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Comparisons of carbon isotope discrimination in populations of aridland plant species differing in lifespan

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Summary. Carbon isotope discrimination (Δ) was compared between populations of dominant perennial plant species, differing in life expectancy, in two deserts with contrasting vegetation types. In both deserts, plants of the shorter-lived species showed significantly higher Δ and greater intrapopulation variance in this character compared to the long-lived species. These results indicate underlying differences in gas-exchange physiology, and suggest a positive correlation between water-use efficiency and lifespan in desert plants. Differences in variance for this character may reflect greater microenvironmental variation experienced by shorter-lived plants and/or different forms of selection acting on water-use traits. Spatial distributions were significantly clustered for the shorter-lived species and significantly uniform for the long-lived species, indicating that competition has been important in the development of the long-lived populations. The long-lived *Larrea tridentata* showed a significant, negative correlation between Δ and Thiessen polygon area, suggesting a positive relationship between water-use efficiency and longevity within this species. This relationship was weakly supported in the other warm desert species, *Encelia farinosa*, but was not observed within populations of the cold desert species, *Gutierrezia microcephala* and *Coleogyne ramosissima*. These results suggest that Δ reflects key aspects of plant metabolism related to lifespan; these differences may ultimately influence interactions among desert plants and the structure of desert plant communities.

Key words: Carbon isotope ratio – Desert ecology – Plant community structure – $^{13}C/^{12}C$ – Water-use efficiency

In arid environments, water availability and competition among plants for this limiting resource are considered to be primary determinants of plant density and species composition (Fonteyn and Mahall 1978; MacMahon and Schimpf 1981; Fowler 1986). However, the patterns generated by these factors are better understood than the mechanisms responsible. Consistent patterns of community composition across soil moisture gradients suggest that differences in plant water-use may underlie differential patterns of establishment and growth. Community-wide data on water-use characteristics are generally lacking, however, due to the difficulty of obtaining the necessary measurements on large numbers of plants in the field.

The carbon isotope composition of plant tissues provides a time-integrated measure of plant physiological behavior that can circumvent this difficulty (Farquhar et al. 1989). In C_3 plants, the $^{13}C/^{12}C$ ratio is a function of the intercellular leaf concentration of CO_2 (c_i), during carbon fixation. The operational c_i is determined by the balance of influx through the stomata, and consumption through carbon fixation during photosynthesis (A). Stomatal opening also influences transpiration rate (E). As a result, the isotopic composition of a leaf can be related to both photosynthetic metabolism and water loss. Given similar environmental conditions among plants being compared, the $^{13}C/^{12}C$ ratio can be used to compare plant water-use efficiency (A/E; Farquhar and Richards 1984; Farquhar et al. 1989). Carbon isotope composition is frequently reported as discrimination (Δ), relating the $^{13}C/^{12}C$ ratio of plant tissues to that of the CO_2 in the surrounding atmosphere.

Desert C_3 plants exhibit a range of over 10‰ in Δ, indicating substantial differences in physiological characteristics (Ehleringer 1988). Intraspecific differences of more than 4‰ have been reported for C_3 species in the same habitat (DeLucia et al. 1988; Ehleringer and Cooper 1988; Toft et al. 1989; Smedley et al. 1991; DeLucia and Schlesinger 1991). For comparison, a 2‰ difference in Δ indicates a difference of approximately 30 $\mu l\, l^{-1}$ in the average operational c_i, and given similar leaf temperatures, a difference in water-use efficiency of about 30% (Ehleringer and Cooper 1988; Ehleringer et al. 1992). While some of the field-based variation in Δ results from environmental differences, several studies have demonstrated a significant, genetic basis for differences in Δ (Hubick et al. 1988; Martin et al. 1989; Geber and

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Dawson 1990; Schuster et al. 1992). Recent investigations into the causes and consequences of variation in Δ are beginning to reveal how the underlying physiological characteristics can affect plant establishment and growth, and may directly influence the structure of plant communities (Ehleringer and Cooper 1988; Geber and Dawson 1990; DeLucia and Schlesinger 1991; Smedley et al. 1991).

