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Short communication

Leaf-twig carbon isotope ratio differences in photosynthetic-twig desert shrubs*

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Summary. Carbon isotope ratios were determined for bulk tissues of both leaves and current season twigs of 29 species of Mohave Desert shrubs. Leaf and twig tissues were found to differ in their carbon isotope ratios only in those species which had photosynthetic twigs. These data suggest that the twigs of these species operate at lower intercellular CO_2 values than leaves, an interpretation which is consistent with available gas-exchange data. An effect of microhabitat was also evident between the mean isotope ratios of leaves from wash versus slope habitats.

Key words: Stable isotopes – Intercellular carbon dioxide – Water-use efficiency – Desert shrubs

A significant proportion of the perennial plants in desert habitats have chlorophyllous stem and twig tissues (Cannon 1908; Stocker 1960; Shreve and Wiggins 1964; Adams and Strain 1968; Gibson 1983). These twig tissues maintain positive photosynthetic rates and for some species represent the major photosynthetic surface (Adams and Strain 1968; DePuitt and Caldwell 1975; Szarek and Woodhouse 1978).

Photosynthetic pathways among species having twig and stem photosynthesis can be assessed through carbon isotope ratio analyses. From such surveys, there is evidence indicating that all three major pathways (C_3, C_4, and CAM) exist in stem-photosynthesizing species (Mooney et al. 1977; Shomer-Ilan et al. 1981). While carbon isotope ratios have been used primarily as a means of distinguishing among photosynthetic pathways, there is a theoretical basis (Farquhar et al. 1982b) and experimental evidence (Farquhar et al. 1982a; Ehleringer et al. 1985; Downton et al. 1985) indicating that the leaf carbon isotope ratios are also a reliable indication of the average daytime intercellular CO_2 concentration in C_3 plants. Using the relationship between carbon isotope ratio and intercellular CO_2 proposed by Farquhar et al. (1982b), the carbon isotope ratio is expected to be:

$$\delta^{13}C = -12.2 - 22.6\, c_i/c_a$$

where c_i and c_a are the intercellular and ambient CO_2 concentrations, respectively.

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Recently, Comstock and Ehleringer (1987) have measured photosynthetic characteristics of leaves and twigs of *Hymenoclea salsola*, a common shrub from wash habitats within the Mohave and Sonoran Deserts. They observed a consistent difference of 27 $\mu l\ l^{-1}$ CO_2 between the intercellular CO_2 concentrations of leaves (247 $\mu l\ l^{-1}$) and twigs (220 $\mu l\ l^{-1}$) under ambient conditions with well-watered plants. This intercellular CO_2 difference has implications for differences in instantaneous water-use efficiency (WUE) by leaves and twigs, since:

$$WUE = (c_a - c_i)/(1.6\, \Delta w)$$

where Δw is the leaf to air water vapor concentration gradient. As both leaves and twigs are quite narrow (less than 3 mm diameter) in *H. salsola*, leaf temperatures are similar and thus Δw values are equivalent (Comstock and Ehleringer 1987). Therefore, carbon isotope ratios in *H. salsola* become an indicator of potential differences in WUE between photosynthetic tissue types.

The purpose of this study is to evaluate carbon isotope ratios in a number of twig-photosynthesizing desert shrubs to see if there are differences between leaf and twig tissues consistent with the gas exchange observations reported for *Hymenoclea salsola*.

Methods and materials

Tissues for carbon isotope ratio analyses were collected from field sites near Oatman, Arizona (lat. 34°57′ N, long. 114°25′ W) and Littlefield, Arizona (lat. 37°01′ N, long. 113°52′ W). The vegetation sampled in both locations is at 500–700 m elevation and is typical of the upper portions of the Sonoran Desert in transition to the higher elevation Mohave Desert (Shreve and Wiggins 1964). Paired leaf and current-year twig tissues were collected from the same plant, air dried and brought back to the laboratory for analyses. Carbon isotope ratios were measured on tissues (ground to 40 mesh in a Wiley mill) using an isotope ratio mass spectrometer (Tieszen et al. 1979); the carbon isotope ratios are expressed relative to the PDB standard. Carbon isotope differences were evaluated using paired Student's *t*-tests.

