SHORT COMMUNICATION

Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: comparison across tropical forests and tree life history

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Despite the progress made in understanding the ecophysiology of tropical plants during the past two decades (Lüttge 1997, Mulkey *et al.* 1996), questions regarding relationships between the environment and physiological diversity remain. It is now recognized that tropical climate can be quite variable (see Coen 1983) which could lead to significant functional diversity (increased variation in life history traits) among species due to the tight association between gas exchange physiology and the environment (see Enquist & Leffler 2001, Guehl *et al.* 1998, Huc *et al.* 1994, Martinelli *et al.* 1998, Sobrado 1993). It remains unclear, however, how the subtleties of variation in tropical climate and tree life history traits are related to the functional diversity of tropical communities (Borchert 1994, 1998).

The stable carbon isotope composition ($\delta^{13}C$) of plant tissue can be used to quantify certain aspects of functional diversity among species. $\delta^{13}C$ has been suggested as a surrogate for water use efficiency (WUE, the ratio of carbon gained to water lost during gas exchange) (Farquhar *et al.* 1988). Generally plants with high $\delta^{13}C$ are thought to have high WUE while those with low $\delta^{13}C$ have low WUE. Several researchers have examined $\delta^{13}C$ values in tropical forests (see Martinelli *et al.* 1998) however, additional studies are necessary to fully understand the extent of $\delta^{13}C$ variation and its correlates.

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In this study, we compare variation in $\delta^{13}C$ among co-occurring tropical dry forest species of north-western Costa Rica (see Enquist & Leffler 2001) in order to quantify functional diversity. The goals of this study are to (1) present $\delta^{13}C$ data from the dominant species in this region; (2) determine if the $\delta^{13}C$ variation among these species is related to functional differences in phenology (evergreen or deciduous), canopy position (emergent or understorey), and leaf morphology (soft or coriaceous); and (3) place our data in the context of other tropical forest $\delta^{13}C$ studies.

We obtained leaf tissue from herbarium specimens collected from June through August in 1995 and 1996 by B. J. Enquist. These samples were dried and not treated with any preservative. All individuals came from within a study plot in San Emilio forest, Area de Conservación de Guanacaste (Enquist *et al.* 1999). All samples were collected from lower branches (*c.* 2 m above ground) within the forest and one mature leaf was taken from each voucher which corresponded to a separate individual. Twenty-three species from 17 families were sampled (Table 1). These species possessed both simple and compound leaves. Simple leaves generally ranged from 6–19 cm with one species, *Genipa americana*, having leaves to 40 cm in length. Leaflets ranged in length from 5–13 cm. Leaf samples were analysed for $\delta^{13}C$ at the University of New Mexico using the methods described by Ehleringer & Osmond (1989). Our data were

Table 1. $\delta^{13}C$ and penetrometer values for the 23 species examined. In the 'Functional groups' column, D = deciduous, E = evergreen, Co = coriaceous, S = soft, Ca = canopy, U = understorey. Values are the mean of all samples for that species with the SE in parentheses, n is the number of individuals from each species anlaysed for $\delta^{13}C$. The Tukey HSD minimum significant difference for $\delta^{13}C$ between two species is 2.72%.

