

QUANTIFICATION OF GROWTH BENEFIT OF CARNIVOROUS PLANTS FROM PREY

LUBOMÍR ADAMEC • Institute of Botany of the Czech Academy of Sciences • Dukelská 135 • CZ-379
82 Třeboň • Czech Republic • lubomir.adamec@ibot.cas.cz

Keywords: Cost-benefit relationships, mineral cost and benefit, stimulation of root nutrient uptake, growth benefit.

Abstract: The growth of carnivorous plants is usually limited or co-limited by shortage of available mineral nutrients N, P, and K in barren soils or waters. Carnivorous plants capture animal prey, absorb mineral nutrients from digested prey, and partly overcome the nutrient limitation. Therefore, prey capture leads invariably to marked and significant growth increase as the main ecophysiological benefit of carnivory. Here, a novel functional-ecological approach of how to quantify growth benefit efficiency of carnivory is explained. It expresses plant growth increase due to prey catching or feeding per amount of N or P or K theoretically absorbed from prey (or applied in mineral solution onto the traps) in growth experiments.

Introduction

Carnivorous plants (CPs) usually grow in soils and waters poor in available mineral nutrients (N, P, K, Ca, Mg) and, at least in terrestrial species, their foliar or shoot N, P, or K contents are on average somewhat lower than those in non-CPs (e.g. Juniper *et al.* 1989; Adamec 1997, 2011; Ellison 2006). Therefore, their natural or greenhouse growth is usually limited or co-limited by shortage of N, P, and K in their organs (Ellison & Adamec 2011). Carnivorous plants capture animal prey (mostly arthropods), absorb mineral nutrients from digested prey, and partly overcome the nutrient limitation. Consequently, prey capture leads invariably to marked and significant growth increase as the main ecophysiological benefit of carnivory. However, animal prey is a relatively rich source only for N and P as their tissue contents in typical preys (per unit dry weight, DW) are 5-10 times higher than those in CP shoots, but the tissue K, Ca, and Mg contents in preys are comparable with those in plants or lower. Therefore, CPs can cover commonly >50% of their seasonal N and P gain from carnivory, but only around 1-5% of K, Ca, or Mg (Adamec 1997, 2011).

It has been found for various *Drosera* and *Pinguicula* species that prey capture leads to a marked stimulation of mineral nutrient uptake by roots; the same effect is also attained if drops of a mineral nutrient solution are applied onto the traps (Hanslin & Karlsson 1996; Adamec 1997, 2002, 2011). The amount of mineral nutrients (N, P, K, Ca, Mg) absorbed consequently by stimulated roots *minus* unfed controls can be ca. 1.6-27 times higher than that directly absorbed from prey carcasses or nutrient solution. It characterizes the efficiency of the use of foliar nutrient uptake for mineral nutrient uptake by roots in total plant biomass (Adamec 2002, 2011). Yet the physiological nature of this root uptake stimulation remains unknown.

As introduced by Givnish *et al.* (1984) on the basis of a cost-benefit model, carnivory could only evolve when the marginal benefit associated with carnivory (in term of increased photosynthesis or growth) exceeded the marginal cost (in term of carbon or biomass needed for trap construction as structural cost of carnivory). The model has become the fundamental platform underlying ecophysiological research on CPs since its origin (see Ellison & Gotelli 2001, 2009; Ellison 2006; Ellison & Adamec 2011; Pavlovič & Saganová 2015). Knight (1992) supplemented the model and

hypothesized that CPs invest a greater metabolic (energetic) cost in their traps as an increased dark respiration rate because the traps are physiologically more active than leaves. This maintenance cost was investigated for a variety of CP species with different types of traps and was confirmed for mobile traps (Adamec 2006, 2010a,b; Pavlovič *et al.* 2007, 2009; Hájek & Adamec 2010). Traps usually represent not only higher metabolic cost than leaves, but simultaneously also higher photosynthetic cost due to their specialization for carnivory as trap photosynthetic rate per unit DW is usually (much) lower than that of leaves (cf. Knight 1992; Adamec 2006, 2010a,b; Pavlovič *et al.* 2007, 2009; Hájek & Adamec 2010).

