Variation in leaf carbon isotope discrimination in *Encelia farinosa*: implications for growth, competition, and drought survival

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Abstract. Population-level variation in the leaf carbon isotope discrimination (Δ) values was examined in *Encelia farinosa*, a common Sonoran Desert shrub. There was approximately a 2‰ range in Δ values among different plants. These differences in Δ values among neighboring plants were maintained through time, both under conditions when neighbors were present and after neighbors had been removed. Individuals with high Δ values were found to have an accelerated growth rate when these plants were released from competition for water. Individuals with low Δ values were better able to persist through long-term drought. These data suggest possible tradeoffs between conditions favoring high- and low-Δ-value plants within a natural population. Given the temporal variability in precipitation between years and spatial variability in microhabitat quality in the Sonoran Desert, variation in Δ values among *E. farinosa* plants will be maintained within a population.

Key words: Carbon isotope ratio – Desert ecology

Intercellular CO_2 concentration (c_i) has been suggested as a key parameter in plant gas exchange, indicative of a metabolic set point and of the relative gas exchange constraints imposed by water and nutrient limitations (Ehleringer 1993a, b). As a set point, long-term estimates of c_i may provide an integrated measure of the biochemical and structural factors that relate both CO_2 uptake and water loss in plants. Over extended 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, 1989; Farquhar and Richards 1984). 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) and Farquhar and Richards (1984) has been the most extensively tested. In its simplest form, their expression for discrimination in leaves of C_3 plants is

$$\Delta = a + (b-a)\frac{c_i}{c_a},\qquad(1)$$

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.

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 perhaps to underestimate the importance of this character, since other aspects of water relations are also directly related to the c_i value. For instance, both λ, a set point describing the optimal pattern of stomatal behavior that maximizes carbon gain for a given amount of water loss (Cowan 1977), l_s, the extent of stomatal limitation on photosynthesis (Farquhar and Sharkey 1982; Jones 1985), and stem hydraulic conductivity (Meinzer et al. 1993) are directly related to a leaf's c_i value. Moreover, it is not unambiguously 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 (Ehleringer 1993a, b), providing an integrated measure of the biochemical and structural factors that relate both CO_2 uptake and water loss in plants.

At the species level, variation in Δ values appears to be related to life-history patterns. Ehleringer and Cooper

(1988) observed that Δ values of different plant species were inversely correlated with longevity in a Sonoran Desert community. Similar trends were noted by Smedley et al. (1991) for annuals and herbaceous perennials within a Great Basin grassland. Within a single species, Geber and Dawson (1990) *(Polygonum arenastrum)*, Ehleringer et al. (1990) *(Phaseolus vulgaris)*, and Richards and Condon (1993) *(Triticum aestivum)* reported that age to flowering among different families or cultivars was inversely related to leaf carbon isotope discrimination. Few data are available to examine carbon isotope variation within single populations. In the single study available, Schuster et al. (1992a) reported significant intrapopulational variation in Δ for four shrub species, but could not partition that variation into environmental versus genetic components, although a previous study had noted a high heritability for Δ (Schuster et al. 1992b).

A greater understanding of the potential significance of Δ might come from looking at variation among individual plants and its consequence for performance in the field. In this study, I determined the variation in Δ values among individuals of *Encelia farinosa* Gray, a common drought-deciduous shrub of the Sonoran Desert. I then evaluated the significance of variation in Δ values to growth under competitive and non-competitive situations and the significance of Δ values for extended drought survival. The underlying hypotheses for this study were that (1) Δ-value differences among plants had a genetic basis and therefore ranking differences would be maintained through time, (2) high Δ values would be associated with a greater capacity to respond to high soil moisture conditions, and (3) low Δ values would be associated with a greater capacity to survive limited soil moisture conditions.

Materials and methods

Study site

This study was conducted in west central Arizona (34° 57' N, 114° 25' W, 550 m elevation) at a site approximately 8 km south of Oatman, Arizona and 25 km northeast of Needles, California. Four sites on adjacent south-facing slopes were used in this study. The vegetation of this area is typical of the Lower Colorado Valley portion of the Sonoran Desert (Shreve and Wiggins 1964). On south-facing slopes and bajadas, the vegetation is dominated by the shrub *Encelia farinosa*. Throughout much of this region, *E. farinosa* forms monospecific stands with a clumped distribution, especially on south-facing slopes (Ehleringer 1984; Schuster et al. 1992a). More than 80% of the *E. farinosa* shrubs in each of the populations were within 50 cm of each other. At other sites in this area, it is co-dominant with the shrub *Larrea tridentata* and the cactus *Opuntia bigelovii*. Soils at this site are thin, volcanically-derived, and low in nutrients (Ehleringer 1984).

