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3. Carbon Isotope Ratios and Physiological Processes in Aridland Plants

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Carbon isotope ratios in plants were initially used to investigate photosynthetic pathway types and have more recently been extended to studies of water-use efficiency in C_3 plants. The previous chapter by Farquhar et al. laid down the theoretical framework for why carbon isotope ratios should provide valuable insights into plant water-use efficiency studies and also provided strong experimental evidence of these patterns among agronomically important species. In this chapter, I focus on how carbon isotope ratios can be utilized in studies of aridland plants to understand ecophysiological processes.

Carbon Isotope Ratio and Photosynthetic Pathways

Since the initial observations of Bender (1968, 1971) and Smith and Epstein (1971), there has been an interest in using carbon isotope ratios as a means of screening plants for C_3 versus C_4 photosynthetic pathway differences. It also became clear that plants with Crassulacean acid metabolism (CAM) exhibited carbon isotope ratios similar to C_4 plants or in some species had carbon isotope ratios intermediate between those of C_3 and C_4 plants (Osmond et al. 1982). We now know that the carbon isotope ratios of leaves can vary from −7 to −35‰, with C_4 plants having values of −7 to −15‰, CAM plants −10 to −22‰, and C_3 plants −20 to −35‰. The source for this discrimination in C_3

photosynthesis is the initial carboxylating enzyme ribulose bisphosphate (RuBP) carboxylase, which discriminates strongly against the heavier isotope (O'Leary 1981; Osmond et al. 1982). Phosphoenolpyruvate (PEP) carboxylase (as in C_4 and CAM species) appears not to discriminate against ^{13}C, but diffusional and recarboxylation factors play an important role in determining the isotopic composition. Little further discrimination occurs after photosynthesis within the leaf, except during lipid metabolism (DeNiro and Epstein 1977).

Carbon isotope ratio surveys to determine the presence and abundance of C_3, C_4, and CAM photosynthetic pathways have been made in the deserts of northern and southern Africa (Schulze and Schulze 1976; Winter et al. 1976; Mooney et al. 1977; Winter 1979; Werger and Ellis 1981; Ziegler et al. 1981), central and western Asia (Winter and Troughton 1978; Zelenskiĭ and Glagoleva 1981; Frey and Kürschner 1983; Shomer-Ilan et al. 1981; Winter 1981; Ziegler et al. 1981), the Indian subcontinent (Sankhla et al. 1975; Ziegler et al. 1981), North America (Mooney et al. 1974; Philpott and Troughton 1974; Eickmeier and Bender 1976; Syvertsen et al. 1976; Eickmeier 1978), and South America (Mooney et al. 1974). Several general patterns have emerged from these surveys. First, although C_3, C_4, and CAM photosynthetic pathways occur in plants from each of these aridland regions, it appears that the greatest fraction of the nonsucculent species are C_3 plants. The succulent species tend to be obligate-CAM or facultative-CAM plants, with the distinction correlated with stem versus leaf succulence. When the C_4 photosynthetic pathway occurs, it is most frequent among perennial halophytes and annuals. There is a correlation between photosynthetic pathway and precipitation, so that C_3 plants tend to predominate at the mesic sites, while CAM plants are most frequent at the driest locations (Teeri et al. 1978). In nonsaline regions, C_4 plants tend to predominate only on those arid locations where there is significant summer precipitation (Stowe and Teeri 1978).

Perhaps some of the most interesting observations to come from these carbon isotope ratio surveys are data indicating the broad range of $\delta^{13}C$ values to be found in both CAM and C_3 plants. CAM values range from -10 to $-22‰$ (Eickmeier and Bender 1976; Szarek and Troughton 1976; Mooney et al. 1977; Troughton et al. 1977; Winter et al. 1978), with this range reflecting the different proportions of C_3 and CAM photosynthetic activity. In general, these facultative-CAM plants exhibit C_3 photosynthesis during wet periods and then the photosynthetic tissues change to CAM under drought conditions. As a variation on this theme, some plants such as *Frerea indica* have leaves which exhibit C_3 photosynthesis while their succulent stems exhibit CAM photosynthesis (Lange and Zuber 1977).

