



# Ecophysiological Traits of Terrestrial and Aquatic Carnivorous Plants: Are the Costs and Benefits the Same?

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| Citation          | Ellison, Aaron M. and Lubomír Adamec. Forthcoming. Ecophysiological traits of terrestrial and aquatic carnivorous plants: are the costs and benefits the same? <i>Oikos</i> .  |
| Published Version | <a href="http://onlinelibrary.wiley.com/journal/10.1111/%28ISSN%291600-0706">http://onlinelibrary.wiley.com/journal/10.1111/%28ISSN%291600-0706</a>  |
| Citable link      | <a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:4777759">http://nrs.harvard.edu/urn-3:HUL.InstRepos:4777759</a>  |
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1 **Ecophysiological traits of terrestrial and aquatic carnivorous plants: are the costs and**  
2 **benefits the same?**

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18 14 March 2011

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20 **Abstract**

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

42 broader insights into similarities and differences between aquatic and terrestrial plants of all  
43 types.  
44

45 **Introduction**

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

55 Givnish et al. (1984) provided one of the most significant applications of a cost-benefit  
56 model to a long-standing problem in evolutionary ecology – an explanation for the repeated  
57 evolution of botanical carnivory among at least six disparate plant lineages (Darwin 1875; Lloyd  
58 1942; Benzing 1987; Juniper et al. 1989; Albert et al. 1992; Ellison and Gotelli 2001, 2009;  
59 Chase et al. 2009). In short, Givnish et al. (1984) proposed that botanical carnivory – the  
60 attraction, capture, and digestion of animal prey, and the subsequent direct uptake and use of  
61 nutrients from that prey – would evolve when the marginal benefit derived from carnivory  
62 (expressed as increased rates of photosynthesis or growth) exceeded the marginal cost  
63 (expressed in units of carbon) required to construct animal traps. Because of its clarity and its  
64 quantitative framework, the cost-benefit model for the evolution of botanical carnivory has been  
65 the fundamental framework underlying carnivorous plant research since its publication in 1984  
66 (see reviews in Adamec 1997a; Ellison 2006; Ellison and Gotelli 2009; and see Brewer et al.  
67 2011 for an alternative approach).

68           The cost-benefit model for the evolution of botanical carnivory was developed based on  
69 data collected from a single carnivorous plant, the bromeliad *Brocchinia reducta* (Givnish et al.  
70 1984), but it has been applied routinely to all carnivorous plants (Givnish et al. 1984; Benzing  
71 1987; Ellison 2006). The majority of these *ca.* 650 species inhabit nutrient-poor habitats in  
72 which light and water are rarely limiting (Benzing 1987, 2000; Brewer et al. 2011).  
73 Approximately 90 % of carnivorous plants can be considered “terrestrial”; they are firmly rooted  
74 in sandy or peaty wetland soils (Juniper et al. 1989; Taylor 1989; Guisande et al. 2007), and  
75 virtually all of the empirical studies applying the cost-benefit model for the evolution of  
76 carnivory have examined terrestrial carnivorous plants (Ellison 2006). But the remaining ~10%  
77 of carnivorous plants, including ~50 species of bladderworts (*Utricularia*: Lentibulariaceae) and  
78 the water-wheel plant *Aldrovanda vesiculosa* (Droseraceae) are unrooted submerged or  
79 amphibious aquatic plants (Taylor 1989; Adamec 1997b). Here, we ask whether the cost-benefit  
80 model applies equally well to aquatic carnivorous plants and what general insights into trade-off  
81 models are gained by this comparison.

82           In applying the cost-benefit model, why should it matter whether plants are aquatic or  
83 terrestrial? First, the physical environments of aquatic and terrestrial habitats are quite different  
84 (Sand-Jensen 1989; Barko et al. 1991; Sand-Jensen and Frost-Christensen 1998; Colmer and  
85 Pedersen 2008). On land, CO<sub>2</sub> is available as a gas at a relatively constant concentration and  
86 diffuses rapidly into plant tissues through stomata (e.g., Lambers et al. 1998). In water, CO<sub>2</sub> and  
87 O<sub>2</sub>, the critical gases for photosynthesis and respiration, are dissolved in solution and diffusion  
88 rates of dissolved solutes limit photosynthetic rate. Furthermore, uptake of CO<sub>2</sub> by aquatic plants  
89 is strongly dependent on pH and total alkalinity, and direct uptake of CO<sub>2</sub> by aquatic plants  
90 increases with concentrations of dissolved inorganic carbon, dissolved organic matter, and

91 mineral nutrients in the aquatic environment. Although the shallow standing, oligo-mesotrophic  
92 and dystrophic (organically-rich, humic) waters in which aquatic carnivorous plants grow may  
93 have low concentrations of O<sub>2</sub>, these same waters usually (but not strictly) are very rich in free  
94 CO<sub>2</sub> (Adamec 1997a, 1997b, 2008a). These physical differences between aquatic and terrestrial  
95 environments strongly suggest that key ecophysiological traits and processes (e.g.,  
96 photosynthesis, growth rate, nutrient uptake) should differ between terrestrial and aquatic plants,  
97 whether or not they are carnivorous (e.g., Sand-Jensen 1989; Lambers et al. 1998; Colmer and  
98 Pedersen 2008).

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

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

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

134           Although most carnivorous plants are perennial, some are annual, and both life-histories  
135 can be found among terrestrial and aquatic carnivorous plants. Among aquatic carnivorous



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

142         Finally, aquatic plants are not found in all angiosperm clades, and aquatic carnivorous  
143 plants are notable for their taxonomic restriction. All but one of the aquatic carnivorous plants  
144 are in the single genus *Utricularia* (Lamiales: Lentibulariaceae), and are found only in a few  
145 derived clades within that genus (Taylor 1989; Guisande et al. 2007). The one other aquatic  
146 carnivorous plant is *Aldrovanda vesiculosa*, a derived carnivorous plant in the Droseraceae  
147 (Caryophyllales). Thus, phylogenetic constraints may play a greater role in determining the  
148 evolution of specific types or mechanisms of carnivory in (aquatic) *Utricularia* (Jobson et al.  
149 2004) than in the more phylogenetically diverse terrestrial carnivorous plants.

150         In this paper, we first review our understanding of differences and similarities in  
151 fundamental ecophysiological traits – structural characteristics, growth patterns and rates,  
152 photosynthesis, and nutrient uptake and use – of aquatic and terrestrial carnivorous plants  
153 (henceforth ACPs and TCPs, respectively). We then use these contrasts to assess cost-benefit  
154 relationships among these traits in ACPs and TCPs and ask whether these patterns can inform  
155 trait-based models for plants growing in either terrestrial or aquatic habitats. We then return to  
156 the question of how phylogeny may have constrained observed patterns of the evolution of  
157 botanical carnivory. Finally, we outline a set of research needs to further our understanding of  
158 the evolutionary physiology of carnivorous plants and to incorporate them fully into general

159 trait-based models of plant form and function (compare Wright et al. 2004, 2005; Reich et al.  
160 2009; and Ordoñez et al. 2009 with Ellison 2006; and Karagatzides and Ellison 2009).

