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Ecophysiological traits of terrestrial and aquatic carnivorous plants: are the costs and benefits the same?

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Abstract

Identification of trade-offs among physiological and morphological traits and their use in cost-benefit models and ecological or evolutionary optimization arguments have been hallmarks of ecological analysis for at least 50 years. Carnivorous plants are model systems for studying a wide range of ecophysiological and ecological processes and the application of a cost-benefit model for the evolution of carnivory by plants has provided many novel insights into trait-based cost-benefit models. Central to the cost-benefit model for the evolution of botanical carnivory is the relationship between nutrients and photosynthesis; of primary interest is how carnivorous plants efficiently obtain scarce nutrients that are supplied primarily in organic form as prey, digest and mineralize them so that they can be readily used, and allocate them to immediate versus future needs. Most carnivorous plants are terrestrial – they are rooted in sandy or peaty wetland soils – and most studies of cost-benefit trade-offs in carnivorous plants are based on terrestrial carnivorous plants. However approximately 10% of carnivorous plants are unrooted aquatic plants. In this Forum paper, we ask whether the cost-benefit model applies equally well to aquatic carnivorous plants and what general insights into trade-off models are gained by this comparison. Nutrient limitation is more pronounced in terrestrial carnivorous plants, which also have much lower growth rates and much higher ratio of dark respiration to photosynthetic rates than aquatic carnivorous plants. Phylogenetic constraints on ecophysiological trade-offs among carnivorous plants remain unexplored. Despite differences in detail, the general cost-benefit framework continues to be of great utility in understanding the evolutionary ecology of carnivorous plants. We provide a research agenda that if implemented would further our understanding of ecophysiological trade-offs in carnivorous plants and also would provide

broader insights into similarities and differences between aquatic and terrestrial plants of all types.

Introduction

Organisms cannot do everything equally well. Identification of trade-offs among physiological and morphological traits (Shipley 2002; Shipley et al. 2006; He et al. 2009) and the use of such traits in cost-benefit models and ecological or evolutionary optimization arguments (e.g., Givnish 1986; Raven et al. 2004; Ellison and Gotelli 2009) have been hallmarks of ecological analysis for at least 50 years. Despite their obvious drawbacks and limitations (e.g., Gould and Lewontin 1979; Lenormand et al. 2009; Nielsen 2009), cost-benefit models and their kin have framed many ecological research programs and continue to provide new insights and generalizations (Wright et al. 2004, 2005; Santiago and Wright 2007; Reich et al. 2007, 2009; Ordoñez et al. 2009).

Givnish et al. (1984) provided one of the most significant applications of a cost-benefit model to a long-standing problem in evolutionary ecology – an explanation for the repeated evolution of botanical carnivory among at least six disparate plant lineages (Darwin 1875; Lloyd 1942; Benzing 1987; Juniper et al. 1989; Albert et al. 1992; Ellison and Gotelli 2001, 2009; Chase et al. 2009). In short, Givnish et al. (1984) proposed that botanical carnivory – the attraction, capture, and digestion or animal prey, and the subsequent direct uptake and use of nutrients from that prey – would evolve when the marginal benefit derived from carnivory (expressed as increased rates of photosynthesis or growth) exceeded the marginal cost (expressed in units of carbon) required to construct animal traps. Because of its clarity and its quantitative framework, the cost-benefit model for the evolution of botanical carnivory has been the fundamental framework underlying carnivorous plant research since its publication in 1984 (see reviews in Adamec 1997a; Ellison 2006; Ellison and Gotelli 2009; and see Brewer et al. 2011 for an alternative approach).

The cost-benefit model for the evolution of botanical carnivory was developed based on data collected from a single carnivorous plant, the bromeliad *Brocchinia reducta* (Givnish et al. 1984), but it has been applied routinely to all carnivorous plants (Givnish et al. 1984; Benzing 1987; Ellison 2006). The majority of these *ca.* 650 species inhabit nutrient-poor habitats in which light and water are rarely limiting (Benzing 1987, 2000; Brewer et al. 2011). Approximately 90 % of carnivorous plants can be considered "terrestrial"; they are firmly rooted in sandy or peaty wetland soils (Juniper et al. 1989; Taylor 1989; Guisande et al. 2007), and virtually all of the empirical studies applying the cost-benefit model for the evolution of carnivory have examined terrestrial carnivorous plants (Ellison 2006). But the remaining ~10% of carnivorous plants, including ~50 species of bladderworts (*Utricularia*: Lentibulariceae) and the water-wheel plant *Aldrovanda vesiculosa* (Droseraceae) are unrooted submerged or amphibious aquatic plants (Taylor 1989; Adamec 1997b). Here, we ask whether the cost-benefit model applies equally well to aquatic carnivorous plants and what general insights into trade-off models are gained by this comparison.

In applying the cost-benefit model, why should it matter whether plants are aquatic or terrestrial? First, the physical environments of aquatic and terrestrial habitats are quite different (Sand-Jensen 1989; Barko et al. 1991; Sand-Jensen and Frost-Christensen 1998; Colmer and Pedersen 2008). On land, CO_2 is available as a gas at a relatively constant concentration and diffuses rapidly into plant tissues through stomata (e.g., Lambers et al. 1998). In water, CO_2 and O_2, the critical gases for photosynthesis and respiration, are dissolved in solution and diffusion rates of dissolved solutes limit photosynthetic rate. Furthermore, uptake of CO_2 by aquatic plants is strongly dependent on pH and total alkalinity, and direct uptake of CO_2 by aquatic plants increases with concentrations of dissolved inorganic carbon, dissolved organic matter, and mineral nutrients in the aquatic environment. Although the shallow standing, oligo-mesotrophic and dystrophic (organically-rich, humic) waters in which aquatic carnivorous plants grow may have low concentrations of O_2, these same waters usually (but not strictly) are very rich in free CO_2 (Adamec 1997a, 1997b, 2008a). These physical differences between aquatic and terrestrial environments strongly suggest that key ecophysiological traits and processes (e.g., photosynthesis, growth rate, nutrient uptake) should differ between terrestrial and aquatic plants, whether or not they are carnivorous (*e.g.*, Sand-Jensen 1989; Lambers et al. 1998; Colmer and Pedersen 2008).

Aquatic carnivorous plants are not common in all aquatic habitats. Shallow non-dystrophic (clear) lakes usually host diverse communities of rooted and non-carnivorous aquatic plants (Sand-Jensen 1989; Barko et al. 1991), whereas in dystrophic lakes and streams, species diversity of rooted aquatic plants is relatively poor but the two genera of aquatic carnivorous plants are abundant (e.g., Kamiński 1987a). Typical dystrophic waters are dark, have high concentrations of humic acids and tannins, and loose, anoxic sediments (Kamiński 1987a, b, Adamec 1997a, b); these conditions are not especially favorable for the growth and development of rooted aquatic plants. In contrast, aquatic carnivorous plants float freely near the water's surface where there is more light and free oxygen, but without roots to absorb nutrients, these plants may have evolved carnivory to maximize nutrient capture. Similar selective pressures may apply in terrestrial wetlands where terrestrial carnivorous plants are most common. In these habitats, anoxic peats or excessively well-drained and leached sands creates strong nutrient limitation and may have favored investment in alternative (i.e., carnivorous) structures for capturing nutrients.

Second, rooted plants take up nutrients through specialized structures – roots (and often associated mycorrhizae) – and can store these nutrients in other specialized structures such as rhizomes (when they are present).

