Stable Isotopes and Plant Carbon–Water Relations

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Environmental and Physiological Influences on Carbon Isotope Composition of Gap and Understory Plants in a Lowland Tropical Forest

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I. Introduction

The stable carbon isotope composition of plant tissue ($\delta^{13}C$) is determined both by the isotopic composition of the CO_2 source and by discrimination against the heavier isotope ^{13}C during photosynthetic CO_2 fixation (see O'Leary, Chapter 3, and Farquhar and Lloyd, Chapter 5, this volume). In C_3 plants this discrimination has two main components: one associated with diffusion of CO_2 through the stomata and one due to discrimination against ^{13}C by the primary carboxylating enzyme, RuBisCO. The balance between carboxylation and stomatal limitation of CO_2 diffusion is reflected in the ratio of intercellular to atmospheric partial pressure of CO_2 (p_i/p_a). When stomatal limitation of CO_2 diffusion is small, p_i/p_a will be large and biochemical discrimination against ^{13}C by RuBisCO predominates. Because the biological effects on carbon isotope composition are usually of more interest than source CO_2 effects, it is often more informative to define tissue carbon isotope composition in terms of a discrimination value (Δ) which takes temporal and spatial variation in the $\delta^{13}C$ of the source CO_2 into account (see Farquhar, Chapter 5, this volume). If variation in the isotopic composition of the CO_2 source is known, then analyses of foliar Δ can be used as a powerful tool to understand integrated responses of leaf gas exchange (p_i/p_a) to variations in light, water availability, and other environmental factors (e.g., Farquhar *et al.*, 1982a; Winter *et al.*, 1982; Guy *et al.*, 1986; Hubick *et al.*, 1988; Zimmerman and Ehleringer, 1990).

In closed tropical forests, vertical stratification in the isotopic composition of the source CO_2 may confound the interpretation of foliar $\delta^{13}C$ values (Medina and Minchin, 1980; Farquhar *et al.*, 1989; Sternberg *et al.*, 1989); as a result of soil respiration and relatively poor ventilation, CO_2 concentrations may build up in the understory (Allen and Lemon, 1976; Medina and Minchin, 1980). Since this respiratory CO_2 is derived from material already depleted in ^{13}C, $\delta^{13}C$ values for air in dense tropical forests (Fig. 1) should lie somewhere between the bulk atmospheric value (-7.8 to -8‰) and the value for CO_2 derived from soil respiration (-25 to -28.3‰). For example, air $\delta^{13}C$ values should become progressively more negative as the soil surface is approached, particularly in the understory (Fig. 1). By contrast, in gaps, openings in the forest created by one or more canopy tree falls, greater air mixing may result in air $\delta^{13}C$ values closer to those of the bulk atmosphere. In forests with pronounced wet and dry seasons the $\delta^{13}C$ value of the air should be less negative during the dry season when soil respiration is reduced.

Foliar $\delta^{13}C$ values of tropical forest plants will thus be a function both of physiological processes leading to discrimination against ^{13}C and of the magnitude of refixation of respiratory CO_2. Despite considerable spatial and temporal heterogeneity of $\delta^{13}C$ values in air of tropical forests, recent studies suggest that variations in the $\delta^{13}C$ of the air can be predicted from measurements of the ambient CO_2 concentration alone, providing reason for optimism concerning the utility of foliar $\delta^{13}C$ analyses in forest species (Sternberg *et al.*, 1989; Broadmeadow *et al.*, 1992).
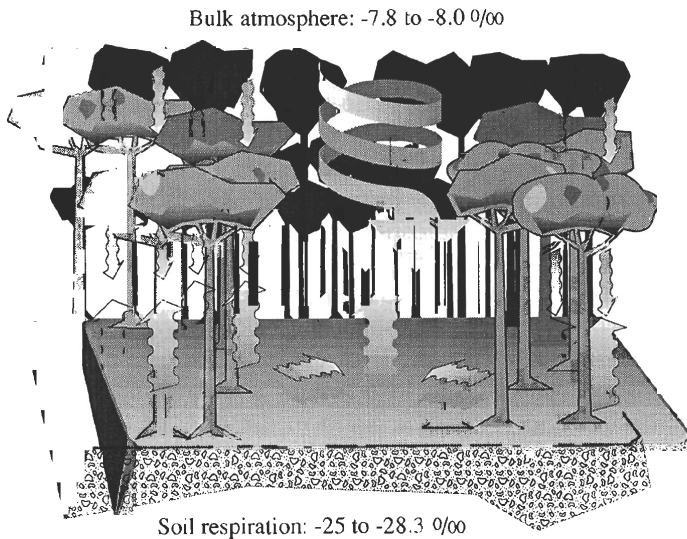
Bulk atmosphere: -7.8 to -8.0 ⁰/oo