In a survey of one Sonoran Desert plant community, Ehleringer and Cooper (1988) reported a striking correlation of carbon isotope composition and life expectancy. Within each of the three microhabitats they examined (slope, transition and wash), there was a negative relationship between Δ and species life expectancy. Ehleringer and Cooper (1988) proposed a mechanistic explanation: species with low water-use efficiency are more likely to successfully establish during wet periods because they can operate at higher c_i (high Δ) and accumulate biomass rapidly. A number of studies have observed significant positive correlations between growth rate and Δ (Farquhar et al. 1989). However, periodic drought conditions should favor long-lived species that are conservative in their use of water (a correlate of low Δ).

In this study we compared the carbon isotope composition of populations (100 plants) of two dominant perennial plant species with contrasting life expectancies in each of two different desert plant communities. These large population samples allowed us to study intraspecific variation in Δ, and thus in c_i, an area largely ignored until recently (Farquhar et al. 1989). Such variation can influence plant growth and reproduction, and can be the key to understanding the interaction of individuals with their environment (e.g. Geber and Dawson 1990). We specifically addressed the following questions: Do populations of plant species with different life expectancies, operating under similar environmental conditions, differ in carbon isotope composition? How much variation in Δ exists within these populations, and does the variance differ among species? Is Δ correlated with factors such as plant size or spacing, that may reflect competitive interactions? Finally, we discuss our results in relation to a conceptual framework in which desert community structure and dynamics are directly influenced by differences in gas exchange physiology and water use.

Methods

Warm desert site

The warm desert site was located southwest of Oatman, Arizona (Mohave Co.) and 18 km east of the Colorado River. This area is within the Lower Colorado Valley portion of the Sonoran Desert (Shreve and Wiggins 1964). Mean annual precipitation at nearby Needles, CA is 111.5 mm (Fig. 1). Mean annual temperature is 22.7° C, with air temperatures seldom below freezing (mean of 7 days per year). The long-lived species at this site was *Larrea tridentata* (DC.) Cov. (Zygophyllaceae), an ubiquitous and frequently dominant shrub throughout much of the Mohave, Sonoran and Chihuahuan Deserts. Age estimates for the largest clones of this species exceed 10,000 years (Vasek 1980). The shorter-lived species at this site was *Encelia farinosa* Gray (Asteraceae), a common shrub of the Mohave and Sonoran Deserts; individuals of this species attain ages of 30–50 years at most (Goldberg and Turner 1986; Turner 1990)

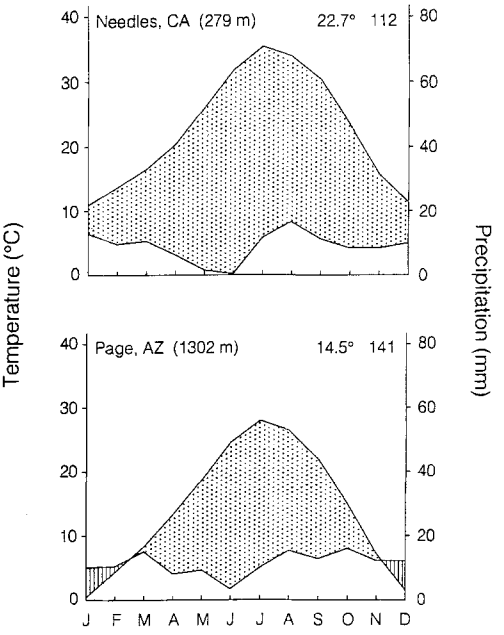


Fig. 1. Climate diagrams compiled from National Weather Service data for stations at Needles, CA (warm desert), and Page, AZ (cold desert)