Moreover, traps of CPs usually contain a high proportion of total plant amount of growth-limiting mineral nutrients N, P, K, Ca, and Mg. Therefore, Adamec (2010c) postulated mineral cost of carnivory as the total nutrient amount in all traps which could also be expressed in percent of total plant nutrient amount. In aquatic CP species, mineral cost of carnivory for N, P, K, and Ca could extend even 60%. Although a great proportion of trap N, P, and K is reutilized from senescent traps, a part of them and all Ca and Mg are lost in senescent traps (Adamec 2002, 2011, 2014). Adamec (2010c) thus suggested a concept of mineral cost-benefit relationships which maximize mineral nutrient uptake from prey per minimal nutrient (N, P) losses invested into carnivory. This concept does not deny the above classic model (Givnish *et al.* 1984) proposed for terrestrial CPs but rather supplements it, as it specifies mineral nutrient economy of CPs after which carnivory is beneficial for the plants. Quantitatively, Adamec (2011) expressed the efficiency of mineral nutrient investment in traps (termed “total nutritional benefit of carnivory”) as a ratio between the total amount of nutrients (N, P, K, Ca, Mg) coming from carnivory (either directly from prey or indirectly *via* stimulated root uptake) and that amount of nutrients lost in senescent traps over their lifespan. When this value for a given nutrient exceeds 1, carnivory will be ecologically beneficial. However, this nutritional model to date has received much less attention.

A marked stimulation of growth is commonly the final benefit of carnivory with significant ecological consequences. Givnish *et al.* (1984) predicted that carnivory would evolve among plants when the marginal photosynthetic benefits of carnivory exceeded its marginal costs. As foliar N and P contents in terrestrial CPs are low and photosynthesis commonly increases in well-fed CPs relative to starved ones (for review see Pavlovič & Saganová 2015), the low growth rates of CPs are at least partially limited by a shortage of mineral nutrients. So far, the stimulation of photosynthesis by prey capture has been confirmed in *Drosera capensis* (Pavlovič *et al.* 2014), 10 *Sarracenia* species (Farnsworth & Ellison 2008), *Nepenthes talangensis* (Pavlovič *et al.* 2009) and *N. alata* (He & Zain 2012) but some results are non-significant (Méndez & Karlsson 1999; Kruse *et al.* 2014). In *N. talangensis*, photosynthetic rate also rose after mineral enrichment of the soil (Pavlovič *et al.* 2010; cf. results for *Darlingtonia californica*; Ellison & Farnsworth 2005). On the contrary, the stimulation of photosynthesis in aquatic CPs by prey capture is quite ambiguous (Adamec 2008).

In feeding experiments in various terrestrial CP species, a marked growth increase in fed plants (usually 1.5-5 times) was observed (Adamec 1997, 2011) and it is therefore probable that the predicted increase in the specific foliar photosynthetic rate (per unit biomass) is very common in most of terrestrial CP species. Even if the specific foliar photosynthetic rate remains unchanged after prey capturing, another additional mechanism could ensure attaining of higher growth rate. In aquatic *Utricularia* species, prey capture can reduce significantly the proportion of traps to the total plant biomass (Adamec 2011, 2015). This reduction of structural investment in carnivory should consequently not only decrease the energetic cost of traps but also photosynthetic cost of shoots (*sensu* Knight 1992). The higher proportion of photosynthetically active leaves (over the traps) should ensure an increase of total plant photosynthetic rate as the photosynthetic benefit and, there-

fore, also of increased plant growth rate as the growth benefit, even if the specific photosynthetic foliar rate is not increased (Adamec 2008).