161

## 162 **Traits of aquatic and terrestrial carnivorous plants**

### 163 *Structural traits*

164 The growth forms of TCPs most commonly are sessile or erect rosettes, but there also are  
165 carnivorous vines (*Triphyophyllum*) and erect-stemmed herbs (*Drosophyllum*, *Roridula*, *Byblis*)  
166 (Juniper et al. 1989). Most TCPs possess true roots and many species also produce thick  
167 rhizomes. Root-like rhizomes or stolons are produced even by otherwise rootless terrestrial  
168 species of *Utricularia* and *Genlisea* (Juniper et al. 1989; Taylor 1989; Adamec 2005). The root  
169 systems of TCPs are usually small, short, and poorly branched (the proportion of root dry mass  
170 to the total plant dry mass ranges from 3 – 23%; Adamec 1997a). Nonetheless, roots, rhizomes,  
171 and/or stolons anchor the plants, root uptake may contribute substantially to the nutrient budget  
172 of TCPs (Adamec 1997a), and the physiological root activity per unit biomass is surprisingly  
173 high (Adamec 2005). In contrast, ACPs are submerged or partially amphibious, rootless plants  
174 that float freely in the water column or are weakly attached to loose sediments (Taylor 1989;  
175 Guisande et al. 2007). Uptake of nutrients from the surrounding water supplements nutrients  
176 obtained from captured prey (Lollar et al. 1971; Knight and Frost 1991; Friday and Quarmby  
177 1994; Ulanowicz 1995; Guisande et al. 2000; Chiang et al. 2000; Adamec 2008a). Most ACPs  
178 have a linear, modular shoot structure consisting of regularly produced and regularly shed nodes  
179 with filamentous leaves and tubular, fragile internodes. In some species, the leaves are arranged  
180 in true whorls. The linear shoots are either monomorphic (non-differentiated) or dimorphic,  
181 differentiated into green photosynthetic shoots and pale carnivorous shoots with many traps

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

188

### 189 *Growth*

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

201       The relative growth rate of both ACPs and TCPs is generally significantly lower than  
202 most groups of non-carnivorous herbaceous plants ( $F_{5,423} = 80.26$ ,  $P < 2 \times 10^{-16}$ , ANOVA; Fig.  
203 1). Based on a broad review of published values (references in legend to Fig. 1), the RGRs of  
204 ACPs and TCPs, along with rooted aquatic herbaceous plants (non-carnivorous) were low (of the

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

217

### 218 *Photosynthesis and dark respiration*

219 In all TCPs, the traps are modified from leaves or leaf parts (Arber 1941; Lloyd 1942). In many  
220 TCPs, the traps function simultaneously as nutrient capture organs and as photosynthetic organs,  
221 although in the ca. 100 species of *Nepenthes*, the lamina (an expanded petiole) accounts for at  
222 least 90% of photosynthesis and the traps (modified leaf blades) have negligible photosynthetic  
223 rates (Pavlovič et al. 2007; Karagatzides and Ellison 2009). In ACPs, the situation is similar.

224 *Aldrovanda* traps both acquire nutrients and photosynthesize, but in *Utricularia*, traps are  
225 specialized for prey capture and have much lower photosynthetic rates than the leaves.

226 Therefore, in comparing photosynthetic rates among groups, we use data from the primary  
227 photosynthetic organs, but where possible, we also highlight differences between photosynthetic

228 rates of leaves/lamina and traps. In discussing respiratory (maintenance) costs, we focus on the  
229 ratio of dark respiration to photosynthesis.

230 Both TCPs and ACPs are C-3 plants (Lüttge 1983). However, maximum photosynthetic  
231 rates vary dramatically between TCPs and ACPs ( $F_{5, 259} = 24.12$ ,  $P < 2 \times 10^{-16}$ , ANOVA; Fig. 2).  
232 Mass-based maximum photosynthetic rates ( $A_{MAX}$ ) measured for TCPs range from 17-153 nmol  
233  $\text{CO}_2 \text{ g}^{-1}$  (dry mass)  $\text{s}^{-1}$ , approximately 4-fold less than values commonly found for leaves non-  
234 carnivorous herbs (Wright et al. 2004; Ellison and Farnsworth 2005; Ellison 2006; Fig. 2). In  
235 contrast,  $A_{MAX}$  of ACPs range from 73-517 nmol  $\text{g}^{-1} \text{ s}^{-1}$ , whereas the usual values for submerged,  
236 aquatic, non-carnivorous plants generally range from 75 to 240 (for rooted aquatic herbs) or 200  
237 – 450 (for floating, unrooted aquatic herbs) nmol  $\text{g}^{-1} \text{ s}^{-1}$  (Fig. 2). That is,  $A_{MAX}$  of ACPs is similar  
238 to both unrooted aquatic non-carnivorous plants ( $P = 0.98$ ) and rooted aquatic non-carnivorous  
239 plants ( $P = 0.22$ ), whereas  $A_{MAX}$  of TCPs not only is significantly lower than that of terrestrial  
240 non-carnivorous plants ( $P < 1 \times 10^{-8}$ ), but it is also significantly lower than that of ACPs and  
241 other aquatic plants ( $P < 1 \times 10^{-8}$ ). The photosynthetic  $\text{CO}_2$  affinity (compensation  
242 concentration) measured for ACPs averages 4.5  $\mu\text{M}$  and ranges from 0.7-13  $\mu\text{M}$  (Adamec  
243 1997b, 2009a; Adamec and Kovářová 2006; Pagano and Titus 2007), quite similar to that found  
244 in non-carnivorous aquatic plants, which ranges from 1.5 – 10  $\mu\text{M}$  (Maberly and Spence 1983).  
245 We note that in general,  $\text{HCO}_3^-$  is of a very minor ecological importance in carbon budgets of  
246 ACPs, although  $\text{HCO}_3^-$  may be used for photosynthesis by *U. australis* grown at very high pH  
247 (Adamec 2009b).

