

Carnivorous Plants: Physiology, ecology, and evolution

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<https://doi.org/10.1093/oso/9780198779841.001.0001>

Published: 2017

Online ISBN: 9780191825873

Print ISBN: 9780198779841

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CHAPTER

18 Why are plants carnivorous? Cost/benefit analysis, whole-plant growth, and the context-specific advantages of botanical carnivory

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<https://doi.org/10.1093/oso/9780198779841.003.0018> Pages 232–255

Published: December 2017

Abstract

The 1984 cost/benefit model for the evolution of carnivorous plants addresses their potential energetic and ecological advantages. It has provided a conceptual framework for research on distribution, variation in trap allocation and mechanisms, association with low rates of photosynthesis and whole-plant growth, and ecology of carnivorous plants relative to noncarnivorous ones. We re-assess this model, its potential extensions, and the validity of its assumptions and predictions. We review what is known about photosynthesis, respiration, relative growth rates, and resource allocation in carnivorous and noncarnivorous plants, and growth, nutrient limitation and stoichiometry, adaptation to different prey, and optimal trap allocation of carnivorous plants. We propose explanations for six ecological and evolutionary paradoxes involving carnivorous plants. Future advances will hinge on better quantification of the cost/benefit model and comparing model predictions with data.

Keywords: [Coprophagy](#), [cost/benefit model](#), [detritivory](#), [epiphytes](#), [fitness](#), [fire](#), [myrmecotrophy](#), [nitrogen](#), [nutrient availability](#), [optimal trap allocation](#), [soil anoxia](#)

Subject: [Plant Sciences and Forestry](#), [Animal Pathology and Diseases](#)

Collection: [Oxford Scholarship Online](#)

18.1 Introduction

Most plant species are consumed, in whole or part, by animals acting as herbivores, pollinators, or seed dispersers, but carnivorous plants have turned the ecological tables and consume animals as prey. Carnivorous plants thus interact in unique ways with animals that serve as competitors for prey, digestive symbionts, food guards, butlers, kleptoparasites, or even prey mutualists and sources of nutrients via excreta (Chapters 21–26 and below). More importantly, carnivorous plants—by absorbing mineral nutrients from animals via costly traps that attract, capture, and/or digest prey—have gained the ability to live and compete successfully in nutrient-poor environments, but at the expense of reduced competitive ability elsewhere (Givnish et al. 1984, Ellison and Gotelli 2002, Ellison and Adamec 2011, Pavlovič and Saganová 2015; Chapter 2).

Darwin (1875) devoted only a few lines to the ecological value of botanical carnivory, stating that “[t]he absorption of animal matter from captured insects explains how *Drosera* can flourish in extremely poor peaty soils ... considering the nature of the soil where it grows, the supply of nitrogen would be extremely limited, or quite deficient, unless the plant had the power of obtaining this important element from captured insects” (pp. 14–15). Darwin (1875) focuses almost entirely on the structure and workings of the traps in different groups, with little said about the functional consequences of carnivory. The beneficial impacts of prey capture on growth and seed production by *Drosera* were first documented three years later by his son, Francis Darwin (1878).

Givnish et al. (1984) addressed the ecological value of carnivory in detail for the first time with a cost/benefit model for the evolution of carnivory in plants. This model explained why carnivorous plants are common in habitats that are not only nutrient-poor but also sunny and moist, and why plants might adjust their allocation to carnivory in different circumstances. This model has stimulated a large amount of research over the past 32 years, and provided a conceptual framework for many studies of ecophysiology, ecological distribution, resource allocation, and evolution of carnivorous plants (Givnish 1989, Adamec 1997a, Ellison and Gotelli 2002, Ellison 2006, Anderson and Midgley 2007, Gibson and Waller 2009, Ellison and Adamec 2011, Clarke and Moran 2016; Chapters 2, 3, 10, 17, 19).

Here we re-assess this model, discuss how its predictions can be extended in a number of important ways, and evaluate its assumptions and predictions in terms of what is now known about photosynthesis, respiration, relative growth rate (RGR), and resource allocation in carnivorous versus noncarnivorous plants, nutrient limitation and stoichiometry, and adaptation to different kinds of prey.

18.2 The cost/benefit model for the evolution of plant carnivory

Traps in carnivorous plants provide an alternative source for the nutrients absorbed by roots in other plants, but they involve additional energetic costs, including production of attractive nectars or aromas (Chapter 12), secretion of digestive enzymes (Chapters 13, 16), absorption of nutrients (Chapter 16), trap activation or resetting (Chapter 14), and reduced carbon gain associated with production of photosynthetically inefficient leaves (Givnish et al. 1984, Givnish 1989, Adamec 2006, 2010a, 2010c, Hájek and Adamec 2010, Ellison and Adamec 2011, Pavlovič and Saganová 2015). Botanical carnivory—the attraction, capture, or digestion of prey, and subsequent uptake of nutrients from dead prey resulting in increased plant growth or reproduction (Chapter 1)—should be favored whenever the energetic benefits of a small investment in carnivory exceed the costs (Figure 18.1).

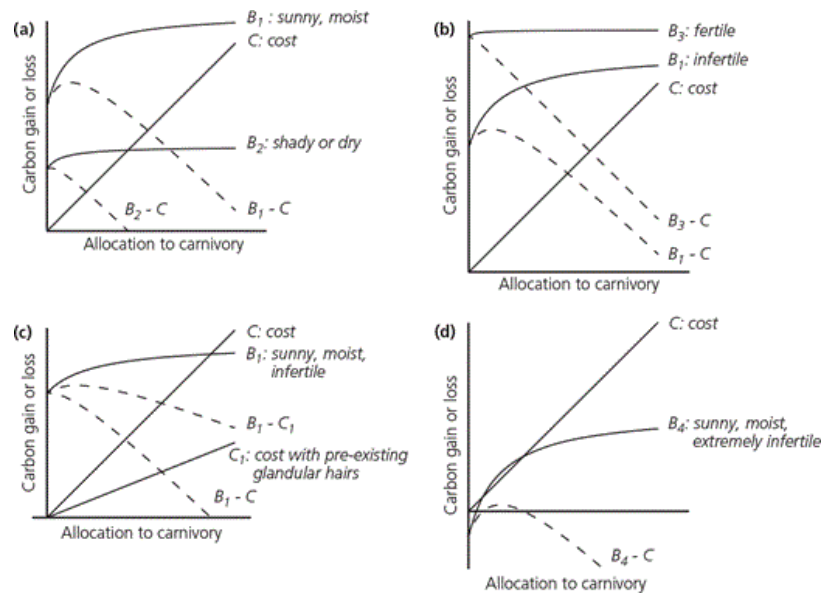


Figure 18.1 Cost/benefit model for the evolution of carnivory in plants, plotting photosynthetic benefits and costs against different levels of investment in carnivorous adaptations under different conditions. **(a)** On nutrient-poor sites, the rate at which photosynthesis (B) increases with investment in carnivory (as a result of greater nutrient supply) should be higher, and show less tendency to plateau, in well-lit and moist microsites (B_1) than where light or water more strongly limit carbon uptake (B_2). Dashed lines show net difference between photosynthetic benefit and cost (C) of obtaining nutrients through carnivory. Carnivory should evolve whenever the benefit of a small investment in carnivory exceeds its own cost; that is, when $dB/dx > dC/dx$, or when the net profit curve $B-C$ slopes upward near $C = 0$. **(b)** On sunny, moist, nutrient-rich sites, photosynthetic rates (B_3) should be elevated relative to otherwise similar but nutrient-poor sites where carnivory can make little or no increment to photosynthesis ($dB/dx \approx 0$), so carnivory is unlikely to be favored. **(c)** In lineages in which glandular hairs are already present and co-used in carnivorous mutants, the cost curve (C_1) should be reduced, favoring the evolution of carnivory. **(d)** On bare rock or extremely sterile soil, noncarnivorous ancestors should show negative carbon balance; even under well-lit and -watered conditions, nutrients gained from a small investment in carnivory are unlikely to result in positive carbon balance, even if a greater, optimal investment would.

Thus, adaptation to extremely infertile sites via carnivory is unlikely to arise directly, but instead in steps, with small initial investments favored on sunny, moist, somewhat infertile sites, leading to plants being able to survive on, and later become adapted to, extremely infertile sites.

p. 234 18.2.1 The benefits of carnivory

The cost/benefit model assumes that advantages in energy capture translate into advantages in intra- and interspecific competition that lead to gains in fitness. It also assumes that any initial trap structure (or subsequent refinement thereof) is a simple phenotypic step from ancestral forms (Chapter 3); no matter what the energetic or fitness advantage of carnivory, it is extremely unlikely that a single mutation or set of mutations encoding a complex trapping mechanism could arise all at once. Finally, it also assumes that investment in carnivory is scalable once traps have evolved; this is straightforward, given the modular construction of plants and resulting ability to vary trap number, size, and nectar and digestive enzyme secretion rates once traps have evolved. Given these assumptions, selection within species or competition among species should favor carnivory whenever the initial marginal benefit obtained by carnivory (measured as increased rates of photosynthesis per unit leaf mass or whole-plant growth) exceeds the marginal cost (measured in the same units of carbon) of constructing traps (Givnish et al. 1984, Givnish 1989; Figure 18.1).

Based on first principles, carnivory might provide four kinds of energetic benefits that would enhance whole-plant carbon gain: (1) an increased rate of photosynthesis per unit leaf mass; (2) an increased rate of conversion of photosynthate to new leaf tissue; (3) reduction in allocation of photosynthate to unproductive roots as nutrient absorption by trap leaves increases; or (4) partial replacement of autotrophy with heterotrophy (Givnish et al. 1984, Givnish 1989). Uptake of N, P, or other nutrients via carnivory (Chapters 17, 19) could result in increased concentrations of Rubisco or other photosynthetic proteins in new leaf tissue (Pavlovič et al. 2016), increased stores of nutrients to produce such proteins and convert stocks of carbohydrates into new leaves, or decreased demand for nutrients supplied by roots.

Increased photosynthesis.

Many studies show that feeding enhances the growth of carnivorous plants, especially under nutrient-poor conditions (Chapters 17, 19), but few have tested the proposed elevation of leaf nutrient levels and photosynthesis by feeding (Hypothesis 1). The strongest support for Hypothesis 1 is provided by Farnsworth and Ellison (2008) for ten *Sarracenia* species and by Pavlovič et al. (2014) for *Drosera capensis*. Gao et al. (2015) supported Hypothesis 2 by showing that fed *Dionaea* produce larger petioles and smaller traps. Comparative data indicate that carnivores often have substantially smaller root systems than noncarnivores in the same habitat (Darwin 1875, Brewer 2003, Brewer et al. 2011)—3.4 to 23% of total biomass for the few species studied (Adamec 1997a)—providing circumstantial support for Hypothesis 3. However, some experiments have shown increased root growth and nutrient uptake following prey capture (Hanslin and Karlsson 1996, Adamec 1997a, 2002, Lenihan and Schulz 2014, Gao et al. 2015).

Heterotrophy or autotrophy?

There is little support for Hypothesis 4. Terrestrial plants appear to obtain mostly nutrients, not carbon, from carnivory (e.g., Chandler and Anderson 1976, Adamec 1997a), although some carbon uptake does occur, perhaps via absorption of amino acids (Dixon et al. 1980, Rischer et al. 2002). Fasbender et al. (2017) showed that *Dionaea* uses prey-derived amino acid carbon to fuel respiration. However, the situation may be different for aquatic *Utricularia*, which can grow in complete darkness if supplied with a carbohydrate-rich medium (Harder 1970). Terrestrial species of *Utricularia* allocate < 9% of their biomass to leaves, calling into question whether they are fully autotrophic (Porembski et al. 2006). Michalko et al. (2013) showed that *Drosera rotundifolia* secretes a β -1, 3-glucanase that can cleave plant glucans and lead to absorption of simple sugars. The magnitude of carbon uptake via this pathway, however, has yet to be quantified and may be quite low, because insects do not contain glucans. Glucanases in carnivorous plants have traditionally been viewed as defenses against microbial pathogens (Juniper et al. 1989, Hatano and Hamada 2008, Schulze et al. 2012).