Soil respiration: -25 to -28.3 ⁰/oo

Figure 1.   Schematic representation of CO_2 mixing processes in a tropical forest showing the two principal CO_2 sources: the bulk atmosphere and soil respiration (decomposer respiration and root respiration) and their respective $\delta^{13}C$ values.

In this study foliar $\delta^{13}C$ and photosynthetic gas exchange of high light-requiring species growing in gaps and of shade-tolerant shrub species growing in the understory and in gaps in a lowland tropical forest were examined. Our principal objective was to determine the extent to which the variation in foliar $\delta^{13}C$ observed could be attributed to differences in internal physiological features or to differences in the isotopic composition of the source CO_2. The $\delta^{13}C$ of the air was estimated from the ambient CO_2 concentration using a recently published model (Sternberg *et al.*, 1989). Additional objectives included comparing leaf gas exchange responses of shade-tolerant shrub species growing in the understory and the same species growing in gaps and comparing gas exchange responses of shade-tolerant and high light-requiring species both growing in gaps.

II. Materials and Methods

The study was carried out in a semi-evergreen, moist tropical forest on Barro Colorado Island (BCI), Panama (9° 09′N, 79° 51′W). Mean annual rainfall is approximately 2600 mm and is characterized by a marked seasonality, with a dry season from mid-December until the beginning of May when rainfall is only 160−260 mm (Windsor, 1990). The results presented here were obtained during the dry season of 1991 (February−March).

Piper cordulatum C.DC. (Piperaceae) and *Psychotria limonenesis* Krause (Rubiaceae) were chosen as representative shade-tolerant shrub species. Both are common in the forest understory on BCI. *Palicourea guianensis* Aubl. (Rubiaceae) and *Cecropia obtusifolia* Bertol. (Moraceae) were chosen as the representative high light-requiring species. These species occur only in gaps. Two gap and two understory sites were selected. Both gaps were relatively small, between 8 and 12 m in diameter. The understory sites were located within 100 m of a gap and were slightly larger than the gap sites. All study sites were in secondary growth forest. Three individuals of each species were selected per site (with the exception of *C. obtusifolia* for which only one individual was found) and four of the youngest fully expanded leaves were marked for gas exchange measurements. All gas exchange measurements were made by sealing the gas exchange cuvette over the same premarked area of each leaf. Gas exchange measurements were made between 0900 and 1600 h during 3 to 4 days at each site using a LI-COR LI-6200 portable photosynthesis system. Photosynthetic photon flux density (PPFD) was measured with a quantum sensor during the gas exchange measurements. These data were used to calculate overall average PPFD values for each type of site.

For determination of foliar $\delta^{13}C$ the delineated portions of the leaves used for gas exchange measurements were pooled per plant (with the exception of *C. obtusifolia*), oven-dried at 40°C, and finely ground. Subsamples were combusted and the relative abundance of ^{13}C and ^{12}C in the CO_2 released by the combustion was analyzed by mass spectrometry. Stable

carbon isotope composition was expressed as the $^{13}C/^{12}C$ ratio relative to that of the Pee Dee belemnite standard with a precision of 0.2‰. The resulting $\delta^{13}C$ values were used to estimate carbon isotope discrimination (Δ) as

$$\Delta = (\delta^{13}C_a - \delta^{13}C_p)/(1 + \delta^{13}C_p), \tag{1}$$

where a and p represent air and plant, respectively.