248 The large differences in photosynthetic rates between TCPs and ACPs only partly reflect  
249 their minor differences in RGRs. An assessment of the relationship between respiration and  
250 photosynthesis in ACPs and TCPs (Fig. 3), however, illuminates linkages between carbon

251 fixation rates and RGR. Non-carnivorous herbaceous plants typically have dark respiration rates  
252 ( $R_D$ ) < 50 % of  $A_{MAX}$  (Bazzaz and Carlson 1982). In contrast, the average  $R_D/A_{MAX}$  ratio of TCPs  
253 is much higher (63 %), whereas ACPs have a much lower ratio of  $R_D/A_{MAX}$  (mean = 34 %, range  
254 4 – 190 %;  $F_{1,40} = 5.88$ ,  $P = 0.03$  ANOVA on  $\ln$ -transformed data). Interestingly,  $R_D$  tends to  
255 increase with  $A_{MAX}$  for TCPs, but varies little for ACPs;  $R_D/A_{MAX}$  is little affected by  
256 supplemental feeding (Fig. 3). The much higher (absolute) values of  $R_D$  in aquatic *Utricularia*  
257 traps than in traps of TCPs support the observation of very energetically demanding  
258 physiological function of water pumping that is unique to *Utricularia* (Jobson et al. 2004;  
259 Adamec 2006).

260         The averages also mask significant differences between traps and leaves or  
261 photosynthetic lamina in species where trapping and photosynthesis are accomplished by  
262 different organs ( $F_{5,32} = 18.84$ ,  $P = 0.002$ , nested ANOVA on  $\ln$ -transformed data). In the TCPs  
263 *Nepenthes*, *Sarracenia*, and *Dionaea* for which those  $A_{MAX}$  and  $R_D$  have been measured  
264 separately on traps (pitchers and snap-traps, respectively) and laminae (lamina, phyllodia, and  
265 petioles, respectively), the traps have much higher respiratory costs (mean  $R_D/A_{MAX} = 158\%$ ,  
266 range = 13 – 325%) than do the laminae (mean = 19%, range = 9 – 33%) (Fig. 3). For TCPs such  
267 as *Drosera*, *Pinguicula* and *Sarracenia* in which traps are modified leaves and both  $R_D$  and  $A_{MAX}$   
268 were measured on these modified leaves,  $R_D/A_{MAX}$  averages 68% (range 10 – 149%). Similarly,  
269 respiratory costs of very weakly photosynthesizing traps of the aquatic *Utricularia* (mean  $R_D/A_{MAX}$   
270 = 106%, range 32 – 190%) are much higher than its leaves (mean = 9%, range 4 – 90%). Even  
271 when traps and leaves of *Utricularia* are assayed together, their  $R_D/A_{MAX}$  ratio is much lower  
272 than that of TCPs (mean = 21%, range 9 – 38%) (Fig. 3).

273           The substantial differences in the relative respiratory costs between ACPs and TCPs are  
274 related to their distinct methods of growth. We conclude that low  $A_{MAX}$  values and high  $R_D/A_{MAX}$   
275 ratios of TCPs are a typical, convergent, attribute of this group of plants and reflect  
276 physiological consequences of slow growth, and storage of C over often long lifespans (Butler  
277 and Ellison 2007). On the other hand, the very low  $R_D/A_{MAX}$  of ACPs reflects their rapid growth  
278 and turnover of senescent shoots that leads to large and predictable losses of structural and non-  
279 structural carbohydrates (Adamec 2000). Unlike TCPs that store C for future use, a substantial  
280 amount (~ 20-25 %) of the total photosynthetically fixed C is secreted by aquatic *Utricularia*  
281 traps into trap fluid where it supports the commensal assemblage within the trap (Sirová et al.  
282 2010).

283

#### 284 *Nutrient uptake and use*

285 It has been demonstrated repeatedly that the primary benefit of trapping and consuming insect  
286 prey is to obtain growth-limiting mineral nutrients, mainly N and P (see reviews in Juniper et al.  
287 1989; Adamec 1997a, 2002; Ellison 2006). How this benefit is expressed, however, differs  
288 among some carnivorous plant taxa and is unknown for others. For example, in several pitcher  
289 plants (*Sarracenia* and *Nepenthes*),  $A_{MAX}$  increases with foliar N or P (Ellison and Farnsworth  
290 2005; Pavlovič et al. 2007; Farnsworth and Ellison 2008). In *Drosera* and *Pinguicula*, capture of  
291 prey by traps stimulates additional uptake of mineral nutrients from the soil (Hanslin and  
292 Karlsson 1996; Adamec 1997a, 2002). Root uptake can further enhance  $A_{MAX}$  (Pavlovič et al.  
293 2010). Downstream, the consequence of prey addition usually results in increased growth  
294 expressed as more leaves, branches, and/or biomass (Ellison 2006). These data lead us to  
295 hypothesize that N and P derived from prey enhance essential growth processes in ACPs such as

296 cell division, DNA replication, and protein synthesis in the young, meristematic tissues of shoot  
297 apices (Adamec 2008b). This hypothesis is supported only for *Aldrovanda* but not for two  
298 *Utricularia* species (Adamec 2011a). Together with observations that TCPs shunt excess N to  
299 new growth (Butler and Ellison 2007), these data all suggest that the effects of enhanced prey  
300 capture are manifest on young, developing tissues and organs rather than on mature, existing  
301 organs (Ellison and Gotelli 2002, 2009).

302 TCPs have significantly lower foliar N, P, and K than all other functional groups of  
303 terrestrial non-carnivorous plants (Ellison 2006). In contrast, macronutrient content in shoots of  
304 ACPs is ~2 – 5 times greater than that of TCPs (Fig. 4) and comparable to that of aquatic non-  
305 carnivorous plants (Dykyjová 1979). Phosphorus content is much more variable among ACPs  
306 than among TCPs – up to 10- to 20-fold within the same species – but it could be overestimated  
307 in ACPs with their closed traps if remnants of captured prey are inadvertently analyzed (Adamec  
308 2008a). Like TCPs, K content in ACPs is substantially greater than N content, and P content of  
309 ACPs is nearly double that of terrestrial forbs, which otherwise have the highest foliar nutrient  
310 content among the different functional groups examined by Wright et al. (2005). Also unlike  
311 TCPs, average tissue macronutrient contents of ACPs are well above the “critical levels” (blue  
312 lines in Fig. 4) that limit growth in both aquatic and terrestrial plants (Gerloff and Krombholz  
313 1966; Ellison 2006). Stoichiometrically, ACPs show no consistent patterns with respect to  
314 nutrient limitation, whereas TCPs tend to be primarily P or P+N limited (Fig. 5).