In contrast, rootless aquatic plants obtain nutrients from the water column by diffusion through unspecialized leaves and stems and specialized structures for long-term storage of nutrients are rarely present. Although strictly speaking, the ~170 species of terrestrial *Utricularia* lack roots, these species do have root-like underground shoots or stolons that, like true roots, anchor the plants to the substrate and store nutrients (Taylor 1989). Thus, we consider terrestrial *Utricularia* to be functionally "rooted" plants. In both terrestrial and aquatic habitats, carnivorous plants also obtain nutrients from prey captured by specialized traps modified from leaves (Arber 1941; Lloyd 1942; Adamec 1997a; Ellison and Gotelli 2009) and in terrestrial habitats, prey capture has been shown to enhance nutrient uptake by roots (Aldenius et al. 1983; Hanslin and Karlsson 1996; Adamec 2002). Analogous effects have not been found in aquatic carnivorous plants (Adamec et al. 2010), nor have they been examined in terrestrial *Utricularia*. In both terrestrial and aquatic habitats, an increase in availability of dissolved nutrients (in soil or in the water column) is associated with a decrease in the production of carnivorous traps (Knight and Frost 1991; Chiang et al. 2000; Guisande et al. 2000, 2004; Ellison and Gotelli 2002), suggesting a clear energetic and/or mineral "cost" to their production. By examining and synthesizing available data on growth and ecophysiological processes of carnivorous plants, we assess whether or not there are differences in the associated marginal costs of nutrient uptake by carnivorous plants growing in terrestrial and aquatic habitats.

Although most carnivorous plants are perennial, some are annual, and both life-histories can be found among terrestrial and aquatic carnivorous plants. Among aquatic carnivorous plants, annual life-histories are uncommon in typical dystrophic habitats but are more common in very shallow waters on sandy or clayish bottom in (sub)tropical regions where rapid growth and reproduction may have been selected for in ephemeral habitats (Taylor 1989). Similarly, among terrestrial carnivorous plants, annual life-histories are most frequent in sundews (*Drosera* sp.) and rainbow plants (*Byblis* sp.) that occur in seasonally dry or episodically disturbed habitats (Lowrie 1998).

Finally, aquatic plants are not found in all angiosperm clades, and aquatic carnivorous plants are notable for their taxonomic restriction. All but one of the aquatic carnivorous plants are in the single genus *Utricularia* (Lamiales: Lentibulariaceae), and are found only in a few derived clades within that genus (Taylor 1989; Guisande et al. 2007). The one other aquatic carnivorous plant is *Aldrovanda vesiculosa*, a derived carnivorous plant in the Droseraceae (Caryophyllales). Thus, phylogenetic constraints may play a greater role in determining the evolution of specific types or mechanisms of carnivory in (aquatic) *Utricularia* (Jobson et al. 2004) than in the more phylogenetically diverse terrestrial carnivorous plants.

In this paper, we first review our understanding of differences and similarities in fundamental ecophysiological traits – structural characteristics, growth patterns and rates, photosynthesis, and nutrient uptake and use – of aquatic and terrestrial carnivorous plants (henceforth ACPs and TCPs, respectively). We then use these contrasts to assess cost-benefit relationships among these traits in ACPs and TCPs and ask whether these patterns can inform trait-based models for plants growing in either terrestrial or aquatic habitats. We then return to the question of how phylogeny may have constrained observed patterns of the evolution of botanical carnivory. Finally, we outline a set of research needs to further our understanding of the evolutionary physiology of carnivorous plants and to incorporate them fully into general trait-based models of plant form and function (compare Wright et al. 2004, 2005; Reich et al. 2009; and Ordoñez et al. 2009 with Ellison 2006; and Karagatzides and Ellison 2009).

Traits of aquatic and terrestrial carnivorous plants

Structural traits

The growth forms of TCPs most commonly are sessile or erect rosettes, but there also are carnivorous vines (*Triphyophyllum*) and erect-stemmed herbs (*Drosophyllum, Roridula, Byblis*) (Juniper et al. 1989). Most TCPs possess true roots and many species also produce thick rhizomes. Root-like rhizomes or stolons are produced even by otherwise rootless terrestrial species of *Utricularia* and *Genlisea* (Juniper et al. 1989; Taylor 1989; Adamec 2005). The root systems of TCPs are usually small, short, and poorly branched (the proportion of root dry mass to the total plant dry mass ranges from 3 – 23%; Adamec 1997a). Nonetheless, roots, rhizomes, and/or stolons anchor the plants, root uptake may contribute substantially to the nutrient budget of TCPs (Adamec 1997a), and the physiological root activity per unit biomass is surprisingly high (Adamec 2005). In contrast, ACPs are submerged or partially amphibious, rootless plants that float freely in the water column or are weakly attached to loose sediments (Taylor 1989; Guisande et al. 2007). Uptake of nutrients from the surrounding water supplements nutrients obtained from captured prey (Lollar et al. 1971; Knight and Frost 1991; Friday and Quarmby 1994; Ulanowicz 1995; Guisande et al. 2000; Chiang et al. 2000; Adamec 2008a). Most ACPs have a linear, modular shoot structure consisting of regularly produced and regularly shed nodes with filamentous leaves and tubular, fragile internodes. In some species, the leaves are arranged in true whorls. The linear shoots are either monomorphic (non-differentiated) or dimorphic, differentiated into green photosynthetic shoots and pale carnivorous shoots with many traps

(Taylor 1989; Guisande et al. 2007). Traps of both TCPs and ACPs are derived from modified leaves (Arber 1941; Lloyd 1942; Juniper et al. 1989; see Ellison and Gotelli 2001 for a review and illustrations). The traps of both terrestrial and aquatic *Utricularia* species are hollow bladders, 2 cells thick and 1-6 mm in diameter (Juniper et al. 1989; Taylor 1989). The 4-6 mm wide snap-traps of the aquatic *Aldrovanda* are similarly shaped, albeit much smaller, than those of its terrestrial sister-group, the Venus' fly-trap, *Dionaea muscipula* (Juniper et al. 1989).

Growth

Aquatic and terrestrial carnivorous plants grow in different ways. Like most familiar plants, TCPs produce new shoots and leaves while retaining, at least for a time, older shoots and leaves. The result is a plant whose main axis and branches increase in size through time. In striking contrast, ACPs have very rapid apical shoot growth but their basal shoot segments age and die at about the same rate. For example, under favorable conditions, the apical shoot growth rate ranges from 1.0 – 1.2 whorls d^{-1} in *Aldrovanda* to as much as 2.8 – 4.2 nodes/d in field or culture-grown aquatic *Utricularia* species (Friday 1989; Adamec 2000, 2008c, 2009b, 2010a; Adamec and Kovářová 2006), although *relative* growth rate (RGR in $g\ g^{-1}\ d^{-1}$) may appear to approach zero (Adamec 2009b). The result of this "conveyer-belt" growth system is that ACPs maintain a relatively constant length of the main shoot. Under normal conditions, however, shoot branching accompanies main shoot extension, leading to RGRs of ACPs far exceeding zero.

The relative growth rate of both ACPs and TCPs is generally significantly lower than most groups of non-carnivorous herbaceous plants ($F_{5,423} = 80.26$, $P < 2 \times 10^{-16}$, ANOVA; Fig. 1). Based on a broad review of published values (references in legend to Fig. 1), the RGRs of ACPs and TCPs, along with rooted aquatic herbaceous plants (non-carnivorous) were low (of the order of 0.055 g g^{-1} d^{-1} for ACPs and 0.035 g g^{-1} d^{-1} for TCPs) and statistically indistinguishable ($P = 0.83$), but significantly lower than RGRs of terrestrial herbs ($P < 1 \times 10^{-8}$, *post-hoc* multiple comparisons among means with Tukey's HSD test). We note that most of these data are from seedlings or small plants, but in general these RGR values are not corrected for plant size and so may confound relative growth rates and size (Rose et al. 2009; Rees et al. 2010). However, relatively few data on RGR have been size-corrected, and previously published papers on RGR generally do not provide sufficient information to apply the size-corrected models suggested by Rose et al. (2009) or Rees et al. (2010). More definitive comparisons of RGR between carnivorous and non-carnivorous plants, whether terrestrial or aquatic, will require reassessment of relative growth rates in light of overall plant sizes at the time of measurement. In any case, branching rate of the main shoot in ACPs is of crucial importance for both overall plant growth and RGR (Kamiński 1987a; Adamec 2000, 2008c, 2009b, 2010a, 2011c).

