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Leaf carbon isotope ratios from a tropical dry forest in Venezuela

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Summary

Leaf carbon isotope ratios were measured on dominant deciduous-leaved and evergreen-leaved species in a seasonally dry tropical forest in Venezuela. Carbon isotope ratios were higher and the intercellular to ambient CO_2 concentrations were lower in the deciduous-leaved species. Associated with this are predicted lower water-use efficiencies in evergreen-leaved than in deciduous-leaved species. Predawn water potentials were more positive in evergreen-leaved species, leading to a negative correlation between leaf carbon isotope ratio values and predawn water potential among the different species.

Key words: $\delta^{13}C$, intercellular CO_2, carbon isotope ratio, tropical forest, water potential

Introduction

Analysis of the carbon isotope composition of C_3 plants has been a useful technique for investigating the variations in intercellular to ambient CO_2 concentrations of photosynthetically-active leaves and of the resulting implications for water-use efficiency and stomatal limitation on the photosynthetic rate (O'LEARY 1988, FARQUHAR et al. 1989, EHLERINGER et al. 1993). Carbon isotope fractionation occurs during the initial photosynthetic fixation and the resulting $^{13}C/^{12}C$ composition in plant tissues is dependent on both $^{13}C/^{12}C$ of air CO_2 (source) and of intercellular to ambient CO_2 concentration ratio (c_i/c_a) (FARQUHAR et al. 1982). Since these fractionation events occur continuously as leaves photosynthesize, the analysis of leaf carbon isotope composition provides an integrated, long-term estimate of the intercellular to ambient CO_2 concentration. The c_i/c_a ratio changes in response to limitations imposed by stomatal diffusion limitations and/or photosynthetic demand for CO_2. Thus the c_i/c_a ratio is influenced by a variety of environmental stresses (see review by FARQUHAR et al. 1989). Life history and physiological characteristics interact and there tends to be a positive correlation between longevity and the c_i/c_a ratio at both the intra- and interspecific levels (see contributions in EHLERINGER et al. 1993).

The aim of this study was to analyze seasonal changes in the carbon isotope composition of dominant drought-deciduous and evergreen species, co-occurring in a tropical dry forest in Venezuela. The seasonally dry forests here consist primarily of drought-deciduous species and sparse but occasional evergreen species. We selected four deciduous and two evergreen species, spanning a range of foliage longevity of from 6 to 12 months. Previous ecological studies of these species have focused on water relations and instantaneous gas-exchange characteristics (SOBRADO 1986, 1991, 1993, 1994). One objective of this study was to determine if the carbon isotope analyses, which provide an integrated, long-term estimate of gas-exchange parameters, exhibited a pattern similar to that seen in previous studies.

Materials and methods

Study site

The experimental site was a tropical dry forest located at Charallave, Venezuela (latitude 10° N, longitude 67° W, elevation 400 m). Average annual precipitation is 900 mm, with the majority of the rains occurring from May through October. The landscape is defined by wide valleys flanked by smooth hills. The forest had three well-defined layers (trees, shrubs and annuals) and few vines (GORDON 1977). The highest trees were from 8 to 10 m tall in the valley areas, but plant height became progressively shorter on the hill slopes. The most

common trees were drought-deciduous species: *Beureria cumanensis* SCHULZ (Boraginaceae), *Lonchocarpus dipteroneurus* PITTIER (Papilionaceae), *Pithecellobium dulce* BENTH. (Mimosaceae), *Coursetia arborea* [= *Humboldtiella arborea* GRISEB.] (Papilionaceae), *Albizzia colombiana* BRITTON et KILLIB. (Mimosaceae) and *Acacia macracantha* GRISEB. (Mimosaceae). Few evergreen species occurred in the area; all were shrubs in the Capparidaceae, except for the tree *Morisonia americana* L. (also Capparidaceae).

