



**Heritability of Carbon Isotope Discrimination in *Gutierrezia microcephala*  
(Asteraceae)**

William S. F. Schuster, Susan L. Phillips, Darren R. Sandquist, James R. Ehleringer

*American Journal of Botany*, Volume 79, Issue 2 (Feb., 1992), 216-221.

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*American Journal of Botany*  
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## HERITABILITY OF CARBON ISOTOPE DISCRIMINATION IN *GUTIERREZIA MICROCEPHALA* (ASTERACEAE)<sup>1</sup>

WILLIAM S. F. SCHUSTER,<sup>2</sup> SUSAN L. PHILLIPS,  
DARREN R. SANDQUIST, AND JAMES R. EHLERINGER

Department of Biology and Stable Isotope Ratio Facility (SIRFER),  
University of Utah, Salt Lake City, Utah 84112

The carbon isotope composition (<sup>13</sup>C/<sup>12</sup>C) of C<sub>3</sub> plant tissues provides a long-term, integrated measure of photosynthetic metabolism. Quantitative genetic methods were used to study the inheritance of carbon isotope composition and several morphological characters in *Gutierrezia microcephala*, a short-lived desert perennial. Open-pollinated seed was collected from a population located near Lee's Ferry, Arizona, in an area that was disturbed approximately 20 years ago. Seeds were germinated and seedlings grown in a common greenhouse environment. Carbon isotope discrimination ( $\Delta$ ) and all morphological characters varied significantly among maternal families. Heritability of  $\Delta$  was estimated as 81% in the greenhouse and as 92% using the regression of family mean  $\Delta$  on parent  $\Delta$  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  $\Delta$ . The corresponding genetic correlations were similar in magnitude and direction, but did not differ significantly from zero. These results imply the existence of heritable differences in physiology associated with carbon assimilation and water loss within populations, and the potential for microevolutionary change through natural selection.

Over the past two decades, many studies have documented interspecific variation in plant carbon isotope composition (<sup>13</sup>C/<sup>12</sup>C) (Farquhar, Ehleringer, and Hubick, 1989). The <sup>13</sup>C/<sup>12</sup>C composition of plant materials is lower than that of atmospheric carbon dioxide, because of discrimination processes by photosynthetic carboxylation enzymes and the slower diffusion of <sup>13</sup>CO<sub>2</sub> relative to <sup>12</sup>CO<sub>2</sub> (Farquhar, O'Leary, and Berry, 1982). While carbon isotope composition has historically been presented in delta notation ( $\delta$ ) as carbon isotope ratio relative to the Pee Dee belemnite (PDB) standard, Farquhar and Richards (1984) proposed a more direct measure, carbon isotope discrimination ( $\Delta$ ), which reflects the fractionation relative to the source carbon (atmospheric CO<sub>2</sub>).

At the interspecific level, the largest differences in  $\Delta$  (on the order of 22‰) reflect different photosynthetic pathways: C<sub>3</sub>, C<sub>4</sub>, and Crassulacean acid metabolism (O'Leary, 1988; Farquhar, Ehleringer, and Hubick, 1989). Yet among C<sub>3</sub> taxa,  $\Delta$  values can differ by 12‰, and within individual C<sub>3</sub> species by 4‰–5‰. Within C<sub>3</sub> plants, differences in carbon isotope discrimination have been correlated with differences in physiological processes such as intercellular CO<sub>2</sub> concentration (Farquhar, Ehleringer, and Hubick, 1989), water-use efficiency (Farquhar, Ehleringer, and Hubick, 1989), nitrogen-use efficiency (DeLucia and Schlesinger, 1991), and leaf conductance (Ehleringer, 1990), with differences in life history characteristics such as longevity (Ehleringer and Cooper, 1988), life form

(Smedley et al., 1991), and maturity date (Ehleringer et al., 1990; Geber and Dawson, 1990), and with differences in environmental conditions, such as light levels (Zimmerman and Ehleringer, 1990), elevation (Vitousek, Matson, and Turner, 1988), drought stress (Masle and Farquhar, 1988; Toft, Anderson, and Nowak, 1989), air pollution (Martin, Bytnerowicz, and Thorstenson, 1988), and salinity (Guy, Reid, and Krouse, 1980). Thus  $\Delta$  is a complex character, representing an integrated measure of photosynthetic metabolism, water use, and environmental influence.

