

The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO₂ within tropical forest formations in Trinidad

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Summary. A method of monitoring and collecting CO₂ samples in the field has been developed which has been used to study both temporal and spatial variations in canopy CO₂ isotopic signatures in two contrasting tropical forest formations in Trinidad. These have been related to vertical gradients in the carbon isotope ratio ($\delta^{13}\text{C}$) of organic material in conjunction with measurements of other environmental parameters. The $\delta^{13}\text{C}$ of leaf material from two canopies showed a gradient with respect to height, more negative values being found low in the understorey. The deciduous secondary forest, (Simla) showed a difference of 4.6‰ and the semi-evergreen seasonal canopy (Aripo), 2.8‰. The range of $\delta^{13}\text{C}$ values at Simla was 4‰ less negative than those at Aripo. In order to relate these measurements to the interaction between diffusion or carboxylation limitation, and source CO₂ effects, variations in environmental parameters through the canopy have been compared with changes in CO₂ partial pressure (P_a) and isotopic composition (δ_a) throughout the day during the dry season. Values of P_a 20 m above the ground at Aripo varied from 380 vpm at dawn to 340 vpm at midday, at which time the partial pressure 15 cm above the ground was 375 vpm. The CO₂ partial pressure did not stabilise during the course of the day, and there was good correlation ($r^2=0.82$) between δ_a and P_a , with more negative values of δ_a occurring in the understorey. Diurnal changes of 2‰ were evident at all canopy positions. In the more open canopy at Simla, these gradients were similar, but less marked. Leaf-air vapour pressure deficit (VPD) showed no relationship with height, possibly as a result of minimal water flux from both the soil and the canopy due to low soil water content; VPD was 1.5 kPa higher at midday than dawn. A 3° C temperature gradient between the understorey and upper canopy was observed at Aripo but not in the more open Simla canopy. CO₂ partial pressure stabilised for only 4 h in the middle of the day, while other parameters showed no stable period. The proportion of floor respired CO₂ reassimilated at

Aripo has been calculated as 26%, 19%, and 8% for the periods 0600–1000, 1000–1400, and 1400–1800 hours. In order to quantify source CO₂ effects, measurements of the environmental parameters and assimilation rate must be made at all canopy positions and throughout the day.

Key words: Carbon isotope ratios – Tropical canopies – CO₂ fluxes – Respired carbon dioxide

Fractionation against ¹³CO₂ during photosynthesis results in organic material depleted in ¹³C as compared to source CO₂, with a more negative carbon isotope ratio ($\delta^{13}\text{C}$, ‰). This may be expressed in terms of discrimination (Δ^2), when the isotope ratios of plant (δ_p) and atmospheric CO₂ (δ_a) are taken into account to produce a positive term directly related to the extent of fractionation (Farquhar et al. 1989a, b).

These processes have been characterised by several models which have been refined by G.D. Farquhar and co-workers to account for the inherent discrimination by RuBisCO (ribulose biphosphate carboxylase oxygenase) in terms of carboxylation limitation and diffusion limitation, as well as discrimination resulting from secondary carboxylase activity, respiration and carbon partitioning (Farquhar et al. 1982; 1989a, b; Raven and Farquhar 1990).

Applications using stable isotopes of carbon have developed from initially categorising photosynthetic pathways, (C₃, C₄, CAM: Bender 1968) to evaluating more critically the interactions between water use and C₃ photosynthetic efficiency. This latter approach has resulted from the analysis of P_i/P_a (internal:external partial pressure of CO₂), which is related independently through stomatal conductance to both water use efficiency and the extent of carbon isotope discrimination

$$^1 \delta^{13}\text{C} = \left(\frac{R_{44/45}_{\text{Sample}}}{R_{44/45}_{\text{Standard}}} - 1 \right) \times 1000$$

$$^2 \Delta = (\delta_a - \delta_p) / (1 + \delta_p)$$

(O'Leary 1988; Farquhar 1989a, b; Griffiths 1991). However difficulties remain in "scaling-up" these applications to whole canopies and natural ecosystems, particularly when there may be significant variation in source CO₂ isotope composition (Griffiths 1991).

For forest canopies, δ_p has often been observed to have a more negative value (depleted in ¹³C) associated with leaves and plants from the understorey. The magnitude of this gradient varies depending on the type of forest studied, but has typically ranged from 2.5‰ (*Lagarostrobos franklinii*: Francey et al. 1985) up to 5‰ in temperate and tropical hardwood canopies (Vogel 1978; Medina and Minchin 1980; Schleser and Jayasekera 1985; Van der Merwe and Medina 1989; Sternberg et al. 1989).