Species	Family	Functional groups	n	$\delta^{13}C$ (%)	Penetrometer value (g)
Trophis racemosa (L.) Urban	Moraceae	E, S, U	5	−31.5(0.407)	10.8(3.19)
Tabebuia ochracea Standl.	Bignoniaceae	D, S, Ca	3	−31.4(0.644)	5.00(2.90)
Piper amalgo L.	Piperaceae	E, S, U	5	−31.2(0.878)	—
Chrysophyllum brenessii Cronquist	Sapotaceae	E, S, U	6	−31.1(0.591)	—
Ateleia herbert-smithii Pittier	Fabaceae	D, S, Ca	5	−31.1(0.172)	4.74(4.74)
Calycophyllum candidissimum (Vahl) DC.	Rubiaceae	D, S, Ca	5	−30.7(0.591)	16.6(6.38)
Ocotea veraguensis (Meisn.) Mez	Lauraceae	E, S, U	5	−30.7(0.235)	23.1(4.23)
Guettarda macrosperma Donn. Sm.	Rubiaceae	D, S, Ca	5	−30.5(1.081)	9.44(6.49)
Brosimum alicastrum Swartz	Moraceae	E, S, Ca	4	−30.5(0.402)	57.1(8.81)
Diospyros nicaraguensis Standl.	Ebenaceae	D, S, Ca	5	−30.4(0.701)	64.3(13.6)
Cupania guatemalensis (Turcz.) Radlk.	Sapindaceae	E, S, U	5	−30.3(0.331)	8.86(4.02)
Astronium graveolens Jacq.	Anacardiaceae	D, S, Ca	5	−30.3(0.222)	4.35(3.32)
Bunchosia biocellata Schlecht.	Malpighiaceae	D, S, Ca	5	−30.0(0.275)	8.64(4.01)
Casearia sylvestris Sw.	Flacourtiaceae	E, S, U	5	−30.0(0.230)	7.34(4.00)
Genipa americana L.	Rubiaceae	D, Co, Ca	5	−29.5(0.584)	22.4(5.06)
Guarea glabra Vahl	Meliaceae	E, S, Ca	5	−29.5(0.325)	30.7(9.59)
Capparis indica (L.) Fawc. & Rendle	Capparidaceae	E, Co, Ca	6	−29.3(0.575)	228(13.9)
Hymenaea courbaril L.	Fabaceae	E, Co, Ca	5	−29.0(0.491)	30.6(7.00)
Manilkara chicle (Pittier) Gilly	Sapotaceae	E, Co, Ca	3	−28.6(0.991)	120(9.66)
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	D, Co, Ca	5	−28.6(0.221)	13.0(5.85)
Sideroxylon capiri (A. DC.) Pittier	Sapotaceae	E, Co, Ca	5	−28.5(0.286)	92.8(13.8)
Semialarium mexicanum (Miers) Mennega	Hippocrateaceae	D, Co, Ca	5	−28.2(0.187)	65.3(7.68)
Zanthoxylum setulosum P. Wilson	Rutaceae	E, Co, Ca	5	−27.7(0.386)	—

analysed for significant differences among species using ANOVA and among functional groups using t-tests.

In addition to categorizing species as having soft or coriaceous leaves we also quantified leaf 'toughness' using a penetrometer-type device (Lucas *et al.* 1991, Sagers & Coley 1995). Toughness (penetrometer value), is reported as the mass required to push a 3-mm-diameter rod through a leaf. Depending upon local abundance, the number of individuals from each species sampled varied from 10 to 60. One leaf, collected from *c.* 2 m above the forest floor, was measured from each individual for 20 out of the 23 species examined (Table 1). The relationship between $\delta^{13}C$ and penetrometer value was analysed using a rank regression.

In order to place our results in a broader context, we compiled $\delta^{13}C$ and precipitation data from numerous tropical studies. While many studies report $\delta^{13}C$, only those which reported annual precipitation and $\delta^{13}C$ of several species with a variety of physiological strategies were utilized (n = 17). The relationship between $\delta^{13}C$ and precipitation among studies was then examined using regression and the best possible curve fit determined.

The mean $\delta^{13}C$ value for all species in this study was −29.9‰. Other tropical ecosystems are more depleted in ^{13}C than ours. Wet tropical ecosystems range from a low of −32.1‰ (tropical moist forest, Brazil, Martinelli *et al.* 1998) to a high of −30.6‰ (subtropical wet/rainforest, Puerto Rico, von Fischer & Tieszen 1995). Values for dry tropical forests are closer to the values observed in our study (−29.0‰ in Venezuela, Sobrado & Ehleringer 1997 and −26.8‰ in northern Australia, Schulze *et al.* 1998).

