



---

From Carnivore to Detritivore? Isotopic Evidence for Leaf Litter Utilization by the Tropical Pitcher Plant *Nepenthes ampullaria*

Author(s): Jonathan A. Moran, Charles M. Clarke, and Barbara J. Hawkins

Reviewed work(s):

Source: *International Journal of Plant Sciences*, Vol. 164, No. 4 (July 2003), pp. 635-639

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/375422>

Accessed: 04/03/2013 18:52

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *International Journal of Plant Sciences*.

<http://www.jstor.org>

## FROM CARNIVORE TO DETRITIVORE? ISOTOPIC EVIDENCE FOR LEAF LITTER UTILIZATION BY THE TROPICAL PITCHER PLANT *NEPENTHES AMPULLARIA*

Jonathan A. Moran,<sup>1,\*</sup> Charles M. Clarke,<sup>†</sup> and Barbara J. Hawkins\*

\*Department of Biology, University of Victoria, P.O. Box 3020, Victoria, British Columbia V8W 3N5, Canada; and †Department of Biology, Hong Kong University of Science and Technology, Clear Water Bay Road, Kowloon, Hong Kong

*Nepenthes* pitcher plants trap prey in specialized leaves formed into pitchers. Most lowland species live in open, sunny habitats and capture prey to obtain nutrients, principally nitrogen (N). *Nepenthes ampullaria* is commonly found under closed canopy forest and possesses morphological traits that indicate adaptation to trap leaf litter as a nutrient source. We tested this hypothesis by comparing foliar stable N isotope abundance ( $\delta^{15}\text{N}$ ) between plants growing under forest canopy at 20 sites (litterfall present) and those growing in 20 open areas (no litterfall) in Borneo. Foliar  $\delta^{15}\text{N}$  values were significantly lower and total N concentrations were higher for the plants with access to litterfall. Using a mixing model, we estimated that *N. ampullaria* plants growing under forest canopy derived  $35.7\% \pm 0.1\%$  of their foliar N from leaf litter inputs.

**Keywords:** Borneo, carnivory, N isotopes, *Nepenthes*.

### Introduction

*Nepenthes* pitcher plants (Nepenthaceae) employ highly specialized fluid-filled traps to attract, kill, and digest invertebrate prey, from which they extract nutrients (Kato et al. 1993; Moran 1996; Schulze et al. 1997; Moran and Moran 1998; Moran et al. 1999). Along with other carnivorous plants, *Nepenthes* typically occur in open, sunny habitats (Lüttge 1983; Givnish et al. 1984; Benzing 1987). *Nepenthes ampullaria* Jack is an anomaly among lowland *Nepenthes* species in that it is most common in closed canopy forest, e.g., heath forest and peat swamp forest (Clarke 1997, 2001). This habitat preference is consistent over the wide geographical range of the species, from Thailand to the islands of the Sunda Shelf to New Guinea.