There is also an equally large range in the carbon isotope ratios in desert C_3 plants. For the perennial species examined in several studies that have broadly surveyed the vegetation, the carbon isotope ratios range from -20.6 to $-30.7‰$ (Figure 3.1). This large range of values does not result from any change in the photosynthetic pathway of these C_3 plants. Instead, it reflects differences in diffusional limitations to leaf performance discussed below.

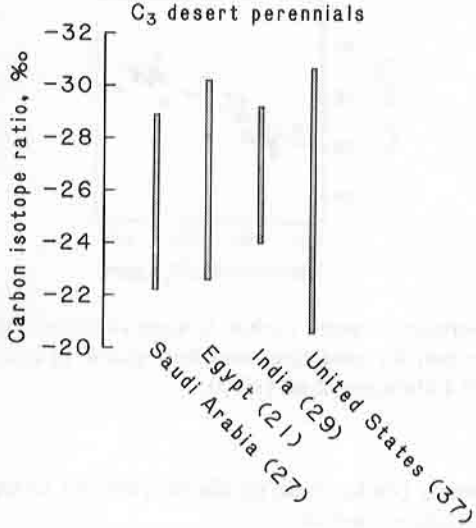

Figure 3.1. The range of carbon isotope ratios for leaves from C_3 perennial plants from the deserts of Saudi Arabia, Egypt, India, and the United States. The numbers in parentheses represent the sample size. Based on data from Philpott and Troughton (1974) and Ziegler et al. (1981). The data sets chosen represent broad surveys of arid-zone plants from specific desert locations.

Carbon Isotope Ratio and Intercellular CO_2 Concentration

Recently, carbon isotope ratio analyses have shown great promise for use as a tool to understand integrated plant behavior. Farquhar et al. (1982b) proposed that variation in the leaf carbon isotope ratio ($\delta^{13}C_{leaf}$) of C_3 plants should be dependent on the intercellular CO_2 concentration (c_i) as:

$$\delta^{13}C_{leaf} = \delta^{13}C_{air} - a - (b - a)c_i/c_a \quad (1)$$

where $\delta^{13}C_{air}$ is the carbon isotope ratio of the CO_2 in the air (about $-8‰$ at current CO_2 levels), a is the fractionation caused by the slower diffusion of $^{13}CO_2$ relative to $^{12}CO_2$ (4.4‰), b is the fractionation caused by discrimination of RuBP carboxylase against $^{13}CO_2$ (27‰), and c_a is the atmospheric CO_2 concentration. Field observations of average diurnal c_i values correlated with whole-leaf carbon isotope ratios support the expected pattern (Figure 3.2). Additional data sets more clearly demonstrate the tight relationship between $\delta^{13}C_{leaf}$ and c_i (Farquhar et al. 1982a; Downton et al. 1985; Seemann and Critchley 1985).

What is extremely useful about the relationship between intercellular CO_2 concentration (c_i) and carbon isotope ratio is that c_i is related to instantaneous

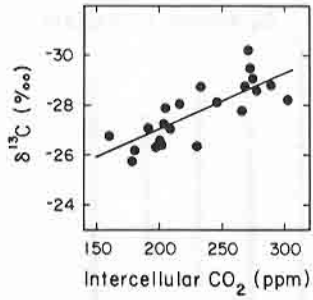

Figure 3.2. The relationship between carbon isotope ratio and average daytime intercellular CO_2 concentration for mistletoes and host plants in central Australia during September 1981. From Ehleringer et al. (1985).

leaf water-use efficiency (molar ratio of photosynthesis to transpiration) as can be seen from the equations below:

$$A = (c_a - c_i)\, g/1.6 \tag{2}$$

$$E = \Delta w g \tag{3}$$

$$A/E = (c_a - c_i)/(1.6\Delta w) \tag{4}$$

where A is the net photosynthetic rate, E is the transpiration rate, g is leaf conductance, and Δw is the leaf to air water vapor concentration gradient. As c_a is essentially constant under normal atmospheric conditions, the leaf carbon isotope ratio should depend only on c_i and Δw. High water-use efficiencies are therefore associated with higher carbon isotope ratios (more positive values) and vice versa. Experimental observations of the correlation between water-use efficiency of entire plants and carbon isotope ratio has been provided by Farquhar and Richards (1984). This approach provides a powerful tool for estimating integrated long-term water-use efficiency by a plant, as was earlier established by Farquhar et al. in Chapter 2. The remainder of this chapter is focused on the application of carbon isotope ratios to better understand both c_i and water-use efficiency (WUE) in desert C_3 plants.

