Annals of Botany **88**: 307–311, 2001
doi:10.1006/anbo.2001.1460, available online at http://www.idealibrary.com on IDEAL®

Termite Prey Specialization in the Pitcher Plant *Nepenthes albomarginata*—Evidence from Stable Isotope Analysis

JONATHAN A. MORAN*†, MARLIS A. MERBACH‡, NIGEL J. LIVINGSTON†, CHARLES M. CLARKE§ and WEBBER E. BOOTH¶

†Department of Biology, University of Victoria, PO Box 3020, Victoria, B.C. V8W 3N5, Canada, ‡Fachbereich Biologie, Zoologisches Institut, J. W. Goethe-Universität, Frankfurt am Main, Germany, §Department of Biology, Hong Kong University of Science and Technology, Clear Water Bay Road, Kowloon, Hong Kong and ¶Department of Biology, Universiti Brunei Darussalam, Jalan Tungku Link, Gadong, BE1410, Brunei Darussalam

Received: 7 September 2000 Returned for revision: 13 December 2000 Accepted: 12 April 2001

Old World pitcher plants (*Nepenthes* spp., Nepenthaceae) trap and digest invertebrate prey to derive nutrients, primarily nitrogen (N). In the majority of lowland *Nepenthes* species studied to date, ants (Hymenoptera, Formicidae) are numerically the dominant prey taxon. *Nepenthes albomarginata* is unusual in showing an apparent bias towards the capture of termites (Isoptera). We tested the hypothesis that *N. albomarginata* derives N from termite capture, by comparison of foliar stable N isotope abundance ($\delta^{15}N$) with a sympatric species (*N. rafflesiana*), whose verified major prey group is ants. *N. albomarginata* showed significantly lower $\delta^{15}N$ values than *N. rafflesiana*, reflecting the lower $\delta^{15}N$ value of termite tissue relative to that of ants, and suggesting a degree of prey segregation between the two *Nepenthes* species. Using mixing models, we estimated that termites (*Hospitalitermes* sp.) contribute 53·8 ± 7·3 % of the total foliar N in *N. albomarginata*, and that ants (*Crematogaster* sp.) contribute 68·1 ± 2·4 % of the total foliar N in *N. rafflesiana*. We also investigated the carbon stable isotope abundance ($\delta^{13}C$) in both species. *N. albomarginata* showed higher $\delta^{13}C$ values and a lower estimated intercellular partial pressure of CO_2 (C_i) than *N. rafflesiana*, indicating either higher water use efficiency (due to water stress) or greater photosynthetic capacity.

Key words: Borneo, carnivory, *Nepenthes albomarginata*, *Nepenthes rafflesiana*, photosynthesis, stable isotopes, termites.

INTRODUCTION

The genus *Nepenthes* (Nepenthaceae) comprises approximately 82 species of carnivorous pitcher plants. To date, most studies of lowland *Nepenthes* species have shown ants (Hymenoptera, Formicidae) to be numerically the dominant prey taxon (Kato *et al*., 1993; Moran, 1996; Adam, 1997; Clarke, 1998; Moran *et al*., 1999). *Nepenthes albomarginata* (T. Lobb ex Lindl.) is a notable exception; analysis of its prey shows an apparent bias towards the capture of termites (Isoptera) in this species in Sumatra and Borneo (Kato *et al*., 1993; Adam, 1997; Clarke, 1997). The presence of a tomentose band of tissue beneath the peristome (pitcher mouth) has been implicated in the attraction of Isoptera to *N. albomarginata* pitchers (Clarke, 1997; Moran *et al*., 1999); the peristome nectaries themselves secrete little or no nectar (Merbach *et al*., 2001).