18.2.2 Benefits vary with environmental conditions

p. 235 Let us consider plants of a given size—with an initial fixed biomass in leaves and roots—and ask how allocation of energy to carnivory would affect their net growth and, thus, competitive ability and fitness (Givnish et al. 1984). As the amount of energy x invested in carnivory (e.g., traps, digestive enzymes) per gram of leaf mass rises (the cost curve $C(x)$ in Figure 18.1), prey capture, nutrient absorption, and effective rate of photosynthesis per unit leaf mass ($\text{g C g}^{-1} \text{ leaf s}^{-1}$) should also increase, rising linearly initially and then plateauing with increasing investments in carnivory (the benefits curve $B(x)$ in Figure 18.1). The initial increase could result from (a) an increase in the absolute rate of photosynthesis; (b) an increase in the rate of conversion of carbon skeletons to new leaf tissue because of the higher availability of nutrients provided by carnivory; or (c) a decline in the fractional allocation of energy to unproductive but nutrient-absorbing roots (Givnish et al. 1984, Givnish 1989). In retrospect, we think that (c) is unlikely to alter the curve $B(x)$, and instead should discount the net cost of carnivory, decreasing the slope of the cost curve $C(x)$.

Photosynthetic enhancement.

The amount by which photosynthesis (or conversion rate of photosynthate to leaf tissue) can be enhanced by increased nutrient input depends on ecological conditions. The effective rate of photosynthesis is unlikely to rise unless nutrients are in short supply and limit photosynthesis or the conversion of photosynthate into new leaf tissue, so the greatest benefit is expected on nutrient-poor sites. The usual increase in the growth of carnivorous plants when supplied with prey on nutrient-poor substrates disappears if nutrient availability is increased by fertilizing the substrate itself (Ellison 2006). Growth is not photosynthesis, but these results are consistent with (and analogous to) how soil fertilization leads to enhanced rates of photosynthesis and whole-plant rates of growth in noncarnivorous plants (e.g., Reich et al. 2003, Ellison 2006, Drenovsky et al. 2012). The well-documented rise following supplemental feeding in the concentrations of N and P in leaf tissue of terrestrial carnivorous plants (Chandler and Anderson 1976, Christiansen 1976, Karlsson and Pate 1992, Chapin and Pastor 1995, Wakefield et al. 2005, Ellison 2006, Farnsworth and Ellison 2008, Pavlovič et al. 2014) implies an increased rate of photosynthesis, based on the rates of carboxylation, electron transport, and net photosynthesis increasing with leaf N and P concentration across plants worldwide (Walker et al. 2014).

If factors such as light or moisture are in limited supply, they should limit photosynthesis and the extent to which additional nutrients provided by carnivory can elevate carbon gain (Givnish et al. 1984). On economic grounds, we expect lower levels of moisture or light to reduce optimal stomatal conductance and, thus, maximum photosynthetic rates (A_{max}) at a given level of leaf N concentration and mesophyll photosynthetic capacity (Givnish and Vermeij 1976, Cowan and Farquhar 1977, Wong et al. 1979), flattening the A_{max} vs. [N] response. Lower moisture supply should favor thicker leaves with more mass per unit area (Givnish 1979), resulting in more internal self-shading and longer average distances for CO_2 to diffuse from the stomata, also flattening the A_{max} vs. N response. As expected, photosynthesis per unit leaf mass at a given leaf N concentration is lower in drier habitats around the world, and increases less rapidly with leaf N concentration (Wright et al. 2005).

Plateauing of benefits.

As the amount of energy x devoted to carnivory rises, the benefit curve $B(x)$ should plateau, perhaps because of saturation in prey capture efficiency (e.g., a Type-II functional response), but certainly as factors other than nutrients limit photosynthesis or the conversion of photosynthate into new leaf tissue (Givnish 1989). For example, $B(x)$ would level off if increased nutrient supply increased the rate of conversion of photosynthate into new leaf tissue at a constant nutrient concentration but not the nutrient concentration per unit leaf mass (Givnish 1989). As nutrient uptake increases with investment in carnivory, the rate at which new leaves can be produced should depend less on limiting nutrients (e.g., N, P) and more on the availability of carbon skeletons. The latter should depend on the availability of light and water, so the conversion rates should rise most quickly and plateau more slowly in well-lit, moist, nutrient-poor areas (Givnish et al. 1984).

The difference between the benefit and cost curves in Figure 18.1 can be used to predict whether carnivory should be favored in a given environment, and if so, what the optimal level of investment in carnivory would be. Carnivory should evolve if benefits rise faster than costs at low levels of investment in carnivory: if $dB/dx > dC/dx$ or, equivalently, if the initial marginal benefit of carnivory exceeds its marginal cost; or the initial slope of the benefit curve is steeper than that of the cost curve. The optimal level of investment in carnivory should occur where the difference between the benefit and cost curves is maximized: $dB/dx = dC/dx$.

p. 236

18.3 Predictions of the cost/benefit model

Thirteen specific predictions emerge from the cost/benefit model.

18.3.1 Carnivory is most likely to evolve and be favored ecologically in habitats that are sunny, moist, and nutrient poor

Sunny, moist, and nutrient-poor conditions are most likely to increase the initial steepness of the benefit curve; carnivory should evolve when nutrients alone limit photosynthesis, either directly or via effects on other processes (e.g., cell division) that limit photosynthesis (Figure 18.1a). This prediction does not depend on potential benefits of carnivory associated with decreased root function in anoxic soils (§18.3.10). Fertile substrates should elevate substantially the benefit curve but largely eliminate the marginal benefits of investment in carnivory, flattening $B(x)$ and working against the evolution and competitive ability of carnivorous plants (Figure 18.1b).

Many habitats are poor in nutrients. Wet soils *per se* are likely to be deficient in nitrate due to anoxia— O_2 diffuses 10,000 times more slowly in water than in air—reducing nitrogen fixation by free-living or symbiotic prokaryotes at $pO_2 < 40\text{--}50$ kPa (Serraj and Sinclair 1996), while denitrifiers remain metabolically highly active and release of nitrogen from dead plant tissue is greatly slowed (Vitousek and Howarth 1991). Ombrotrophic bogs are precipitation-fed and thus deficient in bedrock-derived P; consequently, they are also deficient in N because of the high energy requirements and P demands of N-fixers (Vitousek and Howarth 1991), and to the slow decomposition of dead plant remains. Ancient, highly leached soils and uplifted marine sands are likely to be deficient in both P and N (Chadwick et al. 1999), accounting for highly infertile sites in the boreal zone, the Atlantic and Gulf Coastal Plains of the USA, *tepui*s and adjacent sand plains of the Guyana Shield, and ancient sandy soils of South Africa and southwestern Australia, all hot-spots of carnivorous plant diversity (Givnish 1989). Frequent burning can impoverish soil fertility further by volatilizing leaf N and leading to partial losses of other nutrients from ash via leaching or runoff (Givnish et al. 1984). Paradoxically, calcareous spring-heads and highly calcareous soils may be P-

deficient but extremely rich in cations because of P complexing with Ca, especially as a result of the degassing of CO₂ and co-precipitation of P with CaCO₃ as insoluble calcite around spring-heads (Boyer and Wheeler 1989).

18.3.2 Epiphytism works against carnivory and favors myrmecotrophy

Perches on tree boles and branches are nutrient-poor and often sunny, but also are episodically dry and thus unlikely to support carnivorous plants (Givnish et al. 1984, Benzing 1990). Sunny perches are more likely to support ant-fed plants than carnivores because of reduced rates of evaporation in the internal chambers of ant-fed myrmecophytes versus the active secretion of nectar or digestive fluids in carnivores (Thompson 1981, Givnish et al. 1984). For bromeliads, Benzing (1990) argued that lower costs would permit ant-fed plants to tolerate more shade, and that lax, nearly horizontal-leaved taxa (e.g., *Nidularium*) would be adapted best to the low light and high humidity of forest understories, and obtain added nutrients from fallen leaf debris.

18.3.3 Optimal investment in carnivory in terrestrial plants should increase toward the sunniest, moistest, most nutrient-poor sites

Sunny, moist, and nutrient-poor conditions should increase the initial steepness of the benefit curve and shift the optimum level of investment in carnivory higher (Figure 18.1a). This prediction can help account for both spatial patterns and seasonal variation in the expression of carnivorous traits, including clines in pitcher-plant form and seasonal heterophylly—the production of noncarnivorous leaves at particular times of year.

p. 237

18.3.4 Optimal trap mechanism and form should depend on tradeoffs associated with environmental conditions, prey type, and trap type

Included here are variations in the form of sticky traps in *Drosera* and degree of leaf curling in *Pinguicula*, the advantage of snap-traps versus sticky traps in *Dionaea*, and the tradeoffs between wide-mouthed pitchers with wetttable peristomes versus narrow-mouthed pitchers with waxy scales and viscoelastic fluids in *Nepenthes* from rainier versus drier areas. Also pertinent are the conditions that favor carnivory versus other strategies (e.g., N fixation, myrmecotrophy, coprophagy, and detritus capture) that can provide alternative sources of limiting resources (Givnish et al. 1984, Givnish 1989, Benzing 1990, Bonhomme et al. 2011a, Bazile et al. 2012, C.R. Schöner et al. 2015).

18.3.5 Carnivorous plants should have low photosynthetic rates and RGRs

The advantage of carnivory lies not in absolutely high photosynthetic rates, but rather in an increase in benefits minus costs per unit leaf mass. The poor, wet soils likely to favor carnivory should, by themselves, lead to low photosynthetic rates and RGR. Unless a given investment in carnivory were to yield a substantially greater return of nutrients than the same energy invested in roots, carnivory is unlikely to reverse this situation. If there were such a large return/cost advantage of carnivory versus roots, most plants would have already become carnivorous.

18.3.6 Rainy, humid conditions or wet soils favor carnivores by lowering the costs of glandular secretion or permitting passive accumulation of rainwater

Pitcher plants and functionally similar bromeliads (*Brocchinia hecetioides*, *B. reducta*; *Catopsis berteroniana*) typically are found in areas of heavy rainfall and where the ratio of precipitation to evapotranspiration is high (Givnish 1989). The benefit of heavy rainfall and high humidity is seen most easily for species that impound rainwater (e.g., *Heliamphora*, *Sarracenia purpurea*, *Brocchinia*, *Catopsis*, *Paepalanthus*), but such conditions also should reduce the amount of fluid that others (e.g., *Cephalotus*, *Darlingtonia*, *Nepenthes*) must secrete. Potential origins of carnivorous pitchers as hydathodes (§18.5.6) also would be facilitated by wet soils. Root pressure should be investigated as a mechanism for maintaining abundant glandular secretions. A dry atmosphere or soil would greatly increase the costs of maintaining glandular secretions in plants with sticky traps. There is a tension between increased supplies of soil moisture and decreased rates of evaporation on the one hand, and increased rates at which glandular secretions are washed away on the other, which might work against plants with sticky traps in areas of heavy rainfall (Givnish 1989).

18.3.7 Possession of defensive glandular hairs should facilitate the evolution of carnivory

In essence, the pre-existence and co-use of glandular hairs would reduce the cost curve and favor carnivory for smaller increments to photosynthesis and the benefits curve (Figure 18.1c). This would favor one of Darwin's proposed pathways to carnivory—and one that was almost surely the basis of the evolution of carnivory in five of ten carnivorous clades (Chapter 3)—but do so on economic grounds, adding to Darwin's (1875) functional analogies.

18.3.8 Fire over infertile substrates favors carnivory

Fire increases light availability, and often soil moisture, because of reductions in above-ground biomass and leaf area. Fire also volatilizes N and reduces the availability of this element in the long term (Christiansen 1976). These shifts all tend to elevate and steepen the benefits curve (Figure 18.1a) and thus favor carnivory. Brewer et al. (2011) argue that carnivores may never have an edge over noncarnivores, and that fire favors them simply by opening competition-free space (Chapter 2). But this ignores the advantage in local competition (or at least physiological tolerance) that carnivorous plants have on such cleared sites relative to noncarnivores, and the edge in regional competition obtained by reproducing on such sites. In essence, Brewer hypothesized that carnivorous plants can have an advantage only where other plants cannot grow, and that there is no set of conditions, slightly more fertile, slightly less open, where they continue to have a growth advantage. This seems unlikely, but no experiment has yet tested this proposition.

18.3.9 The ability of carnivorous plants to grow on bare rock or sterile sands must have evolved in stepwise fashion

A progenitor with no alternative source of nutrients would have negative carbon balance (respiration, no photosynthesis) at zero investment in carnivory, so any initial small investment in carnivory still would leave plants with negative growth (Figure 18.1d). However, if a plant evolved carnivory on a slightly more fertile substrate, and then increased its investment to the optimal level there (Figure 18.1a), it might then be able to survive on substrates with zero substrate fertility.

