

FINAL REPORT TO THE
DEPARTMENT OF ENERGY

For

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Water Use, Productivity and Interactions Among Desert Plants

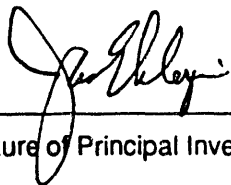
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Table Of Contents

1. Summary of Progress During the Grant Period	2
Water use, water-use efficiency, and primary productivity	2
Carbon isotope discrimination as a tool for ecological studies	5
Carbon isotope discrimination as a general measure of water-use efficiency	5
Water-use efficiency patterns in desert communities	6
Intraspecific studies	6
Heritability of Δ	6
Electrophoretic variation in desert plants	7
Drought and population structure	8
Water sources of desert plants	9
2. Publications Arising From DOE Support During the Grant Period	12
3. Personnel Supported By The Grant and Student Training	15

1. Summary of Progress During the Grant Period

Water plays a central role affecting all aspects of the dynamics in aridland ecosystems. Productivity, stability, and competitive interactions among ecosystem components within aridlands are key processes related directly to water in deserts. The ecological studies in this project revolve around one fundamental premise: that integrated aspects of plant metabolism provide insight into the structure and function of plant communities and ecosystems. While it is difficult to extrapolate from instantaneous physiological observations to higher scales, such as whole plant performance or to the interactions between plants as components of ecosystems, several key aspects of plant metabolism are scalable.

Analyses of stable isotopic composition in plant tissues at natural abundance levels provide a useful tool that can provide insight into the consequences of physiological processes over temporal and spatial scales. Some plant processes continuously fractionate among light and heavy stable isotopic forms of an element; over time this results in integrated measures of plant metabolism. For example, carbon isotope fractionation during photosynthesis results in leaf carbon isotopic composition that is a measure of the set-point for photosynthetic metabolism and of water-use efficiency. Thus it provides information on the temporal scaling of a key physiological process. In contrast, hydrogen is not fractionated during water uptake through the root. Soil water availability in shallow, deep, and/or groundwater layers vary spatially; therefore hydrogen isotope ratios of xylem sap provide a direct measure of the water source currently used by a plant. The longer-term record of carbon and hydrogen isotope ratios is recorded annually in xylem tissues (tree rings). The research in this project addresses variation in stable isotopic composition of aridland plants and its consequences for plant performance and community-level interactions.

Water use, water-use efficiency, and primary productivity. Primary productivity is often limited by water relations characters and/or soil water availability). Productivity and evapotranspiration are linearly correlated in natural vegetation as well, indicating the inevitable tradeoff between transpirational and photosynthetic fluxes as stomata regulate the diffusion rates of water vapor out and carbon dioxide into the leaf. Turbulent flow dynamics within canopies and also between the canopy and the open atmosphere will impact overall canopy photosynthesis and transpiration rates to some extent, depending on canopy coupling characteristics, but there is no doubt that leaf-level gas exchange characters play a dominant role in gas exchange of canopies, particularly in arid habitats where leaf areas are low.

Stomata are the major feature allowing control of water loss in aerially dry environments. Yet at the same time, stomatal control reduces inward CO₂ diffusion and thus reduces photosynthetic rate, creating a fundamental tradeoff influencing primary productivity rates. The set point at which plants operate is highly

variable, depending on both genetic and environmental factors. As one commonly used parameter describing this tradeoff, we can measure water-use efficiency, which is defined as the molar ratio of photosynthetic carbon gain (A) to transpirational water loss (E). Water-use efficiency is measured on an instantaneous, gas-exchange basis as the A/E ratio.

Photosynthetic rates (A) tend to decline in response to a decreased leaf conductance (g), because carbon dioxide diffusion rates into the leaf through the stomata and hence intercellular carbon dioxide concentrations (c_i) are progressively reduced with a reduction in leaf conductance. If leaf temperatures do not change substantially as the stomata close, there may be an increase in the instantaneous water-use efficiency (A/E). This follows because the relationship between photosynthesis and stomatal activity is

$$A = (c_a - c_i) \frac{g}{1.6} = \frac{c_a g}{1.6} \left(1 - \frac{c_i}{c_a} \right) \quad (1)$$

and the transpiration rate (E) is

$$E = v g \quad (2)$$

where c_a is the atmospheric carbon dioxide concentration, 1.6 is the ratio of the diffusivities of water to carbon dioxide in air and is used to convert the conductance to water vapor through the stomata to the conductance to carbon dioxide through the stomata, and v is the gradient in water vapor between the leaf (e_i) and atmosphere (e_a), divided by total atmospheric pressure (in the past we have used " Δw " to denote this term; however that same symbol is easily confused with carbon isotope discrimination, " Δ ", and thus for clarity we have opted for v).

Combining these two equations, we see that the instantaneous water-use efficiency (A/E) becomes

$$A/E = \frac{c_a}{1.6v} \left(1 - \frac{c_i}{c_a} \right) \quad (3)$$

Over time, a fraction of the fixed carbon will be lost through respiration (ϕ_c) and a fraction of the water (ϕ_w) may be lost at night if stomata do not completely close. Therefore, the long-term water-use efficiency, known as the transpiration efficiency (W), measured in terms of biomass or yield with respect to water loss

at the whole plant level will be

$$W = \frac{c_a \left(1 - \frac{c_i}{c_a}\right) (1 - \phi_c)}{1.6v(1 + \phi_w)} \quad (4)$$

Under natural field conditions W depends primarily on both c_i and v . High W values can be achieved by decreasing c_i or by decreasing v (e.g., photosynthesizing during cooler times of the day, which has the effect of reducing leaf temperature during photosynthetically active periods).