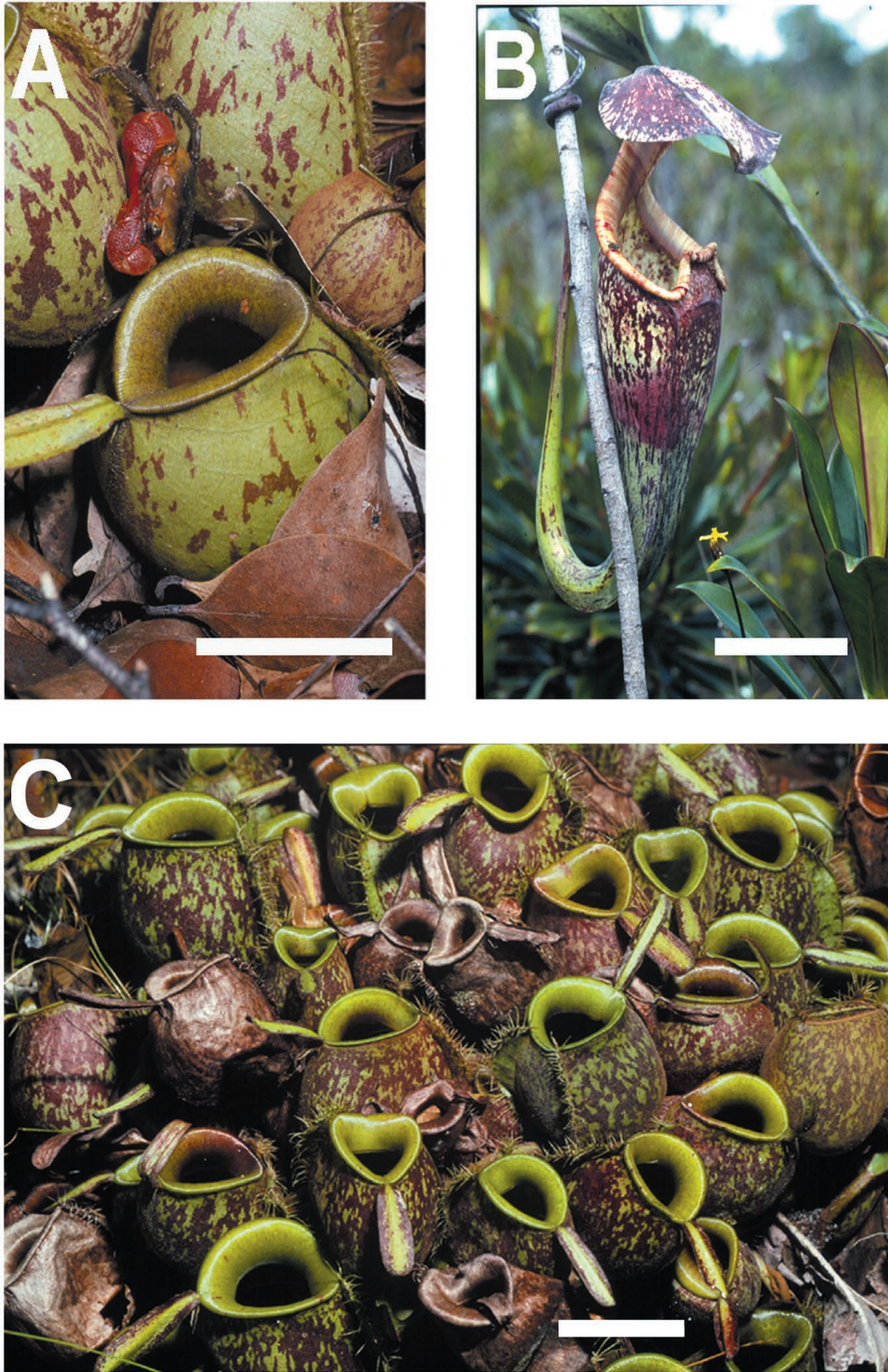
The morphology of *N. ampullaria* is also highly atypical in several respects (fig. 1A). First, the pitcher lid is vestigial and reflexed away from the pitcher mouth, and the leaf blade is unusually small, which allows material to fall directly into the pitcher from above. In most other lowland *Nepenthes* species, the lid is positioned over the pitcher mouth and prevents vertical entry of matter into the pitcher (e.g., *Nepenthes rafflesiana* Jack; fig. 1B). Second, nectar glands (a fundamental component of the prey attraction mechanism [Juniper et al. 1989]) are rare or absent from the pitcher lid, and those surrounding the pitcher mouth are smaller than those of congeners (Macfarlane 1893; Lloyd 1942). The wax-covered zone, which causes prey to lose its foothold within the pitcher in other *Nepenthes* species, is absent (Macfarlane 1893; Juniper and Burras 1962; Clarke 1997, 2001), as are the “lunate” cells, modified overhanging stomatal guard cells with a putatively similar function (Pant and Bhatnagar 1977). Finally, the spatial deployment of pitchers is unique among the genus and often results in an extensive, densely packed “carpet” of pitchers

resting on the forest floor, which thereby minimizes vertical overlap and maximizes the area for interception of material falling from above (fig. 1C).