Photosynthesis and dark respiration

In all TCPs, the traps are modified from leaves or leaf parts (Arber 1941; Lloyd 1942). In many TCPs, the traps function simultaneously as nutrient capture organs and as photosynthetic organs, although in the ca. 100 species of *Nepenthes*, the lamina (an expanded petiole) accounts for at least 90% of photosynthesis and the traps (modified leaf blades) have negligible photosynthetic rates (Pavlovič et al. 2007; Karagatzides and Ellison 2009). In ACPs, the situation is similar. *Aldrovanda* traps both acquire nutrients and photosynthesize, but in *Utricularia*, traps are specialized for prey capture and have much lower photosynthetic rates than the leaves. Therefore, in comparing photosynthetic rates among groups, we use data from the primary photosynthetic organs, but where possible, we also highlight differences between photosynthetic rates of leaves/lamina and traps. In discussing respiratory (maintenance) costs, we focus on the ratio of dark respiration to photosynthesis.

Both TCPs and ACPs are C-3 plants (Lüttge 1983). However, maximum photosynthetic rates vary dramatically between TCPs and ACPs ($F_{5,\,259} = 24.12$, $P < 2 \times 10^{-16}$, ANOVA; Fig. 2). Mass-based maximum photosynthetic rates (A_{MAX}) measured for TCPs range from 17-153 nmol CO_2 g^{-1} (dry mass) s^{-1}, approximately 4-fold less than values commonly found for leaves non-carnivorous herbs (Wright et al. 2004; Ellison and Farnsworth 2005; Ellison 2006; Fig. 2). In contrast, A_{MAX} of ACPs range from 73-517 nmol g^{-1} s^{-1}, whereas the usual values for submerged, aquatic, non-carnivorous plants generally range from 75 to 240 (for rooted aquatic herbs) or 200 – 450 (for floating, unrooted aquatic herbs) nmol g^{-1} s^{-1} (Fig. 2). That is, A_{MAX} of ACPs is similar to both unrooted aquatic non-carnivorous plants ($P = 0.98$) and rooted aquatic non-carnivorous plants ($P = 0.22$), whereas A_{MAX} of TCPs not only is significantly lower than that of terrestrial non-carnivorous plants $P < 1 \times 10^{-8}$), but it is also significantly lower than that of ACPs and other aquatic plants ($P < 1 \times 10^{-8}$). The photosynthetic CO_2 affinity (compensation concentration) measured for ACPs averages 4.5 µM and ranges from 0.7-13 µM (Adamec 1997b, 2009a; Adamec and Kovářová 2006; Pagano and Titus 2007), quite similar to that found in non-carnivorous aquatic plants, which ranges from 1.5 – 10 µM (Maberly and Spence 1983). We note that in general, HCO_3^- is of a very minor ecological importance in carbon budgets of ACPs, although HCO_3^- may be used for photosynthesis by *U. australis* grown at very high pH (Adamec 2009b).

The large differences in photosynthetic rates between TCPs and ACPs only partly reflect their minor differences in RGRs. An assessment of the relationship between respiration and photosynthesis in ACPs and TCPs (Fig. 3), however, illuminates linkages between carbon fixation rates and RGR. Non-carnivorous herbaceous plants typically have dark respiration rates (R_D) < 50 % of A_{MAX} (Bazzaz and Carlson 1982). In contrast, the average R_D/A_{MAX} ratio of TCPs is much higher (63 %), whereas ACPs have a much lower ratio of R_D/A_{MAX} (mean = 34 %, range 4 – 190 %; $F_{1,40} = 5.88$, $P = 0.03$ ANOVA on *ln*-transformed data). Interestingly, R_D tends to increase with A_{MAX} for TCPs, but varies little for ACPs; R_D/A_{MAX} is little affected by supplemental feeding (Fig. 3). The much higher (absolute) values of R_D in aquatic *Utricularia* traps than in traps of TCPs support the observation of very energetically demanding physiological function of water pumping that is unique to *Utricularia* (Jobson et al. 2004; Adamec 2006).

The averages also mask significant differences between traps and leaves or photosynthetic lamina in species where trapping and photosynthesis are accomplished by different organs ($F_{5,32} = 18.84$, $P = 0.002$, nested ANOVA on *ln*-transformed data). In the TCPs *Nepenthes, Sarracenia*, and *Dionaea* for which those A_{MAX} and R_D have been measured separately on traps (pitchers and snap-traps, respectively) and laminae (lamina, phyllodia, and petioles, respectively), the traps have much higher respiratory costs (mean R_D/A_{MAX} = 158%, range = 13 – 325%) than do the laminae (mean = 19%, range = 9 – 33%) (Fig. 3). For TCPs such as *Drosera*, *Pinguicula* and *Sarracenia* in which traps are modified leaves and both R_D and A_{MAX} were measured on these modified leaves, R_D/A_{MAX} averages 68% (range 10 – 149%). Similarly, respiratory costs of very weakly photosynthezing traps of the aquatic *Utricularia* (mean R_D/A_{MAX} = 106%, range 32 – 190%) are much higher than its leaves (mean = 9%, range 4 – 90%). Even when traps and leaves of *Utricularia* are assayed together, their R_D/A_{MAX} ratio is much lower than that of TCPs (mean = 21%, range 9 – 38%) (Fig. 3).

The substantial differences in the relative respiratory costs between ACPs and TCPs are related to their distinct methods of growth. We conclude that low A_{MAX} values and high R_D/A_{MAX} ratios of TCPs are a typical, convergent, attribute of this group of plants and reflect physiological consequences of slow growth, and storage of C over often long lifespans (Butler and Ellison 2007). On the other hand, the very low R_D/A_{MAX} of ACPs reflects their rapid growth and turnover of senescent shoots that leads to large and predictable losses of structural and non-structural carbohydrates (Adamec 2000). Unlike TCPs that store C for future use, a substantial amount (~ 20-25 %) of the total photosynthetically fixed C is secreted by aquatic *Utricularia* traps into trap fluid where it supports the commensal assemblage within the trap (Sirová et al. 2010).

Nutrient uptake and use

It has been demonstrated repeatedly that the primary benefit of trapping and consuming insect prey is to obtain growth-limiting mineral nutrients, mainly N and P (see reviews in Juniper et al. 1989; Adamec 1997a, 2002; Ellison 2006). How this benefit is expressed, however, differs among some carnivorous plant taxa and is unknown for others. For example, in several pitcher plants (*Sarracenia* and *Nepenthes*), A_{MAX} increases with foliar N or P (Ellison and Farnsworth 2005; Pavlovič et al. 2007; Farnsworth and Ellison 2008). In *Drosera* and *Pinguicula*, capture of prey by traps stimulates additional uptake of mineral nutrients from the soil (Hanslin and Karlsson 1996; Adamec 1997a, 2002). Root uptake can further enhance A_{MAX} (Pavlovič et al. 2010). Downstream, the consequence of prey addition usually results in increased growth expressed as more leaves, branches, and/or biomass (Ellison 2006). These data lead us to hypothesize that N and P derived from prey enhance essential growth processes in ACPs such as cell division, DNA replication, and protein synthesis in the young, meristematic tissues of shoot apices (Adamec 2008b). This hypothesis is supported only for *Aldrovanda* but not for two *Utricularia* species (Adamec 2011a). Together with observations that TCPs shunt excess N to new growth (Butler and Ellison 2007), these data all suggest that the effects of enhanced prey capture are manifest on young, developing tissues and organs rather than on mature, existing organs (Ellison and Gotelli 2002, 2009).

