

## Leaf carbon isotope ratios of plants from a subtropical monsoon forest\*

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**Summary.** Carbon isotope ratios were used to survey the distribution of photosynthetic pathways among taxa, the relationship between photosynthetic pathway and habitat light levels, and the relationship between intercellular  $\text{CO}_2$  levels of  $\text{C}_3$  plants and habitat light levels within a subtropical monsoon forest in southern China. Of 128 species, most (94) possessed the  $\text{C}_3$  photosynthetic pathway; 33 species possessed the  $\text{C}_4$  pathway and all of these were restricted to high light locations. There was one epiphytic CAM species. The  $\text{C}_3$  species were classified as occurring in open, intermediate, and closed canopy sites. Among  $\text{C}_3$  species, carbon isotope ratios tended to become more negative with decreasing light availability in the habitat.

**Key words:** Tropical forests –  $\text{C}_3$  –  $\text{C}_4$  – CAM – Intercellular  $\text{CO}_2$

Over the past fifteen years, carbon isotopic analyses have been used as an effective means of surveying the distributions of  $\text{C}_3$  and  $\text{C}_4$  photosynthetic pathways within different vegetation types (Winter and Troughton 1978; Ziegler et al. 1981; Hattersley 1983). More recently, Farquhar et al. (1982b) proposed that carbon isotope ratios in  $\text{C}_3$  plants indicate the average intercellular  $\text{CO}_2$  concentration ( $c_i$ ) during the photosynthetic periods. Experimental evidence to support this prediction is now available (Farquhar et al. 1982a; Ehleringer et al. 1985; Downton et al. 1985). Water-use efficiency, the ratio of photosynthesis to transpiration, can be estimated knowing  $c_i$  and the leaf to air humidity gradient ( $\Delta w$ ) (Pearcy and Ehleringer 1984). If  $\Delta w$  in leaves from different plants is uniform, carbon isotope ratios can be used as an indication of the average leaf water-use efficiency. Farquhar and Richards (1984) verified this prediction for different wheat cultivars and Hubick et al. (1986) have extended this to peanut cultivars.

The purpose of the present study was to survey the carbon isotope ratios for the common plant species in a monsoonal rainforest in southern China. Our objectives were to answer two questions: 1) what species possess the  $\text{C}_4$  photosynthetic pathway and in which microhabitats are they found, and 2) within the  $\text{C}_3$  species, does carbon

isotopic composition vary with either life form or microhabitat implying a relationship between habitat and  $c_i$ ?

### Materials and methods

Naturally-growing plants were sampled at the Ding Hu Shan Biosphere Preserve, Guangdong Province, China (lat.  $23^\circ 08' \text{N}$ , lat.  $112^\circ 35' \text{E}$ ). The preserve, operated by the South China Institute of Botany, is a 1,200 ha parcel of monsoon evergreen broad-leaf forest, most of which has been protected from human disturbance for at least 400 years (Wang et al. 1982). The preserve is part of the MAB World Biosphere Network and is surrounded by lands heavily impacted by human activity for both agricultural and forestry purposes. The climate of this region is distinctly monsoonal. The average annual precipitation is 1,927 mm, of which almost 70% falls between the months of May and September (Huang and Fan 1982). Air temperatures average  $21.4^\circ \text{C}$  annually with a low of  $12.0^\circ \text{C}$  in January. The soils are lateritic with a pH range of 4.5–5.0 (He et al. 1982).

The plant species sampled were subdivided into three categories on the basis of the microhabitat where the species were most abundant. These categories (closed-, intermediate- and open-microhabitat) represent mature closed canopy forest and two types of disturbed forests with much lower biomass and cover. Species most abundant in disturbed forests of intermediate canopy closure were labeled intermediate while species from open woodland with scattered introduced and native trees were labeled open. Wang et al. (1982) and Ehleringer et al. (1986) describe these plant communities in more detail. Taxonomic identification of the species is based on the Handbook of Plants of Ding Hu Shan (Shi et al. 1978).