Competition experiment

Two sequential neighbor-removal competition experiments were conducted, each on separate south-facing slopes. At each of these two sites, more than 98% of the perennial vegetation was *E. farinosa*, with just an occasional *Krameria parvifolia, L. tridentata,* or *O. bigelovii* at the site.

In the first experiment (using population 1), 12 plants of equivalent size (0.22 m²) were chosen as target and control plants on the first slope. Around the six target shrubs, all aboveground perennial vegetation within a 2-m radius was removed (which was thought to be the longest possible lateral root extension; Ehleringer 1984); an effort was made to minimally disrupt the soil surface and no neighbor roots were removed. The target and control plants were then monitored for 24 months. Precipitation and temperatures during this experiment were typical of long-term trends for this region.

In the second experiment (using population 2), 16 plants of equivalent size (0.25 m²) were chosen as target and control plants on a second slope. The intact population was initially monitored for 18 months before any neighbor-removal manipulation. After this initial observation period, all aboveground perennial vegetation within a 2-m radius was removed from around the eight target shrubs; again, an effort was made to minimally disrupt the soil surface and no neighbor roots were removed. The target and control plants were then monitored for 23-months. Precipitation and temperatures during the initial phase of this experiment were typical of this region, but shortly after neighbors had been removed, the region experienced a prolonged drought lasting more than a year.

Population analyses

Plant distribution, carbon isotope discrimination, and shrub canopy characteristics were measured on three of the populations (2, 3, and 4). Population 2 was sampled between February 1987 and September 1991. Population 3 was sampled once in September 1986. In population 4, the population was sampled once each spring beginning in 1982. In populations 2 and 3, there was no detectable seedling establishment during the period of sampling. In population 4, there were occasional recruitment and mortality events, but in no case before the drought was there more than a 1–2% recruitment or mortality in a given year. Recruitment was measured as the addition of individuals that had been new seedlings during the previous spring.

Carbon isotope analyses

Carbon isotope discrimination (Δ) of mature leaf tissues was measured on each of the target and control shrubs. In addition, during the initial observation period of the second competition experiment, Δ values were measured on all *E. farinosa* individuals within the population. Five mature leaves per shrub were bulked for each Δ measurement. Leaf tissues were then dried, ground with a mortar and pestle, and a 2-mg subsample of the ground tissue was combusted and analyzed for $^{13}C/^{12}C$ on an isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, CA). The carbon isotope ratio ($\delta^{13}C$) was calculated as

$$\delta^{13}C = (R_{sample} / R_{standard} - 1) \cdot 1000\%o$$

and then Δ was calculated as

$$\Delta = (\delta^{13}C_{air} - \delta^{13}C_{plant}) / (1 + \delta^{13}C_{plant})$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the plant sample and standard (PDB). The $\delta^{13}C_{air}$ was assumed to be $-8\%o$. The overall precision of the measurement was $\pm 0.11\%o$.

Staistical analyses

All data were analyzed using JMP on a Macintosh computer.

Results

Variation in carbon isotope discrimination

Population-level variation in carbon isotope discrimination was examined on two of the four contiguous populations. In September 1986, a population of 49 mature plants (population 3) exhibited approximately a 2‰ range among all individuals (mean = 17.21‰, SD = 0.46‰) (Fig. 1). In the following spring, the range of Δ values observed for an adjacent population of 89 individuals (population 2) plants was 3‰. The mean spring-time Δ value was 18.81 ± 0.64‰, which was 1.6‰, greater than had been observed on the adjacent population the previous fall. This difference in Δ values translated into approximately a 24 µl l^{-1} change in the operational c_i values. To determine whether these differences reflected seasonal changes or inter-population differences, the Δ values were again measured on population 2 the following September (Fig. 1). The mean Δ value for population 2 at that time was reduced to 17.83 ± 0.64‰, a similar value to that which had been observed for population 3 the previous fall.