The *Larrea tridentata* plot was established on a gravelly plain, 6.1 km south and 3.2 km west of Oatman, at an elevation of 570 m. Shrub cover was almost pure *L. tridentata*, and a rectangular plot of 2000 m^2 contained 100 *L. tridentata* plants. All plants were tagged, measured for height and diameter, and mapped to the nearest 0.5 m in June 1990. Ten leaves representing recent growth were collected at that time from each plant for carbon isotope analysis. The *Encelia farinosa* plot was located on a rocky, *E. farinosa*-dominated slope 8.4 km south of the *L. tridentata* plot, at an elevation of 425 m. The 500 m^2 plot contained 110 *E. farinosa* plants, as well as a limited number of other perennial shrubs. All *E. farinosa* plants were tagged, measured for size and mapped to the nearest 0.1 m in March 1990. Five recently matured leaves, produced following spring 1990 rains, were collected at that time from each *E. farinosa* plant for carbon isotope analysis.

Cold desert site

The cold desert site was located 11.5 km north of Lee's Ferry, AZ (Coconino Co.), at an elevation of 1340 m, in an area of the Colorado Plateau characterized by a cold desert environment (West 1983). Mean annual precipitation at nearby Page, AZ is 140.9 mm (Fig. 1). While mean annual temperature is 14.5° C, air temperatures are below freezing an average of 93 days each year. At this site the long-lived species was *Coleogyne ramosissima* Torr. (Rosaceae), a dominant plant along the margins of the Mohave, Sonoran and Great Basin Deserts that often forms nearly pure stands (Benson and Darrow 1957). Matched photographs indicate that individual lifespans can exceed 100 years (R. Webb, pers. comm.), and one report documented ages up to 240 years based on ring counts (Bounds and West 1976). The shorter-lived species was *Gutierrezia microcephala* (DC.) Gray (Asteraceae), a common plant through much of southwestern North America, especially around disturbed areas. Maximum lifespan in this species has been estimated to be 20–30 years (Parker 1985).

The *Coleogyne ramosissima* plot was established in a level area with nearly monospecific *C. ramosissima* growth. Soils in this area are sandy and poorly developed, with a caliche layer at a depth of 1 m under our plots. The 240-m^2 plot contained 108 *C. ramosissima* plants. The *Gutierrezia microcephala* plot was established 100 m

south of the *C. ramosissima* plot, adjacent to a disturbed area. This 80-m^2 plot contained 103 *G. microcephala* plants as well as several *C. ramosissima* and *Ephedra viridis* shrubs. All plants on each plot were tagged, measured for size and mapped to the nearest 0.1 m in October 1989. At least 10 mature leaves representing recent growth were collected at that time from each *C. ramosissima* and *G. microcephala* plant for carbon isotope analysis.

Isotopic analysis

Sampled leaves were oven-dried at 65° C, ground to a fine powder with a mortar and pestle, and then subsampled for isotopic analysis. Carbon isotope ratio ($\delta^{13}C$), relative to the PDB standard, was determined on an isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, CA). Methods for sample analysis followed Ehleringer and Osmond (1989). Leaf carbon isotope discrimination (Δ) was calculated from leaf carbon isotope ratio (δ_{leaf}) as

$$\Delta = \frac{(\delta_{air} - \delta_{leaf})}{(1 + \delta_{leaf})}$$

where δ_{air} was measured as $-8.0‰$ (i.e. -0.008) in the field (Ehleringer 1991).

Data analysis

The mean and variance of the Δ values were compared between the species at each site. Equality of variance was tested using a ratio test (Sokal and Rohlf 1981). Since the variances differed significantly, means were compared using a nonparametric Kruskal-Wallis test. Since variances were also proportional to the means, we used a *t*-test of the coefficients of variation to test whether the amount of variation in Δ differed between the species at each site. Normality of the distributions was tested using a Komolgorov-Smirnov test.