Cresswell (1998) found that plant material accounted for >50% of the necromass in pitchers of this species in Bornean heath forest, although no suggestion was made that this material was utilized by the plant. Other studies show *N. ampullaria* to have very low invertebrate prey capture rates relative to other *Nepenthes* species in both Sumatra and Borneo (Kato et al. 1993; Adam 1997). *Nepenthes ampullaria* pitchers are long lived, as might be expected of a plant relying on a slow but steady trickle of nutrients. For example, the functional life of pitchers in this species can be >6 mo, compared with a “typical” insectivorous species such as *Nepenthes mirabilis* Druce, whose pitchers are functional for <1 mo (Clarke 1997).

This broad body of circumstantial evidence suggested to us a leaf litter trapping syndrome in *N. ampullaria*. The aim of our study was to use stable N isotope ratio analysis to test the idea that *N. ampullaria* sequesters N from leaf material falling from the forest canopy. The  $^{15}\text{N}$  undergoes trophic enrichment, and the tissues of carnivorous plants (whose N source is  $^{15}\text{N}$  enriched since it is derived from animal tissue) show higher  $\delta^{15}\text{N}$  values than do those of noncarnivorous plants (Schulze et al. 1997; Moran et al. 2001). Although only moderately successful at invertebrate prey capture relative to its congeners, *N. ampullaria* nonetheless captures and presumably utilizes invertebrate prey as a N source. Our hypotheses were as follows: (1) *N. ampullaria* plants growing under forest canopy would derive N from leaf litter in addition to that from invertebrate prey via the pitchers. In contrast, the pitchers of *N. ampullaria* plants growing in the open with no access to litterfall would acquire N from invertebrate prey alone and as a consequence would show more elevated  $^{15}\text{N}$  levels in their tissues. (2) *Nepenthes ampullaria* plants growing in the open, deprived of N from leaf litter, would show lower foliar N concentrations than plants with access to litterfall. In both

<sup>1</sup> Author for correspondence; e-mail jmoran@uvic.ca.



**Fig. 1** Pitcher morphology. *A*, *Nepenthes ampullaria*. *B*, *Nepenthes rafflesiana*, a “typical” species. *C*, Cluster of *N. ampullaria* pitchers forming a continuous carpet on the forest floor. Bar = ca. 5 cm.

hypotheses, the role of N uptake by the roots is ignored. We believe this to be a valid approach because two studies have shown that root uptake of N is minor compared with pitcher uptake in mature *Nepenthes* plants with functional pitchers (Schulze et al. 1997; Moran and Moran 1998).

### Material and Methods

The study was carried out in Brunei, northwest Borneo (4°34'N, 114°25'E, 10–20 m a.s.l.) and focused on two habitat types: tropical heath forest (kerangas) and open, secondary scrub (padang). Detailed accounts of Bruneian heath forest vegetation and stand structure are provided by Brünig (1974) and Davies and Becker (1996). The scrub vegetation was dominated by *Rhodomyrtus tomentosa* (W. Ait) Hassk (Myrtaceae), *Melastoma malabatricum* L. (Melastomataceae), *Dillenia suffruticosa* Griff. Martelli (Dilleniaceae), and *Ploiarium alternifolium* Melchior (Theaceae).

The experimental design was as follows: one *Nepenthes ampullaria* plant was sampled from each of 20 separate and discrete stands of heath forest (litterfall present) and 20 separate and discrete areas of open scrub (litterfall absent) within a highly fragmented mosaic of both habitat types over a ca. 25 × 25-km area. For each plant, a foliar sample (pitcher lid) was collected from its most recent fully developed pitcher. In addition, one recently abscised and physically intact leaf litter sample was collected from the forest floor of 10 of the heath forest stands. All leaf litter samples were ≤2 cm in length and sufficiently small to allow entry into a typical *N. ampullaria* pitcher.