The changes in observed Δ values among sampling dates reflected an acclimation response to progressively increasing soil moisture deficits. While the overall mean Δ value decreased through the year (Fig. 2; Ehleringer et al. 1992), the rankings among individuals within the population remained the same. As a consequence, there were significant correlations in Δ values among sample dates (Fig. 2). These corresponding changes suggested genetic differences among individuals within the popula-
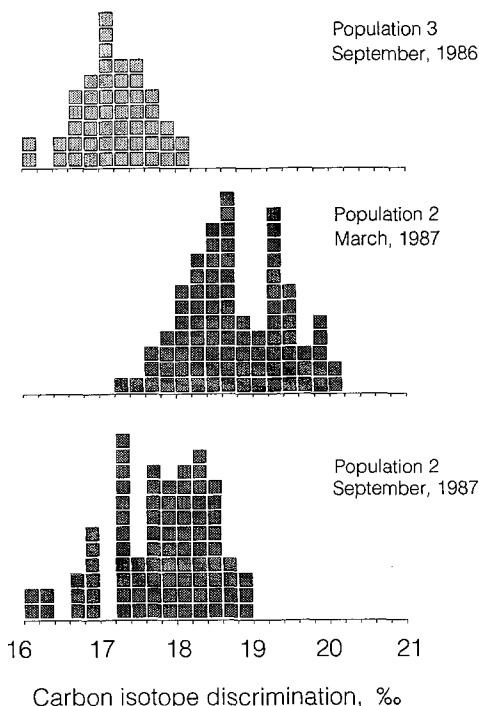

Fig. 1. Frequency distribution of carbon isotope discrimination values for individuals of *Encelia farinosa* populations 2 and 3 at a Sonoran Desert site south of Oatman, Arizona. Each *square* represents a single plant within a population
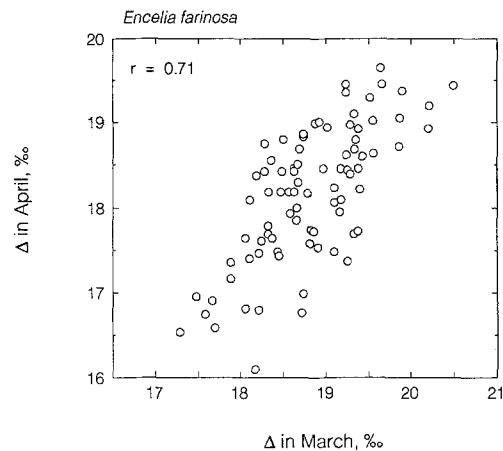

Fig. 2. Carbon isotope discrimination values for individuals of *Encelia farinosa* measured under natural conditions in early March and again on newly produced leaves in late April (approximately 6 weeks later) at a Sonoran Desert site south of Oatman, Arizona. During this peak vegetative growth period, leaf life expectancy was approximately 4 weeks
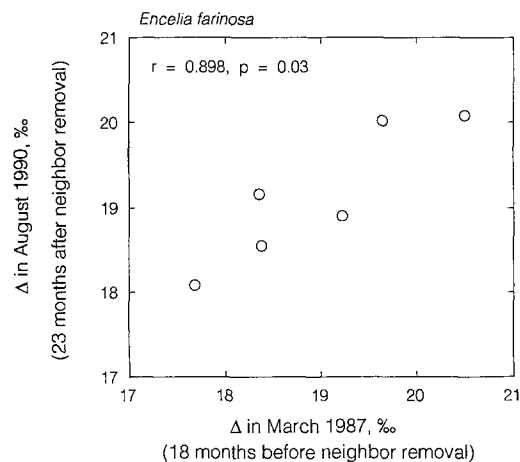

Fig. 3. A comparison of carbon isotope discrimination values measured on *Encelia farinosa* individuals in the field 18 months before neighbors had been removed and 23 months after neighbor removal at a Sonoran Desert site south of Oatman, Arizona

tion. Yet it was also possible that the variation in Δ values among adjacent individuals could have been the product of competitive interactions among individuals, creating a local-scale, spatial variation in soil moisture patterns. To test this, Δ values were followed on six mature individuals from an initial period when these plants had neighbors through a period following neighbor removal. Over this 41-month period, the rankings in Δ values among the six plants remained consistent (Fig. 3). These results allow us to conclude that Δ values were not influenced by the presence of neighbors competing for water. Although the plants acclimated to the differences in soil moisture availability experienced through the year and this changed the absolute Δ value of individual plants, the rankings in Δ values among individuals remained relatively constant both with and without neighbors.