The deciduous species used in this study were *Co. arborea, L. dipteroneurus, P. dulce* and *B. cumanensis;* the evergreen species were *Capparis aristiguetae* ILTIS and *M. americana.* Details on the ecophysiological characteristics of these species can be found elsewhere (SOBRADO & CUENCA 1979, SOBRADO 1986, 1991, 1992, 1993, 1994).

Plant measurements

Plant evaluations were conducted using leaves at three different developmental stages: expanding, recently mature but fully expanded, and very mature. The relative leaf-age scale was based on time of collection, color and texture of the leaves (SOBRADO & MEDINA 1980). Expanding leaves were collected in June for deciduous species and in September for evergreen species. Recently mature leaves were collected after full expansion was completed. Very mature leaves were collected when small yellowish marks (initial sign of senescence) were first observed.

In order to reduce microenvironmental variation, all leaf material was randomly selected from plants growing side by side. Predawn water potential measurements were conducted at the field site on three leaf replicates per species using a pressure chamber (TURNER 1988). For carbon isotope ratios ($\delta^{13}C$) sun-lit leaves were collected, oven-dried and finely ground. These samples were prepared following procedures outlined in EHLERINGER (1991); the measurements were collected using an isotope ratio mass spectrometer (model delta S, Finnigan MAT, Bremen, Germany). The carbon isotope ratios ($\delta^{13}C$) were expressed relative to Pee Dee Belemnite standard and the precision of the measurement was ± 0.11‰.

From FARQUHAR et al. (1982) the long-term, average intercellular to ambient CO_2 concentration (c_i/c_a) was calculated as

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

where $\delta^{13}C_{leaf}$ and $\delta^{13}C_{air}$ (–8‰) are the carbon isotope ratios of leaf and air, a is the fractionation due to slower diffusion of $^{13}CO_2$ in air (4.4‰) and b is the net fractionation associated with CO_2 fixation (27‰).

Short-term leaf c_i/c_a estimates were derived from gas exchange measurements collected on sun-lit leaves using a portable gas analyzer system (LCA-2, ADC Co., Hoddesdon, UK). Conditions for measurements were ambient CO_2 concentration approximately 34 Pa, photosynthetic active radiation >1000 µmol $m^{-2}s^{-1}$ and a leaf temperature between 29 °C (expanding and mature leaves) and 34 °C (very mature leaves). These values are typical of the environmental conditions experienced by these plants.

Results and discussion

Carbon isotope ratios of mature sun-lit leaves differed by more than 3‰ among species (Fig. 1). Evergreen-leaved species exhibited a pattern distinct from deciduous-leaved species; evergreen leaves tended to be more depleted in ^{13}C. A significant change occurred in leaf $\delta^{13}C$ with leaf maturation. Expanding leaves had $\delta^{13}C$ values that were up to 4.2‰ more positive than was observed in mature leaf tissues. Very mature leaves in all six species tended to have $\delta^{13}C$ values that were slightly more positive than recently matured leaves. Comparable developmental changes in the carbon isotopic composition of leaves have been observed in species from contrasting environments (LOWDEN & DICK 1974, GARTEN & TAYLOR 1982, SMITH & OSMOND 1987, DONOVAN & EHLERINGER 1991, SMEDLEY et al. 1991). In those studies, it had been suggested that the most positive $\delta^{13}C$ values seen in the early stages of leaf development represented stored carbon that had been accumulated late in the previous growing season when stomatal limitations had decreased the discrimination against ^{13}C.