Photosynthesis was measured in the field under spring conditions in March–April of 1985 and 1986 using a portable CO_2-depletion-based photosynthesis system (model LI-6000, LICOR Instruments, Lincoln, Nebraska, USA). Photosynthetic rates were measured during midday condi-

Table 1. Carbon isotope ratios (‰) and midday photosynthetic rates (μmol m^{-2} s^{-1}) under springtime conditions for leaves and twigs of a number of shrub and perennial herbaceous plant species from the Sonoran Desert. Carbon isotope ratios are expressed relative to PDB. "Difference" is the twig value less leaf value. "NM" indicates that the leaf photosynthetic rate was not measured and "NG" indicates that the twigs were not green. "W" and "S" indicate that plants were sampled from wash and slope microhabitats, respectively

Species	Carbon isotope ratio			Photosynthesis	
	leaf	twig	difference	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
Gaura 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
$\bar{x} \pm 1$ SE	−26.1±0.4	−25.9±0.3	0.2±0.1		

tions (1000–1300 h) under clear skies and are expressed on a projected area basis.

Results and discussion

The leaves of all shrubs studied had substantial, positive rates of net photosynthesis (Table 1). Carbon dioxide exchange rates of current season twigs, however, differed markedly between those species visually classified as having a well developed chlorenchyma layer in the twigs and those which were not. The average net photosynthetic rates of twigs were 13.0 and 0.06 μmol m^{-2} s^{-1} for green-twigged and nongreen-twigged species respectively.

Leaf and twig carbon isotope ratios were measured on separated leaf and twig samples taken from the same shoot. Of interest was the difference in the intercellular CO_2 values of the leaf versus the twig. The difference between twig and leaf carbon isotope ratios was used as an indicator of this c_i difference. Using gas exchange measurements, Comstock and Ehleringer (1987) observed a 27 μl l^{-1} difference in c_i between leaves and twigs of *Hymenoclea salsola*. From the Farquhar et al. (1982b) equation, the expected difference in $\delta^{13}C$ values for twig minus leaf is approximately 1.8‰. This difference is in the right direction, but is higher than the 1.2‰ measured on *H. salsola* (Table 1). Three factors that play a role in explaining this apparent discrepancy are: 1) bulk tissues were analyzed in the present study and this would tend to minimize leaf-twig isotope differences since during the initial phases of leaf and twig development the two tissues were derived from a common source, 2) the expected 1.8‰ value is based on plants grown under well-watered conditions and does not consider any stress effects, and 3) c_i may have differed less between leaf and twig tissues even when well-watered under ambient conditions differing from those of the gas-exchange measurements such as increased Δ_w.

From a larger survey of carbon isotope ratios presented in Table 1, there was a statistically significant difference in the twig minus leaf carbon isotope ratios between photosynthetic-twig and nonphotosynthetic-twig shrubs ($t = 23.24$, $P < 0.001$). Carbon isotope ratios of twigs from photosynthetic-twig shrubs averaged 1.50±0.17‰ higher than their associated leaves; the difference between twigs and leaves of nonphotosynthetic-twig shrubs averaged 0.16 ± 0.14, which is not significantly different from zero. These data strongly suggest that the average intercellular CO_2 values of leaves was 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 ($t = 3.386$, $P < 0.01$), it arises because of a microdistributional difference in the two shrub types. Photosynthetic-twig shrubs tended to occur in wash habitats, whereas nonphotosynthetic-twig shrubs occurred 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 at on average higher intercellular CO_2 values than those of the slope-habitat shrubs. These data are still preliminary, but they indicate that the measurement of stable carbon isotopes may be of great use in ascertaining broad patterns in the adaptation of photosynthetic physiology to specific microsites.

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