

## **Correlations between carbon isotope ratio and microhabitat in desert plants**

**James R. Ehleringer and Tamsie A. Cooper**

Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

**Summary.** Water is usually considered to be the key limiting factor for growth of desert plants, yet there is little information available of the water-use efficiency of species within a desert community. Leaf carbon isotope ratios, an indicator of long-term intercellular carbon dioxide concentrations and thus of water-use efficiency in  $C_3$  plants, were measured on species occurring within a Sonoran Desert community, consisting of wash, transition and slope microhabitats. Along a soil moisture gradient from the relatively wetter wash to the relatively drier slope, leaf carbon isotope ratios increased in all species, indicating that water-use efficiency increased as soil water availability decreased. Leaf carbon isotope ratios of long-lived perennials were substantially more positive than in short-lived perennials, even though plants were growing adjacent to each other. Leaf carbon isotope ratio and leaf duration (evergreen versus deciduous) were not correlated with each other. The results are discussed in terms of how the efficiency of water use may affect community structure and composition.

**Key words:** Photosynthesis – Transpiration – Stable isotopes

Within the warm deserts of North America, a number of studies have described associations between vegetation zonation patterns and environmental variables. A major conclusion of these studies is that soil water availability and soil particle size are the primary factors responsible for establishment of the observed vegetation patterns on non-disturbed sites (Shreve 1915, 1942; Yang and Lowe 1956; Shreve and Wiggins 1964; Klikoff 1967; Phillips and MacMahon 1978). Implicit within these studies is the notion that soil moisture levels are limiting and that plants are differentially distributed along this cline because of differences in their ability to tolerate low soil moisture availability and/or to compete for this limiting resource. Indeed, despite the earlier suggestion to the contrary by Shreve and Wiggins (1964), there is now ample evidence that plants in deserts do compete with each other, most notably for soil moisture (Fowler 1986). A logical extrapolation of the available competition data is that these plant interactions ultimately affect community composition, although experimental verification of this notion is lacking at present.

Offprint requests to: J.R. Ehleringer

While the concepts of zonation and competition within desert plants are generally accepted, the specifics are not well understood. For instance, there are no data available regarding the critical relationships between productivity and water consumption of desert plants other than the general observation that primary productivity and rainfall are positively correlated (Ehleringer and Mooney 1983). Desert perennials are often classified according to the rate at which water is transpired (e.g. water-wasters, water-conservative, etc.) (MacMahon and Schimpf 1981; Smith and Nobel 1986), but not according to the tradeoffs between photosynthetic carbon gain and water loss. Evolutionary models of optimal plant function in deserts, while noting the tradeoff between photosynthetic carbon gain and water loss governed by stomata, have focused on the rates of primary productivity rather than on the water-use efficiency associated with that biomass production (Johnson 1975; Orians and Solbrig 1977; Solbrig and Orians 1977). Yet the early studies of Briggs and Shantz (1913, 1914) demonstrated that there could be large differences among species in the ratio of dry matter production to water consumption (water-use efficiency), even when plants were grown under common conditions.

The limited success in extending the earlier Briggs and Shantz observations into most ecological situations has been in part because of the destructive nature of the analysis which prevents prolonged comparative analyses and in part because of the tremendous labor efforts involved. However, alternative means of estimating water-use efficiency have been developed which are less labor-intensive, and still yield long-term information about the efficiency of water use by a plant. Since stomata govern the rates at which carbon dioxide and water vapor diffuse into and out of a leaf, the relative differences in water-use efficiency (ratio of photosynthesis to transpiration,  $A/E$ ) of different species or of plants within different microhabitats can be calculated from

$$A/E = (c_a - c_i) / (1.6 \cdot \Delta w) \quad (1)$$

where  $c_a$  is the ambient carbon dioxide concentration (assumed to be  $340 \mu\text{l l}^{-1}$ ),  $c_i$  is the intercellular carbon dioxide concentration,  $\Delta w$  is the leaf to air water vapor concentration gradient, and 1.6 is the ratio of the diffusion coefficients of water to carbon dioxide in air. Long-term estimates of  $c_i$  can be obtained by carbon isotope ratio analysis (Farquhar et al. 1982).