If the principal reason for the growth stimulation is the uptake of relatively small amounts of mineral nutrients N, P, and K from prey, using a functional-ecological approach, it is possible to express the plant growth increase due to prey capture or feeding *per amount* of N or P or K absorbed from prey (or a mineral solution applied onto the traps) in greenhouse or field-growth experiments. This model of growth benefit from carnivory shows the efficiency of biomass production per unit nutrient amount gained from prey. The “growth benefit efficiency” (GBE) of carnivory is defined as a ratio between a measured growth increase of CPs (*minus* unfed controls; in mg DW of the biomass) and a model amount of N, P, and K (in mg) gained theoretically from prey (or a nutrient solution) in published growth experiments. As shown in Table 1, the data on measured growth increase and weight of arthropod prey captured (or volume of a nutrient solution applied) could be drawn from 11 studies for 13 CP species. The model efficiency used for the uptake of N from prey was 40% (field) or 76% (greenhouse) and 90% for P and K, but 100% uptake of the nutrients in the case of nutrient solution (see Adamec 2002, 2011). Unless specified directly in the given study, the following mean nutrient contents in dry insects were taken into account (in % DW): N, 10; P, 1.0; K, 1.2 (Adamec 1997, 2011). As different kinds of arthropod prey as well as the efficiencies of nutrient uptake from these preys can differ considerably from the model values in different CP species or under experimental conditions, it is possible to assume that the true amounts of N, P, and K gained could vary from the model values at most by 30-40%. Thus, the calculated model GBE values in Table 1 could be loaded at most by a 30-40% error. Based on usual values of shoot or foliar nutrient contents (% DW; N, 1.0-1.5; P, 0.08-0.12; K, 0.8-1.5; Ellison & Adamec 2011) in CPs, the values of the GBE far exceeding ca. 70-100 for N, 800-1200 for P, and 70-120 for K can indicate an increase of specific photosynthetic rate per unit foliar DW. In contrast, the GBE in control non-fed plants is zero.

Results and Discussion

The calculated GBE (in mg/mg) for 13 CP species was between 21-5020 for N, for P between 206-13,000, and for K 170-10,400 (Table 1). What can be drawn from the data? The data show that the GBE can greatly vary for a given nutrient not only among different taxa, but also within the same species in different experiments or at different feeding levels (cf. *D. capillaris*, *D. aliciae*, *D. rotundifolia*, *P. vulgaris*, and *S. purpurea*). In *S. purpurea* overfed on prey, the GBE was by two orders of magnitude lower than that in this species naturally catching prey. It indicates that the efficiency is greatly reduced by high prey amount. The very high GBE values in two experiments on application of nutrient solutions onto the leaves (Adamec *et al.* 1992; Adamec 2002) may partly reflect relatively long duration of these experiments (7 and 4 months, respectively), during which the growth effect is amplified. Very high values of the GBE above the theoretical threshold (>100 for N, >1200 for P, >120 for K) indicate that the prey-derived uptake of the given nutrient is either relatively low to cover the increased growth (it could particularly apply for K as arthropods are relatively poor K source; the growth increase is mainly due to the N and P uptake from prey), or that the specific foliar photosynthetic rate is stimulated by the nutrient uptake. If all GBE values for N, P, and K are increased above the threshold, it directly indicates photosynthetic stimulation and, simultaneously, a possibility of the stimulation of root nutrient uptake (Table 1). This was proven for several *Drosera* species and *S. purpurea*, but neither for *P. vulgaris* nor aquatic *Aldrovanda vesiculosa* (cf. Méndez & Karlsson 1999; Adamec 2008; Farnsworth & Ellison 2008; Pavlovič *et al.* 2014).

