

Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline*

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Summary. Leaf carbon isotope ratios and leaf mineral composition (Ca, K, Mg, Mn, N, and P) were measured on the dominant species along an irradiance cline in a subtropical monsoon forest of southern China. This irradiance cline resulted from disturbance caused by fuel-harvesting. Leaf carbon isotope ratios increased from undisturbed to disturbed sites for all species, indicating that leaf intercellular CO₂ concentrations decreased and leaf water use efficiencies increased along this cline. Nitrogen and magnesium levels were lower in leaves of species on the disturbed sites, but there were no clear patterns for calcium, potassium, phosphorus or manganese.

Key words: Water-use efficiency – Nutrient-use efficiency – Photosynthesis – Human impact – ¹³C/¹²C ratios

Within any specific terrestrial ecosystem, there is generally a higher productivity on soils with greater nutrient availability (Epstein 1972; Chapin 1980). Since nutrient levels within the weathered, acidic soils of tropical and subtropical forest ecosystems are often low, one area of strong focus has been on the relationships between productivity and mineral recycling in tropical ecosystems (Golley et al. 1975; Stark and Jordan 1978). Human harvesting of herbaceous layers and wood for fuels within tropical forests may exacerbate the effect of poor soils as it involves removal of both nutrients and biomass from the ecosystem. How this impacts on leaf nutrient levels, productivity, and production efficiency will depend on nutrient availability within the soil and on the effects of an altered microenvironment on leaf photosynthetic rates. Data from temperate forest ecosystems indicate that net primary productivity is decreased under situations involving frequent nutrient removal (Vitousek et al. 1979; Rapp 1983; Vitousek 1983).

Within Guangdong Province in southern China, very little remains of the original subtropical monsoon forests, because most of this region has been subject to varying intensities of timber and firewood harvesting over the past several thousand years. Mineral ash resulting from combustion of harvested materials is not returned to the forest ecosystem, but is instead applied to the rice paddies, thus potentially representing a significant mineral loss from the

forests. While only remnants of the original subtropical monsoon forests persist, most of the hillsides were replanted recently (35–70 years ago) with a combination of *Eucalyptus robusta* (introduced from Australia), *Pinus massoniana* (introduced from central China), and native dominant tree species of different seral stages (Wang et al. 1982). Historically, the herbaceous and shrub layers were used mostly for charcoal and the timber for construction.

Harvesting still occurs to different extents in these regions, and so the forest vegetation in southern China represents a mosaic in terms of canopy development and successional stages; these stages result from both time constraints on successional events and from stresses imposed by human activity. Such a situation provides an opportunity to ask how does long-term harvesting and nutrient removal affect factors related to primary productivity such as levels of leaf nutrients, nutrient-use efficiency, and water-use efficiency?

Nutrient-use efficiency can be thought of in terms of leaf longevity, and nutrient recovery from senescing leaves, but also in terms of nutrient concentrations versus the resulting photosynthetic rates in leaves. Photosynthetic capacity increases in response to increased nutrient levels, and the correlations are especially strong for nitrogen, the macronutrient required in greatest concentration (Field and Mooney 1986). Photosynthetic rates also increase in response to increased intercellular CO₂ levels as stomates open (Farquhar and Sharkey 1982), but higher intercellular CO₂ concentrations result in reduced water use efficiencies (ratio of photosynthesis to transpiration) (Percy and Ehleringer 1984). However, increased intercellular CO₂ concentrations result in a greater nitrogen use efficiency (ratio of photosynthesis to leaf nitrogen content) (Field et al. 1983). Thus, leaf nitrogen use efficiency will increase if water use efficiency decreases and vice versa.

Given the long-term impact of man in southern China and the lateritic soils which are characteristic of this region (Wang et al. 1982), we hypothesized that frequently harvested forests should exhibit characteristics of a stressed ecosystem: lower mineral concentrations in the leaves and increased nitrogen use efficiencies.