Carbon isotope discrimination (Δ) by leaves of C_3 plants is related to photosynthetic gas exchange, because Δ is a measure of the long-term c/c_a value. The c/c_a value will differ among plants because of changes in stomatal opening and in the chloroplast demand for CO_2 . Of the models linking C_3 photosynthesis and $^{13}C/^{12}C$ composition, that of Farquhar et al. (1982) has been the most extensively developed and tested. Their expression for discrimination in leaves of C_3 plants in its simplest form is

$$\Delta = a + (b - a) \frac{c_i}{c_a} \quad (5)$$

where a is the fractionation occurring due to diffusion in air (4.4 ‰), b is the net fractionation caused by carboxylation (mainly discrimination by Rubisco, approximately 27 ‰), and c_a and c_i are the atmospheric and intercellular CO_2 concentrations. The advantage of measuring Δ is that since carbon is being continually fixed by a leaf, measuring Δ provides an integrated estimate of c_i/c_a . Isotopic analyses of different plant components integrate over several times scales. Within leaves, sugar and starch analyses provide integrated estimates of Δ for periods of 3-5 days, respectively. Leaf analyses provides an estimate of Δ during the life period of that leaf and tree ring analyses can be used for an annual integration period. For reviewers more familiar with carbon isotope ratio (δ) as a measure of carbon isotopic composition,

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \quad (6)$$

where subscripts a and p refer to atmospheric CO₂ (source) and plant material (product), respectively. The correlation between Δ and c/c_a have been confirmed for many crop species, but unfortunately data for native species are uncommon.

Carbon Isotope discrimination as a tool for ecological studies. An objective of our current project was to establish that carbon isotope discrimination theory as developed in Eqn. 5 was directly applicable to aridland species. On-line photosynthetic observations of Sonoran Desert species contrasting in life form confirm that these desert species discriminate against ¹³C in a manner consistent with theory (Fig. 1).

Secondary fractionation processes after photosynthetic reduction of CO₂ should not affect the overall leaf isotopic composition (because of mass balance considerations), unless dark-respired CO₂ has a different isotopic composition than that of the CO₂ photosynthetically reduced the previous day or sugar export from the leaf is isotopically different from that fixed during the previous day. The latter is unlikely given the strong isotopic correlation between different plant parts. We are nearing completion of an examination of the hypothesis that the $\delta^{13}\text{C}$ of CO₂ from dark respiration reflects the isotopic composition of carbon fixed during the previous daylight period (current year's work). Although there is nocturnal variation in the $\delta^{13}\text{C}$ of respired CO₂ (possibly reflecting respiration of sugar/starch substrates early and lipids later in the evening), overall mass balance calculations suggest that respired CO₂ does not lead to an alteration in the leaf isotopic composition. Thus from our data sets, it appears that leaf carbon isotopic composition is a reliable indication of long-term c/c_a in desert plants and could be used to extrapolate gas exchange processes as outlined above.

Carbon Isotope discrimination as a general measure of water-use efficiency. In using carbon isotopes to infer water-use efficiency, it is easy to overlook the assumption that leaf temperatures are equivalent among the plants being compared. An analysis of the possible errors introduced when leaf temperatures are not equivalent indicates that, if the differences in leaf temperatures are ≤ 3 °C, a 1% difference in Δ values between plants is more than sufficient to conclude that water-use efficiencies can be unambiguously ranked by measuring their Δ values (Fig. 2). Leaves of desert plants are typically ± 2 °C of air temperature, thus it is likely that Δ values can be reliably used to rank different plants with respect to their water-use efficiencies for a given sampling date (Ehleringer et al., 1991a). While over the course of the year, absolute water-use efficiencies of desert plants will be influenced more by changes in v (essentially beyond control of plants) than Δ , natural selection would be expected to act on the variation in Δ as it represents the differential response of plants when exposed to similar environmental conditions.

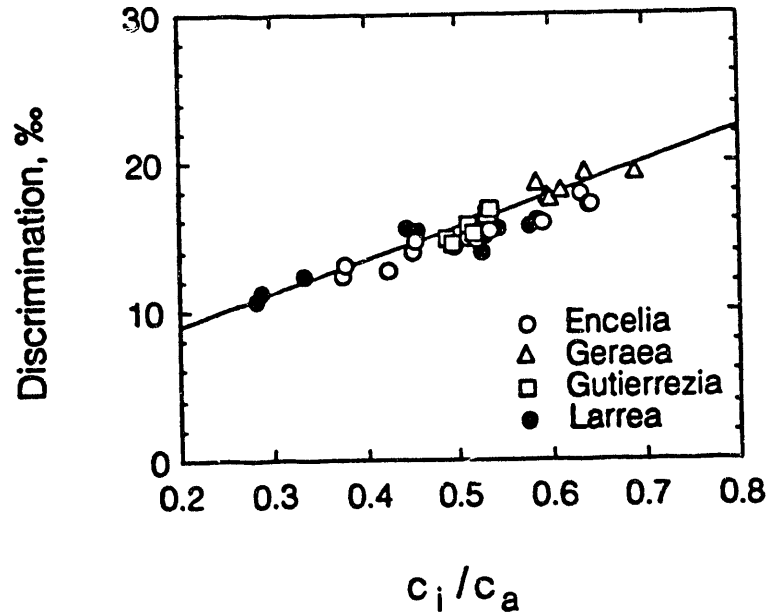


Figure 1. On-line carbon isotope discrimination as a function of intercellular carbon dioxide concentration for common desert species. The line represents the theoretically expected relationship.

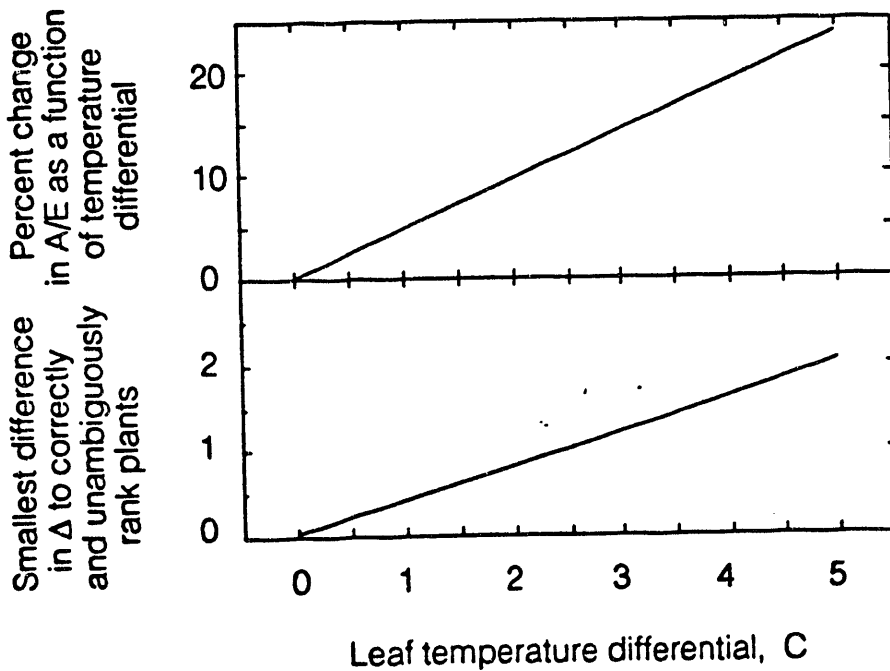


Figure 2. Upper plate. Percent change in water-use efficiency as leaf temperature differential increases between two plants. Lower plate is the minimum difference in Δ necessary to correctly and unambiguously rank plants for water-use efficiency based on Δ values given the temperature effect on water-use efficiency shown in the upper plate.