There is controversy as to the causes of this gradient: some authors attribute the more negative δ_p values in the understorey to the re-fixation of respiratory CO₂, already depleted in ¹³C (Vogel 1978; Medina and Minchin 1980; Medina et al. 1986; Van der Merwe and Medina 1989). Indeed, this "local atmosphere" effect was proposed by Wickman (1952), and later substantiated by Keeling (1958; 1961a, b). Others suggest that it is a response to variations in P_i/P_a due to light limitation of photosynthesis low in the canopy (Francey et al. 1985; Francey and Hubick 1988). Other studies have reported a lateral gradient in δ_p associated with an irradiance cline (Ehleringer et al. 1986; 1987), and a relationship between δ_p and light level in an epiphytic orchid (Zimmerman and Ehleringer 1990). These approaches have been resolved into two types of model, one implicating δ_a (Schleser and Jayasekera 1985; Sternberg 1989; Sternberg et al. 1989) and the other, Δ (Francey et al. 1985; Francey and Hubick 1988) as being the major determinant of δ_p low in the canopy.

However, many of the measurements of δ_a used to validate these models have been of samples collected at various times during the course of the day from different positions within the canopy. Many of the CO₂ collection methods have also been cumbersome to use in the field. We have developed a sample preparation line, which, in conjunction with an air intake which can be raised or lowered within the canopy by means of a pulley, can be used to sample δ_a regularly throughout the day. Studies have been carried out in contrasting forest formations in the field in Trinidad, showing that there are dynamic changes in both P_a and δ_a , as well as in other environmental parameters (see Lemon et al. 1970; Marek and Pirochtova 1990). Such temporal and vertical stratification should be taken into account when future models of forest canopy $\delta^{13}\text{C}$ gradients are reported.

Methodology

The study sites were located in two adjacent valleys, Arima and Heights of Aripo, running north to south and subtending the main ridge of the Northern Mountain Range, Trinidad, West Indies. The sites were at similar altitudes, Simla (grid ref. PS 868 823) at 200 m, and Aripo (grid ref. PS 938 797) at 140 m, and only 7.5 km apart. Aripo was however further east, and in the rain-shadow of Cerro del Aripo, the highest peak of the Northern Range, leading to

greater annual precipitation. Both sites were on the eastern sides of their respective valleys, but Aripo was only 10 m above and 40 m away from a river, in the bottom of a ravine. The valley at Simla was more open, and free-draining with limestone outcrops throughout. The species composition at each site, together with the deciduous nature of the Simla canopy late in the dry season lead to classifications as "deciduous seasonal forest" for Simla, and "semi-evergreen seasonal forest" for Aripo, after Beard (1946).

Canopy structure was similar for both Simla and Aripo, with emergent crowns attaining a height of 25 m and 30 m respectively. A closed canopy formed at 18 m or 20 m, and a secondary canopy of younger trees at 7–8 m from the forest floor. Both canopies had similar light profiles (at midday), 50% transmission in the primary canopy, 12% in the secondary, 8% and 2%, 1 m and 15 cm from the ground, with respect to full sunlight. Values are means of nine readings at each height (measured with ΔT integrating quantum sensors, Δ -T devices, Cambridge, UK).

Canopy access

An emergent tree ("mast" tree after Lemon et al. 1970) was climbed with the aid of spiked leg irons, and a climbing rope attached in the crown. Subsequent ascents could then be made using "Jumar clamps", and descents by abseiling. A rope/pulley system was erected at the highest accessible point in the crown allowing tubing for gas collection and probes for measuring environmental parameters to be positioned in the canopy with minimal disturbance of the site. The canopy positions investigated were primary canopy (approximately 20 m: at Simla this was subdivided into upper and lower), secondary canopy (approximately 8 m), and also 1 m and 15 cm from the ground.

Sampling procedure

The air intake, attached to the rope-pulley system, consisted of a length of PTFE tubing (4 mm internal diameter), to which two copper-constantan thermocouples (Solex instruments, Broughton Astley, England) were attached. One of the thermocouples was taped between two freshly cut leaves of the mast species, to provide an estimate of leaf temperature, while the other monitored air temperature.