18.3.10 Anoxic or toxic soils should favor carnivory on open, moist sites

Anoxic or toxic soils render root function costly; shifting part or all nutrient uptake to trap leaves above-ground would effectively lower the cost curve via reduced allocation to roots, and thereby favor the evolution of carnivory and higher optimal levels of allocation to carnivory. However, this hypothesis ignores the possibly complex interplay of allocation to leaves, roots, and traps and their impact on photosynthesis per unit leaf mass and whole-plant growth. To assess these tradeoffs, we present a simple, two-dimensional model to explore the impact of allocation to roots versus traps, which predicts increased allocation to traps and decreased allocation to roots on sites with unfavorable root environments (Box [18.1](#)).

Box 18.1

We ignore tissue respiration and mortality, assume that all tissues have the same construction cost, and further assume that the fractional allocations f_L , f_R , and f_C to leaf tissue, root tissue, and carnivory are constant and sum to 1. Let the water supply available per unit leaf mass $W = f_R \times \alpha_R / f_L$, where α_R measures the rate of water uptake per unit root mass, a function of root physiology and available water per soil volume. Let the supply of the most limiting nutrient $N = (f_R \times \beta_R + f_C \times \beta_C) / f_L$, where β_R measures the rate of nutrient uptake per unit root mass and β_C measures the rate of nutrient uptake per unit investment in carnivory. The β values reflect the physiology of roots and traps and the availabilities of the most limiting nutrient in soil versus air. Under these conditions, the parameter measuring the exponential rate of growth in whole-plant mass is $f_L \times A(W, N)$, where A_{mass} is photosynthetic rate per unit leaf mass, modeled as a compound Michaelis-Menten process, $A_{\text{mass}} = A_{\text{max}} \times W / (W + k_W) \times N / (N + k_N)$. The k values measure the extent to which additional water and nutrients can enhance photosynthesis; the smaller k is, the more rapidly A_{mass} rises with the supply of each resource and less of each resource is required to saturate photosynthesis.

The optimal allocation strategy (f_R, f_C) will always involve intermediate allocations to roots and leaves ($0 < f_R, f_L < 1$), given that only roots can provide water (this may not be valid for pitfall plants like *Brocchinia reducta*) and that zero growth would result if no energy or all energy were allocated to leaves. Low soil fertility, anoxia, or soil toxins that reduce root efficiency would reduce β_R enough so that it should favor nutrient capture by above-ground trap leaves and decreased allocation to roots.

This analysis is a “toy” model, in that the parameters have not been adjusted to reflect the behavior of real plants. Nevertheless, it can be used to show that carnivorous plants are most likely to evolve when nutrient availability to roots is low and that to traps is high, and when photosynthesis is responsive to nutrient increments and little root allocation is needed to saturate water supply. As expected, optimal allocation to roots (f_R) increases as α_R declines, while optimal allocation to carnivory (f_C) increases as k_N increases and β_C declines; at the transition to carnivory, increases in β_C result in a large increase in allocation to carnivory and large decrease in allocation to roots (Figure 18.2).

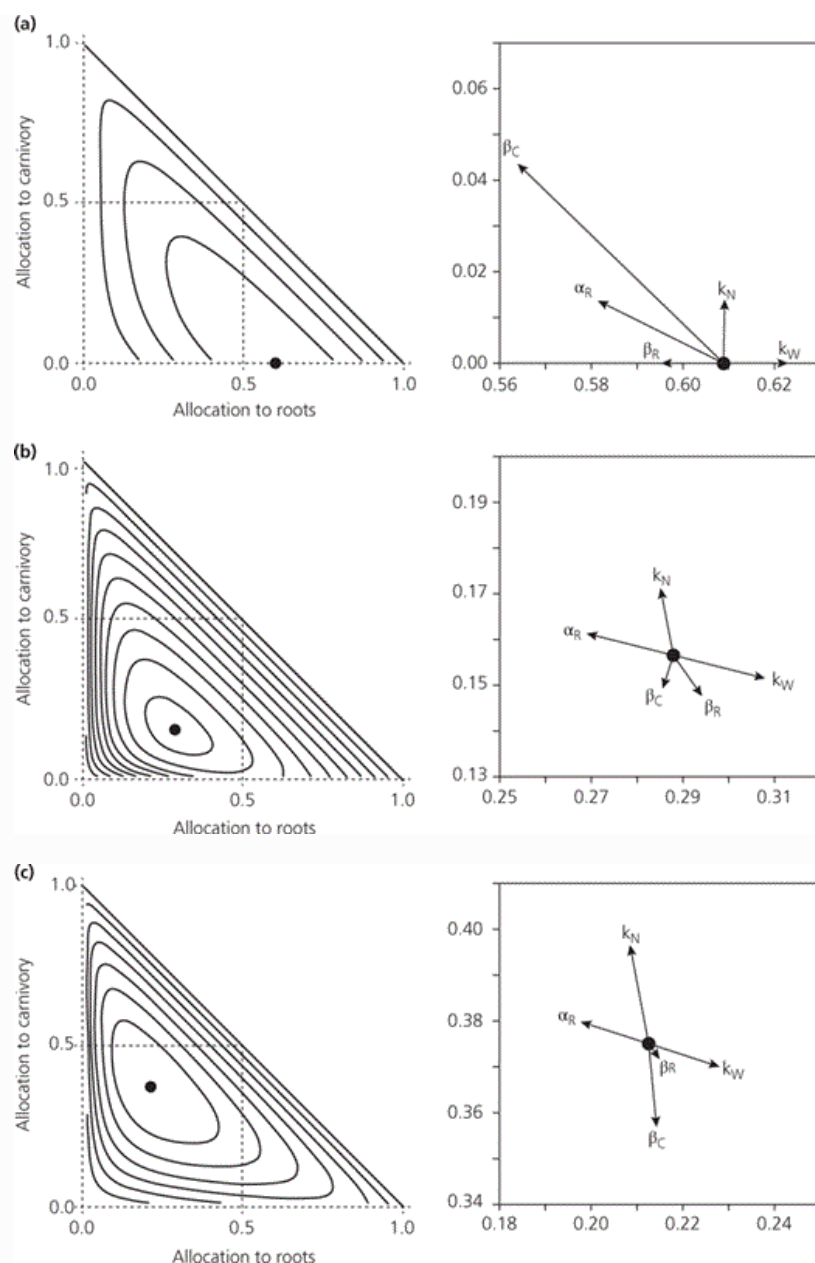


Figure 18.2 Two-dimensional cost/benefit model, plotting contours of the exponential coefficient of whole-plant growth rate against allocation to carnivory (f_C) and roots (f_R). Shown are contours of relative growth rate for (a) an edge optimum ($f_C = 0$) and (b, c) two internal optima ($f_C, f_R > 0$) (see Box 18.1). The dot in each left panel indicates the precise position of the optimum. Arrows in the enlargements (right) indicate shifts in each optimum resulting from a 20% increase in the value of the indicated parameters. For internal optima, increases in the effective delivery of the limiting nutrient per unit investment in carnivory (β_C)—or decreases in the same per unit investment in roots (β_R)—favor increased allocation to carnivory and decreased allocation to roots. A similar pattern may apply to some edge optima if the parameters favor a shift to carnivory. Greater water returns per unit root investment (α_R) favor increased root investment. Increased values of k_W decrease the value of additional small increments of water supply and result in decreased root allocation and increased allocation to carnivory; the opposite results from increased values of k_N , which decrease the value of additional small increments of nutrient supply. Parameter sets ($\alpha_R, \beta_C, \beta_R, k_N, k_W$) are (1.5, 3, 1.51, 1, 1.05) for the edge maximum, and (2.87, 3, 0.42, 0.26, 0.49) and (1.29, 0.92, 0.08, 0.57, 0.16) for the internal maxima in (b) and (c).

p. 239 Brewer et al. (2011) argued against carnivory evolving on wet soils through a mechanism that involved increasing photosynthetic rates because carnivorous plants have comparatively low photosynthetic rates (Ellison 2006); this misinterprets the cost/benefit model, which focuses on marginal, not absolute gains. Brewer et al. (2011) also suggested that carnivorous plants might be absent from dry sites not because such sites limit the benefits of carnivory, but because the shallow root systems of carnivores would exclude them from such sites. This claim involves a conundrum: do carnivorous plants have shallow root systems because
 p. 240 they often grow in wetlands with anoxic soils, or do their shallow root systems restrict them to wetlands?

Given that several carnivorous plants (including at least *Drosera rotundifolia*, *Byblis lamellata*, *Nepenthes pervillei*, and pygmy sundews) have extensive root systems to exploit rock fissures and deep, well-drained sands (Juniper et al. 1989, Conran et al. 2002, Adlassnig et al. 2005b), it appears likely that the shallow root systems of other carnivores were shaped by anoxic soils, rather than being an inevitable consequence of the carnivorous habit. Brewer et al. (2011) also argued that in wetlands, carnivory simply may be an adaptive alternative to the production of deep roots with extensive aerenchyma, and found that all carnivores in a Mississippi wetland lacked aerenchyma. However, this view ignores the negative impact of sodden soils on N availability (S18.3.1). Further, the absence of aerenchyma is simply not characteristic of all carnivores: *Darlingtonia californica* and many species of *Drosera*, *Pinguicula*, and *Sarracenia* have gas-filled intercellular spaces in their root cortex (Adlassnig et al. 2005b).

18.3.11 Growth co-limitation by multiple nutrients may favor the paradoxical increase in root investment seen in carnivorous plants that have recently captured prey

For a single nutrient, the two-dimensional model outlined in Box 18.1 would favor decreased root allocation whenever increases in prey density or capture efficiency elevate β_C . However, if two or more nutrients co-limit plant growth, and prey capture elevates the level of one of them, it could favor increased root growth and nutrient capture. This would be even more likely if one or more of the co-limiting nutrients were retrieved more cheaply from the soil than from prey ($\beta_C > \beta_R$). But increased root growth and metabolism also would likely lead to increased uptake of the nutrient(s) retrieved more efficiently from prey, perhaps explaining the paradoxical finding in some feeding experiments that carnivores absorb more of a limiting nutrient than are contained in the prey captured (Hanslin and Karlsson 1996, Adamec 1997a, 2002).

Without nutrient complementarity, the two-dimensional model would argue against any simple positive feedback involving prey capture leading to increased root allocation (e.g., Ellison and Gotelli 2001): if prey capture in a particular site is a better source of a single limiting nutrient ($\beta_C > \beta_R$), then prey capture should mainly stimulate more trap production. Adamec (1997a, 2002) argues that animal prey are such rich sources of N and P, and such poor sources of K and Mg, that prey capture might favor increased root growth to absorb K and Mg (Chapter 17). This intriguing idea could be tested by modeling the uptake and benefits of several different nutrients while implicitly assuming that all nutrients mentioned essentially co-limit growth (cf. Tilman 1982).

18.3.12 Paradoxically, in aquatic carnivorous *Utricularia*, harder, more fertile waters should favor greater investment in traps

Harder waters contain more cations, and often more P and N, but they also contain more CO₂ when in equilibrium with the atmosphere, and a greater pool of bicarbonate ions from which additional CO₂ can emerge as some is absorbed by photosynthesis (Hanson et al. 2006). Lakes also are often supersaturated in CO₂, presumably because of decomposing organic matter and dissolved inorganic carbon (DIC) delivered by springs (Hanson et al. 2006, Adamec 2008d, 2012b). Because of this large variation in CO₂ availability across lakes, and the much slower diffusibility of CO₂ in water than in air, photosynthesis by submersed aquatic plants can be strongly limited by CO₂ availability. Although there are more mineral nutrients (cations) in ponds with harder waters, and sometimes more PO₄-P and NO₃-N (e.g., Adamec 2008d), we suspect that the dominant effect setting optimal allocation to costly traps is CO₂ availability. The greater [CO₂] is, the greater should be the benefit in realized photosynthesis for a given increment to leaf nutrients via prey capture, favoring greater investment in traps (Adamec 2015a; Chapter 19).

18.3.13 Soil anoxia or extreme infertility militate against tall, woody plants and may restrict carnivory to short, mostly herbaceous plants

Woody plants, because of their secondary thickening, lack aerenchyma linking roots to leaves to air, and thus typically are excluded from sodden, nutrient-poor soils. Extreme soil infertility favors carnivory but not tall, woody plants (Givnish 2003, Givnish et al. 2014b). Together these considerations help explain why carnivory is restricted mostly to short, herbaceous plants.

