Quantification of Growth Benefit
of Carnivorous Plants from Prey

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

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