Nutrient Limitation and Stoichiometry of Carnivorous Plants

A. M. Ellison

Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366, USA

Received: September 13, 2005; Accepted: January 19, 2006

Abstract: **The cost-benefit model for the evolution of carnivorous plants posits a trade-off between photosynthetic costs associated with carnivorous structures and photosynthetic benefits accrued through additional nutrient acquisition. The model predicts that carnivory is expected to evolve if its marginal benefits exceed its marginal costs. Further, the model predicts that when nutrients are scarce but neither light nor water is limiting, carnivorous plants should have an energetic advantage in competition with non-carnivorous plants. Since the publication of the cost-benefit model over 20 years ago, marginal photosynthetic costs of carnivory have been demonstrated but marginal photosynthetic benefits have not. A review of published data and results of ongoing research show that nitrogen, phosphorus, and potassium often (co-)limit growth of carnivorous plants and that photosynthetic nutrient use efficiency is 20 – 50% of that of non-carnivorous plants. Assessments of stoichiometric relationships among limiting nutrients, scaling of leaf mass with photosynthesis and nutrient content, and photosynthetic nutrient use efficiency all suggest that carnivorous plants are at an energetic disadvantage relative to non-carnivorous plants in similar habitats. Overall, current data support some of the predictions of the cost-benefit model, fail to support others, and still others remain untested and merit future research. Rather than being an optimal solution to an adaptive problem, botanical carnivory may represent a set of limited responses constrained by both phylogenetic history and environmental stress.**

Key words: **Carnivorous plants, stoichiometry, potassium, photosynthesis, phosphorus, nitrogen, cost-benefit model.**

Introduction

Carnivory has evolved repeatedly among angiosperms, and ± 600 species of carnivorous plants grow throughout the world in bogs, fens, and outwash plains, atop inselbergs, tepuis, and other mountains, in valleys and on stream banks, and in lakes and ponds – usually wherever light and moisture are abundant and soil macronutrients, especially nitrogen, phosphorus, and potassium, are severely limiting (Givnish et al., 1984, 1989; Benzing, 1987). Charles Darwin (1875) provided the first detailed experimental evidence for carnivory in several genera, and his son Francis was the first to show unequivocally that the growth of a carnivorous plant, the sundew *Drosera rotundifolia* L., was enhanced by nutrients acquired through its carnivorous organs (Darwin, 1878). Through the first 75 years of the 20th century, botanists focused on finding and describing new carnivorous plants, illustrating their unique organs, unravelling their physiological mechanisms for nutrient uptake from captured prey, and determining their evolutionary history (Lloyd, 1942; Lüttge, 1983; Juniper et al., 1989). By the early 1980s, it was clear that carnivory was a convergent trait among a diversity of unrelated plant families (reviews in Albert et al., 1992; Ellison and Gotelli, 2001). This conclusion, together with more detailed habitat data, suggested that carnivory is an adaptive trait in environments where critical nutrients are scarce or unavailable and light is not limiting, a hypothesis that was crystallized in a cost-benefit model (Givnish et al., 1984).

The cost-benefit model has two components. The *marginal* benefit is hypothesized to be an increased rate of photosynthesis per unit of photosynthate invested in (relatively inefficient or costly) carnivorous structures. The *marginal cost* is the unit photosynthate required for the production of additional carnivorous structures. In focusing on enhanced photosynthesis as the primary benefit of carnivory, the cost-benefit model makes three predictions. First, “plants with mutations for such investments (i.e., carnivorous organs) should have an energetic advantage in competing with other (i.e., non-carnivorous) plants” (Givnish et al., 1984: 490). Second, the primary energetic benefit of carnivory would be either an increased rate of photosynthesis per unit leaf mass or an increase in the total leaf mass supported (Givnish et al., 1984: 490). Third, the absolute benefit of carnivory should plateau and the marginal benefit of carnivory should decline with increasing investment in carnivory once factors other than nutrients begin to limit photosynthetic rates (Givnish et al., 1984: 491). Following the publication of the cost-benefit model, botanical research on carnivorous plants shifted to measuring the costs and benefits of carnivory and to attempting to test its predictions (Adamec, 1997 a). Here, I review and synthesize published literature on photosynthesis and nutrient limitation in carnivorous plants, and compare these data with global compilations on relationships among photosynthesis and nutrients in non-carnivorous

Plant Biol. 8 (2006): 740 – 747

DOI 10.1055/s-2006-923956 · Published online May 11, 2006
ISSN 1435-8603

Table 1 Summary of studies (1878 – 2005) of growth of carnivorous plants in response to addition of prey alone, inorganic nutrients (IN) alone (normally to soil or water), or prey + IN. A positive response relative to controls is indicated by a "+", no response by a "0", a negative response by a "–", and no data by "NA". A "0" in the prey + IN column indicates no interaction between these two variables

Species	Growth response to			References[a]
	prey alone	IN alone	prey + IN	
Aldrovanda vesiculosa L.	+	+	+	12
Dionaea muscipula Ellis	NA	–	NA	20
Drosera aliciae R. Hamet	NA	+	NA	1
Drosera binata Labill. var. *multifida* Mazrimas	0	+	NA	23
Drosera capensis L.	0	+	NA	23
Drosera capillaris Poir.	NA	+	NA	1
Drosera closterostigma N. Marchant and Lowrie	+	0	0	14
Drosera filiformis Raf.	+	NA	NA	17
Drosera glanduligera Lehm.	+	0	0	14
Drosera intermedia Hayne	+/0	NA	NA	9, 25, 27
Drosera rotundifolia L.	+ (0)	±	±	6, 15, 17, 21, 22, 25
Drosera spathulata Labill.	NA	+	NA	1
Nepenthes rafflesiana Jack	+	NA	NA	18
Pinguicula alpina L.	+	+	0	15, 24
Pinguicula planifolia Chapman	+	NA	NA	9
Pinguicula vallisneriifolia Webb	+	NA	NA	28, 29
Pinguicula villosa L.	+	0	0	15, 24
Pinguicula vulgaris L.	+	+/0/–	+/0/–	2, 13, 15, 24
Sarracenia alata Wood	+	+	NA	3
Sarracenia flava L.	+	NA	NA	9
Sarracenia leucophylla Raf.	+	NA	NA	9
Sarracenia purpurea L.	0	+/0/–	0	4, 7, 10
Utricularia gibba L.	+	+	0	22
Utricularia macrorhiza Le Conte	+/0	+	NA	8, 16, 19
Utricularia spp.	NA	–	NA	5
Utricularia uliginosa Vahl	0	0	+	11