In the present study, we address the questions of 1) how does water-use efficiency vary among desert plants in a common habitat and 2) does the water-use efficiency of a species vary as soil water availability changes. We used carbon isotope ratios to obtain long-term estimates of  $c_i$ , which then allow us to extrapolate to water-use efficiency if we assume that leaf temperatures of the species sampled are similar during the photosynthetically active period (Farquhar et al. 1982). Field observations of when plants are active and of leaf temperatures generally tend to support this assumption (Comstock et al. 1988; Ehleringer and Cooper, unpublished observations).

## Materials and methods

The study site was approximately 9 km west of Oatman, Arizona (lat. 34° 57' N, long. 114° 25' W, 657 m elevation). The vegetation of this area is transitional between Mohave Desert southwestern portion and the Sonoran Desert Lower Colorado valley portion (Shreve and Wiggins 1964). The site consisted of three definable microhabitats: slope, transition zone, and wash (Fig. 1). The slopes consisted of shallow soils with limited soil development and often having bedrock exposed at the surface. Below the slopes were the bajadas, expansive alluvial fans. These bajadas consisted of two components: the wash and the transition zone. Wash microhabitats are best described as a region of active soil and gravel deposition, soil movement (via flashflooding), and deeper gravelly soils. The transition zone is the stabilized portion of the bajada, originally formed from wash deposits, but no longer subjected to active soil movement in recent times.

In each of the three microhabitats, five randomly placed linear transects of 100 m each were used to describe the plant community composition. Additionally, each microhabitat was traversed several times to identify species present in the microhabitat, but that were missed by limiting our linear sampling to 500 m. Species identification follows Shreve and Wiggins (1964).

Long-term estimates of the intercellular carbon dioxide concentration ( $c_i$ ) were calculated by rearranging the equations originally developed by Farquhar, O'Leary and Berry (1982) as

$$c_i = c_a \cdot (\delta^{13}C_{\text{air}} - \delta^{13}C_{\text{leaf}} - a) / (b - a) \quad (2)$$

where  $\delta^{13}C_{\text{air}}$  and  $\delta^{13}C_{\text{leaf}}$  are the carbon isotope ratios of the air and leaf, respectively,  $a$  is the discrimination associated with the slower diffusion rate of  $^{13}\text{CO}_2$  ( $a = 4.4\%$ ), and  $b$  is the net discrimination against  $^{13}\text{CO}_2$  associated with RuBP carboxylase ( $b = 27$ ).

Carbon isotope ratios were determined on bulked samples collected following summer rains in early October. Each sample consisted of ten leaves from ten different

plants of the same species. The sample was dried, ground to 40 mesh and then subsampled. Carbon isotope ratios were determined on carbon dioxide collected from combusted samples using a Finnigan MAT delta E isotope ratio mass spectrometer. Carbon isotope ratios are expressed relative to the PDB standard using the equation:

$$\delta^{13}C = (R_{\text{sample}}/R_{\text{standard}} - 1) \cdot 1000 \quad (3)$$

where  $\delta^{13}C$  is the carbon isotope ratio of the sample in parts per mil (‰),  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{13}\text{C}/^{12}\text{C}$  ratios of sample and standard, respectively. The precision of each isotopic measurement is 0.02‰ and repeatability of each sample was  $\pm 0.08\%$ .

## Results

Both plant cover and the number of species decreased from the wash, the region of relatively greater soil water availability, to the slopes, the region of relatively less soil water availability (Table 1). Yet at the same time, plant density increased along this cline, going from 24.2 to 43.4 plants per 100 m. The consequence of these two opposite patterns was that the mean plant length intersecting the transect (i.e. average plant size) for all species decreased from 1.75 m to 0.64 m between wash and slope microhabitats, respectively.

Of the 17–21 species occurring within each microhabitat, only 2 or 3 species were common enough to represent 5% or more of the ground cover (Table 2). The wash microhabitat was dominated by *Acacia greggii* (a tall shrub at this site) (14%) and *Chilopsis linearis* (a tree) (11.5%). Two shrubs, *Ambrosia eriocentra* and *Chrysothamnus paniculatus*, were slightly less common, but together comprised 9% of the ground cover. The transition microhabitat was dominated by *Acacia greggii* (8.8%) and *Larrea divaricata* (9.0%). On the slopes, *L. divaricata* continued to predominate, but shared this position with another shrub, *Encelia farinosa* (6.4%).