A negative correlation exists between total annual precipitation and $\delta^{13}C$ among tropical sites. This relationship is best fit by a second-order polynomial (Figure 1) suggesting that $\delta^{13}C$ is correlated with water availability in drier tropical forests but may not be in wetter systems. Hence, a threshold value of annual precipitation may exist above which additional precipitation has little impact on $\delta^{13}C$. Such threshold relationships in biological systems are not uncommon and have been reported in other $\delta^{13}C$/water availability studies (see Leffler & Evans 1999).

Despite the relationship between $\delta^{13}C$ and annual precipitation among tropical sites, unexplained variation remains. Several factors are known to contribute to $\delta^{13}C$ variation among forests, including: variation in canopy density which alters light regimes (Martinelli *et al.* 1998), $[CO_2]$ and the $\delta^{13}C$ of source air for plants (Buchmann *et al.* 1997, Sternberg *et al.* 1989); differences in vapour pressure deficit among forests (Farquhar *et al.* 1988); and mineral nutrient availability (Holbrook *et al.* 1995). There is also a surprising degree of variation in $\delta^{13}C$ among species within San Emilio. $\delta^{13}C$ ranged from a low of −31.5‰ in *Trophis racemosa* to a high of −27.7‰ in *Zanthoxylum setulosum* (Table 1), a range of *c.* 4‰, overlapping with mean values from both wet tropical forests and dry tropical savannas (Figure 1). Hence, substantial physiological
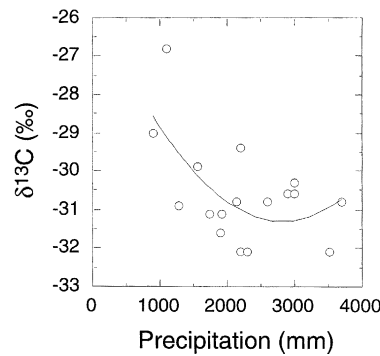
Figure 1. Relationship between $\delta^{13}C$ and total annual precipitation among study sites throughout the tropics. Note the significant curvilinear relationship (n = 17, $\delta^{13}C = 7 \times 10^{-7}(precip)^2 - 0.004(precip) - 25.4$, $r^2 = 0.373$, $P < 0.05$) suggesting the declining importance of precipitation in determining $\delta^{13}C$ as precipitation increases. Data for this figure come from Bonal *et al.* (2000), Buchmann *et al.* (1997), Ducatti *et al.* (1991), Ehleringer *et al.* (1987), Guehl *et al.* (1998), Jackson *et al.* (1993), Kapos *et al.* (1993), Martinelli *et al.* (1998), Medina & Minchin (1980), Nagy & Proctor (2000), Schulze *et al.* (1998), Sobrado & Ehleringer (1997), Sternberg *et al.* (1998), Victoria *et al.* (1995), von Fischer & Tieszen (1995).

variation among local species may exist. Martinelli *et al.* (1998) observed an even greater 8‰ range variation, from −28 to −36‰, in Brazilian tropical forests. They attributed variation in $\delta^{13}C$ among species to canopy heterogeneity and differences among species in carbon assimilation and water use. We attribute the variation in $\delta^{13}C$ observed here to species-specific physiological diversity rather than canopy heterogeneity because of our sampling protocol which focused on differences between species found at the same canopy height and the open nature of the canopy in this forest.

To investigate the life history correlates of the observed interspecific variation we placed our species into functional groups based on phenology (deciduous or evergreen), canopy position (understorey or canopy) and leaf morphology (soft or coriaceous). Deciduous and evergreen trees did not have significantly different $\delta^{13}C$ values, however, significant differences were observed between canopy and understorey species and between species with tough, coriaceous leaves and those with soft leaves (Table 2). Leaf penetrometer values ranged from 4.35 ± 3.32 g (mean ± SE) in *Astronium graveolens* to 228 ± 13.9 g in *Capparis indica*. A rank regression between $\delta^{13}C$ and penetrometer value is positive and highly significant (Figure 2).