Despite these observations, no quantitative investigation has been carried out to date into the role of termites in the nitrogen (N) nutrition of *N. albomarginata*. Using stable N isotope analysis ($\delta^{15}N$), our primary aim was to test the hypothesis that this species targets and derives N from the capture of termites. For comparison, we also investigated a sympatric species, *Nepenthes rafflesiana* (Jack), which targets a wide variety of invertebrate species, although ants are numerically predominant (Moran, 1996; Adam, 1997; Moran *et al*., 1999). Termites are caught only rarely and accidentally by *N. rafflesiana*, comprising <4 % of the total prey (Moran, 1996). Since prey capture represents a significant source of N in *Nepenthes* (Schulze *et al*., 1997; Moran and Moran, 1998), we hypothesized that differences in $\delta^{15}N$ between ants (the verified modal prey group for *N. rafflesiana*) and termites (the putative target group for *N. albomarginata*) would be mirrored in the tissues of the two *Nepenthes* species. A secondary aim was to investigate possible differences in the photosynthetic physiology of the two species, via estimation of intercellular CO_2 partial pressure (C_i) from stable carbon (C) isotope abundance ($\delta^{13}C$).

MATERIALS AND METHODS

Study site

The study was undertaken in degraded coastal heath forest overlying an albic arenosol (leached white sand) on a marine terrace of Pleistocene origin in Brunei, northwest Borneo (4° 44′ N, 114° 36′ E, 5-20 m asl). Vegetation overlying this soil type is generally N-limited (Moran *et al*., 2000). The low scrub comprised *Ploiarium alternifolium*

* For correspondence. Fax 001 250 721 7120, e-mail jmoran@uvic.ca

0305-7364/01/080307+05 $35.00/00

Melchior (Theaceae), *Dillenia suffruticosa* Griff. Martelli (Dilleniaceae), *Melastoma malabathricum* L. (Melastomataceae) and *Rhodomyrtus tomentosa* (W. Ait) Hassk (Myrtaceae). In addition to *Nepenthes* species, myrmecophytes (ant-plants) such as *Discidia* sp. (Asclepiadaceae) were also present.

Sample collection and isotopic natural abundance determination

Samples of the leaf blade were collected from 12 *N. albomarginata* and 18 *N. rafflesiana* plants growing sympatrically. The lower sample number for *N. albomarginata* reflects its relative scarcity in Brunei. Each sample was taken from a separate plant, and represented the youngest leaf possessing a fully-developed pitcher. In Brunei, the termite genus most commonly encountered foraging at, and caught in, pitchers of *N. albomarginata* is *Hospitalitermes* (Nasutitermitinae; Merbach, pers. obs.). Worker caste individuals were collected from the same habitat, as were worker ants of a genus commonly caught by *N. rafflesiana* (*Crematogaster* sp.; Moran, pers. obs.). Foliar samples were also collected from four non-carnivorous reference plant species (*M. malabathricum*, *D. suffruticosa*, *R. tomentosa* and *P. alternifolium*). The use of more than one reference plant species reduced the possibility that interspecific differences in rooting depth biased $\delta^{15}N$ values (Schulze *et al.*, 1991).

Samples were oven-dried at 60 °C for 48 h and ground to a fine powder in a vibratory ball mill (Wig-L-Bug Amalgamator, Crescent Dental Co., Chicago, Il, USA). They were sent to the Stable Isotope Facility, University of California Davis (USA), for determination of $^{15}N/^{14}N$ and total N concentrations, as well as $^{13}C/^{12}C$ and total C concentrations, using a mass spectrometer with elemental analyzer (ANCA-Hydra 20-20, PDZEuropa). Natural abundance of the heavy isotopes ($\delta^{15}N$, $\delta^{13}C$) was expressed as per mil (‰) deviation from values for standard materials in the ratio of the heavy to the light isotope (atmospheric N_2 for N; PeeDee Belemnite (PDB) for C), as follows:

$$\delta X = [(R_{\mathrm{SAMPLE}}/R_{\mathrm{STANDARD}}) - 1]1000 \qquad (1)$$

where X is the heavy isotope and R is the ratio of heavy to light isotope. The working standard for $\delta^{13}C$ was beet sucrose with a value of −23·83 ‰ relative to PDB. Precision was ±0·2 ‰ for both $\delta^{15}N$ and $\delta^{13}C$ determinations.