Air was drawn from the intake to a site 40 m distant from the mast tree using an air supply unit (ASU, The Analytical Development Co. Ltd, Hoddesdon, England) through PTFE tubing. CO₂ partial pressure was measured with an infra-red gas analyser (IR-GA: LCA-2, ADC Ltd.), and the relative humidity of the air was determined with a Vaissala type humidity sensor within a porometer head (Dingbat Electronics, Aberdeen, Scotland), with the temperature of the air within the porometer head measured using a thermistor. Leaf-air vapour pressure deficit (VPD) could therefore be calculated for each canopy position, using leaf and air temperature at each height. Following a change in position of the air intake, air was drawn through the system for 10 min prior to CO₂ collection. Measurements were made continuously from 0430 to 1900 hours, with dawn and dusk at 0600 and 1800 hours (local time) respectively.

Collection of atmospheric CO₂

CO₂ for isotopic analysis was collected cryogenically using the apparatus shown in Fig. 1. The method was developed from that of Evans et al. (1986). Air was drawn from the air intake through PTFE tubing using a rotary vacuum pump, with the flow rate restricted to 200 cm³ min⁻¹ through the needle valve. This resulted in a partial vacuum between the valve and the pump, with CO₂ collected in a single pass through the cold trap (liquid N₂). After a 10 min collection period, the line was evacuated to a final

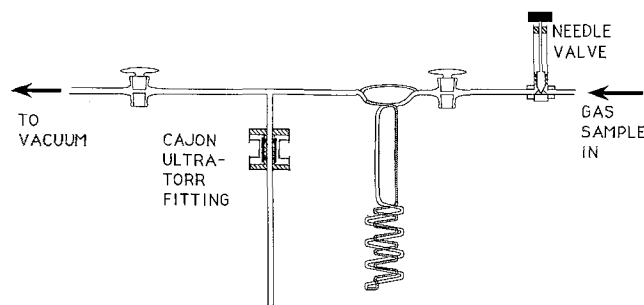


Fig. 1. Apparatus used for the collection of carbon dioxide samples in the field. The cold trap was constructed from 6 mm/4 mm (O.D./I.D.) pyrex, stopcocks were high vacuum pyrex stopcocks (4 mm key orifice: Springham, Stafford, UK), the needle valve was a fine metering needle valve (Nupro Co, Ohio, U.S.A.), and 6 mm (O.D.) Cajon "ultra torr" fittings (Cajon Co. Ltd, Macedonia, U.S.A.) attached the side arm to the collection line

pressure of 1×10^{-2} Torr by closing the stopcock upstream from the cold trap. The system was then isolated from the rotary pump, and the cold trap warmed to release the CO_2 which was freeze-distilled into the side-arm using liquid N_2 . After 5 min the pyrex tube was sealed to form a vial using a butane gas torch. These samples could then be stored for subsequent purification and analysis (see below).

Measurements of ambient atmospheric conditions were made from a ridge in a clearing, at a height of 15 m above the ground. CO_2 was collected and environmental parameters measured throughout the day.

Collection and analysis of organic material

Leaf samples were collected from species near the mast tree, at the five heights described under canopy access (at Aripo, samples were taken from both upper and lower primary canopy).

Organic material was combusted as described by Griffiths et al. (1990), with CO_2 from both combusted and atmospheric CO_2 collections repurified through oxidation and reduction columns, to

remove remaining volatile organic compounds, and N_2O . Analysis was performed on an Isospec 44 dual inlet isotope ratio mass spectrometer (Spectramass Ltd, Congleton, U.K., modified by C.J.S. Sciences, Winsford, U.K.) with respect to a working standard, with $\delta^{13}\text{C}$ of -43.2% vs PDB.

Results

A summary of the data regarding the isotope ratio, $\delta^{13}\text{C}$ of leaf material (δ_p) at different heights in the two canopies is presented in Fig. 2. Results are expressed as the mean (\pm SE) of analyses of all species present at a particular canopy position. Both canopies demonstrate a similar trend in δ_p , tending towards more negative values (i.e. more depleted in ^{13}C) low in the understorey. At Simla, this difference assumed a value of 3.6% (-24.7 to -29.1%), while a smaller difference of 2.8% (-29.7 to -32.5%) was observed at Aripo. Also apparent in the