Of the 30 perennial species present, only 10 species occurred in all three microhabitats. In none of these cases was a single species dominant in all three zones, but rather the pattern was either that the species was present, but uncommon in all three microhabitats (*Ambrosia dumosa*, *Bebbia juncea*, *Cassia covesii*, *Eriogonum fasciculatum*, *E. inflatum*, and *Porophyllum gracile*) or else it was common in two microhabitats and present, but uncommon in the third (*Acacia greggii*, *Ephedra viridis*, *Krameria parvifolia*, and *Larrea divaricata*).

Along the decreasing soil moisture cline from wash to slope microhabitats, leaf carbon isotope ratios of individual species tended to increase (Table 3). In several instances (*Ambrosia dumosa*, *Eriogonum inflatum*, and *Hymenoclea salsola*), leaf carbon isotope ratios increased by 2‰ or more

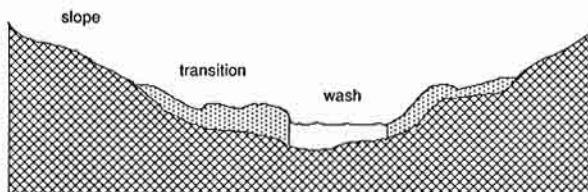


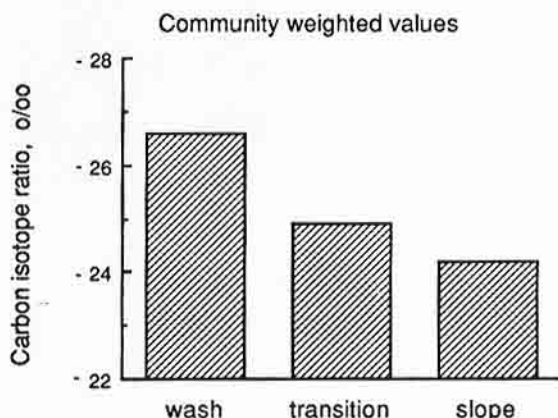
Fig. 1. Cross-sectional depiction of the site, illustrating wash, transition and slope microhabitats

Table 1. Percentage ground cover, plant density, and total number of species at wash, transition and slope microhabitats near Oatman, Arizona

	wash	transition	slope
Per cent plant cover	42.4	30.6	27.9
Number of plants per 100 m	24.2	32.0	43.4
Total number of perennial species in microhabitat	21	20	17

**Table 2.** Per cent cover for individual species in wash, transition and slope microhabitats near Oatman, Arizona. A "+" indicates that the species was present in that microhabitat, but that its frequency was less than 0.1% of the ground cover. NP indicates that the species was not present in that microhabitat

	wash	transition	slope
<i>Acacia greggii</i>	14.4	8.8	0.9
<i>Acamptopappus sphaerocephalus</i>	NP	2.5	NP
<i>Ambrosia dumosa</i>	0.0+	0.1	0.7
<i>Ambrosia eriocentra</i>	3.4	NP	NP
<i>Bebbia juncea</i>	0.5	0.0+	0.9
<i>Cassia covessii</i>	0.0+	0.1	1.7
<i>Cercidium floridum</i>	0.0+	NP	NP
<i>Chilopsis linearis</i>	11.5	NP	NP
<i>Chrysothamnus paniculatus</i>	5.6	NP	NP
<i>Encelia farinosa</i>	NP	0.2	6.4
<i>Encelia frutescens</i>	0.1	NP	NP
<i>Ephedra viridis</i>	0.5	3.2	1.8
<i>Eriogonum fasciculatum</i>	0.2	1.2	0.0+
<i>Eriogonum inflatum</i>	0.1	0.6	0.3
<i>Echinocereus</i> sp.	NP	NP	0.1
<i>Hymenoclea monogyra</i>	1.4	NP	NP
<i>Hymenoclea salsola</i>	1.3	0.0+	NP
<i>Krameria parvifolia</i>	0.6	2.0	2.4
<i>Larrea divaricata</i>	1.6	9.0	10.5
<i>Lycium andersonii</i>	0.0+	0.0+	NP
<i>Phoradendron californicum</i>	0.5	0.7	NP
<i>Porophyllum gracile</i>	0.3	0.4	1.5
<i>Psilotrophe cooperi</i>	NP	0.4	0.0+
<i>Opuntia acanthocarpa</i>	NP	NP	0.6
<i>Opuntia basilaris</i>	NP	0.0+	0.1
<i>Salazaria mexicana</i>	NP	1.5	NP
<i>Senecio douglasii</i>	0.2	NP	NP
<i>Sphaeroclea ambigua</i>	NP	0.0+	0.0+
<i>Stellaria</i> sp.	0.0+	NP	NP
<i>Viguiera laciniata</i>	NP	0.0+	0.0+