From recent studies, we know that substantial variation in  $\Delta$  values can occur within seemingly homogeneous populations of aridland species (J. Ehleringer et al., unpublished data). It is unclear how much of this variation was the result of environmental vs. genetic components (but see Geber and Dawson, 1990). If plant populations possess significant additive genetic variance for  $\Delta$ , it would imply that heritable differences in carbon acquisition physiology exist with the potential for microevolutionary change through natural selection.

In this paper, we present results of a quantitative genetic study of carbon isotope discrimination and growth characteristics in thread snakeweed (*Gutierrezia microcephala* [DC.] Gray), a short-lived perennial of the Asteraceae common to the deserts of the American southwest. Since *G. microcephala* frequently colonizes disturbed areas yet is also able to persist in undisturbed communities, we hypothesized that genetic variation for physiological behavior could be a factor in its success. In one natural population near Lee's Ferry, Arizona, we found wide variation in  $\Delta$  values despite the appearance of environmental homogeneity. To study the inheritance of  $\Delta$  and growth characters, we randomly selected 24 individuals from this population and grew their open-pollinated progeny in a greenhouse. The experiment was designed to address three basic questions: 1) How similar are  $\Delta$  values of individuals in the field to those of their offspring grown in a common greenhouse environment? 2) Is there significant among-family variation in discrimination, and what is the esti-

<sup>1</sup> Received for publication 22 April 1991; revision accepted 26 September 1991.

The authors thank Mary Alyce Kobler and the greenhouse staff at the University of Utah for assistance, Steve Klassen and Christina Thomson for help with plant measurement, harvest, and data handling; Windy Ike for carbon isotope analyses; the Bureau of Land Management for allowing study at our field site; Lisa Donovan, Vince Eckhart, Monica Geber, Todd Dawson, Thomas Mitchell-Olds, and Barry Martin for helpful reviews of the manuscript; and Sara Via for suggestions on calculating genetic correlations. This research was supported by grants from the Ecological Research Division, Office of Health and Environmental Research, U.S. Department of Energy.

<sup>2</sup> Author for correspondence.

mated heritability of  $\Delta$ ? and 3) Is  $\Delta$  genetically or phenotypically correlated with morphological characters?

## MATERIALS AND METHODS

**Field population and sampling**—Our field population was located 11.5 km north of Lee's Ferry, Arizona, at an elevation of 1,340 m. The plant community is dominated by blackbrush (*Coleogyne ramosissima* Torr.), with *Gutierrezia microcephala* especially prevalent in disturbed areas. All 214 *G. microcephala* plants within a 200-m<sup>2</sup> area were tagged and mapped in early October 1989. In late October, we randomly selected 24 of these plants with adequate seed set and collected seed for the greenhouse study. Our sample was biased toward the larger, more fecund plants in the population at that time since most of the smaller plants and some of the largest plants did not produce enough seed for collection. In April 1990 we sampled leaves for carbon isotope analysis from each of the 24 parent plants as well as from 50 additional, randomly selected plants. This collection consisted of ten leaves per plant from the first matured flush of leaves produced following the spring rains.

**Greenhouse experiment**—Seeds were air dried for 4 wk and then placed under a mist bench in a perlite/vermiculite mixture for germination. Three weeks later 30 seedlings from each family were planted in individual 15-cm pots. Ten pots from each family were placed in each of three blocks in a greenhouse at the University of Utah in Salt Lake City, Utah (elev. 1,450 m above sea level). Pot positions were randomized within blocks every 1 to 2 wk. Plants were started under natural light, then slowly increased to 14-hr days under banks of sodium vapor and mercury halide high-intensity lamps (light intensity > 800  $\mu\text{E m}^{-2} \text{s}^{-1}$ ). All plants were watered daily and fertilized weekly with 1/2-strength Hoagland's solution (Epstein, 1972) or Peter's Professional 20-20-20 fertilizer. Air temperatures were maintained between 32 C during the day and 17 C at night, and soil temperature varied between 28 C and 18 C. Relative humidity was maintained at 26%, and fans were used to ensure adequate ventilation and mixing of air. All plants were harvested after 12 wk of growth. Mortality was less than 1%.

The following characters were measured on each plant at harvest: plant height, maximum plant width, plant width perpendicular to the maximum width, and length and maximum width of each of three randomly selected leaves. Plants were then separated into above- and belowground parts. Roots were carefully washed to remove soil, then all parts were dried to constant weight.