All samples were oven dried for 48 h at 60°C, ground to a fine powder, and sent to the University of California, Davis, for isotopic determination using a mass spectrometer and elemental analyzer (ANCA-Hydra 20-20, PDZEuropa). Natural abundance of the heavy isotope ( $\delta^{15}\text{N}$ ) was expressed as per mil (‰) deviation from that of a standard material in the ratio of heavy to light isotope (atmospheric  $\text{N}_2$ ) using the general formula

$$\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 1000, \quad (1)$$

where  $X$  is the heavy isotope and  $R$  is the ratio of heavy to light isotope. Precision was  $\pm 0.2\text{‰}$ .

The contribution of leaf litter-derived N ( $\%N_{\text{litter}}$ ) to total foliar N content of *N. ampullaria* was estimated using the ISOERROR1\_03 two end-member mixing model (Phillips and Gregg 2001):

$$\%N_{\text{litter}} = \left( \frac{\delta^{15}\text{N}_{\text{amp forest}} - \delta^{15}\text{N}_{\text{amp open}}}{\delta^{15}\text{N}_{\text{litter}} - \delta^{15}\text{N}_{\text{amp open}}} \right) 100, \quad (2)$$

where  $\delta^{15}\text{N}_{\text{amp forest}}$ ,  $\delta^{15}\text{N}_{\text{amp open}}$ , and  $\delta^{15}\text{N}_{\text{litter}}$  are the mean  $\delta^{15}\text{N}$  values for *N. ampullaria* under forest canopy (i.e., with leaf litter input), *N. ampullaria* from open scrub (no leaf litter input), and leaf litter samples from the forest floor, respectively. The two end-member approach was used originally by Shearer and Kohl (1989) to determine the contribution of fixed atmospheric N to plants. In that model, the end members were plants using 0% and 100% fixed N, respectively. For this study, it was not possible to obtain material from *N. ampullaria* plants whose N was

100% leaf litter derived, since this species traps invertebrate prey in both open and forested habitats. Therefore, we used leaf litter itself as a substitute and effectively ignored the possibility of isotopic fractionation during N uptake from this source. The implications of this are dealt with in “Discussion.”

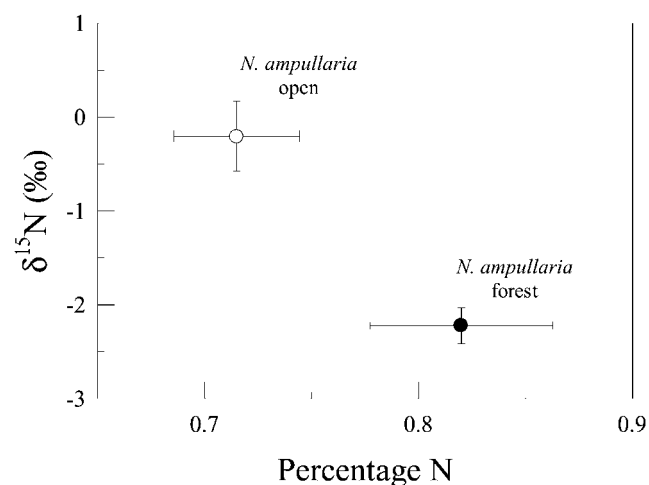
Statistical analyses were carried out using SigmaStat v. 2.0 (SPSS, Chicago). Data were analyzed for normality and homogeneity of variance before performing  $t$ -tests (Sokal and Rohlf 1981).

### Results

The  $\delta^{15}\text{N}$  values of *Nepenthes ampullaria* foliage under closed canopy forest sites were significantly more negative than for conspecifics growing in open scrub sites (mean  $\pm 1$  SE =  $-2.22\text{‰} \pm 0.19\text{‰}$  and  $-0.20\text{‰} \pm 0.37\text{‰}$ , respectively;  $t = 4.83$ ,  $P < 0.001$ ,  $df = 38$ ; fig. 2). Foliar N concentrations were significantly higher for plants growing within the forest sites than for those growing in the open sites with no access to litterfall ( $0.82\% \pm 0.04\%$  and  $0.71\% \pm 0.03\%$ , respectively;  $t = -2.03$ ,  $P < 0.05$ ,  $df = 38$ ; fig. 2).