315 Variation in nutrient content within individual ACPs reflects the steep nutrient polarity  
316 along shoots, localization of traps along the shoot, and also captured prey (Adamec 1997a, 2000,  
317 2008a). Thus, the growth rates of ACPs (Fig. 1) are associated with high  $A_{MAX}$  (Fig. 2),  
318 relatively low  $R_D$  (Fig. 3), and high shoot nutrient contents (Fig. 4). Nevertheless, very rapid



319 growth of ACPs that were experimentally fed additional prey in situations led to significant  
320 decrease in tissue N and P content in apical shoot segments (Adamec 2000; 2008a, 2011a).  
321 Similar results also have been observed in non-carnivorous aquatic plants (e.g., Titus and  
322 Andorfer 1996) and in adult shoots of several TCPs (Adamec 1997a, 2002). This observation  
323 may be partly the result of an apparent “dilution” of mineral nutrients by organic substances in  
324 plant tissues of rapidly growing plants.

325 Potassium (K) has been much less studied in carnivorous plants (Adamec 1997a; Ellison  
326 2006), but tissue K content in traps of aquatic *Utricularia* species (3.7-8.7 % of dry mass) is  
327 much higher than in its leaves or shoots (Adamec 2008a, 2010b), probably reflecting particular  
328 trap functions. The highest concentrations of K found in *Utricularia* traps exceed any reported  
329 for non-carnivorous aquatic plants (cf. Dykyjová 1979). However, it is not known whether this  
330 high K content is restricted to trap walls or the specialized quadrifid glands within the trap.

331 The effect of supplemental prey on growth of both TCPs and ACPs is generally positive  
332 (Adamec 1997a; Ellison 2006), but weak in aquatic *Utricularia* species, in which the effect  
333 depends markedly on pH and CO<sub>2</sub> availability (Kosiba 1992a; Adamec 2008a; Adamec et al.  
334 2010). However, both ACPs and TCPs efficiently take up nutrients from prey carcasses. Thirty  
335 to 76% of prey-N is taken up by TCPs (Hanslin and Karlsson 1996; Adamec 1997a, 2002; Butler  
336 and Ellison 2007; Butler et al. 2008) and over 80% is taken up by the aquatic *U. vulgaris* (Friday  
337 and Quarmby 1994). Similarly, TCPs take up 57 – 96% of P, K, Mg, and micronutrients from  
338 prey (Plummer and Kethley 1964; Adamec 2002; Adlassnig et al. 2009). Although comparable  
339 quantitative data are lacking for ACPs, we hypothesize that uptake of P, K, and Mg in ACPs  
340 should also be very efficient.

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

349

### 350 **Cost-benefit relationships in aquatic and terrestrial carnivorous plants**

351

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

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

378           Both ACPs and TCPs have relatively high respiration rates, but  $R_D$  increases much more  
379 rapidly with  $A_{MAX}$  in TCPs than it does in ACPs (Fig. 3). At least for *Utricularia*, this may reflect  
380 the aforementioned mutation in the cytochrome *c* oxidase pathway (Jobson et al. 2004), but the  
381 parallel high  $A_{MAX}$  relative to  $R_D$  observed in *Aldrovanda* cannot be explained in the same way.  
382 However, *Aldrovanda* and *Utricularia*, like terrestrial carnivorous plants in the genera *Dionaea*,  
383 *Nepenthes*, *Cephalotus*, *Genlisea*, have traps that are distinctly separate from photosynthetic  
384 laminae. Although most studies of ACPs measure photosynthesis and respiration separately in  
385 leaves and traps, only recently have comparable studies of TCPs distinguished between traps and

386 lamina (Pavlovič et al. 2007; Hájek and Adamec 2009; Karagatzides and Ellison 2009). The  
387 relationship between  $A_{MAX}$  and  $R_D$  in all carnivorous plants may become clearer as these  
388 characteristics are measured separately on traps and leaves or laminae of a larger number of  
389 species.

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

395

## 396 **Conclusions and challenges for further research**

397

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

409           **It remains crucial, however, to resolve clearly linkages between prey capture and**  
410 **nutrient uptake on the one hand and photosynthesis on the other.** The majority of pitcher  
411 plants (*Darlingtonia californica*, *Sarracenia* spp., *Nepenthes* sp.) show correlated increases in  
412 foliar N and P content, growth rate, and  $A_{MAX}$  following prey addition (Ellison and Farnsworth  
413 2005; Wakefield et al. 2005; Farnsworth and Ellison 2008; Pavlovič et al. 2009). Comparable  
414 data for aquatic carnivorous plants are rare and inconsistent (Adamec 2000, 2008c, 2011a;  
415 Adamec et al. 2010). In part, this contrast reflects the relative ease of studying prey  
416 mineralization and nutrient uptake in terrestrial pitcher plants with their large pitchers (e.g.,  
417 Butler and Ellison 2007; Butler et al. 2008; Karagatzides et al. 2009) and the difficulty of  
418 studying similar phenomena in aquatic *Utricularia* with their tiny bladders (e.g., Englund and  
419 Harms 2003; Adamec 2008a, 2008c).

420           Studies on TCPs have focused primarily on N, and to a lesser extent, P, which have been  
421 shown repeatedly to be limiting nutrients for these plants (Figs. 4, 5). Aquatic carnivorous  
422 plants, on the other hand, show much more variability both in tissue nutrient content (Fig. 4) and  
423 stoichiometric nutrient limitation (Fig. 5). A few studies have suggested that uptake of P, K, and  
424 Mg from prey could enhance photosynthesis of ACPs (Adamec 2008c) and that these nutrients  
425 may be as important to ACPs as N is to TCPs (Friday and Quarmby 1994; Adamec et al. 2010).  
426 However, methodological barriers must be overcome before direct measurements of linkages  
427 between these nutrients and  $A_{MAX}$  can be made in ACPs. Similar barriers have limited studies of  
428 the efficiency of mineral nutrient uptake from prey carcasses in ACPs (Friday and Quarmby  
429 1994; Adamec et al. 2010).

430           **What other core cellular and physiological processes are directly tied to nutrient**  
431 **uptake from prey capture by carnivorous plants?** We have previously suggested that prey-

432 derived N and P increase cell division, DNA replication, and protein synthesis in young  
433 meristematic tissues of shoot apices of ACPs account for the very rapid growth of their apical  
434 shoots (Adamec 2008c). Because effects of prey addition are manifest primarily on young,  
435 developing tissues and organs rather than in mature, existing organs (Ellison and Gotelli 2002,  
436 2009), such effects may not be apparent in short-term experiments. Because of the large  
437 differences in shoot morphology and growth dynamics of ACPs and TCPs (e.g. Fig. 1) there is  
438 unlikely to be a single mechanism by which carnivory stimulates growth in both groups.