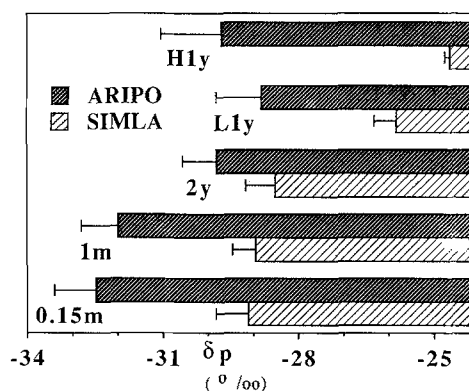


Fig. 2. Mean δ_p of leaf material from 0.15 m, 1 m, secondary (2y), lower primary (L1y), and upper primary (H1y) canopy in the two forest formations. Values are means of between two and six species, \pm SEM, each sample consisting of ten pooled leaves

Table 1. δ_p for species collected from the two canopies, in relation to height

Species	Growth form	δ_p				
		15 cm	1 m	2y	L1y	H1y
Simla						
<i>Brosimum alicastrum</i> (Sw.)	d	-27.2	-27.5	-28.1	-26.9	-24.6
<i>Philodendron krugii</i> (L.) C. Koch	e	-27.9	-27.5	-26.1	-24.6	-
<i>Lundia corymbifera</i> (Vahl.) Sandwith	e	-27.9	-28.1	-28.8	-26.3	-24.8
<i>Tabernaemontanum attenuata</i> (Miers.) Urb	d	-30.2	-29	-28.9	-	-
<i>Swietenia macrophylla</i> King (introduced)	d	-28.7	-29.5	-	-25.8	-
<i>Casearia guianensis</i> (Aubl.) Urb.	s	-29.6	-29.7	-28.3	-	-
<i>Aphelandra pulcherrima</i> (Jacq.-Kunth.)	s	-32.4	-31.4	-31.1	-	-
Aripo						
<i>Clathrotropis brachpetala</i> (Tul) Kleinh.	d	-31.8	-30.0	-28.7	-28.3	-27.6
<i>Ryania speciosa</i> Vahl.	s	-32.0	-31.7	-29.1	-	-
<i>Calliandra guildingii</i> Beuth.	d	-31.0	-31.8	-30.2	-29.7	-29.3
<i>Philodendron lingulatum</i> Schott.	e	-35.9	-35.0	-31.6	-	-
<i>Bactris cusea</i> Crueg.	d	-	-	-32.2	-31.1	-32.3
<i>Miconia affinis</i> DC.	d	-31.8	-31.7	-27.3	-26.3	-

Values are single analyses of a pooled sample of ten leaves
d=dominant canopy tree, s=sub-canopy tree, e=epiphyte

2y=secondary canopy, L1y=lower primary canopy, H1y=upper primary canopy

range of δ_p values is an overall difference of 4‰ between the two canopies.

Individual δ_p data for the species analysed are presented in Table 1, and demonstrate that δ_p is generally independent of growth form. However, the palm *Bactris cusea* appears anomalous, exhibiting no gradient in δ_p with height, and more negative δ_p values in the upper canopy than other species, while the epiphytic aroid, *Philodendron lingulatum*, and the sub-canopy shrub, *Aphelandra pulcherrima*, both demonstrate more negative δ_p values in the lower canopy than other species in their respective formations. Shaded material from the upper primary canopy of the mast tree at Simla, *Brosimum alicastrum*, was also analysed, and δ_p found to be 1.5‰ more negative than exposed material (data not shown). Apart from these species (also see Discussion), there was a constant gradient observed in δ_p for the two canopies.

Variations in environmental parameters and δ_a for the forest formations at Simla and Aripo

The diurnal variations in environmental parameters for each site are presented in Fig. 3, with data averaged over 5 or 4 consecutive days for Simla and Aripo respectively. Measurements have been pooled at each height over arbitrary 2-h periods (e.g. all data collected 0500–0700 hours, for all days, is presented as a mean at 0600 hours, including days when CO_2 was collected for isotopic analysis).

At the open canopy of Simla, there was a large gradient in P_a both within the canopy, and throughout the day (Fig. 3c). At dawn, P_a at 20 m (358 vpm) was 25 vpm lower than at 15 cm (383 vpm), although both were reduced to 338 and 346 vpm, respectively, at midday. Thus stratification was more marked at dawn, but still statistically significant during the steady-state period in the middle of the day (Student's *t*-test). There was no significant stratification of leaf temperature (data not shown), air temperature or leaf air VPD, although there were