The similar $\delta^{13}C$ values in deciduous and evergreen species (Table 2) is in contrast to the idea that evergreen species maintain higher WUE than deciduous species (Mooney & Gulmon 1982). In fact, WUE in tropical trees appears more complex than previously thought. Sobrado & Ehleringer (1997) observed higher $\delta^{13}C$ in deciduous species than evergreen species. The lack of variation between deciduous and evergreen species in our study suggests that the maintenance of leaves throughout the dry season does not necessarily require differences in WUE and may imply that long-term WUE is similar in the two groups. This relationship, however, could be confounded because, at the landscape
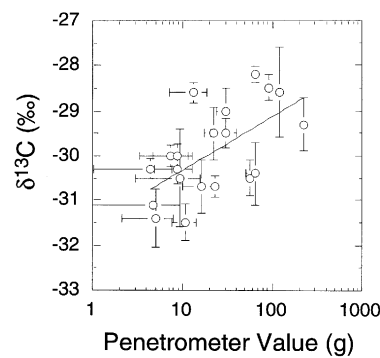
Figure 2. Relationship between $\delta^{13}C$ and penetrometer value. Each data point represents the mean value for an individual species ± SE. The relationship is statistically significant using Kendell's rank correlation (n = 20, $r^2 = 0.140$, P < 0.023).

level, the distributions of evergreen and deciduous species differ due to topographic and edaphic features of the environment. Additionally, leaf N and P content differs among evergreen and deciduous tropical tree species (see Holbrook *et al.* 1995) which may play a role in leaf $\delta^{13}C$. Nevertheless, it is important to note that differences in life history traits are correlated with habitat affinity and possibly leaf tissue N and P content. This suggests that inherent physiological differences influence which species can co-occur by influencing local distribution within a community, a conclusion also reached by Goldstein *et al.* (1989, 1996) and Borchert (1994).

We observed significant differences between understorey and emergent canopy species (Table 2). Numerous studies have examined vertical $\delta^{13}C$ gradients in tropical systems. In all cases, leaves collected from lower canopy levels were more depleted in ^{13}C than those from the upper canopy (Buchmann *et al.* 1997, Ehleringer *et al.* 1987, Medina *et al.* 1991). This difference is due to the 'canopy effect' which Buchmann *et al.* (1997) explain with light levels and [CO_2]. Our study indicates that leaves collected from multiple species, at the same canopy position, can also show substantial variation. Since the growth environment is similar, inherent physiological differences, possibly related to

Table 2. T-test analysis for differences between categories in each functional group. $\delta^{13}C$ is the mean value for each category with the SE in parentheses.

Functional group	$\delta^{13}C$ (‰)	P
Phenology		0.239
Evergreen	−29.7(0.323)	
Deciduous	−30.3(0.280)	
Canopy position		0.022
Canopy	−29.6(0.263)	
Understorey	−30.8(0.231)	
Toughness		0.001
Soft	−30.6(0.144)	
Coriaceous	−28.7(0.202)	

root distribution (Goldstein *et al.* 1996, Holbrook *et al.* 1995), stomatal control (Meinzer *et al.* 1993) or vulnerability to cavitation (Sobrado 1993), could exist between canopy and understorey species within this forest. Nevertheless, it is important to stress that although our results are consistent with the hypothesis of functional diversity among species, controlled physiological experiments are necessary.

We observed significant differences in $\delta^{13}C$ between species with tough, coriaceous leaves and those with soft leaves (Table 2) and a significant correlation between leaf $\delta^{13}C$ and penetrometer value (Figure 2); soft-leaved species had more negative $\delta^{13}C$. Variation in $\delta^{13}C$ between these species is likely the result of differences in leaf construction (i.e. lignin and lipid content, Sprent *et al.* 1996) which stem from inherent differences in physiological strategy. Moreover, since tough leaves are advantageous in water-limited environments (Turner 1994) this correlation may arise from the high WUE of these trees. Previous studies have demonstrated that structural composition can impact $\delta^{13}C$ (Broadmeadow & Griffiths 1993, Hubick *et al.* 1986). Vitousek *et al.* (1990) report a positive relationship between $\delta^{13}C$ and SLA among ecotypes of *Metrosideros polymorpha*, however Turner *et al.* (2000) did not find any relationship between $\delta^{13}C$ and leaf toughness in a dipterocarp and heath forest in Brunei. They did, however, observe a relationship between $\delta^{13}C$ and %C, a variable not measured in this study.