**Carbon isotope analysis**—Carbon isotope composition was determined on bulked samples. For field-grown materials, this consisted of ten leaves per plant from the April field collection. For the greenhouse harvests, this consisted of all aboveground material from each plant in Block 1 (ten plants from each family). Sample storage and preparation followed Ehleringer and Osmond (1989). All samples were dried in an oven for 24 hr at 60 C, ground to a fine powder with mortar and pestle, and then subsampled for isotopic analysis. Carbon isotope ratio ( $\delta^{13}\text{C}$ ) relative to the PDB standard was determined on an iso-

tope ratioing mass spectrometer (delta S, Finnigan MAT, San Jose, CA; Ehleringer and Osmond, 1989). Standard deviation of each measurement as estimated from long-term observations of a cabbage standard was  $\pm 0.10\%$ . Leaf carbon isotope discrimination ( $\Delta$ ) was calculated from leaf carbon isotope ratios ( $\delta_{\text{leaf}}$ ) as

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

where  $\delta_{\text{air}}$  was measured as  $-9.0\%$  in the greenhouse experiments and  $-8.0\%$  in the field (Ehleringer, 1991).

**Data analysis**—Computations and statistical analyses were performed using Statistical Analysis Systems procedures GLM, VARCOMP, and CORR (SAS Institute, 1985). Composite variables mean leaf length and width per individual, mean plant width, and root-to-shoot biomass ratios were calculated from the raw data. Several characters showed significant deviations from normality and thus were log-transformed prior to analysis (leaf length, plant width, and  $\Delta$  did not require transformation). Log transformation may remove the dependence of variance on the mean, and most characters had homogeneous variances after the transformation. Leaf width still exhibited departures from normality after transformation; thus results for this variable should be interpreted with caution.

Significant family effects were tested for all characters using a Model II analysis of variance. All variables were analyzed using two-way analysis of variance with family and block treated as random effects, except for  $\Delta$ , which was measured only in block 1, thus constraining the analysis to family effects. We estimated the heritability of each character by equating the observed variance components to causal components of variance according to the methods for a half-sib analysis in Falconer (1981). In this design, the among-families component of variance estimates one-fourth of the additive genetic variance plus 1/16 of the epistatic variance, which we assumed to be zero for our analyses (Falconer, 1981). We calculated the intraclass correlation coefficient ( $t$ ) for each character as the ratio of the among-families variance to total variance, and estimated heritabilities as  $4t$ . Since heritability is estimated as  $2t$  in a full-sib design, this method overestimated actual heritabilities to the extent that full-sibs were present in our greenhouse families. However, we chose a half-sib design based on several lines of evidence: only one seed is produced per flower, we randomly sampled seeds from a much larger total number of seeds produced on most plants, the flowers are mechanically adapted for outbreeding (Solbrig, 1960), and preliminary electrophoretic data indicated an outbreeding mating system in the population (W. Schuster, personal observation). Standard errors of our estimates were based on Falconer (1981). Our choice of a least-squares approach rather than a maximum-likelihood approach as advocated by Shaw (1987) was based on the nearly complete balance of our design.

The heritability of  $\Delta$  was also estimated using a regression of family mean  $\Delta$  on parent  $\Delta$  (Falconer, 1981). Narrow-sense heritability was estimated as twice the regression coefficient (again assuming half-sib families), and the standard error of the coefficient was doubled to obtain the standard error of these heritability estimates. Heri-

tability in nature was estimated using the method of Riska, Prout, and Turelli (1989). This method provides a minimum estimate of heritability in nature, using the formula:

$$h^2 \geq 4B^2(\sigma^2_{(PN)}/\sigma^2_{(AL)})$$

where  $B$  is the regression coefficient of offspring on parent,  $\sigma^2_{(PN)}$  is the phenotypic variance in nature (estimated by the observed variance of the selected parents), and  $\sigma^2_{(AL)}$  is the additive genetic variance in the laboratory (estimated from the half-sib analysis).

Phenotypic correlations among characters were calculated as Pearson's product-moment correlations of transformed values. Genetic correlations were calculated by two methods: the product-moment correlation of family means between all pairs of characters (Via, 1984) and the ratio of the genetic covariance between each pair of traits divided by the square root of the product of the genetic variances for each trait (Falconer, 1981). Results from the latter method are presented here, but these did not differ substantially from family means estimates. Standard errors were calculated according to Falconer (1981).