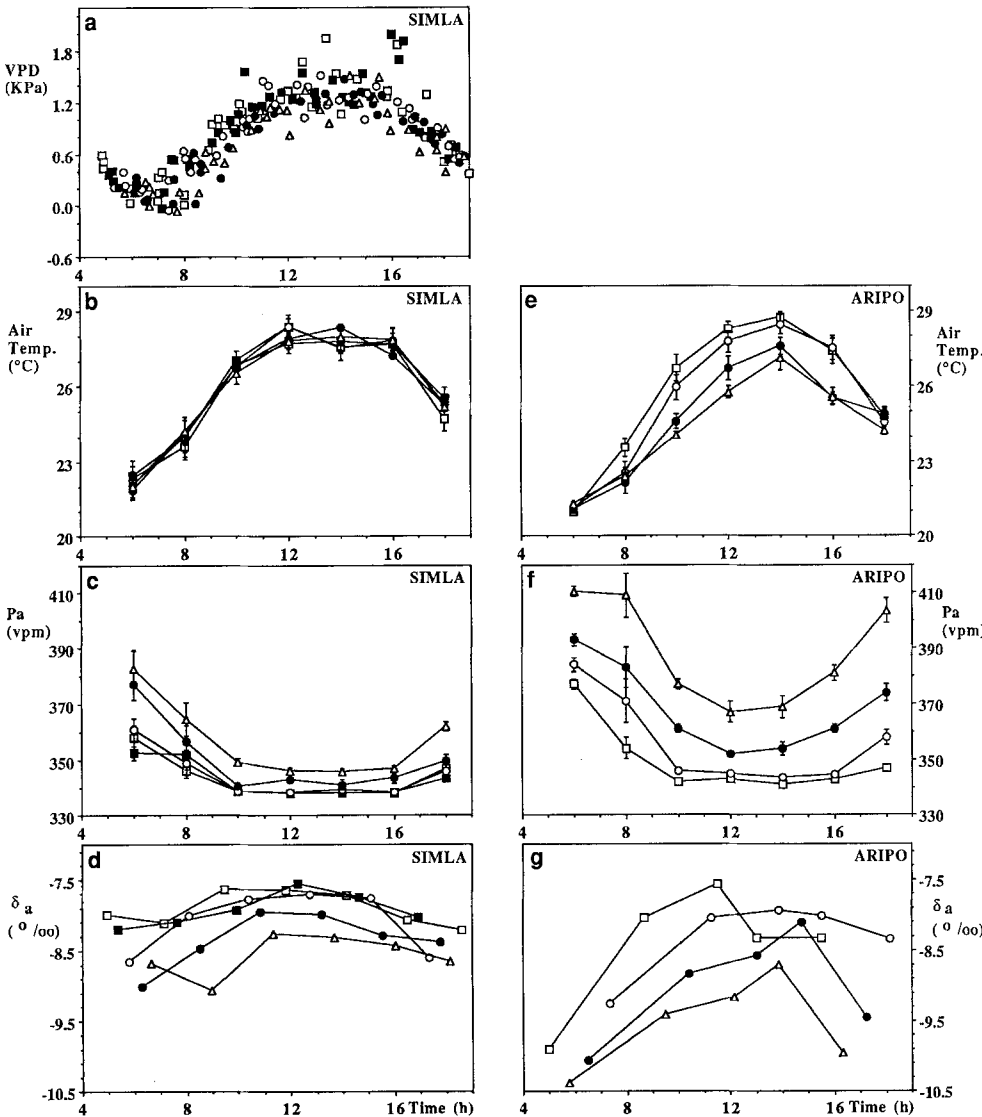


Fig. 3a–g. Diurnal courses of environmental parameters at five heights in the two forest formations: Δ 0.15 m, \bullet 1 m, \circ secondary canopy; \square primary canopy (upper at Simla); \blacksquare lower primary canopy at Simla. Values of VPD at Simla are all points measured over: 5 days 9 March, 10 March, 13 March, 14 March, 17 March 1990. Values of air temperature and CO_2 partial pressure are means of all values \pm SEM measured over 2 h periods on the same 5 days at Simla and 22 March, 23 March, 28 March, and 30 March 1990 at Aripo. δ_a was measured on 14 March at Simla and 22 March at Aripo

consistent variations for all canopy positions through the course of the day, air temperature varying from 22° C at dawn to 28° C at midday (Fig. 3b), while leaf-air VPD ranged from 0.1 kPa to 1.3 kPa (Fig. 3a).