TCPs have significantly lower foliar N, P, and K than all other functional groups of terrestrial non-carnivorous plants (Ellison 2006). In contrast, macronutrient content in shoots of ACPs is ~2 – 5 times greater than that of TCPs (Fig. 4) and comparable to that of aquatic non-carnivorous plants (Dykyjová 1979). Phosphorus content is much more variable among ACPs than among TCPs – up to 10- to 20-fold within the same species – but it could be overestimated in ACPs with their closed traps if remnants of captured prey are inadvertently analyzed (Adamec 2008a). Like TCPs, K content in ACPs is substantially greater than N content, and P content of ACPs is nearly double that of terrestrial forbs, which otherwise have the highest foliar nutrient content among the different functional groups examined by Wright et al. (2005). Also unlike TCPs, average tissue macronutrient contents of ACPs are well above the "critical levels" (blue lines in Fig. 4) that limit growth in both aquatic and terrestrial plants (Gerloff and Krombholz 1966; Ellison 2006). Stoichiometrically, ACPs show no consistent patterns with respect to nutrient limitation, whereas TCPs tend to be primarily P or P+N limited (Fig. 5).

Variation in nutrient content within individual ACPs reflects the steep nutrient polarity along shoots, localization of traps along the shoot, and also captured prey (Adamec 1997a, 2000, 2008a). Thus, the growth rates of ACPs (Fig. 1) are associated with high A_{MAX} (Fig. 2), relatively low R_D (Fig. 3), and high shoot nutrient contents (Fig. 4). Nevertheless, very rapid growth of ACPs that were experimentally fed additional prey in situations led to significant decrease in tissue N and P content in apical shoot segments (Adamec 2000; 2008a, 2011a). Similar results also have been observed in non-carnivorous aquatic plants (e.g., Titus and Andorfer 1996) and in adult shoots of several TCPs (Adamec 1997a, 2002). This observation may be partly the result of an apparent "dilution" of mineral nutrients by organic substances in plant tissues of rapidly growing plants.

Potassium (K) has been much less studied in carnivorous plants (Adamec 1997a; Ellison 2006), but tissue K content in traps of aquatic *Utricularia* species (3.7-8.7 % of dry mass) is much higher than in its leaves or shoots (Adamec 2008a, 2010b), probably reflecting particular trap functions. The highest concentrations of K found in *Utricularia* traps exceed any reported for non-carnivorous aquatic plants (cf. Dykyjová 1979). However, it is not known whether this high K content is restricted to trap walls or the specialized quadrifid glands within the trap.

The effect of supplemental prey on growth of both TCPs and ACPs is generally positive (Adamec 1997a; Ellison 2006), but weak in aquatic *Utricularia* species, in which the effect depends markedly on pH and CO_2 availability (Kosiba 1992a; Adamec 2008a; Adamec et al. 2010). However, both ACPs and TCPs efficiently take up nutrients from prey carcasses. Thirty to 76% of prey-N is taken up by TCPs (Hanslin and Karlsson 1996; Adamec 1997a, 2002; Butler and Ellison 2007; Butler et al. 2008) and over 80% is taken up by the aquatic *U. vulgaris* (Friday and Quarmby 1994). Similarly, TCPs take up 57 – 96% of P, K, Mg, and micronutrients from prey (Plummer and Kethley 1964; Adamec 2002; Adlassnig et al. 2009). Although comparable quantitative data are lacking for ACPs, we hypothesize that uptake of P, K, and Mg in ACPs should also be very efficient.

Finally, a number of TCPs efficiently re-use N, P, and K from senescent leaves, and this re-use is much greater than that found in terrestrial non-carnivorous plants that co-occur with TCPs in bogs or fens (Adamec 1997a, 2002; Butler and Ellison 2007). In contrast, in the aquatic *Aldrovanda* and *U. australis*, only N and P, not K, has been found to be re-utilized from old shoots (Adamec 2000, 2008a). It appears that rapidly growing ACPs lose *all* stored K with their old shoots and have to acquire *all* K needed for new growth from prey or from the ambient water. When it has been studied, reutilization rates of Mg and Ca by both ACPs and TCPs have been found to be very low or even zero (Adamec 1997a, 2000, 2002, 2008a).

Cost-benefit relationships in aquatic and terrestrial carnivorous plants

The cost-benefit model for the evolution of carnivory by plants posits that (a) carbon costs of carnivorous structures increase linearly (or at least monotonically), (b) that benefits of prey capture are manifest in increased photosynthesis (or growth), but that these benefits increase only up to a point and then reach an asymptote, and (c) that carnivory is favored when the marginal benefits exceed the marginal costs (Givnish et al. 1984). Our review of ecophysiological characteristics, structural traits, and patterns of growth illustrate that cost-benefit trade-offs are likely to differ between ACPs and TCPs in some ways but are similar in others. In summarizing the costs and benefits, we note that very few studies have simultaneously measured both costs and benefits for any carnivorous plant (Méndez and Karlsson 1999; Ellison and Farnsworth 2005; Adamec 2008c, 2011a; Farnsworth and Ellison 2008; Karagatzides and Ellison 2009). Such studies are clearly an important area for future research.

Measurements of tissue nutrient content suggest that TCPs are much more strongly limited by nutrient availability than are ACPs (Fig. 4), and this difference is expressed in the somewhat higher RGR (Fig. 1) and much higher A_{MAX} (Fig. 2) of ACPs relative to TCPs. Stoichiometrically, ACPs appear to be K- or P-limited whereas TCPs tend to be N-limited (Fig. 5). The cost-benefit model for the evolution of botanical carnivory emphasized N limitation, as N often limits A_{MAX}. Because traps of ACPs are energetically very costly, it is plausible that P limitation (of, e.g., ATP) might be of more consequence for ACPs than for TCPs. Evolutionary innovations within respiratory pathways of *Utricularia* also appear to reflect the selective pressures attendant to these costs (Jobson et al. 2004). Similarly, cellular signalling within the rapidly responsive traps of both *Aldrovanda* and *Utricularia* may be limited by K availability (Adamec 2010b); it would be of interest to determine if similar limitation is observed in *Dionaea* (the sister group of *Aldrovanda*). In support of this hypothesis, mineral costs of carnivory – especially of K and P – exceed 50% of total plant K and P amount in several ACP species (Adamec 2010b); we hypothesize that the proportion will be lower in most TCP species with separate traps.

Both ACPs and TCPs have relatively high respiration rates, but R_D increases much more rapidly with A_{MAX} in TCPs than it does in ACPs (Fig. 3). At least for *Utricularia*, this may reflect the aforementioned mutation in the cytochrome *c* oxidase pathway (Jobson et al. 2004), but the parallel high A_{MAX} relative to R_D observed in *Aldrovanda* cannot be explained in the same way. However, *Aldrovanda* and *Utricularia*, like terrestrial carnivorous plants in the genera *Dionaea, Nepenthes, Cephalotus, Genlisea*, have traps that are distinctly separate from photosynthetic laminae. Although most studies of ACPs measure photosynthesis and respiration separately in leaves and traps, only recently have comparable studies of TCPs distinguished between traps and lamina (Pavlovič et al. 2007; Hájek and Adamec 2009; Karagatzides and Ellison 2009). The relationship between A_{MAX} and R_D in all carnivorous plants may become clearer as these characteristics are measured separately on traps and leaves or laminae of a larger number of species.

Despite the differences in detail, however, the general cost-benefit framework continues to be of great utility in understanding the evolutionary ecology of carnivorous plants. Both ACPs and TCPs are limited by available resources and must allocate nutrients and carbon to base metabolic functions, current and future growth (storage), and development of organs – traps and/or roots – to provide additional opportunities for obtaining and taking up nutrients.