Water-use efficiency patterns in desert communities. In our currently-funded proposal, we hypothesized that long-lived plants were more conservative in their use of water than short-lived plants, and, thus, we expected a negative correlation between Δ and life expectancy among perennials in desert ecosystems. Contrasting desert plant communities, differing in drought duration and in winter vs. summer precipitation, were examined by collecting leaf material from 10 individuals of all common perennial species within a habitat and measuring their isotopic composition. The results of these comparisons support our hypothesis of an inverse relationship between longevity of a species within the ecosystem and its water-use efficiency (Fig. 3a). Long-lived species have lower Δ values and this pattern is maintained across years (Fig. 3b). It also appears that invading species, which are generally very short-lived, have higher Δ values. This difference in c/c_a is likely to be one of the components that confers an advantage for rapid colonization of disturbed sites during periods of sufficient moisture availability. Genetic studies described below indicate that high Δ values are linked with a number of morphological and physiological features that may be important in early establishment.

Intraspecific studies. While variation in isotopic composition provides insight into community-level patterns, analyses of single-species populations should provide equivalent insight into the dynamics affecting population structure in response to biotic and abiotic stresses. Tagged populations of *Encelia farinosa* (medium-lived, warm desert), *Larrea tridentata* (long-lived, warm desert), *Coleogyne ramosissima* (long-lived, cold desert), and *Gutierrezia microcephala* (medium-lived, cold desert) were analyzed for carbon isotope discrimination value, genetic variation (by gel electrophoresis), photosynthetic gas exchange, and water relations characters.

In the field, we found significant variation in Δ values among adjacent plants for different species (Fig. 4). Long-lived species were less variable than medium-lived species (Table 1), consistent with our hypothesis that plants persisting through repeated drought periods over an extended period should be characterized by higher water-use efficiencies and more uniform in this character. The biological bases for differences in carbon isotopic composition are unclear, except to say that some aspect(s) of gas exchange are inducing the differences. These differences may be direct, such as genetic differences in the sensitivity to environment (such as stomatal sensitivity to humidity) or absolute magnitude of the leaf conductance, or they may be indirect, such as influenced by differences in hydraulic architecture and the xylem water transport system.

Heritability of Δ . We used quantitative genetic methods to study heritability of Δ and several morphological parameters in *Gutierrezia microcephala*, a short-lived cold desert perennial (Schuster et al.,

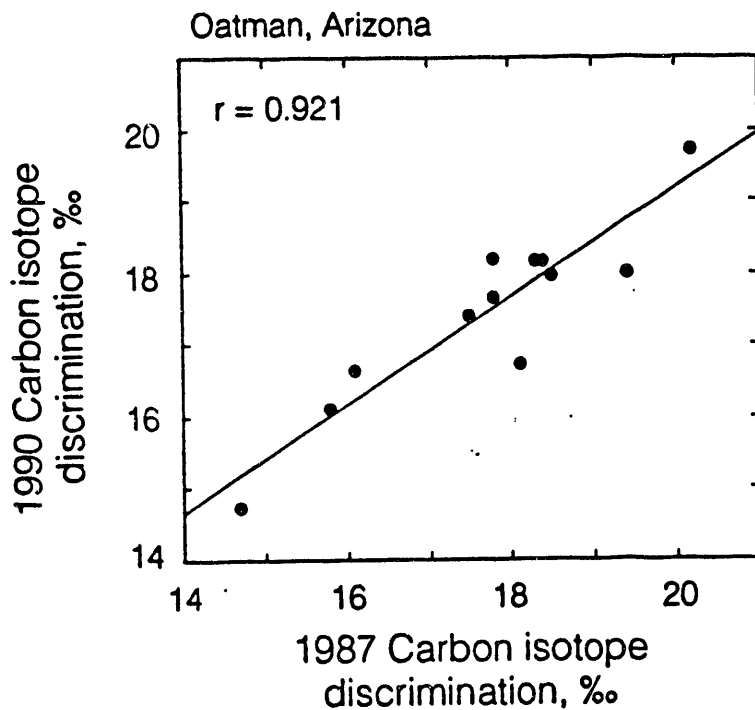
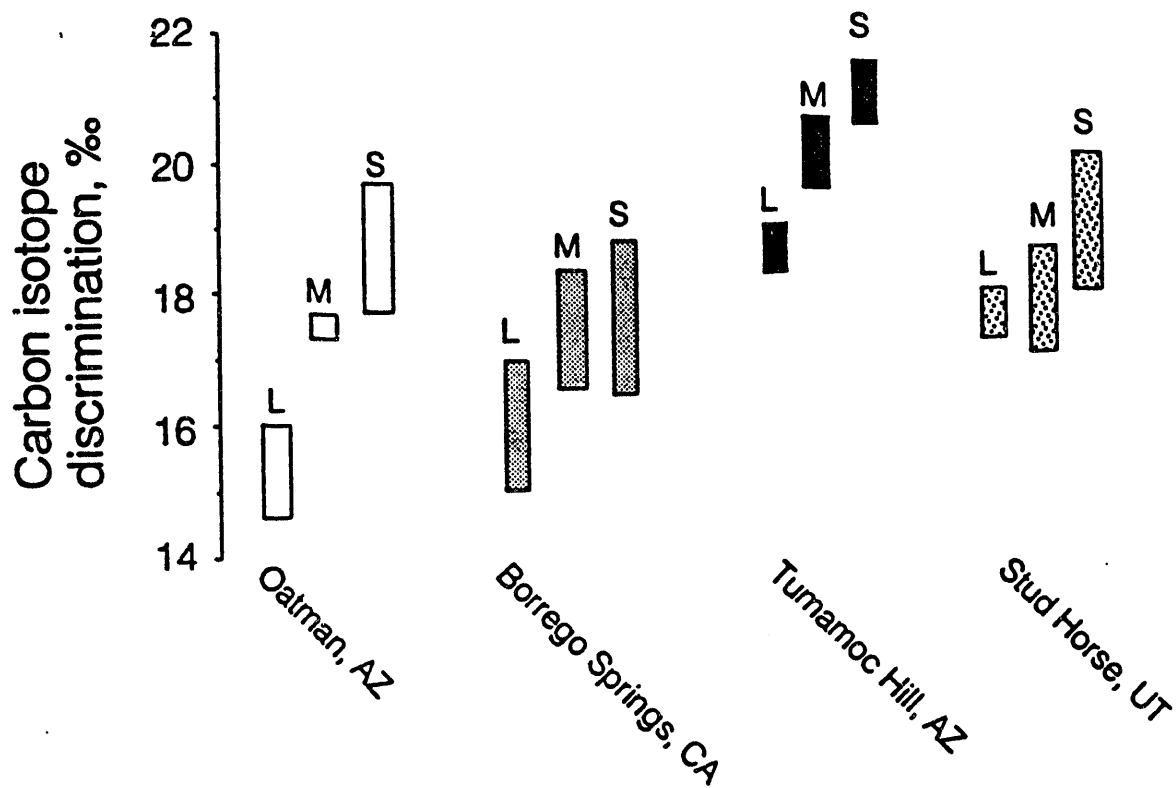