439 **Of great curiosity is the repeated finding that mineral nutrient uptake from the soil**  
440 **by roots of TCPs is stimulated following prey capture** (Hanslin and Karlsson 1996; Adamec  
441 1997a, 2002). Aquatic carnivorous plants lack roots; might prey addition stimulate mineral  
442 nutrient uptake by shoots from the ambient water? Adamec et al. (2010) found that shoot N and  
443 P uptake by *A. vesiculosa* increases following prey capture, but a similar effect was not observed  
444 for *U. australis*. What is the mechanism for these effects in TCPs and *Aldrovanda*? Does  
445 nutrient uptake affinity or capacity increase with prey capture or tissue nutrient content, leading  
446 to a positive feedback loop that ultimately increases uptake rate? Detailed examination of  
447 physiological and hormonally regulated processes – photosynthetic rates, transport of  
448 photosynthates to roots, tissue mineral nutrient content in both shoots and roots, root anatomy,  
449 mineral nutrient uptake by excised roots, and phytohormone content in roots – should be taken  
450 into account.

451 Furthermore, as animal prey is a poor source of K, and because  $[K^+]$  in the ambient water  
452 can be very low and growth limiting (Adamec 1997a), **we hypothesize that  $K^+$  uptake affinity**  
453 **of ACPs is extremely high**. A focus on studying K uptake characteristics in shoots of ACPs is  
454 warranted by the fact that, unlike TCPs, ACPs reutilize virtually no K from senescent shoots

455 although the shoot content of K in ACPs is very high (Fig. 4). We also were unable to find any  
456 studies on K reutilization from senescent shoots in non-carnivorous plants, and so comparative  
457 studies of K dynamics in any aquatic plant would be welcome. Finally, we suggest that the  
458 nature of the stimulation of root nutrient uptake by the foliar nutrient uptake should be studied in  
459 model species of TCPs as well, with particular attention to *Drosera* and *Dionaea*, the terrestrial  
460 sister taxa of *Aldrovanda*.

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

471 **Finally, what is the phylogenetic signal in linkages between prey capture, nutrient**  
472 **dynamics, growth, and photosynthesis in carnivorous plants?** Although robust species-level  
473 phylogenies of most carnivorous plant groups are now available (reviewed by Ellison and  
474 Gotelli 2009), experimental work, especially on ACPs, is taxonomically restricted. Jobson et al.  
475 (2004) found a unique mutation in the cytochrome *c* oxidase pathway in *Utricularia* that helps to  
476 deal with the high energetic cost of its unique trap. Aquatic *Utricularia* are all derived from  
477 terrestrial ancestors, and both the loss of true roots (but not root-like structures) preceded

478 colonization of, and adaptation to, aquatic habitats. The cytochrome *c* oxidase mutation is not  
479 restricted to aquatic *Utricularia* but it is possible that there are other synapomorphies that are  
480 present only in aquatic members of this genus. For example, does the apparent absence of a  
481 feedback between prey addition and shoot uptake of dissolved nutrients by *Utricularia* reflect  
482 phylogenetic constraints in the aquatic clades of this genus? In light of the recent finding of food  
483 web operation inside traps of aquatic *Utricularia* (Sirová et al. 2009), the proposed nutritional  
484 benefit for the plants from these mutualistic interactions – uptake of N and P from phytoplankton  
485 and detritus – deserves focused attention.

486

487



488 **Acknowledgements**

489 AME's work on carnivorous plant has been supported by grants from the US National Science  
490 Foundation: 98-05722, 02-35238, 03-01361, 03-30605, and 05-41680. LA's work on this study  
491 was supported by the Research Programme of the Academy of Sciences of the Czech Republic,  
492 No. AV0Z60050516. Three anonymous reviewers provided constructive comments on the  
493 manuscript.

494

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790 **Figure Legends**

791 **Figure 1.** Relative growth rates (RGR:  $\text{g g}^{-1} \text{d}^{-1}$ ) for a wide variety of herbaceous plants. Boxes  
792 illustrate median RGR (center horizontal line), upper and lower quartiles (limits of grey boxes),  
793 upper and lower deciles (horizontal lines delimiting ends of vertical lines), and individual  
794 observations beyond the upper and lower deciles (solid circles). Box width is proportional to  
795 sample size, and ranges from  $N = 2$  (for aquatic unrooted herbs exclusive of ACPs) to  $N = 208$   
796 (for herbaceous dicotyledonous angiosperms, exclusive of TCPs). Data compiled from Grime  
797 and Hunt (1975), Fenner (1983), Eissenstat and Caldwell (1987), Poorter and Remkes (1990),  
798 Shipley and Peters (1990), Nielsen and Sand-Jensen (1991), Marañón and Grubb (1993), Hunt  
799 and Cornelissen (1997), Keddy et al. (1998), Adamec (1999; 2000; 2002; 2008b; 2010a),  
800 Adamec and Lev (1999), Leishman (1999), Shipley (2002), Pagano and Titus (2004; 2007), and  
801 Farnsworth and Ellison (2008). The full dataset is available from the Harvard Forest Data  
802 Archive (<http://harvardforest.fas.harvard.edu/data/archive.html>), Dataset HF-168.

803

804 **Figure 2.** Maximum dry mass-based photosynthetic rates ( $\text{nmol CO}_2 \text{ fixed g}^{-1} \text{ s}^{-1}$ ) for leaves or  
805 shoots of herbaceous plants. Boxes as in Fig. 1; box width is proportional to sample size, and  
806 ranges from  $N = 8$  (for aquatic unrooted herbs exclusive of ACPs) to  $N = 141$  (for herbaceous  
807 dicotyledonous angiosperms, exclusive of TCPs). Data for terrestrial plants are from Ellison  
808 (2006), Pavlovič et al. (2007; 2009; 2010), Farnsworth and Ellison (2008), Karagatzides and  
809 Ellison (2009), Hájek and Adamec (2010) and Bruzzese et al. (2010). Data for aquatic plants are  
810 from Boston et al. (1989), Nielsen and Sand-Jensen (1989), Madsen et al. (1991, 1996), Madsen  
811 and Brix (1997), Adamec (1997b; 2006; 2008c), Maberly and Madsen (2002), Kahara and  
812 Vermaat (2003), Pierini and Thomaz (2004), and Klavsen and Maberly (2010). The full dataset



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

815

816 **Figure 3.** Mass-based dark respiration and photosynthetic rates ( $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ ) for  
817 carnivorous plants for which both were measured on the same plants. Different symbols are used  
818 for different genera. Colors represent types of carnivorous plants: blue – aquatic carnivorous  
819 plants (ACPs: *Aldrovanda* and *Utricularia*); dark green – terrestrial carnivorous plants (TCPs)  
820 with separate traps and lamina (*Nepenthes*, *Dionaea*) or phyllodia (*Sarracenia*); light green with  
821 black border – TCPs without separate traps and lamina (*Drosera*, *Drosophyllum*, *Pinguicula*).  
822 Solid symbols are leaves, lamina, phyllodia, or entire plants, as appropriate; open symbols are  
823 traps measured separately of *Utricularia*, *Nepenthes*, and *Sarracenia*. Solid symbols with a  
824 central cross are for *Aldrovanda*, *Utricularia*, and *Nepenthes* that had received supplemental  
825 prey or nutrients. Data compiled from Knight (1992), Adamec (1997b; 2008c), Mendéz and  
826 Karlsson (1999), Pavlovič et al. (2007; 2009; 2010); Bruzzese et al. (2010), and Hájek and  
827 Adamec (2010). Regression lines are shown for all TCPs (green line) and ACPs (blue line). The  
828 full dataset is available from the Harvard Forest Data Archive  
829 (<http://harvardforest.fas.harvard.edu/data/archive.html>), Dataset HF-168.