18.4 Assumptions of the cost/benefit model

The modified cost/benefit model (Figures 18.1, 18.2) has five important assumptions: (1) the costs of carnivory, including the low photosynthetic capacity of trap leaves, are substantial relative to photosynthetic inputs; (2) as allocation to traps increases or prey density rises, prey capture should also increase; (3) benefits of carnivory include an increased rate of photosynthesis per unit leaf mass, an increased rate of conversion of photosynthate to new leaf tissue, or a reduction in photosynthate allocation to unproductive roots; (4) the marginal net benefits of carnivory should peak and then decline with increasing investments in carnivory as factors other than nutrients limit photosynthesis; and (5) prey capture should result in carnivorous plants having a higher growth rate than noncarnivores in the same microsites.

18.4.1 Costs of carnivory

The costs of carnivory can be substantial. *Drosera* from southwestern Australia allocate 3–6% of total photosynthesis to mucilage production alone (Pate 1986). *Darlingtonia californica*, *Sarracenia purpurea*, and two species of *Drosera* have photosynthetically inefficient trap leaves with lower photosynthetic rates per unit leaf mass at a given% leaf N content and specific leaf mass (SLM, g m⁻²), and a lower N content at a given SLM, than across noncarnivorous plants worldwide (Ellison and Farnsworth 2005). Ellison (2006) documented significantly lower rates of photosynthesis per unit leaf mass and whole-plant growth in carnivorous plants than in any of the other growth forms tabulated from a global database (Figure 18.3).

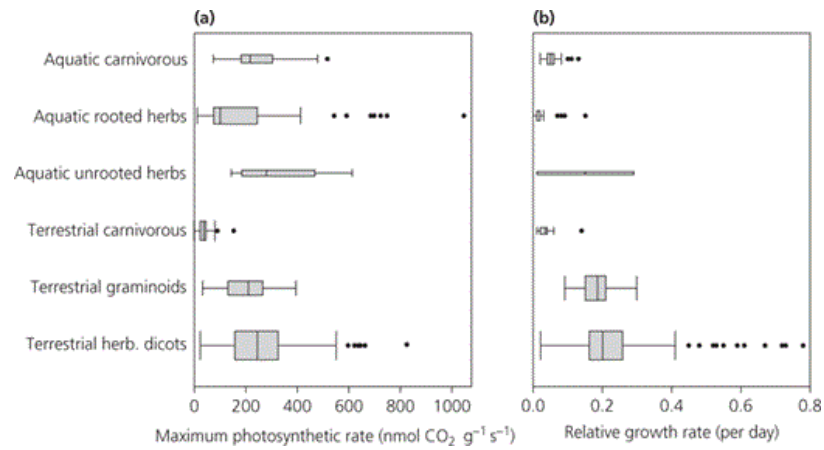


Figure 18.3 (a) Maximum photosynthetic rates per unit leaf mass ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) for species in six growth-form categories of herbaceous plants. Boxes indicate median rates (center horizontal line), upper and lower quartiles (limits of grey boxes), upper and lower deciles (horizontal lines delimiting ends of vertical lines), and individual observations beyond the latter range. Box width is proportional to sample size, from $n = 8$ for unrooted, submersed noncarnivores to $n = 141$ for terrestrial, herbaceous, noncarnivorous dicots. Note low rates for terrestrial carnivores vs. terrestrial noncarnivores; aquatic carnivores have rates comparable to those for aquatic noncarnivores. (b) Relative growth rates (RGR, $\text{g g}^{-1} \text{ day}^{-1}$) for the same growth forms. Boxes as above, with sample sizes ranging from $n = 2$ for unrooted, submersed noncarnivores to $n = 208$ for terrestrial, herbaceous, noncarnivorous dicots. Note the low values of RGR for terrestrial carnivores vs. noncarnivores. Growing conditions were not controlled across either dataset.

Redrawn from Ellison and Adamec (2011).

Although these data suggest either an opportunity cost (Givnish et al. 1984) or little increase in photosynthesis associated with carnivory, such interpretations neglect the fact that few of the noncarnivorous species included in Figure 18.3 occur in the same extremely unproductive habitats as the carnivorous ones. To identify differences between species that result from differences in traits rather than environments, it is necessary to control for ecological distribution. Pavlovič et al. (2007, 2009) and Pavlovič and Saganová (2015) avoided this problem by studying variation between lamina (leaf) and trap (pitcher) tissues in three species of *Nepenthes*, each grown under identical greenhouse conditions; their findings clearly identify an opportunity cost associated with trap production. Leaves outperformed pitchers in photosynthesis per unit mass for most levels of light availability and internal CO_2 concentration (c_i), apparent photochemical quantum yield (ϕ_{PSII}), stomatal density and conductance, tissue N and P concentration, and the concentrations of chlorophyll and carotenoids (Figure 18.4). Leaf tissue also had higher concentrations of Rubisco, consistent with the higher initial slopes of the $A-c_i$ curve.

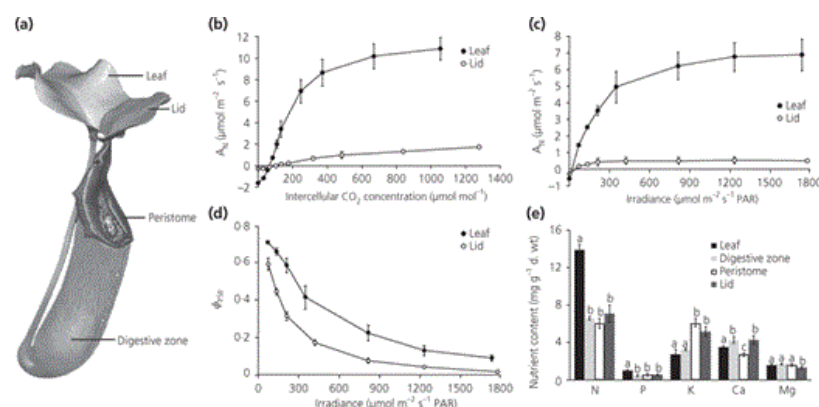


Figure 18.4 Data bearing on the cost/benefit model for evolution of carnivory in *Nepenthes*, based on comparisons between the pitcher (the lid being a flat part of the pitcher) and the leaf. (a) Leaf and pitcher of *Nepenthes truncata*. (b) A vs. c_i photosynthetic response curves. (c) Light response curves. (d) Light responses of effective photochemical quantum yield of photosystem II (Φ_{PSII}). (e) Elemental composition of the leaf vs. different portions of the pitcher. Data shown are means \pm SE ($n = 5$); different letters indicate significant differences among tissue types ($P < 0.05$; one-way ANOVA).

Redrawn from Pavlovič and Saganová (2015).

18.4.2 Allocation to carnivorous structures

The structural and opportunity costs of carnivory in trap construction are slightly smaller than estimates based solely on biomass allocation. A survey of 23 terrestrial carnivorous species showed that traps have a significantly lower construction cost per unit mass ($CC_{\text{mass}} = 1.29 \pm 0.20$ g glucose/g dry mass) than leaves or laminae (1.41 ± 0.14 g glucose/g DM) of the same species under the same conditions; the latter costs were similar to those of leaves of 267 noncarnivorous species across a wide variety of habitats (Karagatzides and Ellison 2009). Slightly lower CC_{mass} and much lower photosynthetic rates result in a long payback time for traps (Karagatzides and Ellison 2009).

Aquatic species of *Utricularia* allocate up to 61% of their vegetative mass to traps, which have dark respiration rates R_d (mmol kg⁻¹ dry mass h⁻¹) two to three times higher than leaves, and maximum photosynthetic rates A_{max} 7–10 times lower (Adamec 2006, 2008d). As a result, traps have high construction costs per plant, and high maintenance costs and low photosynthetic capacities per unit of bladder mass: R_d/A_{max} is 0.50–1.40 in traps but only 0.036–0.082 in leaves. High rates of trap respiration in *Utricularia* probably are related to the costs of pumping water from the trap (Adamec 2006, 2011f) and may underlie the evolution of a highly unusual, \downarrow energy-efficient mutation in the sequence of cytochrome c oxidase in *Utricularia* (Jobson et al. 2004).

Other continuing costs of carnivory, including nectar, mucilage, and enzyme secretion (Chapter 12); digestion and nutrient resorption (Chapters 3, 16); elemental allocation (Chapters 17, 19); electrical and jasmonate signaling in *Dionaea* and *Drosera* (Chapters 14–16); and resetting of aquatic trap leaves in *Utricularia* (Chapter 14) may be substantial, but many of these remain unquantified (Pavlovič and Saganová 2015). The peristome of *Sarracenia purpurea* secretes ≈ 70 μg cm⁻² h⁻¹ of carbohydrate as nectar (Deppe et al. 2000). Pitcher plants (*Cephalotus*, *Nepenthes*, Sarraceniaceae) secrete abundant nectar to attract prey, often ants (Givnish et al. 1984, Givnish 1989); observations on *Sarracenia alata* (Horner et al. 2012) and experiments on *S. purpurea* (Bennett and Ellison 2009) indicate that nectar secretion is critical in determining the rate of prey attraction and capture.

Respiration rates of traps often are very high during periods of high metabolic activity, including water pumping from *Utricularia*, rapid trap closure and prey retention in *Dionaea* (Pavlovič et al. 2010a, 2011a), and rapid tentacle movement in *Drosera* (Adamec 2010a). Costs of pumping water from recently triggered

Utricularia bladders may be increased further by spontaneous triggering of those bladders in the absence of animal prey, which can occur ≈ 15 –40 times during a typical trap's three-week lifetime (Adamec 2011f; Chapter 14). In two *Utricularia* species, 20–25% of newly fixed carbon is secreted into the trap fluid, including simple sugars (which may help feed symbiotic microbiota; Chapter 25), lactic acid, and phosphatases (Sirová et al. 2010, 2011). In aquatic *Aldrovanda* and *Utricularia*, the mineral costs of carnivory exceed 50% of total plant K and P, which may be related to the high energetic and elemental costs of pumping water from the traps that lead to very high concentrations of K in bladders (3.7–8.7% dry mass) and needs for ATP (Adamec 2010c).

p. 244 The costs to *Nepenthes* of producing waxes (0.02 – $0.61 \mu\text{g cm}^{-2}$) composed of aldehydes and viscoelastic fluids composed of long-chain polysaccharides are not yet known (Riedel et al. 2007, Bonhomme et al. 2011b). During the triggering and closure of \hookleftarrow *Dionaea* traps and the generation and propagation of action potentials, leaf respiration spikes to at least ten times the background rate, while non-photochemical quenching rises, and apparent quantum yield (ϕ_{PSII}) and photochemical quenching fall, each in successive waves (Pavlovič et al. 2010a, 2011a, Pavlovič and Saganová 2015). During trap closure, 29% of cellular ATP is lost (Jaffe 1973). During the digestive phase, respiration rates of *Dionaea* traps more than double, while net photosynthetic rates in bright light fall by roughly 20% (Pavlovič and Saganová 2015).

Given the high costs of prey digestion, water pumping, and electrical signaling, Pavlovič and Saganová (2015) proposed that the inducible rather than constitutive nature of these processes is key to the evolution of rapidly closing traps and plant-mediated digestion. Jasmonates, well-known plant defense hormones, are involved in this inducibility and their accumulation can also affect photosynthetic reactions (Krausko et al. 2017). In noncarnivorous plants, jasmonates act as signals to redirect the gene expression and biosynthetic capacity from photosynthesis and growth to defense (Chapter 16), a significant allocation cost for plants that may be offset by the fitness benefit of not incurring these costs when defense is not needed. In carnivorous plants, jasmonates induce production of digestive enzymes, which are pathogenesis-related proteins (Buch et al. 2015, Bemm et al. 2016), and their accumulation also can affect photosynthetic reactions in *D. capensis* (Krausko et al. 2017). Given the long time between meals for snap-traps of *Dionaea* (≈ 23 days; Gibson and Waller 2009), the savings from inducible carnivory might be large.

18.4.3 Prey capture increases with allocation to carnivory

Increased mucilage production, droplet size, and gland density increase the apparent rate of prey capture in *Pinguicula vallisneriifolia* (Zamora 1995). Prey capture in *Sarracenia alata* increases with trap size (Green and Horner 2007, Bhattarai and Horner 2009) and nectar secretion rate (Horner et al. 2012). Larger traps of *Dionaea* capture larger prey at roughly the same rate as smaller traps capture smaller prey, so larger traps capture far more biomass per unit time (Gibson and Waller 2009). *Dionaea* releases a cocktail of more than 60 volatile organic compounds (VOCs), including terpenes, benzenoids, and aliphatics, that increase attraction of *Drosophila* under lab conditions (Kreuzwieser et al. 2014). Field studies in Borneo have shown a similar value of VOCs in attracting flies and ants to *Nepenthes rafflesiana* pitchers (Di Giusto et al. 2010). Absence of benzenoids in pitchers near ground level led to the attraction mainly of ants.