Air $\delta^{13}C$ was calculated using the equation developed by Sternberg *et al.* (1989) for data collected at BCI,

$$\delta^{13}C_a = 6703(1/[CO_2]) - 28.3‰ \tag{2}$$

where $[CO_2]$ is the ambient CO_2 concentration in μliter liter^{-1}. The prevailing ambient CO_2 concentration at each site was estimated by circulating ambient air through the infrared gas analyzer of the portable photosynthesis system used for the leaf gas exchange measurements. This procedure was carried out at frequent intervals between the leaf measurements. Our preliminary data concerning the relationship between $\delta^{13}C_a$ and the ambient CO_2 concentration were consistent with the model presented above and with findings by other authors (see Griffiths *et al.*, Chapter 14, this volume). This suggests that variation in the isotopic composition in the source CO_2 can be adequately predicted from logistically and technically simpler measurements of ambient CO_2 concentration alone. Nevertheless, ambient CO_2 concentration at a height of about 1 m was only 353 μliter liter^{-1} ($\delta^{13}C_a$ of $-9.3‰$) in the present study compared with about 376 μliter liter^{-1} ($\delta^{13}C_a$ of $-10.5‰$) in the study by Sternberg *et al.* (1989).

III. Results

Foliar $\delta^{13}C$ values differed among high light-requiring and shade-tolerant species and among individuals of the same species growing in gap and understory sites (Table I). The least negative foliar $\delta^{13}C$ values were observed in the high light-requiring species *C. obtusifolia* and *P. guianensis* (mean = $-30.8‰$). Foliar $\delta^{13}C$ of the shade-tolerant species *P. cordulatum* and *P. limonensis* growing in a gap site were less negative (mean = $-33.3‰$) than in individuals of these two species growing in understory sites (mean = $-35.2‰$).

Measurements of the ambient CO_2 concentration in gap and understory sites indicated that $\delta^{13}C_a$ was 0.9 to 1.6‰ more negative than the value of $-8‰$ generally attributed to the bulk atmosphere (Table I). However, consistent differences in $\delta^{13}C_a$ in gap and understory sites were not observed. A comparison of foliar $\delta^{13}C$ values with those of the air for shade-tolerant species growing in gap and understory sites showed that only 20 to 35% of the difference in foliar $\delta^{13}C$ could be attributed to differences in the isotopic composition of the air. This was more clearly seen by using $\delta^{13}C_a$ to calculate Δ, a procedure which allows direct comparison of physiological

Table I Gas Exchange and Carbon Isotope Composition of Leaves and Air for Plants Growing in Forest Gap and Understory Sites[a]

Site	Species	$\delta^{13}C_p$ (‰)	$\delta^{13}C_a$ (‰)	Δ (‰)	A/g (μmol/mol)
Gap 2	*C. obtusifolia*	-30.5 ± 0.7	-9.6 ± 0.1	21.6 ± 0.9	54.1 ± 9.7
Gap 2	*P. guianensis*	-31.2 ± 0.5	-9.6 ± 0.1	22.3 ± 0.6	60.4 ± 7.8
	mean	-30.8	-9.6	22.0	57.3
Understory 1 and 2	*P. cordulatum*	-35.9 ± 0.2	-9.4 ± 0.1	27.5 ± 0.3	8.6 ± 1.8
Gap 1	*P. codulatum*	-33.4 ± 0.1	-8.9 ± 0.1	25.3 ± 0.02	42.8 ± 5.6
	difference	-2.5	-0.5	2.2	-34.2
Understory 1 and 2	*P. limonensis*	-34.6 ± 0.2	-9.4 ± 0.1	26.1 ± 0.4	9.5 ± 2.0
Gap 1	*P. limonensis*	33.2 ± 0.4	-8.9 ± 0.0	25.1 ± 0.4	40.7 ± 5.9
	difference	-1.4	-0.5	1.0	-31.2