**Fig. 2.** Mean carbon isotope ratio of the perennial vegetation, weighted for species abundance, in wash, transition and slope microhabitats

(Table 3). This pattern implied an overall decrease in intercellular carbon dioxide levels ( $c_i$ ) as soil moisture became less available. Of the 17 species which occurred in at least two different microhabitats, leaf carbon isotope ratios were more positive (lower  $c_i$ ) on the drier sites for 14 of these species. In the three cases for which carbon isotope ratios appeared to decrease instead of increase (*Eriogonum fasci-*

**Table 3.** Leaf carbon isotope ratio of bulked samples for individual species in wash, transition and slope microhabitats near Oatman, Arizona. A blank indicates that the species was not present in that microhabitat. Leaf types are dd=drought deciduous, wd=winter deciduous, e=evergreen, and es=evergreen stem. Species are categorized according to their longevity, which is based upon information in Shreve and Hinckley (1937), Wells (1961), Vasek, Johnson and Brum (1975), Vasek, Johnson and Eslinger (1975), Beatley (1979), Carpenter, Barbour, and Bahre (1986), Goldberg and Turner (1986), Webb, Steiger and Turner (1987)

	leaf type	wash	transition	slope
long-lived (50+ years)				
<i>Cercidium floridum</i>	dd	-24.07		
<i>Chilopsis linearis</i>	wd	-25.37		
<i>Chrysothamnus paniculatus</i>	wd	-26.69		
<i>Ephedra viridis</i>	es		-23.30	-23.82
<i>Krameria parvifolia</i>	dd		-24.60	-23.87
<i>Larrea divaricata</i>	e	-24.12	-23.60	-22.67
<i>Lycium andersonii</i>	e	-25.32	-25.09	
		-25.11	-24.15	-23.45
medium-lived (10-40 years), opportunistic				
<i>Acacia greggii</i>	wd	-27.40	-25.82	
<i>Ambrosia dumosa</i>	dd	-27.37	-26.04	-25.37
<i>Encelia farinosa</i>	dd		-26.13	-25.46
<i>Encelia frutescens</i>	dd	-27.51		
<i>Hymenoclea salsola</i>	dd	-26.45	-23.54	
mean		-27.18	-25.38	-25.42
short-lived (1-10 years), opportunistic				
<i>Ambrosia eriocentra</i>	dd	-29.29		
<i>Bebbia juncea</i>	dd	-28.33	-26.66	-25.80
<i>Cassia covessii</i>	dd	-26.03	-26.71	-26.83
<i>Eriogonum fasciculatum</i>	dd		-26.40	-26.53
<i>Eriogonum inflatum</i>	dd	-28.17	-25.82	-25.70
<i>Phoradendron californicum</i>	es	-27.14	-26.96	
<i>Porophyllum gracile</i>	dd	-27.47	-26.75	-26.55
<i>Psilotrophe cooperi</i>	dd		-27.65	-27.02
<i>Sphaeroclea ambigua</i>	dd		-27.38	-27.57
<i>Viguiera laciniata</i>	dd		-26.08	-26.40
mean		-27.74	-26.71	-26.55

*culatum*, *Sphaeroclea ambigua*, and *Viguiera laciniata*), the differences in isotope values between sites were rather small (0.13-0.32‰). Since in each instance, each of these plant species was also uncommon, it is possible that this apparent countertendency represented a sampling error.