Comparisons among *Nepenthes* species highlight a complex series of tradeoffs among energy allocation to a large peristome, slippery waxes, and viscoelastic trap fluids (Chapters 12, 15). In species without viscoelastic fluids, prey capture increases with allocation to trap waxes, whereas species with viscoelastic fluids capture more prey than species dependent on slippery waxes alone; investments in these two mechanisms are negatively correlated (Bonhomme et al. 2011b).

Small investments in carnivory can yield intermittent but predictable bonanzas. The peristome of several *Nepenthes* is extremely slippery when wet by rain, fog, or nectar, but not when dry (Bauer et al. 2008;

Chapters 12, 15). The inefficiency of traps during dry periods allows scout ants to recruit large numbers of workers to extrafloral nectaries (EFNs); large batches of workers then can be captured under wet conditions (Bauer et al. 2015a). Continuous experimental wetting of the peristome increases the number of non-recruiting prey but decreases that of ants, with trapping shifting from batches to individuals. A wettable peristome thus appears to be an adaptation for capturing ants or other social insects (Bauer et al. 2015a; Chapter 15). Waxy zones below the peristome are effective under both wet and dry conditions; the latter are likely in the seasonal lowlands. Capture rates of ants by *Nepenthes* increase with extrafloral nectar and slippery wax walls (Gaume et al. 2016), whereas termite capture increases with the presence of a rim of edible trichomes (Merbach et al. 2002) and symbiotic association with ants. Capture of flying insects increases with pitcher aperture and presence of alluring odors.

p. 245

The unique status of *Nepenthes bicalcarata* as both a carnivorous plant and a myrmecophyte long has been puzzling (Beccari 1904, Givnish 1989; Chapters 23, 26). It invests in domiciles in the form of swollen tendrils for its ant partner, *Camponotus schmitzi*, and its EFNs prove the ants with food. *Camponotus schmitzi* can run safely over the slippery trapping surfaces, and dives into the pitchers to retrieve prey (Clarke and Kitching 1995, Merbach et al. 2007). The benefits of this kleptoparasitism are unclear, but the plant gains two advantages from investing in ants. First, ants attack and prey on inquiline dipteran larvae that feed on prey captured by the pitcher, preventing their escape from traps and loss of prey-derived nutrients (Bonhomme et al. 2011a, Scharmann et al. 2013). Second, the ants clean the peristome surface and maintain its ability when wet to “aquaplane” prey into the pitcher fluid (Thornham et al. 2012; Chapters 12, 15); the presence of *C. schmitzi* increases prey capture by 45%. Fungal hyphae contaminate the peristomes of ant-free older pitchers; experimental contamination of clean peristomes with starch also greatly reduced capture efficiency. Peristomes of ant-colonized pitchers were cleaned and returned to high capture efficiency in about one week. *Nepenthes bicalcarata* has unusually long-lived pitchers, which may have driven its unusual investment in what we might term ant butlers (Thornham et al. 2012).

18.4.4 Benefits of carnivory

Experimenting with *Drosera rotundifolia*, Francis Darwin (1878) provided the first demonstration that prey capture increased the growth and reproduction of carnivorous plants. Pavlovič and Saganová (2015) recently showed that feeding increased the photosynthetic rates of carnivorous plants in 16 of 19 species spread across *Aldrovanda*, *Dionaea*, *Drosera*, *Nepenthes*, and *Sarracenia*. In most terrestrial carnivorous plant species, increases in photosynthetic rates are positively correlated with increases in leaf N or P concentration and whole-plant growth (Ellison 2006, Pavlovič and Saganová 2015; Chapter 17). Comparable findings for aquatic carnivores are rare and inconsistent (Adamec 2000, 2008d, Adamec et al. 2010c; Chapter 19). Ellison and Adamec (2011) argued that this difference might simply reflect the greater methodological challenges of working with *Utricularia*’s tiny bladders.

Early studies that failed to show an impact of prey capture on photosynthetic rate (e.g., Méndez and Karlsson 1999, Wakefield et al. 2005) measured gas exchange on fully expanded leaves that had been fed for a short period, in which up-regulation of photosynthesis might not have occurred for several reasons. In contrast, measurements of photosynthesis on newly produced leaves (e.g., Farnsworth and Ellison 2008) generally find up-regulation following feeding. This result is consistent with increased allocation of nutrients in newly formed leaves in many carnivorous genera (Schulze et al. 1997, Butler and Ellison 2007, Kruse et al. 2014).

Increased flowering and seed production as a consequence of feeding has been reported in several terrestrial species (e.g., Darwin 1878, Karlsson and Pate 1992, Thorén and Karlsson 1998, Pavlovič et al. 2009; Chapter 17). The question remains whether these phenomena are caused by increased photosynthesis and plant growth, or direct limitation of reproduction by certain critical nutrients, not carbon (Givnish et al. 1984).

Increased growth after feeding also may reduce the time required to achieve minimum flowering size (Pavlovič et al. 2009).

18.4.5 Plateauing benefits of carnivory

A meta-analysis of 29 studies demonstrated a significant positive effect of feeding on growth ($P < 0.02$), but no significant effect of nutrient additions ($P = 0.15$) or nutrient \times prey interaction ($P = 0.81$), showing that additional nutrients contributed by carnivory are less valuable when plants are growing on more nutrient-rich substrates (Ellison 2006). Direct evidence of a plateauing of the photosynthetic benefits of carnivory, however, is sparse. Increased feeding of ten *Sarracenia* species in a greenhouse led to a rapid rise to a maximum A_{mass} ($r^2 = 0.51$, $P < 0.02$) and fluorescence ratio F_v/F_m ($r^2 = 0.74$, $P < 0.0015$) (Farnsworth and Ellison 2008; Figure 18.5). Additional studies should be conducted to test whether this effect applies to a wide range of carnivores.

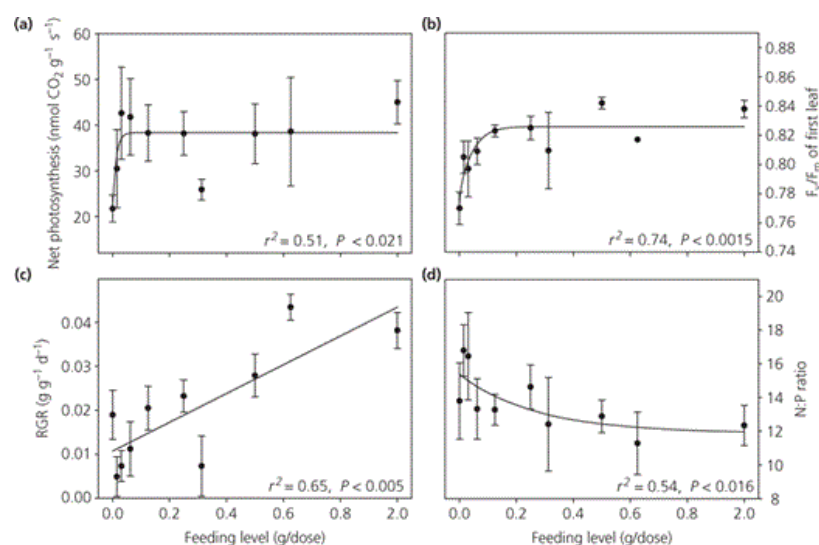


Figure 18.5 Responses of (a) net photosynthesis per unit leaf mass, (b) fluorescence ratio F_v/F_m of the first leaf, (c) RGR ($\text{g g}^{-1} \text{ day}^{-1}$), and (d) N:P ratio to experimental feeding in ten *Sarracenia* species ($n = 12/\text{species}$). Points are means \pm SE for all plants at each feeding level and all variables showed significant responses across species to feeding ($P < 0.05$, ANOVA). Curves for (a) and (b) are non-linear regressions fit to a three-parameter exponential rise to a maximum [$y = y_0 + a(1 - e^{-bx})$]; (c) is a linear regression; and (d) is a non-linear fit to a three-parameter exponential decay ($y = y_0 + ae^{-bx}$).

Redrawn from Farnsworth and Ellison (2008).

18.4.6 Growth advantage of carnivorous plants

Experiments supporting a growth advantage of carnivorous versus noncarnivorous plants have not been done, perhaps because they would require a unique combination of physiological and ecological approaches under field conditions for both types of plants. The studies that come closest to supporting this assumption are those that show a significant advantage of fed carnivores over unfed carnivores in photosynthesis or growth under the same lab or field conditions (§18.4.4, 18.4.5). For example, van der Ent et al. (2015) found that five montane *Nepenthes* species had similar leaf N but higher leaf P contents relative to 34 co-occurring noncarnivorous plants. This study needs to be followed up with investigations of gas exchange, whole-plant growth, and competitive interactions.

18.5 Tests of predictions of the cost/benefit model

18.5.1 Botanical carnivory is most likely in nutrient-poor, sunny, and moist habitats

The great majority of carnivorous plants in fact grow in sites that are nutrient-poor, sunny, and moist, at least during the growing season (Heslop-Harrison 1978, Thompson 1981, Lüttge 1983, Givnish et al. 1984, Juniper et al. 1989, Midgley and Stock 1998, McPherson 2010, Pereira et al. 2012, Nishi et al. 2013). Such habitats include bogs and wet tundra, open sites on moist to wet sands and other highly leached soils, fire-swept substrates, bare rock, and oligotrophic ponds and streams.

There are few exceptions to this rule. *Drosophyllum lusitanicum* actively grows on arid sites during the dry Mediterranean summer, but has a relatively extensive, deep root system that may tap groundwater (Adamec 1997a, 2009a, Adlassnig et al. 2005b) and hygroscopic glandular secretions that may allow substantial water uptake from fog (Adamec 2009a). A few shade-loving *Drosera* (*D. adelae*, *D. prolifera*, *D. schizandra*) inhabit the understories of Queensland rain forests, but they are only weakly carnivorous, possessing few glandular tentacles per leaf or slow-moving to stationary tentacles (Givnish et al. 1984, McPherson 2008). Other *Drosera* (e.g., *D. erythrorhiza*, *D. falconeri*) occur on calcareous sands (Adlassnig et al. 2005b). *Nepenthes* vines mostly inhabit forest openings on nutrient-poor soils, but several grow on base-rich calcareous or serpentine soils; few species are epiphytic or grow under closed canopies (Givnish et al. 1984, Clarke and Moran 2016). *Darlingtonia* also is endemic to serpentine soils (Ellison and Farnsworth 2005). Most *Utricularia* are aquatic or grow on moist open ground in highly oligotrophic sites (Adamec 1997a), but a few species grow in hard, cation-rich waters (e.g., the Florida Everglades, McCormick et al. 2011) or tolerate shade (Adamec 2008a); 12 of ~240 species are epiphytic in cloud forests (Fleischmann 2015a; Chapter 8).

Substantial numbers of species (>30) of *Pinguicula* occur on calcareous substrates, especially in México but also at mid- to high latitudes in Europe (Basso 2009). Karlsson and Carlsson (1984) found that growth of *Pinguicula vulgaris* on a calcareous mire substrate was more limited by P. This result is consistent with our expectations: calcareous soils may be base-rich but P available to plants may be in short supply (§18.3.1). Several *Pinguicula* species in México and Europe occupy partly to densely shaded microsites, with the distribution of some apparently representing an adaptive compromise between sunny but dry and insect-poor microsites and shady but moist and insect-rich microsites (Zamora 1995, Zamora et al. 1998, Alcalá and Domínguez 2003, 2005).

Seasonal growth or expression of carnivory explains other apparent exceptions. Several tuberous *Drosera* occupy extremely nutrient-poor but semiarid upland sites in southwestern Australia, but are active mostly during the moist winter and spring (Erickson 1978) and thus are not an exception to predictions. Similarly, butterworts in México stop producing sticky mucilage during the dry season, when few insects are present (Alcalá and Domínguez 2005). The single species of *Triphyophyllum* undergoes its carnivorous phase in the understory of seasonally waterlogged forests on shallow lateritic soils in West Africa, with carnivorous individuals seen both under canopy openings and dense shade (Green et al. 1979, A. Fleischmann *personal communication*).