[a] References: 1. Adamec (2002); 2. Aldenius et al. (1983); 3. Brewer (2003); 4. Chapin and Pastor (1995); 5. Chiang et al. (2000); 6. F. Darwin (1878); 7. Ellison and Gotelli (2002); 8. Englund and Harms (2003); 9. Gibson (1983); 10. Gotelli and Ellison (2002); 11. Jobson et al. (2000); 12. Kaminski (1987b); 13. Karlsson and Carlsson (1984); 14. Karlsson and Pate (1992); 15. Karlsson et al. (1991); 16. Knight and Frost (1991); 17. Krafft and Handel (1991); 18. Moran and Moran (1998); 19. Otto (1999); 20. Roberts and Oosting (1958); 21. Schulze and Schulze (1990); 22. Sorenson and Jackson (1968); 22. Stewart and Nilsen (1992); 23. Stewart and Nilsen (1993); 24. Thorén et al. (1996); 25. Thum (1988); 26. Wakefield et al. (2005); 27. Wilson (1985); 28. Zamora et al. (1997); 29. Zamora et al. (1998).

plants (Wright et al., 2004, 2005). I use this synthesis to test predictions of the cost-benefit model and assess the support for it in light of over two decades of focused research.

Benefits and Costs of Carnivory

More than two dozen studies have tested whether growth of carnivorous plants is, in fact, enhanced by carnivory (Table **1**). A meta-analysis of these data suggests there is a significant positive effect of prey addition on plant growth ($p = 0.02$, binomial test of 29 studies), but no significant effect of nutrient additions ($p = 0.15$) or nutrient × prey interaction ($p = 0.81$). In other words, additional nutrients gained from carnivory are less valuable when plants are growing in relatively nutrient-rich soils (Dixon et al., 1980; Aldenius et al., 1983; Karlsson et al., 1991; Méndez and Karlsson, 2005) or eutrophied lakes (Knight and Frost, 1991; Guisande et al., 2000; Jobson et al., 2000), where plants are subject to atmospheric deposition of nitrogen (Ellison and Gotelli, 2002), or when they are competing for light with non-carnivorous plants (Brewer, 2003). Overall, these studies provide some support for the predictions that there is a marginal benefit to carnivory, and that the absolute benefit plateaus with increasing level of nutrient availability. However, the cost-benefit model expresses benefits in terms of photosynthetic rates, not in terms of growth, so the support provided for the cost-benefit model by these studies is only indirect.

There have been fewer measurements of the costs of carnivory. Three studies directly measured the carbon costs of mucilage used in sticky traps by *Drosera* (Pate, 1986 [In his 1986 review, Pate cites his own unpublished data that 3 – 6% of photosynthate is used for mucilage production by *Drosera*. Although this figure (and this paper) are subsequently cited in the literature, these data were never published.]; Thorén et al., 2003) or *Pinguicula* (Zamora et al., 1998). Two studies examined changes in photosynthetic efficiency of traps relative to conventional foliage (Knight, 1992; Ellison and Gotelli, 2002) following experimental changes in nutrient availability. Ellison and Farnsworth (2005) showed that *Darlingtonia californica* Torrey had significantly lower photosynthetic rates for its tissue nitrogen and phosphorus content than was predicted by

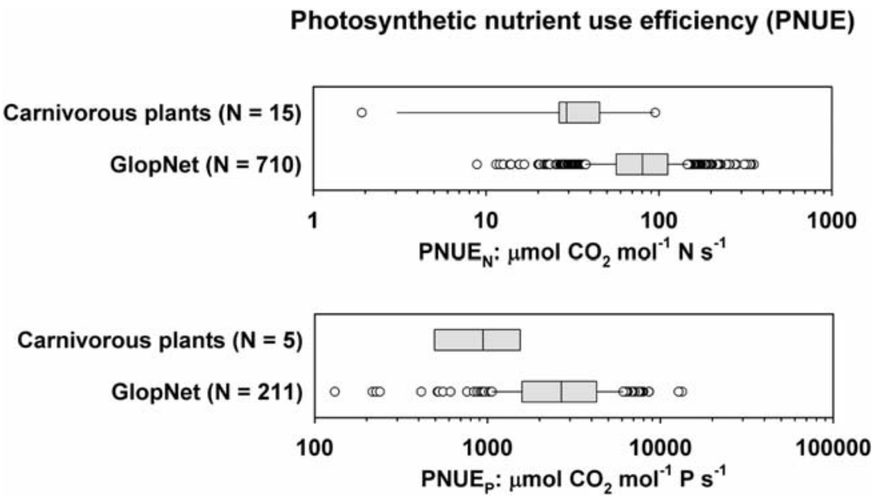

Fig. 1 Photosynthetic nitrogen (top) and phosphorus (bottom) use efficiency by carnivorous plants and non-carnivorous plants. The data on PNUE$_N$ and PNUE$_P$ for non-carnivorous plants are derived from the GlopNet data base compiled by Wright et al. (2004); the GlopNet data in the figure lack the four records of carnivorous plants (*Sarracenia purpurea* and *Drosera* spp.) entered in this data base. The carnivorous plant data are from Weiss (1980), Knight (1992), Adamec (1997 b), Méndez and Karlsson (1999), Wakefield et al. (2005), and Ellison and Farnsworth (2005). PNUE for carnivorous plants is significantly lower than PNUE for non-carnivorous plants (PNUE$_N$: $t = 4.1$, df = 723, $p < 1 \times 10^{-6}$; PNUE$_P$: $t = 2.3$; df = 214; $p = 0.03$). Data for aquatic and terrestrial carnivorous plants are pooled so that there are sufficient data for statistical analysis.