[a]Data are means ± 1 SE for four measurements on three plants per species and site (with the exception of *C. obtusifolia* for which averages are for four measurements on one plant). $\delta^{13}C_a$ values were estimated using ambient CO_2 concentrations and the equation $\delta^{13}C_a = 6703(1/[CO_2]) - 28.3$ from Sternberg *et al.* (1989). Values of Δ were calculated from $\delta^{13}C_a$ and $\delta^{13}C_p$ as described in the text.

influences on tissue carbon isotope composition. A relatively large range in Δ was observed, from 22‰ in high light-requiring species to 26.8‰ in shade-tolerant individuals growing in the understory. Independent estimates of intrinsic water-use efficiency expressed as the ratio of CO_2 assimilation to stomatal conductance (A/g) determined from leaf gas exchange measurements (see Meinzer *et al.*, Chapter 22, this volume) during the dry season (Table I) were highly correlated with foliar Δ ($r^2 = 0.76$). The patterns of Δ and A/g observed suggested that intrinsic water-use efficiency was highest in the high light-requiring species, intermediate in shade-tolerant species growing in gaps, and lowest in shade-tolerant species growing in the understory.

An additional manifestation of the strong correlation between A/g and Δ was a linear relationship between Δ and p_i/p_a (Fig. 2). There was good agreement between the higher values of Δ and p_i/p_a exhibited by shade-tolerant species growing in the understory and the model proposed by Farquhar *et al.* (1982b). At lower values of Δ and p_i/p_a, however, the deviation between observed and predicted values became increasingly large. Although the difference in slopes between predicted and observed Δ values was not statistically significant, this increase in deviation may have resulted from an underestimation of $\delta^{13}C_a$ in gaps or from the difference in time scale involved in the types of measurements. Δ values represent integrated physiological responses of leaves, whereas gas exchange measurements represent instantaneous responses to prevailing conditions. Field determinations of $\delta^{13}C_a$ for both sites should be made in order to resolve this question.

Because p_i/p_a and therefore Δ is determined largely by the ratio A/g, A
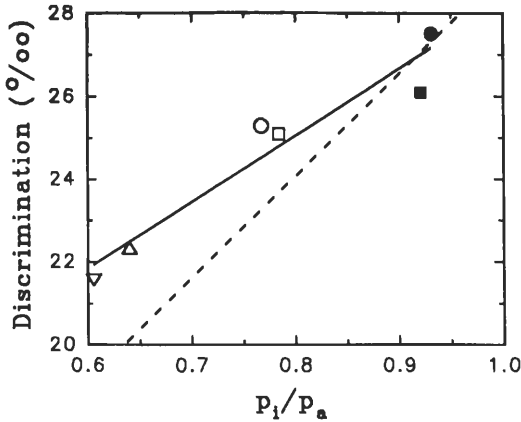
Figure 2. Relationship between foliar carbon isotope discrimination and the ratio of intercellular to ambient partial pressure of CO_2 (p_i/p_a) for high light-requiring and shade-tolerant species growing in gap (open symbols) and understory (closed symbols) sites. (∇) *Cecropia obtusifolia*, ($\triangle$) *Palicourea guianensis*, ($\bigcirc$) *Piper cordulatum*, ($\square$) *Psychotria limonensis*. The dashed line represents the theoretical relationship between discrimination and p_i/p_a ($\Delta = a + (b - a)p_i/p_a$, with $a = 4.4‰$ and $b = 29‰$), proposed by Farquhar *et al.* (1982b).
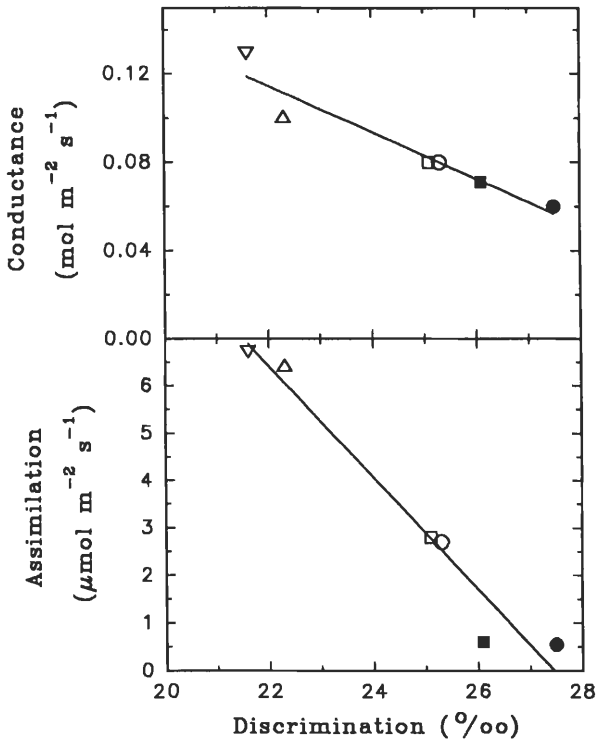