Correlations of $\delta^{13}C$ with Photosynthetic Tissue Type and with Habitat

A significant proportion of the perennial plant species in desert habitats have chlorophyllous stem and twig tissues which maintain positive photosynthetic rates (Cannon 1908; Shreve and Wiggins 1964; Adams and Strain 1968; Gibson 1983). In desert plants that maintain leaves for only a portion of the growing season, twigs and stems can represent a major photosynthetic surface. Photosynthetic pathways among species having twig and stem photosynthesis have been assessed through carbon isotope ratio analyses. The results of such surveys

indicate that all three major pathways (C_3, C_4, and CAM) can be found in stem-photosynthesizing species (Mooney et al. 1977; Shomer-Ilan et al. 1981).

Carbon isotope ratios can also be used as a means of estimating relative water-use efficiencies of these different photosynthetic tissues (eq. 4). Comstock and Ehleringer (1988) have shown that leaves and twigs of *Hymenoclea salsola*, a common photosynthetic-twig shrub of the Mohave and Sonoran Deserts, are quite narrow and exhibit similar leaf and twig temperatures. Thus, Δw values are equivalent, and carbon isotope ratios in *H. salsola* become an indicator of potential differences in WUE between photosynthetic tissue types. They also observed a consistant average difference of 27 μl liter^{-1} CO_2 between the intercellular CO_2 concentrations of leaves (247 μl liter^{-1}) and twigs (220 μl liter^{-1}) under ambient conditions with well-watered plants. These gas-exchange data indicate that the instantaneous WUE is greater in twigs than in leaves, a trend which is also borne out in the carbon isotope ratio differences between leaves and twigs of *H. salsola* (Table 3.1).

The results of a larger survey of Mohave Desert and Sonoran Desert perennials indicate a statistically significant difference between the twig and leaf carbon isotope ratios of photosynthetic-twig and nonphotosynthetic-twig shrubs (Table 3.1). Twigs from photosynthetic-twig shrubs averaged 1.50 ± 0.17‰ higher than leaves; those twigs from nonphotosynthetic-twig shrubs averaged only 0.16 ± 0.14 higher than leaf values, a difference that is not significantly different from zero. These data suggest that the average intercellular CO_2 values of leaves were higher than in twigs for photosynthetic-twig desert shrubs.

In addition, the average leaf carbon isotope ratio from photosynthetic-twig shrubs (−26.50‰) was higher than in nonphotosynthetic-twig shrubs (−26.05‰). Although this difference is statistically significant ($t = 3.86$, $p < 0.01$), it arises because of a microdistributional difference in the two shrub types and not because of obvious intrinsic differences in leaves from photosynthetic-twig and nonphotosynthetic-twig shrubs. Photosynthetic-twig shrub species tend to occur in wash habitats, whereas nonphotosynthetic-twig shrub species occur primarily on slope habitats. These two microhabitats are adjacent, but distinct; slopes tend to have a much shallower alluvial soil than do washes, and washes clearly receive more soil water through runoff than do the slopes. When the leaf carbon isotope ratio data are evaluated according to microhabitat, wash-habitat shrubs averaged −26.51 ± 0.25‰ and slope-habitat shrubs −25.63 ± 0.40‰. These means are significantly different ($t = 7.15$, $p < 0.001$), indicating that leaves of wash-habitat shrubs tended to operate on average at higher intercellular CO_2 values than those of the slope-habitat shrubs. This may translate into differences in WUE between microhabitats, but the absence of Δw values for the different species prevents this extrapolation. However, during the drought periods, when both sets of plants would be expected to be leafless, the photosynthetic twigs appear to operate at lower c_i values (and thus presumably higher WUE) than either of the two sets of leaves, and this may have a direct bearing on performance of plants under water-limited conditions.