Conclusions and challenges for further research

Carnivorous plants have been model systems for studying a wide range of ecophysiological and ecological processes (Adamec 1997a; Ellison and Gotelli 2001; Ellison et al. 2003) and have provided novel insights into trait-based models of ecological and evolutionary trade-offs. Central to the cost-benefit model for the evolution of botanical carnivory is the relationship between nutrients and photosynthesis. How do carnivorous plants efficiently obtain scarce nutrients that are supplied primarily in organic form as prey, digest and mineralize them so that they can be readily used, and allocate them to immediate needs (e.g., increase photosynthetic activity to provide energy for “expensive” traps) as opposed to future needs (e.g., storage for subsequent years’ growth or flowering)? Beginning with Darwin (1875), studies of carnivorous plants have elaborated the diversity of mechanisms used by carnivorous plants to capture and digest prey (e.g., reviews in Juniper et al. 1989, Ellison and Gotelli 2009).

It remains crucial, however, to resolve clearly linkages between prey capture and nutrient uptake on the one hand and photosynthesis on the other. The majority of pitcher plants (*Darlingtonia californica*, *Sarracenia* spp., *Nepenthes* sp.) show correlated increases in foliar N and P content, growth rate, and A_{MAX} following prey addition (Ellison and Farnsworth 2005; Wakefield et al. 2005; Farnsworth and Ellison 2008; Pavlovič et al. 2009). Comparable data for aquatic carnivorous plants are rare and inconsistent (Adamec 2000, 2008c, 2011a; Adamec et al. 2010). In part, this contrast reflects the relative ease of studying prey mineralization and nutrient uptake in terrestrial pitcher plants with their large pitchers (e.g., Butler and Ellison 2007; Butler et al. 2008; Karagatzides et al. 2009) and the difficulty of studying similar phenomena in aquatic *Utricularia* with their tiny bladders (e.g., Englund and Harms 2003; Adamec 2008a, 2008c).

Studies on TCPs have focused primarily on N, and to a lesser extent, P, which have been shown repeatedly to be limiting nutrients for these plants (Figs. 4, 5). Aquatic carnivorous plants, on the other hand, show much more variability both in tissue nutrient content (Fig. 4) and stoichiometric nutrient limitation (Fig. 5). A few studies have suggested that uptake of P, K, and Mg from prey could enhance photosynthesis of ACPs (Adamec 2008c) and that these nutrients may be as important to ACPs as N is to TCPs (Friday and Quarmby 1994; Adamec et al. 2010). However, methodological barriers must be overcome before direct measurements of linkages between these nutrients and A_{MAX} can be made in ACPs. Similar barriers have limited studies of the efficiency of mineral nutrient uptake from prey carcasses in ACPs (Friday and Quarmby 1994; Adamec et al. 2010).

What other core cellular and physiological processes are directly tied to nutrient uptake from prey capture by carnivorous plants? We have previously suggested that prey-derived N and P increase cell division, DNA replication, and protein synthesis in young meristematic tissues of shoot apices of ACPs account for the very rapid growth of their apical shoots (Adamec 2008c). Because effects of prey addition are manifest primarily on young, developing tissues and organs rather than in mature, existing organs (Ellison and Gotelli 2002, 2009), such effects may not be apparent in short-term experiments. Because of the large differences in shoot morphology and growth dynamics of ACPs and TCPs (e.g. Fig. 1) there is unlikely to be a single mechanism by which carnivory stimulates growth in both groups.

Of great curiosity is the repeated finding that mineral nutrient uptake from the soil by roots of TCPs is stimulated following prey capture (Hanslin and Karlsson 1996; Adamec 1997a, 2002). Aquatic carnivorous plants lack roots; might prey addition stimulate mineral nutrient uptake by shoots from the ambient water? Adamec et al. (2010) found that shoot N and P uptake by *A. vesiculosa* increases following prey capture, but a similar effect was not observed for *U. australis*. What is the mechanism for these effects in TCPs and *Aldrovanda*? Does nutrient uptake affinity or capacity increase with prey capture or tissue nutrient content, leading to a positive feedback loop that ultimately increases uptake rate? Detailed examination of physiological and hormonally regulated processes – photosynthetic rates, transport of photosynthates to roots, tissue mineral nutrient content in both shoots and roots, root anatomy, mineral nutrient uptake by excised roots, and phytohormone content in roots – should be taken into account.

Furthermore, as animal prey is a poor source of K, and because [K^+] in the ambient water can be very low and growth limiting (Adamec 1997a), **we hypothesize that K^+ uptake affinity of ACPs is extremely high**. A focus on studying K uptake characteristics in shoots of ACPs is warranted by the fact that, unlike TCPs, ACPs reutilize virtually no K from senescent shoots although the shoot content of K in ACPs is very high (Fig. 4). We also were unable to find any studies on K reutilization from senescent shoots in non-carnivorous plants, and so comparative studies of K dynamics in any aquatic plant would be welcome. Finally, we suggest that the nature of the stimulation of root nutrient uptake by the foliar nutrient uptake should be studied in model species of TCPs as well, with particular attention to *Drosera* and *Dionaea*, the terrestrial sister taxa of *Aldrovanda*.

The nutritional benefit of carnivory, defined as the ratio between the gain (direct and indirect) of certain mineral nutrients from carnivory and the loss of those nutrients in construction of traps, has recently been introduced by Adamec (2011b) to supplement the classic cost-benefit model (Givnish et al. 1984). To be nutritionally beneficial, carnivorous plants must not only capture prey efficiently but also maximize nutrient uptake from prey and minimize nutrient losses in senescent traps. Therefore, it is expected that the **nutritional cost-benefit ratio** was of principal importance during the evolution of different carnivorous plant taxa, both terrestrial and aquatic. New data on nutritional benefit in TCPs show relatively high cost-benefit ratios for N and P but smaller ones for K and Mg (Adamec 2011b). Future research will reveal if there any differences in nutritional benefits of carnivory between TCPs and ACPs.

Finally, what is the phylogenetic signal in linkages between prey capture, nutrient dynamics, growth, and photosynthesis in carnivorous plants? Although robust species-level phylogenies of most carnivorous plant groups are now available (reviewed by Ellison and Gotelli 2009), experimental work, especially on ACPs, is taxonomically restricted. Jobson et al. (2004) found a unique mutation in the cytochrome *c* oxidase pathway in *Utricularia* that helps to deal with the high energetic cost of its unique trap. Aquatic *Utricularia* are all derived from terrestrial ancestors, and both the loss of true roots (but not root-like structures) preceded colonization of, and adaptation to, aquatic habitats. The cytochrome *c* oxidase mutation is not restricted to aquatic *Utricularia* but it is possible that there are other synapomorphies that are present only in aquatic members of this genus. For example, does the apparent absence of a feedback between prey addition and shoot uptake of dissolved nutrients by *Utricularia* reflect phylogenetic constraints in the aquatic clades of this genus? In light of the recent finding of food web operation inside traps of aquatic *Utricularia* (Sirová et al. 2009), the proposed nutritional benefit for the plants from these mutualistic interactions – uptake of N and P from phytoplankton and detritus – deserves focused attention.

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Figure Legends

Figure 1. Relative growth rates (RGR: g g^{-1} d^{-1}) for a wide variety of herbaceous plants. Boxes illustrate median RGR (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 upper and lower deciles (solid circles). Box width is proportional to sample size, and ranges from $N = 2$ (for aquatic unrooted herbs exclusive of ACPs) to $N = 208$ (for herbaceous dicotyledonous angiosperms, exclusive of TCPs). Data compiled from Grime and Hunt (1975), Fenner (1983), Eissenstat and Caldwell (1987), Poorter and Remkes (1990), Shipley and Peters (1990), Nielsen and Sand-Jensen (1991), Marañón and Grubb (1993), Hunt and Cornelissen (1997), Keddy et al. (1998), Adamec (1999; 2000; 2002; 2008b; 2010a), Adamec and Lev (1999), Leishman (1999), Shipley (2002), Pagano and Titus (2004; 2007), and Farnsworth and Ellison (2008). The full dataset is available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), Dataset HF-168.