The average carbon isotope ratio in each microhabitat was determined by weighting the isotopic ratio of each species by its abundance in that microhabitat (Fig. 2). These calculations revealed that carbon isotope ratios were most negative in plants from the wash microsite (-26.59‰), intermediate in the transition microsite (-24.89‰), and most positive at the slope microsite (-24.19‰). These average carbon isotope ratios translated into average  $c_i$  values of 213, 188 and 178  $\mu\text{l l}^{-1}$  for wash, transition and slope microhabitat plants, respectively.

## Discussion

Within almost all species from this survey, carbon isotope ratios declined with decreasing soil water availability (wash



to transition to slope microsites). The magnitude of this isotope ratio change depended upon the individual species, but the trend clearly indicates that  $c_i$  values decreased with decreasing soil water availability. Since a 1‰ change in  $\delta^{13}\text{C}$  is equivalent to approximately a  $15 \mu\text{l l}^{-1}$  difference in  $c_i$ , the data from Table 3 imply that  $c_i$  values of an individual species vary on average approximately  $20 \mu\text{l l}^{-1}$ , and may vary by as much as  $43 \mu\text{l l}^{-1}$  in some species, such as *Hymenoclea salsola*.

A decrease in the operational  $c_i$  value indicates an increase in the stomatal diffusion limitation to photosynthesis and also an increase in leaf water-use efficiency (unless offset by a substantial rise in leaf temperature). Thus, the  $\delta^{13}\text{C}$  data show that both the stomatal limitations and water-use efficiency of a species increases as soil water availability decreases. At the community level, it appears that there are substantial decreases in the average  $c_i$  value in the wash and transition microhabitats (weighted values of 213 versus  $188 \mu\text{l l}^{-1}$ ), but less so between transition and slope microsites ( $188$  versus  $178 \mu\text{l l}^{-1}$ ).

Do the  $c_i$  values and hence water-use efficiency correlate with life form? The data are somewhat limited, but there is a tendency for trees to have lower  $c_i$  values than shrubs and for evergreen-leaved shrubs to have lower  $c_i$  values than deciduous-leaved shrubs.

Perhaps more striking is the correlation between  $\delta^{13}\text{C}$  and life expectancy. Actual life expectancy data for desert shrubs are limited, but there is a strong consensus that desert perennials can be roughly divided into three groups: short-lived (1–10 years), medium-lived (10–40 years), and long-lived (greater than 50 years) (see Table 3 for references). In Table 3, the species from this study have been segregated into one of these three categories based on life expectancy observations from other studies. Within each microhabitat, there is the consistent pattern that plant life expectancy and carbon isotope ratio are positively correlated. That is to say, longer-lived perennials tend to have lower  $c_i$  values and therefore to also have higher water-use efficiencies than shorter-lived perennials. These patterns are not the result of differences in plant size as there are both large and small perennials within the long-lived and medium-lived classifications.

Mooney and Gulmon (1982) have pointed out that as a general rule evergreen leaves tend to have lower photosynthetic rates than deciduous leaves. It is therefore perhaps surprising that our results suggest water-use efficiency and longevity at the leaf level need not be correlated with each other.

A positive correlation between plant longevity and its water-use efficiency suggests a physiological mechanism that may provide insight into competitive interactions, community dynamics and plant establishment. If a high water-use efficiency also means a greater stomatal limitation on photosynthesis and therefore a lower rate of carbon gain (assuming for simplicity that leaves had the same photosynthetic dependence on  $c_i$ ), it may be that plants with a high water-use efficiency grow more slowly than plants with a low water-use efficiency under periods of high soil moisture availability. If limiting, but relatively high amounts of soil moisture are equally available to both high and low water-use efficiency plants, the low water-use efficiency plant should be the better competitor if both plants have equal access to the same soil moisture. However, high water-use efficiency plants should be able to maintain a relatively

higher productivity rate when soil water becomes very limiting and growth in the low water-use efficiency plants is substantially reduced.