In a separate analysis, twenty two of the most common plant species were again sampled near Oatman, Arizona. However, in this second set of mea-

Table 3.1. Carbon Isotope Ratios and Midday Photosynthetic Rates Under Midday Springtime Conditions for Leaves and Twigs of a Number of Shrub and Perennial Herbaceous Plant Species from the Sonoran Desert[a]

Species[b]	Carbon Isotope Ratio (‰)[c]			Photosynthetic Rate (μmol m^{-2} s^{-1})[e]	
	Leaf	Twig	Difference[d]	Leaf	Twig
Photosynthetic-twig shrubs					
Bebbia juncea (W)	−27.1	−26.2	0.9	20.7	10.7
Chrysothamnus paniculatus (W)	−27.6	−26.5	1.2	23.6	15.2
Dyssodia porophylloides (S)	−27.0	−24.6	2.4	6.5	5.4
Gutierrezia microcephalum (W)	−27.2	−24.7	2.5	21.1	17.9
Gutierrezia sarothrae (W)	−26.2	−24.9	1.3	16.7	4.4
Hymenoclea salsola (W)	−26.1	−24.9	1.2	24.8	16.6
Lepidium fremontii (W)	−25.4	−24.2	1.2	12.6	8.8
Porophyllum gracile (W)	−27.8	−26.1	1.7	37.7	23.9
Psiolostrophe cooperi (W)	−27.0	−25.6	1.4	12.8	12.9
Salizaria mexicana (W)	−26.4	−25.1	1.3	15.1	16.7
Senecio douglasii (W)	−25.2	−23.0	2.2	26.0	1.5
Sphaeralcea parvifolia (W)	−25.7	−23.5	2.2	22.3	13.7
Stephanomeria paucifolia (W)	−26.6	−26.3	0.3	22.3	23.3
Thamnosma montana (W)	−25.7	−24.5	1.2	21.7	10.5
$\bar{x} \pm 1$ SE	−26.5 ± 0.2	−25.0 ± 0.3	1.5 ± 0.2		

Nonphotosynthetic-twig shrubs					
Acamptopappus sphaerocephalus (W)	−28.2	−28.0	0.2	9.2	2.7
Ambrosia dumosa (S)	−25.9	−26.1	−0.2	13.0	1.8
Ambrosia eriocentra (W)	−26.5	−26.0	0.6	12.7	−1.5
Cowania mexicana (W)	−24.6	−25.2	−0.6	NM	NG
Encelia farinosa (S)	−25.3	−25.2	0.1	20.0	0.2
Encelia frutescens (W)	−28.3	−28.5	−0.2	25.0	NG
Eriogonum fasciculatum (S)	−26.4	−25.8	0.6	4.4	−3.2
Eurotia lanata (S)	−26.1	−25.9	0.2	3.9	−0.4
Guara coccinea (W)	−26.8	−26.7	0.1	NM	NG
Happlopappus linearfolius (S)	−25.0	−25.1	−0.1	NM	NG
Larrea divaricata (S)	−23.3	−24.3	−1.0	NM	NG
Lycium andersonii (W)	−26.6	−25.9	0.7	NM	NG
Prunus fasciculatus (S)	−26.0	−25.1	0.9	NM	NG
Rhus trilobata (W)	−23.9	−23.5	0.4	NM	NG
Salvia dorrii (W)	−27.9	−26.8	1.1	16.9	0.8
$\bar{x}$ + 1 SE	−26.1 ± 0.4	−25.9 ± 0.3	0.2 ± 0.1		

[a] From Ehleringer et al. (1987).
[b] "W" and "S" indicate that plants were sampled from wash and slope microhabitats, respectively.
[c] Expressed relative to PDB.
[d] Twig value less leaf value.
[e] NM: not measured; NG: not green.

surements, plants were collected from each of the three principal microhabitat types (wash, transition, and slope), not just the microhabitat in which the species was most common. Again, leaf carbon isotope ratios were higher in plants from wash microhabitats (−26.72‰) compared to those from slope microhabitats (−25.66‰). These differences are similar to those observed above and are again statistically significant ($t = 7.08$, $p < 0.001$). Moreover, for all six of the species which span from wash to slope habitats, there was an increase in carbon isotope ratio (decrease in c_i) in plants from slope habitats, ranging from 0.9 to 2.5‰. Of the remaining species whose distributions spanned across microhabitats,