Leaf tissues for carbon isotope ratio analysis were collected from mature leaves on plants in their natural habitat within the preserve. Carbon isotope ratios were measured on ground leaf tissues, using an isotope rationing mass spectrometer (Tieszen et al. 1979) and are expressed relative to the PDB standard.

### Results and discussion

There has been limited research on photosynthetic pathways in tropical and subtropical vegetation types. Chazdon (1978) and Rundel (1980), focusing on  $\text{C}_4$  grasses, noted that in Costa Rica and in the Hawaiian Islands, the  $\text{C}_4$

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**Table 1.** Carbon isotope ratio, life form and habitat of plants from the Ding Hu Shan Preserve

Family	Species	Carbon isotope ratio (parts per thousand)	Life form	Habitat
<b>Lycopodiophyta</b>				
Lygodiaceae	<i>Lygodium japonicum</i> (Thunb.) Sw.	-27.84	herb	intermediate
Selaginellaceae	<i>Selaginella uncinata</i> (Desv.) Spring	-28.66	herb	closed
<b>Pteridophyta</b>				
Adiantaceae	<i>Adiantum capillus-veneris</i> L.	-29.20	fern	intermediate
	<i>Adiantum flabellulatum</i> L.	-32.76	fern	closed
Angiopteridaceae	<i>Angiopteris fokiensis</i> Heiron.	-30.74	fern	closed
Aspidiaceae	<i>Hemigramma decurrens</i> (Hook.) Copel.	-33.40	fern	closed
Cyatheaceae	<i>Cyathea podophylla</i> (Hook.) Copel.	-30.57	tree fern	closed
Dicksoniaceae	<i>Cibotium barometz</i> (L.) J. Sm.	-29.71	fern	closed
Gleicheniaceae	<i>Dicranopteris linearis</i> (Burm.) Underw.	-27.99	fern	open
Lindsaeaceae	<i>Stenoloma chusanum</i> (L.) Ching	-28.34	fern	closed
Osmundaceae	<i>Osmunda vachellii</i> Hook.	-31.04	fern	closed
Polypodiaceae	<i>Lemmaphyllum microphyllum</i> Presl.	-26.50	fern	open
Thelypteridaceae	<i>Abacopteris multilineatum</i> (Wall) Ching	-29.88	fern	closed
<b>Spermatophyta Gymnospermae</b>				
Cupressaceae	<i>Platycladus orientalis</i> (L.) Franco	-27.77	tree	open
Pinaceae	<i>Pinus massoniana</i> Lamb.	-26.40	tree	open
<b>Angiospermae Dicotyledonae</b>				
Acanthaceae	<i>Rostellularia procumbens</i> (L.) Nees	-29.09	herb	intermediate