Nitrogen use efficiency is difficult to estimate without continuous information on photosynthetic rates. However, knowing the average intercellular CO₂ concentration of leaves would provide comparative information on whether nitrogen-use efficiency or water-use efficiency was relatively higher. Farquhar et al. (1982b) first proposed that the car-

bon isotope ratio could be used as a measure of the average intercellular CO_2 concentration and several studies are now available in support of this (Farquhar et al. 1982a; Bradford et al. 1983; Farquhar and Richards 1984; Ehleringer et al. 1985; Downton et al. 1985). Our approach has been to use leaf carbon isotope ratios as a tool for interpreting water-use versus nitrogen-use limitations in forest sites with differing degrees of human impact.

Site description

Plants were sampled at the Ding Hu Shan Biosphere Preserve, China, (lat. $23^\circ 08' \text{N}$, lat. $112^\circ 35' \text{E}$). This is a 1200 ha preserve of monsoon evergreen broad-leaf forest which is part of the MAB World Biosphere Network. The climate of this region is distinctly monsoonal. The average annual precipitation is 1927 mm, of which almost 70% falls between the months of May and September (Huang and Fan 1982). Air temperatures are warm, averaging 21.4°C annually and with a low of 12.0°C in January. Soils at Ding Hu Shan are uniform and typically thin with a pH range of 4.5–5.0 (Wang et al. 1982). Limited information is available on soil characteristics. He et al. (1982) classified these lateritic soils as "thin, heavily leached red soils". Average soil phosphorus levels were reported as $0.4 \mu\text{g}$ per g soil and soil potassium values at $28 \mu\text{g g}^{-1}$. No soil nitrogen values were reported for the locations used in our study, but He et al. (1982) did report that C/N ratios were approximately 12. In our study we did not measure soil nutrient characteristics.

The specific sites sampled contrasted in the extent of human interference. Three sites were chosen to reflect the range of human impact on forest composition and productivity. The first site was an undisturbed closed canopy forest site, hereafter referred to as the "closed canopy" site. The second and third sites were disturbed by the occasional gathering of branches and herbage to be used as cooking fuel. Because the overstory canopy development was intermediate between the undisturbed and third sites, this second site is referred to as the "mid" site. The third site was disturbed by harvesting of branches and herbage for cooking and by occasional tree cutting. The understory at this site was much more exposed than at the other two sites and is referred to as the "open" site. Both the mid site and open site had been replanted with *Pinus massoniana* and *Eucalyptus robusta*, two nonnative species, during the 1930's. In addition to these three forest sites, plants were sampled at a fully-exposed nursery location located at the edge of the Ding Hu Shan Preserve.

The vegetation of the closed canopy site is more than 400 years old, having been protected because of its proximity to a Buddhist monastery (Wang et al. 1982). This vegetation formed a closed canopy at approximately 24 m. The dominant trees are *Castanopsis chinensis*, *Cryptocarya chinensis*, *C. concinna*, and *Schima superba*. The understory vegetation consisted primarily of a subcanopy tree layer at 10–15 m, with *Machilus velutina* and younger canopy-level trees as dominants, and a shrub layer with *Aporosa yunnanensis*, *Ardisia quinquevaga*, *Blastus cochinchinensis*, and *Psychotria rubra* as the most common species. Herbs were infrequent at this site.

The mid site had a semi-closed canopy and had well defined tree, shrub and herb layers. The overstory trees were *Eucalyptus robusta* and *Pinus massoniana*. The shrub

layer consisted primarily of *Castanopsis chinensis*, *Evodia leptota*, *Psychotria rubra*, *Rhodomyrtus tomentosa*, *Schefflera octophylla* and *Schima superba*. The herb layer was dominated by the fern *Dicranopteris linearis*.

The open site was very similar in species composition to the mid site. The main differences between these two sites were the more open canopy in the open site, perhaps as a result of increased tree harvesting (of both *Eucalyptus robusta* and *Pinus massoniana*) and a change in shrub frequencies. *Ardisia* and *Schefflera* were more frequent at the mid site, while *Evodia*, *Psychotria* and *Rhodomyrtus* were more important at the open site.

Methods

Sites were ordinated by the amount of the daily total irradiance incident on the forest floor during the summer solstice, which is the active period for growth. This was determined from hemispherical photographs taken at 0.5 m at five randomly chosen locations at each site.

At each site, mature leaves were sampled from several plants for each species and these were combined to form a single sample for later analyses. For each species at each site, there were three combined samples. Plants were sampled once during January (dry season) and then again in July (wet season). Leaf tissues were oven dried and then ground to a 40 mesh in a Wiley mill.