## RESULTS

Leaf samples from the parent plants and a subsample of the surrounding population indicated that  $\Delta$  was approximately normally distributed within the natural population (Kolmogorov-Smirnov one-sample test,  $P > 0.28$ ), with a range of nearly 4‰ (Fig. 1). Discrimination in the selected parent plants did not differ significantly from the rest of the sampled plants in the population (Kolmogorov-Smirnov two-sample test,  $P > 0.25$ ), and thus they were judged to be a representative sample. However, the range of  $\Delta$  values in the parents was less than 3‰, and they did not include plants from either tail of the population distribution.

All of the measured traits exhibited significant family-based variation (Table 1). Discrimination exhibited the highest heritability of any character ( $h^2 = 0.81$ ), and low overall variation as measured by the coefficient of variation (3.3%). All plant size and leaf characters showed highly significant variation among families. Dry weight of above- and belowground tissues showed the greatest amount of variation and the lowest heritabilities among the measured traits.

Regression of family mean  $\Delta$  on adult plant  $\Delta$  yielded a highly significant relationship ( $P < 0.001$ ). The slope of the relationship ( $b = 0.46$ ) provided a heritability estimate of 0.92. In all cases  $\Delta$  was greater in greenhouse-

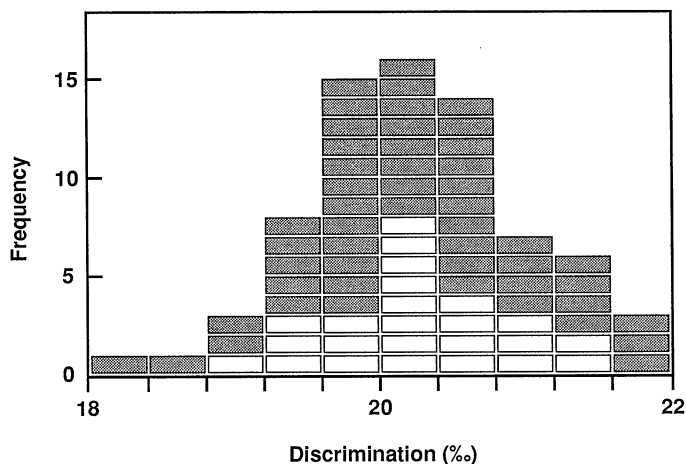


Fig. 1. Frequency histogram of carbon isotope discrimination values ( $\Delta$ ) of leaves from 74 plants in the snakeweed study population, including those 24 plants chosen as maternal parents in the greenhouse study (parent values shown in white).

grown progeny than in parent leaf tissues produced in the field. These data resulted in a minimum field heritability estimate for  $\Delta$  of 0.54.

Phenotypic and genetic correlations among traits were generally of the same sign, although some differences in magnitude were evident (Table 2). Phenotypic correlations among all plant size traits were highly significant, and genetic correlations among these traits were similar or somewhat lower in magnitude. Phenotypically, plant height, plant width, and leaf size characters were significantly correlated with  $\Delta$ , with the direction being positive for all traits except leaf width. Phenotypic correlations between  $\Delta$  and components of plant weight were also positive, but nonsignificant at the 0.05 level. None of the genetic correlations between  $\Delta$  and other traits were significant. However, the direction and magnitude of these estimates were generally quite similar to the phenotypic correlations, and the genetic correlation between  $\Delta$  and leaf width approached statistical significance ( $P = 0.06$ ).

## DISCUSSION

**Genetic control of  $\Delta$** —Our results indicate that there is genetic variation influencing carbon isotope discrimination in *Gutierrezia microcephala*. Carbon isotope composition reflects the ratio of intercellular to ambient  $\text{CO}_2$

TABLE 1. Mean, coefficient of variation, range, significance of family effects and heritability estimates for all measured traits

Character	Mean	CV	Range of family means		F (sig.) <sup>a</sup>	h <sup>2</sup> (SE)
			Low	High		
$\Delta$ (‰)	22.0	3.3	21.4	22.9	3.56***	0.81 (0.280)
Plant height (mm)	38.6	48.2	24.3	53.9	3.26***	0.40 (0.139)
Plant width (mm)	67.1	31.8	50.3	82.4	2.73**	0.32 (0.123)
Leaf length (mm)	37.7	27.0	28.9	45.4	3.78***	0.43 (0.146)
Leaf width (mm)	3.5	21.5	3.1	4.2	4.83***	0.44 (0.148)
Shoot weight (mg)	245.1	85.9	159.1	392.4	2.01*	0.22 (0.099)
Root weight (mg)	169.5	87.5	88.4	279.2	2.12*	0.28 (0.112)
Root/Shoot ratio	0.69	28.5	0.56	0.91	2.22*	0.38 (0.137)