Based on tissue stoichiometry, most terrestrial carnivorous plants appear to be limited by N, P, or both N and P (Figure 18.6). In contrast, aquatic *Aldrovanda* and *Utricularia* may be limited by K, which may reflect their heavy investment of K in below-water traps and water pumping (Adamec 2010c), lack of K recycling from old tissues, and low [K] in some waters (Ellison and Adamec 2011; Chapter 19). Two points should be made regarding these inferences. First, the N:P:K stoichiometry of leaf tissue shown is downstream of elemental inputs via carnivory. Data for a limited number of terrestrial species indicate that nutrient inputs from prey enhance both foliar N and P contents by small to quite large amounts (Ellison 2006), but the

effect appears reversed in aquatic *Aldrovanda* and several *Utricularia* species (Adamec 1997a, 2000, 2008d). Second, N:P:K stoichiometry only indicates relative amounts of growth limitation by these elements (Olde Venterink et al. 2003), not the total amount by which plant growth could be increased by *ad libitum* nutrient additions. This total limitation is likely to be quite large for carnivorous plants, but it has never been measured.

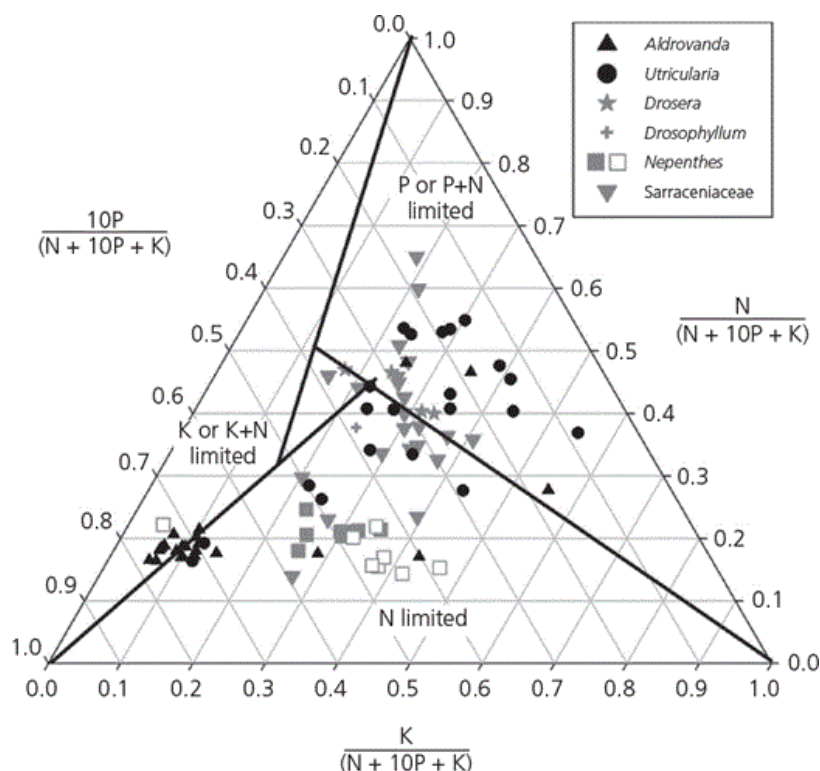


Figure 18.6 Tissue stoichiometry for aquatic submersed carnivorous plants (black) and terrestrial carnivorous plants (grey). Solid symbols indicate entire plants or traps; open symbols indicate leaves (laminae) measured separately on *Nepenthes*. Sarraceniaceae here includes *Darlingtonia* and *Sarracenia*. Dark diagonals separate regions of N, P or P + N, and K or K + N limitation following Olde Venterink et al. (2003).

Redrawn from Ellison and Adamec (2011).

18.5.2 Carnivorous epiphytes should be rare but myrmecophytic epiphytes should be more common

Tree branches and boles are nutrient-poor, but often are shady and moist or sunny and dry. Thus the cost/benefit model would predict that epiphytes rarely should be carnivorous.

Of the nearly 800 species of carnivorous plants, only 17 (2%) are epiphytic, including four *Nepenthes* (Chapter 5), twelve *Utricularia* (all in *U. sect. Orchidoides*; Chapter 8), and one *Catopsis* (Chapter 10). This compares with an estimated 9% of epiphytic species among all the nearly 300,000 species of angiosperms (Zotz 2013). If carnivory were randomly distributed among angiosperms, we would expect there to be ~70 carnivorous epiphytes, four times more than are known.

True epiphytism among carnivorous plants may be even rarer than these numbers suggest, as many carnivorous epiphytes live in wet microsites that differ little, functionally, from those typically occupied by aquatic bladderworts. Five of the 12 epiphytic *Utricularia* species often grow as emergent aquatic plants in open microsites, frequently living in the tanks of sunlit bromeliads, including the carnivorous *Brocchinia*

hechtioides and *B. reducta*. A single truly epiphytic species (*U. quelchii*) studied by Porembski et al. (2006) allocated only 15% of its biomass to leaves, just above the average of $8.1 \pm 1.5\%$ (SD) in six small terrestrial *Utricularia* species and well below the average of $59.1 \pm 1.0\%$ in three aquatic species. Even more remarkably, the leaf:trap biomass ratio for epiphytic *U. quelchii* was 0.50, much smaller than the ratios of 3.9 ± 1.3 for aquatic species and 32.4 ± 17.6 for terrestrial species. This raises the question of whether *U. quelchii* and the few other epiphytic species growing on densely shaded, mossy boles and branches can obtain carbon autotrophically via photosynthesis or heterotrophically via carnivory. *Utricularia* can grow in the dark when provided with sucrose (Harder 1970), and the tiny leaves of many annual terrestrial species suggests they might be heterotrophic. These terrestrials produce so few traps, however, that heterotrophy seems unlikely (Porembski et al. 2006). Such is not the case for epiphytic species like *U. quelchii*, which should be investigated as possible heterotrophs or mixotrophs.

As predicted by cost/benefit analysis, myrmecotrophy is far more common in epiphytes than carnivory. Almost all the ≈ 200 ant-fed plants originally tallied by Thompson (1981) are epiphytes, mostly occupying sunny or partly shaded perches; many more species (e.g., in *Tillandsia*) would be added to this list if it were recompiled today. At least 93 more species—all epiphytes—receive nutrients from ant gardens growing around their roots, as well as possibly other services, including seed dispersal and protection against herbivores (Orivel and Leroy 2011).

18.5.3 Investment in carnivory by terrestrial plants should increase toward the sunniest, moistest, most nutrient-poor sites

One confirmation of this prediction is the cline in the relative size of the photosynthetic keel versus the carnivorous tube of the northern pitcher plant (*Sarracenia purpurea*) across a nitrogen deposition gradient in New England (Ellison and Gotelli 2002; Figure 18.7a). Across 26 bogs, carnivorous pitchers were smaller while photosynthetically more efficient keels were larger where the concentration of ammonium in the pore water (and, presumably, in precipitation) was greater. The two exceptions to this rule apparently involved cases where tissue N:P stoichiometry suggested that P rather than N was limiting (Ellison and Gotelli 2002). Within a single bog remote from coastal industrial areas, plots experimentally sprayed with different concentrations of NH_4NO_3 developed pitchers that exhibited a similar pattern to that seen across the N deposition gradient (Figure 18.7b). Pitchers in another bog that were fed N and P solutions exhibited a regular shift toward relatively large keels and small tubes with increasing N (Figure 18.7c). As expected, pitchers with larger keels had higher photosynthetic rates. Similarly, feeding *Sarracenia* (Weiss 1980) and fertilizing *Nepenthes* (Pavlovič et al. 2010b) often suppresses trap formation and facilitates phyllode production. Variation in relative tube and keel size also occurs in response to natural variation in macronutrient availability in different wetland types (Bott et al. 2008). Feeding *Dionaea* decreases the trap:petiole ratio and red trap pigmentation (Gao et al. 2015).

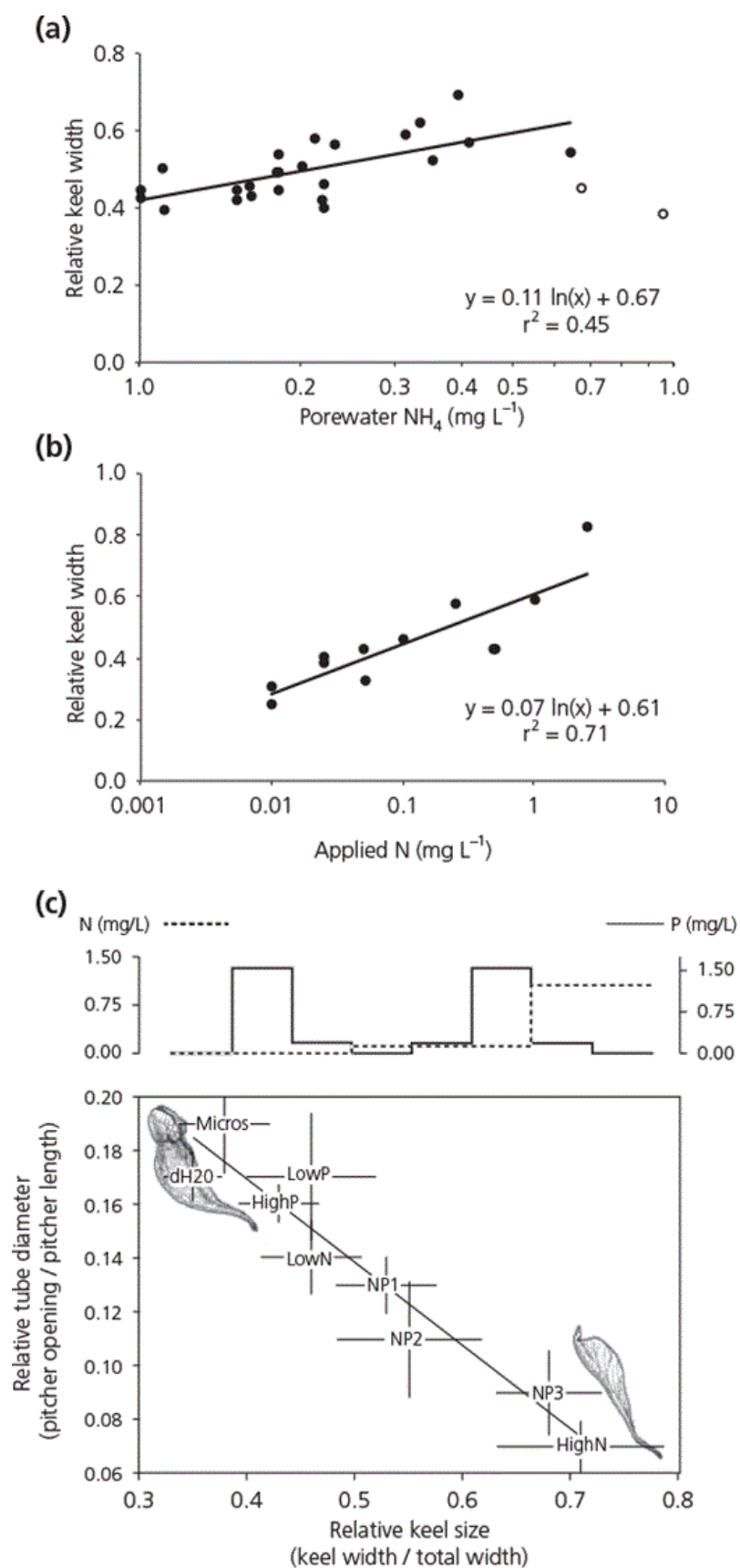


Figure 18.7 (a) Allocation to photosynthesis vs. carnivory measured by relative keel width [keel width/(keel width + tube width)] in *Sarracenia purpurea* growing in 26 bogs along an anthropogenic nitrogen deposition gradient (measured as pore-water NH_4) in Massachusetts and Vermont, USA. RKW (relative keel width) = $0.11 \times \ln [\text{NH}_4] + 0.67$ ($r^2 = 0.45$, $P < 0.001$), excluding two Vermont outliers that appear to be P-limited (hollow symbols). (b) Relative keel width as a function of the concentration of N

experimentally sprayed on the substrate at Molly Bog, Vermont, USA: $RKW = 0.07 \times \ln [N] + 0.61$ ($r^2 = 0.71$, $P < 0.001$). (c) Relative keel width and tube diameter as a function of the concentrations of N and P (upper panel) regularly added to the tank fluid of 90 plants at Hawley Bog, Massachusetts, USA. Insets show form of leaves at either end of the nutritional gradient.

Redrawn from data provided by Ellison and Gotelli (2002).

