encelia farinosa
r = 0.898, p = 0.03
Δ in August 1990, %
(23 months after neighbour removal)
Δ in March 1987, %
(18 months after neighbour removal)

only be maintained through gene flow with neighbouring populations. In both possibilities, variation in Δ values would be expected, but it is only the latter possibility that offers an explanation for differences in the variance of Δ values between longer- and shorter-lived species. Since Δ values are an indication of a set point for gas exchange that involves water loss, it is conceivable that some aspect of stomatal physiology, water-use efficiency, water-use maximization or drought tolerance is under strong selective pressure, particularly in arid lands.

While the evaporative gradient may place some restrictions on water loss rates, an increased efficiency in the use of soil water is only reasonable if plants can exert some control over the rates of soil water extraction from the soil volume in which its roots are located. If plants are competing for the same limited water, there may be selection against conservative water use, and for rapid resource capture, since that water cannot be stored internally, except in succulents. On this basis, arguments could be constructed to suggest that under competitive situations low Δ-value genotypes may be selected against, and under low competitive environments high Δ-value genotypes would be selected against. From studies of Mojave and Sonoran Desert plants, it is clear that not only is water present in limiting quantities, but that there is strong competition for that water resource (Fowler, 1986). Why then do plants persist that are not conservative in their use of water unless water-use efficiency and growth are unrelated?

Viewed from a different perspective, an alternative argument might be advanced that would lead to the opposite conclusion. For example, if the Δ value is a relatively fixed control point for metabolism, other aspects of growth or carbon allocation may be affected so as to allow the plant to maintain that Δ value. In particular, carbon allocation to root versus shoot growth may be influenced by a plant's Δ value. Virgona et al. (1990) provided evidence in support of this idea by showing that in sunflowers there was a strong positive correlation between Δ and the ratio of leaf area to root area (τ). Genotypes with high Δ values also tended to have high τ values.

Consider the possibility that carbon allocation patterns exhibited substantial plasticity, while the Δ value was relatively invariant. If the shoot to root allocation pattern was influenced by a plant's Δ value, then competition for limiting water should influence that pattern. Virgona et al. (1990) showed that under well-watered, single-pot conditions τ was positively correlated with Δ as suggested in Figure 17.8. If Δ is a relatively fixed control point, then under competition for water, plants with high Δ values will have to allocate proportionally more carbon to root growth in order to get sufficient water to maintain that Δ value, which is effectively describing the rate of carbon gain to water loss (Figure 17.8). Reallocating carbon to below-ground structures will result in a reduced above-ground growth rate, suggesting that high Δ-value genotypes would be selected against under water-competitive situations. If this model is correct, then high Δ-value plants


Figure 17.8. Hypothesized relationship between shoot-to-root areas (τ) among genotypes of a species and leaf carbon isotope discrimination (Δ) as a function of soil moisture availability. The two lines represent hypothesized responses to situation with and without water competition.
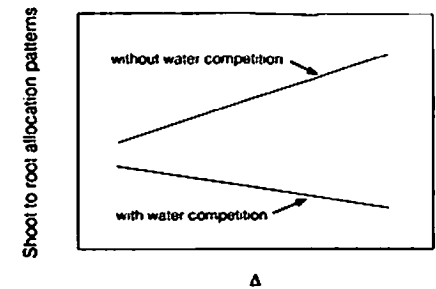
should exhibit greater plasticity in response to changes in water stress induced either by abiotic or biotic factors.