Figure 2. Maximum dry mass-based photosynthetic rates (nmol CO_2 fixed g^{-1} s^{-1}) for leaves or shoots of herbaceous plants. Boxes as in Fig. 1; box width is proportional to sample size, and ranges from $N = 8$ (for aquatic unrooted herbs exclusive of ACPs) to $N = 141$ (for herbaceous dicotyledonous angiosperms, exclusive of TCPs). Data for terrestrial plants are from Ellison (2006), Pavlovič et al. (2007; 2009; 2010), Farnsworth and Ellison (2008), Karagatzides and Ellison (2009), Hájek and Adamec (2010) and Bruzzese et al. (2010). Data for aquatic plants are from Boston et al. (1989), Nielsen and Sand-Jensen (1989), Madsen et al. (1991, 1996), Madsen and Brix (1997), Adamec (1997b; 2006; 2008c), Maberly and Madsen (2002), Kahara and Vermaat (2003), Pierini and Thomaz (2004), and Klavsen and Maberly (2010). The full dataset

is available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), Dataset HF-168.

Figure 3. Mass-based dark respiration and photosynthetic rates (nmol CO_2 g-^{1} s^{-1}) for carnivorous plants for which both were measured on the same plants. Different symbols are used for different genera. Colors represent types of carnivorous plants: blue – aquatic carnivorous plants (ACPs: *Aldrovanda* and *Utricularia*); dark green – terrestrial carnivorous plants (TCPs) with separate traps and lamina (*Nepenthes, Dionaea*) or phyllodia (*Sarracenia*); light green with black border – TCPs without separate traps and lamina (*Drosera, Drosophyllum, Pinguicula*). Solid symbols are leaves, lamina, phyllodia, or entire plants, as appropriate; open symbols are traps measured separately of *Utricularia, Nepenthes,* and *Sarracenia*. Solid symbols with a central cross are for *Aldrovanda, Utricularia,* and *Nepenthes* that had received supplemental prey or nutrients. Data compiled from Knight (1992), Adamec (1997b; 2008c), Mendéz and Karlsson (1999), Pavlovič et al. (2007; 2009; 2010); Bruzzese et al. (2010), and Hájek and Adamec (2010). Regression lines are shown for all TCPs (green line) and ACPs (blue line). The full dataset is available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), Dataset HF-168.

Figure 4. Tissue nutrient content of nitrogen (N), phosphorus (P), and potassium (K) in leaves or shoots of aquatic (ACP) and terrestrial (TCP) carnivorous plants. Box plots as in Fig. 1, but not scaled to sample size, which is given in axis labels. The vertical blue lines indicate the value below which the nutrient is considered to limit plant growth. Data for TCPs are from Ellison (2006), Osunkoya et al. (2007) Pavlovič et al. (2007; 2009; 2010), Farnsworth and Ellison

(2008), Karagatzides and Ellison (2009), Karagatzides et al. (2009), Adamec (2009a), and Moon et al. (2010). Data for ACPs are from Moeller (1980), Kamiński (1987a; 1987b), Kosiba and Sarosiek (1989), Kosiba (1992a; 1992b; 1993), Friday and Quarmby (1994), Bern (1997), and Adamec (2000; 2008a; 2010b). The full dataset is available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), Dataset HF-168.

Figure 5. Stoichiometric relationships for ACPs (blue) and TCPs (green) in which N, P, and K all were measured simultaneously on the same individual. Solid symbols indicate entire plants or traps; open symbols indicate laminae measured separately on *Nepenthes*. “Sarraceniaceae” includes both *Sarracenia* and *Darlingtonia*. Dark lines indicate regions of N, P or P+N, and K or K+N limitation following the criteria of Olde-Venterink (2003). Data sources as in Fig. 4. The full dataset is available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), Dataset HF-168.