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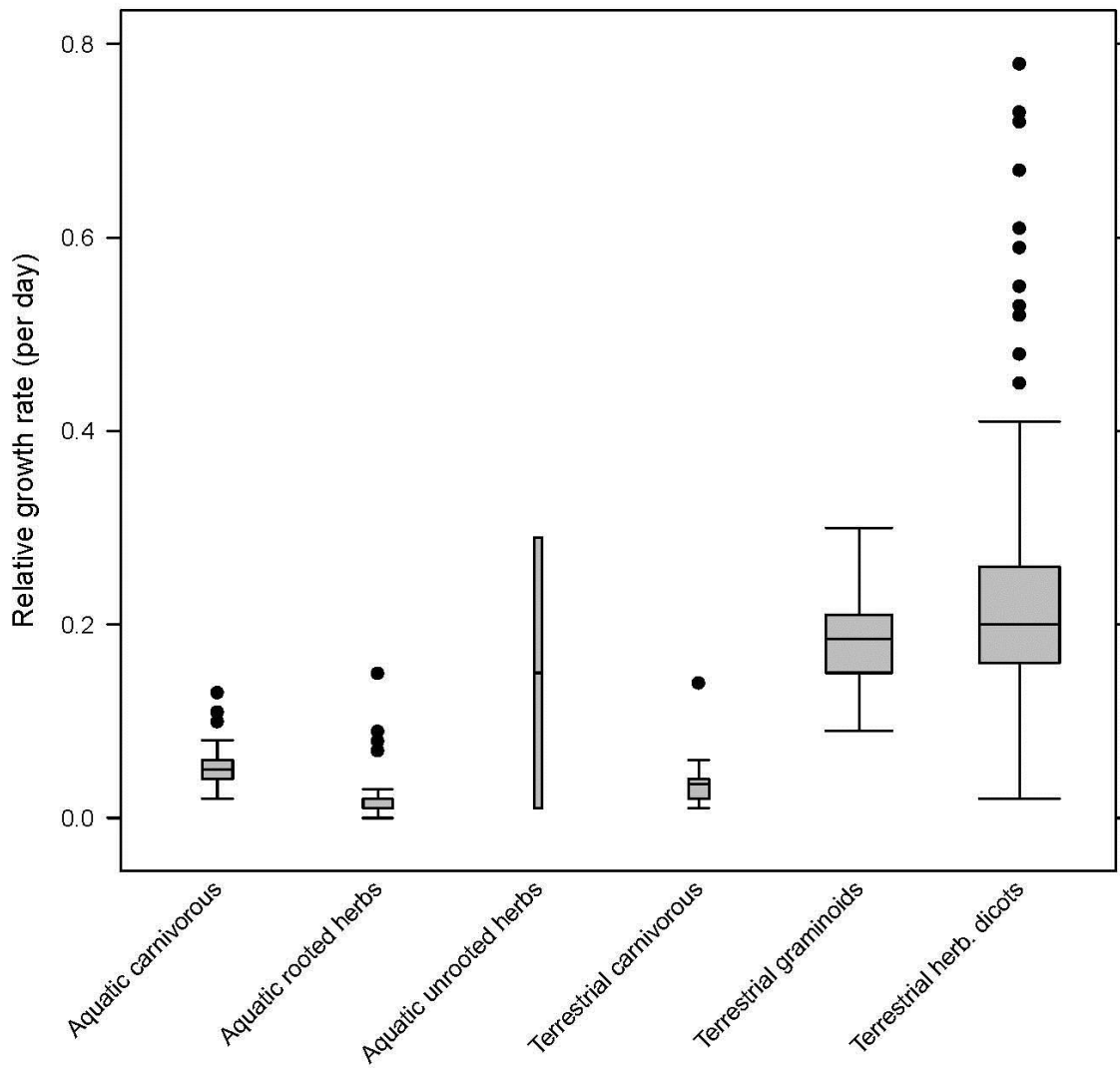
831 **Figure 4.** Tissue nutrient content of nitrogen (N), phosphorus (P), and potassium (K) in leaves or  
832 shoots of aquatic (ACP) and terrestrial (TCP) carnivorous plants. Box plots as in Fig. 1, but not  
833 scaled to sample size, which is given in axis labels. The vertical blue lines indicate the value  
834 below which the nutrient is considered to limit plant growth. Data for TCPs are from Ellison  
835 (2006), Osunkoya et al. (2007) Pavlovič et al. (2007; 2009; 2010), Farnsworth and Ellison

836 (2008), Karagatzides and Ellison (2009), Karagatzides et al. (2009), Adamec (2009a), and Moon  
837 et al. (2010). Data for ACPs are from Moeller (1980), Kamiński (1987a; 1987b), Kosiba and  
838 Sarosiek (1989), Kosiba (1992a; 1992b; 1993), Friday and Quarmby (1994), Bern (1997), and  
839 Adamec (2000; 2008a; 2010b). The full dataset is available from the Harvard Forest Data  
840 Archive (<http://harvardforest.fas.harvard.edu/data/archive.html>), Dataset HF-168.

