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# FOLIAR REFLECTANCE AND VECTOR ANALYSIS REVEAL NUTRIENT STRESS IN PREY-DEPRIVED PITCHER PLANTS (*NEPENTHES RAFFLESIANA*)

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Pitcher plants of the genus *Nepenthes* trap invertebrate prey in pitchers formed from modified leaf tips. This study investigates the benefits of carnivory to *Nepenthes rafflesiana*, a common Bornean lowland species. Plants were denied prey capture in their natural habitat for 18 wk and were compared with a control group that was allowed to trap, digest, and assimilate prey as usual over the same period. Resource limitation was demonstrated in prey-deprived plants, which produced significantly fewer and smaller pitchers than did control plants. Analysis of foliar spectral reflectance showed increased reflectance within part (608–738 nm) of the photosynthetically active wave band in the prey-deprived plants, signifying a reduction in chlorophyll content. Decreased reflectance at 550 nm in the prey-deprived plants also indicated increased production of anthocyanins, denoting possible nitrogen or phosphorus limitation. Although no difference was found in tissue concentrations of nitrogen or phosphorus between treatments, vector analysis identified a reduction in content of both elements as a result of reduced biomass production in prey-deprived plants. Our findings demonstrate the key role carnivory plays in the nutrition of this species in its natural habitat.

## Introduction

In common with other carnivorous plants, pitcher plants of the genus *Nepenthes* (family Nepenthaceae) are found predominantly in sunny and wet or waterlogged habitats that are believed to be nutrient limited (Lüttge 1983; Benzing 1987). *Nepenthes* pitchers have evolved to trap, digest, and absorb the breakdown products of invertebrates and in some species have developed floral traits to attract anthophilous (flower-visiting) insects. For example, those of *Nepenthes rafflesiana* Jack, a common Bornean species, possess both a flower-like fragrance and ultraviolet patterns that have been shown to contribute to prey attraction (Moran 1996). The production of elaborate and complex trapping mechanisms indicates strong evolutionary pressure to augment the more usual mode of nutrient uptake via the roots with nutrients from animal prey.

The family Nepenthaceae comprises 82 species (Jebb and Cheek 1997), making it the largest pitcher plant family, and one of the larger taxa among the carnivorous plants (Juniper et al. 1989; Clarke 1997). However, while the benefits of prey capture are documented for other carnivorous plant families (Sarraceniaceae [Christensen 1976; Chapin and Pastor 1995], Lentibulariaceae [Aldenius et al. 1983], Droseraceae [Chandler and Anderson 1976; Wilson 1985; Thum 1988; Schulze and Schulze 1990; Gibson 1991; Karlsson and Pate 1992]), to date there have been no published quantitative studies on *Nepenthes* species to investigate this aspect of their biology. We explored this question by assessing the consequences of zero prey capture to *N. rafflesiana* in its natural habitat via analysis of pitcher production, tissue nutrient status, and foliar reflectance. *Nepenthes rafflesiana* attracts and catches a wide spectrum of invertebrate prey in its pitchers, although the dominant prey group are Formicidae (Moran [1996] provides an account of the prey spectrum of this species in Brunei). The null hypotheses were that denial of prey would have no significant effect on growth performance, tissue nutrient status (nitrogen and phosphorus), or foliar chlorophyll content in plants that were denied prey.

## Material and Methods

The investigation was carried out in a small (<300 $m^2$) area of degraded coastal heath forest in Brunei, northwest Borneo (4°44′N, 114°36′E), overlying an albic arenosol (heavily leached, white sand) on a Pleistocene marine terrace (Brünig 1974). The vegetation was low scrub dominated by *Ploiarium alternifolium* Melchior (Theaceae) and *Dillenia suffruticosa* Griff. Martelli (Dilleniaceae). In March 1995, 30 *Nepenthes rafflesiana* plants were selected for study. Small plants (<0.5 m height) with one to three live pitchers were chosen to minimize the possibility of nutrient reserves reducing the effect of prey deprivation on the treated individuals. Since all plants used in the study were necessarily small and prereproductive, sex was impossible to determine (Dellaporta and Calderа-Urrea 1993). The following two treatments were allocated randomly. (1) The live pitchers of 15 plants were emptied of their contents by rinsing with deionized water into a container that was emptied outside of the study site. The pitchers were then packed with a wad of cotton wool moistened with deionized water to provide a barrier to prey entry without damaging the pitcher in any observable way. Before insertion, the cotton