<sup>a</sup> Significance levels for family effects: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

TABLE 2. Genetic (above the diagonal) and phenotypic (below the diagonal) correlation matrix and significance level (below the correlations) for all measured traits

Character	Plant		Leaf		Shoot weight	Root weight	Root/shoot ratio	$\Delta$
	Height	Width	Length	Width				
Plant height		0.55 (0.01)	0.65 (0.00)	-0.40 (0.06)	0.61 (0.00)	0.48 (0.02)	-0.07 (0.76)	0.19 (0.24)
Plant width	0.74 (0.00)		0.92 (0.00)	0.03 (0.91)	0.67 (0.00)	0.55 (0.01)	0.09 (0.67)	0.07 (0.72)
Leaf length	0.72 (0.00)	0.91 (0.00)		-0.04 (0.85)	0.59 (0.00)	0.47 (0.02)	0.13 (0.13)	0.12 (0.44)
Leaf width	-0.34 (0.00)	-0.17 (0.00)	-0.15 (0.00)		-0.10 (0.64)	-0.02 (0.94)	0.09 (0.68)	-0.39 (0.06)
Shoot weight	0.70 (0.00)	0.82 (0.00)	0.74 (0.00)	-0.04 (0.33)		0.92 (0.00)	-0.12 (0.59)	0.11 (0.50)
Root weight	0.67 (0.00)	0.79 (0.00)	0.71 (0.00)	-0.05 (0.21)	0.95 (0.00)		0.05 (0.83)	0.14 (0.40)
Root/shoot	0.00 (0.99)	0.00 (0.99)	-0.02 (0.68)	-0.05 (0.20)	0.03 (0.51)	0.33 (0.00)		0.18 (0.25)
$\Delta$	0.21 (0.00)	0.21 (0.00)	0.22 (0.00)	-0.22 (0.00)	0.11 (0.10)	0.10 (0.12)	0.03 (0.64)	

( $c_i/c_a$ ; Farquhar, O'Leary, and Berry, 1982), and thus these results imply the existence of genetically controlled differences in average daytime  $c_i$ . Our estimate of heritability from the sib analysis suggests that genotype is the most important factor determining the carbon isotope composition of these plants in a common environment. Regression of family mean  $\Delta$  on parent  $\Delta$  yielded a similarly high estimate of heritability. However, since field plants can exhibit significant temporal variation in  $\Delta$  (see references cited in introduction), sib analysis may be a more reliable method for estimating heritability of this trait than parent-offspring regression.

This is one of the first reports of genetic control of  $\Delta$  in a nonagricultural, perennial plant species. Geber and Dawson (1990) reported significant family-based variation for  $\Delta$  in the introduced, self-fertilizing annual, *Polygonum arenastrum*. Several studies of agricultural plants have produced broad-sense estimates of the heritability of  $\Delta$  between 60% and 90% (Hubick, Shorter, and Farquhar, 1988; Hall et al., 1990; Johnson et al., 1990). Such estimates describe the proportion of phenotypic variance that is due to underlying genetic factors, but cannot be used to accurately predict parent-to-offspring transmission or the response of a trait to selection, since the contributions of nonadditive genetic factors are unknown. In our study, both the parent-offspring and half-sib estimates are of narrow-sense heritability, although they may be upwardly biased if families were not strictly related as half-sibs (discussed in Materials and Methods). In the extreme case of all families consisting entirely of full-sibs, our heritability estimates would need to be halved. Some variance due to a common maternal environment may also be included in these estimates, although some studies have indicated that maternal effects on discrimination may not be significant (Hubick, Shorter, and Farquhar, 1988; M. Brick, personal communication).

We expect the heritability of discrimination in field populations to be less than our greenhouse estimate due to greater environmental variation (e.g., Primack and Antonovics, 1981). Our best estimate of a lower bound for

the heritability of  $\Delta$  within our field population is 0.54, using the relationship between the additive genetic variance for  $\Delta$  in the greenhouse and the phenotypic variance in the field population. The existence of significant, additive genetic variance for discrimination within this natural population suggests that  $\Delta$  is a trait that can respond to natural selection.

**Correlation of  $\Delta$  and growth**—We found a significant, positive phenotypic correlation between  $\Delta$  and growth (as measured by final plant size measurements), although the correlation coefficients were only in the range of 0.20 to 0.22. Positive phenotypic correlations between  $\Delta$  and biomass or yield have been previously reported in wheat (Condon, Richards, and Farquhar, 1987), tomato (Martin and Thorstenson, 1988), beans (White, Castillo, and Ehleringer, 1990), and wheatgrass (Johnson et al., 1990). In contrast, Hubick, Farquhar, and Shorter (1986) reported negative correlations between  $\Delta$  and yield in peanut. Such phenotypic correlations all have underlying genetic and environmental components. Significant genetic correlations generally indicate pleiotropy, the existence of genes that affect both traits, although they can also result from linkage disequilibrium (Falconer, 1981; Mitchell-Olds and Rutledge, 1986).

None of the genetic correlations between  $\Delta$  and size traits were significant at the 0.05 level. This was partly a result of the reduced statistical power of genetic correlations as compared to phenotypic correlations, as only genetic correlations in excess of 0.40 could be considered significantly different from zero. Nevertheless, the genetic correlations between  $\Delta$  and plant biomass or size characters were always of the same sign and generally of the same magnitude as the phenotypic correlations. This was true also when family means were used to estimate the genetic correlations. Thus some of the same genes that affect carbon isotope discrimination may indeed be important to plant growth, although the resulting correlations are not very large.

**Evolutionary implications**—Falconer (1981) and Mousseau and Roff (1987) have noted that fitness-related traits in animals typically exhibit lower heritabilities than traits expected to have little impact on fitness. While simple, directional selection should act to reduce additive genetic variance over time, several studies have shown that heritable variation for some fitness-related characters is maintained in natural populations (van Noordwijk, van Balen, and Sharloo, 1980; Findlay and Cooke, 1983; Coyne and Beecham, 1987; Mousseau and Roff, 1987; Prout and Barker, 1989). A variety of mechanisms have been implicated for the maintenance of this variation including mutation, heterozygote advantage, fluctuating selection pressures, antagonistic pleiotropy, and the lack of an equilibrium state (summarized in Mousseau and Roff, 1987).

Several previous reports have linked  $\Delta$  to overall plant performance. For instance, a negative relationship is expected between  $\Delta$  and water-use efficiency (A/E) in  $C_3$  plant species based on theory (Farquhar, O'Leary, and Berry, 1982), and this expectation has been realized in many studies (Farquhar and Richards, 1984; Hubick, Farquhar, and Shorter, 1986; Hubick, Shorter, and Farquhar, 1988; Martin and Thorstenson, 1988; Ehleringer et al., 1990; Geber and Dawson, 1990; Johnson et al., 1990). If this is also true in *G. microcephala*, plants with low  $\Delta$  may have an advantage in the field due to higher A/E. However, plants in our experiment with higher  $\Delta$  values were larger both in terms of biomass and plant size after 12 wk of growth, and these traits could significantly affect plant fitness in natural communities. If these relationships do hold in nature, high and low  $\Delta$  values might indicate different adaptive strategies including suites of correlated characters such as photosynthesis and transpiration rates, growth rate, and water-use efficiency (see also Lechowicz, 1984; Lechowicz and Blais, 1988; Geber and Dawson, 1990). Such differences may also have important effects on plant fecundity.

A variety of theoretical models and empirical evidence indicates that heterogenous environments can be important in the maintenance of genetic variation (Hedrick, Ginevan, and Ewing, 1976; Ewing, 1979; Gillespie and Turelli, 1989), and the spatial and temporal variation in selective regimes associated with such heterogeneity might explain the persistence of significant additive genetic variance for  $\Delta$  in our study population. *G. microcephala* dominates most areas that were disturbed approximately 20 years ago during the construction of power lines for the Glen Canyon dam. However, it is also a common component of relatively undisturbed neighboring communities that have a much greater plant density and are dominated by the long-lived blackbrush (*Coleogyne ramosissima*). Temporally, these arid environments are characterized by unpredictable precipitation regimes and extended periods of drought. In view of this heterogeneity, we suggest that there may be an advantage to more conservative use of water and correspondingly lower  $\Delta$  under some situations, but that an opposite strategy may be favored under other conditions. For instance, Donovan and Ehleringer (1991) present evidence that characteristics associated with low  $\Delta$  may be selectively advantageous for established plants, while selection may favor high  $\Delta$  during seedling establishment. Thus, advantages associated with different physiological strategies might result in

fluctuating, and possibly disruptive, selection and the maintenance of genetic variation for  $\Delta$ .

Our heritability estimates indicate an ongoing potential for evolutionary response to selection in *G. microcephala*. However, the response to natural selection acting on any quantitative character will depend on the parameters of the genetic variance-covariance matrix for affected and correlated traits (Lande, 1982; Lande and Arnold, 1983). Genetic correlation of  $\Delta$  with other characters such as growth rate could constrain the rate and direction of evolutionary changes. Further inquiries into correlations between  $\Delta$  and growth characters, as well as studies of the response of  $\Delta$  to selection, will be needed to improve our understanding of the evolution of physiological solutions to trade-offs between carbon gain and water loss in arid environments.

#### LITERATURE CITED

- CONDON, A. G., R. A. RICHARDS, AND G. D. FARQUHAR. 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field-grown wheat. *Crop Science* 27: 996–1001.
- COYNE, J. A., AND E. BEECHAM. 1987. Heritability of two morphological characters within and among natural populations of *Drosophila melanogaster*. *Genetics* 117: 727–737.
- DELUCIA, E. H., AND W. H. SCHLESINGER. 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* 72: 51–58.
- DONOVAN, L. A., AND J. R. EHLERINGER. 1991. Ecophysiological differences among juvenile and reproductive plants of several woody species. *Oecologia* 86: 594–597.
- EHLERINGER, J. R. 1990. Correlations between carbon isotope discrimination and leaf conductance to water vapor in common beans. *Plant Physiology* 93: 1422–1425.
- . 1991.  $^{13}C/^{12}C$  fractionation and its utility in terrestrial plant studies. In D. C. Coleman and B. Fry [eds.], *Carbon isotope techniques*, 187–200. Academic Press, New York, NY.
- , AND T. A. COOPER. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76: 562–566.
- , AND C. B. OSMOND. 1989. Stable isotopes. In R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel [eds.], *Plant physiological ecology*, 281–300. Chapman and Hall, New York, NY.
- , J. W. WHITE, D. A. JOHNSON, AND M. BRICK. 1990. Carbon isotope discrimination, photosynthetic gas exchange, and transpiration efficiency in beans and range grasses. *Acta Oecologia* 11: 611–625.
- EPSTEIN, E. 1972. *Mineral nutrition of plants: principles and perspectives*. John Wiley and Sons, New York, NY.
- EWING, E. P. 1979. Genetic variation in a heterogenous environment. VII. Temporal and spatial heterogeneity in infinite populations. *American Naturalist* 114: 197–212.
- FALCONER, D. S. 1981. *Introduction to quantitative genetics*. Longman, New York, NY.
- FARQUHAR, G. D., J. R. EHLERINGER, AND K. T. HUBICK. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503–537.
- , M. H. O'LEARY, AND J. A. BERRY. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* 9: 121–137.
- , AND R. A. RICHARDS. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* 11: 539–552.
- FINDLAY, C. S., AND F. COOKE. 1983. Genetic and environmental components of clutch size variance in a wild population of lesser snow geese (*Anser caerulescens caerulescens*). *Evolution* 37: 724–734.
- GEBER, M. A., AND T. E. DAWSON. 1990. Genetic variation in and covariation between leaf gas exchange, morphology, and develop-

- ment in *Polygonum arenastrum*, an annual plant. *Oecologia* 85: 153–158.
- GILLESPIE, J. H., AND M. TURELLI. 1989. Genotype-environment interaction and the maintenance of polygenic variation. *Genetics* 121: 129–138.
- GUY, R. D., D. M. REID, AND H. R. KROUSE. 1980. Shifts in carbon isotope ratios of two C<sub>3</sub> halophytes under natural and artificial conditions. *Oecologia* 44: 241–247.
- HALL, A. E., R. G. MUTTERS, K. T. HUBICK, AND G. D. FARQUHAR. 1990. Genotypic differences in carbon isotope discrimination by cowpea under wet and dry field conditions. *Crop Science* 30: 300–305.
- HEDRICK, P. W., M. E. GINEVAN, AND E. P. EWING. 1976. Genetic polymorphism in heterogenous environments. *Annual Review of Ecology and Systematics* 7: 1–32.
- HUBICK, K. T., G. D. FARQUHAR, AND R. SHORTER. 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germ plasm. *Australian Journal of Plant Physiology* 13: 803–816.
- , R. SHORTER, AND G. D. FARQUHAR. 1988. Heritability and genotype × environment interactions of carbon isotope discrimination and transpiration efficiency in peanut (*Arachis hypogaea* L.). *Australian Journal of Plant Physiology* 15: 799–813.
- JOHNSON, D. A., K. H. ASAY, L. L. TIESZEN, J. R. EHLERINGER, AND P. G. JEFFERSON. 1990. Carbon isotope discrimination—potential in screening cool-season grasses for water-limited environments. *Crop Science* 30: 338–343.
- LANDE, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63: 607–615.
- , AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1227.
- LECHOWICZ, M. J. 1984. The effects of individual variation in physiological and morphological traits on the reproductive capacity of the common cocklebur, *Xanthium strumarium* L. *Evolution* 38: 833–844.
- , AND P. A. BLAIS. 1988. Assessing the contributions of multiple interacting traits to plant reproductive success: environmental dependence. *Journal of Evolutionary Biology* 1: 255–273.
- MARTIN, B., A. BYTNEROWICZ, AND Y. R. THORSTENSON. 1988. Effects of air pollutants on the composition of stable carbon isotopes,  $\delta^{13}\text{C}$ , of leaves and wood, and on leaf injury. *Plant Physiology* 88: 218–223.
- , AND Y. R. THORSTENSON. 1988. Stable carbon isotope composition ( $\delta^{13}\text{C}$ ), water use efficiency, and biomass productivity of *Lycopersicon esculentum*, *Lycopersicon pennellii*, and the F<sub>1</sub> hybrid. *Plant Physiology* 88: 213–217.
- MASLE, J., AND G. D. FARQUHAR. 1988. Effects of soil strength on the relation of water-use efficiency and growth to carbon isotope discrimination in wheat seedlings. *Plant Physiology* 86: 32–38.
- MITCHELL-OLDS, T., AND J. J. RUTLEDGE. 1986. Quantitative genetics in natural plant populations: a review of the theory. *American Naturalist* 127: 379–402.
- MOUSSEAU, T. A., AND D. A. ROFF. 1987. Natural selection and the heritability of fitness components. *Heredity* 59: 181–197.
- O'LEARY, M. H. 1988. Carbon isotopes in photosynthesis. *BioScience* 38: 328–336.
- PRIMACK, R. B., AND J. ANTONOVICS. 1981. Experimental ecological genetics in *Plantago*. V. Components of seed yield in the ribwort plantain *Plantago lanceolata*. *Evolution* 35: 1069–1079.
- PROUT, T., AND J. S. F. BARKER. 1989. Ecological aspects of the heritability of body size in *Drosophila buzzatii*. *Genetics* 123: 803–813.
- RISKA, B., T. PROUT, AND M. TURELLI. 1989. Laboratory estimates of heritabilities and genetic correlations in nature. *Genetics* 123: 865–871.
- SAS INSTITUTE. 1985. SAS user's guide, version 5. SAS Institute Inc., Cary, NC.
- SHAW, R. G. 1987. Maximum-likelihood approaches applied to quantitative genetics of natural populations. *Evolution* 41: 812–826.
- SMEDLEY, M. P., T. E. DAWSON, J. P. COMSTOCK, L. A. DONOVAN, D. E. SHERRILL, C. S. COOK, AND J. R. EHLERINGER. 1991. Seasonal carbon isotope discrimination in a grassland community. *Oecologia* 85: 314–320.
- SOLBRIG, O. T. 1960. Cytotaxonomic and evolutionary studies in the North American species of *Gutierrezia* (Compositae). *Contributions of the Gray Herbarium* 184: 1–63.
- TOFT, N. L., J. E. ANDERSON, AND R. S. NOWAK. 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. *Oecologia* 80: 11–18.
- VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SHARLOO. 1980. Heritability of ecologically important traits in the great tit (*Parus major*). *Ardea* 68: 193–203.
- VIA, S. 1984. The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. *Evolution* 38: 896–905.
- VITOUSEK, P. M., P. A. MATSON, AND D. R. TURNER. 1988. Elevational and age gradients in Hawaiian montane rainforest: foliar and soil nutrients. *Oecologia* 77: 565–570.
- WHITE, J. W., J. A. CASTILLO, AND J. R. EHLERINGER. 1990. Associations between productivity, root growth and carbon isotope discrimination in *Phaseolus vulgaris* under water deficit. *Australian Journal of Plant Physiology* 17: 189–198.
- ZIMMERMAN, J. K., AND J. R. EHLERINGER. 1990. Carbon isotope ratios are correlated with irradiance levels in the Panamanian orchid *Cata-setum viridiflavum*. *Oecologia* 83: 247–249.