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Contrasting growth effects of prey capture in two aquatic carnivorous plant species

Lubomír Adamec[1], **Dagmara Sirová**[2] and **Jaroslav Vrba**[2]

With 2 tables

Abstract: A detailed 11-day growth analysis was performed under greenhouse conditions on two aquatic, carnivorous plants in order to determine growth effects caused by supplemental feeding on zooplankton. The two species surveyed were the rare, stenotypic *Aldrovanda vesiculosa* and the more common, eurytopic *Utricularia australis*. While a highly significant increase in shoot biomass (by 60 %) was found for *Aldrovanda* plants supplemented with prey, no significant effect of prey addition occurred in *Utricularia*. However, main shoots of fed plants of both species were significantly longer, had more mature leaf nodes, and their mean apical growth rate was higher than in unfed plants. Branching was markedly supported by prey in *Aldrovanda* only. Feeding significantly increased the structural investment in carnivory in *Utricularia* but had no effect on *Aldrovanda*, although significantly increasing maximum trap length in both species. Measurements of total nutrient concentrations in fed *Aldrovanda* plants revealed much more total N, P, K, and Mg at the end of the experiment, compared with unfed plants. In *Utricularia*, however, fed plants contained only more N than unfed plants but the opposite was true for the total amount of P, K and Mg. In *Aldrovanda*, a large proportion of N, P, K, and Mg consumption could be covered from prey. The different growth effect of prey addition in the two species could be explained by the operation of a complex food web in *Utricularia* traps, which possibly substitute for prey capture in barren waters.

Key words: *Aldrovanda vesiculosa*, *Utricularia australis*, prey capture, growth analysis, shoot mineral nutrient content, nutrient uptake.

Introduction

Aquatic (or amphibious) carnivorous plants of the genera *Aldrovanda* (Droseraceae) and *Utricularia* (Lentibulariaceae) are rootless and generally grow in shallow, standing, dystrophic waters (Juniper et al. 1989, Taylor 1989). These dystrophic waters are usually nutrient poor, commonly low in K, but especially low in N and P (Adamec 1997a, 2008a, Guisande et al. 2007). The most typical feature of these dystrophic waters is a high concentration of free CO_2 (Adamec 1997a, b, 2007, 2008a, Adamec & Kovářová 2006). Aquatic carnivorous plants assimilate all necessary nutrients either directly from water or from captured prey. Principal adaptations of *Utricularia* and *Aldrovanda* include carnivory, efficient nutrient re-utilisation from senescent shoots, and, likely, a very high nutrient uptake affinity from ambient water (e.g., Kamiński 1987b, Kosiba 1992a, b, Adamec 2000, 2008a, Englund & Harms 2003). Considering the ecological cost-benefit relationships, Givnish et al. (1984) hypothesised that for terrestrial carnivorous plants, carnivory provides a greater mineral nutrient availability and, most importantly, may lead to an increase in plant's total rate of

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Author's addresses:
[1] Institute of Botany AS CR, Section of Plant Ecology, Dukelská 135, CZ-379 82 Třeboň, Czech Republic.
Corresponding author; e-mail address: adamec@butbn.cas.cz
[2] University of South Bohemia, Faculty of Science, and Biology Centre AS CR, Institute of Hydrobiology, České Budějovice, Czech Republic.