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wool was soaked and rinsed three times in deionized water over a 48-h period to remove possible contaminating nutrient elements. The plants were examined at 10–14-d intervals throughout the 18-wk course of the study, and any newly opened pitchers were treated in the same way. (2) The remaining 15 plants served as controls. The pitchers were not emptied and were allowed to catch prey over the period of the experiment. At the end of the study, all plants were harvested. The number and length (cm) of all live pitchers were recorded for each plant at the beginning and end of the study. For plants with no live pitchers at the end of the study, mean pitcher length was recorded as zero. Because of mortality losses, only 13 control and 14 experimental plants were harvested. A further two experimental plants were removed from the study after they were found to be linked by runners to larger plants.

All roots and live leaves (lamina and tendril only) were removed from each plant and washed briefly in deionized water, dried at 60°C for 48 h, and ground to pass a 40-mesh screen. Pitchers were not assayed as it would have been impossible to exclude the possibility of nutrient contamination from prey remains in those of the control plants. A Kjeldahl digestion was carried out on a random subsample of the leaf and root material from each plant, using a Lachat model BD 46 block digestor (Lachat Instruments, Milwaukee) with concentrated sulfuric acid and a potassium sulfate/copper sulfate catalyst. The resulting solutions were analyzed using a Lachat QuickChem Flow Injection Analyzer (Lachat Instruments, Milwaukee), employing the indophenol-blue reaction for total nitrogen and the acid molybdate reaction for total phosphorus (Allen 1989). Precision was assessed by calculating coefficients of variation (CVs) for results from six replicates of the same sample (Sokal and Rohlf 1981). The CVs for nitrogen and phosphorus concentration were 3% and 7%, respectively. Accuracy was determined by comparison with external reference materials (Standard Reference Material #1515 [apple leaves], National Institute of Standards and Technology, U.S.A., for nitrogen; external material from Department of Chemistry, Universiti Brunei Darussalam, for phosphorus). Observed values deviated from certified values by the following amounts: nitrogen +4%, phosphorus −10%.

From the results of the chemical analyses and morphological measurements, a vector diagram was constructed (Timmer 1991) to represent graphically the effects of prey deprivation on foliar nutrient concentration (unit mass of nutrient per unit mass of tissue), dry matter production, and nutrient content (nutrient concentration × mass of tissue). Mean control values for unit dry weight, nutrient concentration, and nutrient content were normalized to represent 100%, and the mean prey-deprived values were calculated and plotted in relation to these (Haase and Rose 1995). Since there were no direct measurements of biomass production made, an estimate was derived by multiplying mean pitcher number by mean pitcher length to give a productivity index. This was deemed valid, as it is *relative* changes that are important in vector analysis, and a significant allometric relationship exists between pitcher length and dry weight in this species ($R = 0.76$, $P < 0.001$, $n = 34$; J. Moran, unpublished data).