### Discussion

*Nepenthes ampullaria* plants growing on the closed canopy forest sites, with consequent access to litterfall, showed significantly more negative  $\delta^{15}\text{N}$  values than did those growing at the open sites. Given the depleted  $\delta^{15}\text{N}$  signature of the leaf litter samples ( $-5.88\text{‰} \pm 0.45\text{‰}$ ,  $n = 10$ ), this result supports the hypothesis that under forest canopy, *N. ampullaria* sequesters N from leaf litter trapped in its pitchers. In addition, plants growing within the forest sites showed significantly higher foliar N concentrations than did those at the open sites with no access to litterfall. Moran and Moran (1998) demonstrated that *N. rafflesiana* plants that were denied prey capture for several months were nonetheless able to maintain foliar N concentra-



**Fig. 2** Comparison of foliar  $\delta^{15}\text{N}$  (‰) and N concentration (%) for *Nepenthes ampullaria* plants growing in open scrub areas (no litterfall present;  $n = 20$ ; open circle) and closed canopy heath forest stands (litterfall present;  $n = 20$ ; filled circle). Points represent means; bars represent 1 SE.

tions similar to those of control plants. In this study, the fact that *N. ampullaria* plants growing at the open sites were unable to maintain N concentrations comparable to those growing on the forest sites suggests an unusually high degree of nutrient stress over a prolonged period in the absence of litter input. We believe that this observation may account in part for the scarcity of *N. ampullaria* at open sites. Cresswell (1998) reported that in Bornean heath forest, >50% of the necromass in *N. ampullaria* pitchers was plant tissue, and using the mixing model, we estimated that *N. ampullaria* plants growing in the forest derived  $35.7\% \pm 0.1\%$  of their total foliar N from leaf litter.

Alternatively, the more negative  $\delta^{15}\text{N}$  values for *N. ampullaria* growing on the forest sites might be due to enhanced N uptake via the roots in this habitat type, relative to the open sites. This is highly unlikely, however, since it has been demonstrated that the pitchers are the primary means of N uptake in the *Nepenthes* species studied so far (Schulze et al. 1997; Moran and Moran 1998). When the pitchers are rendered inoperative by blocking the mouth, N uptake by the roots alone is insufficient to make up for the shortfall (Moran and Moran 1998). Uptake by the roots (rather than the pitchers) would not, therefore, produce the observed increase in foliar N concentrations in *N. ampullaria* plants growing in the forest sites. Another potential source of N is via  $\text{N}_2$ -fixing bacteria in the pitcher fluid, which occurs in some epiphytic bromeliads (Bermudes and Benzing 1991) and New World pitcher plants (Sarraceniaceae; Prankevicus and Cameron 1991). However, in the absence of a plausible reason why  $\text{N}_2$  fixation would occur preferentially under forest canopy, we believe that this possibility can also be discounted for the present.

Litterfall is a fundamental pathway in nutrient cycling within tropical forests (Vitousek 1984; Attiwill and Adams 1993), and N transfer to the forest floor via litterfall in Bornean heath forest is in the order of  $5\text{--}6 \text{ g m}^{-2} \text{ yr}^{-1}$ , primarily in abscised leaves (Proctor et al. 1983; Moran et al. 2000). More than 45% of the common tree species in Bornean heath forest are microphyllous (Brüning 1974), which increases the probability of unimpeded entry of abscised leaves into *N. ampullaria* pitchers. A common strategy of plants in heath forest and other oligotrophic forests is the deployment of a shallow fine root mat to trap litterfall nutrients before they are leached down the soil column (Stark and Jordan 1978; Davies and Becker 1996). Sitting above the soil surface, the pitchers of *N. ampullaria* are ideally positioned to intercept litter-held nutrients before they reach the fine roots of competing plant species. In this respect, the strategy of *N. ampullaria* is comparable to that of some epiphytic “tank” bromeliads of the New World tropics (Benzing 2000).