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photosynthesis. Although the hypothesis was verified in 12 terrestrial species, the results still remain partly ambiguous, as a significant photosynthesis increase per unit leaf biomass has not been demonstrated in all species tested so far (cf. Méndez & Karlsson 1999, Ellison & Farnsworth 2005, Wakefield et al. 2005, Farnsworth & Ellison 2008). This hypothesis has also recently been tested in two aquatic carnivorous species. Both *Aldrovanda vesiculosa* and *Utricularia australis* grew faster in an outdoor culture when fed on zooplankton, but the net photosynthetic rate of shoots was stimulated by prey only in *A. vesiculosa*, while it decreased in *U. australis*. The dark respiration rate remained unchanged (Adamec 2008b). Moreover, tissue N content in mature shoot segments was significantly higher in the unfed plants of both species (see also Adamec 2000). For these reasons, Adamec (2008b) hypothesised that the main physiological effect of catching prey is to provide N and P for essential growth processes, such as cell division, DNA replication, and synthesis of RNA and proteins in young tissues of shoot apices. According to the growth rate hypothesis (Sterner & Elser 2002), this effect could occur even in aquatic carnivorous species due to their very rapid growth. Unlike terrestrial carnivorous plants, most of the aquatic species exhibit very rapid apical shoot growth (1–4 leaf nodes d^{-1}) and high relative growth rates (Friday 1989, Adamec 2000, 2002, 2009, Adamec & Kovářová 2006, Farnsworth & Ellison 2008). To support their very rapid growth, aquatic carnivorous plants exhibit high net photosynthetic rates, which are close to the maximum values known for submerged plants (Adamec 1997b, 2006).

In aquatic carnivorous plants, prey capture can be important to attain a high growth rate (for review, see Adamec 1997a, Adamec 2000, Englund & Harms 2003). While this positive growth effect is consistent in *A. vesiculosa*, the results of the relatively few experiments in *Utricularia* spp. are rather ambiguous as they greatly depend on experimental conditions; mainly CO_2 concentration, mineral nutrient availability, or irradiance (cf. Sorenson & Jackson 1968, Kosiba 1992a, b, Jobson et al. 2000, Englund & Harms 2003, Adamec 2008b). The principal difference between *Utricularia* spp. and *Aldrovanda* in their growth response to prey could be due to the different trap structure and even different trap ecology. Snapping traps of *Aldrovanda* are permanently open and close only during a period of prey digestion (Juniper et al. 1989). In contrast, suction traps of *Utricularia* spp. are permanently closed, with commensal communities of mainly bacteria and unicellular algae occurring and propagating in the trap fluid (Richards 2001, Sirová et al. 2003, 2009, Peroutka et al. 2008).

Aldrovanda vesiculosa L. and *Utricularia australis* R. Br. are free-floating, submerged, carnivorous plants growing commonly in the same shallow dystrophic waters (e.g., Kamiński 1987a). While stenotopic *Aldrovanda* is a very rare and critically endangered plant species throughout its European range (Adamec 1999), eurytopic *U. australis* represents a very common submerged plant species (Taylor 1989). Both species have recently been used for studying growth and mineral nutrition (Adamec 1999, 2000, 2008a, b, 2009, Adamec & Kovářová 2006). The present paper describes a detailed growth analysis of these two species, performed in greenhouse conditions in order to evaluate the growth effects caused by feeding on zooplankton. The aim is to determine whether different trap structure and operation in the two species can predetermine different growth effects. Plant biometric data, structural investment in carnivory as well as total plant nutrient (N, P, K, and Mg) amount were estimated to determine the effect of carnivory.

Material and methods

Experimental plants

Adult, 8–10 cm long plants of *A. vesiculosa* (collected from E. Poland) were pre-cultivated outdoors in a 2.5 m^2 plastic container simulating natural conditions (for details see Adamec 1997b, 2008b, Sirová et al. 2003). Subadult, 20–40 cm long plants of *U. australis* (collected from Ruda fishpond, Třeboňsko Biosphere Reserve, Czech Republic), were pre-cultivated in a 0.8 m^2 plastic container under similar conditions for two weeks. In both containers, plants were gently fed on fine zooplankton. The growth experiment on both species proceeded in two 0.8 m^2 white, plastic containers, which stood in a naturally lit greenhouse with open lateral walls for cooling. Each container (30 cm high) contained 200 l of tap water and 80 g dry weight (DW) of *Carex elata* litter as substrate. For 19 days preceding the experiment, the pre-soaked substrate allowed water in the containers to mimic that of an oligotrophic and slightly dystrophic environment. On 19 June 2008, three days before the growth experiment started, 50 shortened apical segments of both *A. vesiculosa* (ca. 4 cm long) and *U. australis* (ca. 15–20 cm long) from the pre-cultivation were put in one 200 l experimental container and allowed to digest all captured prey for three days.