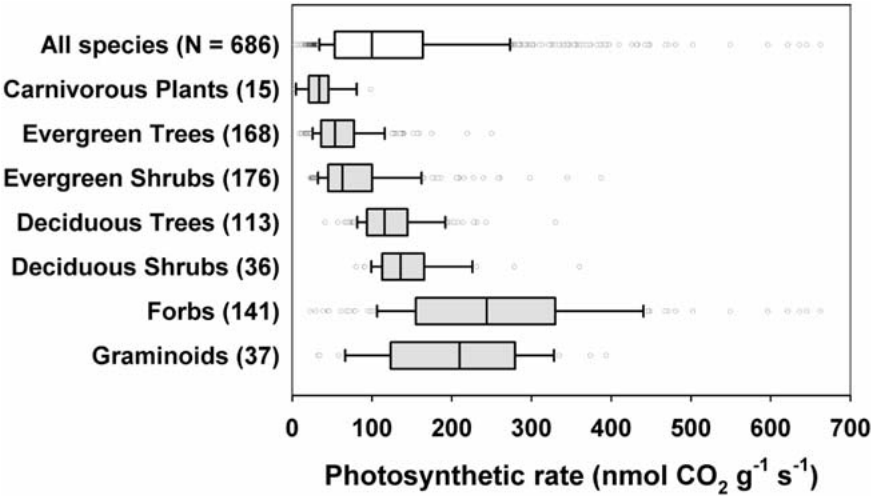

Fig. 2 Photosynthesis per unit leaf mass for carnivorous plants (data sources in Fig. **1**) and non-carnivorous plants (from the GlopNet data base: Wright et al., 2004). Numbers in parentheses are the total number of observations (each observation is a unique species × site combination).

general scaling relationships (Wright et al., 2004). This appears to be a general property of carnivorous plants (Ellison and Farnsworth, 2005). In contrast to predictions of the cost-benefit model, however, photosynthetic nutrient use efficiency (PNUE, expressed as µmol CO$_2$ fixed per mol nutrient per unit time) is significantly lower for carnivorous plants than for non-carnivorous plants (Fig. **1**). Further, the photosynthetic rate per unit leaf mass of carnivorous plants is dramatically lower than the photosynthetic rate per unit leaf mass of non-carnivorous plants, including graminoids, forbs, and evergreen or deciduous shrubs and trees (Fig. **2**).

What Nutrients are Limiting for Carnivorous Plants?

Physiological processes and plant growth may be limited by absolute concentrations of available nutrients or by their relative concentrations (Aerts and Chapin, 2000). Although Givnish et al. (1984, 1989) discussed how nitrogen, phosphorus, or other nutrients could limit photosynthesis of carnivorous plants, virtually all subsequent studies have assumed that only nitrogen is the primary nutrient gained through carnivory, and that the primary benefit derived from carnivory is nitrogen used to produce additional RuBP carboxylase-oxygenase to increase CO$_2$ fixation rates. Although prey contribute 10 – 90% of the nitrogen budget of carnivorous plants (reviewed by Ellison and Gotelli, 2001), only two studies have examined directly the linkage between nitrogen uptake by carnivorous plants and photosynthetic rate. Ellison and Gotelli (2002) showed an increase in photosynthetic rate following addition of inorganic N (as NH$_4$Cl) to pitchers of *Sarracenia purpurea* L., but this response resulted from plants producing non-carnivorous phyllodia following N addition; phyllodia photosynthesize 25% more rapidly than carnivorous pitchers on the same plant. In contrast, Wakefield et al. (2005) found no change in either leaf morphology or photosynthetic rate of *S. purpurea* fed additional prey. Their study also suggested that *S. purpurea* was preferentially absorbing phosphorus from prey, and plants receiving supplemental prey were *more* N-limited than control plants.

Nutrient content of carnivorous plants

Concentrations of N, P, and K in carnivorous plant leaves generally are lower than those in leaves of non-carnivorous plants (Fig. **3**) and normally well below concentrations at which each nutrient is generally thought to limit growth or physiology. The median leaf N content for "control" carnivorous plants

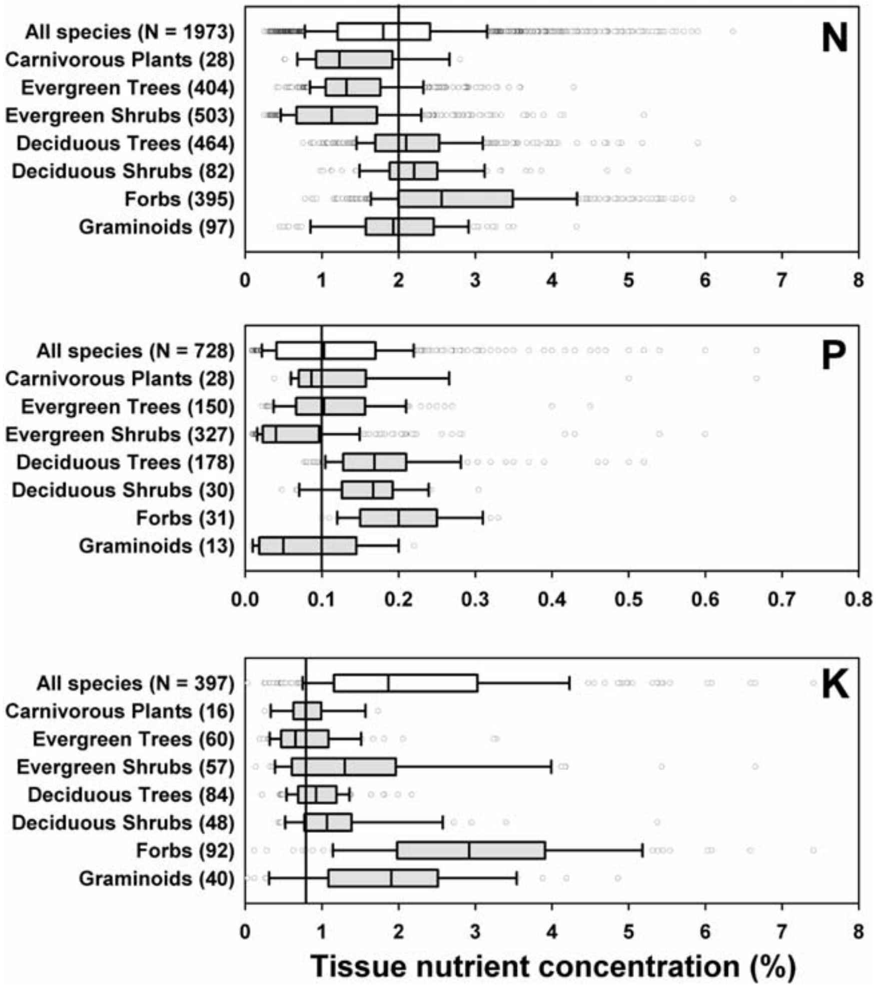

Fig. 3 Concentrations of N, P, and K in leaves of carnivorous plants and non-carnivorous plants. Numbers in parentheses are total number of observations (each observation is a unique species × site combination). The thick vertical line on each panel is the concentration below which the nutrient is considered to be limiting based on its absolute concentration (Aerts and Chapin, 2000). Data for concentrations of N and P in leaves of non-carnivorous plants come from the GlopNet data base (Wright et al., 2004), whereas data for concentrations of K in leaves of non-carnivorous plants are from Wright et al. (2005) with additional data compiled for this study from Siccama et al. (1970), Likens and Bormann (1970), Woodwell et al. (1975), Garten (1978), and Thompson et al. (1997). Carnivorous plant data from Small (1972), Christensen (1976), Chandler and Anderson (1976), Watson et al. (1982), Karlsson and Carlsson (1984), Kaminski (1987 a), Karlsson and Pate (1992), Foulds (1993), Chapin and Pastor (1995), Adamec (1997 a), Thorén and Karlsson (1998), Moran and Moran (1998), Méndez and Karlsson (1999), Ellison and Gotelli (2002), Wakefield et al. (2005), and Ellison and Farnsworth (2005).