Figure 3. A - Upper plate. Distribution of carbon isotope discrimination values among long (L, > 50 yr), medium (M, 10-40 yr), and short lived (S, 2-5 yr) perennials at four desert sites. B - Lower plate. Stability of carbon isotope discrimination values across different sampling years. Each point represents a single species.

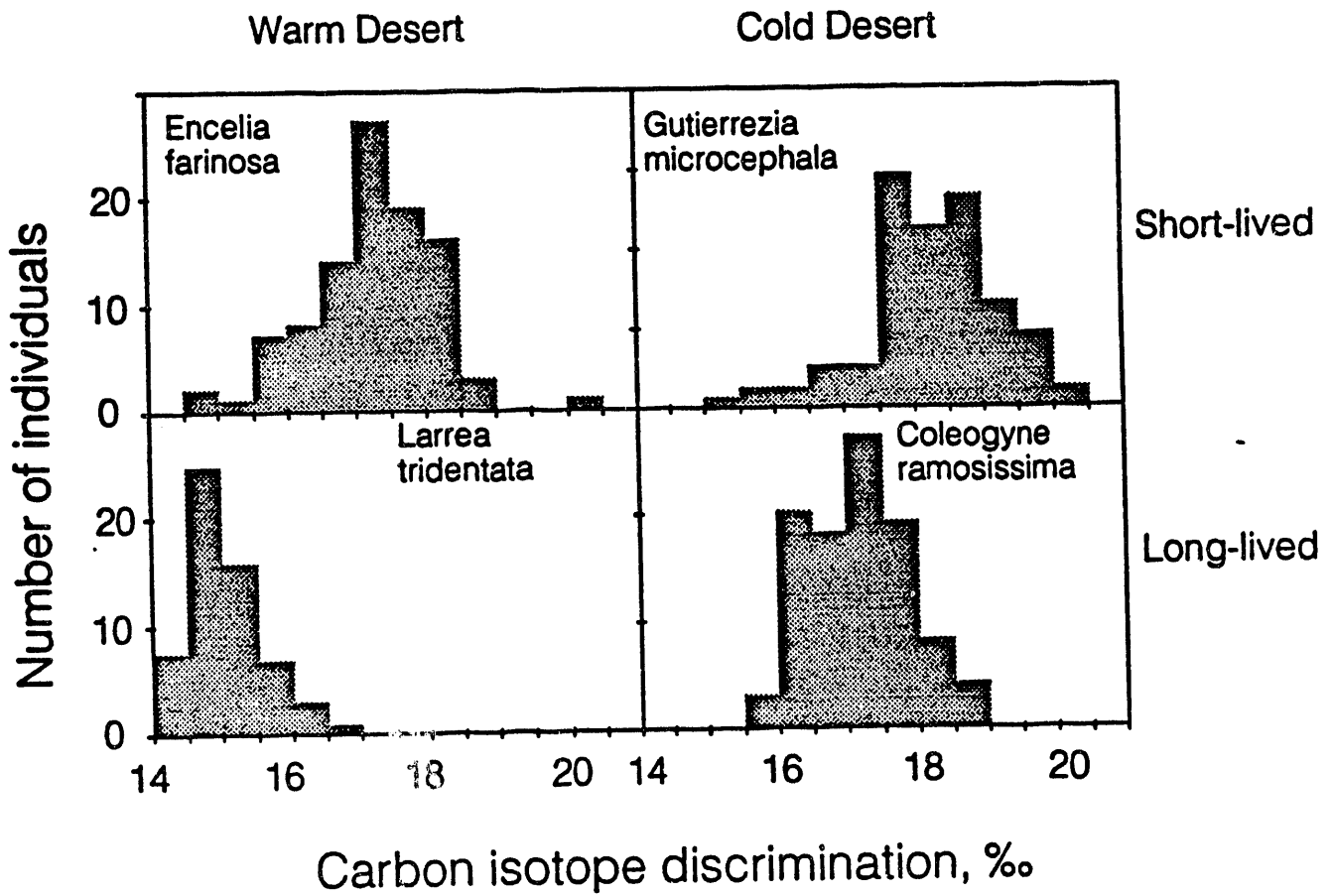


Figure 4. Distribution of carbon isotope discrimination values among subpopulations of dominant shorter-lived and longer-lived perennials in a warm desert and a cold desert site. Each value represents a bulked subsample from an individual plant in the population.