Growth experiment

On 22 June 2008, 40 randomly selected, homogeneous non-branched *A. vesiculosa* shoot segments were shortened to 6 (or 6.5) mature apical leaf nodes (shoot length about 3 cm) and 20 individuals were put into each container. Similarly, 40 selected *U. australis* shoot segments were shortened to 15 mature apical leaf nodes (shoot length about 7–9 cm), all visible branches excised, and 20 individuals were put into each container. We are aware that these plants were pseudoreplicates but the treatment (feeding on prey) was strictly the same for all plants. Shoot length and maximum trap size (to the nearest 0.5 mm) were estimated in all experimental plants (Adamec 2009). The remaining 10 plant replicates of each species were used for destructive analyses. In the 4th–6th mature leaf nodes of *A. vesiculosa*, traps were counted, the proportion of traps with captured prey was estimated using a binocular loupe, and the structural investment in carnivory, as the proportion of trap DW (80 °C; prey was removed from the traps) to the total DW of the leaf nodes, was estimated in four plants (Adamec 2009). The other six plant replicates were used for estimation of tissue N, P, K, and Mg content (prey was removed from traps). All 10 plants were dried (80 °C) and weighed for the initial DW. The same protocol was performed for the 10 remaining *U. australis* plants in the 11th–12th mature leaf nodes, but the captured prey was not removed.

The water continuously circulated between both experimental containers using a couple of submersible aquarium pumps that equalised water chemistry. The pumps were fitted with fine nylon nets to prevent any transfer of added zooplankton from one container to the other. Zooplankton prey mixture was regularly added to one container, while the other remained without any prey. The dominant prey captured was about 1.2-mm large, undetermined ostracod in *A. vesiculosa*, and *Eudiaptomus* sp. (1.4 mm) were trapped preferentially by *U. australis*. The containers were covered with a neutral-density nylon filter and the irradiance (PAR) at plant level was about 38 % of that in the open area, which is an optimum level for both species (Adamec 1997b, Adamec & Kovářová 2006). A submersible temperature data logger (Minikin T, EMS, Brno, Czech Rep.) monitored water temperature in each container at plant level. During the growth period of 11 days (22 June–3 July), the mean water temperature at plant level was 26.0 °C (range of 21.5–30.6 °C), the difference between the containers was always ≤ 0.2 °C. Basic water chemistry parameters were estimated in both containers several times during the growth period (for the methods see Adamec 1999, 2000). During the experiment, pH in the both containers was 7.34–8.00, dissolved O_2 concentration 0.11–0.25 mM, total alkalinity 0.98–1.03 meq l^{-1}, electrical conductivity 30.0–31.4 mS m^{-1}, free CO_2 concentration 0.02–0.10 mM, and the sum of concentrations of humic acids and tannins 2.6–2.9 mg l^{-1}. The water was very poor in mineral nutrients (0 µg l^{-1} NO_3-N; 0–21 µg l^{-1} NH_4-N; 9–12 µg l^{-1} PO_4-P; 4.8–4.9 mg l^{-1} K^+; 23.3–24.2 mg l^{-1} Ca^{2+}; 5.2 mg l^{-1} Mg^{2+}). Differences between the container with and without prey were negligible for any water chemistry parameter. Distilled water compensated for evaporative water losses.