Correlation of Δ with population-level plant characters

The coordinates of each plant in population 2 were mapped and plant size was measured to determine the spatial relationships between size and neighbor proximity. As in the other two populations, population 2 consisted only of mature individuals. There were no seedlings or recently established *E. farinosa* and plant size averaged 0.27±0.08 m² (95% C.I.). Proximity to neighbors was estimated from the Thiessen polygon size (using JMP), which should be an approximate estimate of the area available for root exploitation of available soil moisture (Mithen et al. 1984). Larger plants occurred only in locations with few other plants and plant size (m²) was positively correlated with Thiessen polygon area ($r = 0.462$, $n = 89$, $P < 0.001$). While this result might have been expected on the basis of previous studies showing that *E. farinosa* competed for soil moisture (Ehleringer 1984), it was surprising to note that the Δ value of individual shrubs was not significantly correlated with Thiessen polygon area ($r = 0.029$, $n = 89$, NS). Nor was there a significant correlation between Δ and plant resource availability, expressed as the ratio of the Thiessen polygon size to overall plant size ($r = -0.200$, $n = 89$, NS).

There was a significant negative correlation between plant size and Δ value ($r = -0.386$, $n = 89$, $P < 0.001$); larger plants tended to have lower Δ values. These data would suggest that either a low Δ value was an advantage to plants, allowing them to increase in size for an unknown reason, or perhaps that plants with low Δ values tended to survive longer in the population and therefore be larger. The lack of a significant correlation between Δ values and Thiessen polygon size would suggest that the latter is the more likely explanation. There are no known mechanisms for determining the age of *E. farinosa* and, because of the suffrutescent habit, it is not possible to count annual rings on the largest base stem as a reliable estimate of plant age.

Soil fertility is also not likely to be a basis for either differences in leaf Δ values or plant size. Leaf Kjeldahl nitrogen content varied between 11 and 23 mg g⁻¹ among individuals within the population, but there was no significant correlations between Δ and leaf Kjeldahl nitrogen content ($r = -0.155$, $n = 89$, NS). Overall plant size exhibited no significant relationship with leaf nitrogen content ($r = 0.011$, $n = 89$, NS).

Leaf Δ value and competitive interactions

The previous results suggested that under natural conditions the Δ value was unlikely to be related to plant size, but provided no evidence for how individual plants might respond to the removal of neighbors. Yet other studies had indicated that gas exchange rates were often positively correlated with Δ values (Condon et al. 1987; Ehleringer 1990; Ehleringer et al. 1990). To examine the possibility that changes in gas exchange rate might be detectable when plants were released from competition,
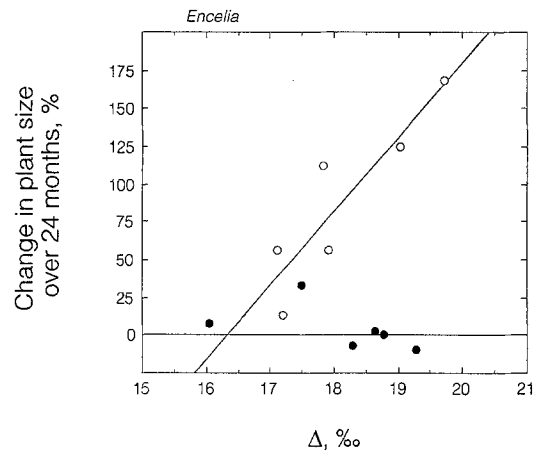

Fig. 4. Relative changes in plant size of *Encelia farinosa* individuals following neighbor removal *(open circles)* and of control plants whose neighbors were not removed *(full circles)* as a function of the carbon isotope discrimination value of the plant at a Sonoran Desert site south of Oatman, Arizona

growth was monitored on plants following neighbor removal. Over a 24-month period, there was no detectable change in plant size among control plants (Fig. 4). However, plants released from neighbor competition significantly increased in size and the magnitude of that response was positively related to the plant's Δ value (Fig. 4).

Long-term drought survival and leaf Δ value

A second experiment (using population 2) was established to repeat the previous observations (Fig. 4), using the entire range of Δ values found within a population. However, shortly after the neighboring plants had been removed around the target plants, the region experienced a severe drought that lasted for more than a year. During that time, precipitation recorded at the surrounding meteorological stations was only 39% of the long-term mean values (US Weather Records). The last time an equivalent drought had occurred in this region was 28 years earlier.