17.4.2 Competitive interactions

To address the possibility that high and low Δ-value genotypes would respond differentially to water availability, Ehleringer (1993) examined relationships between growth, water relations and Δ in monospecific stands of Encelia farinosa under natural and neighbour-removed situations. In a series of long-term observations, plant performance was measured on individuals varying in their Δ value. All neighbours were removed around some individuals for a distance of 2 m, which was thought to be the longest possible lateral root extension; other similar-sized plants remained with neighbours as controls. Growth rate was measured as the change in plant size during the experimental period, which was characterized as having average to above average precipitation inputs. While plants with neighbours exhibited essentially no growth during this period, irrespective of their Δ value, plants without neighbours grew substantially and growth was related to the plant's Δ value (Figure 17.9). These data indicate that plants not competing for limiting soil moisture grew at a faster above-ground rate, and that Δ was in some way associated with the capacity of a plant to respond to these less restricting soil moisture conditions. One possibility is that Δ is correlated with leaf conductance, as has been shown for a number of species (Condon et al., 1987; Ehleringer, 1990; Ehleringer et al., 1990). If that were the case, conductance-driven differences among plants could result in increased photosynthesis and growth of high Δ-value plants exposed to reduced water stress. An alternative but not exclusive explanation is that carbon-allocation patterns within plants changed in response to increased soil moisture availability, as hypothesized in Figure 17.8. The available data do not allow us to distinguish among these possibilities, but only to conclude that under reduced competition and greater soil moisture availability high Δ-value plants have a greater growth rate than low Δ-value plants. Ehleringer (1984) and Ehleringer and Clark (1988) showed that carbon gain and growth rate differences in Encelia farinosa translated into higher fitness values, indicating a selective
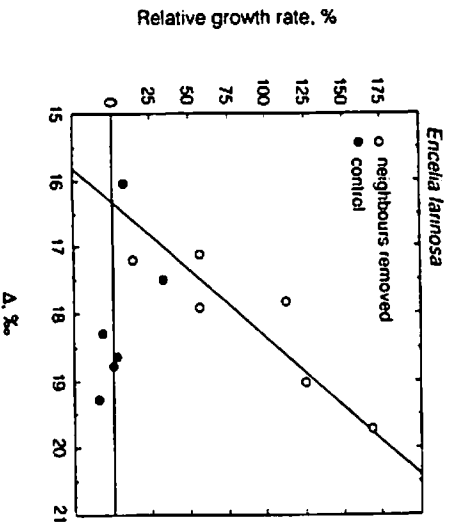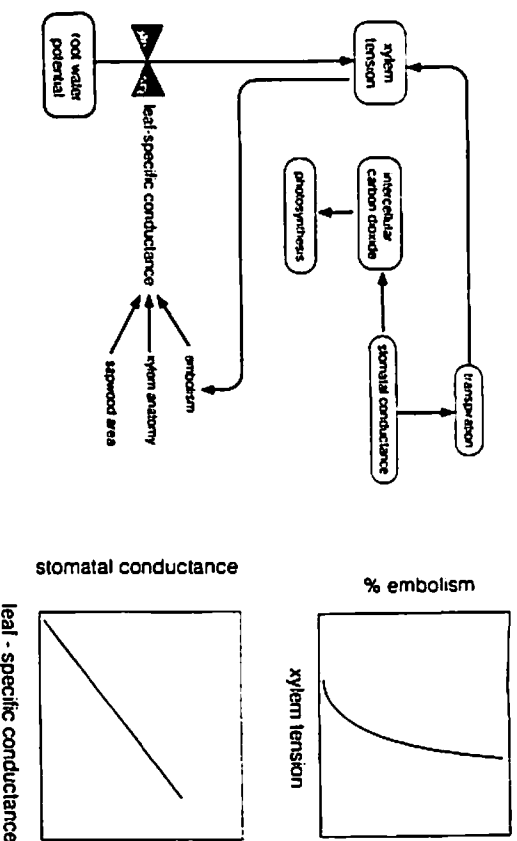
Figure 17.9. Growth rates of Encelia farinosa individuals following neighbour removal and of control plants whose neighbours were not removed as a function of the carbon isotope discrimination value of the plant at a Sonoran Desert site near Oatman, Arizona. (Data are from Ehleringer, 1993.)

advantage for high Δ-value plants under greater water availability conditions. The question still remains as to why, then, are low Δ-value individuals maintained within a population?