In contrast to Simla, stratification was more pronounced in the dense canopy at Aripo. At dawn, a significant gradient of 34 vpm (377–411 vpm) in P_a existed between 18 m and 15 cm, which was reduced to 24 vpm (343–367 vpm) at midday (Fig. 3f), as opposed to gradients of 25 vpm and 8 vpm at Simla. P_a did not reach steady-state during the day, and values were consistently greater than observed at Simla. At midday, a significant gradient in air temperature of 3° C (18 m: 29° C, 15 cm: 26° C; Fig. 3e) was evident ($P < 0.01$, Student's t -test). Although continuous measurement of air humidity (and thus leaf-air VPD) was not possible due to equipment failure, a minimum leaf-air VPD gradient at midday may be calculated: assuming the partial pressure of water vapour is constant throughout the canopy (2.65 kPa recorded in preliminary measurements), values of leaf temperature at midday (data not shown) yield leaf-air VPD of 1.18 kPa, 1.08 kPa, 0.86 kPa and 0.67 kPa at heights of 18 m, 8 m, 1 m and 15 cm. Air temperature (at 18 m) fluctuated between 21° C and 29° C through the course of the day (21–26° C at 15 cm), of similar magnitude to that observed at Simla, where no stratification in leaf-air VPD was seen.

Measurements of δ_a over a single daily timecourse are presented for the two canopies in Figs. 3d and g as averages of two samples at each time point (a period of 20 min). Values of δ_a changed in parallel with those of P_a and showed consistent variations throughout the day, at Simla varying between –9‰ and –8.3‰ at 15 cm, and –7.9‰ and –7.5‰ at 20 m, between dawn and midday. At Aripo, the diurnal fluctuations were greater, varying between –10.4‰ and –8.7‰ at 15 cm, and –9.8‰ and –7.5‰ at 18 m. The δ_a gradient at midday was greater at Aripo (1.3‰) than at Simla (0.7‰), again indicating more stratification in the denser canopy (see discussion for statistical correlations). Values were in general more negative at Aripo as a result of either the denser canopy structure, or greater CO₂ flux from the soil. Measurements of “ambient” P_a and δ_a were made 15 m above a clearing on a ridge, demonstrating that the boundary layer above vegetation affects CO₂ levels and extends beyond the canopy (see Nobel 1983). CO₂ partial pressure varied from 346 vpm at dawn to 334 vpm at midday, with a mean value of δ_a of -7.7 ± -0.1 ‰ (data not shown), similar to other current values (Sternberg 1989).

Discussion

The gradients in δ_p presented here are of a similar magnitude to those reported by other workers (Vogel 1978; Medina and Minchin 1980; Schleser and Jayasekera 1985; Francey et al. 1985; Medina et al. 1986; Sternberg et al. 1989; Medina et al. 1991). The gradient in δ_p was greater at Simla (4.6‰) than Aripo (2.8‰) although at present it is uncertain whether this is due to edaphic effects, (Simla being less moist), or differences in the

microclimates of the two canopies, (the Aripo site was at the bottom of a ravine). Analysis of *Brosimum alicastrum* at Simla perhaps demonstrates the effect of light limitation of photosynthesis, in that δ_p of peripheral primary canopy leaves was less negative than that of leaves from the middle of that canopy (–24.6‰ vs –26.2‰) (data not shown). Light limitation of photosynthesis could also be implicated in the very negative δ_p values recorded for *P. lingulatum*, which grew in deep shade even in the secondary canopy.

The mean difference in δ_p between the two canopies indicates either reduced diffusion limitation to photosynthesis, or a greater contribution of isotopically light CO₂ from soil respiration (Medina et al. 1986; Schleser and Jayasekera 1985) at Aripo. The shading effect of the valley sides may also explain the difference in absolute δ_p values between the two sites, with total daily incident PPFD at Aripo lower than at Simla, leading to greater light limitation of photosynthesis, and thus larger values of Δ . This would not have been apparent from midday measurements of canopy light transmission.

However, differences in plant water status and the influence on leaf conductance could also explain both the large spread in values of δ_p for the sites, and the 4‰ difference in mean δ_p between the two sites. Measurements of leaf water potential in the future would enable the principal factor to be identified. Leaf-air VPD and air temperature are unlikely to contribute to the gradient in δ_p at Simla in the dry season, since no gradient was observed in those parameters in this more open canopy. At Aripo there was stratification of both air temperature and (calculated) VPD, indicating the denser canopy structure, with the ground level to upper canopy gradient being 2.5° C in the middle of the day. Temperature effects on Δ have been demonstrated in a number of studies (Friend et al. 1989; Troughton et al. 1974; Christeller et al. 1976; Smith et al. 1973), although the results have been ambiguous, and thus further work must be performed on the relevant species before the contribution of temperature gradients to the gradient in δ_p is known. Gas exchange analysis will also be required to determine the contributions of leaf-air VPD and PPFD to the gradient in δ_p .