There was a high mortality of *E. farinosa* shrubs in response to this episodic drought event. In population 4, where population size had been monitored for almost a decade, population size decreased dramatically. Of the *E. farinosa* shrubs (all adult plants) 48% died during the drought (Fig. 5). Prior to this drought, mortality rates had been low (0–5% per year) and recruitment into the population had been of similar magnitude.

A slightly higher mortality rate occurred in *E. farinosa* population 2, the population used for the second set of neighbor removal experiments. In this population, 66% of the *E. farinosa* shrubs died during the drought period. Based on analysis of the control plants, the likelihood of death during the drought was not dependent on plant size ($t = 0.065$, $n = 37$, $P = 0.949$). Instead an analysis of covariance (factoring out any effect of plant size) revealed that those plants that died during the drought had significantly higher Δ values than those plants that sur-
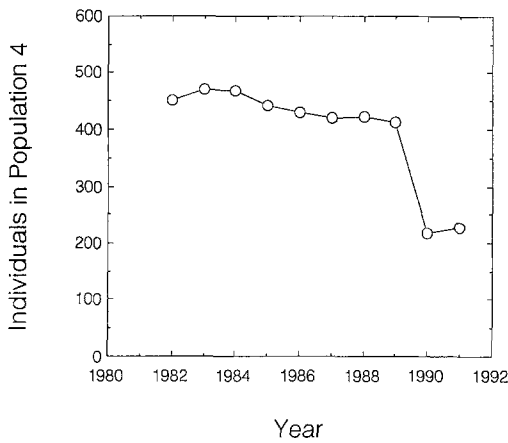
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Fig. 5. Numbers of mature *Encelia farinosa* individuals in a 312-m^2 plot on a south-facing slope 8 km south of Oatman, Arizona. The plot was sampled once each spring
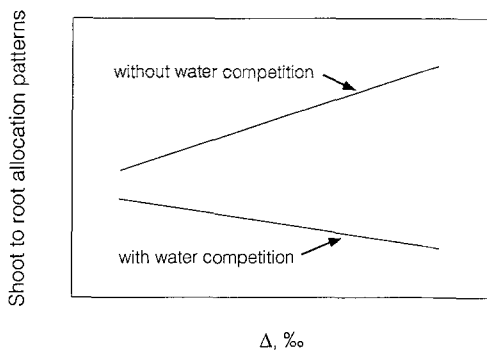

Fig. 6. Hypothetical relationship of shoot-to-root areas (τ) among genotypes of a species and leaf carbon isotope discrimination (Δ). The two *lines* represent hypothesized responses by plants to water-limiting situations, where neighbor competition for soil moisture accelerates the extraction rates of water from the soil. In this model, genotypes with a high Δ value would substantially alter τ values in response to changes in the level of competition for water

vived the drought (F-ratio $= 16.04$, $P = 0.0003$). The average Δ value of surviving plants was 18.17‰, whereas for those plants dying the average was 18.62‰. Interesting spatial patterns can be seen in the mortality patterns between those plants with and without neighbors during the drought. Between the control and neighbor-removed plants, plants without neighbors were more likely to survive the drought than those plants with immediate neighbors ($X^2 = 9.143$, $P = 0.0025$). This increased survival probability was not dependent on the Δ value of the neighbor-removed plant, suggesting that access to greater soil volume may also have contributed to survival of all plants without neighbors irrespective of their Δ value.

Discussion

The notion of c_i/c_a as a measure of a photosynthetic set point that is related to life-history patterns (Ehleringer 1993a, b) is supported by a number of recent studies.

Higher c_i/c_a values are associated with shorter life expectancies (DeLucia et al. 1988; Ehleringer and Cooper 1988; Ehleringer et al. 1990; Smedley et al. 1991). The maintenance of ranking differences in *Encelia farinosa* leaf Δ values among plants over a range of environmental conditions and even following neighbor removal is additional indirect evidence. Further support for this pattern has been detected in crop species. Maturity date among cultivars under uniform garden conditions was inversely related to Δ value (Ehleringer et al. 1990; Richards and Condon 1993; White 1993). Variation in flowering date likely reflects carbon gain, allocation, and developmental rate differences among genotypes. The rankings of Δ values of different genotypes within a crop species remained constant through development within a growing season, suggesting 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.