Table 1. The comparison of experimental growth increase of CPs (*minus* unfed controls) by foliar prey feeding or natural prey capture or by application of a mineral nutrient solution (NS) onto the traps from literature data. This growth benefit from carnivory shows the efficiency of biomass production per unit nutrient amount gained theoretically from prey. The values shown in denominator in italics denote the efficiency of the total accumulation of the given mineral nutrient applied onto the trap. For detailed model assumptions see the text. Based on usual values of shoot or foliar nutrient contents, values far exceeding ca. 70-100 for N, 800-1200 for P, and 70-120 for K (in bold) can indicate an increase of specific photosynthetic rate per unit foliar DW. AQ, aquarium; GR, greenhouse; FI, field. 1: Adamec (2002); 2: Adamec *et al.* (1992); 3: Chandler & Anderson (1976); 4: Karlsson & Pate (1992); 5: Krafft & Handel (1991); 6: Thum (1988); 7: Thum (1989); 8: Aldenius *et al.* (1983); 9: Karlsson & Carlsson (1984); 10: Chapin & Pastor (1995); 11: Adamec *et al.* (2010).

Species	Growth condit.	Growth period (d)	Nutrient applic.	Biomass increase (DW) per amount of nutrients absorbed (mg/mg)			Comment	Refer.
				N	P	K		
<i>D. capillaris</i>	GR	125	NS	702/14.4	2045/0.67	1948/25.1	Droplets of NS	1
<i>D. aliciae</i>	GR	125	NS	741/7.9	2158/0.87	2056/27.2	-****-	1
<i>D. spatulata</i>	GR	95	NS	659/8.7	1920/0.85	1828/21.1	-****-	1
<i>D. adelaie</i>	AQ	217	NS	5018	13,128	10,406	-****-	2
<i>D. aliciae</i>	AQ	217	NS	1298	3398	2693	-****-	2
<i>D. capillaris</i>	AQ	217	NS	3062	8009	6349	-****-	2
<i>D. whittakeri</i>	GR	75-87	Flies	24.3-49.7	206-419	171-349		3
<i>D. closterostigma</i>	GR	121	Collemb.	242	1345	1121	Perennial species	4
<i>D. glanduligera</i>	FI	77	Flies	69.5	309	258	Annual species	4
<i>D. rotundifolia</i>	GR	2 seas.	Flies	56.3-69.0	313-384	261-320	5 or 10 flies/week	5
<i>D. filiformis</i>	GR	2 seas.	Flies	51.2-97.0	284-546	237-455	5 to 20 flies/week	5
<i>D. rotundifolia</i>	FI	162	Flies	250	1110	834	Corrected for	6,7
<i>D. intermedia</i>	FI	104	Flies	171	760	571	robbing prey	6,7
<i>P. vulgaris</i>	GR	45	Insects	21.3-26.6	94.6-118	78.8-98.4	Nutrient-fed peat	8
<i>P. vulgaris</i>	GR	47	NS	27.3	577	--	N or P application	9
<i>P. vulgaris</i>	GR	47	NS	68.5	377	--	N+P application	9
<i>S. purpurea</i>	FI	110	Nat. prey	202	2024	1687		10
<i>S. purpurea</i>	FI	110	Flies	1.37	11.0	10.4	Plants overfed	10
<i>A. vesiculosa</i>	GR	11	Zoopl.	39.4	372	29.6	Fed on ostracods	11

Conclusions

The GBE parameter defined in this study expresses the production of extra dry biomass per unit of N, P, and K taken up directly from prey but it tells nothing about the efficiency of the stimulation of mineral nutrient uptake by roots by foliar nutrient uptake and *vice versa* – both efficiency

parameters are independent of each other. This fact also follows from the data (Table 1). A direct measurement of foliar photosynthetic rate and the stimulation of root nutrient uptake by the foliar uptake are very demanding and costly. However, in growth experiments, an exact estimation of the growth increase as the growth benefit of carnivory and the DW of applied prey bodies for calculation of the growth benefit efficiency is relatively simple.

Acknowledgements: This study was partly funded by the Long-term research project of the Czech Academy of Sciences (RVO 67985939). Thanks are due to Dr. Andrej Pavlovič, Olomouc University, Czech Republic, for valuable comments.