(plants provided with neither supplemental prey nor supplemental inorganic nutrients) = 12.6 mg/g, which is well below the 10th percentile for forbs, deciduous shrubs and deciduous trees, and below the 25th percentile for graminoids. Similarly, the median leaf P for "control" carnivorous plants (0.94 mg/g,) is well below the 10th percentile for forbs, deciduous shrubs, and deciduous trees, and modestly above that of graminoids. Median leaf K of carnivorous plants is also quite low, but does not differ dramatically from non-carnivorous species. Overall, despite their generally herbaceous habit (among the carnivorous plants, only the liana *Triphyophyllum peltatum* [Hutch. and Dalziel] Airy Shaw [Dioncophyllaceae] produces wood and its leaves no longer produce carnivorous glands once it is a woody adult [Green et al., 1979]), carnivorous plants are more similar to evergreen shrubs and trees than they are to forbs or graminoids in terms of their leaf nutrient concentrations (Fig. **3**). Among non-carnivorous plants, evergreen trees and shrubs have some of the lowest PNUE (Wright et al., 2005), albeit still much higher than carnivorous plants.

Nutrient stoichiometry of carnivorous plants

Stoichiometric relationships among different nutrients can be used to determine if their relative concentrations limit plant growth (Koerselman and Meuleman, 1996; Aerts and Chapin, 2000; Olde Venterink et al., 2002; Sterner and Elser, 2002; Ågren, 2004; Güsewell, 2004) and productivity of entire communities or ecosystems (Bedford et al., 1999; Aerts and Chapin, 2000; Sterner and Elser, 2002; Schade et al., 2005). Historically, N and P have received the most attention: N limitation is implied by $N < 20$ mg/g and $N:P < 14$, whereas P limitation is implied by $P < 1$ mg/g and $N:P > 16$ (Koerselman and Meuleman, 1996; Aerts and Chapin, 2000). Co-limitation of N and P is implied when concentrations of N and P are individually limiting and when $14 \leq N:P \leq 16$.

Using these criteria, both N and P generally co-limit carnivorous plant growth (cross-hatched area in Fig. **4**). Tissue N is usually below 2% (= 20 mg/g – Fig. **3** top panel, and left-to-right shading in Fig. **4**), tissue P is usually below 0.1% (= 1 mg/g – Fig. **3** centre panel, and right to left shading in Fig. **4**), and with few exceptions, the N : P ratios are not distinguishable from 15 : 1 (black reference line in Fig. **4**). Unsurprisingly, addition of inorganic nutrients alone shifts plant nutrient content in the expected direction (Fig. **5 A**): P addition results in N-limitation, N addition results in P-limitation, and N + P addition results in somewhat more P-limitation than addition of P alone. Ellison and Gotelli (2002) illustrated this in more detail by varying the N : P ratio of the complete nutrient solution added to the plants (see also Wakefield et al., 2005). In contrast, addition of prey alone tends to shift plant nutrient content in the direction of N-limitation (Fig. **5 B**). When prey and nutrients

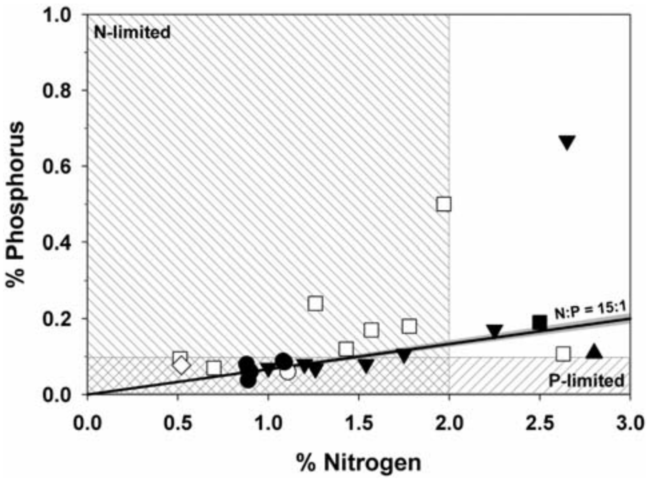

Fig. 4 Nitrogen and phosphorus content of carnivorous plant genera. (▲) *Aldrovanda;* (▼) *Drosera;* (◇) *Nepenthes;* (●) *Sarracenia;* (○) *Darlingtonia;* (□) *Pinguicula;* (■) *Utricularia*. Data sources as in Fig. **3**. Critical concentrations of N and P, and critical N : P ratios based on criteria of Koerselman and Meuleman (1996) and Aerts and Chapin (2000). The 15 : 1 N : P ratio is indicated with a solid black line, and the range $14 \leq N:P \leq 16$ is shaded in solid grey around the black line.

are added in combination in full factorial experiments, the interaction is essentially the resultant of the vector changes in nutrient limitation resulting from the addition of prey or nutrients alone (Fig. **5C**). Overall, these studies lend further support to the hypothesis that the primary nutrient gained from carnivory is P (Chandler and Anderson, 1976; Stewart and Nilsen, 1993; Wakefield et al., 2005).

More recently, Olde Venterink et al. (2002, 2003) focused attention on the tri-partite relationship between N, P, and K. In particular, they focus on the critical role of K, and suggest that if K < 8 mg/g then its availability can limit plant growth. They further suggest critical ratios for P or P + N limitation ($N:P > 14.5$, $K:P > 3.4$), K or K + N limitation ($N:K > 3.1$, $K:P < 3.4$), and pure N limitation ($N:P < 14.5$, $N:K < 2.1$). From these criteria, most carnivorous plants for which tissue concentrations of N, P, and K have been published appear to be P-limited or N + P co-limited (Fig. **3**). Two experiments suggest that relatively more P than other nutrients is taken up either from prey or from complete nutrient solution (8-8-8 N-P-K fertilizer). Additions of prey shifted *Sarracenia purpurea* from being P-limited to K- or K + N-limited (Wakefield et al., 2005; Fig. **6**). *Sarracenia flava* L. control plants are stoichiometrically P-limited, and addition of prey, complete N-P-K fertilizer, or prey × N-P-K shifted plants to being stoichiometrically N-limited (Christensen, 1976; Fig. **6**). *Triphyophyllum* leaf tissue is K-enriched in a surrounding K-poor soil (unpublished data cited by Green et al., 1979), perhaps because this species preferentially takes up K from prey. A prediction from these data would be that growth of *Triphyophyllum* is co-limited by N and P.