Geber and Dawson (1990), Schuster et al. (1992a), and Dawson and Ehleringer (1993) all observed significant intra-populational variation in Δ values. In a study of the extent of population-level variance in Δ values of species in warm and cold desert ecosystems, Schuster et al. (1992a) observed that variance was greater in populations of the shorter-lived species. If there is a relationship between longevity and Δ value, then lower Δ values would be expected in longer-lived populations because these plants must persist through more drought events (Ehleringer 1993a, b). Over time, natural selection may favor genotypes with specific Δ values, which would then result in a narrower variance in the longer-lived species. However, for shorter-lived organisms (10–25 years), such as *Encelia farinosa*, a distribution of Δ values may reflect environmental heterogeneity on a scale that maintains Δ variability within the population rather than narrowing that variation.

The results of this study suggest that there may be selection for either of the two tails of the Δ distribution within a population. Both spatial and temporal heterogeneity in soil moisture are common in desert environments (Noy-Meir 1979; Ehleringer 1993b). In addition, episodic events such as prolonged drought and extremely wet years are known to have a significant impact in structuring aridland ecosystems (Noy-Meir 1979). If these water-related factors affecting spatial and temporal heterogeneity of soil moisture are of sufficient magnitude, they should influence variance in gas exchange characteristics.

High Δ values appear to be of selective value under high-resource (soil moisture) conditions, such as would occur *spatially* if plants were not competing with neighbors for water or at particular microsites where moisture was more available (such as wash versus slope sites in the Sonoran Desert). In addition, such conditions could occur *temporally* such as during wet years when precipita-

tion exceeds median annual input levels. The data from Fig. 4 strongly suggest that plants with high Δ values are better able to capitalize on high resource conditions than are plants with low Δ values. These data indicate that plants not competing for limiting soil moisture grew at a faster aboveground 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 (Condon et al. 1987; Ehleringer 1990; Ehleringer et al. 1990). If that were the case, conductance-driven differences in Δ values among plants could result in increased photosynthesis and an increased growth rate of high Δ-value plants when not exposed to water stress. Livingston and Spittlehouse (1993) have shown that transpiration-induced differences in leaf Δ values of Douglas fir did correspond with seasonal changes in productivity similar to the patterns observated in Fig. 4.

An alternative but not exclusive explanation is that carbon-allocation patterns within plants changed in response to increased soil moisture availability as hypothesized in Fig. 6. Virgona et al. (1990) have shown a correlation between leaf Δ values and root/shoot carbon allocation patterns. The model in Fig. 6 suggests that if the Δ value is a relatively fixed set point, then other allocation or growth adjustments between above- and belowground components may be necessary in order to maintain a specific Δ value. That is, plants competing for water may have to allocate a greater fraction of their current photosynthate to roots. Those genotypes with a high Δ value may have to allocate proportionally more to roots under water competition than do plants with low Δ values. When competition for water is relieved, the increased availability of carbon in high-Δ plants may be now allocated to aboveground growth resulting in the greater growth rate observed in Fig. 4. Unfortunately, the data in Fig. 4 do not allow us to distinguish among these possibilities, but only to conclude that under reduced competition and greater soil moisture availability, plants with high Δ values have a greater growth rate than plants with low Δ values. Ehleringer (1984) and Ehleringer and Clark (1988) showed that carbon gain and growth rate differences in *E. farinosa* translated into higher fitness values, indicating a selective advantage for high Δ-value plants under greater water availability conditions.

A high Δ value may not be without disadvantages though, particularly if 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. Given equal stem hydraulic conductances between two genotypes, a relatively higher stomatal conductance by one should result in an increased transpiration rate and a decreased leaf water potential in that genotype. The increased survival probability of low-Δ genotypes is suggestive that these plants experienced lower xylem embolism rates. While evidence of variation in xylem hydraulic or xylem embolism characters are not available yet for *E. farinosa*, corroborating evidence has been detected in another peren-

nial. Meinzer et al. (1993) observed that variation in Δ values among coffee cultivars was positively correlated with hydraulic conductance.

As soil moisture availability decreases during drought, the water potential gradient between leaf and root in *E. farinosa* 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, 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 aridland shrubs.

These data indicate an advantage to plants with low Δ values and suggest possible tradeoffs between conditions favoring plants with high and low Δ values 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 neighbors 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 in the Sonoran Desert, variation in Δ values among *E. farinosa* plants will be maintained within a population.

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