Table 1. Comparison of carbon isotope discrimination distributions for the four study species. Samples size is 100 per population. All comparisons of long- and medium-lived species within a desert are significant at the $p < 0.05$ level.

species	normality	mean	variance	c.v.
Warm desert				
<i>Encelia farinosa</i>	yes ($p > 0.215$)	17.25	0.817	5.24
<i>Larrea tridentata</i>	yes ($p > 0.161$)	15.05	0.279	3.51
Cold desert				
<i>Gutierrezia microcephala</i>	yes ($p > 0.225$)	18.25	0.916	5.24
<i>Coleogyne ramosissima</i>	yes ($p > 0.235$)	17.13	0.472	4.01

Table 2. Electrophoretic variation for the four study species. Samples size is 100 per population. At least twenty different enzyme systems were scored for each species.

species	Percent polymorphism	Observed heterozygosity	Number of alleles per locus
Warm desert			
<i>Encelia farinosa</i>	79.0	0.153	2.2
<i>Larrea tridentata</i>	50.0	0.130	1.8
Cold desert			
<i>Gutierrezia microcephala</i>	71.5	0.175	2.0
<i>Coleogyne ramosissima</i>	59.2	0.136	1.8

Table 3. Comparison of levels of electrophoretic variation in adjacent slope and wash populations of *Encelia farinosa*. Parker Dam, is a temporary composite of two nearby sites to give sufficient sample sizes for statistical comparisons in this proposal. The patterns between the two Parker sites are similar, but not all plants had been scored at the time this proposal was submitted. Thus, when completed, the comparison will be for three different wash-slope sites.

Population habitat	Polymorphism	Heterozygosity	Alleles per locus
Oatman slope	78.9	0.161	2.2
wash	73.7	0.148	2.2
Parker Dam slope	83.3	0.201	2.5
wash	76.7	0.181	2.2

1991a). Seed collected from open-pollinated seed from the Stud Horse population were germinated and seedlings grown in a common greenhouse environment. Carbon isotope discrimination and all morphological characters varied significantly among maternal families. The variation was of similar magnitude to that observed in the field (Schuster et al., 1991b). Heritability of Δ was estimated at 81% in the greenhouse and as 92% using the regression of family mean Δ on parent Δ from field samples. Using both field and greenhouse data, we estimated a lower bound for heritability in nature of 54%. Offspring size and biomass both showed significant, positive correlations with Δ , similar to that observed for crop species (Ehleringer et al., 1990). The corresponding genetic correlations were similar in magnitude and direction. These results imply the existence of heritable differences in physiology associated with water-use efficiency within populations, and the potential for rapid microevolutionary change through natural selection. While simple, directional selection should act to reduce additive genetic variance over time leading to low heritability of a character, many plant studies have shown that substantial heritable variation is often maintained in natural populations with heterogeneous or fluctuating environments (Hamrick and Godt, 1990), such as deserts which are characterized by both drought versus wet years and competitive, low resource habitats versus disturbed, relatively high resource habitats.

Electrophoretic variation in desert plants. We have used electrophoretic techniques to quantify the overall level of genetic variation in populations of these four species, as well as to examine correlations between habitat, physiology (i.e., Δ), and genetic background. The overall level of genetic variation in a species is an important parameter that indicates the potential for microgeographic differentiation, development of population structure, and evolutionary change. In a 1979 review, Hamrick, Linhart and Mitton indicated that electrophoretic variation was lower in plants from aridlands when compared to other environments. However, this statement was based on a very limited data set, and few data have been collected since that time. The results of our electrophoretic survey dispute this notion: populations of these four dominant aridland taxa exceed the mean level of genetic variation reported for all dicot species in nearly every case (Table 2). The high genetic variation demonstrates a high potential for rapid evolutionary response to natural selection and to the development of population structure.

Previous comparisons of levels of variation among species have yielded many insights into factors associated with high levels of genetic variation. One of the most interesting comparisons available in our data is with respect to differences in life expectancy. Previous surveys have often found that genetic variation and lifespan are positively correlated. However, we have reason to believe that natural selection may select for a conservative response in long-lived species, at least in water use, but that short-lived species may be much more variable due to temporal and spatial heterogeneity in the environment. Our data on genetic variation are not entirely consistent with either hypothesis, and point to the obvious

importance of other factors in determining level of genetic variation. However, relatively shorter-lived *Encelia* was significantly more variable than longer-lived *Larrea* in each measure of genetic variation, and shorter-lived *Gutierrezia* was more variable than *Coleogyne*, at least in terms of observed heterozygosity.

In *Encelia farinosa* we have further explored the relationships between genetic variation and microhabitat. Estimates of genetic variation between adjacent slope and wash microhabitat populations of *E. farinosa* in three different populations show significant microhabitat variation in percent polymorphism, heterozygosity, and number of alleles per locus (Table 3). Wash microhabitat plants appear to be less variable for each of these characters. In addition, allele frequencies were significantly different at several loci between these adjacent populations, despite the fact that they are clearly close enough to experience significant gene flow. Moreover, the differences were frequently at the same gene loci (e.g. PGI, DIA, ACP, ALKP), indicating that natural selection acting on these or closely linked gene loci is responsible for the observed genetic differentiation. Carbon isotope discrimination was significantly greater in the wash population than in the slope population ($p < 0.01$). We also found that Δ was significantly correlated with heterozygosity in the slope samples at Oatman ($p < 0.01$), a result we are following follow-up at the other two locations. The wash population has a greater variation in water-use efficiency. The basis for this difference is unclear, but may be related to establishment probabilities and the highly disturbed nature of wash microhabitats. However, it is more likely that the more severe nature of the slope habitat is eliminating less water-use efficient genotypes.

The electrophoretic studies to date have established the importance of knowing more about the genetic structure in desert species. Genetic variability appears to be large and the potential for differentiation exists across microhabitat gradients; it is unfortunate that so few other data sets exist. Given what we know now, genetic studies should play a much greater role in understanding the nature of ecological dynamics and adaptive patterns in these species, particularly in *Encelia* for which a wealth of ecological, morphological, and physiological data already exist. Since alternative molecular genetic approaches (e.g., RFLP) are necessary to better understand the nature of the differentiation and of possible linkages between morphological and physiological characters to form adaptive combinations in response to abiotic and biotic factors, such studies will not be proposed in this proposal as we do not have the molecular or genetic expertise to conduct such studies.