Carbon isotope ratios were determined by mass spectrometry (Tieszen et al. 1979) and are expressed in parts per mil relative to the PDB standard.

Leaf tissue analyses of Ca, K, Mg, Mn and P were conducted by optical emission spectroscopy at the Laboratory of Biomedical and Environmental Science at the University of California, Los Angeles. Each sample was replicated three times. Data presented are mean and standard error of three different samples. Leaf Kjeldahl nitrogen analyses were made on an autoanalyzer (Technicon, Tarrytown, New York).

The response of intercellular CO_2 concentration to changes in photon flux were measured on intact leaves of several different species using an open gas exchange system (Ehleringer 1983). All measurements were made on potted plants grown in the summer months under greenhouse conditions at the University of Utah. The gas exchange measurement conditions were typical of the greenhouse environment: ambient CO_2 levels of $350 \mu\text{l l}^{-1}$, leaf temperature of 25°C and a leaf to air water vapor concentration gradient of 15 mbar bar^{-1} .

Results

Leaf carbon isotope values indicated that all species investigated were C_3 plants and that within a species carbon isotope values increased as the habitats became more open (Fig. 1, Table 1). This pattern was consistent for tree, shrub and herb species. The range in carbon isotope values for a single species was almost 5 ‰ in *Ardisia*, *Castanopsis* and *Psychotria*, and 2–3 ‰ for other species. These data suggest that there were large changes in the average intercellular CO_2 concentrations (c_i) and that c_i decreased with increasing light levels in the habitat.

At the closed canopy site, leaf carbon isotope values decreased with canopy depth, again suggesting that c_i decreased with increasing light level (Fig. 2). The four species

Ding Hu Shan, China

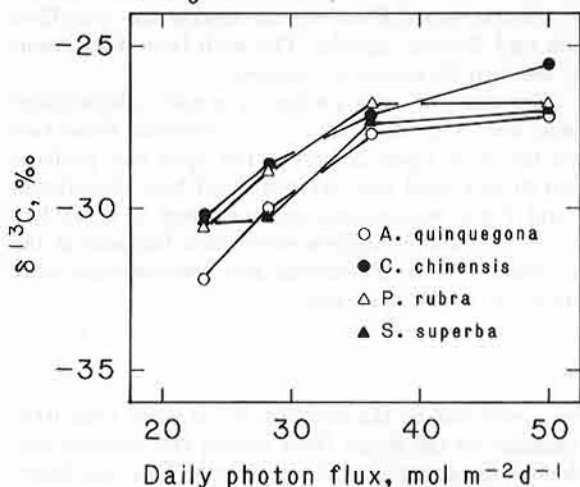


Fig. 1. Leaf carbon isotope values from different species along a light availability cline in a monsoonal forest habitat at Ding Hu Shan, China. Data are means of three values, except nursery plants which are single observations

Ding Hu Shan, China

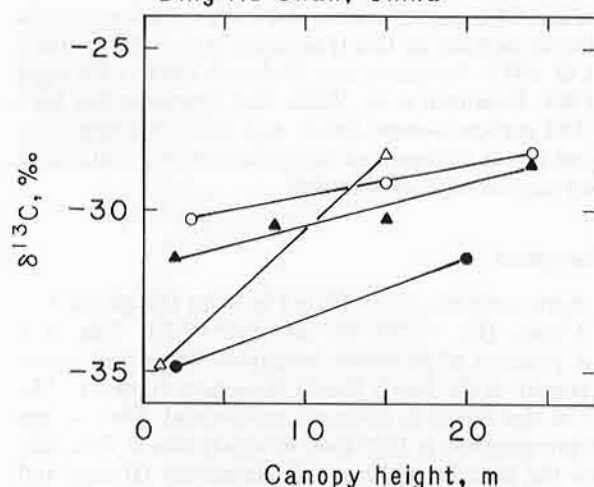


Fig. 2. Leaf carbon isotope values from different tree species as a function of height in a mature monsoonal tropical forest at Ding Hu Shan, China. Data are means of three values. *Cryptocarya chinensis* ●, *Machilus velutina* △, *Castanopsis chinensis* ○, *Schima superba* ▲