Plant densities were calculated based on the number of tagged plants within the plots. Data from only the first 100 plants on each plot were used for subsequent comparisons. Plant spacing and pattern were evaluated using nearest neighbor analysis (Clark and Evans 1954). We compared the observed mean nearest-neighbor distances to expected values based on a null hypothesis that individuals were randomly distributed, and calculated a standard normal deviate to test that hypothesis. We also evaluated plant spacing by calculating the Thiessen polygon domains of each plant, defined as the area closer to that plant than any other (Mead 1971; Mithen et al. 1984). Plant canopy area and volume were calculated from the height and width measurements for each plant. We evaluated the relationships among Δ and plant size measurements, distance to nearest neighbor, and Thiessen polygon area using nonparametric (Spearman) correlation analysis. For these calculations we eliminated individual plants from the data sets that were too close to plot borders to determine nearest neighbors with certainty.

Results

Mean carbon isotope discrimination was significantly greater in the species with the shorter lifespan at each site (Fig. 2, Table 1). Mean Δ for *G. microcephala* was 1.1‰ greater than the mean for the relatively long-lived *C. ramosissima*, and the mean difference between *E. farinosa* and *L. tridentata* was 2.2‰. The range and variance of Δ were also greater for the shorter-lived species at each site. Significant differences in the coefficient of variation revealed that differences in variance were not artifacts of variance-mean proportionality: the shorter-lived species exhibited greater intrapopulation variation in Δ, independent of the mean, at each site. Δ values were higher for the

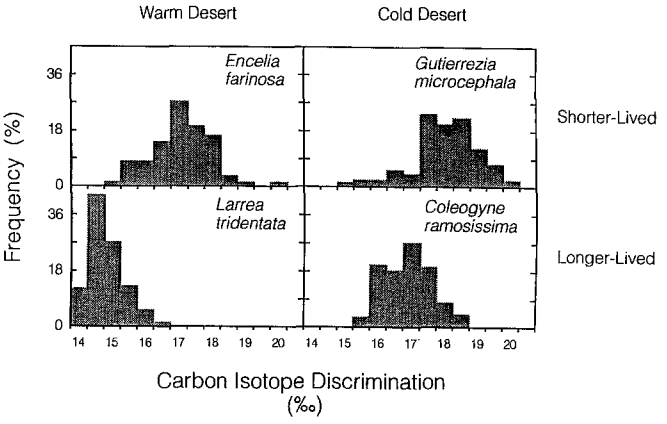


Fig. 2. Distribution of carbon isotope discrimination in leaf samples from populations of dominant perennial plants, differing in lifespan, from warm and cold desert sites ($n = 100$ for each species)

cold desert species than the warm desert species, indicating higher operating c_i in the cold desert plants. However, interpretation of this comparison is complicated by differences in sampling times and environmental conditions, as well as the different phenologies of the two species at each site.

Plants of the shorter-lived species exhibited a highly significant clumped, or aggregated, spatial pattern at each site (Table 2). In contrast, *L. tridentata* exhibited a highly significant regular, or uniformly dispersed, pattern. *C. ramosissima* also exhibited a significant regular spacing pattern (one-tailed test, $P = 0.05$).

Correlation coefficients of Δ with plant size were consistently negative, but were only significant for *L. tridentata* (Table 3; correlations with area and volume were similar, thus only results for area are shown). Δ was also negatively correlated with distance to the nearest neighbor for *L. tridentata* and *E. farinosa*, and with Thiessen polygon area for *L. tridentata*. Neither measure of plant spacing was correlated with Δ in plots of the two cold desert species.

Discussion

Our findings confirm and extend the trend reported by Ehleringer and Cooper (1988), that desert plants with short lifespans have higher carbon isotope discrimination relative to the dominant long-lived species in the same area. Furthermore, annual plants previously sampled near these field sites had even higher Δ values than the *E. farinosa* and *G. microcephala* plants in this study (Ehleringer et al. 1991). Since Δ is primarily a function of average intercellular leaf CO_2 concentration (c_i), these differences reflect underlying differences in gas exchange physiology that are associated with longevity.