17.4.3 Impact of long-term drought

A high Δ value may not be without disadvantages, particularly if the Δ value is strongly correlated with leaf conductance to water loss. 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 (see also Chapter 7). Given equal stem hydraulic conductances between two genotypes, a relatively high stomatal conductance by one should result in an increased transpiration rate and a decreased leaf water potential in that genotype (Figure 17.10). As soil moisture availability decreases, 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 (see Chapter 7). In theory, these cavitation events could restrict water flow sufficiently and result in stem death. This may in part be the explanation for why suffrutescent growth (many stems emerging from a common root base) is so common among arid-land shrubs. Long-term droughts of 6–18 months occur frequently in arid lands and can result in high shrub mortality. Ehleringer (1993) monitored survival in *E. farinosa* shrubs differing in Δ values through a year-and-a-half drought in the Sonoran Desert. As with the previous competition experiment, plants differing in their Δ value were divided into two groups: control plants in a naturally

occurring monospecific stand and individuals within that stand that had their neighbours removed. In response to the drought, there was significant mortality. More than 60% of the individuals in the control population died. On a neighbouring hillside used for long-term demographic studies, almost 50% of the *E. farinosa* population died (Ehleringer, unpublished). Of interest was that, irrespective of Δ value, none of the individuals without neighbours died during the drought. Only those plants competing for water (those with neighbours) died during the drought. Plant size (Student's *t* test, *p* = 0.949) was not a factor related to mortality or survival through the drought. However, mortality was significantly related to a shrub's Δ value. Plants surviving the drought had significantly lower Δ values than those that died (Student's *t* test, *p* = 0.022).

These data indicate an advantage to low Δ-value plants and suggest possible trade-offs between conditions favouring high and low Δ-value plants within a natural population. Genotypes with low Δ values may persist through long-term drought or competitive situations better than high Δ-value genotypes. However, under conditions of high resource availability, induced by either microsites without neighbours or possibly wet years, the high Δ-value genotypes significantly outperform the low Δ-value genotypes. Given the temporal variability in precipitation between years and spatial variability in microhabitat quality, variation in Δ values will be maintained in the population.

Figure 17.10. 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. Shown at the right are the expected relationships between xylem tension and extent of embolism and between the leaf-specific conductance and stomatal conductance.

17.5 Implications of carbon isotopic variation for community structure

The idea of trade-offs associated with Δ value and habitat quality has many ramifications at both the intra- and interspecific levels. At the population level, the previous results imply that variability should be a function of the advantage to be gained by a high growth rate offset by the potential disadvantages associated with drought-induced mortality. Schuster *et al.* (1992) showed that the extent of variability with populations of longer- and shorter-lived desert species was inversely related to the life expectancy of that species. This is exactly the pattern expected in the predictions taken from Figures 17.2 and 17.10. Individuals of longer-lived species will be exposed to more drought events, reducing the likelihood that a high Δ-value individual could persist through time in the population.

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. Under common garden conditions, the isotopic variation was greater than 2‰ and was negatively related to ω, the average leaf-to-air water vapour gradient weighted for periods when soil moisture was available (Figure 17.11). *Hymenoclea salsola* has both photosynthetic twigs and leaves, with twigs always having lower ω, and Δ values. Since leaves and twigs both have small diameters, resulting in
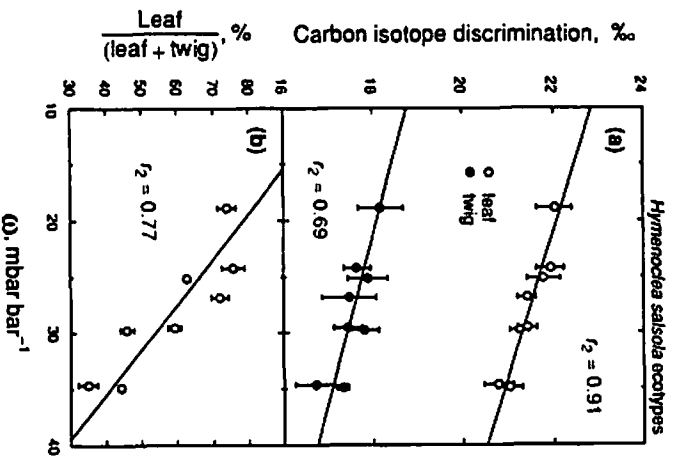
strong convective exchange and equivalent tissue temperatures, twigs also always have a greater water-use efficiency (Comstock and Ehleringer, 1988). The fraction of leaf to twig photosynthetic areas is also negatively related to ω, resulting in plants from drier habitats (atmospheric drought) having 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 trade-offs 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).