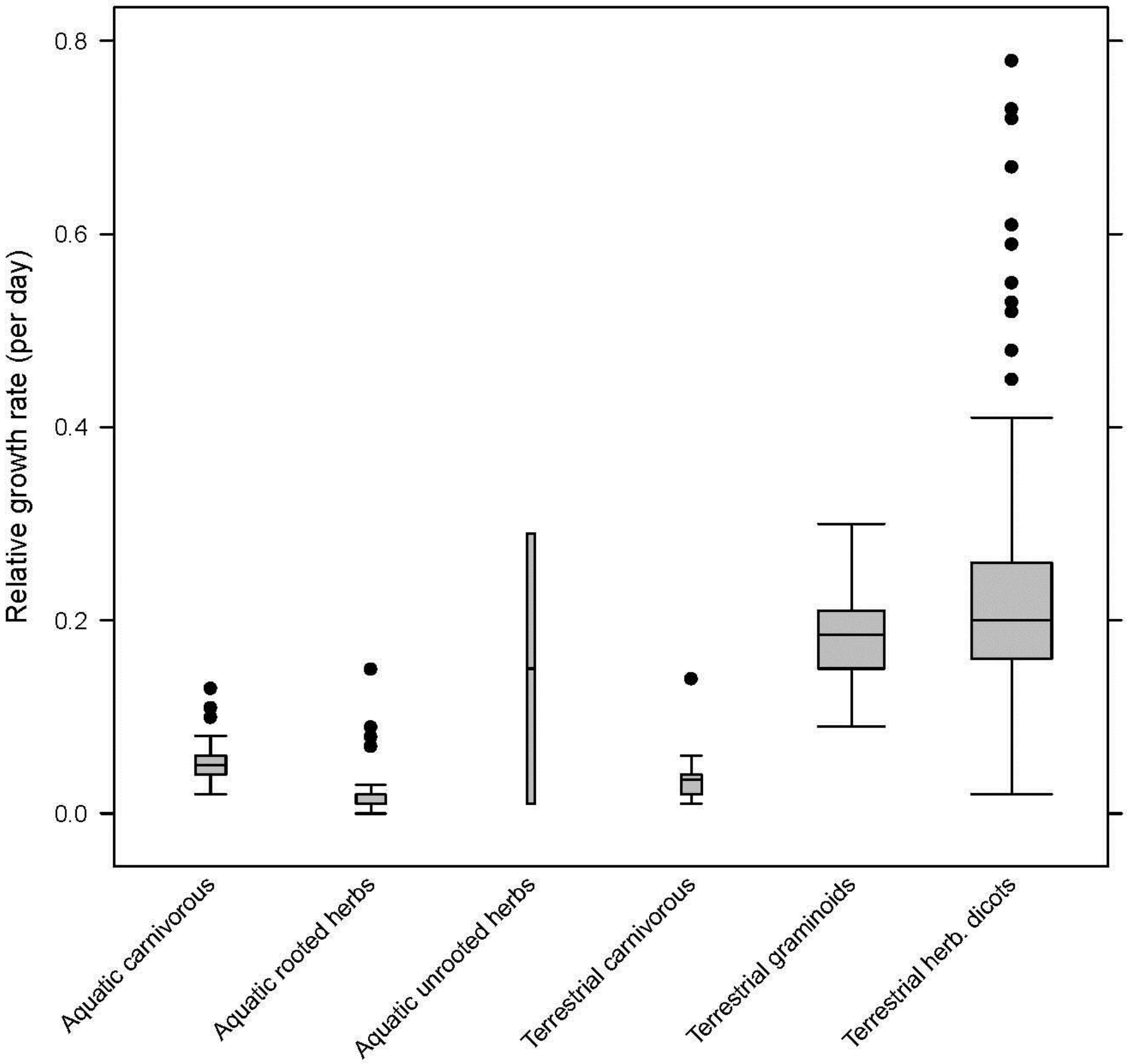
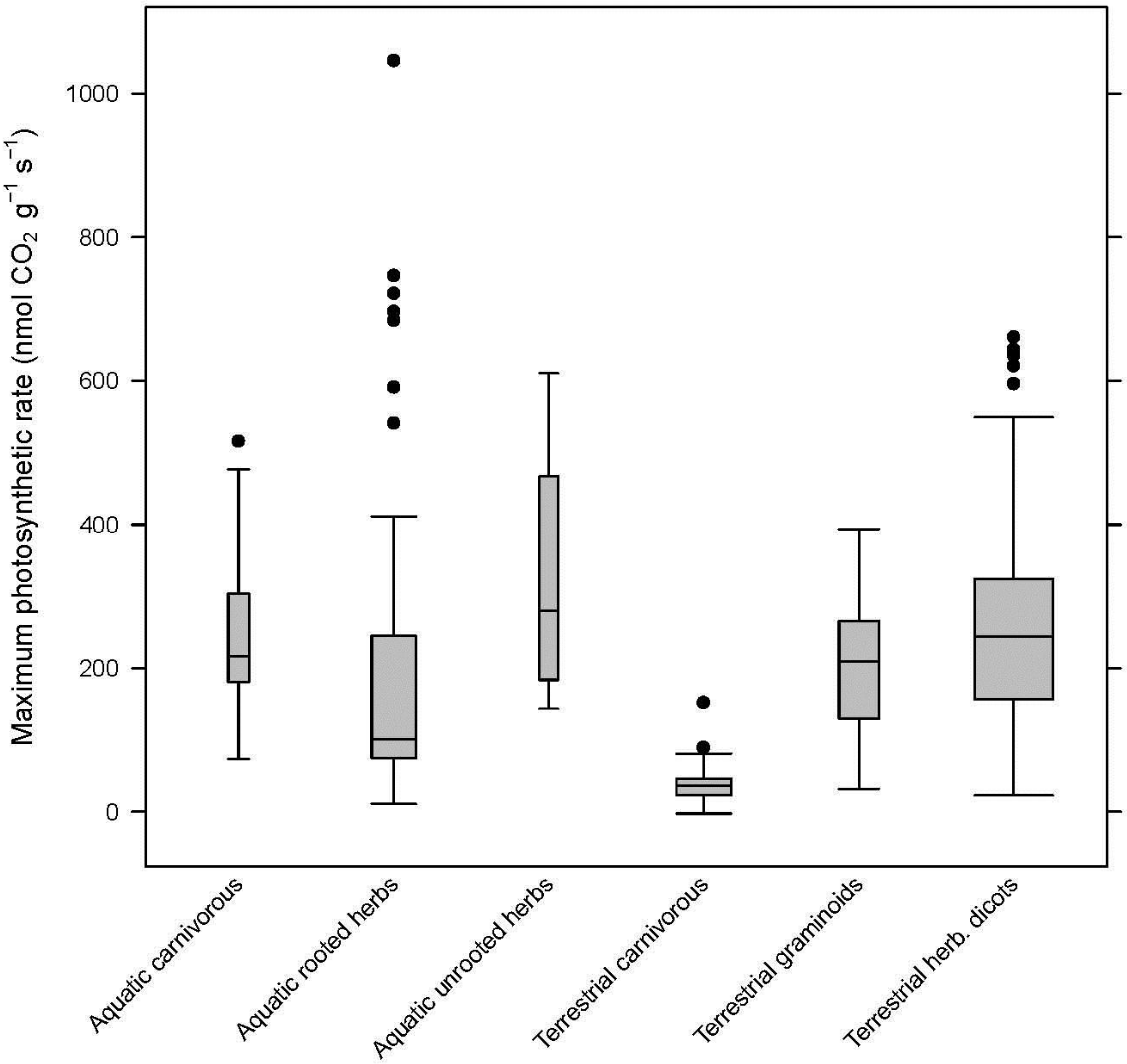

Relative growth rate (per day)
0.0
0.2
0.4
0.6
0.8
Aquatic carnivorous
Aquatic rooted herbs
Aquatic unrooted herbs
Terrestrial carnivorous
Terrestrial graminoids
Terrestrial herb. dicots

Figure 1



Maximum photosynthetic rate (nmol CO$_2$ g^{-1} s^{-1})
1000
800
600
400
200
0
Aquatic carnivorous
Aquatic rooted herbs
Aquatic unrooted herbs
Terrestrial carnivorous
Terrestrial graminoids
Terrestrial herb. dicots

Figure 2

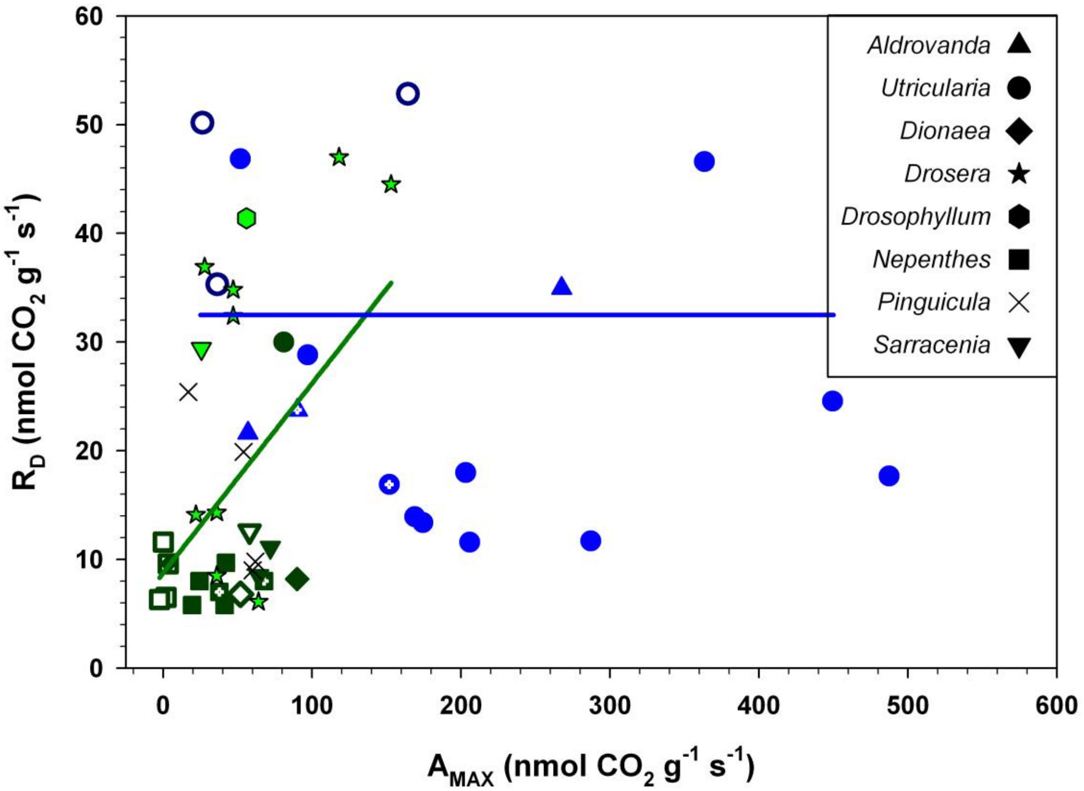

R_D (nmol CO_2 g^{-1} s^{-1})
0
10
20
30
40
50
60
A_{MAX} (nmol CO_2 g^{-1} s^{-1})
0
100
200
300
400
500
600
Aldrovanda ▲
Utricularia ●
Dionaea ◆
Drosera ★
Drosophyllum ⬢
Nepenthes ■
Pinguicula ×
Sarracenia ▼