References

- Adamec, L. 1997. Mineral nutrition of carnivorous plants: A review. *Bot. Rev.* 63: 273-299.
- Adamec, L. 2002. Leaf absorption of mineral nutrients in carnivorous plants stimulates root nutrient uptake. *New Phytol.* 155: 89-100.
- Adamec, L. 2006. Respiration and photosynthesis of bladders and leaves of aquatic *Utricularia* species. *Plant Biol.* 8: 765-769.
- Adamec, L. 2008. The influence of prey capture on photosynthetic rate in two aquatic carnivorous plant species. *Aquat. Bot.* 89: 66-70.
- Adamec, L. 2010a. Dark respiration of leaves and traps of terrestrial carnivorous plants: are there greater energetic costs in traps? *Cent. Eur. J. Biol.* 5: 121-124.
- Adamec, L. 2010b. Ecophysiological look at organ respiration in carnivorous plants: A review. In: Osterhoudt G., Barhydt J. (eds.), *Cell Respiration and Cell Survival: Processes, Types and Effects*. Nova Science Publishers, Inc., New York, pp. 225-235.
- Adamec, L. 2010c. Mineral cost of carnivory in aquatic carnivorous plants. *Flora* 205: 618-621.
- Adamec, L. 2011. Ecophysiological look at plant carnivory: Why are plants carnivorous? In: Seckbach, J., and Dubinski, Z. (eds.), *All Flesh is Grass. Plant-Animal Interrelationships. Cellular Origin, Life in Extreme Habitats and Astrobiology* Vol. 16. Springer Science + Business Media B. V., Dordrecht - Heidelberg - London - New York, pp. 455-489.
- Adamec, L. 2014. Different reutilization of mineral nutrients in senescent leaves of aquatic and terrestrial carnivorous *Utricularia* species. *Aquat. Bot.* 119: 1-6.
- Adamec, L. 2015. Regulation of the investment in carnivory in three aquatic *Utricularia* species: CO₂ or prey availability? *Phyton* 55: 131-148.
- Adamec, L., Dušáková, K., and Jonáčková, M. 1992. Growth effects of mineral nutrients applied to the substrate or onto the leaves in four carnivorous plant species. *Carniv. Pl. Newslett.* 21(1-2): 18-24.
- Adamec, L., Sirová, D., and Vrba, J. 2010. Contrasting growth effects of prey capture in two carnivorous plant species. *Fundam. Appl. Limnol.* 176: 153-160.
- Aldenius, J., Carlsson, B., and Karlsson, S. 1983. Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. *New Phytol.* 93: 53-59.
- Ellison, A.M. 2006. Nutrient limitation and stoichiometry of carnivorous plants. *Plant Biol.* 8: 740-747.
- Ellison, A.M., and Farnsworth, E.J. 2005. The cost of carnivory for *Darlingtonia californica* (Sarraceniaceae): evidence from relationships among leaf traits. *Am. J. Bot.* 92: 1085-1093.
- Ellison, A.M., and Gotelli, N.J. 2001. Evolutionary ecology of carnivorous plants. *Trends Ecol. Evol.* 16: 623-629.