It would be naive to assume that the differences we observed between canopy and understorey species and between soft- and coriaceous-leaved species are independent because canopy species often have coriaceous leaves (Table 1). Within Guanacaste, canopy leaves are exposed to strong, desiccating winds which can result in high water loss and structural damage and coriaceous leaves are both resistant to wind damage and also have a high WUE. Additionally, since coriaceous leaves can be an adaptation to water limitation the distribution of these species may be tied to soil water content which also influences $\delta^{13}C$. Since soil water availability is known to vary throughout San Emilio (Enquist, unpubl. data) vouchers were collected from individuals throughout the forest to minimize its impact on our analyses. However, when examined at the landscape level, many of the species investigated here appear to have preferences across the mesotopographic gradient. Nevertheless, the strong correlations of $\delta^{13}C$ with canopy position and penetrometer value indicate that intrinsic $\delta^{13}C$ variation among species exists.

In conclusion, values of $\delta^{13}C$ appear to reflect a surprising degree of functional diversity both within and among tropical forests. At large scales there is a negative correlation between $\delta^{13}C$ and annual precipitation. The negative correlation provides further evidence that tropical forests experience varying degrees of water stress. On a local community scale, there is also substantial variation among dry tropical forest species. While this variation may be confounded by numerous factors, differences in life history traits among species

appear to also play an important role in $\delta^{13}C$ variation. These results indicate that spatial and temporal variation in tropical climate has resulted in a surprising degree of physiological diversity. These findings have important implications for understanding species-specific responses to potential climatic change and for general theories concerning the origin and maintenance of species diversity both within and across tropical forest communities.

LITERATURE CITED

BONAL, D., SABATIER, D., MONTPIED, P., TREMEAUX, D. & GUEHL, J. M. 2000. Interspecific variability of $\delta^{13}C$ among trees in rainforests of French Guiana: functional groups and canopy integration. *Oecologia* 124:454–468.

BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449.

BORCHERT, R. 1998. Responses of tropical trees to rainfall seasonality and its long-term changes. *Climate Change* 39:381–393.

BROADMEADOW, M. S. J. & GRIFFITHS, H. 1993. Carbon isotope discrimination and the coupling of CO_2 fluxes within forest canopies. Pp. 109–129 in Ehleringer, J. H., Hall, A. E. & Farquhar, G. D. (eds). *Stable isotopes and plant carbon-water relations*. Academic Press, San Diego.

BUCHMANN, N., GUEHL, J. M., BARIGAH, T. S. & EHLERINGER, J. R. 1997. Interseasonal comparison of CO_2 concentrations, isotopic composition, and carbon dynamics in an Amazonian rainforest (French Guiana). *Oecologia* 110:120–131.

COEN, E. 1983. Climate. Pp. 35–46 in Janzen, D. H. (ed.). *Costa Rican natural history*. University of Chicago Press, Chicago.

DUCATTI, C., SALATI, E. & MARTINS, D. 1991. Measurement of the natural variation of $^{13}C : ^{12}C$ ratio at Reserva Ducke Forest, central Amazonia. *Forest Ecology and Management* 38:201–210.

EHLERINGER, J. R. & OSMOND, B. C. 1989. Stable isotopes. Pp. 281–300 in Pearcy, R. W., Ehleringer, J. R., Mooney, H. A. & Rundel, P. W. (eds). *Plant physiological ecology*. Chapman and Hall, London.