Amaranthaceae	<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	-29.30	herb	intermediate
	<i>Amaranthus ascendens</i> Loisel.	-13.20	herb	open
Annonaceae	<i>Fissistigma glaucescens</i> (Hance) Merr.	-29.59	Liana	closed
Araliaceae	<i>Schefflera octophylla</i> (Lour.) Harms	-31.95	tree	intermediate
Asclepiadaceae	<i>Dischidia chinensis</i> Champ. ex Benth.	-15.24 CAM	epiphyte	open
Asteraceae	<i>Ageratum conyzoides</i> L.	-30.85	herb	open
	<i>Senecio hoi</i> Dunn	-34.50	Liana	closed
	<i>Senecio scandens</i> Buch.-Ham.	-31.92	herb	intermediate
Begoniaceae	<i>Begonia fimbriatipula</i> Hance	-33.10	herb	closed
Burseraceae	<i>Canarium album</i> Racusch.	-28.31	tree	open
Euphorbiaceae	<i>Alchornea trewioides</i> (Benth.) Muell.-Arg.	-29.65	shrub	intermediate
	<i>Aporosa yunnanensis</i> Metc.	-30.82	tree	closed
	<i>Croton lachnocarpus</i> Benth.	-34.40	shrub	intermediate
	<i>Croton tiglium</i> L.	-29.50	tree	closed
	<i>Euphorbia antiquorum</i> L.	-28.80	shrub	intermediate
	<i>Mallotus apelta</i> (Lour.) Muell.-Arg.	-26.74	shrub	intermediate
	<i>Phyllanthus urinaria</i> L.	-30.61	herb	open
	<i>Sapium discolor</i> Muell. Arg.	-31.30	tree	closed
Fagaceae	<i>Castanopsis chinensis</i> Hance	-29.80	tree	intermediate
Guttiferae	<i>Garcinia oblongifolia</i> Champ	-30.02	tree	closed
Lauraceae	<i>Cryptocarya chinensis</i> (Hance) Hemst.	-33.62	tree	closed
	<i>Cryptocarya concinna</i> Hance	-34.86	tree	closed
	<i>Evodia leptota</i> (Spreng.) Merr.	-31.29	shrub	closed
	<i>Lindera chunii</i> Merr.	-31.42	tree	closed
	<i>Lindera communis</i> Hemsl.	-29.10	tree	intermediate
	<i>Machilus velutina</i> Champ. ex Benth.	-32.34	tree	closed
Lamiaceae	<i>Perilla frutescens</i> (Linn.) Britt.	-29.35	herb	open
Lobeliaceae	<i>Lobelia chinensis</i> Lour.	-30.80	herb	open
Loranthaceae	<i>Elytranthe cochinchinensis</i> (Lour.) G. Don	-29.80	parasite	intermediate
	<i>Loranthus pentapetalus</i> Roxb.	-30.80	parasite	intermediate
	<i>Taxillus chinensis</i> (DC.) Danser	-30.80	parasite	intermediate
Magnoliaceae	<i>Tsoongiodendron odoratum</i> Chun	-31.18	tree	closed