Shoot length, the number of mature leaf nodes, and the branching of shoots were estimated in all plants after four and eight days, and at the end of the experiment (after 11 days; for details see Adamec 2000, Adamec & Kovářová 2006). Apical shoot growth rate (ASGR) was estimated from the number of mature leaf nodes. After eight days of plant growth, all plants of the variant with prey addition were gently washed with tap water and transferred to the container without prey. To digest all pre-captured prey, the plants grew in the container without prey for the next three days, after which the experiment was terminated. There were no dead basal parts of shoots at the end of the experiment. Twelve randomly selected plants of each variant were used to estimate the doubling time of biomass (T_2) and other parameters, while the remaining eight plants were used for other analyses. In 10 plants of *A. vesiculosa* of each variant, the proportion of traps with captured prey was estimated in the 11th–12th mature leaf nodes (nodes newly produced during the experiment). The same was performed in the 29th–30th mature leaf nodes in 10 *U. australis* plants. Thus, in both plant species, the final prey estimation in the traps was a measure of prey capture during the whole experiment.

Trap number, mean trap DW, and structural investment in carnivory (see above) were estimated in the 4th–6th mature leaf nodes in *A. vesiculosa* (n = 6) and in the 11th–12th mature leaf nodes in *U. australis* (n = 4). Maximum trap size was estimated in all 20 plants of each treatment. Total DW was estimated in all 12 plants selected in each treatment. Large prey was removed from all traps of *A. vesiculosa*.

Tissue nutrient content and statistical treatment

The final biomass from six plants of each variant was used for mineral nutrient analyses. The total dry biomass of each plant was weighed and used for estimating tissue N, P, K, and Mg content after acid mineralisation (for all details, see Adamec 2002). To assess the total nutrient amount in the dominant prey species, 5–20 diaptomids or ostracods were mineralised and analysed in the same way. It was assumed that all mineral nutrients were taken up exclusively from the ambient water by the unfed plants, or both from the water and prey in the fed treatment. Hence, the difference in the total nutrient amount between the fed and unfed variant should have been caused by the effect of feeding. The total nutrient amount, estimated as a product of mean tissue nutrient content and mean plant biomass, was calculated for the initial and final plant biomass. These values were used to assess the proportion of mineral nutrients which could theoretically be taken up from prey and cover the increased nutrient amount in fed plants compared to that in unfed ones. A model budget of the nutrient amount taken up from prey during the 8-day growth period with prey was calculated, taking into consideration the number of leaf nodes and traps, the proportion of traps with captured prey, prey nutrient amount measured, and presumed efficiencies of mineral nutrient uptake from prey (76 % for N, see Dixon et al. 1980, Friday & Quarmby 1994; 90 % for P, K, Mg, see Adamec 2002). The model budget is based on the observation that *Aldrovanda* captured about 67 ostracods and *Utricularia* 314 diaptomids during the experiment. Furthermore, the calculated, model-based nutrient amount taken up from prey was expressed in percentage of the increased nutrient amount in fed plants taken up during the experiment, while the remainder expressed the theoretical nutrient uptake from the water. Based on these model data, the percentage of the nutrient amount theoretically taken up from prey in the fed variants was calculated where possible. Values above > 100 % indicate that the efficiency of nutrient uptake from prey may have been lower than was assumed.

Throughout the paper, the mean with standard error is shown wherever possible. Differences were tested by two-way ANOVA (species and prey as fixed effects, values for species not shown) and those within each species by one-way ANOVA (Tukey HSD test). Apical shoot growth rate was evaluated by a two-tailed t-test.

Results

At the start of the experiment, about 19 % of *Aldrovanda* traps but only about 0.5 % of *Utricularia* traps had

Table 1. Results of 11-d greenhouse growth experiment with *Aldrovanda vesiculosa* and *Utricularia australis*, grown with or without prey. After 8 days of the experiment, prey was removed from the +prey variant. The experiment was terminated 3 days after. The ASGR, apical shoot growth rate (nodes d^{-1}, t-test). Different sets of parameters are separated by dotted line. Means ± 1 SE are shown. Significant difference in the final parameters (1-way ANOVA, Tukey HSD test) within each species: $^{**}P < 0.01$, $^{*}P < 0.05$, $^{\text{ns}}P > 0.05$; significance (prey application, and species × prey interaction; 2-way ANOVA) in the right columns: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, $^{\text{ns}}P > 0.05$.

	Aldrovanda vesiculosa		*Utricularia australis*		Prey	Sp. × