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Correlating genetic variation in carbon isotopic composition with complex climatic gradients

(desert ecology/humidity gradient/stable isotope/transpiration efficiency/water-use efficiency)

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ABSTRACT **Genetic variation in both carbon isotope discrimination and the proportions of leaf and photosynthetic twig tissues were observed in ecotypes of *Hymenoclea salsola* T.G., a common shrub in the deserts of the western United States, when grown under common garden conditions. These variations were correlated with climatic conditions in the habitats of origin through a model that described the leaf-to-air water vapor gradients experienced by plants during the growing season. Both carbon isotope discrimination and the proportion of leaves in the canopy were lower in plants derived from habitats with higher leaf-to-air water vapor gradients, despite the fact that some of these sites received relatively high amounts of annual precipitation. These patterns were consistent with the notion that plants are able to maintain substantial control of water-use efficiency over large environmental gradients of temperature and moisture availability.**

Continuous, genetically determined variation occurs in physiological and morphological traits of many organisms along climatic gradients (1–3). Understanding the biological responses to geographic and climatic variation is of great importance in evaluating ecological adaptation. Unfortunately, the underlying functional relationships often remain obscure. The biological characters of interest often vary with a large number of highly correlated environmental parameters, such as temperature, precipitation, humidity, and insolation (1–4). In other cases, individual climatic variables may show very little correlation with the traits of interest, and descriptive parameters, such as elevation and latitude, which subsume both quantitative and qualitative patterns in several climatic variables, may show the tightest correlation with biological traits (5). Complex environmental gradients can be meaningfully interpreted only if explicit functional mechanisms linking organismal traits and environmental parameters can be defined.

One such mechanistic relationship for plants can be derived from standard diffusion equations describing the processes of CO_2 uptake during photosynthesis (A) and water-loss during transpiration (E) by photosynthetic organs:

$$A = (c_a - c_i)\frac{g}{1.6}, \qquad \nu = \frac{(e_i - e_a)}{p_{total}}, \qquad E = g\nu, \qquad [1]$$

where c is the CO_2 concentration as mol fraction; e is the absolute water vapor pressure; subscripts i and a represent intercellular and ambient locations, respectively; g is the leaf conductance to water vapor; and p_{total} is the total atmospheric pressure. Instantaneous water-use efficiency (A/E) is the ratio of net photosynthesis to transpiration, and it reduces to a constant multiplied by the ratio of the diffusion gradients in CO_2 and water vapor between a photosynthesizing organ and the surrounding atmosphere (6):

$$A/E = \frac{(c_a - c_i)}{1.6\nu}. \qquad [2]$$

Environmental temperatures and atmospheric humidity exert the major control over the magnitude of the leaf-to-air water vapor gradient (ν), especially when leaf and air temperatures are closely coupled as in microphyllous species (7, 8). In contrast, a number of biochemical, physiological, and morphological plant characters predominate in determining the magnitude of the gradient in CO_2 between the leaf intercellular spaces and the atmosphere. The effects of variation in these plant characters on photosynthetic gas exchange are temporally integrated by carbon isotope discrimination during photosynthesis, and this discrimination is recorded in the isotopic composition of accumulated plant biomass (9), providing a reliable long-term indicator of the gradient in CO_2 between atmosphere and intercellular air spaces.

We hypothesized that plant characters affecting intercellular CO_2 concentration would show compensatory genetic differentiation in response to climatic variation in the leaf-to-air water vapor gradient, thereby reducing climatic control over water-use efficiency. That is, in climates with drier atmospheres and/or higher air and leaf temperatures, plants should evolve to have lower intercellular CO_2 concentrations so that overall water-use efficiency remains constant across the climatic gradient. This relationship should be especially robust in hot, arid environments, where availability of water drives most ecological processes (10–12), and where ν reaches some of its highest values for terrestrial vegetation. We evaluated this hypothesis using *Hymenoclea salsola* T.G., a common drought-deciduous shrub widely distributed across the North American warm deserts.

A model was constructed to estimate direct environmental influences on water-use efficiency and to simultaneously account for differences across sites in the seasonal timing of photosynthetic activity. When tissue and air temperatures are tightly coupled as they are in arid lands (7, 8), ν is determined primarily by variation in air temperature; because humidity levels are low, ν can be closely approximated by calculating the saturation vapor pressure of the air ($e_{a,sat}$) based on temperature data from standard meteorological records (mean daily maxima for each month) and assuming in the first approximation that $\nu = e_{a,sat}/p_{total}$.

Annual mean values of ν, however, have limited physiological or ecological significance, because plants in desert ecosystems are inactive much of the year. Moreover, different rainfall patterns will result in phenological variation among sites, and environmental factors influencing water-use efficiency are relevant only during periods when sufficient soil moisture is available to permit photosynthetic activity. Temporal variations in the growing season among sites can be

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incorporated without bias by averaging the saturation vapor pressure expressed as a mol fraction ($p_{\mathrm{w,sat}}/p_{\mathrm{tot}}$) over each month of the year, using the monthly ratio of precipitation (P) to potential evapotranspiration (E_{p}) (calculated from ref. 13) as a weighting factor. We used the algorithm of Thornthwaite (13) in calculating E_{p}, because it has proven to be robust, and it can be calculated from easily available meteorological data from even very remote stations. More recent and sophisticated models could be substituted when input data are available. The effective seasonal leaf-to-air water vapor gradient (ω) is then calculated as

$$\omega = \left[\frac{1}{p_{\mathrm{total}}} \sum_{\mathrm{Jan}}^{\mathrm{Dec}} \left(e_{\mathrm{a,sat}} \frac{P}{E_{\mathrm{p}}}\right)\right] \Bigg/ \sum_{\mathrm{Jan}}^{\mathrm{Dec}} \frac{P}{E_{\mathrm{p}}}. \qquad [3]$$

ω is an index that ranks sites according to the mean evaporative demand expected during the most likely growing seasons throughout the year and has the same units as ν. If the assumptions of equivalent tissue and air temperatures and zero atmospheric humidity are satisfied [they are closely approached in many arid ecosystems (5, 14)], the value of ω converges on the actual mean growing-season value of ν. Since atmospheric humidity is always greater than zero, ω tends to overestimate mean growing-season ν but still accurately ranks sites if variation in e_{a} is small relative to variation in $e_{\mathrm{a,sat}}$. The ratio P/E_{p} is not allowed to exceed 1, indicating for that month that water was not limiting to growth. In the data analyses presented below, monthly precipitation in excess of potential evapotranspiration is assumed to be lost as runoff. The alternative assumption that excess precipitation is stored in the soil profile until lost as E_{p} was also evaluated. This alternative assumption would have the effect of increasing the moisture available for evapotranspiration in the warmer spring months, and thus increasing the relative importance of these months in the calculation of ω as described above. This effectively increased the value calculated for ω for all sites (data not shown), but it did not alter the ranking of any sites in this study nor significantly alter any of the measured correlations between ω and biological traits.

H. salsola is a warm desert sub-shrub (height 0.5–1.0 m) that is found from the northern extremes of the Mojave Desert in southern Nevada and east-central California southward through the Sonoran Desert into Mexico and Baja California. It is commonly found on deep sandy soils and has a taproot with moderate rooting depth. It often occurs in washes and small gullies, but it is not at all phreatophytic and readily takes up summer rainfall from surface soil layers when available (15). *H. salsola* is typical of most desert species in opportunistically responding to rainfall at any time of the year (10, 12, 16). Nonetheless, most vegetative growth occurs in the winter and spring even when rainfall is strongly bimodal with respect to winter and summer seasons. This is because the high summer temperatures cause rapid soil drying (10, 16) and mitigate growth responses to any but the largest precipitation events. This phenological behavior is incorporated in ω by using the monthly precipitation sufficiency ratio, P/E_{p} (13), as a weighting factor representing potential physiological activity. *H. salsola* is a microphyllous species with long terete leaves 1–2 mm in diameter (leaves are needle-shaped but not sclerophyllous). It also typifies a common desert specialization by having photosynthetic twigs as well as leaves engaging in net carbon assimilation (18). Relative to this discussion, photosynthetic twigs in *H. salsola* intrinsically operate at higher water-use efficiencies than leaves, and this is a general feature of shrubs that have photosynthetic twigs (18–20). Therefore, in photosynthetic-twigged, desert species, intraspecific variation in water-use efficiency may be achieved by changes in photosynthetic physiology (i.e., stomatal behavior or carboxylation capacity) at the organ level affecting intercellular $\mathrm{CO_2}$ concentration, by changes in the relative production of leaf versus twig photosynthetic surfaces at the canopy level, or both.

Individuals of *H. salsola* from native populations located throughout the Mojave and Sonoran Deserts of North America were transplanted and grown in a common garden in Littlefield, Arizona (Fig. 1). Naturally occurring young adults at each original field site were cut back to the ground, and dug up such that *ca.* 80–90% of the taproot biomass was collected intact. These taproots were planted in the common garden and allowed to grow for 2 years prior to sampling. Plants in the garden were spaced 4 m apart, and for these small shrubs little root overlap or competition for water should have occurred during the experiment. Natural, highly branched canopies had been reestablished at the end of the first year. Plants received modest supplemental watering during the first year of establishment but not during the second year, when measurements were made. Three current-year shoots per individual (five individuals per site of origin) were sampled in May for leaf/twig area ratios and leaf carbon isotopic ratio, and in September for twig carbon isotopic ratio. All samples represented new tissues produced that year, but while the May sample represents peak canopy development during the growing season, twig isotopic ratio samples had endured a summer drought.

The sites of origin for different *H. salsola* collections encompassed considerable climatic variation within the warm desert, with mean annual temperature ranging among sites from 15°C to 22°C, total annual precipitation from 92 to 254 mm, and the percentage of total rainfall coming in the warm summer months (June–September) from 14% to 49% (Table 1). When the plants collected from these diverse sites were sampled under uniform garden conditions, there was genetic differentiation in both carbon isotope discrimination and the degree to which leaves contributed to whole-plant photosynthetic surface area (Fig. 2). Carbon isotope discrimination was always lower in twig than in leaf tissues regardless of the population of origin, indicating that photosynthetic twigs always maintained lower intercellular $\mathrm{CO_2}$ concentrations than leaves. For both leaf and twig tissues, population-level differentiation in carbon isotope discrimination was a linear function of ω calculated for the site of origin. This means that, in the common garden, water-use efficiency was greatest in individuals originating from sites with high ω and lowest in individuals originating from sites with low ω. The slopes of the relationship between carbon isotope discrimination and ω did not differ [$F(1,12) = 0.23$, not significant] between leaf and twig photosynthetic tissues (Fig. 2*A*); both

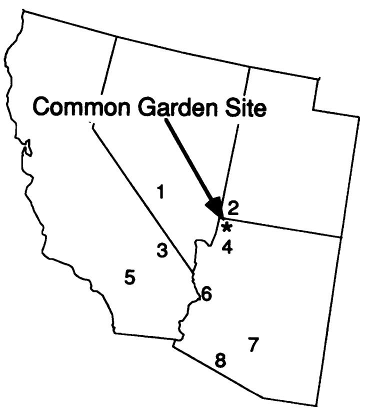

FIG. 1. Locations of source populations of *H. salsola*: 1, Mina, NV; 2, Joshua Tree Natural Area, UT; 3, Death Valley National Monument, CA; 4, Oatman, AZ; 5, Palm Desert, CA; 6, Parker, AZ; 7, Redrock, AZ; and 8, Organ Pipe Cactus National Monument, AZ. Common garden site near Littlefield, AZ, is indicated.

Table 1. Selected climatic parameters for each site of origin and ω evaluated for the eight sites indicated in Fig. 1

Site of origin	Mean annual temperature, °C	Summer precipitation,* % of annual	Total annual precipitation, mm	Latitude of source population, degrees	ω of source population, $\text{mbar}\cdot\text{bar}^{-1}$
1	12.1	26.6	93	38.4	18.9
3	17.9	32.5	113	35.8	24.2
2	15.2	28.1	243	37.0	25.1
4	18.9	32.7	200	35	26.8
5	22.0	13.5	159	33.8	29.6
6	22.5	29.6	97	34.2	29.8
7	20.8	48.7	254	32.3	34.7
8	20.6	49.0	234	31.9	34.9

The climatic parameters shown are those which contribute to the calculation of ω by determining leaf temperature (and ν) and phenology. 1 bar = 100 kPa.

*June 1 through September 30.

organ types were similarly affected by climate at the site of origin.

There were also important differences among populations in allocation patterns between leaf and photosynthetic-twig tissue production in the common garden (Fig. 2*B*). As ω increased across sites of origin, there was also a large shift in canopy architecture toward reduced production of leaf and increased production of twig, the more water-use efficient of the two photosynthetic organs. Thus, the regulation of plant characters balancing the relative magnitudes of CO_2 and water diffusion gradients involved a close coordination of both physiological and morphological traits within the canopy. We examined the generality of this phenomenon by comparing leaf and twig photosynthetic areas on eight photosynthetic-twigged shrub species co-occurring at two desert sites differing in ω (16). These species were *Acamptopappus sphaerocephalus* Gray, *Chrysothamnus paniculatus* Greene, *Hymenoclea salsola, Gutierrezia sarothrae* Britt. and Rusby, *Senecio douglasii* var. *monoensis* Jepson, *Psilostrophe cooperi* Greene, *Sphaeralcea parvifolia* A. Nels., and *Salizaria mexicana* Torr. As predicted, populations of all species exhibited leafier canopies at the site with the lower ω (paired Student's *t* test, $t = -3.872$, $P = 0.006$, $n = 8$).

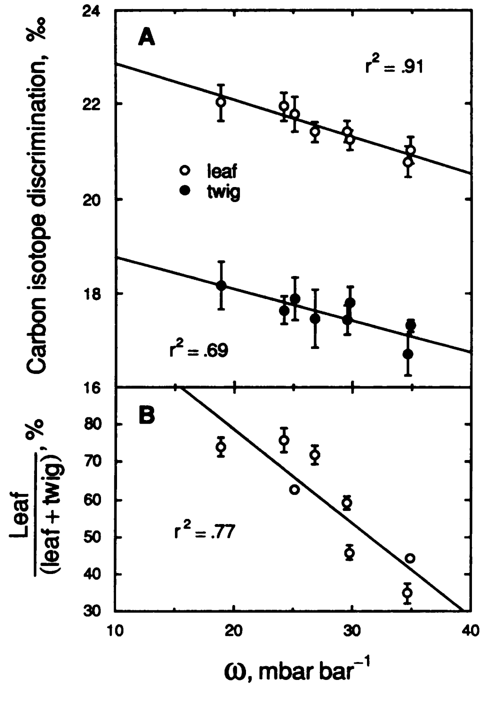

FIG. 2. Relationships between the climatic variation in ω across sites of population origin and the expression of traits affecting water-use efficiency under common garden conditions. Regression lines are based on the mean value for plants from each population in the common garden, and error bars represent ±1 SE. (*A*) Tissue-level variation for carbon isotope discrimination in leaves and twigs. The lines indicated are the least-squares best fits: discrimination(leaf) = $23.6 - 0.078\omega$ ($P < 0.001$), and discrimination(twig) = $19.4 - 0.068\omega$ ($P < 0.01$). Carbon isotope discrimination was measured on bulked samples collected during peak vegetative growth in spring and measured on a Finnigan MAT delta E isotope-ratio mass spectrometer (9, 20). (*B*) Variation in leaf contribution to total canopy surface area. Leaf area development is expressed as the percentage of the total photosynthetic surface area (combined leaves and twigs) in the canopy contributed by leaves alone. Relative leaf area, % = $128.5 - 2.5\omega$ ($P < 0.005$).

Since ν was constant under common garden conditions, the genetically based variation in carbon isotope discrimination should have resulted in proportional variation in water-use efficiency for plants growing in the common garden. In the native sites, however, the same variation in carbon isotope discrimination would have reduced variation in water-use efficiency expected from climatically caused variation in ν (Fig. 3). The variations in water-use efficiency indicated for

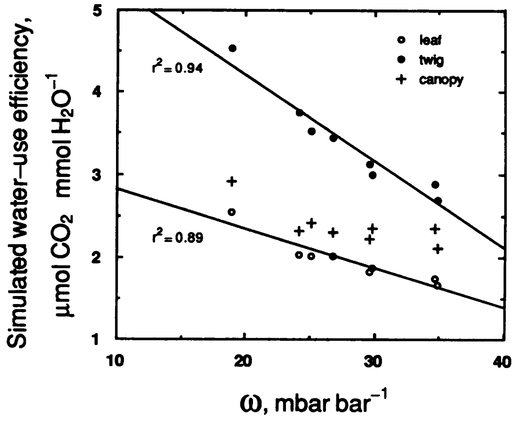

FIG. 3. Estimates of mean growing-season water-use efficiency in the native sites for each respective population plotted relative to the climatic gradient. Leaf and twig values are based on late-spring carbon isotope discrimination of newly produced leaf and twig tissues (Fig. 2*A*) and on calculated values of ω for the respective sites of origin for each population. Canopy water-use efficiency further incorporates the relative proportions of leaf and twig photosynthetic surface area in the canopy (Fig. 2*B*), and a relative gas exchange rate per unit of twig surface area equal to 0.62 times that of a leaf (16). The diffusion gradient for CO_2 assimilation was calculated from theory (9) as $(c_a - c_i) = c_a\{1 - [(\text{discrimination} - a)/(b - a)]\}$, where a and b are fractionation constants having values of 4.4 and 27 and relating to diffusional and biochemical events, respectively, and c_a is assumed to be constant at 350 µl/liter. Water-use efficiency (A/E) was calculated as $(c_i - c_a)/1.6\nu$, and ν was taken to be equal to ω for the respective sites of origin. Lines shown are the least-squares best fits: $(A/E)_{\text{twig}} = 6.31 - 0.105\omega$; and $(A/E)_{\text{leaf}} = 3.30 - 0.048\omega$.

leaf and twig tissues are based both on the estimate of mean growing season ν embodied in ω and on the gradient in CO_2 predicted for each tissue and population from the carbon isotope discrimination data (Fig. 2*A*). Both leaves and twigs develop greater CO_2 diffusion gradients ($c_a - c_i$) in high-ω ecotypes, but the changes in c_i are not sufficient to counteract the magnitude of variation in ν. Thus strong, almost linear decreases in the water-use efficiencies of each tissue are predicted in the native sites as ω increases (Fig. 3). Variation in c_i (Fig. 2*A*) has reduced the magnitude of these slopes, but only by 28% for leaves and 16% for twigs. The steeper slope for twigs is due to their lower initial c_i making high initial water-use efficiency possible, and also the fact that, since $c_a - c_i$ is much larger initially in twigs, when both tissues have the same absolute change in c_i it is a smaller percentage change in $c_a - c_i$ for twigs than for leaves. At the whole-canopy level, however, there is also a shift in the proportion of each tissue type represented. If the shift from leafy to twiggy canopies (Fig. 2*B*) is also incorporated into the calculations, we find that whole-canopy water-use efficiency is relatively stable across the climatic gradient. Only at the site at the extreme low end of the ω gradient is water-use efficiency of the canopy predicted to differ from that at all other sites. It is not surprising that plant characters fail to fully compensate for environmental variation at this extreme, where the proportional changes in ω are extremely rapid and have a great effect on water-use efficiency.

Several caveats should be mentioned regarding the estimates of water-use efficiency discussed here. (*i*) We do not mean to imply that water-use efficiency is constant throughout the growing season at an individual site but only that an average value can be assigned in each case. (*ii*) The values of ω given here and used to calculate water-use efficiency are based on maximum daily air temperatures. Calculations based on mean temperatures would give lower values of ω and higher values of water-use efficiency but would not change any of the rankings of sites or the qualitative conclusions drawn. (*iii*) Both leaves and twigs are produced primarily in the spring growing season, but the tissue samples for isotopic analysis were collected on different dates. Although most of the twig biomass is produced in the spring (which would thus be the season most influencing isotopic composition), the difference between the two tissue types shown above may be slightly exaggerated by water stress. Nonetheless, it is well established that twigs do maintain lower c_i values than leaves (18–20), and the disjunct sampling will not change the main effects of shifting from one tissue type to the other. (*iv*) The physiological data incorporate only the genetic differentiation revealed in a common garden. Growing under differing ν in the native sites, plastic response to immediate growth conditions would augment these genetic tendencies. Thus the full role of physiological adjustment in controlling water-use efficiency may be somewhat underestimated in this analysis, which considers only the effects of ecotypic differentiation. What the simulation clearly shows, however, is that genetically based variation in plant characters is sufficient to exert substantial control over water-use efficiency along this climatic gradient.

Leaf area development among *H. salsola* ecotypes was significantly correlated with ω, but not with any other single climatic parameter investigated (Table 2). Carbon isotope discrimination was correlated with annual temperature, but the association between isotopic discrimination and ω was much stronger (Table 2). Since ω incorporates the nonlinear dependence of vapor pressure on temperature, both annual and seasonal, as well as differences in the timing of growing seasons driven by the interaction of seasonal temperature and precipitation, it is likely that this is the explanation for the stronger correlation with ω than with temperature. This is particularly important because variables determining seasonal timing (total annual precipitation and seasonal distribution of precipitation) may be independent of both one another and variation in annual temperature (Table 2).

ω provides a single parameter that is relevant to plant performance, and it generates nontrivial predictions concerning biological response to climatic variation. Under common garden conditions, intercellular CO_2 concentrations were lowest in plants originating from native habitats characterized by high ω. Lower intercellular CO_2 concentrations in high-ω ecotypes imply greater stomatal limitation of photosynthesis and may therefore be characterized as "more conservative" water-use behavior. In general for winter-wet climates with even moderate summer drought, higher values of ω will be calculated for climates with higher annual temperature, higher annual precipitation, or a larger percentage of the total precipitation occurring during the summer. That plants originating from sites with greater total precipitation should be more conservative in their gas-exchange behavior may appear counterintuitive, but it follows from the way in which total precipitation and seasonal temperature variation interact to affect the seasonality of growth. In winter-wet climates, the P/E_p ratio almost always achieves unity during the coolest months. Because of the exponential relationship between saturation vapor pressure and temperature, much more precipitation is required in summer to achieve a P/E_p ratio approaching unity. As total precipitation

Table 2. Correlation matrix of biological traits measured under common garden conditions, selected climatic parameters, and ω evaluated for the respective source locations of the eight *H. salsola* populations indicated in Fig. 1

	Leaf carbon isotope discrimination	Relative leaf-area development*	Mean annual temperature	Summer precipitation	Total annual precipitation	Latitude of source population	ω of source population
Leaf carbon isotope discrimination	1.00						
Relative leaf-area development	0.90	1.00					
Mean annual temperature	−0.77	−0.65	1.00				
Summer precipitation	−0.60	−0.56	0.15	1.00			
Total annual precipitation	−0.57	−0.47	0.18	0.54	1.00		
Latitude of source population	0.93	0.80	−0.87	−0.54	−0.48	1.00	
ω of source population	−0.95	−0.88	0.83	0.57	0.60	−0.97	1.00

The climatic parameters shown are those which contribute to the calculation of ω by determining leaf temperature (and ν) and phenology. The critical value of $r = 0.71$ ($P \leq 0.05$); $n = 8$ sites of origin.

*Leaf area/leaf and twig area.

increases in more mesic sites, only the warmer months in which P/E_p has not yet reached unity are affected, increasing their weighting relative to the cool winter and early spring. Wetter sites will have a longer growing season, but a greater fraction of it will occur in warmer months, resulting in higher values for ω. Thus ω ranks sites in a fundamentally different manner than indices calculating total resource (water) availability. We suggest that the conditions under which water is used may be a more important influence on water-use efficiency than is the total amount of water available over an annual cycle.

Read and Farquhar (21) recently reported variation in carbon isotope discrimination among congeneric species of *Nothofagus* from tropical and subtropical latitudes. Even among these plants of wet forests, substantial genetic variation in c_i occurs. In their study, the best climatic factor explaining variation in isotopic discrimination was the amount of summer rainfall. Those authors speculate that the relationship is due to greater adaptation for water uptake in those species adapted for enduring summer drought, which they suggest would result in less sensitive stomata under conditions of mild water deficits in the soil. While the assumptions permitting easy computation of ω are not met in these forests (leaf temperatures ≠ air temperatures; humidity is not low and constant), it is of interest to note how qualitative assumptions embodied in ω might relate to these data. For physiological traits related directly to carbon uptake, if suppression of summer activity by water deficits results in greater emphasis by forces of natural selection on the milder portions of the growing season, this scenario would also predict the observed relationship of decreasing carbon isotopic discrimination with increasing summer rainfall.

Climatic variation is of great interest to both ecological studies of plant adaptation and agricultural questions of plant performance across different environments. Nonetheless, studies showing a mechanistic link between climatic variation and genetic differentiation of photosynthetic characters are limited. While previous studies have shown important relationships between environmental temperatures and ecotypic differentiation in metabolic temperature optima (17), most approaches have evaluated instantaneous or short-term physiological parameters, whose impact is often difficult to extrapolate over extended time periods. The development of the theory of carbon isotope discrimination during photosynthesis (9) is now facilitating more detailed evaluations of morphological and physiological characters related to long-term patterns of water-use efficiency. Emerging evidence indicates substantial intraspecific genetic variation in carbon isotope discrimination (9), although the evolutionary significance of these differences is not fully understood. The description of intraspecific, genetically based differentiation in carbon isotope discrimination with broad-scale climatic variation adds a further dimension to the understanding of mechanisms associated with plant water-use regulation in arid environments.

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