Contribution of prey-derived N

The contribution of termite-derived N to the total N content of *N. albomarginata* foliage ($\%N_{\mathrm{TERM}}$) was calculated using a mixing model following Treseder *et al.* (1995):

$$\%N_{\mathrm{TERM}} = [(\delta^{15}N_{\mathrm{Na}} - \delta^{15}N_{\mathrm{Nr}})/(\delta^{15}N_{\mathrm{H}} - \delta^{15}N_{\mathrm{Nr}})]100 \qquad (2)$$

where $\delta^{15}N_{\mathrm{Na}}$, $\delta^{15}N_{\mathrm{Nr}}$ and $\delta^{15}N_{\mathrm{H}}$ are the mean $\delta^{15}N$ values for *N. albomarginata*, *N. rafflesiana* and *Hospitalitermes* sp., respectively. Ants have been reported to constitute up to 40 % of the prey of *N. albomarginata* (Kato *et al.*, 1993), and so this species could not be used as the 'non-ant' reference for *N. rafflesiana*. Therefore, the percent contribution of ant-derived N to *N. rafflesiana* foliage was calculated following the model of Schultze *et al.* (1991):

$$\%N_{\mathrm{ANT}} = [(\delta^{15}N_{\mathrm{Nr}} - \delta^{15}N_{\mathrm{R}})/(\delta^{15}N_{\mathrm{C}} - \delta^{15}N_{\mathrm{R}})]100 \qquad (3)$$

where $\delta^{15}N_{\mathrm{Nr}}$, $\delta^{15}N_{\mathrm{R}}$ and $\delta^{15}N_{\mathrm{C}}$ are the mean $\delta^{15}N$ values for *N. rafflesiana*, the non-insectivorous reference plant foliage and *Crematogaster* sp., respectively.

Determination of intercellular CO_2 partial pressure (C_i)

C_i was calculated in two stages. First, discrimination against $\delta^{13}C$ (Δ) was calculated as:

$$\Delta = (\delta^{13}C_a - \delta^{13}C)/(1 + \delta^{13}C/1000) \qquad (4)$$

where $\delta^{13}C_a$ is the isotopic composition of ambient air (−8 ‰). Following Farquhar *et al.* (1982) and Livingston *et al.* (1998), C_i was then derived from:

$$C_i = [(\Delta - a)/(b - a)]C_a \qquad (5)$$

where a is the degree of discrimination from diffusion in air (4·4 ‰), b is the net discrimination from carboxylation (27 ‰) and C_a is the ambient CO_2 partial pressure (370 μmol mol^{-1}).

Statistical analyses were undertaken using Systat V 5·05 (Systat Inc., Evanston, IL, USA; Wilkinson, 1990). Prior to *t*-tests, data were analysed for normality and homogeneity of variance. Data which violated the assumptions were analysed using the non-parametric Mann-Whitney *U* test (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION

Differences in $\delta^{15}N$ between N. albomarginata *and* N. rafflesiana

Our results support the hypothesis that *N. albomarginata* is a termite specialist, and suggest a degree of prey partitioning between it and the sympatric *N. rafflesiana*. $\delta^{15}N$ values for the former species were significantly more negative than for the latter (*N. albomarginata*: −2·1 ± 0·31 ‰; *N. rafflesiana*: 1·9 ± 0·14 ‰; $t = 7{\cdot}40$, $P < 0{\cdot}001$, d.f. = 28; Fig. 1), reflecting the ^{15}N depletion of *Hospitalitermes* sp. (termites) relative to *Crematogaster* sp. (ants) caught by *N. rafflesiana* ($\delta^{15}N = -4{\cdot}0 \pm 0{\cdot}07$ ‰ and 2·0 ± 0·02 ‰ for termites and ants, respectively, $n = 8$, 5). Using the mixing model we estimated that 53·8 ± 7·3 % of total foliar N in the *N. albomarginata* plants sampled was derived from termites.