Figure 3. Stomatal conductance and assimilation in relation to foliar carbon isotope discrimination for plants growing in forest gap and understory sites. Symbols are as defined in Fig. 2.

and g were examined individually as functions of Δ in order to determine the nature of the adjustments in leaf gas exchange characteristics responsible for the variation in Δ observed. Both A and g were greatest in the high light-requiring species and declined linearly with increasing Δ (Fig. 3). The 5.9‰ range of Δ was associated with a greater than 10-fold variation in A and only a 2-fold variation in g. This indicates that the lower Δ of plants growing in gaps, particularly in the high light-requiring species, was primarily due to large increases in A. The increase in A associated with higher PPFD in gaps more than compensated for the increase in g, which, in the absence of a change in A, would have raised Δ. Average PPFD during the gas exchange measurements was an order of magnitude higher in the gaps ($288\ \mu mol\ m^{-2}\ s^{-1}$) than in the understory ($28\ \mu mol\ m^{-2}\ s^{-1}$). The relationship between A and Δ and between g and Δ for all species and sites suggested that the physiological basis for the adjustments in gas exchange to differences in the light regime was similar for both shade-tolerant and high light-requiring species.

IV. Discussion

The relatively abrupt decline in wind speed within the canopy of tropical forests (e.g., Roberts *et al.*, 1990) and the release of CO_2 depleted in ^{13}C from the soil may cause the isotopic composition of the source CO_2 near the forest floor to differ substantially from that above the canopy. Within tree fall gaps, however, greater turbulence and hence mixing of the bulk air with the respired CO_2 derived from the forest floor biomass might be expected to result in values of $\delta^{13}C_a$ closer to those of the bulk atmosphere than in the adjacent understory. The 0.5‰ difference in $\delta^{13}C_a$ between gap site 1 and nearby understory sites 1 and 2 were consistent with this idea (Table I). Nevertheless, values of $\delta^{13}C_a$ in gaps may be as negative as those in understory sites (gap site 2, Table I). This is probably a consequence of differences in air turbulence patterns associated with gap size and also of horizontal heterogeneity in the amount of CO_2 released by decomposition processes.

When differences in the isotopic composition of the air among sites were taken into account, it appeared that 65 to 80% of the difference between gap and understory in foliar $\delta^{13}C$ of the shade-tolerance species *P. cordulatum* and *P. limonensis* was the result of internal adjustments in leaf gas exchange characteristics. Contrasting results for forest species growing in the Luquillo Mountains of Puerto Rico were obtained by Medina *et al.* (1991) who reported the expected vertical stratifcation in foliar $\delta^{13}C$ values but no difference in foliar $\delta^{13}C$ between plants growing in gap and understory sites.