Analysis of foliar reflectance has proven effective in identifying stress from a number of agents (e.g., ozone, drought, pathogens) for several plant species (Carter 1993, 1994; Carter and Miller 1994) and relies on the fact that absorption of radiation by leaves between ca. 400 and 700 nm results primarily from chlorophyll (Knipling 1970). According to the Beer-Lambert Law, the fraction of incident radiation absorbed is proportional to the number of absorbing molecules in its path (Salisbury and Ross 1992), and thus a reduction in foliar chlorophyll content will result in increased reflectance in this wave band (Carter et al. 1992; Mariotti et al. 1996). As chlorophyll content decreases, absorptance within the 400–700-nm wave band will decrease and reflectance will increase first at those wavelengths in which absorptance by the pigments is relatively weak. Only after further reduction in pigment concentration will decreased absorptance be noticed at wavelengths in which the pigments are strongly absorptive (Carter and Miller 1994). Thus, a ratio of reflectance at a stress-sensitive wavelength to one at an insensitive wavelength can be used to compare stress levels between groups via foliar chlorophyll content. Reflectance analysis was carried out as follows: before processing for nutrient assays, the youngest mature leaf possessing a fully developed pitcher was removed from each plant and a scan of reflected energy ($W\ m^{-2}$) was carried out on the center of the adaxial (upper) side of the lamina, using a LI 1800 Spectroradiometer with an 1800-12S Integrating Sphere (Li-Cor, Lincoln, Nebr.) under illumination by a halogen lamp. The scan was made at 2-nm resolution from 400 nm (violet) to 1100 nm (infrared). Leaves were selected to obtain a sample population of approximately the same stage of development, as reflectance characteristics change with leaf age (Gausman and Quisenberry 1990). Percentage reflectance at each wavelength was then determined by dividing the measured reflected radiation value from the leaf by that from a standard reference material (barium sulfate, Li-Cor, Lincoln, Nebr.), the reflectance of which was assumed to be 100%, and multiplying by 100. Sensitivity analysis (*sensu* Carter 1993, 1994) was then conducted to determine which wavelengths were most responsive to the effects of prey deprivation. Sensitivity was calculated in two stages. First, the mean percentage reflectance values of the control plants were subtracted from those of the prey-deprived plants at each wavelength (fig. 2*a*) to give reflectance difference (fig. 2*b*). Sensitivity at each wavelength was then calculated by dividing the reflectance difference values in figure 2*b* by the reflectance values of the control plants at each wavelength (fig. 2*c*). On the basis of the results of the sensitivity analysis, reflectance ratios were determined and compared between experimental and control plants.

All analyses were carried out using the SigmaStat version 2.0 statistical package (Jandel Scientific, San Rafael, Calif.). For *t*-tests, data were first analyzed for normality and homogeneity of variance. Nonnormal data were square-root-transformed before running the test, and in cases where transformation was ineffective, the nonparametric Mann-Whitney *U*-test was employed (Sokal and Rohlf 1981).

## Results

By the end of the 18-wk study period, prey-deprived plants produced significantly smaller pitchers (ca. 45%) and in smaller numbers (ca. 46%), compared with the control group (table 1). There were no significant differences in root or leaf

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**Table 1**

**Summary of Response Categories between *Nepenthes rafflesiana* Plants without and with Prey Input over an 18-wk Period**

| Response | Without prey | With prey | df | *P* |
|---|---|---|---|---|
| Total pitcher number per plant: | | | | |
| Initial | 1.4 (0.2) | 1.3 (0.1) | 23 | ns[a] |
| Final | 0.7 (0.2) | 1.3 (0.2) | 23 | 0.036 |
| Mean pitcher length per plant (mm): | | | | |
| Initial | 7.9 (0.3) | 8.6 (0.6) | 23 | ns |
| Final | 4.5 (1.1) | 8.3 (0.6) | 23 | 0.005 |
| Nitrogen wt/wt (%): | | | | |
| Leaf | 0.52 (0.04) | 0.57 (0.04) | 23 | ns |
| Root | 0.18 (0.02) | 0.17 (0.01) | 22 | ns |
| Phosphorus wt/wt (%): | | | | |
| Leaf | 0.077 (0.007) | 0.085 (0.008) | 23 | ns |
| Root | 0.013 (0.001) | 0.015 (0.003) | 22 | ns[b] |
| Foliar reflectance ratios (nm): | | | | |
| λ 692 : 420 | 3.25 (0.16) | 2.76 (0.10) | 23 | 0.019 |
| λ 692 : 760 | 0.25 (0.01) | 0.21 (0.00) | 23 | 0.015 |
| λ 636 : 420 | 2.84 (0.12) | 2.46 (0.09) | 23 | 0.018 |
| λ 636 : 760 | 0.22 (0.01) | 0.19 (0.00) | 23 | 0.014 |

Note. Values denote mean (±SE in parentheses). Unless otherwise noted, *P* was determined using a *t*-test. ns = not significant (i.e., $P > 0.05$).