EHLERINGER, J. R., LIN, Z. F., FIELD, C. B., SUN, G. C. & KUO, C. Y. 1987. Leaf carbon isotope ratios of plants from a subtropical monsoon forest. *Oecologia* 72:109–114.

ENQUIST, B. J. & LEFFLER, A. J. 2001. Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. *Journal of Tropical Ecology* 17:41–60.

ENQUIST, B. J., WEST, G. B., CHARNOV, E. L. & BROWN, J. H. 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401:907–911.

FARQUHAR, G. D., HUBICK, K. T., CONDON, A. G. & RICHARDS, R. A. 1988. Carbon isotope fractionation and plant water-use efficiency. Pp. 21–40 in Rundel, P. W., Ehleringer, J. R. & Nagy, K. A. (eds). *Stable isotopes in ecological research*. Springer-Verlag, New York.

GOLDSTEIN, G., RADA, F., RUNDEL, P., AZOCAR, A. & OROZCOS, A. 1989. Gas exchange and water relations of evergreen and deciduous tropical savanna trees. *Annals of Forestry* 46 Suppl:448s–453s.

GOLDSTEIN, G., MEINZER, F. C., STERNBERG, L. S. L., JACKSON, P., CAVELIER, J. & HOLBROOK, N. M. 1996. Evaluating aspects of water economy and photosynthetic performance with stable isotopes from water and organic matter. Pp. 244–267 in Mulkey, S. S., Chazdon, R. L. & Smith, A. P. (eds). *Tropical forest plant physiology*. Chapman and Hall, New York.

GUEHL, J. M., DOMENACH, A. M., BEREAU, M., BARIGAH, T. S., CASSABIANCA, H., FERHI, A. & GARBAYE, J. 1998. Functional diversity in an Amazonian rainforest of French Guyana: a dual isotope approach (δ^{15}N and δ^{13}C). *Oecologia* 116:316–330.

HOLBROOK, N. M., WHITBECK, J. L. & MOONEY, H. A. 1995. Drought responses of neotropical dry forest trees. Pp. 243–276 in Bullock, S. H., Mooney, H. A. & Medina, E. (eds). *Seasonally dry tropical forests*. Cambridge University Press, Cambridge.

HUBICK, K. T., FARQUHAR, G. D. & SHORTER, R. 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. *Australian Journal of Plant Physiology* 13:803–816.

HUC, R., FERHI, A. & GUEHL, J. M. 1994. Pioneer and late stage tropical rainforest tree species (French Guiana) growing under common conditions differ in leaf gas exchange regulation, carbon isotope discrimination and leaf water potential. *Oecologia* 99:297–305.

JACKSON, P. C., MEINZER, F. C., GOLDSTEIN, G., HOLBROOK, N. M., CAVELIER, J. & RADA, F. 1993. Environmental and physiological influences on carbon isotope composition of gap and understorey plants in a lowland tropical forest. Pp. 131–140 in Ehleringer, J. H., Hall, A. E. & Farquhar, G. D. (eds). *Stable isotopes and plant carbon-water relations*. Academic Press, San Diego.

KAPOS, V., GANADE, G., MATSUI, E. & VICTORIA, R. L. 1993. δ^{13}C as an indicator of edge effects in tropical rainforest reserves. *Journal of Ecology* 81:425–432.

LEFFLER, A. J. & EVANS, A. S. 1999. Variation in carbon isotope composition among years in the riparian tree *Populus fremontii*. *Oecologia* 119:311–319.

LUCAS, P. W., CHOONG, M. F., TAN, H. T. W., TURNER, I. M. & BERRICK, A. J. 1991. The fracture toughness of the leaf of the dicotyledon *Calophyllum inophyllum* L. (Guttiferae). *Philosophical Transactions of the Royal Society of London, Series B* 334:95–106.

LÜTTGE, U. 1997. *Physiological ecology of tropical plants*. Springer, Berlin. 384 pp.