N. rafflesiana catches a wide variety of invertebrate prey (15 Orders) including Diptera, non-formicine Hymenoptera, Coleoptera, Thysanoptera and Hemiptera. However, Formicidae are numerically the dominant prey category, accounting for between 50 and 90 % of prey items in pitchers (Moran, 1996; Moran *et al.*, 1999). A number of formicine genera regularly caught by *N. rafflesiana* are

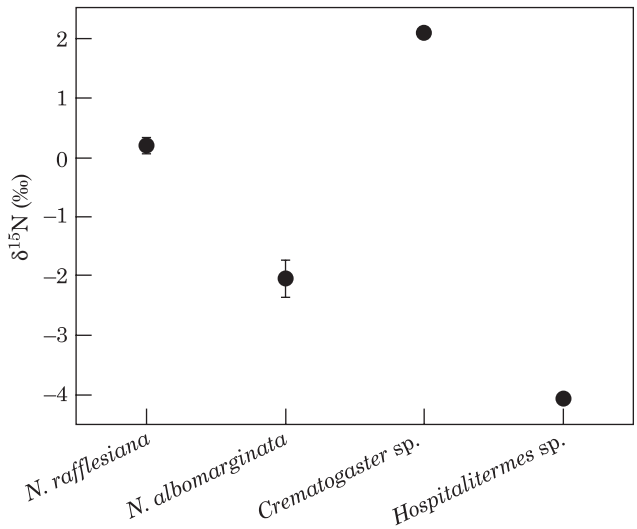

FIG. 1. $\delta^{15}N$ values (‰) for *N. rafflesiana* ($n = 18$), *N. albomarginata* ($n = 12$), *Crematogaster* sp. (ants) ($n = 5$) and *Hospitalitermes* sp. (termites) ($n = 8$). Points represent means, bars represent 1 s.e. and are not visible if narrower than the symbol.

omnivorous (Tobin, 1994), and thus would be expected to show elevated $\delta^{15}N$ values relative to *Hospitalitermes* sp., since ^{15}N undergoes trophic enrichment (DeNiro and Epstein, 1981; Minagawa and Wada, 1984). This was the case for *Crematogaster* sp., and using the mixing model we estimated that the ants contributed $68{\cdot}1 \pm 2{\cdot}4$ % of the total foliar N in *N. rafflesiana* (all the non-carnivorous reference plant species used in the model showed negative $\delta^{15}N$ values: *M. malabathricum* $-5{\cdot}9 \pm 0{\cdot}8$ ‰; *D. suffruticosa* $-3{\cdot}3 \pm 0{\cdot}3$ ‰; *R. tomentosa* $-2{\cdot}2 \pm 0{\cdot}5$ ‰; *P. alternifolium* $-4{\cdot}1 \pm 0{\cdot}3$ ‰; $n = 5$ per species). Although studies of stable isotope ratios have been used to infer diet in animal predators (see Kelly, 2000, for a recent review), ours is the first study to demonstrate differentiation between trophic level of prey (i.e., grazers *vs.* omnivores) between sympatric carnivorous plant species.

An alternative explanation for the lower $\delta^{15}N$ in *N. albomarginata* is that, in this species, all of the N is root-derived, with the pitchers making no nutritional contribution. However, we believe that the conspicuous production of these highly specialized and, presumably, photosynthate-costly trapping structures by the plant renders this possibility remote. Also, two pieces of evidence support the view that under typical conditions the pitchers, not the roots, are the key N-sequestering structures in *Nepenthes*. Firstly, Moran and Moran (1998) demonstrated that *N. rafflesiana* plants whose pitchers were prevented from trapping prey showed a reduction in growth rate, foliar chlorophyll content and foliar N content compared to control plants in which the pitchers were allowed to function normally. Uptake of N via the roots was insufficient to compensate completely for the shortfall resulting from pitcher blockage. The second piece of evidence comes from a study of *Nepenthes mirabilis* (Druce) by Schulze *et al.* (1997) who showed that very young plants are dependent solely on root uptake, whereas once functional pitchers are produced, invertebrate prey becomes the main source of N, as demonstrated by a sharp increase in $\delta^{15}N$ from older to younger leaves. In the current study, all the foliar material from *Nepenthes* was collected from mature plants producing fully functional pitchers.