at the closed canopy site appeared to behave differently; two of the species (*Cryptocarya chinensis* and *Machilus*) exhibited large changes in carbon isotope ratio with height and two species (*Castanopsis* and *Schima*) much smaller changes. Variation in tissue carbon isotope composition with height could be due to either changes in the operational c_i or to differences in the isotopic composition of the source CO_2 . If the atmospheric CO_2 in the lower canopy levels were derived primarily from decomposed humus material at the ground level, its carbon isotope value should be closer to -25 ‰ than to the -8 ‰ expected in the open atmosphere. Leaves of both *Cryptocarya* and *Machilus* at the 1–2 m height had lower carbon isotope ratios than either *Castanopsis* or *Schima* at the same height, even though all plants were at the same location. From these observations we might infer there was more variation in $\delta^{13}\text{C}$ of leaf tissues associated with c_i differences among species than caused by potential changes in $\delta^{13}\text{C}$ of the source which should have affected all species equally.

The leaf carbon isotope ratio patterns observed for individual species were also evident as community-wide pat-

terns (Table 2). The increase in carbon isotope ratio with increased habitat irradiance indicated that the average c_i values decreased along this gradient. Using the relationship between carbon isotope ratio and intercellular CO_2 as proposed by Farquhar et al. (1982b) and inserting the most recent estimate for RuBP carboxylation discrimination (29 ‰) from Roeske and O'Leary (1984), the carbon isotope ratio is expected to be:

$$\delta^{13}\text{C}_{\text{leaf}} = \delta^{13}\text{C}_{\text{air}} - a \frac{(c_a - c_i)}{c_a} - b \frac{c_i}{c_a}$$

where $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{13}\text{C}_{\text{air}}$ are the carbon isotope ratios of the leaf and air, respectively, a is the discrimination due to diffusion (4.4 ‰), b is the discrimination by RuBP carboxylase, and c_a is the ambient CO_2 concentration. Based on this equation, the calculated average intercellular CO_2 concentrations are 258, 236, 205, and 195 $\mu\text{l l}^{-1}$ for the closed, mid, open, and nursery sites. These values should be regarded as preliminary since the $\delta^{13}\text{C}$ values used do not consider isotopic discrimination associated with source or respiratory effects.

Table 1. Carbon isotope values of different species occurring at three sites differing in canopy development and at a nursery site at Ding Hu Shan, China. Data are $\bar{x} \pm 1$ SE. $n=3$ unless otherwise noted. Units are parts per mil. Values within a row are significantly different from each other at the $P<.05$ or better level if followed by different letters. NP indicates that the species is not present at that site

species	Closed	Mid	Open	Nursery
<i>Ardisia quequegona</i>	-32.17 ± 0.18 a	-30.00 ± 0.15 b	-27.80 ± 0.03 c	-27.2 d
<i>Castanopsis chinensis</i>	-30.30 ± 0.10 a	-28.63 ± 0.03 b	-27.07 ± 0.07 c	-25.6 d
<i>Dicranopteris linearis</i>	NP	-28.60 ± 0.57 a	-26.47 ± 0.27 b	NP
<i>Eucalyptus robusta</i>	NP	-29.40 ± 0.33 a	-27.40 ± 0.49 b	NP
<i>Evodia lepta</i>	NP	-29.40 ± 0.07 a	-26.53 ± 0.28 b	-24.0 c
<i>Pinus massoniana</i>	NP	-28.5 a	-26.40 ± 0.62 b	-26.5 b
<i>Psychotria rubra</i>	-30.67 ± 1.11 a	-28.87 ± 0.07 b	-26.77 ± 0.07 c	-26.9 c
<i>Rhodomyrtus tomentosa</i>	NP	-31.20 ± 0.12 a	-28.40 ± 0.23 b	-27.2 c
<i>Schefflera octophylla</i>	NP	-27.93 ± 0.23 a	-26.59 ± 0.06 b	NP
<i>Schima superba</i>	-30.27 ± 0.12 a	-30.33 ± 0.09 a	-27.27 ± 0.14 b	-27.0 c

Table 2. Average carbon isotope values and Kjeldahl nitrogen contents for plants at the four different sites. Data are $\bar{x} \pm 1$ SE. Values within a column followed by different letters are significantly different from each other at the $P < .05$ level or less