Among the three *Drosera* species native to the New Jersey Pine Barrens, leaves of *D. rotundifolia* growing on partly shaded hummocks are horizontal and broad, with a relatively small trap surface. In contrast, leaves of *D. filiformis*, which grows on wet sand and *Sphagnum*, are vertical and thread-like with a relatively large trap surface. *Drosera intermedia* is intermediate in leaf shape, relative trap volume, and likelihood of shading (Givnish 1989). In *Drosera rotundifolia* grown in outdoor plots, Thorén et al. (2003) documented significant declines in leaf stickiness—reflecting the amount of mucus secreted by the tentacles and the polysaccharide concentration of the secretions—with experimental shading and additions of nutrients, with nutrients having a larger effect. These patterns are consistent with the cost/benefit model for carnivory, although Thorén et al. (2003) interpreted them in light of the carbon/nutrient-balance theory of Bryant et al. (1983). However, the quantitative pattern of secretion of the anti-microbial agent 7-methyljuglone contradicted the carbon/nutrient-balance theory.

p. 250 Mucilage secretion in *Pinguicula vallisneriifolia* increased from deeply shaded to sunny microsites in Spain; leaves varied from curled and more secretory in sun to nearly flat and dry in shade (Zamora et al. 1998). During the Mediterranean summer, sunny sites offer maximum amounts of light, while shaded sites offer maximum amount of moisture and prey, shaping allocation to carnivory and resulting in highest reproduction in intermediate sites. Similarly, peak fitness of *P. moranensis* growing in México occurred in the middle of a light–water–prey gradient, where selection for, and investment in, capture glands was greatest in N-poor environments (soil and prey supplies). Selection for, and investment in, digestive glands was greatest in N-rich environments (Alcalá and Domínguez 2005).

Many carnivorous plants do not produce traps, or produce leaves with a lower allocation to carnivory, during unfavorable seasons when factors other than nutrients may limit growth. Such patterns of seasonal heterophylly also appear to support the predictions of the cost/benefit model (Givnish et al. 1984, Givnish 1989). *Sarracenia flava*, *S. oreophila*, and *S. leucophylla* develop trapless phyllodes during late summer droughts (Christiansen 1976, Weiss 1980). *Cephalotus* develops phyllodes during winter; *Dionaea* produces leaves with broader photosynthetic petioles and smaller traps in winter as well (Slack 1979). Many Mexican *Pinguicula* lose their carnivorous leaves and sprout succulent leaves, or die back to resting stages to survive the winter drought (Alcalá and Domínguez 2005). *Nepenthes* may not develop pitchers in excessively dry or shady sites (Slack 1979). The seasonal flush of glandular leaves in juvenile *Triphyophyllum* occurs at the beginning of the rainy season, as the soil becomes waterlogged and insect abundance may peak, and before the heavy rains likely to wash away glandular secretions (Green et al. 1979).

18.5.4 Form and function of traps depends on tradeoffs associated with environmental conditions and prey type

Studies on *Nepenthes* over the past decade provide some of the most compelling examples illustrating this prediction. Most *Nepenthes* occur in forests edges and openings over highly infertile soils and prey on arthropods, mainly ants (Juniper et al. 1989, Clarke 1997, Clarke and Moran 2016), using one or more of three trapping mechanisms, involving epicuticular waxes, a wetttable peristome, and viscoelastic pitcher fluid (Moran et al. 2013; Chapters 12, 15, §18.4.3).

Bonhomme et al. (2011b) proposed that the nature of insect prey helped determine which of these mechanisms was most effective, and showed that waxier pitchers were more effective at capturing ants,

that viscoelastic fluids were more effective against flies than ants, and that flies were more prevalent than ants in cloud forests at higher elevations. Moran et al. (2013) argued instead that climate shaped pitcher form and trapping mechanism, showing that perhumid cloud forests were strongly associated with large peristomes (with a large limb inside the pitcher), waxless pitchers, and viscoelastic fluid, whereas more seasonal lowlands were associated with small peristomes, waxy pitchers, and non-viscoelastic fluid. Gaume et al. (2016) proposed that both climate and insect prey shape pitchers: waxy traps and cylindrical pitchers with narrow apertures are associated with seasonal lowland areas and mainly capture ants and termites, whereas funnel-shaped traps with wide apertures, viscoelastic fluids, and aromatic traps dominate perhumid cloud forests and mainly capture flying prey. Wettable peristomes also can be highly effective in the seasonal lowlands, based on mass recruitment to nectaries during dry periods, when the pitchers are “safe,” followed by mass captures under wet conditions (Bauer et al. 2012a).

Three *Nepenthes* species with giant pitchers at high elevations—*N. lowii*, *N. macrophylla*, *N. rajah*—have become partly to largely dependent on the feces of tree shrews and rats for N capture (Clarke et al. 2009, Chin et al. 2010, Greenwood et al. 2011; Chapters 15, 26). All three have large, concave lids that secrete abundant nectar and are held at nearly right angles to the pitcher; the distance from the lid glands to the front of the pitcher orifice precisely matches the length of the head plus body of the tree shrew (*Tupaia montana*) to ensure capture of feces when it visits the pitcher to feed from the lid. Feces account for 57–100% of foliar N in *N. rajah*, but all three species continue to capture arthropod prey presumably because of its superiority as a source of N (9.8% of insect mass versus 4.9% for feces).

Nepenthes ampullaria, with its unusually short, wide-aperture pitchers with highly reflexed lids at ground level, is adapted to detritivory and obtains >35% of leaf N from fallen leaves that collect in its pitchers, despite N content of those leaves being only 1.2% (Moran et al. 2003, Pavlovič et al. 2011b). It is one of three species with highly specialized nutrient-capture strategies adapted to densely shaded conditions under closed-canopy heath forests and peat swamps. The others are *N. bicalcarata*, with ant butlers that keep its long-lived pitchers functional (§18.4.3), and *N. hemsleyana*, that serves as a bat roost and obtains substantial amounts of its foliar N in that way (Grafe et al. 2011, C.R. Schöner et al. 2015; Chapter 15). Presumably, these three species can tolerate densely shaded conditions because they have substantially or greatly reduced secretion of nectar and tank fluid (especially in *N. hemsleyana* and *N. ampullaria*; C.R. Schöner et al. 2015), because the costs of bat-plant mutualism are low for each partner (C.R. Schöner et al. 2015), or because ant guarding and long-lived pitchers in *N. bicalcarata* increase the efficiency of those pitchers and reduce their cost of replacement (Thornham et al. 2012).

Darwin (1875) suggested that the rapidly closing snap-traps of *Dionaea* and *Aldrovanda* facilitate escape of small prey through the spaces between the marginal teeth. This feature, together with digestion in an enclosed chamber, may have arisen to capture larger, and consequently more rewarding, prey than could be immobilized by the sticky traps ancestral to Droseraceae. Gibson and Waller (2009) supported this hypothesis using a simple economic model and data on the distribution of body masses of insect prey and escape from both snap traps and sticky traps as a function of body size. Larger plants with larger traps should have a very large advantage in growth, making early prey capture especially important. Prey capture enhances long-term photosynthesis in *Dionaea* (Kruse et al. 2014), but in the short term leads to a spike in respiration and reduced photosynthesis associated with trap closure, prey retention, and digestion (Pavlovič et al. 2010a, 2011a), leading Pavlovič and Saganová (2015) to argue that the inducibility of costly enzyme secretion in plants with active traps may be crucial to their evolution (§18.4.2).

Finally, the return on carnivory in *Roridula dentata* is strongly context-dependent, and varies non-linearly with the density of hemipterans (*Pameridea*) that cruise its leaves, eating trapped insects and defecating on leaves. At very low and very high hemipteran density, growth of *Roridula* is negative, reflecting little or no N input due to the absence of bugs or their abandonment of host plants after consuming all prey (Anderson

and Midgley 2007). Variation in the density of *Pameridea* predators or competitors may thus determine the value of carnivory in *Roridula*.

Other forms of trophic interactions also may facilitate the origin or maintenance of carnivory. Joel (1988) and Givnish (1989) independently proposed that pitcher plants in the genera *Cephalotus*, *Nepenthes*, and *Sarracenia*—all of which prey primarily on ants—may actually be mutualists with their prey. Plants in nutrient-poor habitats are long on carbohydrates but short on N, P, and other mineral nutrients, whereas ants in the same environment may be relatively long on nutrients, because of their predation on insects, but short on carbon. Given the large amount of nectar provided by ant-specialist pitcher plants, and the few individuals from colonies that are lost to pitchers, it might pay ant colonies to sacrifice the occasional sister into the well for all the sugar gained, just as it might pay plants to provide ants with large amounts of sugar if they obtain enough nutrients from the occasional ant prey to elevate photosynthesis by a greater amount. Moon et al. (2010) demonstrated experimentally that *Sarracenia minor* earns a net benefit from its interactions with ants; the question remains whether a net benefit also accrues to the ants. If these ant specialists are mutualists with their prey, there would be a positive feedback between the potential benefits from carnivory and increasing prey density—an outcome not originally envisioned by either Joel (1988) or Givnish (1989).

18.5.5 Carnivorous plants should have low photosynthetic rates and RGR

p. 252 Meta-analyses support these predictions (Ellison 2006, Ellison and Adamec 2011). Both terrestrial and aquatic carnivorous plants have lower rates of photosynthesis and whole-plant growth than most other types of plants, but aquatic carnivorous plants have rates of both that are similar to or exceed those of aquatic noncarnivorous plants (Adamec 2013; Figure 18.3). Initially, these comparisons led Ellison (2006) to conclude they were evidence against the cost/benefit model. However, they are not; the model only predicts that carnivory will evolve if it produces a net increase in growth, not a high absolute growth rate. The key question, therefore, is how the photosynthetic rates and RGRs of fed and unfed carnivorous plants would differ from one another and from noncarnivorous species growing in the same nutrient-poor habitat. None of the comparisons presented by Ellison (2006) or Ellison and Adamec (2011) are controlled in this way, and no such experiments yet have been done.

18.5.6 Rainy, humid conditions or wet soils favor carnivorous plants by lowering the costs of glandular secretion or allowing passive accumulation of rainwater

The occurrence of the great majority of carnivorous plants under rainy and humid conditions or on wet soils, and the growth of most pitcher plants in areas of high rainfall and low evaporation rate (Givnish 1989, Moran et al. 2013) are consistent with this prediction. No studies using modern hydraulic approaches have examined how secretory glands and traps are connected to a carnivorous plant's hydraulic system, and whether any carnivores exhibit root pressure, although Adamec (2005a) did demonstrate water exudation by roots in 12 carnivorous plant species.

The hydathode hypothesis.

Root pressure and water exudation might have played a key role in the evolutionary origin of pitchers in *Nepenthes* and possibly other groups. Biologists have long recognized that different clades of carnivorous plants have evolved either from ancestors with glandular hairs (Darwin 1875) or from ancestors with peltate leaves that capture and hold rainwater in areas with heavy precipitation (Baillon 1870, Franck 1976; Chapter 3). Available data suggest that five of the ten carnivorous plant clades (carnivorous Nepenthales, *Roridula* in Ericales, and Byblidaceae, Lentibulariaceae, and *Philcoxia* in indumentum-rich Lamiales; Chapter 3) evolved from ancestors with glandular hairs. Two others—*Cephalotus* and Sarraceniaceae—are natural candidates for the peltate-leaf pathway, but none of their relatives have peltate leaves, and Fukushima et al. (2015) provide detailed genetic and developmental evidence that the *Sarracenia* trap leaf was not derived from a peltate form and instead reflects shifts in the orientation of the planes of cell division. We hypothesize that pitchers in these two groups, and in *Nepenthes*, are derived from terminal hydathodes in ancestral taxa. Hydathodes can allow plants to refill embolized xylem vessels under root pressure without flooding the leaf mesophyll and thereby adversely affecting photosynthesis (Feild et al. 2005). Often, hydathodes lie at the end of secondary or tertiary veins; they are inherently tubular in nature, providing a key step in the evolution of pitchers, although in almost all species the hydathodal tubes themselves are quite small and flattened.

In *Nepenthes*, the secondary veins converge toward the leaf apex and terminal tendril; a young pitcher begins as a slightly concave depression in the tendril tip (Owen and Lennon 1999). Similarly, in Sarraceniaceae and *Cephalotus*, young pitchers begin as tiny tubular excrescences of the leaf tip. One can imagine an evolutionary pathway in which a terminal hydathode or gland, fed by converging secondary veins, attracts minute prey that drown and are then digested by bacteria, leading to nutrient uptake and a fitness advantage, favoring the evolution of a larger and more complex trap derived from the hydathode. This proposal is close to Hooker's (1859) appendicular theory. Seedling leaves of *Nepenthes* have a depression at the end of the tendril terminating the leaf, and the adult leaves and stem are beset with hydathodes (Cheek and Jebb 2001). In both *Nepenthes* and *Cephalotus*, the tank fluid is supplied by hydathodes inside the trap (Adlassnig et al. 2011). The hydathode hypothesis seems plausible, and a first test of it would be to determine if *Cephalotus* and *Nepenthes* exhibit root pressure, and whether guttation occurs in the terminal tendril of the seedling leaves of *Nepenthes*.