17.6 Responses to seasonal moisture inputs

Recent evidence suggests that not all arid-land plants have the capacity to utilize summer moisture inputs. If summer moisture is a small fraction of total annual precipitation, then plants might not invest in shallow roots and thus would not be expected to utilize much of these infrequent precipitation events. That is, in arid regions with dry summers, carbon may be allocated for deep root growth; roots involved principally in water uptake are not active in the surface layers, but occur only in deeper soil layers where moisture is persistent during summer periods. Surface roots may be involved only in nutrient uptake and represent a relatively small proportion of the belowground structures. As such, water taken up with nutrients would not be detected since it represents such a small fraction of the total water uptake. When infrequent summer precipitation events do occur, the lack of an active upper root layer would prevent significant water uptake from that upper soil layer. As average summer precipitation increases along a precipitation cline, at some point precipitation becomes sufficiently predictable, or achieves some minimal threshold, so that plants develop a dimorphic root system (Figure 17.12) consisting of two zones of active roots, one in the upper soil layers capturing summer precipitation and a second deeper zone for utilizing the more reliable groundwater. The presence of a dimorphic root system depends upon the predictability of moisture sources and the costs associated with producing and maintaining these roots. Although fine root turnover at a high rate may represent a significant cost to plants in their carbon balance (see Chapters 10 and 13), differential root development for water uptake could put plants at
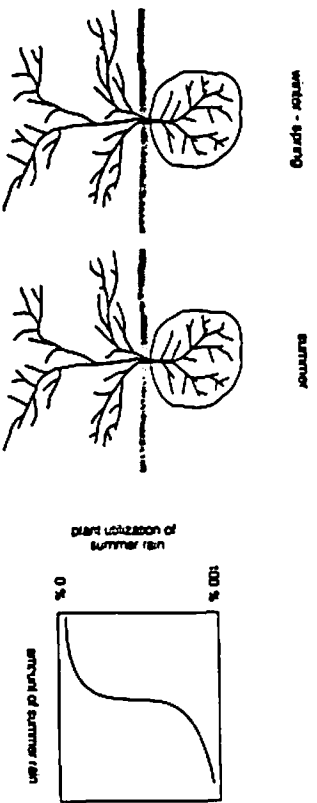

Figure 17.11. (a) *Carbon isotope ratio of leaves and twigs from different ecotypes of Hymenoclea salsola grown under common garden conditions as a function of ω, the leaf-to-air evaporative gradient weighted for seasonal precipitation input.* (b) *The ratio of leaf area as a proportion of total photosynthetic area plotted as a function of ω.*

Figure 17.12. *Left: a drawing of the hypothesized distributions of utilized water by perennial shrubs in arid-land regions during winter–spring and summer growing seasons. Specifically, it is anticipated that shrubs growing in regions with infrequent summer rains will have limited capacity to utilize those precipitation events. Right: a conceptual model of the anticipated relationship between the capacity of a desert shrub to utilize summer precipitation as a function of the amount of summer precipitation received during the summer growing season.*

a selective advantage if the reliability of surface moisture is variable. Some roots must remain active near the surface, because of their role in active mineral nutrient uptake rather than water uptake *per se* (functional specialization).

Analysis of the hydrogen isotope composition (δD) of xylem sap in plants provides a succinct measure of water sources. Groundwater and recent precipitation usually differ markedly in δD signal because of the climatic factors controlling evaporation and precipitation at different times of the year depending on geographical location (Ehleringer et al., 1993; Flanagan and Ehleringer, 1991). Flanagan and Ehleringer (1991) evaluated water uptake patterns in a semiarid pinyon–juniper ecosystem site in southern Utah, which received between 30 and 40% of its annual moisture during the summer months. *Chrysothamnus nauseosus* (rabbitbrush) and *Juniperus osteosperma* (Utah juniper) did not utilize summer precipitation during the year of study: the δD of xylem sap remained close to that of the groundwater (effectively the same as the winter recharge precipitation). In contrast, *Pinus edulis* (pinyon pine) and *Artemisia tridentata* (sagebrush) did utilize summer precipitation. In a follow-up study, Flanagan et al. (1992) showed that the Utah juniper would take up summer precipitation in some situations, but that the xylem sap of the rabbitbrush retained the same δD as the groundwater source.