Habitat	Carbon isotope value (o/oo)	Kjeldahl nitrogen (mg g^{-1})	
		January	July
Closed canopy	-30.85 ± 0.45 a	16.1 ± 1.2 a	19.6 ± 3.0 a
Mid-canopy	-29.29 ± 0.31 b	11.6 ± 0.8 b	14.4 ± 1.1 b
Open canopy	-27.07 ± 0.21 c	12.6 ± 1.2 ab	14.0 ± 1.5 b

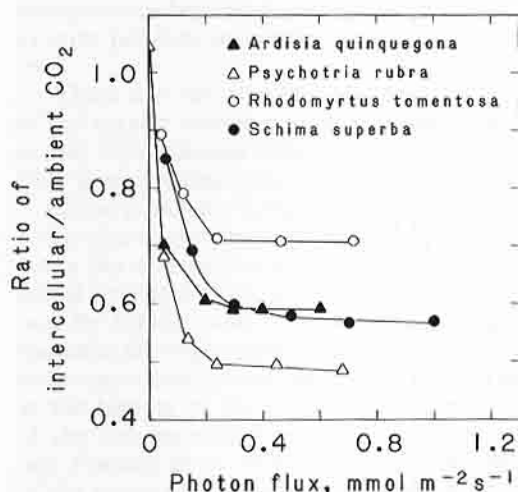


Fig. 3. Ratio of intercellular to ambient carbon dioxide concentrations in four species from Ding Hu Shan as a function of incident photon flux. These response curves were measured at a leaf temperature of 25°C , ambient carbon dioxide concentration of $350 \mu\text{l l}^{-1}$, and a leaf to air water vapor concentration gradient of 15 mbar bar^{-1} . Data are averages of three leaves per species

To verify that changes in leaf carbon isotopic composition were correlated with a change in c_i , the c_i/c_a ratio was measured in four of the dominant species as a function of incident photon flux levels (Fig. 3). The c_i/c_a value changed sharply with irradiance, especially at photon flux levels below $0.5 \text{ mmol m}^{-2} \text{ s}^{-1}$. The ranking of absolute c_i/c_a values for the different species is in agreement with what would be predicted on the basis of the observed carbon isotope ratios in Table 1 and Fig. 1.

Based on leaf carbon isotope ratios and assuming that the leaf to air water vapor gradient (Δw) remained more or less equal at all sites, it appears that water use efficiency differed among sites. Absolute leaf water use efficiency (WUE) can be calculated as

$$\text{WUE} = (c_a - c_i) / (1.6 \Delta w)$$

Using a c_a of $340 \mu\text{l l}^{-1}$, a July average Δw of 12 mbar bar^{-1} (Field et al. 1986), and average carbon isotope values from Table 3, the water use efficiencies varied from $4.3 \text{ mmol mol}^{-1}$ at the least disturbed site to $7.0 \text{ mmol mol}^{-1}$ at the most disturbed site (open).

As frequent fuel harvesting may affect the most mobile and most essential mineral elements, nitrogen levels in leaves at the different sites were analyzed to determine any potential influence of harvesting. Leaf Kjeldahl nitrogen

Table 3. Kjeldahl nitrogen contents of leaves from sites differing in canopy development due to fuel harvesting at Ding Hu Shan. Plants were sampled twice, once during the relatively inactive time of year (January) and active during the active rainy season (July). Data are means ± 1 SE of three lumped samples unless otherwise noted. Units are mg g^{-1} . Values within a row are significantly different from each other at the $P < .05$ or better level if followed by different letters. NP indicates that the species is not present at that site