Long term assessment of c_i/c_a values from carbon isotope ratio measurements gave values similar to values derived from instantaneous gas-exchange measurements, except for the expanding drought-deciduous leaves (Table 1). Conditions during which gas exchange measurements were collected were typical of seasonal values; thus, even though these gas-exchange observations represented short-term measurements, we believe that they are typical of seasonal values for that

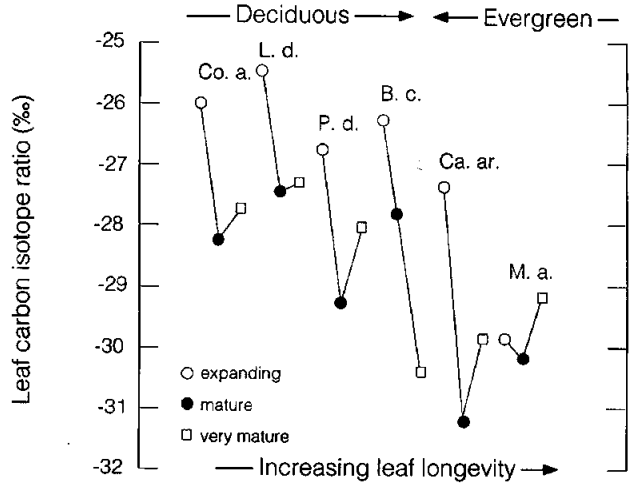

Fig. 1. Leaf $\delta^{13}C$ values as a function of leaf longevity for four drought-deciduous species *Co. arborea* (Co. a.), *L. dipteroneurus* (L. d.), *P. dulce* (P. d.) and *B. cumanensis* (B. c.) and two evergreen species *Ca. aristiguetae* (Ca. ar.) and *M. americana* (M. a.). Values are for expanding (○), mature (●) and very mature (□) leaves.

Table 1. Ratio of intercellular to ambient CO_2 concentration values at different developmental stages of leaves in four drought-deciduous and two evergreen species co-existing in a Venezuelan forest. "T" represents theoretically-expected values based on carbon isotope ratio observations and equation 1. "E" represents experimentally measured values using gas exchange techniques. "T" values were derived from organic materials produced during the entire leaf life time, whereas "E" values were derived from short-term observations. Environmental conditions during periods when "E" measurements were collected were typical of seasonal conditions.

Species	Expanding		Mature		Very Mature	
	T	E	T	E	T	E
Drought-Deciduous						
Co. arborea	0.60	0.77	0.71	0.71	0.75	0.69
L. dipteroneurus	0.59	0.82	0.68	0.71	0.67	0.71
P. dulce	0.64	0.69	0.76	0.72	0.70	0.76
B. cumanensis	0.63	0.71	0.70	0.74	0.81	0.74
Evergreen						
Ca. aristiguetae	0.67	nd	0.84	0.78	0.78	0.75
M. americana	0.79	0.78	0.80	0.76	0.75	0.78

nd = no data

period of the growing season (SOBRADO 1994). This further substantiates the suggestion that during the early stages of leaf development carbohydrates with a different carbon isotope ratio may have been imported from reserves stored elsewhere in the plant (Fig. 1).

It is notable that the $\delta^{13}C$ results indicated that drought-deciduous leaved species were operating at lower c_i/c_a ratio than evergreen-leaved species (Table 1). Previous field studies with these species had shown that the drought-deciduous species maintained lower stomatal conductances and had less water loss during midday during seasonal water deficit conditions than did evergreen-leaved species (SOBRADO & CUENCA 1979).

Interspecific variations in leaf $\delta^{13}C$ were also associated with leaf longevity (Fig. 1). The most positive leaf $\delta^{13}C$ values (–28‰) and lowest c_i/c_a values were found in drought-deciduous species with the shortest foliage longevity; the opposite was observed for evergreens (–31‰). Similarly, trends in the life expectancy of different leaves were positively related with carbon isotope ratio as has been shown previously for plants from contrasting ecosystems (EHLERINGER & COOPER 1988, SMEDLEY et al. 1991, SCHUSTER et al. 1992, RICHARDS & CONDON 1993, WHITE 1993). Interspecific comparisons of $\delta^{13}C$ values can be used to evaluate possible differences in water-use efficiency (CO_2 assimilation to transpiration ratio *A/E*) if differences in the evaporative demand associated with variations in leaf temperature are minimal among species (EHLERINGER et al. 1992). During the rainy season, such differences in this forest are minimal (SOBRADO & CUENCA 1979), and a comparison of adult (mature) leaves would give realistic insights about long term A/E values. Based on $\delta^{13}C$ values from mature leaves, we suggest that drought-deciduous species ($c_i/c_a \sim 0.71$) may be fixing carbon at a higher water-use efficiency value than evergreen ($c_i/c_a \sim 0.82$) species. Instantaneous water-use efficiency from gas-exchange measurements of these drought-deciduous species also gave values that were higher than in the evergreen species (SOBRADO 1991, 1993). These patterns contrast with the generally observed pattern that evergreen-leaved species are more water-use efficient than drought-deciduous-leaved species (MOONEY & GULMON 1982).