841

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

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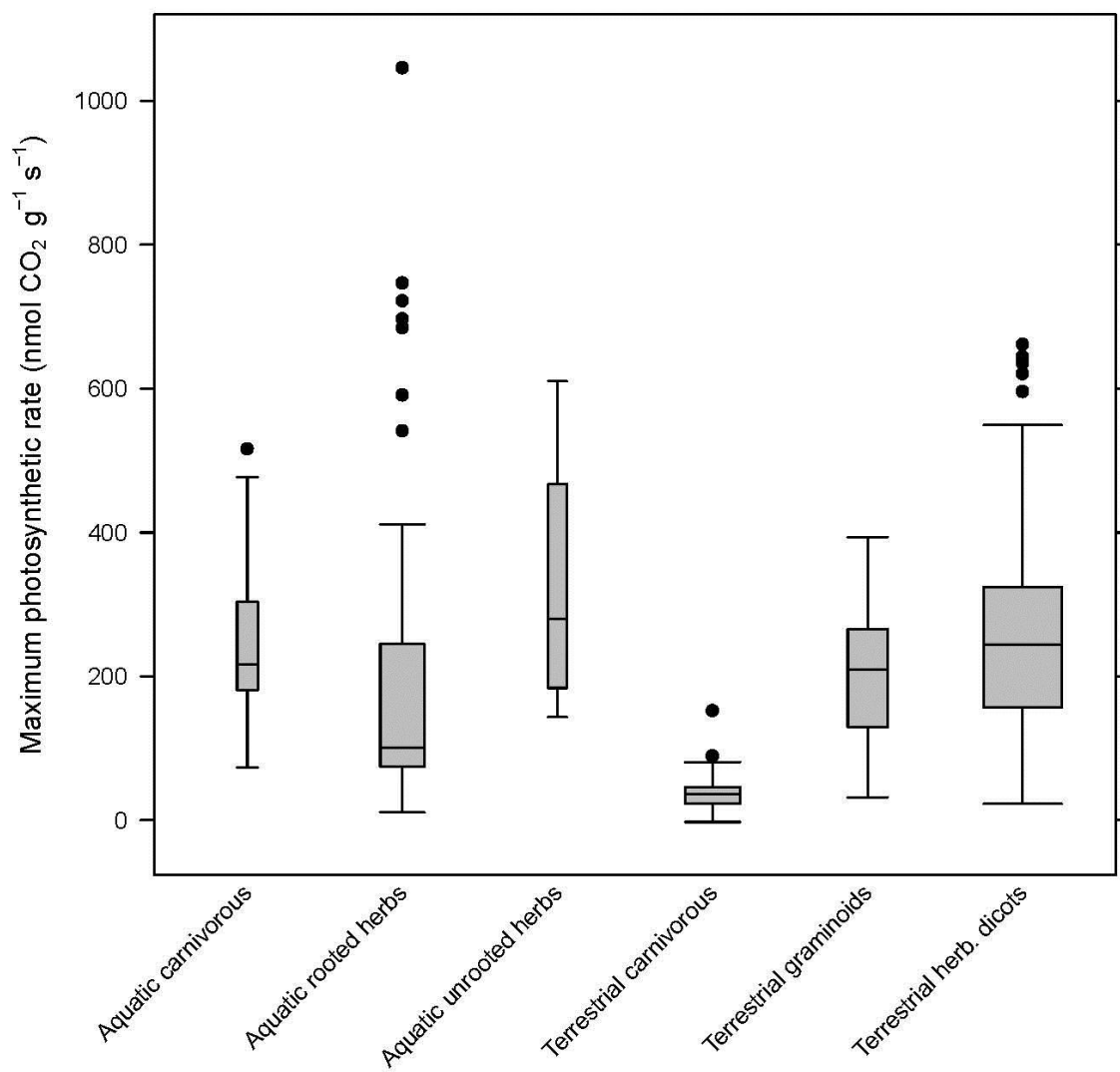


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**Figure 1**

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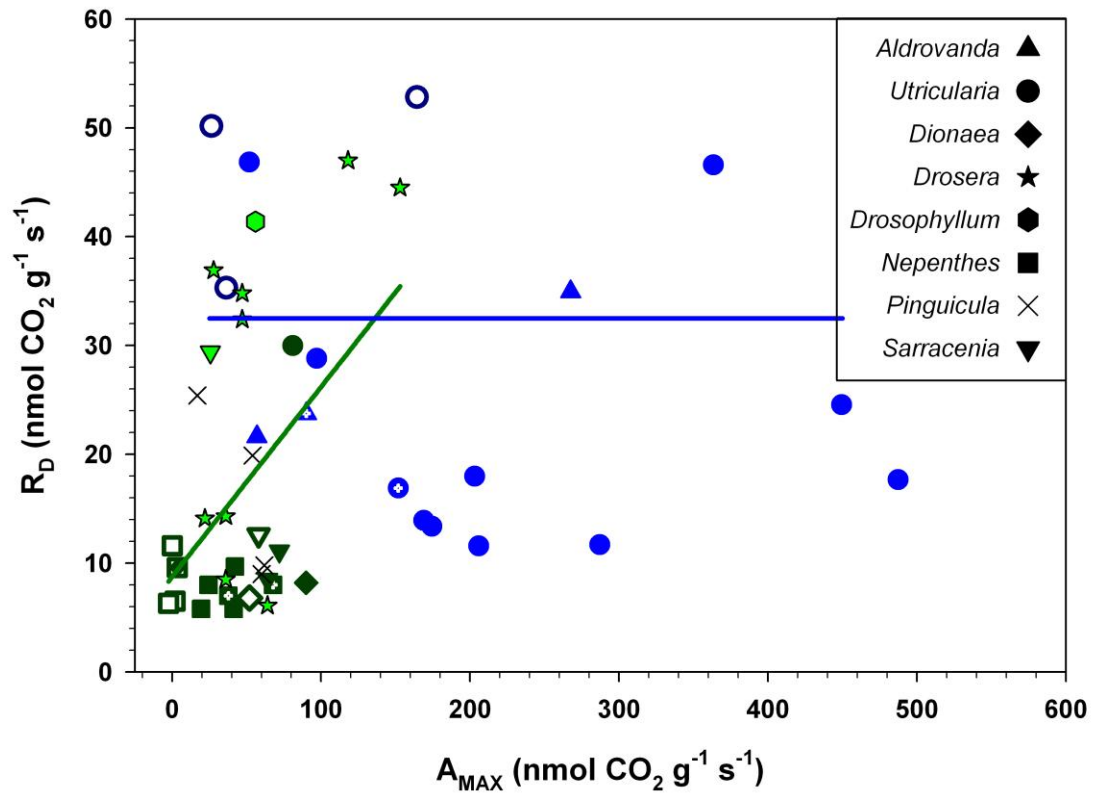