	closed	mid	open
<i>Ardisia quinquegona</i>			
January	13.6 ± 0.5^a	11.4 ± 0.1^b	13.6 ± 0.7^a
July	17.6 ± 0.1^a	14.5 ± 0.5^b	—
<i>Castanopsis chinensis</i>			
January	11.7 ± 0.2^a	12.9 ± 0.3^b	10.7 ± 0.7^{ab}
July	12.6 ± 0.2^a	14.4 ± 0.2^b	15.4 ± 0.3^c
<i>Dicranopteris linearis</i>			
January	NP	10.0 ± 0.7^a	10.4 ± 0.2^a
July	NP	13.2 ± 1.1^a	9.8 ± 0.4^b
<i>Eucalyptus robusta</i>			
January	NP	11.5 ± 3.8^a	9.1 ± 1.5^a
July	NP	—	13.0 ± 0.3
<i>Evodia lepta</i>			
January	NP	16.3 ± 0.5^a	21.5 ± 0.8^b
July	NP	23.0 ± 1.7^a	23.4 ± 0.6^a
<i>Pinus massoniana</i>			
January	NP	$11.3 (1)^a$	10.1 ± 1.0^a
July	NP	—	10.6 ± 0.3
<i>Psychotria rubra</i>			
January	14.5 ± 0.3^a	10.8 ± 0.4^b	14.5 ± 0.2^a
July	17.2 ± 0.6^a	13.9 ± 0.2^b	15.2 ± 0.2^c
<i>Rhodomyrtus tomentosa</i>			
January	NP	8.7 ± 0.3^a	10.1 ± 0.5^b
July	NP	11.1 ± 0.4^a	12.6 ± 0.5^b
<i>Schefflera octophylla</i>			
January	NP	15.2 ± 0.1^a	15.9 ± 1.7^a
July	NP	16.9 ± 0.7^a	15.5 ± 0.7^b
<i>Schima superba</i>			
January	11.9 ± 1.4^a	10.1 ± 0.2^a	10.1 ± 0.7^a
July	20.1 ± 1.4^a	14.3 ± 0.5^b	15.0 ± 0.3^b

contents were measured during both the dry season in winter (January) and again during the wet season (July).

Leaf Kjeldahl nitrogen contents were generally higher in July than in January in all species and at all sites (19 out of 21 observations) (Table 3). For three of the four species that spanned the entire transect, nitrogen contents during the growing season were higher in the leaves from the undisturbed site than from the disturbed sites. Comparing leaf nitrogen contents at the two disturbed sites during either sample period, there were no clear patterns.

In fact, despite the frequent harvesting at the mid and open sites in these forests and their overall low soil nutrient quality (Wang et al. 1982), there were no consistent patterns among individual species in tissue nutrient levels of Ca, Mn, P and K at the different sites (Table 4). For these macronutrients, there were no consistent reductions in tis-

Table 4. Calcium, phosphorus, potassium, magnesium, and manganese contents of leaves from different sites differing in canopy development for a monsoon tropical forest site at Ding Hu Shan, China. Units are $\mu\text{g g}^{-1}$ for Mn and P and mg g^{-1} for Ca, K, and Mg. Data are means ± 1 SE, except as noted. Values within a row are significantly different from each other at the $P < .05$ or better level if followed by different letters