Larger seasonal fluctuations in predawn water potentials occurred in drought-deciduous species (from –0.9 to 5.0 MPa) than in evergreen species (from –1.6 to –2.5 MPa). In these forests, the drought-deciduous species have shallower roots than the deeply-rooted evergreen species (SOBRADO & CUENCA 1979). Therefore, drought-deciduous species may depend on surface water which is intermittent and/or limited. In contrast, evergreen species may be able to exploit a more reliable resource of water through the year. This is consistent with the higher c_i/c_a values in evergreen-leaved species. The $\delta^{13}C$ values of mature leaves were significantly correlated with minimum predawn water potentials (Fig. 2). Similar correlations have been observed among co-occurring species with differential belowground resource acquisition capacities in semi-arid and arid ecosystems (FLANAGAN et al. 1992; VALENTINI et al. 1992).

The differences in leaf $\delta^{13}C$ values of drought-deciduous and evengreen-leaved species are consistent with previous observations of the relationships between leaf

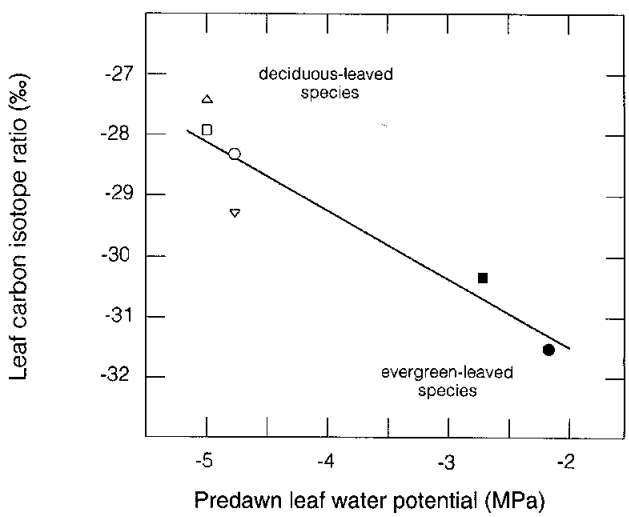

Fig. 2. Leaf $\delta^{13}C$ values as a function of minimum predawn leaf water potential ($r = 0.91$, $p < 0.01$) in four drought-deciduous species ○ *Co. arborea*, △ *L. dipteroneurus*, ▽ *P. dulce* and □ *B. cumanensis* and two evergreen species ● *Ca. aristiguetae* and ■ *M. americana*.

ecophysiology and plant ecology in this tropical dry forest. Despite the fact that evergreen species retain their leaves through very dry periods in this ecosystem and have potentially greater carbon gaining capacity by virtue of longevity, drought-deciduousness more commonly typifies species in this ecosystem. The greater stomatal limitation for carbon fixation and higher *A/E* values in deciduous leaves may allow species with this life form to better maintain activity as soil moisture becomes limiting. Evergreeness may be only of benefit to plants able to tap isolated pockets of deep water that allow these shrubs to persist through dry periods. Given the patchy nature of these deep soil moisture sources and/or temporal variation in the availability of moisture in the deeper layers, the evergreen-leaved species are far less common in this seasonally dry forest.

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