Conclusions and Directions for Future Research

The cost-benefit model makes three predictions: 1) the primary energetic benefit of carnivory would be either an increased rate of photosynthesis per unit leaf mass or an increase in the total leaf mass supported; 2) the absolute benefit

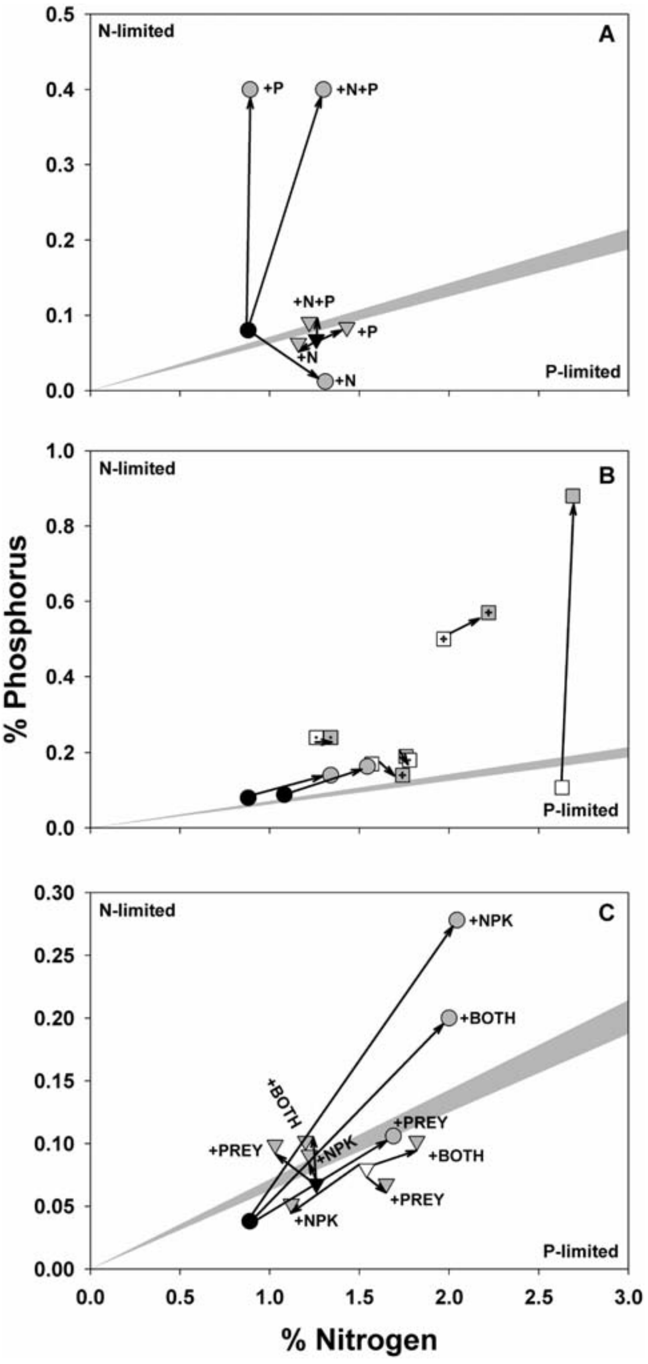

Fig. 5 Response of carnivorous plants to: (**A**) addition of inorganic nutrients only (circles: *Sarracenia purpurea* [data of Chapin and Pastor, 1995]; inverse triangles: *Drosera whittakeri* [data of Chandler and Anderson, 1976]); (**B**) addition of prey only (circles: *Sarracenia purpurea* [data of Chapin and Pastor, 1995 and Wakefield et al., 2005]; squares: *Pinguicula villosa;* squares with crosses: *Pinguicula vulgaris;* squares with dots: *Pinguicula alpina* [data of Thorén and Karlsson, 1998]); (**C**) addition of prey and/or inorganic nutrients in a full factorial design (circles: *Sarracenia flava* [data of Christensen, 1976]; inverse black and grey triangles: *Drosera whittakeri;* inverse white and grey triangles [data of Chandler and Anderson, 1976]: *Drosera glanduligera* [data of Karlsson and Pate, 1992]). The black or white symbols are the controls and the grey symbols are the prey, nutrient, or prey × nutrient additions. Arrows indicate the direction of response to the treatments. The grey shading indicates the zone of N and P co-limitation of growth defined by Koerselman and Meuleman (1996): $14 \leq N:P \leq 16$. Note that the limits of the y-axis (% phosphorus) differ among the three panels.

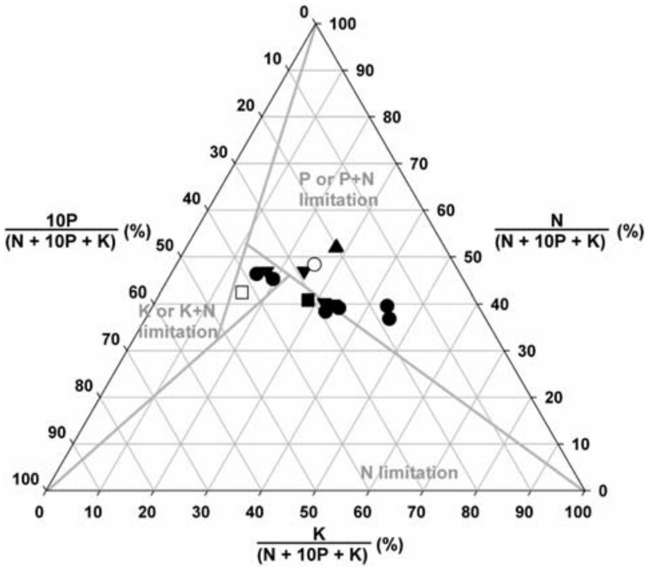

Fig. 6 Ternary plot illustrating potential stoichiometric limitation of N, P, and/or K in carnivorous plant genera. Grey lines indicate boundaries for nutrient limitation (criteria of Olde Venterink et al., 2002, 2003). Symbols as in Fig. **1** (but no *Nepenthes* data on this figure). Data from Small (1972), Christensen (1976), Watson et al. (1982), Kaminski (1987 a), Foulds (1993), Adamec (1997 a), Ellison and Gotelli (2002), Wakefield et al. (2005), and Ellison and Farnsworth (2005).

of carnivory should plateau and the marginal benefit of carnivory should decline with increasing investment in carnivory once factors other than nutrients begin to limit photosynthetic rates; 3) carnivorous plants should have an energetic advantage in competing with non-carnivorous plants (Givnish et al., 1984).