Table 1 (continued)

Family	Species	Carbon isotope ratio (parts per thousand)	Life form	Habitat
Melastomaceae	<i>Memecylon ligustrifolium</i> Champ. ex Benth.	-29.64	tree	closed
Mimosaceae	<i>Pithecellobium clypearia</i> Benth.	-30.33	tree	closed
Molluginaceae	<i>Mollugo pentaphylla</i> L.	-26.90	herb	open
Myrsinaceae	<i>Ardisia quinquegona</i> Bl.	-31.35	shrub	closed
Myrtaceae	<i>Baeckea frutescens</i> L.	-29.36	shrub	intermediate
	<i>Eucalyptus robusta</i> Sm.	-27.40	tree	open
	<i>Rhodomyrtus tomentosa</i> (Ait.) Hassk.	-30.38	shrub	open
	<i>Syzygium rehderianum</i> Merr. & Perry	-29.95	tree	intermediate
Oxalidaceae	<i>Oxalis corniculata</i> L.	-30.15	herb	open
	<i>Oxalis corymbosa</i> DC.	-30.76	herb	open
Piperaceae	<i>Peperomia pellucida</i> (L.) Kunth	-26.90	herb	open
Plantaginaceae	<i>Plantago major</i> L.	-28.20	herb	open
Polygalaceae	<i>Salomonina cantoniensis</i> Lour.	-30.65	herb	intermediate
Polygonaceae	<i>Polygonum hydropiper</i> L.	-29.77	herb	open
Primulaceae	<i>Lysimachia fortunei</i> Maxim.	-30.92	herb	closed
Proteaceae	<i>Helicia reticulata</i> W.T. Wang	-28.40	tree	intermediate
Rosaceae	<i>Pygeum topengii</i> Merr.	-30.23	tree	closed
	<i>Rhapirolepis indica</i> Lindl.	-27.14	shrub	open
Rubiaceae	<i>Psychotria rubra</i> (Lour.) Poir.	-33.82	shrub	closed
	<i>Hedyotis diffusa</i> Willd.	-28.64	herb	open
Sarcospermataceae	<i>Sarcosperma laurinum</i> (Benth.) Hook. f.	-29.58	tree	closed
Scrophulariaceae	<i>Adenosma glutinosum</i> (L.) Druce var. <i>caeruleum</i> (R. Br.) Tsoong	-30.32	herb	open
Sterculiaceae	<i>Sterculia lanceolata</i> Cav.	-29.74	tree	closed
Theaceae	<i>Eurya chinensis</i> R. Br.	-29.03	shrub	open
	<i>Schima superba</i> Gardn. & Champ.	-31.55	tree	closed
Monocotyledoneae				
Araceae	<i>Alocasia macrorrhiza</i> (L.) Schott	-27.74	herb	intermediate
Cyperaceae	<i>Cyperus alternifolius</i> L. ssp. <i>flabelliformis</i> (Rottb.) Küenth.	-30.40	sedge	intermediate
	<i>Cyperus pilosus</i> Vahl	-10.82	sedge	open
	<i>Fimbristylis aestivalis</i> (Retz.) Vahl	-12.70	sedge	open
	<i>Fimbristylis annua</i> (All.) Roem.	-11.04	sedge	open
	<i>Fimbristylis complanata</i> (Retz.) Link.	-10.61	sedge	open
	<i>Fimbristylis schoenides</i> Vahl	-10.77	sedge	open
	<i>Hypolytrum nemorum</i> (Vahl) Spreng.	-34.70	sedge	intermediate
	<i>Lipocarpha microcephala</i> (R. Br.) Kunth	-10.47	sedge	open
	<i>Scleria levis</i> Retz.	-33.00	sedge	intermediate
	<i>Scleria terrestris</i> (L.) Fassett	-32.00	sedge	intermediate
Eriocaulaceae	<i>Eriocaulon wallichianum</i> Mart.	-28.63	herb	closed
Liliaceae	<i>Dianella ensifolia</i> (L.) DC.	-29.70	herb	intermediate
	<i>Hemerocallis fulva</i> L.	-29.49	herb	intermediate
	<i>Ophiopogon japonicus</i> (Thunb.) Ker-Gawl.	-31.70	herb	closed
Orchidaceae	<i>Arundina chinensis</i> Bl.	-29.86	herb	open
Palmae	<i>Daemonorops margaritae</i> (Hance) Becc.	-29.58	liana	closed
Pandanaceae	<i>Pandanus austrosinensis</i> T.L. Wu	-31.28	herb	closed
Poaceae	<i>Arundinella setosa</i> Trih.	-11.93	grass	open
	<i>Capillipedium parviflorum</i> (R. Br.) Stapf	-13.60	grass	open
	<i>Cenchrus calyculatus</i> Caran.	-10.26	grass	open
	<i>Cymbopogon caesius</i> Staph.	-12.90	grass	open
	<i>Digitaria longiflora</i> (Retz.) Pers.	-12.20	grass	open
	<i>Digitaria microbachne</i> (Presl.) Henr.	-10.90	grass	open
	<i>Digitaria violascens</i> Link	-11.53	grass	open
	<i>Eragrostis amabilis</i> (L.) Wright et Arn.	-11.73	grass	open
	<i>Eragrostis perennans</i> Keng	-13.10	grass	open

Table 1 (continued)