These results suggest greater water-use efficiency (A/E) in the long-lived species (Farquhar and Richards 1984). Previous studies have demonstrated correlations between Δ and both instantaneous A/E and long-term transpiration efficiency (summarized in Farquhar et al. 1989), and

Table 1. Comparison of Δ distributions in study populations of four dominant aridland plants

Species	Normality	Mean	Variance	CV
Warm desert				
Encelia farinosa	Yes ($P>0.215$)	17.25[a]	0.817[a]	5.24[a]
Larrea tridentata	Yes ($P>0.161$)	15.05[b]	0.279[b]	3.51[b]
Cold desert				
Gutierrezia microcephala	Yes ($P>0.225$)	18.25[a]	0.916[a]	5.24[a]
Coleogyne ramosissima	Yes ($P>0.235$)	17.13[b]	0.472[b]	4.01[b]

Within deserts, values for mean, variance and coefficient of variation (CV) followed by different letters differ significantly at $\alpha=0.05$

Table 2. Plant density and spacing patterns on study plots of four dominant aridland plants

Species	Density (no./m^2)	Mean distance to nearest neighbor (m)	Spacing pattern
Warm desert			
Encelia farinosa	0.22	0.70	Clumped***
Larrea tridentata	0.05	2.77	Regular***
Cold desert			
Gutierrezia microcephala	1.38	0.29	Clumped***
Coleogyne ramosissima	0.45	0.81	Regular*

* differs from random at $\alpha=0.05$; *** differs from random at $\alpha=0.001$

Table 3. Correlation (Spearman's) of Δ with plant size, distance to nearest neighbor, and Thiessen polygon area in study populations of four dominant aridland plants

Species	Correlation of Δ with		
	Size	Distance to nearest neighbor	Polygon area
Warm desert			
Encelia farinosa	−0.14	−0.24*	−0.17
Larrea tridentata	−0.27**	−0.22*	−0.34**
Cold desert			
Gutierrezia microcephala	−0.13	−0.08	−0.08
Coleogyne ramosissima	−0.16	0.02	0.06

* differs significantly from 0 at $\alpha=0.05$; ** differs significantly from 0 at $\alpha=0.01$

Ehleringer et al. (1992) have demonstrated that Δ values can be used to unambiguously rank the water-use efficiencies of aridland plants in the absence of substantial differences in leaf temperature. Water-use efficiency characteristics may significantly affect the outcome of competitive interactions (Cohen 1970), and may ultimately underlie differences in community composition.

Our results do not support Cowan's (1982) suggestion that perennials in water-limited environments should converge on similar patterns of water-use. Instead Δ values varied widely in these habitats, suggesting a wide range in A/E. Other authors have argued that natural selection will favor either high A/E (Fischer and Turner 1978) or low A/E (Cohen 1970; DeLucia and Schlesinger 1991) in arid environments. Our results suggest that there may be mechanisms selecting for both characteristics in the same environment. The high Δ values of *G. microcephala* and *E. farinosa* support the notion of Cohen (1970) that low A/E can be advantageous, especially to shorter-lived plants with shallow root systems. DeLucia and Schlesinger (1991) have also suggested that low A/E may be advantageous in water-limited environments. However, the values of Δ for *L. tridentata* reported in this study are quite low, and suggest extremely high A/E in one of the most abundant plant species of North American deserts. Interspecific differences in Δ may help explain the association of shorter-lived species with microsites expected to be more mesic within each of these desert environments.

We observed wide intrapopulation variance in Δ, which may reflect both genetic and environmental variation. We attempted to minimize microenvironmental variation in our selection of highly uniform sites. In a separate study we estimated that at least 53% of the variation in Δ in our population of *G. microcephala* is due to underlying genetic variance (Schuster et al. 1992), and there is evidence that Δ is under similar genetic control in many other plant species (Hubick et al. 1988; Martin et al. 1989; Geber and Dawson 1990). Thus our results suggest that the shorter-lived species may have greater intrapopulation genetic variance for Δ than the long-lived species. In species with relatively short persistence times, such as *G. microcephala* and *E. farinosa*, spatial and temporal variation may result

in disruptive selection and the maintenance of high levels of genetic variation for Δ and *A/E* (Schuster et al. 1992). In the long-lived species, the greater likelihood of experiencing severe drought may result in a strong stabilizing selection, and thus a narrower range of inherent Δ values.