Table 3.2. Leaf Carbon Isotope Ratio of Bulked Samples for Individual Species in Wash, Transition, and Slope Microhabitats near Oatman, Arizona[a]

Species[b]	Leaf Type[c]	Wash[d]	Transition[d]	Slope[d]
Long-lived (50+ years)				
Cercidium floridum	dd	−24.07		
Chilopsis linearis	wd	−25.37		
Chrysothamnus paniculatus	wd	−26.69		
Ephedra viridis	es		−23.30	−23.82
Krameria parvifolia	dd		−24.60	−23.87
Larrea divaricata	e	−24.12	−23.60	−22.67
Lycium andersonii	e	−25.32	−25.09	
Mean		−25.11	−24.15	−23.45
Medium-lived (10–40 years), opportunistic				
Acacia greggii	wd	−27.40	−25.82	
Ambrosia dumosa	dd	−27.37	−26.04	−25.37
Encelia farinosa	dd		−26.13	−25.46
Encelia frutescens	dd	−27.51		
Hymenoclea salsola	dd	−26.45	−23.54	
Mean		−27.18	−25.38	−25.42
Short-lived (1–10 years), opportunistic				
Ambrosia eriocentra	dd	−29.29		
Bebbia juncea	dd	−28.33	−26.66	−25.80
Cassia covesii	dd	−26.03	−26.71	−26.83
Eriogonum fasciculatum	dd		−26.40	−26.53
Eriogonum inflatum	dd	−28.17	−25.82	−25.70
Phoradendron californicum	es	−27.14	−26.96	
Porophyllum gracile	dd	−27.47	−26.75	−26.55
Psilostrophe cooperi	dd		−27.65	−27.02
Sphaeralcea ambigua	dd		−27.38	−27.57
Viguiera laciniata	dd		−26.08	−26.40
Mean		−27.74	−26.71	−26.55

[a] From Ehleringer and Cooper (1988).
[b] Species are categorized according to their longevity.
[c] Leaf types are dd = drought deciduous, wd = winter deciduous, e = evergreen, and es = evergreen stem.
[d] A blank indicates that the species was not present in that microhabitat.

only two of them (*Eriogonum fasciculatum* and *Lycium andersonii*) did not show any change in carbon isotope ratio.

It is interesting to note that among the species thought to be longer-lived, leaf carbon isotope ratios tended to be more positive (suggestive of greater water-use efficiencies). Within the wash microhabitat, *Chrysothamnus paniculatus* (−26.69‰) and *Lycium andersonii* (−25.32‰) are long-lived and attain the largest sizes. Firm life history data are lacking, but the available data indicate that expected life spans exceed twenty-five years. In contrast, smaller wash species such as *Bebbia juncea* (−28.33‰) and *Eriogonum inflatum* (−28.17‰) have shorter life spans, on the order of about five years. A similar pattern holds for the slope plants as well. Species such as *Krameria parviflora* (−23.87‰) and *Larrea divaricata* (−22.67‰) are longer-lived, whereas *Porophyllum gracile* (−26.55‰) and *Psilotrophe cooperi* (−27.02‰) are shorter-lived.

The extent to which the structuring of plants within desert communities can be revealed by carbon isotope ratios has not been examined, but these ratios may prove insightful, given the large differences in isotope ratios among species (and hence similarly large differences in water-use efficiency). A number of recent studies have clearly demonstrated that there are strong intraspecific and interspecific competitive effects for water in deserts (Fonteyn and Mahall 1978; Robberecht et al. 1983; Ehleringer 1984). The consequences of competition for water by these plants are manifested through both reduced growth rates and reduced reproductive output. Fonteyn and Mahall (1978) found that neighboring *Ambrosia dumosa* and *Larrea divaricata* shrubs competed for the same water. It may be fortuitous that carbon isotope ratios from Table 3.2 suggest that the shorter-lived *Ambrosia* have a lower water-use efficiency than the longer-lived *Larrea*, or this may be suggestive of a mechanism by which short-lived shrubs can successfully compete with longer-lived shrubs.