*Nepenthes ampullaria* pitchers possess an abnormally broad peristome (pitcher mouth) in relation to their size (Moran et al. 1999) and effectively form a funnel capable of collecting water (fig. 1A, 1C). Therefore, a small amount of additional N may be available to the pitchers via throughfall (i.e., water dripping from canopy foliage), which contains N leached from the canopy as well as N fixed by lightning during electrical storms (Whitmore 1984). However, N fluxes to the forest floor via throughfall are considerably less than in litterfall (Edwards 1982; Vitousek 1982; Attiwill and Adams 1993), so the contribution of precipitation-borne N to the total N budget of the plant is likely to be minimal.

Since the majority of the N in leaf litter is organically bound

(Attiwill and Adams 1993), how might *N. ampullaria* access it? The *Nepenthes* pitcher contains an aquatic environment (or “phytotelm”; Frank and Lounibos 1983), and litter decomposition rates in water are reduced as acidity increases, primarily because of inhibition of microbial activity (Kok and Van der Velde 1994). Clarke and Kitching (1993) reported a mean pH of  $3.72 \pm 0.09$  ( $n = 20$ ) for *N. ampullaria* pitcher fluid, a degree of acidity that might be expected to hinder decomposition. However, *Nepenthes* pitchers provide a habitat for a wide range of aquatic fauna; in Borneo, *N. ampullaria* pitchers support a complex food web containing up to 13 invertebrate species, with mosquito larvae predominant (Clarke and Kitching 1993). Research elsewhere has demonstrated that mosquito larvae play a key role in leaf litter decomposition within tree holes, microenvironments that are analogous to *Nepenthes* pitchers (Carpenter 1982; Fish and Carpenter 1982; Yanoviak 1999). Mosquito larvae excrete N as ammonium ions (Bradshaw and Creelman 1984), which are also produced by bacterial degradation of leaf material (Walker et al. 1991). Since ammonium transporters are present in the digestive glands of *Nepenthes* pitchers (Schulze et al. 1999), there exists a potential pathway for the transfer of N from leaf litter to *N. ampullaria* via the pitcher fauna.

In the mixing model, we used the mean  $\delta^{15}\text{N}$  value of leaf litter as representative of the “100% leaf litter” end member (eq. [2]) and ignored fractionation during transfer from leaf litter to pitcher. The  $\delta^{15}\text{N}$  undergoes enrichment at ca. 3‰ per trophic level (DeNiro and Epstein 1981; Minagawa and Wada 1984), so nitrogenous waste from mosquito larvae grazing on leaf litter with a value of  $-5.88\text{‰}$  would have a  $\delta^{15}\text{N}$  value in the order of  $-2.88\text{‰}$ . If we assume that this is then absorbed by the pitcher and substitute the value of  $-2.88\text{‰}$  for the “100% leaf litter” end member in equation (2), the model produces an estimate of  $76.9\% \pm 0.2\%$  N derived from leaf litter. Therefore, our original estimate, although subject to the errors previously outlined, may be overly conservative.

The genus *Nepenthes* shows a remarkable diversity of pitcher form and prey specialization. Trapping strategies range from those of relatively simple “generalist” species such as *Nepenthes bicalcarata* Hook. f. and *Nepenthes gracilis* Korth (Clarke 1998; Moran et al. 1999) to species that target anthophilous insects (*N. rafflesiana*; Moran 1996; Moran et al. 1999) to sophisticated specialists such as *Nepenthes albo-marginata* Lobb, which targets termites (Kato et al. 1993; Moran et al. 2001; Merbach et al. 2002). Our study indicates that the diversity of trapping strategies in *Nepenthes* may be even broader than was previously assumed. The evolution of a singular combination of morphological adaptations has enabled *N. ampullaria* to occupy a unique nutritional niche within the genus, that of a leaf litter “scavenger.”