18.5.7 Possession of defensive glandular hairs facilitates the evolution of carnivory

- p. 253 Five carnivorous clades are derived from ancestors with glandular hairs (§18.5.6). An additional two to three origins (in Poales) involve ancestors with eglandular but absorptive leaf hairs. A pre-existing investment in hairs would have reduced the energetic threshold for carnivory. In addition, to the extent that the evolution of sticky hairs also may protect carnivores from herbivores, it would increase selection for their evolution. A field experiment involving the removal of secretory glands from the leaves of *Pinguicula moranensis* showed that glandless plants sustained 18 times more damage than control plants (Alcalá et al. 2010). Even if some of the observed effect is due to trauma increasing the attractiveness of glandless plants, this study suggests that much of the benefit this carnivore obtains is through a reduction in herbivory. A similar effect is seen in the ant-specialist *Sarracenia minor*, in which increased ant visitation independent of their capture as prey reduced herbivory and pitcher mortality, and increased the number of pitchers per plant (Moon et al. 2010).

18.5.8 Fire over infertile soils favors carnivorous plants

Many carnivorous plants are associated strongly with nutrient-poor, moist habitats that burn frequently (Givnish 1989). Fire should favor carnivores on such sites by volatilizing N from burnt tissue, and increasing light levels and soil moisture by removing competing plants and foliage (Givnish 1989). Other forms of disturbance over sterile substrates, including logging, lake drainage, or fractures or landslides that expose bare rock, also can favor carnivores without volatilizing N. However, fire also can increase levels of many cations and P, raising the question of whether the greater supply of such nutrients would select against botanical carnivory, or instead enhance its benefits through nutrient complementarity (Givnish 1989). The possibility of the latter is reinforced by the degree to which fire enhances the abundance of N-fixing plants in prairies and pinelands (Towne and Knapp 1996), although wet anoxic soils where carnivorous plants grow are unfavorable for N-fixing legumes.

18.5.9 Gradual evolution of carnivory is essential in extreme habitats

Small allocations to carnivory probably would not provide enough nutrients to maintain plant life when there is essentially no P or N in the substrate. Presumably, the origin of carnivores like *Brocchinia reducta* or *Dionaea muscipula* that can grow on substrates with essentially no nutrients occurred through their initial colonization of nutrient-poor substrates, subsequent optimization (and thus, increase) in allocation to carnivory, and eventual colonization of more-or-less nutrient-free substrates. Testing this hypothesis will require simulation studies with properly parameterized versions of our new model for the evolution of carnivory (Box 18.1) or genetic manipulations that reduce allocations to carnivory.

18.5.10 Anoxic or toxic soils should favor carnivory on open, moist sites

This hypothesis is supported by the widespread occurrence on saturated or toxic soils of carnivorous plants with small root systems. At least fifteen species of *Nepenthes* are restricted to serpentine outcrops in northern Borneo, Palawan, and parts of Wallacea (Clarke and Moran 2016), and *N. vieillardii* is restricted to serpentine outcrops in New Caledonia (Kurata et al. 2008). Van der Ent et al. (2015) found that the serpentine *Nepenthes* from Mt. Kinabalu and Mt. Tambuyukon were heavy-metal excluders; their restriction to serpentine may reflect lowered costs of heavy-metal exclusion because of their carnivory, limited root systems, and the open nature of the vegetation over serpentine. In northern California and southern Oregon, *Darlingtonia californica* is endemic to serpentine (Ellison and Farnsworth 2005), where it co-occurs with another serpentine endemic, *Pinguicula macroceras* ssp. *nortensis*, and non-endemic *Drosera*. In western Newfoundland, *Sarracenia purpurea* grows luxuriantly on open serpentine gravel with water not far below the surface (T. J. Givnish unpublished data).

18.5.11 Co-limitation of growth by multiple nutrients may favor the paradoxical increase in root investment by carnivorous plants that recently have captured prey

This hypothesis provides the only plausible explanation for this puzzling phenomenon. An approach to testing this idea would be to feed plants on a series of defined media that are lacking one or more nutrients, and determine whether additional root growth occurs only in those circumstances in which the elements available from prey and soil are complementary.

18.5.12 Harder, more fertile waters should favor greater investment in traps by *Utricularia*

Knight and Frost (1991) found that the number of traps in *Utricularia macrorhiza* increased with water hardness across nine lakes in northern Wisconsin. They quantified water hardness as specific conductance, a measure that increases with cation concentration in the water column and, most likely, bicarbonate concentration, $[\text{CO}_2]$, total dissolved inorganic carbon (DIC), and possibly [P] weathered from the substrate (Hanson et al. 2006). Their experiments did show that water chemistry, not prey supply, was responsible for this pattern but direct measurements of DIC and $[\text{CO}_2]$ were not provided. In two of the lakes, variation in bladder numbers per leaf reflected the proportional allocation of biomass (Knight and Frost 1991).

Adamec (2008a) found that the percentage of biomass allocation to traps (T) in *U. australis* in 29 Czech fishponds and bog or fen pools was correlated significantly with only one external factor: dissolved CO_2 : $T = 14.33 [\text{CO}_2] + 32.21$ ($r^2 = 0.33$, $P < 0.001$; Figure 18.8). In moving from oligotrophic to eutrophic waters in this landscape, dissolved $[\text{CO}_2]$ increased two-fold (from 0.26 ± 0.20 mM to 0.54 ± 0.56 mM), while $\text{NO}_3\text{-N}$ also increased two-fold (from 3.6 ± 4.1 to 8.0 ± 7.1 $\mu\text{g/L}$), $\text{NH}_4\text{-N}$ increased four-fold (from 27 ± 10 to 102 ± 135 $\mu\text{g/L}$), and $\text{PO}_4\text{-P}$ increased more than six-fold (from 11.7 ± 5.2 to 71.3 ± 86.1 $\mu\text{g/L}$). However, no measure of available N or P showed a significant correlation with trap allocation under two-tailed t -tests ($r = -0.09$, -0.19 , and -0.3 for $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$, respectively; all $P > 0.05$). As expected, shading or feeding *Utricularia vulgaris* stopped trap formation (Englund and Harms 2003), whereas trap allocation in *U. foliosa* increased as water $[\text{NO}_3]$ declined along an Amazonian creek (Guisande et al. 2004). Adamec (2008a, 2015a) argued that proportional biomass allocation to traps is set by the balance of a positive effect of water $[\text{CO}_2]$ and a negative effect of tissue N (or P) concentration, which he viewed as a homeostatic mechanism without reference to optimal energy capture. Alternatively, Adamec's data may be an exemplar of optimal allocation to carnivory in an aquatic carnivore and a mechanism for generating and maintaining a favorable pattern of allocation.

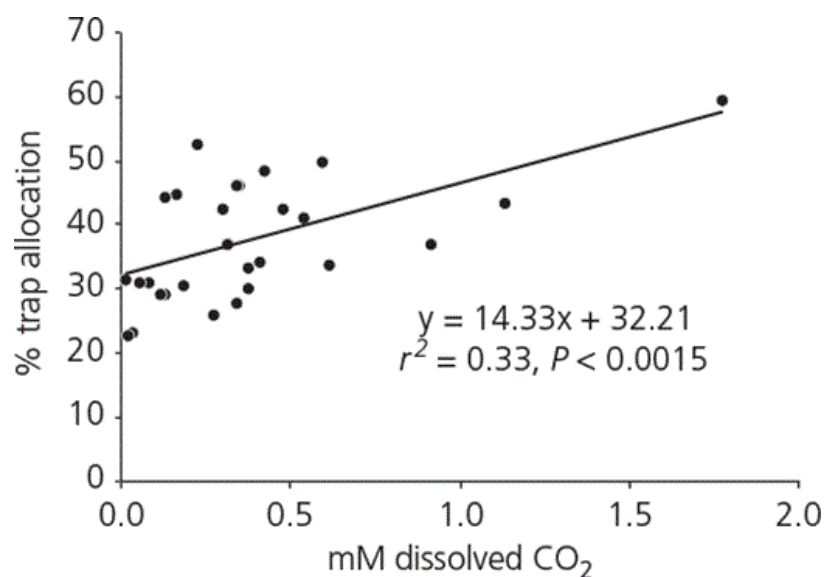


Figure 18.8 Percent allocation of biomass to traps as a function of dissolved $[\text{CO}_2]$ across 29 Czech sites of *Utricularia australis* studied by Adamec (2008a). Line is least-mean-squares regression, % trap allocation = $14.33 \times \text{mM dissolved CO}_2 + 32.21$.

Original data kindly made available by Lubomír Adamec.

18.5.13 Soil anoxia or extreme infertility makes tall, woody carnivores impossible

Almost all carnivorous plants are relatively short herbs. Perhaps the simplest explanation for this prediction is that the wet soils that favor carnivory (§18.5.1, §18.5.6, §18.5.10) often disfavor woody plants. However, the decrease in leaf-specific hydraulic conductance with height in woody plants (Mencuccini 2003) also might be important. That decrease would militate against gigantic carnivores by decreasing water potential and selecting for small leaves with low photosynthetic rates (Koch et al. 2004, Ishii 2011) that are unlikely to be increased by nutrient inputs via carnivory. Thus, the restriction of the carnivorous phase to relatively short juveniles (≈ 1 m tall) in *Triphyophyllum* should be re-examined and the role of decreasing water potential in limiting the photosynthetic rate with increasing height of adult vines studied.

18.6 Future research

p. 255 The cost/benefit model for the evolution of carnivorous plants provides a qualitative explanation for patterns in their distribution, allocation to traps, variation in trap mechanism, association with growth form, low rates of carbon uptake and whole-plant growth, and ecological characteristics relative to plants with other “non-standard” mechanisms of nutrient capture, including myrmecotrophy and nitrogen fixation.

In some ways, it is remarkable that Darwin himself did not advance something analogous to the cost/benefit model. On July 21, 1875, Alfred Russel Wallace—co-creator of the theory of natural selection—wrote to Darwin:

Many thanks for your kindness in sending me a copy of your new book. ... The account of Utricularia is most marvellous, and quite new to me. I'm rather surprised that you do not make any remarks on the origin of these extraordinary contrivances for capturing insects. ... I daresay there is no difficulty, but I feel sure they will be seized on as inexplicable by Natural Selection, and your silence on the point will be held to show that you consider them so!... Here are plants which lose their roots and leaves to acquire the same results by infinitely complex modes! What a wonderful and long-continued series of variations must have led up to the perfect “trap” in Utricularia, while at any stage of the process the same end might have been gained by a little more development of roots and leaves, as in 9,999 plants out of 10,000!

A day later, Darwin responded to Wallace, pointing out that he had in fact traced an evolutionary pathway to carnivory in Droseraceae, a proposal that continues to inspire research (e.g., Gibson and Waller 2009). But Darwin did not respond to the thrust of Wallace’s suggestion—that plants might have responded to shortages of soil nutrients by increased allocation to roots or decreased allocation to leaves, rather than evolve carnivory—a suggestion which, if considered carefully, would almost surely have led Darwin to a consideration of the relative costs and benefits of carnivory.

Perhaps the one direction in which our own responses to this central question might be improved over the coming years is to produce a fully quantitative model for the evolution of carnivory, and compare quantitative predictions of optimal plant form and allocation with reality. Studies by Zamora et al. (1998), Ellison and Gotelli (2002), Alcalá and Domínguez (2005), Adamec (2008a), Gibson and Waller (2009), Bonhomme et al. (2011b), and Gaume et al. (2016) are all steps in this direction. Developing quantitative optimality models, especially for *Utricularia* or *Nepenthes* species that have a clear distinction between photosynthetic and carnivorous organs, and comparing them with alternative approaches (e.g., Adamec 2015a; Chapter 19) would enable the most powerful tests of cost/benefit analysis (Mäkela et al. 2002). Experiments comparing photosynthesis and whole-plant growth by noncarnivorous plants with those of

carnivorous plants in the same field locations and with and without simultaneous access to prey are a very high priority. Such experiments will provide the critical data needed to test many of the predictions of the cost/benefit model.

Givnish, T. J., Sparks, K. W., Hunter, S. J., and Pavlovič, A., *Why are plants carnivorous? Cost/benefit analysis, whole-plant growth, and the context-specific advantages of botanical carnivory*. In: *Carnivorous Plants: Physiology, ecology, and evolution*. Edited by Aaron M. Ellison and Lubomír Adamec: Oxford University Press (2018). © Oxford University Press. DOI:

10.1093/oso/9780198779841.003.0018