		closed	mid	open
<i>Ardisia quinquegona</i>	Ca	7.9 \pm 1.6 ^a	8.9 \pm 0.4 ^a	2.0 \pm 0.3 ^b
	P	867 \pm 116 ^a	779 \pm 76 ^a	1,580 \pm 19 ^b
	K	17.1 \pm 0.9 ^a	15.8 \pm 2.8 ^a	15.5 \pm 0.5 ^a
	Mg	9.7 \pm 1.0 ^a	3.4 \pm 0.4 ^b	2.0 \pm 0.1 ^c
	Mn	396 \pm 4 ^a	1,008 \pm 196 ^b	363 \pm 29 ^a
<i>Castanopsis chinensis</i>	Ca	0.4 \pm 0.1 ^a	1.2 \pm 0.1 ^b	0.7 \pm 0.1 ^c
	P	1,084 \pm 33 ^a	1,462 \pm 111 ^b	1,186 \pm 56 ^a
	K	7.9 \pm 0.8 ^a	10.8 \pm 0.0 ^b	11.5 \pm 0.5 ^c
	Mg	1.4 \pm 0.1 ^a	1.2 \pm 0.0 ^b	1.2 \pm 0.0 ^b
	Mn	129 \pm 21 ^a	650 \pm 79 ^b	131 \pm 5 ^a
<i>Dicranopteris linearis</i>	Ca	NP	0.8 \pm 0.2 ^a	0.2 \pm 0.0 ^b
	P	NP	326 \pm 134 ^a	634 \pm 66 ^b
	K	NP	10.5 \pm 0.3 ^a	5.4 \pm 0.3 ^b
	Mg	NP	1.3 \pm 0.2 ^a	0.8 \pm 0.1 ^b
	Mn	NP	545 \pm 161 ^a	54 \pm 5 ^b
<i>Eucalyptus robusta</i>	Ca	NP	12.5 \pm 3.2 ^a	6.1 \pm 0.3 ^b
	P	NP	1,842 \pm 375 ^a	1,222 \pm 38 ^a
	K	NP	10.7 \pm 1.3 ^a	9.8 \pm 0.4 ^a
	Mg	NP	1.7 \pm 0.1 ^a	1.9 \pm 0.2 ^a
	Mn	NP	423 \pm 66 ^a	236 \pm 15 ^b
<i>Evodia lepta</i>	Ca	NP	5.1 \pm 0.2 ^a	1.2 \pm 0.1 ^b
	P	NP	992 \pm 44 ^a	1,647 \pm 76 ^b
	K	NP	17.1 \pm 0.2 ^a	15.3 \pm 0.5 ^b
	Mg	NP	2.2 \pm 0.1 ^a	1.5 \pm 0.1 ^b
	Mn	NP	1,103 \pm 45 ^a	140 \pm 4 ^b
<i>Pinus massoniana</i>	Ca	NP	0.7 (1) ^a	0.8 \pm 0.2 ^a
	P	NP	1,643 (1) ^a	1,106 \pm 357 ^a
	K	NP	12.6 (1) ^a	7.2 \pm 1.2 ^b
	Mg	NP	0.5 (1) ^a	0.5 \pm 0.0 ^a
	Mn	NP	309 (1) ^a	119 \pm 69 ^b
<i>Psychotria rubra</i>	Ca	3.8 \pm 0.5 ^a	7.1 \pm 0.2 ^b	2.2 \pm 0.7 ^c
	P	1,210 \pm 5 ^a	1,423 \pm 85 ^b	1,506 \pm 84 ^b
	K	8.7 \pm 0.5 ^a	18.0 \pm 0.5 ^b	15.4 \pm 1.5 ^b
	Mg	4.6 \pm 0.2 ^a	3.3 \pm 0.1 ^b	2.8 \pm 0.4 ^b
	Mn	505 \pm 25 ^a	1,592 \pm 81 ^b	203 \pm 32 ^c
<i>Rhodomyrtus tomentosa</i>	Ca	NP	1.0 \pm 0.4 ^a	1.0 \pm 0.2 ^a
	P	NP	881 \pm 130 ^a	1,032 \pm 102 ^a
	K	NP	5.8 \pm 1.3 ^a	10.6 \pm 0.1 ^b
	Mg	NP	0.5 \pm 0.1 ^a	0.7 \pm 0.1 ^a
	Mn	NP	227 \pm 63 ^a	80 \pm 9 ^b
<i>Schefflera octophylla</i>	Ca	NP	4.4 \pm 0.7 ^a	1.9 \pm 0.1 ^b
	P	NP	1,445 \pm 128 ^a	1,253 \pm 35 ^a
	K	NP	23.6 \pm 0.6 ^a	12.9 \pm 0.4 ^b
	Mg	NP	2.5 \pm 0.0 ^a	2.0 \pm 0.1 ^b
	Mn	NP	1,034 \pm 61 ^a	122 \pm 5 ^b
<i>Schima superba</i>	Ca	1.6 \pm 0.5 ^a	2.3 \pm 0.9 ^a	2.5 \pm 1.0 ^a
	P	1,074 \pm 203 ^a	952 \pm 150 ^a	548 \pm 237 ^a
	K	8.3 \pm 1.1 ^a	11.2 \pm 3.4 ^a	11.4 \pm 2.4 ^a
	Mg	1.8 \pm 0.3 ^a	1.1 \pm 0.1 ^b	1.4 \pm 0.2 ^a
	Mn	288 \pm 58 ^a	492 \pm 48 ^b	275 \pm 87 ^a

sue element concentration that might be related to the removal of nutrients by human activity. However, for all four species that spanned the entire transect Mg concentrations at the undisturbed site were higher than at the disturbed sites.