With regard to the mixing models used in this study, it is important to bear in mind their inherent limitations and potential sources of error. Both models are variations on the two end-member approach used originally by Shearer and Kohl (1989) to estimate the contribution of atmospherically-fixed N to plants. The two end-members of the original model were N_2-fixing plants grown hydroponically in an N-free medium (100 % atmospherically-fixed N), and conspecifics using other N sources (0 % atmospherically-fixed N). In our first model, to estimate the contribution of termite-derived N to *N. albomarginata*, we used the $\delta^{15}N$ value of termite tissue as a surrogate for plant material whose N is 100 % termite-derived (since no such plant material was available). Similarly, in the second model we used the $\delta^{15}N$ value of ant tissue rather than that of plant material whose N derives solely from ants. In both cases, the possibility of fractionation during N uptake from the invertebrate sources is disregarded. Another potential source of error is that only one genus each of ant and termite were used, whereas other genera besides these (whose individuals will almost certainly vary in their N isotope signature) are also trapped and digested by the plants. These *caveats* aside, however, we believe the models to be a useful first attempt at explaining the interspecific differences in $\delta^{15}N$ values between the two *Nepenthes* species in terms of targeted prey types.

Termites are the most numerous terrestrial invertebrates in many tropical ecosystems (Collins, 1980; Jones, 1996), and *Hospitalitermes* species in particular forage in large numbers, up to 500 000 individuals per foray (Miura and Matsumoto, 1998). Compared to ants, a smaller proportion of the N in termites is bound up in indigestible chitin (Redford and Dorea, 1984), leaving a correspondingly larger fraction available for assimilation (*Nepenthes* do not produce chitinase, and once digestion is complete only the exoskeleton of the prey is left in the pitcher). It should come as little surprise, therefore, that a *Nepenthes* species has evolved the necessary characteristics to specialize in utilizing such an abundant nutrient resource.

Isotopic clues to the diet of Hospitalitermes *sp.*

What can be deduced about the diet of *Hospitalitermes* sp. from their isotopic composition? Members of the genus feed primarily on epiphytic lichens (Lee and Wood, 1971; Jones and Gathorne-Hardy, 1995; Miura and Matsumoto, 1997, 1998), and the following discussion assumes that lichens formed the major part of the diet of the individuals analysed in this study. The low $\delta^{15}N$ value of the termite tissues suggests that the lichens were diazotrophic, i.e. N_2-fixing (Shearer and Kohl, 1989; Pate *et al.*, 1998; Roggy *et al.*, 1999). Since $\delta^{15}N$ increases by approx. 3 ‰ per trophic level (DeNiro and Epstein, 1981; Minagawa and Wada, 1984), the putative $\delta^{15}N$ of the lichens would be in the order of -7 ‰, a value suggesting an unusually high degree of discrimination against ^{15}N during N_2-fixation (Shearer and

Kohl, 1986). Although some termite groups possess diazotrophic gut flora, this is not the case in the so-called 'higher' termites, including *Hospitalitermes* (Ohkuma *et al.*, 1999). Since 'higher' termites do not possess diazotrophic gut flora, they obtain N from their relatively N-rich foods (e.g. lichens), whereas the possession of diazotrophic gut flora by the 'lower' termites enables them to survive on N-poor foodstuffs such as decaying wood.

The mean $\delta^{13}C$ value of the termites was $-27{\cdot}9 \pm 0{\cdot}05$ ‰ ($n = 8$), and as animals are enriched in ^{13}C to only a small degree relative to their food (approx. 1 ‰; DeNiro and Epstein, 1978), we deduce that lichens on which the *Hospitalitermes* sp. fed would have showed $\delta^{13}C$ values in the region of −29 ‰. Based on this, we make the tentative suggestion that the photosynthetic compartment of the modal target lichens may have comprised phycobionts (green algae) plus cyanobionts (cyanobacteria), since this combination yields $\delta^{13}C$ values close to −29 ‰; lichens in which the photosynthetic compartment comprises green algae or cyanobacteria alone show significantly higher $\delta^{13}C$ values (Máguas *et al.*, 1995). Furthermore, the high degree of discrimination against ^{13}C suggests the absence of pyranoids in the green algal compartment (Smith and Griffiths, 1996).