### Acknowledgments

Samples were collected during a Universiti Brunei Darussalam Research Fellowship to J. Moran. We thank S. Robbins and D. Harris for sample processing. U. Ouanquez, A. Moran, O. Warwick-Hunt, and two anonymous reviewers provided comments on early drafts of the manuscript.

## Literature Cited

- Adam JH 1997 Prey spectra of Bornean *Nepenthes* species (Nepenthaceae) in relation to their habitat. *Pertanika J Trop Agric Sci* 20: 121–134.
- Attwill PM, MA Adams 1993 Tansley review no. 50: nutrient cycling in forests. *New Phytol* 124:561–582.
- Benzing DH 1987 The origin and rarity of botanical carnivory. *Trends Ecol Evol* 2:364–369.
- 2000 Bromeliaceae: profile of an adaptive radiation. Cambridge University Press, Cambridge.
- Bermudes D, DH Benzing 1991 Nitrogen fixation in association with Ecuadorean bromeliads. *J Trop Ecol* 7:531–536.
- Bradshaw WE, RA Creelman 1984 Mutualism between the carnivorous purple pitcher plant and its inhabitants. *Am Midl Nat* 112: 294–304.
- Brüning EF 1974 Ecological studies in the kerangas forests of Sarawak and Brunei. Borneo Literature Bureau, Kuching.
- Carpenter SR 1982 Comparisons of equations for decay of leaf litter in tree-hole ecosystems. *Oikos* 39:17–22.
- Clarke CM 1997 *Nepenthes* of Borneo. Natural History, Kota Kinabalu.
- 1998 Initial colonisation and prey capture in *Nepenthes bicalcarata* (Nepenthaceae) pitchers in Brunei. *Sandakaniana* 12:27–36.
- 2001 *Nepenthes* of Sumatra and Peninsular Malaysia. Natural History, Kota Kinabalu.
- Clarke CM, RL Kitching 1993 The metazoan food webs from six Bornean *Nepenthes* species. *Ecol Entomol* 18:7–16.
- Cresswell JE 1998 Morphological correlates of necromass accumulation in the traps of an Eastern tropical pitcher plant, *Nepenthes ampullaria* Jack, and observations on the pitcher infauna and its reconstitution following experimental removal. *Oecologia* 113:383–390.
- Davies SJ, P Becker 1996 Floristic composition and stand structure of mixed-dipterocarp and heath forests in Brunei Darussalam. *J Trop For Sci* 8:542–569.
- DeNiro MJ, S Epstein 1981 Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351.
- Edwards PJ 1982 Studies of mineral cycling in a montane rain forest in New Guinea. V. Rates of cycling in throughfall and litter fall. *J Ecol* 70:807–827.
- Fish D, SR Carpenter 1982 Leaf litter and larval mosquito dynamics in tree-hole ecosystems. *Ecology* 63:283–288.
- Frank JH, LP Lounibos 1983 Phytotelmata: terrestrial plants as hosts for aquatic insect communities. Plexus, Medford, N.J.
- Givnish TJ, EL Burkhardt, R Happel, J Weintraub 1984 Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *Am Nat* 124:479–497.
- Juniper BE, JK Burras 1962 How pitcher plants trap insects. *New Sci* 269:75–77.
- Juniper BE, RJ Robins, DM Joel 1989 The carnivorous plants. Academic Press, London.
- Kato M, M Hotta, R Tamin, T Itino 1993 Inter- and intra-specific variation in prey assemblages and inhabitant communities in *Nepenthes* pitchers in Sumatra. *Trop Zool* 6:11–25.
- Kok CJ, G Van der Velde 1994 Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water. *Freshwater Biol* 31:65–75.
- Lloyd FE 1942 The carnivorous plants. Plenum, Medford.