[a] Mann-Whitney *U*-test used.

[b] Data were square-root-transformed.

tissue concentrations of nitrogen or phosphorus between groups (table 1), although foliar content of both elements in prey-deprived plants decreased relative to controls (by 67% and 78%, respectively, for nitrogen and phosphorus; fig. 1). Prey-deprived plants showed significantly higher foliar reflectance than the controls in the wave band 608–738 nm ($P < 0.05$, *t*-test, denoted by the shaded region in fig. 2*b*, *c*), and a tendency (not statistically significant) toward reduced reflectance at 550 nm (fig. 2*a*, *b*). Significant sensitivity maxima occurred at 636 nm and 692 nm (fig. 2*c*). Foliar reflectance ratios were significantly higher in prey-deprived plants for 692 : 420 nm, 692 : 760 nm, 636 : 420 nm and 636 : 760 nm (table 1), indicating a reduction in foliar chlorophyll content (Carter et al. 1992; Mariotti et al. 1996).

## Discussion

Initially, the lack of significant differences in tissue concentrations of nitrogen and phosphorus between the experimental and control groups appears at odds with the other findings of this study, and with those of studies on other carnivorous plant species. Increased foliar concentrations of these elements as a result of digesting insect prey have been reported for *Sarracenia* spp. (Christensen 1976; Chapin and Pastor 1995), *Pinguicula vulgaris* (Aldenius et al. 1983), and *Drosera* sp. (Chandler and Anderson 1976). However, analysis of nutrient concentration (the amount of the element in a unit amount of tissue) cannot always be relied on to identify cases of nutrient deficiency, especially with regard to nitrogen (Comerford and Fisher 1984). This is primarily because of the fact that under conditions of resource limitation, plants are able to maintain critical foliar nutrient concentrations by a reduction in growth rate (Farnum et al. 1983). Because there was a decrease in

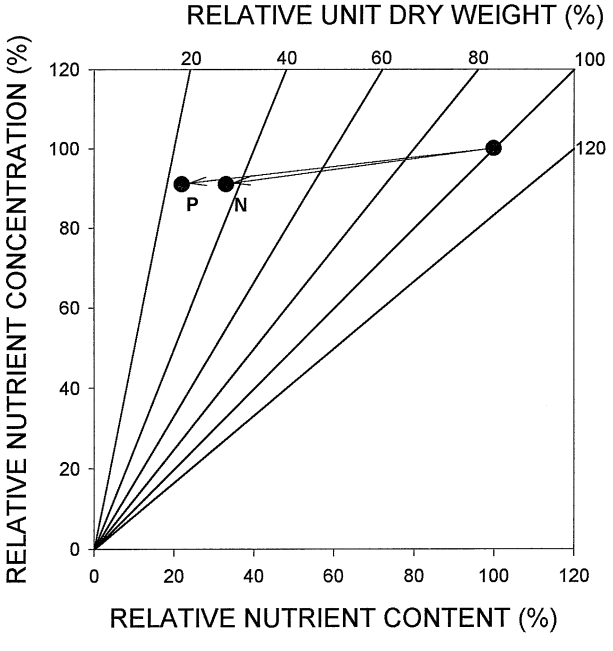


**Fig. 1** Vector diagram of mean foliar nutrient concentration (unit mass of nutrient per unit dry weight of tissue), nutrient content (nutrient concentration × dry weight of tissue), and dry weight for prey-deprived plants, relative to the mean values for controls (point at right, no label), which are normalized to 100% for all three axes. $n = 12$, 13 for prey-deprived and control groups, respectively. *N* = nitrogen, *P* = phosphorus. Arrows indicate direction of change relative to the control group; length of arrow is proportional to the magnitude of change.