To conclude, based on our results we suggest that the probable major carnivory-mediated N pathway in *N. albomarginata* is:

Atmospheric N_2 → diazotrophic lichens → termites → *N. albomarginata*

Ecophysiological implications of $\delta^{13}C$ differences between species

The range of foliar $\delta^{13}C$ values (−32·3 to −28·5 ‰) identifies both *N. albomarginata* and *N. rafflesiana* as C_3 plants (Ehleringer, 1991). Foliar C isotope composition is a function of both the supply of CO_2 to the site of fixation and the photosynthetic capacity (chloroplast demand). These relations are formalized for C_3 plants in models that link photosynthesis to $\delta^{13}C$ through C_i/C_a (Farquhar *et al.*, 1982). *N. albomarginata* showed significantly higher $\delta^{13}C$ values than *N. rafflesiana* ($-29{\cdot}6 \pm 0{\cdot}2$ ‰ and $-31{\cdot}3 \pm 0{\cdot}1$ ‰, respectively; $t = -5{\cdot}8$, $P < 0{\cdot}001$, d.f. = 28) and lower C_i values (Fig. 2). There are two possible explanations for this result. The first is that *N. albomarginata* possesses a higher photosynthetic capacity than *N. rafflesiana*. Between 50 and 80 % of foliar N is typically incorporated in photosynthetic proteins (Evans, 1989), and the fact that *N. albomarginata* showed a significantly higher N concentration than *N. rafflesiana* ($P < 0{\cdot}001$, Mann-Whitney *U* test; Fig. 2), in combination with the lower C_i values, supports the idea that the former species has a higher photosynthetic capacity than the latter. The second possibility is that the lower C_i value of *N. albomarginata* simply reflects greater water stress (manifested in greatly reduced stomatal conductance) relative to *N. rafflesiana*: the relationship between C_i and water stress, via estimated water use efficiency, is well documented (e.g. Farquhar *et al.*, 1982; Farquhar and Richards, 1984; Farquhar *et al.*, 1989; Sun *et al.*, 1996; Pate *et al.*, 1998; Korol *et al.*, 1999). The possibility that *N. albomarginata* is susceptible to water stress is supported by observations of its distribution. The species is very rare and localized in Brunei relative to other parts of its range in Borneo and elsewhere on the Sunda Shelf (Phillipps and Lamb, 1996). Brunei experiences a drier climate than many other parts of Borneo, with two annual dry seasons, in February/March and July/August (Becker, 1992; Cooper, 1992). Episodes of physiological drought (sliding 30 d total rainfall <100 mm; *sensu* Brünig, 1969) occur periodically in the study area (Moran *et al.*, 2000). Furthermore, *N. albomarginata* appears to inhabit wetter microsites than *N. rafflesiana* in areas where the two species are sympatric (Clarke, pers. obs.). Unfortunately, in the absence of gas exchange data, it is not possible to resolve which of these two possibilities is the more likely.

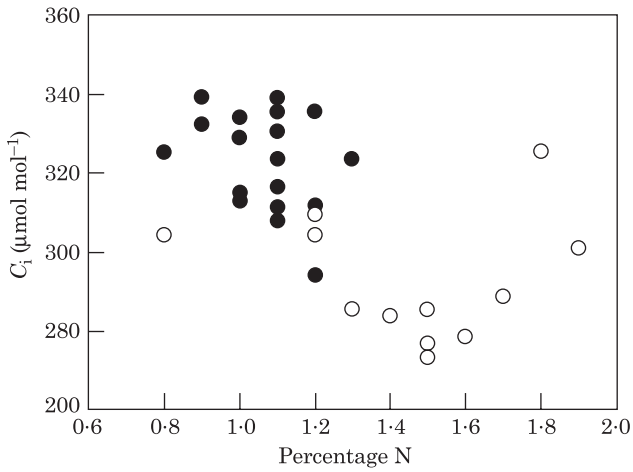

FIG. 2. Estimated intercellular CO_2 partial pressure C_i (μmol mol^{-1}) *vs.* N concentration (%) for *N. rafflesiana* (●; $n = 18$) and *N. albomarginata* (○; $n = 12$).

ACKNOWLEDGEMENTS

We thank S. Robbins and D. Harris for sample preparation and processing. A. Moran, D. Mathewson, C. Maslovat and two anonymous referees improved the manuscript considerably.