Family	Species	Carbon isotope ratio (parts per thousand)	Life form	Habitat
	<i>Eragrostis perlaea</i> Keng	-12.50	grass	open
	<i>Eragrostis pilosissima</i> L.	-13.50	grass	open
	<i>Eragrostis reflexa</i> Hack.	-12.51	grass	open
	<i>Eragrostis tenella</i> (L.) Beauv.	-13.66	grass	open
	<i>Eragrostis tephrosanthos</i> Nees et. Merr.	-12.30	grass	open
	<i>Eragrostis zeylanica</i> Nees et Mey.	-11.64	grass	open
	<i>Eriachne pallescens</i> R. Br.	-11.70	grass	open
	<i>Eulalia quadrinervis</i> (Hack) Kuntze	-12.07	grass	open
	<i>Garnotia patula</i> (Munro) Benth.	-12.63	grass	open
	<i>Indocalamus longiauritus</i> Hand. Mazz.	-32.90	grass	closed
	<i>Isachne globosa</i> (Thunb.) Kuntze	-28.66	grass	intermediate
	<i>Ischaemum aristatum</i> L.	-11.36	grass	open
	<i>Ischaemum ciliare</i> Retz.	-10.88	grass	open
	<i>Leersia hexandra</i> SW.	-29.90	grass	closed
	<i>Leptochloa chinensis</i> (L.) Nees	-12.41	grass	open
	<i>Miscanthus floridulus</i> (Labill.) Wesb.	-12.43	grass	open
	<i>Oplismenus compositus</i> (L.) Beauv.	-27.58	grass	open
	<i>Paspalum orbiculare</i> G. Forst.	-13.40	grass	open
	<i>Pogonatherum crinitum</i> (Thunb.) Kunth	-12.20	grass	open
	<i>Sacciolepis indica</i> (L.) A. Chase	-10.94	grass	open
	<i>Setaria pallide-fusca</i> (Schum.) Stapf et C.E. Hubb.	-11.62	grass	open
	<i>Thysanolaena maxima</i> (Roxb.) Kuntze	-28.35	grass	intermediate
Zingiberaceae	<i>Alpinia chinensis</i> Rosc.	-33.20	herb	closed
	<i>Alpinia pumila</i> Hook. f.	-28.20	herb	intermediate
	<i>Alpinia zerumbet</i> (Pers.) Burt. & Smith	-34.60	herb	closed
	<i>Costus speciosus</i> (Koenig) Smith	-29.60	herb	intermediate
	<i>Costus tonkinensis</i> Gagnep.	-27.40	herb	intermediate
	<i>Zingiber zerumbet</i> (L. Smith)	-32.00	herb	closed

grasses reach their greatest abundances at lowland sites. Medina and Minchin (1980) reported carbon isotope ratios for 35 species from upper and lower canopy positions within an Amazonian rainforest and all were typical of  $C_3$  species. While the relatively low initial slope of the light response of photosynthesis may tend to place  $C_4$  species at a competitive disadvantage in low-light habitats (Ehleringer 1978),  $C_4$  plants are not totally absent from shaded sites. Percy and Troughton (1975) reported that *Euphorbia forbesii*, a lower-canopy tree of Hawaiian Islands forests, possesses the  $C_4$  pathway.

We surveyed 128 of the 2,054 species of higher and lower plants described in Shi et al. (1978). These were the most common species at the sites. Of these, 94 or 73% possessed the  $C_3$  photosynthetic pathway, 33 (26%) the  $C_4$  photosynthetic pathway and 1 species (1%) the CAM pathway (Table 1). Of the  $C_4$  species in the flora, only one was a dicot (*Amaranthus ascendens*). The remainder of the  $C_4$  species were either grasses or sedges. The single CAM species present, *Dischidia chinensis*, belonged to the Asclepiadaceae.

There were several interesting distribution patterns with respect to photosynthetic pathways. The  $C_3$  grasses included species most abundant in each of the major microhabitats (open, intermediate, and closed canopy) (Tables 1 and 2). However, the  $C_4$  grasses were most abundant only in open habitats. In contrast, the  $C_3$  sedges on Ding Hu Shan were typical of intermediate habitats, while the  $C_4$  sedges were most abundant in open habitats. Since *A. ascendens*, the sole  $C_4$  dicot, also occurred in open habitats, all

of the  $C_4$  species we sampled reached greatest abundance in open, high-light environments.