Despite positive associations between Δ and productivity in several other species, the negative relationship between Δ and size in *L. tridentata* suggests that Δ and longevity may be coupled within this species. Other studies have reported significant negative correlations between Δ and plant size, particularly in comparisons of seedlings and established adults (Donovan and Ehleringer in review; Sandquist et al. prep.). Such differences might reflect metabolic changes associated with larger size, but could also result from natural selection (Donovan and Ehleringer 1991). High Δ, if accompanied by higher growth rate, may be favored during establishment, while low Δ may be more important for long-term survival. However, the lack of a significant correlation between Δ and size in *E. farinosa*, *G. microcephala* and *C. ramosissima* suggests that size in these populations may be a function of other factors.

The correlation of Δ with plant spacing in both *E. farinosa* and *L. tridentata* could also reflect either environmentally-induced physiological changes or natural selection. If widely spaced individuals primarily indicate poor microsites, then low Δ in these individuals could reflect physiological response. However, competitive interactions and natural selection could also explain these patterns. Additional controlled experiments will be needed to distinguish among these hypotheses.

Plant growth in cold deserts is limited by cold winter temperatures; in contrast, growth can occur in the warm desert at any time that water is available. Thus for the cold desert species, we would not have expected a significant relationship between Δ and plant spacing, even for the long-lived *Coleogyne ramosissima*. Thus while certain interspecific patterns appear to be general (i.e. spatial clustering, high Δ, and high variance in Δ in shorter-lived species), the intraspecific relationships between Δ and plant spacing differ between the two deserts.

Patterns of plant community composition in aridlands are often repeated along environmental gradients (Shreve and Wiggins 1964; Whittaker and Niering 1965; Yeaton and Cody 1979; MacMahon 1988). From a physiological perspective, traits that influence water loss and the ability to compete for limited soil water should determine which plants will occupy given locations along these gradients. The broad correlation of Δ with lifespan in desert plants indicates underlying physiological differences that may lead to differences in establishment, persistence, and competitive ability. Further study of the effects of differences in Δ on plant performance under competitive conditions and in a variety of environments should refine our understanding of the linkage of physiological processes and community patterns.

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References

Benson L, Darrow R (1957) The trees and shrubs of the southwestern deserts. University of Arizona Press, Tucson, Arizona

Bounds J, West NE (1976) Blackbrush (*Coleogyne ramosissima*) on Southwest Utah rangelands. Res Rep 27, Utah Agric Exp Sta, Logan, Utah

Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445–453

Cohen D (1970) The expected efficiency of water utilization in plants under different competition and selection regimes. Isr J Bot 19: 50–54

Cowan IR (1982) Regulation of water use in relation to carbon gain in higher plants. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of Plant Physiology, New Series, vol 12D. Springer, Heidelberg, pp 589–613

DeLucia EH, Schlesinger WH (1991) Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. Ecology 72: 51–58

DeLucia EH, Schlesinger WH, Billings WD (1988) Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. Ecology 69: 303–311

Donovan LA, Ehleringer JR (1991) Ecophysiological differences among juvenile and reproductive plants of several woody species. Oecologia 86: 594–597

Donovan LA, Ehleringer JR Contrasting water use patterns among size and life history classes of a semiarid shrub. Funct Ecol, in review

Ehleringer JR (1988) Carbon isotope ratios and physiological processes in aridland plants. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Springer-Verlag, New York, pp 41–54

Ehleringer JR (1991) $^{13}C/^{12}C$ fractionation and its utility in terrestrial plant studies. In: Coleman DC, Fry B (eds) Carbon isotope techniques. Academic Press, New York, pp 187–200