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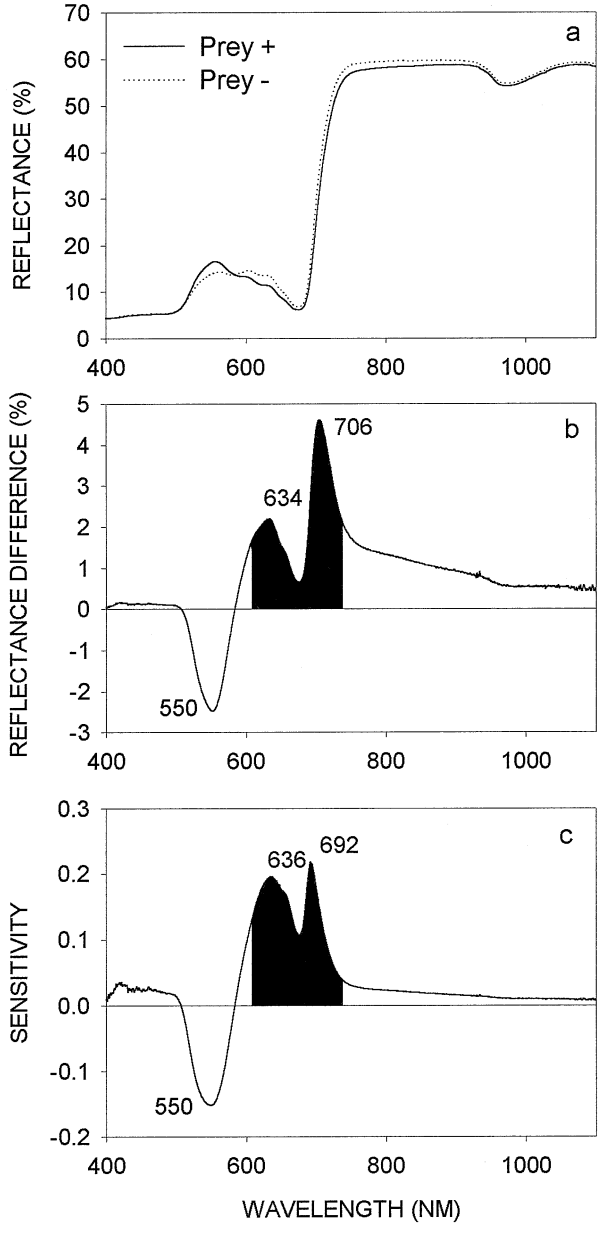


**Fig. 2** Reflectance response of adaxial surface of leaves from prey-deprived plants ($n = 12$) compared with controls ($n = 13$). Methodology is after Carter (1993, 1994). *a*, Percentage reflectance compared to a barium sulfate reference surface (assumed to be 100%). The solid and dotted lines denote mean values for control and prey-deprived plants, respectively. *b*, Percentage reflectance difference, produced by subtracting the mean values for control plants from those of the prey-deprived plants. *c*, Sensitivity (no units; %/%), produced by dividing percentage reflectance difference (*b*) by percentage reflectance values for control plants (solid line, *a*). The shaded areas in *b* and *c* indicate the regions for which there was a significant difference in percentage reflectance between experimental and control plants ($P < 0.05$, *t*-test).