Turning to the interactions between source CO₂ partial pressure and carbon isotope composition, there has been conflicting evidence relating to the stability and absolute values of CO₂ partial pressures within forest canopies. While the dynamic nature of CO₂ fluxes has been demonstrated in some studies (Lemon et al. 1970; Marek and Pirochtova 1990), this was not evident in other investigations (Medina et al. 1986; Sternberg et al. 1989).

Sternberg et al. (1989) observed values of 375 and 349 vpm, 1 and 25 m above ground level in a Panamanian tropical forest canopy, while Francey et al. (1985), presented values of 356 and 339 ppm, at heights of 1 and 14 m, in a Tasmanian temperate rainforest. These two studies stated that CO₂ partial pressure was constant between 0800 hours and 1300 hours, and 0900 hours and 1700 hours respectively, but made no measurements beyond these times. In the second of these studies, assimila-

tion rate was shown to have reached a maximum in both sun and shade branches before 0800 hours, and that there was a "midday depression of photosynthesis" with net respiration from 1300 hours onwards. The period of CO₂ collection and measurement did not therefore correspond with times of net carbon assimilation. With values of δ_a extrapolated from values of CO₂ partial pressure, a significant shortfall may have been introduced in the calculation of the contribution of re-assimilated CO₂ to values of δ_p by this discrepancy in sampling times.

The results presented in this study are the first to follow concomitant changes in δ_a in relation to P_a diurnally, and throughout a forest canopy. With variations of up to 2‰ in δ_a during the early morning, we may visualise photosynthesis acting as a sink for CO₂, drawing ambient atmospheric CO₂ down into the canopy at midday, which may contribute significantly to values of δ_p . At this time, values of δ_a at Aripo of -7.9‰ at 18 m and -9‰ at 15 cm compare with an ambient atmospheric CO₂ value of -7.7‰ (± 0.1), indicating that in dense canopies, gradients in δ_a may contribute to the gradient in δ_p , even at midday. At Simla, the gradient (-7.7‰ to -8.3‰) was reduced, and values of δ_a much closer to ambient values, the minimal gradient with respect to height indicating that CO₂ fluxes were low, and that mixing with the atmosphere was rapid, again illustrating the different natures of the two canopies.

A comparison of the gradient in δ_a at midday suggests that δ_a alone contributes 9% and 30% to the observed gradient in δ_p for Simla and Aripo, respectively, both well below previous estimates (Sternberg 1989).

Modelling of CO₂ fluxes

Only four previous studies have investigated values of δ_a within forest canopies in conjunction with gradients in δ_p . Vogel (1978) collected CO₂ produced in the litter layer overnight, but did not collect gas within the canopy. Francey et al. (1985) calculated values within the canopy from measurements of CO₂ partial pressure described above, using a relationship derived from analysing 18 samples of canopy CO₂ of varying partial pressures. Differences of 0.04‰ at 8 m, and 0.8‰ at 1 m, as compared to ambient values were observed. Figure 4 demon-

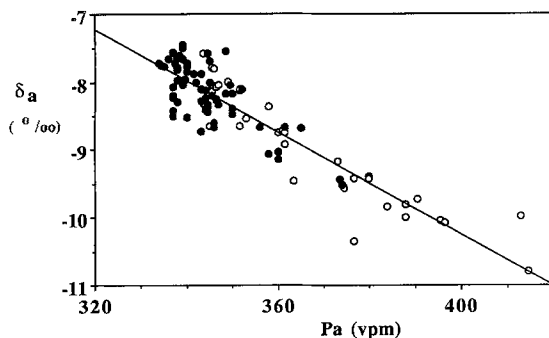


Fig. 4. Relationship between δ_a and P_a for all analyses from the two canopies. Closed symbols represent samples from Simla, and open symbols those from Aripo. The regression for the combined data was $\delta_a = -22.87 + 5073/P_a$, $r^2 = 0.82$

strates that a similar relationship between δ_a and P_a was evident in this study. ($r^2 = 0.82$, $n = 95$, for all samples of CO₂ analysed.) The regression equation for the relationship is: $\delta_a = -22.87 + 5073/P_a$ in comparison with that found by Francey et al. (1985) of: $\delta_a = -23.4 + 5349.3/P_a$. Samples from Simla were generally closer to ambient values than those from Aripo, due to the lack of stratification in that canopy.