Figure 3

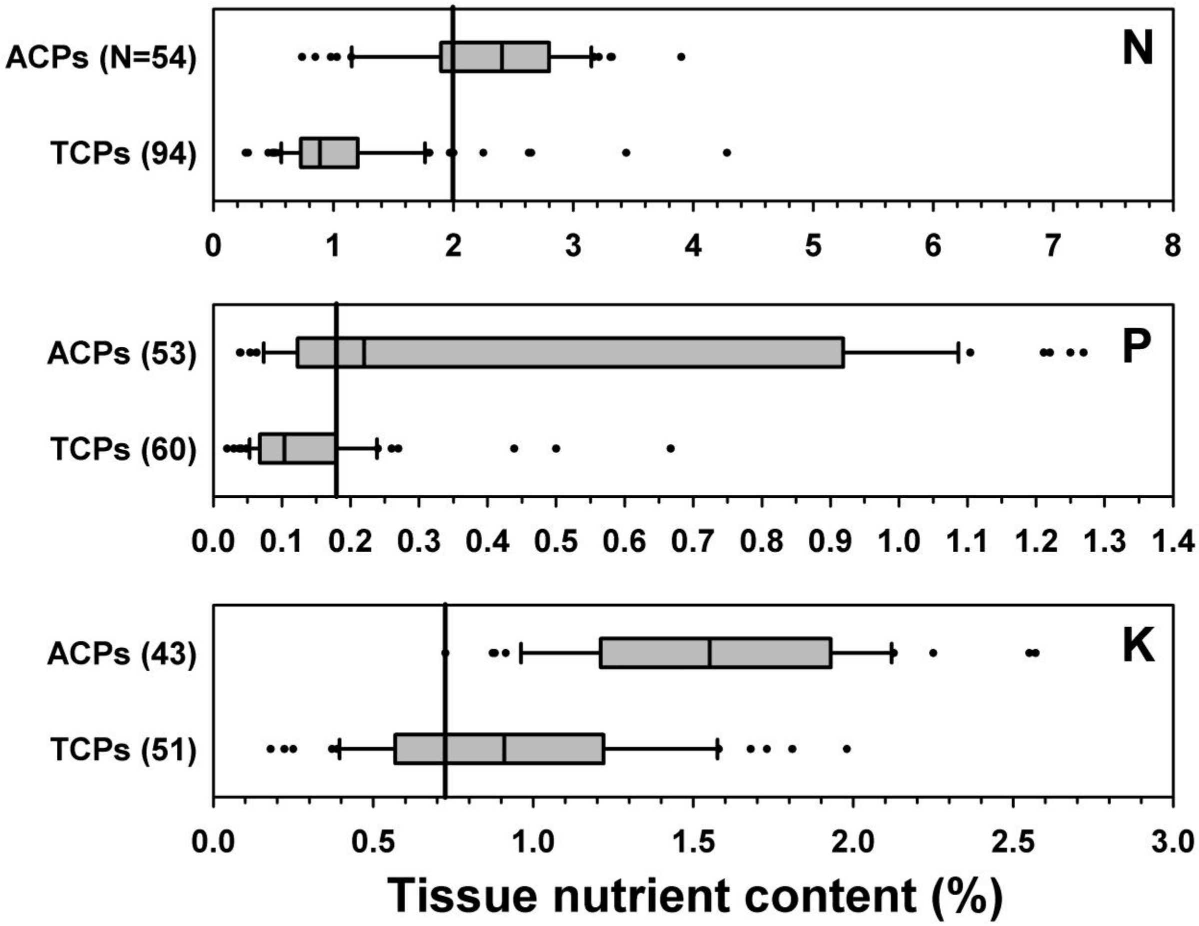
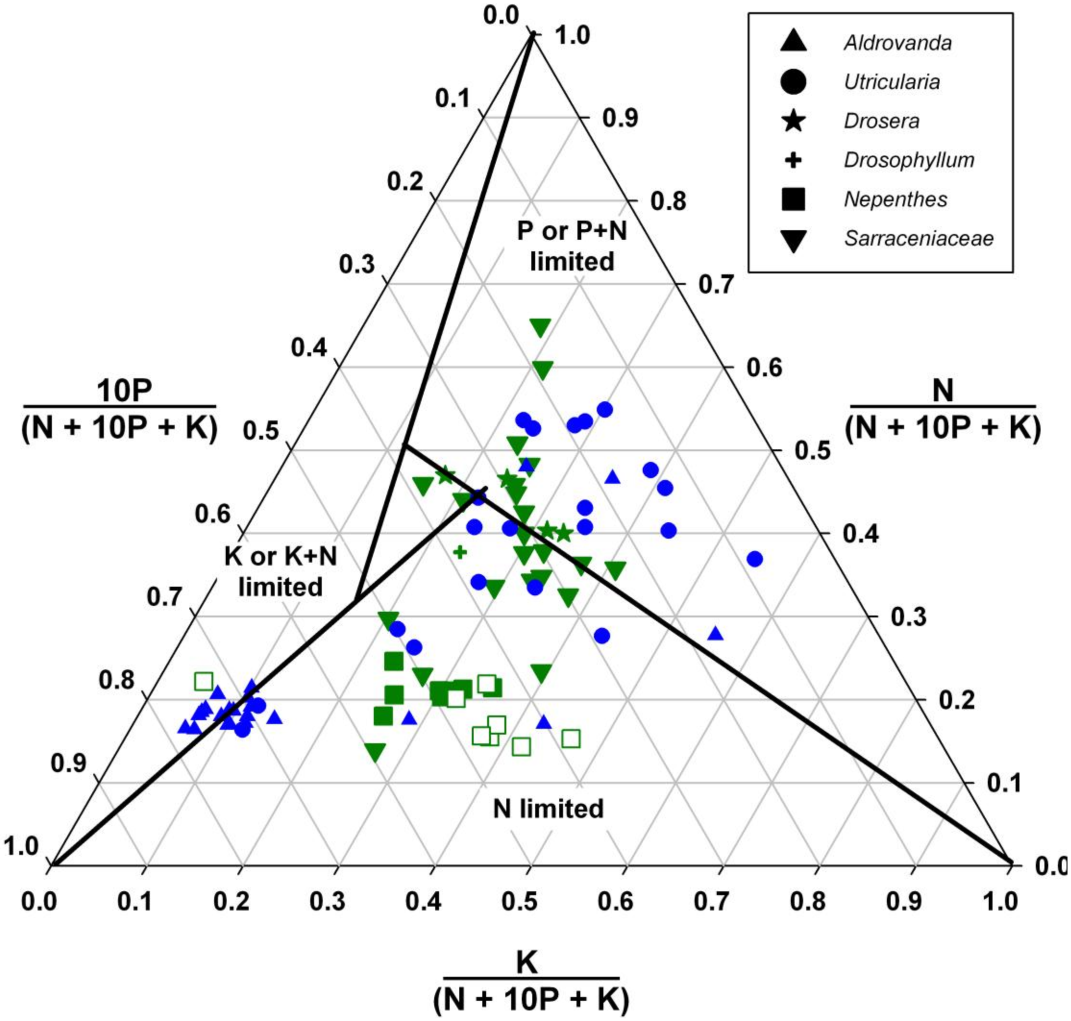

ACPs (N=54)
TCPs (94)
N
0
1
2
3
4
5
6
7
8
ACPs (53)
TCPs (60)
P
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
ACPs (43)
TCPs (51)
K
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Tissue nutrient content (%)

Figure 4



Aldrovanda
Utricularia
Drosera
Drosophyllum
Nepenthes
Sarraceniaceae
P or P+N limited
K or K+N limited
N limited
10P / (N + 10P + K)
N / (N + 10P + K)
K / (N + 10P + K)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure 5