Prediction 1 is not supported by comparative data. Carnivorous plants have lower photosynthetic rates per unit leaf mass than non-carnivorous plants (Fig. **2**), and lower photosynthetic rates per leaf mass area than expected based on universal scaling relationships among leaf traits (Ellison and Farnsworth, 2005). However, most available data address this prediction only indirectly. Direct tests are rare and offer conflicting results. Ellison and Gotelli (2002) showed an increased rate of photosynthesis in *Sarracenia purpurea* following addition of inorganic nutrients, but the response was due to production of non-carnivorous leaves. Wakefield et al. (2005) showed no increased rate of photosynthesis in the same species following addition of prey, but photosynthetic rates were measured on fed leaves. Photosynthetic rates may increase in leaves that are produced subsequent to feeding (E. J. Farnsworth and A. M. Ellison, manuscript in preparation). Overall, data collected to date are inadequate to test prediction 1. Because increased growth rate is an inadequate proxy for marginal photosynthetic benefits, experiments examining physiological responses to prey or nutrient addition by a wide range of carnivorous plants are needed to directly test the cost-benefit model for the evolution of botanical carnivory.

Similarly, prediction 2 cannot be evaluated completely with existing data. The key open question here is what limits photosynthetic rates in carnivorous plants. Both N and P are required for photosynthesis, and available data suggest that growth of carnivorous plants is co-limited by these elements (Figs. **3 – 6**). However, PNUE of carnivorous plants is extremely low (Fig. **1**), and it is possible that rather than being limited by nutrient availability, photosynthetic rates have been constrained through the plants' evolutionary histories. The observation that carnivorous plants are more like evergreen herbs and shrubs in terms of tissue nutrient concentrations and photosynthetic rates suggests an evolved strategy to conserve carbon and nutrients. Carbon costs of carnivorous traps may have been a significant selective pressure in the evolution of carnivory that needs to be accounted for in models of its evolution.

Lastly, prediction 3 is not tied directly to nutrient availability or stoichiometry and I have not addressed it directly in this review. However, available evidence indicates that carnivorous plants do not compete directly with non-carnivorous plants for nutrients (Ellison et al., 2003; Brewer, 2003), and generally are subordinate competitors for light (Brewer, 1998, 1999 a – c, 2003).

The cost-benefit framework is a good model for the optimization of traits by evolution through natural selection (Givnish, 1986). Evolution does not always optimize, however. The phenotypes we see today represent both optimal, adaptive solutions as well as the consequences of constraints imposed by historical accidents (Gould and Lewontin, 1979). I suggest that the evolution of carnivory is more like Hobson's choice – choosing the lesser of two evils in a bad situation – and that the observed poor competitive ability and low photosynthetic rates of carnivorous plants are consequent to a series of evolutionary responses to conditions of extremely low nutrient availability. As our knowledge of the evolutionary history and phylogeny of carnivorous plants continues to expand, we should focus more attention on what constraints limit the range of morphological and physiological responses by these botanical marvels.

Acknowledgements

A version of this paper was presented during the XVIIth International Botanical Congress, as part of the symposium on Advances in Carnivorous Plant Research. I thank the organizers, Stefan Porembski and Wilhelm Barthlott for inviting me to speak there, and discussion with participants in, and attendees of, the symposium focused attention on the central points of the paper. Tom Givnish unwittingly spurred me on to examine photosynthetic nutrient use efficiency and scaling relationships between photosynthesis and leaf mass. Ian Wright and the GlopNet collaborative have generously published and shared their global compilation of leaf traits, which allowed the broad-scale comparisons presented here. Additional data used in this paper are available on request. The research presented has benefited greatly from a decade-long, extensive collaboration with Leszek Błędzki, Jessica Butler, Elizabeth Farnsworth, Nick Gotelli, and many of our students. Our work has been supported by our home institutions – Mount Holyoke College, the University of Vermont, and the Harvard Forest – and by grants from the US Environmental Protection Agency and the US National Science Foundation (nos. 98-05722, 98-08504, 00-82977, 02-35128, 02-34710, and 04-52254).

References

Adamec, L. (1997 a) Mineral nutrition of carnivorous plants: a review. Botanical Review 63, 273 – 299.

Adamec, L. (1997 b) Photosynthetic characteristics of the aquatic carnivorous plant *Aldrovanda vesiculosa*. Aquatic Botany 59, 297 – 306.

Adamec, L. (2002) Leaf absorption of mineral nutrients in carnivorous plants stimulates root nutrient uptake. New Phytologist 155, 89 – 100.

Aerts, R. and Chapin, F. S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30, 1 – 67.

Ågren, G. I. (2004) The C : N : P stoichiometry of autotrophs – theory and observations. Ecology Letters 7, 185 – 191.

Albert, V. A., Williams, S. E., and Chase, M. W. (1992) Carnivorous plants: phylogeny and structural evolution. Science 257, 1491 – 1495.

Aldenius, J., Carlsson, B., and Karlsson, S. (1983) Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. New Phytologist 93, 53 – 59.

Bedford, B. L., Walbridge, M. R., and Aldous, A. (1999) Patterns of nutrient availability and plant diversity of temperate North American wetlands. Ecology 80, 2151 – 2169.

Benzing, D. H. (1987) The origin and rarity of botanical carnivory. Trends in Ecology and Evolution 2, 364 – 369.

Brewer, J. S. (1998) Effects of competition and litter on a carnivorous plant, *Drosera capillaris* (Droseraceae). American Journal of Botany 85, 1592 – 1596.

Brewer, J. S. (1999 a) Effects of competition, litter, and disturbance on an annual carnivorous plant *(Utricularia juncea)*. Plant Ecology 140, 159 – 165.

Brewer, J. S. (1999 b) Effects of fire, competition and soil disturbances on regeneration of a carnivorous plant *(Drosera capillaris)*. American Midland Naturalist 141, 28 – 42.

Brewer, J. S. (1999 c) Short term effects of fire and competition on growth and plasticity of the yellow pitcher plant, *Sarracenia alata* (Sarraceniaceae). American Journal of Botany 86, 1264 – 1271.