Ehleringer JR, Cooper TA (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76: 562–566

Ehleringer JR, Osmond CB (1989) Stable isotopes. In: Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW (eds) Plant physiological ecology. Chapman and Hall, New York, pp 281–300

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR (1991) Differential utilization of summer rains by desert plants. Oecologia 88: 430–434

Ehleringer JR, Phillips SL, Comstock JP (1992) Seasonal variation in the carbon isotopic composition of desert plants. Funct Ecol, accepted pending revision

Farquhar GD, Richards RA (1984) Isotope composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust J Plant Physiol 11: 539–552

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

Fischer RA, Turner NC (1978) Plant productivity in the arid and semiarid zones. Annu Rev Plant Physiol 29: 277–317

Fonteyn PJ, Mahall BE (1978) Competition among desert perennials. Nature 275: 544–545

Fowler N (1986) The role of competition in plant communities in arid and semiarid regions. Annu Rev Ecol Syst 17: 89–110

Geber MA, Dawson TE (1990) Genetic variation in and covariation between leaf gas exchange, morphology, and development in *Polygonum arenastrum*, an annual plant. Oecologia 85: 153–158

Goldberg DE, Turner RM (1986) Vegetation change and plant

demography in permanent plots in the Sonoran Desert. Ecology 67: 695–712
Hubick KT, Shorter R, Farquhar GD (1988) Heritability and genotype × environment interaction of carbon isotope discrimination and transpiration efficiency in peanut (*Arachis hypogaea* L.). Aust J Plant Physiol 15: 799–813
MacMahon JA (1988) Warm deserts. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, pp 231–264
MacMahon JA, Schimpf DJ (1981) Water as a factor in the biology of North American desert plants. In: Evans D, Thames J (eds) Water in desert ecosystems. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp 114–171
Martin B, Nienhuis J, King G, Schaefer A (1989) Restriction fragment length polymorphisms associated with water-use efficiency in tomato. Science 243: 1725–1728
Mead R (1971) Models for interplant competition in irregularly distributed populations. In: Patil GP, Pielou EC, Waters WE (eds) Statistical ecology, volume 2. Pennsylvania State University Press, University Park, Pennsylvania, pp
Mithen R, Harper JL, Weiner J (1984) Growth and mortality of individual plants as a function of "available area". Oecologia 62: 57–60
Parker MA (1985) Size-dependent herbivore attack and the demography of an arid grassland shrub. Ecology 66: 850–860
Schuster WSF, Phillips SL, Sandquist DR, Ehleringer JR (1992) Heritability of carbon isotope discrimination in *Gutierrezia microcephala*. Am J Bot 79: 216–221
Shreve F, Wiggins IL (1964) Vegetation and flora of the Sonoran desert. Stanford University Press, Stanford, California
Smedley MP, Dawson TE, Comstock JP, Donovan LA, Sherrill DE, Cook CS, Ehleringer JR (1991) Seasonal carbon isotope discrimination in a grassland community. Oecologia 85: 314–320
Sokal RR, Rohlf FJ (1981) Biometry. WH Freeman, San Francisco, California
Toft NL, Anderson JE, Nowak RS (1989) Water-use efficiency and carbon isotope composition of plants in a cold desert environment. Oecologia 80: 11–18
Turner RM (1990) Long-term vegetation change at a fully protected Sonoran Desert site. Ecology 71: 464–477
Vasek FC (1980) Creosote bush: long-lived clones in the Mohave desert. Am J Bot 67: 246–255
West NE (1983) Colorado Plateau-Mohavian Blackbrush Semi-desert. In: West NE (ed) Ecosystems of the world, 5. Temperate deserts and semi-deserts. Elsevier, New York, pp 399–411
Whittaker RH, Niering WA (1965) Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology 46: 429–452
Yeaton RI, Cody ML (1979) The distribution of cacti along environmental gradients in the Sonoran and Mohave Deserts. J Ecol 67: 529–541