The epiphytic CAM species, *Dischidia chinensis*, occurred on tree trunks and throughout the canopies of the dominant trees of the closed forest. Because these CAM plants occurred at many levels in the canopy, they encountered a broad range of light environments.

Within the  $C_3$  species in each life form, leaf carbon isotope ratios were more negative in species typical of increasingly closed forest (Table 2). For the life forms represented in all of the habitats, a two-way analysis of variance revealed highly significant effects of habitat, but insignificant effects of life form (Table 3). In fern, grass, shrub and tree life forms, the changes in average carbon isotope ratios exceeded 3.3 per mil in going from open to closed canopy habitats. In the herbs, the changes were closer to 2.5 per mil.

The changes in carbon isotope ratio with habitat could be due to two possible effects: the carbon isotope ratio of the source  $CO_2$  could differ among habitats, or leaves in different habitats could be operating at different average intercellular  $CO_2$  concentrations. Both of these effects would result in more negative carbon isotope ratios in the closed canopy habitats.

Vogel (1978) proposed that in closed forest situations, the source  $CO_2$  for understory plants was largely derived from decomposed surface organic matter. If that were the case, then the carbon isotope ratio of the atmospheric  $CO_2$  in the closed canopy would be close to -25 to -30‰, since this is the isotopic composition of the decaying plant



**Table 2.** Average carbon isotope composition of different life forms arranged according to the microhabitat in which they occurred at the Ding Hu Shan Preserve, China. Data are  $\bar{x} \pm 1$  SE with sample size in parentheses. NP indicates that this life form is not present in that habitat

			Open	Intermediate	Closed canopy
fern	C <sub>3</sub>	11	-27.25 $\pm$ 0.53 (2)	-29.20 (1)	-30.81 $\pm$ 0.54 (8)
grass	C <sub>3</sub>	5	-27.58 (1)	-28.51 $\pm$ 0.11 (2)	-31.40 $\pm$ 1.06 (2)
	C <sub>4</sub>	26	-12.15 $\pm$ 0.17 (26)	NP	NP
sedge	C <sub>3</sub>	4	NP	-32.53 $\pm$ 0.78 (4)	NP
	C <sub>4</sub>	6	-11.07 $\pm$ 0.31 (6)	NP	NP
herb	C <sub>3</sub>	31	-29.47 $\pm$ 0.34 (13)	-29.13 $\pm$ 0.40 (10)	-31.93 $\pm$ 0.59 (8)
	C <sub>4</sub>	1	-13.20 (1)	NP	NP
epiphyte CAM		1	NP	NP	-15.24 (1)
liana	C <sub>3</sub>	3	NP	NP	-31.22 $\pm$ 1.34 (3)
shrub	C <sub>3</sub>	11	-28.85 $\pm$ 0.77 (3)	-29.79 $\pm$ 1.13 (5)	-32.15 $\pm$ 0.68 (3)
tree	C <sub>3</sub>	24	-27.47 $\pm$ 0.35 (4)	-29.84 $\pm$ 0.53 (5)	-31.08 $\pm$ 0.39 (15)

**Table 3.** Two-way ANOVA testing for significant effects of life form (grass, fern, herb, shrub, tree) and habitat of greatest abundance (open, intermediate, closed) on the carbon isotope ratio of leaves of 86 species from Ding Hu Shan