MARTINELLI, L. A., ALMEIDA, S., BROWN, I. F., MOREIRA, M. Z., VICTORIA, R. L., STERNBERG, L. S. L., FERREIRA, C. A. C. & THOMAS, W. W. 1998. Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondônia, Brazil. *Oecologia* 114:170–179.

MEDINA, E. & MINCHIN, P. 1980. Stratification of δ^{13}C values of leaves in Amazonian rain forests. *Oecologia* 45:377–378.

MEDINA, E., STERNBERG, L. & CUEVAS, E. 1991. Vertical stratification of δ^{13}C values in closed natural and plantation forests in the Luquillo mountains, Puerto Rico. *Oecologia* 87:369–372.

MEINZER, F. C., GOLDSTEIN, G., HOLBROOK, N. M. & CAVELIER, J. 1993. Stomatal and environmental control of transpiration in a lowland tropical forest. *Plant, Cell and Environment* 16:429–436.

MOONEY, H. A. & GULMON, S. L. 1982. Constraints on leaf structure and function in reference to herbivory. *BioScience* 32:198–206.

MULKEY, S. S., CHAZDON, R. L. & SMITH, A. P. 1996. *Tropical forest plant ecophysiology*. Chapman and Hall, New York. 675 pp.

NAGY, L. & PROCTOR, J. 2000. Leaf δ^{13}C signatures in heath and lowland evergreen rain forest species from Borneo. *Journal of Tropical Ecology* 16:757–761.

SAGERS, C. L. & COLEY, P. D. 1995. Benefits and costs of defense in a neotropical shrub. *Ecology* 76:1835–1843.

SCHULZE, E.-D., WILLIAMS, R. J., FARQUHAR, G. D., SCHULZE, W., LANGRIDGE, J., MILLER, J. M. & WALKER, B. H. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* 25:413–425.

SOBRADO, M. A. 1993. Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia* 96:19–23.

SOBRADO, M. A. & EHLERINGER, J. R. 1997. Leaf carbon isotope ratios from a tropical dry forest in Venezuela. *Flora* 192:121–124.

SPRENT, J. I., GEOGHEGAN, I. E., WHITTY, P. W. & JAMES, E. K. 1996. Natural abundance of ^{15}N and ^{13}C in nodulated legumes and other plants in the cerrado and neighbouring regions of Brazil. *Oecologia* 105:440–446.

STERNBERG, L. D. S. L., GREEN, L., MOREIRA, M. Z., NEPSTAD, D., MARTINELLI, L. A. & VICTÓRIA, R. 1998. Root distribution in an Amazonian seasonal forest as derived from δ^{13}C profiles. *Plant and Soil* 205:45–50.

STERNBERG, L. S. L., MULKEY, S. S. & WRIGHT, S. J. 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. *Ecology* 70:1317–1324.

TURNER, I. M. 1994. Sclerophylly: primarily protective? *Functional Ecology* 8:669–675.

TURNER, I. M., LUCAS, P. W., BECKER, P., WONG, S. C., YONG, J. W. H., CHOONG, M. F. & TYREE, M. T. 2000. Tree leaf form in Brunei: a heath forest and a mixed dipterocarp forest compared. *Biotropica* 32:53–61.

VICTORIA, R. L., FERNANDES, F., MARTINELLI, L. A., PICCOLO, M. C., CAMARGO, P. B. & TRUMBORE, S. 1995. Past vegetation change in the Brazilian Pantanal arboreal-grassy savanna ecotone by using carbon isotopes in the soil organic matter. *Global Change Biology* 1:165–171.

VITOUSEK, P. M., FIELD, C. B., & MATSON, P. A. 1990. Variation in foliar $\delta^{13}C$ values in Hawaiian *Metrosideros polymorpha*: a case of internal resistance? *Oecologia* 84:362–370.

VON FISCHER, J. C. & TIESZEN, L. L. 1995. Carbon isotope characterization of vegetation and soil organic matter in subtropical forests in Luquillo, Puerto Rico. *Biotropica* 27:138–148.