- Lüttge U 1983 Ecophysiology of carnivorous plants. Pages 489–517 in OL Lange, PS Nobel, CB Osmond, H Ziegler, eds. Encyclopedia of plant physiology. Vol 12C. Springer, Berlin.
- Macfarlane JM 1893 Observations on pitched insectivorous plants. II. *Ann Bot* 7:403–458.
- Merbach MA, DJ Merbach, U Maschwitz, WE Booth, B Fiala, G Zizka 2002 Mass march of termites into the deadly trap. *Nature* 415:36–37.
- Minagawa M, E Wada 1984 Stepwise enrichment of  $^{15}\text{N}$  along food chains: further evidence and the relation between  $\delta^{15}\text{N}$  and animal age. *Geochim Cosmochim Acta* 48:1135–1140.
- Moran JA 1996 Pitcher dimorphism, prey composition and the mechanisms of prey attraction in the pitcher plant *Nepenthes rafflesiana* in Borneo. *J Ecol* 84:515–525.
- Moran JA, MG Barker, AJ Moran, P Becker, SM Ross 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.
- Moran JA, WE Booth, JK Charles 1999 Aspects of pitcher morphology and spectral characteristics of six Bornean *Nepenthes* pitcher plant species: implications for prey capture. *Ann Bot* 83: 521–528.
- Moran JA, MA Merbach, NJ Livingston, CM Clarke, WE Booth 2001 Termite prey specialization in the pitcher plant *Nepenthes albomarginata*: evidence from stable isotope analysis. *Ann Bot* 88:307–311.
- Moran JA, AJ Moran 1998 Foliar reflectance and vector analysis reveal nutrient stress in prey-deprived pitcher plants (*Nepenthes rafflesiana*). *Int J Plant Sci* 159:996–1001.
- Pant DD, S Bhatnagar 1977 Morphological studies in *Nepenthes* (Nepenthaceae). *Phytomorphology* 27:13–34.
- Phillips DL, JW Gregg 2001 Uncertainty in source partitioning using stable isotopes. *Oecologia* 127:171–179.
- Prankevicus AB, DM Cameron 1991 Bacterial dinitrogen fixation in the leaf of the northern pitcher plant (*Sarracenia purpurea*). *Can J Bot* 69:2296–2298.
- Proctor J, JM Anderson, SCL Fogden, HW Vallack 1983 Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litterfall, litter standing crop, and preliminary observations on herbivory. *J Ecol* 71:261–283.
- Schulze W, WB Frommer, JM Ward 1999 Transporters for ammonium, amino acids and peptides are expressed in pitchers of the carnivorous plant *Nepenthes*. *Plant J* 17:637–646.
- Schulze W, E-D Schulze, JS Pate, AN Gillison 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, DH Kohl 1989 Estimates of  $\text{N}_2$  fixation in ecosystems: the need for and basis of the  $^{15}\text{N}$  natural abundance method. Pages 342–374 in PW Rundel, JR Ehleringer, KA Nagy, eds. Stable isotopes in ecological research. Springer, New York.
- Sokal RR, FJ Rohlf 1981 Biometry. WH Freeman, New York.
- Stark NM, CF Jordan 1978 Nutrient retention by the root mat of an Amazonian rain forest. *Ecology* 59:434–437.
- Vitousek PM 1982 Nutrient cycling and nutrient use efficiency. *Am Nat* 119:553–572.
- 1984 Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–298.
- Walker ED, DL Lawson, RW Merritt, WT Morgan, MJ Klug 1991 Nutrient dynamics, bacterial populations, and mosquito productivity in tree hole ecosystems and microcosms. *Ecology* 72: 1529–1546.
- Whitmore TC 1984 Tropical rain forests of the Far East. 2d ed. Oxford University Press, Oxford.
- Yanoviak SP 1999 Effects of leaf litter species on macroinvertebrate community properties and mosquito yield in Neotropical tree hole microcosms. *Oecologia* 120:147–155.