The physiological mechanisms responsible for the decrease in foliar Δ in the gap appeared to be similar for both *P. limonensis* and *P. cordulatum*. The lower Δ values measured under higher light availability in the gap were the

result of large increases in A (Fig. 3). Although g also increased under higher PPFD in the gap, the large increase in the photosynthetic rate and probably in photosynthetic capacity more than compensated for the higher g. Decreases in Δ and or increases in A with increased light availability have been reported for several tropical forest species (Pearcy, 1987; Mulkey, 1986; Strauss-Debendetti and Bazzaz, 1991). The relatively low intrinsic water-use efficiency observed in understory plants is consistent with the idea that under these conditions of low and unpredictable light availability maximization of carbon gain is a more important constraint than is maintenance of high efficiency of water use through stomatal restriction of gas exchange. Higher A in shade-tolerant plants growing in gaps may reflect adjustments in photosynthetic capacity linked to higher foliar nitrogen content (Vitousek and Denslow, 1986). However, in a study of the relationship between irradiance levels and carbon isotope discrimination in the orchid *Catasetum viridiflavum* the 4‰ decrease in Δ observed at high irradiance was attributed to increased stomatal limitation of photosynthesis rather than to changes in photosynthetic capacity (Zimmerman and Ehleringer, 1990). This conclusion was based on measurement of small variation in leaf nitrogen content rather than on measurements of leaf gas exchange.

Recent studies of the relationship between Δ and leaf gas exchange characteristics indicate that there are several mechanisms by which intrinsic water-use efficiency (A/g) can be regulated, each with different implications for plant carbon balance. For example, genotypic variation in A/g in peanut results from variation in photosynthetic capacity at similar levels of g (Wright, Chapter 17, this volume). In contrast, higher intrinsic water-use efficiency (lower Δ) in wheat genotypes resulted from covariance of g and photosynthetic capacity, with the relative reduction in g being greater (Condon *et al.*, 1987). Water-limited coffee plants responded similarly; both A and g were positively correlated with Δ, but the relative change in g was larger (Meinzer *et al.*, 1990). On the other hand, in Hawaiian *Metrosideros polymorpha* populations growing at different levels of soil moisture availability, decreases in Δ were associated with maintenance of nearly constant photosynthetic rates while g declined (Meinzer *et al.*, 1992). In the present study, the increase in A/g (decrease in Δ) in the two shade-tolerant species *P. cordulatum* and *P. limonensis*, associated with higher irradiance in tree fall gaps resulted from an increase in A that compensated for a smaller increase in g. Thus, increases in A/g (as inferred from foliar Δ) associated with increases in light or nutrient availability may reflect an overall increase in rates of carbon accumulation and total gas exchange. This contrasts with increased stomatal limitation of gas exchange and reduced rates of carbon accumulation usually associated with decreases in foliar Δ of water-limited plants.

Shade-tolerant and high light-requiring species differ with respect to a large suite of morphological and physiological features. For example, the high light-requiring species depend on high irradiance and high red to far-red light ratios for germination, exhibit rapid leaf turnover and rapid

growth rates, and invest relatively small amounts of carbon in secondary metabolites (e.g., Denslow *et al.*, 1990). Despite these differences, the shade-tolerant and high light-requiring species exhibit the same relationship between Δ and leaf gas exchange characteristics (Fig. 3).

V. Summary

Our results indicate that interpretation of carbon isotope composition of leaf tissue in tropical forest plants may be confounded by spatial and temporal variation in the isotopic composition of the source CO_2. Concurrent site-specific measurements of either ambient CO_2 concentration or $\delta^{13}C_a$ are therefore necessary in these environments.

Our estimated values of $\delta^{13}C_a$ in gap sites were not consistently higher than those of understory sites, possibly due to small gap size and heterogeneity in the amount of CO_2 released by decomposition processes.

The correlation between A, g, and Δ across light environments and species in the present study suggests that regulation of the relationship between CO_2 acquisition and transpirational losses through biochemical and biophysical responses to light availability represents an important ecological and evolutionary constraint for these species.

Acknowledgments

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