Extending this reasoning, we might expect that low water-use efficiency plants would be more likely to get established in deserts under unusual higher soil moisture years, but perhaps expected to have greater mortality under extended periods of low soil moisture availability. Such a pattern is consistent with the carbon isotope ratio data. It is intriguing to speculate that the differences in water-use efficiency among species contribute directly and in a predictable manner to their long-term growth and survival under the unpredictable and fluctuating drought conditions that characterize desert environments.

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## References

- Beatty JC (1979) Fluctuations and stability in climax shrub and woodland vegetation of the Mohave, Great Basin and Transition Deserts of southern Nevada. *Israel J Bot* 28:149–168
- Briggs LJ, Shantz HL (1913) The water requirements of plants. II. A review of the literature. USDA Bureau Plant Industry Bull 285
- Briggs LJ, Shantz HL (1914) Relative water requirements of plants. *J Agric Res* 3:1–63
- Carpenter DE, Barbour MG, Bahre CJ (1986) Old field succession in Mohave Desert scrub. *Madroño* 33:111–122
- Comstock JP, Cooper TA, Ehleringer JR (1988) Seasonal patterns of canopy development and carbon gain in nineteen warm desert shrub species. *Oecologia* 75:327–335
- Ehleringer JR, Mooney HA (1983) Photosynthesis and productivity of desert and Mediterranean climate plants. In: *Ency Plant Physiology New Series*, vol 12D. Springer, Berlin Heidelberg New York, pp 205–231
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust J Plant Physiol* 9:121–137
- Fowler N (1986) The role of competition in plant communities in arid and semiarid regions. *Ann Rev Ecol Syst* 17:89–110
- Goldberg DE, Turner RM (1986) Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67:695–712
- Johnson HB (1975) Gas-exchange strategies in desert plants. In: Gates DM, Schmerl RB (eds) *Perspectives in Biophysical Ecology*. Springer, Berlin Heidelberg New York, pp 105–120
- Klikoff LG (1967) Moisture stress in a vegetational continuum in the Sonoran Desert. *Am Midl Nat* 77:128–137
- MacMahon JA, Schimpf DJ (1981) Water as a factor in the biology of North American desert plants. In: Evans DD, Thames JL (eds) *Water in Desert Ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg Pennsylvania, pp 114–171
- Mooney HA, Gulmon SL (1982) Constraints on leaf structure and function in reference to herbivory. *BioScience* 32:198–206
- Orians GH, Solbrig OT (1977) A cost-income model of leaves and roots with special reference to arid and semiarid areas. *Am Nat* 111:677–690
- Phillips DL, MacMahon JA (1978) Gradient analysis of a Sonoran Desert bajada. *Southwest Nat* 23:669–680
- Shreve F (1915) The vegetation of a desert mountain range as conditioned by climatic factors. *Carnegie Inst Wash Publ* 217
- Shreve F (1942) The desert vegetation of North America. *Bot Rev* 8:195–246

- Shreve F, Hinckley AL (1937) Thirty years of change in desert vegetation. *Ecology* 18:463-478
- Shreve F, Wiggins IL (1964) *Vegetation and Flora of the Sonoran Desert*. Stanford University Press, Stanford
- Smith SD, Nobel PS (1986) Deserts. In: Baker NR, Long SP (eds) *Photosynthesis in Contrasting Environments*. Elsevier Science Publ, Amsterdam, pp 13-62
- Solbrig OT, Orians GH (1977) The adaptive characteristics of desert plants. *Am Sci* 65:412-421
- Vasek FC (1979) Early successional stages in Mohave Desert shrub vegetation. *Israel J Bot* 28:133-148
- Vasek FC, Johnson HB, Brum GD (1975a) Effects of power transmission lines on vegetation of the Mohave Desert. *Madrono* 23:114-130
- Vasek FC, Johnson HB, Eslinger DH (1975b) Effects of pipeline construction on creosote bush scrub vegetation of the Mohave Desert. *Madrono* 23:1-13
- Webb RH, Steiger JW, Turner RM (1987) Dynamics of Mohave Desert shrub assemblages in the Panamint Mountains, California. *Ecology* 68:478-490
- Wells PV (1961) Succession in desert vegetation on streets of a Nevada ghost town. *Science* 134:670-671
- Yang TW, Lowe CH (1956) Correlation of major vegetation climaxes with soil characteristics in the Sonoran Desert. *Science* 123:542

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