Drought and population structure. The prolonged drought of 1988-1989 in the western US had a significant impact on plants in the Sonoran Desert. The drought was the most extensive in the past 15-25 years, reducing annual precipitation to less than half its average value in most locations and to virtually nothing at the driest sites. Approximately 47% of the population of the medium-lived species (*Encelia*

farinosa, 20-40 yr life expectancy) in Oatman, Arizona died in response to this unusual drought event, whereas none of the individuals in the long-lived species (*Larrea tridentata*, >100 yr life expectancy) died during this drought (Fig. 5). The impact of the extended drought in Death Valley, California was more severe, where 85% of the *E. farinosa* and 4 % of the *L. tridentata* died. Shrub mortality was also common in other species in these ecosystems. For most of the shrubs that survived, there was severe dieback, and growth sprouting from the base of the stems was common.

The probability of drought survival was correlated with intrapopulation variation in water-use efficiency (as measured by Δ). *E. farinosa* have a clumped distribution and water availability has been shown to be influenced by the presence of neighbors (Ehleringer, 1984). An experiment originally designed to investigate growth and competitive interactions in a monospecific stand of *E. farinosa* differing in Δ values provided a fortuitous opportunity to understand the possible interactions between this character and survival through an extended drought. Individual plants had been monitored for a year and a half before the experimental removal of neighbors around individuals of known Δ value. The drought began just after the experiment was underway. At the end of the drought (spring 1990), individuals without neighbors (≥ 2 m distant, either natural or experimental) were more likely to have survived the 2-yr drought ($p = 0.003$) than plants with neighbors. Plant size was not a determinant in the probability of surviving the drought ($p = 0.949$). Individuals that died had lower water-use efficiencies than individuals that survived the extended drought ($p = 0.022$). Yet from a previous neighbor-removal experiment conducted under less severe conditions, we know that the growth rate following neighbor removal is positively related to Δ value ($p < 0.01$). From these data sets and population monitoring, we conclude that drought events play a major role in affecting community structure at the intraspecific level (and at the interspecific level as well since short-lived species are more likely to die during drought). Our results with *Encelia* suggest selection for both high- Δ genotypes that will have greater growth and reproduction in relatively high resource (water) environments and for low- Δ genotypes that can survive long-term drought exposure and may do better under competitive environments as well.

Water sources of desert plants. In our desert communities with high species diversity, to what extent are these plants actually interacting and/or competing for water resources? We have been using hydrogen isotope ratio (δD) analyses of xylem waters to address this question. Winter rains, summer rains, and deep water sources differ in δD values (Ehleringer et al., 1991b). Since there is no fractionation during water uptake (Dawson and Ehleringer, 1991), xylem waters reflect the current water source of plants. Winter rains derived from Pacific frontal storms are utilized by perennial species in both the Painted and Sonoran Deserts (Ehleringer and Cook, 1991; Ehleringer et al., 1991b). In contrast, our data suggest that monsoonal summer precipitation is utilized differentially by species within the ecosystem (Fig. 6, 7). This

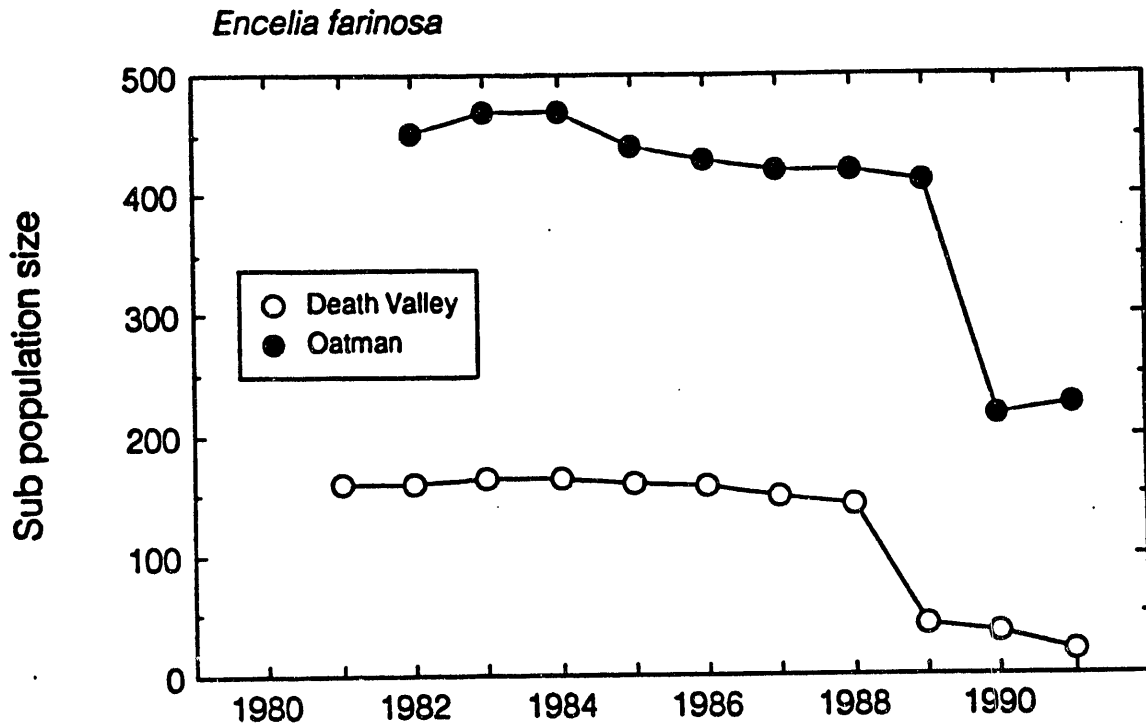


Figure 5. Subpopulation sizes for *Encelia farinosa* growing near Death Valley, California and Oatman, Arizona since 1981. Plot sizes for each are approximately 400 sq. meters. Seedling germination varied between 0-3000 individuals per year. Recruitment as newly established individuals (now as 1 year old) was typically 0-10 individuals per year through 1987. Mortality was typically 0-10 individuals per year through 1987. The drought of 1988-1989 resulted in substantial mortality. That drought was relieved in spring 1991 and was associated with substantial germination so that next year's population size should increase from post-drought low values.