Brewer, J. S. (2003) Why don't carnivorous pitcher plants compete with non-carnivorous plants for nutrients? Ecology 84, 451 – 462.

Chandler, G. E. and Anderson, J. W. (1976) Studies on the nutrition and growth of *Drosera* species with reference to the carnivorous habit. New Phytologist 76, 129 – 141.

Chapin, C. T. and Pastor, J. (1995) Nutrient limitation in the northern pitcher plant *Sarracenia purpurea*. Canadian Journal of Botany 73, 728 – 734.

Chiang, C., Craft, C. B., Rogers, D. W., and Richardson, C. J. (2000) Effects of 4 years of nitrogen and phosphorus additions on Everglades plant communities. Aquatic Botany 68, 61 – 78.

Christensen, N. L. (1976) The role of carnivory in *Sarracenia flava* L. with regard to specific nutrient deficiencies. Journal of the Elisha Mitchell Scientific Society 92, 144 – 147.

Darwin, C. (1875) Insectivorous Plants. New York, NY: Appleton and Company.

Darwin, F. (1878) Experiments on the nutrition of *Drosera rotundifolia*. Journal of the Linnean Society – Botany 17, 17 – 32.

Dixon, K. W., Pate, J. S., and Bailey, W. J. (1980) Nitrogen nutrition of the tuberous sundew *Drosera erythrorhiza* Lindl. with special reference to catch of arthropod fauna by its glandular leaves. Australian Journal of Botany 28, 283 – 297.

Ellison, A. M. and Farnsworth, E. J. (2005) The cost of carnivory for *Darlingtonia californica* (Sarraceniaceae): evidence from relationships among leaf traits. American Journal of Botany 92, 1085 – 1093.

Ellison, A. M. and Gotelli, N. J. (2001) Evolutionary ecology of carnivorous plants. Trends in Ecology and Evolution 16, 623 – 629.

Ellison, A. M. and Gotelli, N. J. (2002) Nitrogen availability alters the expression of carnivory in the northern pitcher plant *Sarracenia purpurea*. Proceedings of the National Academy of Sciences of the USA 99, 4409 – 4412.

Ellison, A. M., Gotelli, N. J., Brewer, J. S., Cochran-Stafira, D. L., Kneitel, J., Miller, T. E., Worley, A. C., and Zamora, R. (2003) The evolutionary ecology of carnivorous plants. Advances in Ecological Research 33, 1 – 74.

Englund, G. and Harms, S. (2003) Effects of light and microcrustacean prey on growth and investment in carnivory in *Utricularia vulgaris*. Freshwater Biology 48, 786 – 794.

Foulds, W. (1993) Nutrient concentrations of foliage and soil in south-western Australia. New Phytologist 125, 529 – 546.

Garten, C. T. Jr. (1978) Multivariate perspectives on the ecology of plant mineral element composition. American Naturalist 112, 533 – 544.

Gibson, T. C. (1983) Competition, disturbance, and the carnivorous plant community in the southeastern United States. PhD dissertation, University of Utah, Salt Lake City, Utah.

Givnish, T. J. (1986) On the Economy of Plant Form and Function. Cambridge, UK: Cambridge University Press.

Givnish, T. J. (1989) Ecology and evolution of carnivorous plants. In Plant-Animal Interactions (Abramson, W. G., ed.), Toronto, Canada: McGraw-Hill Publishers, pp. 243 – 290.

Givnish, T. J., Burkhardt, E. L., Happel, R. E., and Weintraub, J. D. (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. American Naturalist 124, 479 – 497.

Gotelli, N. J. and Ellison, A. M. (2002) Nitrogen deposition and extinction risk in the northen pitcher plant *Sarracenia purpurea*. Ecology 83, 2758 – 2765.

Gould, S. J. and Lewontin, R. C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proceedings of the Royals Society of London B 205, 581 – 598.

Green, S., Green, T. L., and Heslop-Harrison, Y. (1979) Seasonal heterophylly and leaf gland features in *Triphyophyllum* (Dioncophyllaceae), a new carnivorous plant genus. Botanical Journal of the Linnean Society 78, 99 – 116.

Guisande, C., Andrade, C., Granado-Lorencio, C., Duque, S. R., and Núñez-Avellaneda, M. (2000) Effects of zooplankton and conductivity on tropical *Utricularia foliosa* investment in carnivory. Aquatic Ecology 34, 137 – 142.

Güsewell, S. (2004) N : P ratios in terrestrial plants: variation and functional significance. New Phytologist 164, 243 – 266.

Jobson, R. W., Morris, E. C., and Burgin, S. (2000) Carnivory and nitrogen supply affect the growth of the bladderwort *Utricularia uliginosa*. Australian Journal of Botany 48, 549 – 560.

Juniper, B. E., Robins, R. J., and Joel, D. M. (1989) The Carnivorous Plants. New York, NY, USA: Academic Press.

Kaminski, R. (1987 a) Studies on the ecology of *Aldrovanda vesiculosa* L. I. Ecological differentiation of *A vesiculosa* population under the influence of chemical factors in the habitat. Ekologia Polska 35, 559 – 590.

Kaminski, R. (1987 b) Studies on the ecology of *Aldrovanda vesiculosa* L. II. Organic substances, physical and biotic factors and the growth and development of *A. vesiculosa*. Ekologia Polska 35, 591 – 609.

Karlsson, P. S. and Carlsson, B. (1984) Why does *Pinguicula vulgaris* L. trap insects? New Phytologist 97, 25 – 30.

Karlsson, P. S., Nordell, K. O., Carlsson, B. A., and Svensson, B. M. (1991) The effect on soil nutrient status on prey utilization in four carnivorous plants. Oecologia 86, 1 – 7.

Karlsson, P. S. and Pate, J. S. (1992) Contrasting effects of supplementary feeding of insects or mineral nutrients on the growth and nitrogen and phosphorus economy of pygmy species of *Drosera*. Oecologia 92, 8 – 13.

Knight, S. E. (1992) Costs of carnivory in the common bladderwort, *Utricularia macrorhiza*. Oecologia 89, 348 – 355.

Knight, S. E. and Frost, T. M. (1991) Bladder control in *Utricularia macrorhiza*: lake-specific variation in plant investment in carnivory. Ecology 72, 728 – 734.

Koerselman, W. and Meuleman, A. F. W. (1996) The vegetation N : P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology 33, 1441 – 1450.