- Chandler, G.E., and Anderson, J.W. 1976. Studies on the nutrition and growth of *Drosera* species with reference to the carnivorous habit. *New Phytol.* 76: 129-141.
- Chapin, C.T., and Pastor, J. 1995. Nutrient limitations in the northern pitcher plant *Sarracenia purpurea*. *Can. J. Bot.* 73: 728-734.
- Ellison, A.M., and Adamec, L. 2011. Ecophysiological traits of terrestrial and aquatic carnivorous plants: are the costs and benefits the same? *Oikos* 120: 1721-1731.
- Farnsworth, E.J., and Ellison, A.M. 2008. Prey availability directly affects physiology, growth, nutrient allocation and scaling relationships among leaf traits in ten carnivorous plant species. *J. Ecol.* 96: 213-221.
- Givnish, T.J., Burkhardt, E.L., Happel, R.E., and Weintraub, J.D. 1984. Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *Am. Natur.* 124: 479-497.
- Hájek, T., and Adamec, L. 2010. Photosynthesis and dark respiration of leaves of terrestrial carnivorous plants. *Biologia* 65: 69-74.
- Hanslin, H.M., and Karlsson, P.S. 1996. Nitrogen uptake from prey and substrate as affected by prey capture level and plant reproductive status in four carnivorous plant species. *Oecologia* 106: 370-375.
- He, J., and Zain, A. 2012. Photosynthesis and nitrogen metabolism of *Nepenthes alata* in response to inorganic NO₃⁻ and organic prey N in the greenhouse. *Int. Schol. Res. Netw. Botany*, Article ID 63270.
- Juniper, B.E., Robins, R.J., and Joel, D.M. 1989. *The Carnivorous Plants*. Academic Press Ltd, London, UK.
- Karlsson, P.S., and Carlsson, B. 1984. Why does *Pinguicula vulgaris* L. trap insects? *New Phytol.* 97: 25-30.
- Karlsson, P.S., and Pate, J.S. 1992. Contrasting effects of supplementary feeding of insects or mineral nutrients on the growth and nitrogen and phosphorus economy of pygmy species of *Drosera*. *Oecologia* 92: 8-13.
- Knight, S.E. 1992. Costs of carnivory in the common bladderwort, *Utricularia macrorhiza*. *Oecologia* 89: 348-355.
- Krafft, C.C., and Handel, S.N. 1991. The role of carnivory in the growth and reproduction of *Drosera filiformis* and *D. rotundifolia*. *Bull. Torrey Bot. Club* 118: 12-19.
- Kruse, J., Gao, P., Honsel, A., Kreuzwieser, J., Burzlaff, T., Alfarraj, S., Hedrich, R., and Rennenberg, H. 2014. Strategy of nitrogen acquisition and utilization by carnivorous *Dionaea muscipula*. *Oecologia* 174: 839-851.
- Méndez, M., and Karlsson, P.S. 1999. Costs and benefits of carnivory in plants: insights from the photosynthetic performance of four carnivorous plants in a subarctic environment. *Oikos* 86: 105-112.
- Pavlovič, A., and Saganová, M. 2015. A novel insight into the cost–benefit model for the evolution of botanical carnivory. *Ann. Bot.* 115: 1075-1092.
- Pavlovič, A., Krausko, M., Libiaková, M., and Adamec, L. 2014. Feeding on prey increases photosynthetic efficiency in the carnivorous sundew *Drosera capensis*. *Ann. Bot.* 113: 69-78.
- Pavlovič, A., Masarovičová, E., and Hudák, J. 2007. Carnivorous syndrome in Asian pitcher plants of the genus *Nepenthes*. *Ann. Bot.* 100: 527-536.
- Pavlovič, A., Singerová, L., Demko, V., and Hudák, J. 2009. Feeding enhances photosynthetic efficiency in the carnivorous pitcher plant *Nepenthes talangensis*. *Ann. Bot.* 104: 307-314.

- Pavlovič, A., Singerová, L., Demko, V., Šantrůček, J., and Hudák, J. 2010. Root nutrient uptake enhances photosynthetic assimilation in prey-deprived carnivorous pitcher plant *Nepenthes talangensis*. *Photosynthetica* 48: 227-233.
- Thum, M. 1988. The significance of carnivory for the fitness of *Drosera* in its natural habitat. 1. The reactions of *Drosera intermedia* and *D. rotundifolia* to supplementary feeding. *Oecologia* 75: 472-480.
- Thum, M. 1989. The significance of opportunistic predators for the sympatric carnivorous plant species *Drosera intermedia* and *Drosera rotundifolia*. *Oecologia* 81: 397-400.

C Z P WWW.CZPLANTS.COM
carnivorous & exotic plants

World's Rare Plants
Largest Carnivorous Plant Store in San Francisco Bay Area
<http://www.worldsrareplants.com>
Sarracenias • Sundews • Nepenthes • Venus Fly Traps • Terrariums • CP Soil Mixes
Also featuring Fairy Garden Supplies

12511 San Mateo Rd (Highway 92), Half Moon Bay, Ca 94019
Walk-ins welcome or call 650-454-9002