LITERATURE CITED

Adam JH. 1997. Prey spectra of Bornean *Nepenthes* species (Nepenthaceae) in relation to their habitat. *Pertanika Journal of Tropical Agricultural Science* **20**: 121–134.

Becker P. 1992. Seasonality of rainfall and drought in Brunei Darussalam. *Brunei Museum Journal* **7**: 99–109.

Brünig EF. 1969. On the seasonality of droughts in the lowlands of Sarawak (Borneo). *Erdkunde* **23**: 127–133.

Clarke CM. 1997. *Nepenthes of Borneo*. Kota Kinabalu: Natural History Publications.

Clarke CM. 1998. Initial colonisation and prey capture in *Nepenthes bicalcarata* (*Nepenthaceae*) pitchers in Brunei. *Sandakania* **12**: 27–36.

Collins NM. 1980. The distribution of soil macrofauna on the west ridge of Gunung (Mount) Mulu, Sarawak. *Oecologia* **44**: 263–275.

Cooper R. 1992. Forecasting and understanding local weather in Brunei Darussalam. *Brunei Museum Journal* **7**: 88–98.

DeNiro MJ, Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**: 495–506.

DeNiro MJ, Epstein S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* **45**: 341–351.

Ehleringer JR. 1991. $^{13}C/^{12}C$ fractionation and its utility in terrestrial plant studies. In: Coleman DC, Fry B, eds. *Carbon isotope techniques*. San Diego: Academic Press Inc., 187–200.

Evans JR. 1989. Photosynthesis and nitrogen relationships in the leaves of C_3 plants. *Oecologia* **78**: 9–19.

Farquhar GD, Richards RA. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* **11**: 539–552.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**: 503–537.

Farquhar GD, O'Leary MH, Berry JA. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* **9**: 121–137.

Jones DT. 1996. A quantitative survey of the termite assemblage and its consumption of food in lowland mixed dipterocarp forest of Brunei Darussalam. In: Edwards DS, Booth WE, Choy SC, eds. *Tropical rainforest research-current issues*. Dordrecht: Kluwer Academic Publishers, 297–305.

Jones DT, Gathorne-Hardy F. 1995. Foraging activity of the processional termite *Hospitalitermes hospitalis* (Termitidae: Nasutitermitinae) in the rain forest of Brunei, north-west Borneo. *Insectes-Sociaux* **42**: 359–369.

Kato M, Hotta M, Tamin R, Itino T. 1993. Inter- and intra-specific variation in prey assemblages and inhabitant communities in *Nepenthes* pitchers in Sumatra. *Tropical Zoology* **6**: 11–25.

Kelly JF. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* **78**: 1–27.

Korol RL, Kirschbaum MUF, Farquhar GD, Jeffreys M. 1999. Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. *Tree Physiology* **19**: 551–562.

Lee KE, Wood TG. 1971. *Termites and soils*. London: Academic Press.

Livingston NJ, Whitehead D, Kelliher FM, Wang Y-P, Grace JC, Walcroft AS, Byers JN, McSeveny TM, Millard P. 1998. Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young *Pinus radiata* D. Don tree. *Plant, Cell and Environment* **21**: 795–803.

Máguas C, Griffiths H, Broadmeadow MSJ. 1995. Gas exchange and carbon isotope discrimination in lichens: Evidence for interactions between CO_2-concentrating mechanisms and diffusion limitation. *Planta* **196**: 95–102.

Merbach MA, Zizka G, Fiala B, Maschwitz U, Booth WE. 2001. Patterns of nectar secretion in five *Nepenthes* species from Brunei Darussalam, Northwest Borneo, and implications for ant-plant relationships. *Flora* **196**: 153–160.

Minagawa M, Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta* **48**: 1135–1140.

Miura T, Matsumoto T. 1997. Diet and nest material of the processional termite *Hospitalitermes*, and cohabitation of *Termes* (Isoptera, Termitidae) on Borneo Island. *Insectes-Sociaux* **44**: 267–275.