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**Figure 2**

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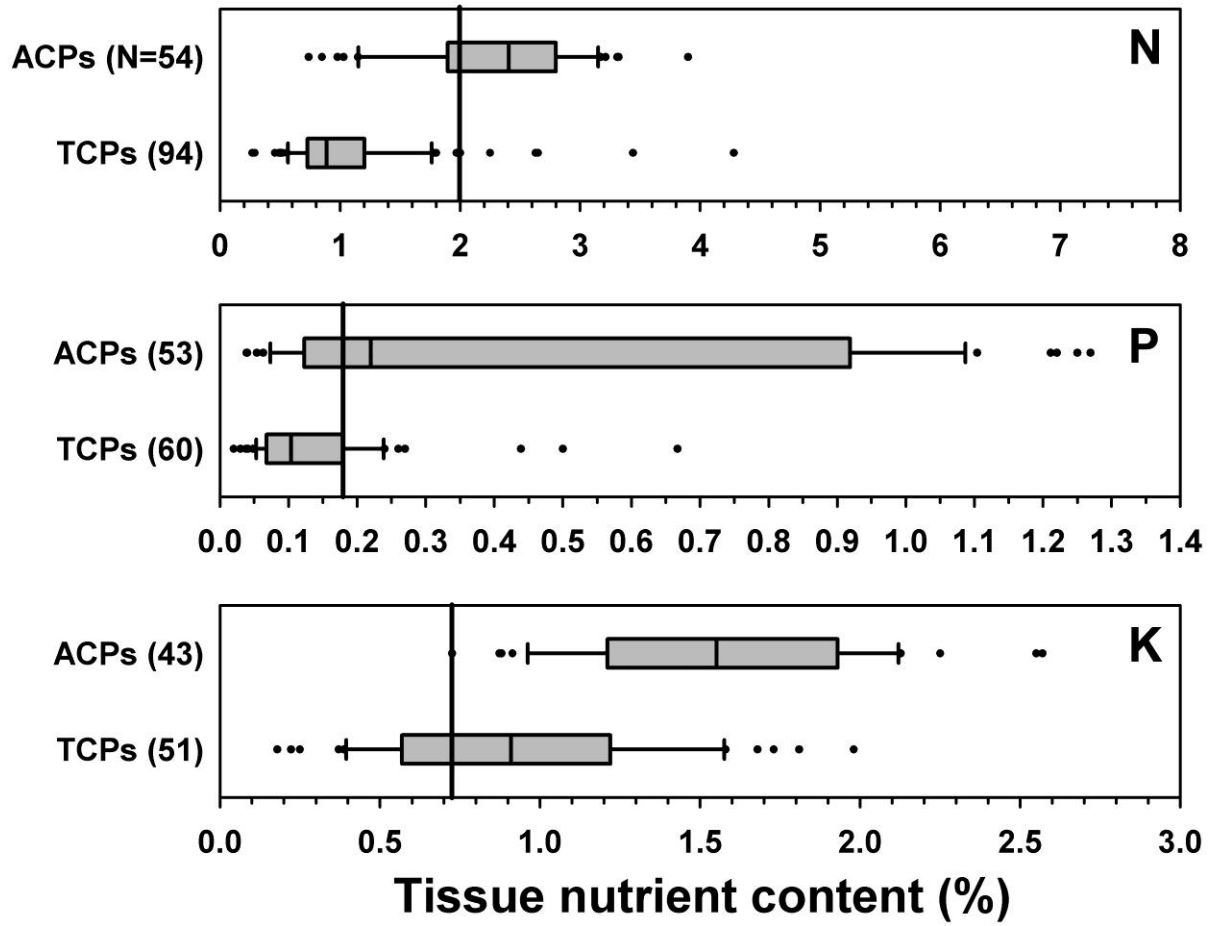


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Figure 3

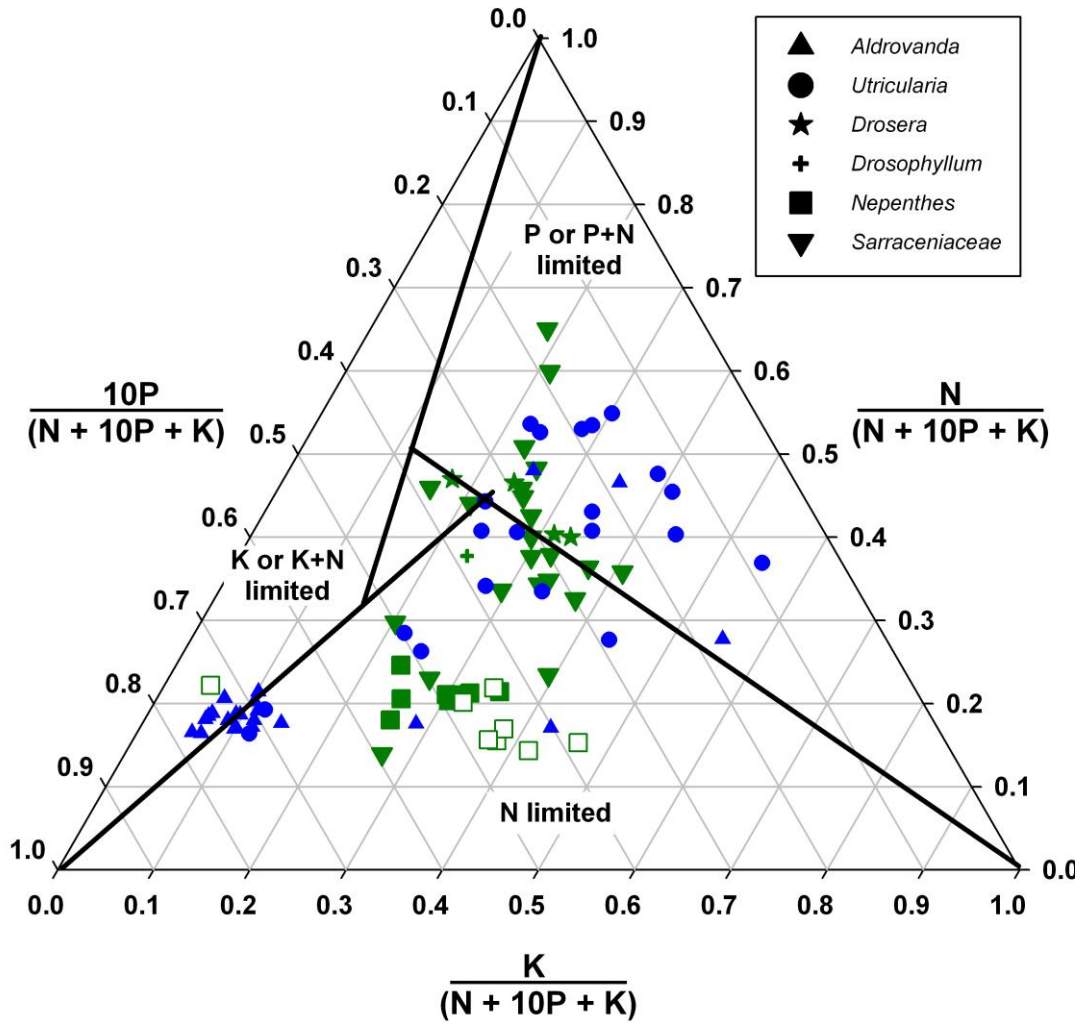


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Figure 4



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Figure 5