Gregg (1991) provided evidence of a cline in the capacity of juniper trees to respond to summer moisture. Along a geographical gradient, where the fraction of summer precipitation varied between 18% and 40%, Gregg (1991) observed that juniper trees on sites with reliable summer precipitation utilized summer precipitation, whereas those on predictably dry summer sites did not respond to summer precipitation (Figure 17.13). It is not surprising that there is ecotypic variation in root structure along a geographical gradient, but the suggestion of a lack of an inducible response to summer rains (Gibson and
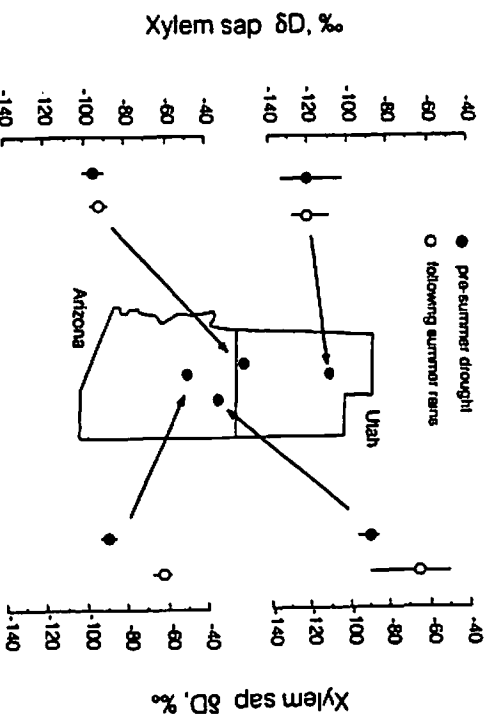
Nobel, 1986) by these arid-land plants is unusual. In a related study from the Mediterranean-climate macchia of Italy, Valentini et al. (1992) observed that *Pistacia lentiscus*, *Phyllirea angustifolia* and *Quercus ilex* responded to summer precipitation, whereas *Q. pubescens* and *Q. cerris* utilized soil moisture from greater depths. Species that did not respond to summer precipitation had xylem sap δD values equivalent to that of the groundwater even after a summer rain event.

Another example of differential species response to summer precipitation was given by Ehleringer et al. (1991) in an investigation of water sources of desert species in southern Utah, at a site which received 45% of the annual precipitation during the summer. Whereas the annual species and the single crassulacean acid metabolism (CAM) succulent species within the desert community responded and fully utilized summer moisture inputs, that was not the case for perennial species. Herbaceous species utilized summer precipitation more than did woody perennials, and a number of perennials appeared not to utilize summer precipitation at all. Moisture at deeper depths was derived primarily from winter and spring recharge events, and this was reflected in the observed groundwater δD values. Spring measurements of water sources confirmed that all species were using the same water source at that time. Thus, it appears that annual, herbaceous and perennial species within the community compete for the same limiting source of water in one growing season (spring), but that herbaceous species have preferential access to a second water source (surface moisture) during the summer growing season.

Figure 17.13. *Hydrogen isotope ratios of xylem sap from Juniperus osteosperma collected before and after summer rains at various location along a north-to-south gradient of increasing summer precipitation in the Intermountain West of the United States. (Data are derived from Gregg, 1991.)*

17.7 Conclusions

Intercellular carbon dioxide concentration (c_i) can be viewed as a set point for gas-exchange metabolism. The carbon isotope discrimination value (Δ) of a leaf is the assimilation-weighted estimate of c_i. Field examination of Δ values in desert plant species reveals a negative correlation with life expectancy. Intraspecific variation in leaf Δ values appears to represent trade-offs between increased growth capacity of high Δ-value genotypes under water-sufficient conditions and increased survival of low Δ-value genotypes under water-limited conditions.

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