Changes in c_i and WUE with Mistletoe Parasitism

Xylem-tapping mistletoes represent an extremely interesting situation for the examination of water use and water-use efficiency in plants. Mistletoes are obligate, epiphytic parasites, dependent on their hosts for both water and mineral nutrient supplies. These parasites reach their highest densities globally in arid lands (Kuijt 1969). Several investigators have shown that mistletoes exhibit higher transpiration rates than their hosts, and it has been hypothesized by Schulze et al. (1984) that this is a mechanism to gather sufficient amounts of required nutrients (in particular nitrogen) from the host xylem fluids. Correlated with this expectation, comparisons of the same mistletoe species on hosts with differing nitrogen contents in their xylem sap indicated that increased nitrogen supply led to increased mistletoe growth rate (Schulze and Ehleringer 1984).

Ehleringer et al. (1985) proposed that variations in water-use efficiency by the mistletoe should be related to the amounts of nitrogen supplied within the host xylem sap and that carbon isotope ratios could be used to evaluate changes in water-use patterns associated with host nutritional quality. The carbon isotope ratios of xylem-tapping mistletoes exhibit a wide range of values, strongly im-

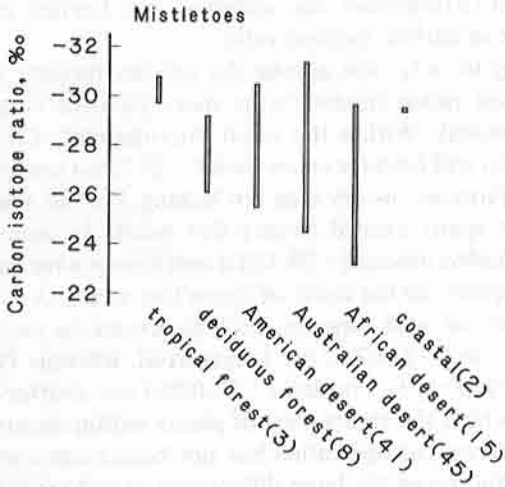

Figure 3.3. The range of carbon isotope ratio values for mistletoe leaves from various habitats. The numbers in parentheses represent the sample size. Based on data from Schulze and Ehleringer (1984), Ehleringer et al. (1985), Ehleringer et al. (1986a, b), and Ehleringer (unpublished observations).

plying substantial variations in the intercellular CO_2 values (Figure 3.3). To estimate the mistletoe response to a change in nitrogen content of the host xylem sap, Ehleringer et al. (1985) compared the difference between mistletoe and host carbon isotope ratios (a measure of the difference in c_i and thus in WUE) on mistletoes growing on nitrogen-fixing (higher resource quality) and non-nitrogen-fixing hosts (lower resource quality). For almost all mistletoes, c_i was higher and WUE lower than for its host. In evaluating mistletoes from Africa, Australia, and North America, there was a clear tendency for mistletoe WUE to improve when supplied with a higher-quality host (Table 3.3). The analysis showed that the difference in carbon isotope ratio between mistletoe–

Table 3.3. Carbon Isotope Ratio Values ($\delta^{13}C$)[a] for Mistletoe–Host Pairs from Different Arid Regions in the United States, Central Australia, and South Africa[b]

Region	Number of Pairs	$\delta^{13}C_{host}$	$\delta^{13}C_{mistletoe}$	$\delta^{13}C_{mistletoe} - \delta^{13}C_{host}$
			High nitrogen hosts	
United States	7	−26.29 ± 0.50	−26.51 ± 0.23	−0.23 ± 0.41
Central Australia	28	−26.87 ± 0.21	−28.28 ± 0.30	−1.41 ± 0.33
South Africa	4	−24.67 ± 0.33	−25.73 ± 0.96	−1.06 ± 0.81
			Low nitrogen hosts	
United States	8	−23.43 ± 0.10	−26.60 ± 0.14	−3.18 ± 0.19
Central Australia	19	−26.54 ± 0.29	−28.83 ± 0.21	−2.30 ± 0.31
South Africa	11	−24.70 ± 0.41	−26.91 ± 0.56	−2.21 ± 0.52

[a] Mean ± SE, in parts per mil.
[b] From Ehleringer et al. (1985).

host pairs (thus difference in WUE) was dependent only on host nitrogen content and not specifically on nitrogen fixation metabolism.