biomass production in terms of pitcher number and size, the nutrient content (i.e., concentration × biomass) was lower in the prey-deprived plants. Vector analysis provides a graphical representation of this effect (Timmer 1991; Haase and Rose 1995). Since biomass estimates were calculated by indirect means (based on an allometric relationship between pitcher length and dry weight), it must be stressed that the vector analysis approach as used here is qualitative rather than quantitative, and therefore useful in identifying general trends only. The direction of the vector line denotes the change relative to the control group, its length denoting the magnitude of the change. The content of both nitrogen and phosphorus is reduced in prey-deprived plants relative to the controls, and the effect of prey deprivation appears to be greater for phosphorus than for nitrogen (fig. 1). There can be little doubt that the prey-deprived plants were nutrient-stressed, resulting in a reduction in both size and number of pitchers. The three other possible stress candidates, light limitation, water stress, and heat stress, can be ruled out since both experimental and control groups were randomly dispersed within a small area (<300 $m^2$), and were thus subject to an equivalent range of edaphic and radiation regimes. It is unlikely that prey-deprived plants were heat-stressed relative to the controls since the cotton wool in the blocked pitchers was kept moist over the course of the experiment. Therefore, the results support the hypothesis that in the natural habitat, biomass production in *Nepenthes rafflesiana* depends largely on nutrient input from prey. Circumstantial support for this conclusion comes from a survey of male and female *N. rafflesiana* plants in the same area, which showed that females produced significantly more pitchers before flowering for the first time than did males (mean ± SE = 23.1 ± 1.3 for males, 29.5 ± 1.8 for females, $P = 0.007$ using *t*-test, $n = 17$ for each sex; J. Moran, unpublished data). Since female plants have a higher nutritional requirement than males for reproduction (Stephenson and Bertin 1983), this result would be expected if prey capture by the pitchers represented a significant source of nutrients.

The foliar reflectance technique identified nutrient stress in the prey-deprived plants, proving a superior method to that of tissue nutrient concentration analysis alone for this species. Sensitivity analysis showed a maximum at 692 nm, which corresponds closely to the fact that chlorophyll is weakly absorptive in that region (Chappelle et al. 1992) and is remarkably close to the sensitivity maximum of 695 nm shown by Carter (1994) for multiple species/multiple stress comparisons. A second sensitivity peak occurred at 636 nm, which corresponds to another region of low absorptance. There is strong absorption by chlorophyll and associated pigments between ca. 415 nm and 420 nm (Chappelle et al. 1992), and so absorptance within this band should be less sensitive to stress-related reductions in foliar chlorophyll content. This was found to be the case in the current study and corresponds with the findings of Carter (1994) and Carter and Miller (1994) for absorptance at 420 nm. Wavelengths outside of the absorption spectra of chlorophylls can also be used as insensitive reference points for reflectance ratios, and following Carter (1993, 1994), we used 760 nm, a wavelength that was also shown to be insensitive in the current study. The concept of a reduction in chlorophyll content and consequent reduction in photosynthetic potential concurs with the morphological find-

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ings of the study, i.e., a reduced capacity for biomass production in plants denied nutrient uptake via carnivory.

Although not significant at $P = 0.05$, there appears to be a tendency toward decreased reflectance at 550 nm (green) in the leaves of prey-deprived plants relative to the controls. Since chlorophyll shows a reflectance maximum at this wavelength (Chappelle et al. 1992; Buschmann and Nagel 1993), the effect may result entirely from a reduction of the pigment content. Another possibility is that the effect is the result of reduced nitrogen content in the experimental plants. Tsay et al. (1982) demonstrated an inverse relationship between foliar nitrogen content and reflectance at 540 nm in loblolly pine (*Pinus taeda* L.). We believe, however, that at least part of the effect results from increased foliar concentrations of anthocyanins, red or blue pigments with absorption maxima in the wave band 500–550 nm (Jurd 1962). Red staining resulting from these compounds is commonly observed on the leaves of *N. rafflesiana* plants in their natural habitat (J. Moran, personal observation). Two factors have been shown to promote anthocyanin production in plants. The first is light intensity (Sato et al. 1996), which is unlikely to have been important in the current study, given that both experimental and control groups were presumed to experience an equivalent range of light climates. The second is nutrient limitation, specifically, nitrogen or phosphorus (Bongue-Bartelsman and Phillips 1995; Hodges and Nozzolillo 1996; Sato et al. 1996), and it is possible that the trend toward increased production of foliar anthocyanins results from deficiencies in one or both of these elements, a hypothesis corroborated by the results of the vector analysis.

To conclude, the results of the study demonstrate the importance of prey-mediated nutrition to growth of *N. rafflesiana* in its natural environment. It is worth bearing in mind that the conclusion reached for this species may not necessarily hold to the same degree across the entire genus, given the apparent diversity of feeding strategies employed among individual species (Kato et al. 1993; Moran 1996; Clarke 1997).

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