Source	Degrees of freedom	F-ratio	P <
Life Form	4	0.27	0.876
Habitat	2	55.8	0.001
Interaction	8	1.89	0.676

materials. This value would then contrast with the carbon isotope ratio of the free atmospheric CO<sub>2</sub>, which is closer to -8‰ (Francey et al. 1985). This is a reasonable explanation for why differences in leaf isotopic composition should be expected in open versus closed habitats, and has been used by Medina and Minchin (1980) and in part by Schleser and Jayasckera (1985) to explain observed variations in leaf carbon isotope ratios within a forest canopy. Measurements of the isotopic composition of atmospheric CO<sub>2</sub> are very limited, but tend to indicate that isotope ratios within the canopy are generally close to the values for the bulk air. Francey et al. (1985) found a gradient of less than 1‰ from the top of a pine canopy to 1 m above the forest floor. Substantial gradients in the isotopic composition of the atmospheric CO<sub>2</sub> are likely to arise only under conditions when little wind penetrates into the canopy.

An alternative explanation for the trend in the carbon isotopic composition of leaves has been proposed by Farquhar et al. (1982a, b). This model predicts that carbon isotope ratios should vary with the ratio of the intercellular (*c<sub>i</sub>*) to atmospheric (*c<sub>a</sub>*) CO<sub>2</sub> concentrations. Using gas exchange techniques, Ehleringer et al. (1986) have demonstrated in a number of species from Ding Hu Shan that the *c<sub>i</sub>/c<sub>a</sub>* ratio changed as a function of light levels. They observed that over the range of light levels expected between open and closed canopy habitats, there were sufficient changes in *c<sub>i</sub>/c<sub>a</sub>* in leaves to account for the observed differences in leaf carbon isotope ratios between habitats.

Our data do not allow a definitive partitioning of the habitat-to-habitat differences in leaf-carbon-isotope com-

position between effects due to the physiological parameter *c<sub>i</sub>/c<sub>a</sub>* and differences due to the environmental parameter, variation in the isotope composition of the source CO<sub>2</sub>. However, the absence of significant differences in the carbon isotope composition of leaves among life forms (Table 3) strongly argues against the importance of source effects. If source effects were important, we would expect the most negative isotope ratios in the herb layer and the least negative values in the trees. Further, we would expect the largest gradient in plants of the closed forest with the least wind penetration and the smallest gradient in plants of the open forest. Neither prediction is supported by the data (Table 2). Thus, the hypothesis supported by the trend in isotope compositions is that average levels of intercellular CO<sub>2</sub> are highest in species typical of closed forest and lowest in species typical of open forest. This interpretation is also consistent with the data of Ehleringer et al. (1986) demonstrating that in several species from Ding Hu Shan, intercellular CO<sub>2</sub> concentration decreases with increasing light.

If source effects are not important and if the humidity gradient is uniform, then differences in carbon isotope composition correspond to differences in water-use efficiency. A more negative isotope ratio indicates a lower ratio of photosynthesis to transpiration. In general, ambient humidities are slightly lower and leaf temperatures are slightly higher in open than in closed forest at Ding Hu Shan (Field et al. 1986). Thus, the indication from the carbon isotope ratios that water-use-efficiency is greatest in plants typical of open habitats and least in plants typical of closed forest is counteracted by the trends in environment.

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## References

- Chazdon RL (1978) Ecological aspects of the distribution of C<sub>4</sub> grasses in selected habitats of Costa Rica. *Biotropica* 10:265-269
- Downton WJS, Grant WJR, Robinson SP (1985) Photosynthetic