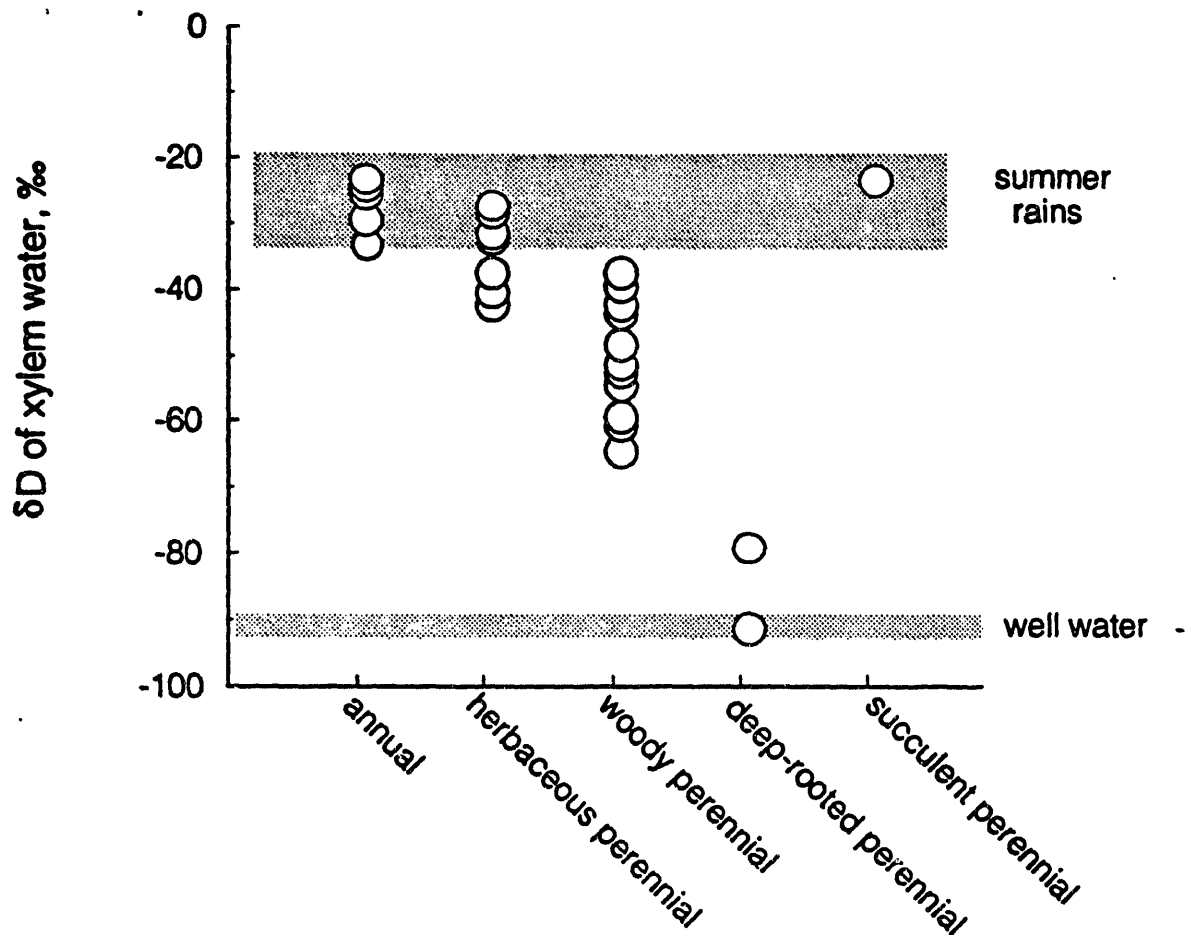


Figure 6. Hydrogen isotope ratios of xylem sap for different perennial species in a sand-shrub community during the summer at Stud Horse Point, Utah. Each point represents a different species. Also shown are the ranges of values for groundwater (from a well) and summer rains.

Table 4. Hydrogen isotope ratios (δD , ‰) in xylem sap of common species representing different life forms in the community at Stud Horse Point, Utah. Data are mean and standard deviation for all species within a life form per sample period.

life form	Number of species	Rain Periods		Drought Periods	
		Spring	Summer	Early Summer	Autumn
annual	5	—	-26.0 ± 3.3	-48.3 ± 5.7	-31.8 ± 4.5
herbaceous perennial	7	-82.5 ± 4.3	-31.9 ± 4.6	-70.7 ± 5.6	-70.8 ± 4.1
woody perennial	13	-91.8 ± 2.4	-53.5 ± 3.4	-79.4 ± 2.8	-76.7 ± 2.8
succulent perennial	1	-84.0 ± 3.0	-22.0 ± 3.0	-54.0 ± 1.0	-25.5 ± 1.5
well water		-91	-90	-92	-92