Miura T, Matsumoto T. 1998. Foraging organization of the open-air processional lichen-feeding termite *Hospitalitermes* (Isoptera, Termitidae) in Borneo. *Insectes-Sociaux* **45**: 17–32.

Moran JA. 1996. Pitcher dimorphism, prey composition and the mechanisms of prey attraction in the pitcher plant *Nepenthes rafflesiana* in Borneo. *Journal of Ecology* **84**: 515–525.

Moran JA, Moran AJ. 1998. Foliar reflectance and vector analysis reveal nutrient stress in prey-deprived pitcher plants (*Nepenthes rafflesiana*). *International Journal of Plant Sciences* **159**: 996–1001.

Moran JA, Booth WE, Charles JK. 1999. Aspects of pitcher morphology and spectral characteristics of six Bornean *Nepenthes* pitcher plant species: Implications for prey capture. *Annals of Botany* **83**: 521–528.

Moran JA, Barker MG, Moran AJ, Becker P, Ross SM. 2000. A comparison of the soil water, nutrient status and litterfall characteristics of tropical heath and mixed dipterocarp forest sites in Brunei. *Biotropica* **32**: 2–13.

Ohkuma M, Noda S, Kudo T. 1999. Phylogenetic diversity of nitrogen fixation genes in the symbiotic microbial community in the gut of diverse termites. *Applied and Environmental Microbiology* **65**: 4926–4934.

Pate JS, Unkovich MJ, Erskine PD, Stewart GR. 1998. Australian mulga ecosystems- ^{13}C and ^{15}N natural abundances of biota components and their ecological significance. *Plant, Cell and Environment* **21**: 1231–1242.

Phillipps A, Lamb A. 1996. *Pitcher-plants of Borneo*. Kota Kinabalu: Natural History Publications.

Redford KH, Dorea JG. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *Journal of Zoology* **203**: 385–395.

Roggy JC, Prévost MF, Gourbiere F, Casabianea H, Garbaye J, Domenach AM. 1999. Leaf natural ^{15}N abundance and total N concentration as potential indicators of plant N nutrition in legumes and pioneer species in a rain forest of French Guiana. *Oecologia* **120**: 171–182.

Schulze E-D, Gebauer G, Schulze W, Pate JS. 1991. The utilization of nitrogen from insect capture by different growth forms of *Drosera* from Southwest Australia. *Oecologia* **87**: 240–246.

Schulze W, Schulze E-D, Pate JS, Gillison AN. 1997. The nitrogen supply from soils and insects during growth of the pitcher plants *Nepenthes mirabilis*, *Cephalotus follicularis* and *Darlingtonia californica*. *Oecologia* **112**: 464–471.

Shearer G, Kohl DH. 1986. N_2-fixation in field settings: estimations based on natural ^{15}N abundance. *Australian Journal of Plant Physiology* **13**: 699–756.

Shearer G, Kohl DH. 1989. Estimates of N_2 fixation in ecosystems: The need for and basis of the ^{15}N natural abundance method. In: Rundel PW, Ehleringer JR, Nagy KA, eds. *Stable isotopes in ecological research*. New York: Springer-Verlag, 342–374.

Smith EC, Griffiths H. 1996. The occurrence of the chloroplast pyrenoid is correlated with the activity of a CO_2-concentrating mechanism and carbon isotope discrimination in lichens and bryophytes. *Planta* **198**: 6–16.

Sokal RR, Rohlf FJ. 1981. *Biometry*. New York: W.H. Freeman.

Sun ZJ, Livingston NJ, Guy RD, Ethier GJ. 1996. Stable carbon isotopes as indicators of increased water use efficiency and productivity in white spruce (*Picea glauca* (Moench) Voss) seedlings. *Plant, Cell and Environment* **19**: 887–894.

Tobin JE. 1994. Ants as primary consumers: diet and abundance in the Formicidae. In: Hunt JH, Nalepa CA, eds. *Nourishment and evolution in insect societies*. San Francisco: Westview Press, 279–307.

Treseder KK, Davidson DW, Ehleringer JR. 1995. Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. *Nature* **375**: 137–139.

Wilkinson L. 1990. *SYSTAT: The system for statistics*. Evanston: SYSTAT Inc.