Krafft, C. C. and Handel, S. N. (1991) The role of carnivory in the growth and reproduction of *Drosera filiformis* and *D. rotundifolia*. Bulletin of the Torrey Botanical Club 118, 12 – 19.

Likens, G. E. and Bormann, F. H. (1970) Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Bulletin of the Yale University School of Forestry 79, 1 – 25.

Lloyd, F. E. (1942) The Carnivorous Plants. New York: Ronald Press.

Lüttge, U. (1983) Ecophysiology of carnivorous plants. In Physiological Plant Ecology III (Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H., eds.), New York: Springer, pp. 489 – 517.

Méndez, M. and Karlsson, P. S. (1999) Costs and benefits of carnivory in plants: insights from the photosynthetic performance of four carnivorous plants in a subarctic environment. Oikos 86, 105 – 112.

Méndez, M. and Karlsson, P. S. (2005) Nutrient stoichiometry in *Pinguicula vulgaris*: nutrient availability, plant size, and reproductive status. Ecology 86, 982 – 991.

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

Olde Venterink, H., Pieterse, N. M., Belgers, J. D. M., Wassen, M. J., and De Ruiter, P. C. (2002) N, P, and K budgets along nutrient availability and productivity gradients in wetlands. Ecological Applications 12, 1010 – 1026.

Olde Venterink, H., Wassen, M. J., Verkroost, A. W. M., and De Ruiter, P. C. (2003) Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. Ecology 84, 2191 – 2199.

Otto, C. (1999) Effects of prey and turion size on the growth and turion production of the carnivorous bladderwort, *Utricularia vulgaris* L. Archiv für Hydrobiologie 145, 469 – 478.

Pate, J. S. (1986) Economy of symbiotic nitrogen fixation. In On the Economy of Plant Form and Function (Givnish, T. J., ed.), Cambridge, UK: Cambridge University Press, pp. 299 – 325.

Roberts, P. R. and Oosting, H. J. (1958) Responses of Venus fly trap *(Dionaea muscipula)* to factors involved in its endemism. Ecological Monographs 28, 193 – 218.

Schade, J. D., Espeleta, J. F., Klausmeier, C. A., McGroddy, M. E., Thomas, S. A., and Zhang, L. (2005) A conceptual framework for ecosystem stoichiometry: balancing resource supply and demand. Oikos 109, 40 – 51.

Schulze, W. and Schulze, E.-D. (1990) Insect capture and growth of the insectivorous *Drosera rotundifolia* L. Oecologia 82, 427 – 429.

Siccama, T. G., Bormann, F. H., and Likens, G. E. (1970) The Hubbard Brook ecosystem study: productivity, nutrients, and phytosociology of the herbaceous layer. Ecological Monographs 40, 389 – 402.

Small, E. (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Canadian Journal of Botany 50, 2227 – 2233.

Sorenson, D. R. and Jackson, W. T. (1968) The utilization of paramecia by the carnivorous plant *Utricularia gibba*. Planta 83, 166 – 170.

Sterner, R. W. and Elser, J. J. (2002) Ecological Stoichiometry: The Biology of Elements From Molecules to the Biosphere. Princeton, NJ, USA: Princeton University Press.

Stewart, C. N. and Nilsen, E. T. (1992) *Drosera rotundifolia* growth and nutrition in a natural population with special reference to the significance of insectivory. Canadian Journal of Botany 70, 1409 – 1416.

Stewart, C. N. and Nilsen, E. T. (1993) Responses of *Drosera capensis* and *D. binata* var. *multifida* (Droseraceae) to manipulations of insect availability and soil nutrient levels. New Zealand Journal of Botany 31, 385 – 390.

Thompson, K., Parkinson, J. A., Band, S. R., and Spencer, R. E. (1997) A comparative study of leaf nutrient concentrations in a regional herbaceous flora. New Phytologist 136, 679 – 689.

Thorén, L. M. and Karlsson, P. S. (1998) Effects of supplementary feeding on growth and reproduction of three carnivorous plant species in a subarctic environment. Journal of Ecology 86, 501 – 510.

Thorén, L. M., Karlsson, P. S., and Tuomi, J. (1996) Somatic cost of reproduction in three carnivorous *Pinguicula* species. Oikos 76, 427 – 434.

Thorén, L. M., Tuomi, J., Kämäräinen, T., and Laine, K. (2003) Resource availability affects investment in carnivory in *Drosera rotundifolia*. New Phytologist 159, 507 – 511.

Thum, M. (1988) The significance of carnivory for the fitness of *Drosera* in its natural habitat. 1. The reactions of *Drosera intermedia* and *D. rotundifolia* to supplementary feeding. Oecologia 75, 472 – 480.

Wakefield, A. E., Gotelli, N. J., Wittman, S. E., and Ellison, A. M. (2005) The effect of prey addition on nutrient stoichiometry, nutrient limitation, and morphology of the carnivorous plant *Sarracenia purpurea* (Sarraceniaceae). Ecology 86, 1737 – 1743.

Watson, A. P., Matthiessen, J. N., and Springett, B. P. (1982) Arthropod associates and macronutrient status of the red-ink sundew (*Drosera erythrorhiza* Lindl.). Australian Journal of Ecology 7, 13 – 22.

Weiss, T. E. J. (1980) The effects of fire and nutrient availability on the pitcher plant *Saracenia flava* L. PhD dissertation, University of Georgia, Athens, Georgia.

Wilson, S. D. (1985) The growth of *Drosera intermedia* in nutrient-rich habitats: the role of insectivory and interspecific competition. Canadian Journal of Botany 63, 2468 – 2469.

Woodwell, G. M., Whittaker, R. H., and Houghton, R. A. (1975) Nutrient concentrations in plants in the Brookhaven oak-pine forest. Ecology 56, 318 – 332.

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Garnier, E., Hikosaka, K., Lamont, B. B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D. I., and Westoby, M. (2005) Assessing the generality of global leaf trait relationships. New Phytologist 166, 485 – 496.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R. (2004) The worldwide leaf economics spectrum. Nature 428, 821 – 827.

Zamora, R., Gómez, J. M., and Hódar, J. A. (1997) Responses of a carnivorous plant to prey and inorganic nutrients in a Mediterranean environment. Oecologia 111, 443 – 451.

Zamora, R., Gómez, J. M., and Hódar, J. A. (1998) Fitness responses of a carnivorous plant in contrasting ecological scenarios. Ecology 79, 1630 – 1644.

A. M. Ellison

Harvard Forest
324 North Main Street
Petersham, MA 01366
USA

E-mail: aellison@fas.harvard.edu

Guest Editor: S. Porembski