The carbon isotope ratio data from the three different continents indicate that mistletoes vary water-use efficiency in response to host quality and support the hypothesis that the differences in transpiration rate are associated with regulation of mineral acquisition. Much of the nitrogen acquired by mistletoes is converted into and stored in vegetation structures as arginine (Ehleringer et al. 1986a), where it is kept temporarily until transferred to developing seeds at the end of the growing season (Schulze and Ehleringer 1984).

Ehleringer et al. (1986a) found that mistletoes *(Phoradendron juniperinum)* had a negative impact on the water potential status of their juniper hosts, but did not seem to influence the host's carbon isotope ratio when compared to neighboring uninfected junipers. In a similar manner, the leaf carbon isotope ratios of *Acacia greggii* were not influenced by parasitism with *Phoradendron californicum* (Table 3.4). However, host carbon isotope ratio was very much dependent on site quality and decreased by almost 2‰ going from the wetter wash microhabitat to the wash–slope transition zone.

P. californicum will also parasitize *Larrea divaricata* from transition-zone microhabitats in this region. In this host species, it is evident that leaf carbon isotope ratios are different between infected and neighboring uninfected shrubs. However, the isotope ratio differences were opposite to what would have been expected if the parasite were having a negative impact on host performance (Table 3.4). Carbon isotope ratios of *Larrea* were more negative (higher c_i values) on infected shrubs, and actually were close to those values observed on *Larrea* in the wash microhabitat (Table 3.2). It appears that in this case, the mistletoes are only successfully infecting *Larrea* individuals in the transition zone whose roots penetrate deep enough to reach the wetter, wash soil layers. Perhaps this is not surprising since it is likely that mistletoes require hosts that can provide a steady transpirational stream during the dry summer months.

Mistletoes can parasitize other mistletoes as well. This occurs as autoparasitism (intraspecific) or as epiparasitism (interspecific). In much the same way that mistletoes have a more negative carbon isotope ratio than their hosts, autoparasitic mistletoes have more negative carbon isotope ratios than the mistletoes they parasitize (Table 3.5). The decreases in leaf carbon isotope ratios

Table 3.4. Carbon Isotope Ratios[a] of Mistletoes *(Phoradendron californicum)* and Their Hosts in Wash and Transition Microhabitats near Oatman, Arizona

	Wash Microhabitat[b]		Transition Microhabitat	
	$\delta^{13}C_{host}$	$\delta^{13}C_{mistletoe}$	$\delta^{13}C_{host}$	$\delta^{13}C_{mistletoe}$
Nonparasitized hosts				
Acacia greggii	−27.40 ± 0.23	—	−25.53 ± 0.50	—
Larrea divaricata	NP	—	−21.97 ± 0.29	—
Parasitized hosts				
Acacia greggii	−27.00 ± 0.41	−27.14 ± 0.42	−25.82 ± 0.51	−26.96 ± 0.66
Larrea divaricata	NP	NP	−23.60 ± 0.89	−24.61 ± 0.09

[a] Mean ± SE for $m = 3$ individuals in each microhabitat.
[b] NP: not present.

Table 3.5. Carbon Isotope Ratios of Hosts, Mistletoes, and Mistletoes Parasitic on Those Mistletoes[a]

	$\delta^{13}C$ (‰)
Acacia gregii (host)	−27.3
Phoradendron californicum (parasite)	−27.9
Phoradendron californicum (autoparasite)	−28.5

[a] Data from Schulze and Ehleringer (1984).

imply progressively more water wasting by the mistletoes along this parasitic chain. In conjunction with this, Ehleringer and Schulze (1985) have shown that these autoparasitic mistletoes also have proportionally more nitrogen than the mistletoes they parasitize.

Summary

Carbon isotope ratios are a reliable indicator of photosynthetic pathway for aridland plants. Surveys of carbon isotope ratios of desert plants indicate that photosynthetic pathway distributions are strongly correlated with environmental conditions. Within aridland C_3 plants, there are substantial variations in leaf carbon isotope ratios. These variations relate to differences in intercellular CO_2 concentration. The application of stable carbon isotopes to these desert plants is providing new insights into the variations in water-use patterns with habitat and of the interactions between mineral metabolism and water use.

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