- and stomatal responses of spinach leaves to salt stress. *Plant Physiol* 77:85–88
- Ehleringer JR (1978) Implications of quantum yield differences on the distributions of  $C_3$  and  $C_4$  grasses. *Oecologia* (Berlin) 31:255–267
- Ehleringer JR, Field CB, Lin ZF, Kuo CY (1986) Leaf carbon isotope ratio and mineral composition in subtropical plants along an irradiance cline. *Oecologia* (Berlin) 70:520–526
- Ehleringer JR, Schulze E-D, Ziegler H, Lange OL, Farquhar GD, Cowan IR (1985) Xylem-tapping mistletoes: water or nutrient parasites? *Science* 227:1479–1481
- Farquhar GD, Ball MC, von Caemmerer S, Roksandic Z (1982a) Effect of salinity and humidity on  $\delta^{13}C$  values of halophytes – evidence for diffusional isotopic fractionation determined by the ratio of intercellular/atmospheric partial pressure of  $CO_2$  under different environmental conditions. *Oecologia* (Berlin) 52:121–124
- Farquhar GD, O'Leary MH, Berry JA (1982b) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust J Plant Physiol* 9:121–137
- Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust J Plant Physiol* 11:539–552
- Francey RJ, Gifford RM, Sharkey TD, Weir B (1985) Physiological influences on carbon isotope discrimination in huon pine (*Lagarostrobos franklinii*). *Oecologia* (Berlin) 66:211–218
- Hattersley PW (1983) The distribution of  $C_3$  and  $C_4$  grasses in Australia in relation to climate. *Oecologia* (Berlin) 57:113–128
- He CH, Chen SQ, Liang YA (1982) The soils of Ding Hu Shan Biosphere Reserve. Tropical and Subtropical Forest Ecosystems Popular Science Press, Guangzhou Branch, China (in Chinese), vol 1, pp 38–46
- Huang ZF, Fang ZG (1982) The climate of Ding Hu Shan. Tropical and Subtropical Forest Ecosystems. Popular Science Press, Guangzhou Branch, China (in Chinese) (vol 1 pp 11–16)
- Hubick KT, Farquhar GD, Shorter R (1986) Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. *Aust J Plant Physiol*
- Medina E, Minchin P (1980) Stratification of  $\delta^{13}C$  values of leaves in Amazonian rain forests. *Oecologia* (Berlin) 45:377–378
- Pearcy RW, Ehleringer JR (1984) Ecophysiology of  $C_3$  and  $C_4$  plants. *Plant Cell Environ* 7:1–13
- Pearcy RW, Troughton JH (1975)  $C_4$  photosynthesis in tree form *Euphorbia* species from Hawaiian rainforest sites. *Plant Physiol* 55:1054–1056
- Rundel PW (1980) The ecological distribution of  $C_4$  and  $C_3$  grasses in the Hawaiian Islands. *Oecologia* (Berlin) 45:354–359
- Schleser GH, Jayasekera R (1985)  $\delta^{13}C$ -variations of leaves in forests as an indication of re-assimilated  $CO_2$  from the soil. *Oecologia* (Berlin) 65:536–542
- Shi GL, Chen DR, Ding GJ (1978) A Handbook of Plants of Ding Hu Shan. South China Institute of Botany, Academia Sinica, p 647
- Smith BN, Oliver J, McMillan C (1976) Influence of carbon source, oxygen concentration, light intensity and temperature on  $^{13}C/^{12}C$  ratios for higher plants. *Bot Gaz* 137:99–104
- Teeri JA, Stowe LG (1976) Climatic patterns and the distribution of  $C_4$  grasses in North America. *Oecologia* (Berlin) 23:1–12
- Tieszen LL, Hein D, Qvortrup SH, Troughton JH, Imbamba SK (1979) Use of  $\delta^{13}C$  values to determine vegetation selectivity in east African herbivores. *Oecologia* (Berlin) 37:351–359
- Vogel GC (1978) Recycling of carbon in a forest environment. *Oecol Plant* 13:89–94
- Wang ZH, He DQ, Song SD, Chen SP, Chen DR, Tu MZ (1982) The vegetation of Ding Hu Shan Biosphere Preserve. Tropical and Subtropical Forest Ecosystems. Popular Science Press, Guangzhou Branch, China (in Chinese) vol 1 pp 77–141
- Ziegler H, Batanouny KH, Sankhla N, Vyas OP, Stichler W (1981) The photosynthetic pathway types of some desert plants from India, Saudia Arabia, Egypt, and Iraq. *Oecologia* (Berlin) 48:93–99

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