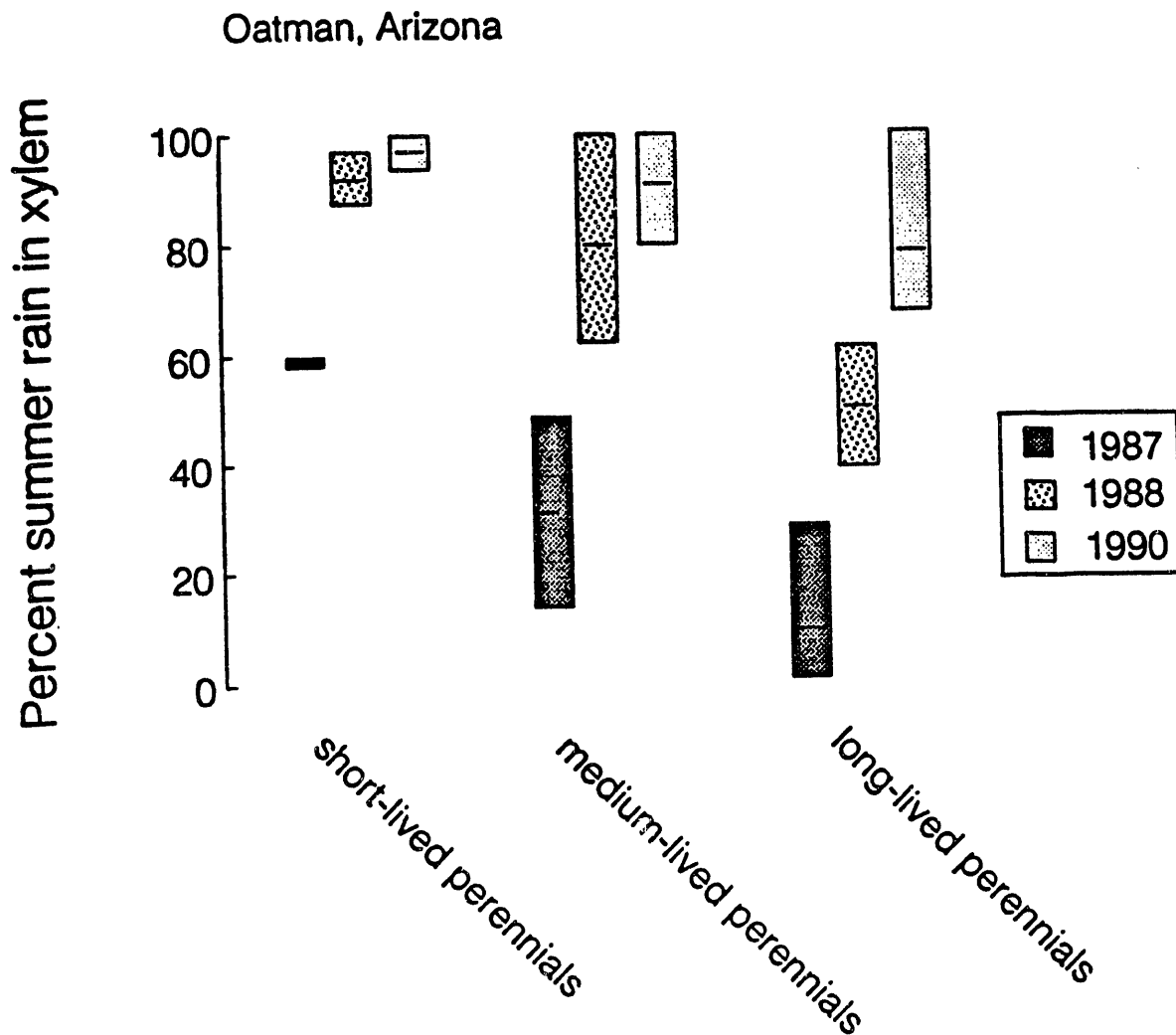


Figure 7. The percentage of summer rain in xylem sap of perennial species at a Sonoran Desert site near Oatman, Arizona during successive summers. There was no summer precipitation during 1989. Boxes represent entire range of values observed for short-lived (2-5 yr), medium-lived (10-50 yr), and long-lived (> 50 yr) perennials from both wash and slope microhabitats. Horizontal bar indicates the average value for that life form.

result is surprising, since root excavation studies show that virtually all perennials have some roots in the upper soil layers. At the Sonoran Desert site in Oatman, substantial use of summer rains by long-lived perennials occurred only in the unusually wet summer of 1990 (but may be confounded by microsite effects).

At Stud Horse Point, summer precipitation was above average in both 1989 and 1990, yet a number of the common perennial species at Stud Horse Point appear to have a limited capacity to utilize summer rains. As a result, δD values of xylem sap differed significantly among life forms during the summer (ANOVA, $F = 35.37$, $df = 3$, $p < .001$) (Table 4). Annuals and the one succulent perennial in the community utilized only the summer rains, whereas herbaceous and woody perennials used different mixtures of winter and summer water sources. Two deeply-rooted perennials utilized little of the summer precipitation and appeared instead to be accessing ground water or remaining winter soil moisture, since the δD values of stem waters were similar to that of well water. The difference in δD values of herbaceous versus all woody perennials was significant (Student's t -test, $t = 3.46$, $df = 18$, $p = .003$). Using a two-end-member linear mixing model, we calculated that, on average, 91% of the waters in herbaceous perennials and 57% of the waters in woody species were from summer rains.

By the autumn drought period, both herbaceous and woody perennials had shifted between possible water sources. With the upper soil layers depleted, perennial species switched back to exploit the remaining moisture in deeper soil layers (Table 4) and there was no difference in the δD values of stem waters among perennial types at that time ($p = 0.273$). Consequently during this drought period, woody and herbaceous perennials all competed for limiting moisture from the same depths. A similar pattern was seen when perennial plants were sampled in the drought period in early July before the onset of summer rains (Table 4). During that early summer drought period, δD values of herbaceous and woody perennial stem waters were again not different from each other ($p = .192$). Thus, in the drought periods of early summer and again in fall, as well as in the wet periods following winter rains, herbaceous and woody perennials utilized the same water source, soil moisture at greater depths. During drought periods plants may compete for soil moisture, and the effects of limited moisture would impact growth, reproduction, and survival (Ehleringer, 1984). In contrast, it is only during the rainy summer months that herbaceous perennials have apparent greater access to soil moisture (from summer rains) than do woody perennials, and thus should be able to gain a competitive advantage by utilizing this critical resource which seems not as utilized by woody perennials.

The δD values for xylem sap of all species during the summer were marginally correlated with water stress levels as measured by midday water potentials, indicating that species with access to summer rains were

less water stressed (1989: $r = 0.396$, $n = 24$, $p = .055$; 1990: $r = 0.373$, $n = 26$, $p = .061$). This pattern, however, was obscured by including in the analysis the two deeply-rooted woody perennials that appeared to be accessing ground water. When these two species were eliminated from the analysis, water source and water stress were significantly correlated (1989: $r = 0.608$, $n = 22$, $p = .003$; 1990: $r = 0.449$, $n = 24$, $p = .028$). The negative relationship between plant access to summer precipitation and water stress was also reflected in the efficiency with which that water was used (again excluding the two species with direct access to ground water). When water stress was regressed against carbon isotope discrimination, there was a significant positive relationship ($p = .023$). Greater access to and utilization of summer rains was associated with decreased plant water-use efficiency in different species. The lack of uptake of appreciable amounts of summer precipitation by most woody perennials resulted in significantly lower water potentials in these species and presumably corresponding reductions in growth rate.

Community-level productivity studies have in the past indicated that growth of most woody desert perennials was limited to the spring, and that little aboveground growth occurred in some perennials in response to limited summer rains. There is a progressive change in root activities of Great Basin shrubs to greater soil depths during spring dry-down in response to decreasing soil moisture as a means of providing water to maintain photosynthetic activity into the summer period. Yet no studies that we are aware of provide information on why roots in the upper layers might not respond to summer rains. Why several of these perennial species seem not to utilize summer rains is unclear.

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