Nutrient Limitation and Stoichiometry of Carnivorous Plants

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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 plateu 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...
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 \( (p = 0.02, \text{ binomial test of 29 studies}) \) and no significant effect of nutrient additions \( (p = 0.15) \) or nutrient \( \times \) 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

<table>
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<tr>
<th>Species</th>
<th>Growth response to</th>
<th>IN alone</th>
<th>prey + IN</th>
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<tbody>
<tr>
<td><em>Aldrovanda vesiculosa</em> L.</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>12</td>
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<tr>
<td><em>Dionaea muscipula</em> Ellis</td>
<td>NA</td>
<td>–</td>
<td>NA</td>
<td>20</td>
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<td><em>Drosera aliciae</em> R. Hamet</td>
<td>NA</td>
<td>+</td>
<td>NA</td>
<td>1</td>
</tr>
<tr>
<td><em>Drosera binata</em> Labill. var. <em>multifida</em> Mazrimas</td>
<td>0</td>
<td>+</td>
<td>NA</td>
<td>23</td>
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<td><em>Drosera capensis</em> L.</td>
<td>0</td>
<td>+</td>
<td>NA</td>
<td>23</td>
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<tr>
<td><em>Drosera capillaris</em> Poir.</td>
<td>NA</td>
<td>+</td>
<td>NA</td>
<td>1</td>
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<tr>
<td><em>Drosera clusosterstigma</em> N. Marchant and Lowrie</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>14</td>
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<td><em>Drosera filiformis</em> Raf.</td>
<td>+</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td><em>Drosera glanduligera</em> Lehm.</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>14</td>
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<td><em>Drosera intermedia</em> Hayne</td>
<td>+/0</td>
<td>NA</td>
<td>NA</td>
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<td><em>Drosera rotundifolia</em> L.</td>
<td>+ (0)</td>
<td>±</td>
<td>±</td>
<td>6, 15, 17, 21, 22, 25</td>
</tr>
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<td><em>Drosera spatulata</em> Labill.</td>
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<td>+</td>
<td>NA</td>
<td>1</td>
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<tr>
<td><em>Nepenthes rafflesiana</em> Jack</td>
<td>+</td>
<td>NA</td>
<td>NA</td>
<td>18</td>
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<td><em>Pinguicula alpina</em> L.</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>15, 24</td>
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<td>+</td>
<td>NA</td>
<td>NA</td>
<td>9</td>
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<tr>
<td><em>Pinguicula vallisiaefolia</em> Webb</td>
<td>+</td>
<td>NA</td>
<td>NA</td>
<td>28, 29</td>
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<tr>
<td><em>Pinguicula villosa</em> L.</td>
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<td>0</td>
<td>0</td>
<td>15, 24</td>
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<td><em>Pinguicula vulgaris</em> L.</td>
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<td>+/0/–</td>
<td>+/0/–</td>
<td>2, 13, 15, 24</td>
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<td>+</td>
<td>+</td>
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<td>+</td>
<td>NA</td>
<td>NA</td>
<td>9</td>
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<tr>
<td><em>Sarracenia leucophylla</em> Raf.</td>
<td>+</td>
<td>NA</td>
<td>NA</td>
<td>9</td>
</tr>
<tr>
<td><em>Sarracenia purpurea</em> L.</td>
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<td>+/0/–</td>
<td>0</td>
<td>4, 7, 10</td>
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<td><em>Utricularia gibba</em> L.</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>22</td>
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<tr>
<td><em>Utricularia macrorhiza</em> Le Conte</td>
<td>+/0</td>
<td>+</td>
<td>NA</td>
<td>8, 16, 19</td>
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<tr>
<td><em>Utricularia spp.</em></td>
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<td>–</td>
<td>NA</td>
<td>5</td>
</tr>
<tr>
<td><em>Utricularia uliginosa</em> Vahl</td>
<td>0</td>
<td>0</td>
<td>+</td>
<td>11</td>
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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 CO₂ 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 CO₂ 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 NH₄Cl) to pitchers of Sarracenia purpurea L., but this response resulted from plants producing non-carnivorous phylloidia 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...
(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 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 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 ≤ N:P ≤ 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. 5A); 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. 5B). When prey and nutrients
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 Nilsson, 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.

...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 P 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...
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).
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