The carbon isotope data from Table 2 suggest that if leaf nitrogen levels had remained constant at all sites, 1) photosynthetic rates would have been highest at the closed site and would have decreased as site disturbance increased

(because of changes in c_i) and 2) nitrogen use efficiency (photosynthetic rate per unit nitrogen) would have improved in going from the open to the closed canopy sites. Since absolute leaf nitrogen contents were higher at the undisturbed site during the growing season than at the disturbed sites, this implied that higher photosynthetic rates (resulting from increased leaf nitrogen levels) combined with increased c_i would result in even greater nitrogen use efficiencies at the undisturbed site.

Discussion

Our results indicate that leaf carbon isotope ratios change within a species depending on position within the canopy and on the extent of overstory canopy development. The environmental parameter mostly likely responsible for these variations is light level. This is supported by the laboratory observations indicating that intercellular CO_2 levels change in the expected direction with irradiance. Several recent studies have also shown that leaf carbon isotope composition can vary with canopy position (Vogel 1978; Medina and Minchin 1980; Schleser and Jayasekera 1985; Francey et al. 1985). In our results as well as the other studies, leaf carbon isotope ratios became more negative in going from exposed, exterior portions to interior, more shaded portions of the trees.

There are two possible explanations for the patterns of leaf carbon isotope ratio with canopy position. The first is that these changes reflect differences in the intercellular CO_2 levels as first proposed by Farquhar et al. (1982b). A second possibility is that the decreases in carbon isotopic composition with depth in the canopy are caused by changes in the isotopic composition of the source CO_2 (as suggested in Vogel 1978; Medina and Minchin 1980; and in part by Schleser and Jayasekera 1985). That is, the CO_2 source in the upper parts of the canopy should be the same as the open atmosphere (approximately -8 o/oo), whereas at the bottom of the canopy it should be closer to that of the decomposing humus layer (approximately -25 o/oo). Francey et al. (1985) measured isotopic composition of the source CO_2 at different canopy positions and could not detect more than a 0.8 o/oo difference from the open atmospheric value anywhere in the canopy, implying that intercellular CO_2 levels were primarily responsible for the observed isotopic differences. Our results also suggest that substantial source isotopic changes did not exist within the canopy, although at the lowest positions within the closed canopy we would expect a small component of the change in leaf carbon isotope composition to be due to source differences.

The close agreement of the leaf carbon isotope ratio data and the observed c_i/c_a dependence on photon flux indicates that carbon isotope ratios can be used to indicate average irradiance levels during photosynthetic active periods. An earlier observation by Smith et al. (1976) had shown that irradiance could influence carbon isotope composition, but the basis of the observation was at that time unknown. Now that a clearer understanding is emerging, leaf carbon isotope analyses may prove useful as integrators of irradiance and other environmental factors in ecological studies along irradiance clines such as in response to disturbance or succession.

Although fuel harvesting removes substantial amounts of biomass from these forests on a regular basis, it does not appear that this is reflected in a decrease in leaf mineral composition of all minerals. Among sites, leaf nitrogen and magnesium contents were lower on those sites which were disturbed. This is consistent with previous observations in other managed ecosystems (Rapp 1983; Vitousek 1983). These studies had demonstrated that highly mobile ions that are poorly buffered can be lost through disturbance.

In our study, other minerals (Ca, Mn, K, and P) did not show a consistent trend with disturbance. Mineral composition of these elements increased in some species with

disturbance, decreased in others, or remained unchanged. The factors responsible for the individual patterns in leaf mineral composition of these elements remains unclear. Of these minerals, K is mobile in the soil and also easily leachable from leaves, and so its concentration might have been expected to have remained constant. While this was evident in a few species, it did not hold for all.

In a study of chaparral species, Field et al. (1983) found that differences in nitrogen use efficiency (NUE) and water use efficiency (WUE) existed in different species within the same community. A similar pattern is evident in our data; both within a single site and among sites differing in disturbance there were pronounced changes in carbon isotope ratio (and thus WUE). Although Δw values were not measured in this study and are necessary to make quantitative statements regarding WUE, Δw values have been measured at these three sites. Their observations indicated only small differences in Δw among sites, and thus our carbon isotope ratio data do indeed indicate relative differences in WUE among sites.

Our study has indicated that in going from undisturbed to disturbed monsoonal forest sites, leaf intercellular CO_2 concentrations and leaf nitrogen levels are lower at sites that are more disturbed.

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