Van der Merwe and Medina (1989) analysed δ_a in the same canopies where Medina et al. (1986) had measured CO₂ partial pressure. Measurements were only made before dawn and after dusk, again not corresponding with times of carbon assimilation. Sternberg et al. (1989) measured δ_a at three heights in a Panamanian rainforest canopy between 0800 hours and 1300 hours. No change in δ_a with respect to time was observed in this period (although a scatter of 3‰ was evident), but a constant gradient of 2.5‰ was found between 0.5 m and 25 m above the forest floor.

These values were used by Sternberg (1989) to model CO₂ fluxes within forest canopies, and the results presented here will be analysed in a similar manner. Using a plot of δ_a vs. $1/P_a$, he determined the proportion of floor-respired CO₂ re-assimilated (R) to be 7–8%. These measurements were made between 0800 hours and 1300 hours, with no diurnal fluctuations apparent. Figure 5 shows plots of δ_a vs. $1/P_a$ for Aripo, with the daylight period divided into three portions, producing regressions of:

$$\delta_a = -24.02 + (5553/P_a), \text{ (0600–1000 hours)}$$

$$\delta_a = -24.95 + (5840/P_a), \text{ (1000–1400 hours)}$$

$$\delta_a = -27.35 + (6646/P_a), \text{ (1400–1800 hours)}$$

We may assume that the isotopic signature of floor-respired CO₂ (δ_r), was -30‰, equivalent to the mean δ_p for the primary canopy, since that is the major source of organic material degraded by the soil microflora (Sternberg 1989). The proportion of respired CO₂ re-assimilated (R), may then be calculated, using the relationship derived by Sternberg (1989):

$$M(t) = M(0\%) (1 - R)$$

where $M(t)$ is the gradient of the line at time (t), and $M(0\%)$ is the gradient of a line corresponding to 0% recycling of respired CO₂, calculated from ambient val-

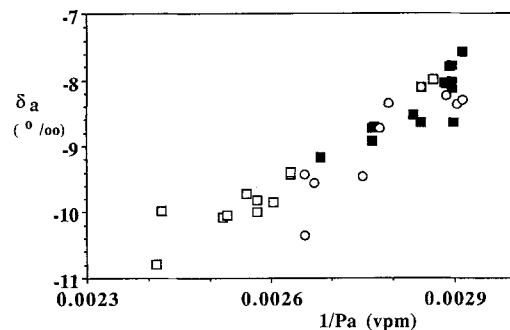


Fig. 5. Regression of δ_a and $1/P_a$ for all points from 0600–1000 hours ($r^2 = 0.92$) (open squares), 1000–1400 hours ($r^2 = 0.72$), (filled squares), and 1400–1800 hours ($r^2 = 0.78$) (open circles) at Aripo. See text for regression equations

ues of P_a and δ_a (measured as 334 vpm and -7.8%). Values of R at Aripo are calculated as 23% for 0600–1000 hours, 19% for 1000–1400 hours, and 8% for 1400–1800 hours.

At Simla, for the period 0600–1000 hours a similar treatment produced a regression of:

$$\delta_a = -24.50 + (5656/P_a), r^2 = 0.83$$

A value of 4% was calculated for the proportion of respired CO_2 reassimilated (assuming $\delta_r = -25.8$), again demonstrating the more open nature of this canopy. Due to the minimal stratification of CO_2 after 1000 hours, a poor fit was obtained, indicating that the model may break down under conditions of minimal P_a and δ_a gradients.

Analysis of canopy values of δ_a are therefore a useful tool for the investigation of CO_2 fluxes in canopies, but with the model inapplicable under low CO_2 gradients. Future studies should also monitor changes in assimilation rate, δ_a and P_a throughout the day as well as measuring δ_r . We have shown that during the dry season in Trinidad, contrasting forest formations have different CO_2 flux characteristics within canopies. Carbon isotope ratio analysis of source CO_2 and plant material indicate contributions from both environmental effects on P_i/P_a and variations in δ_a to the gradient in δ_p . The dynamic nature of the fluxes in δ_a throughout the day indicate that measurements need to be made over both wet and dry seasons in order to investigate these variations completely. The development of the field portable CO_2 collection line, as detailed in this communication, will enable such measurements to be made in the future.

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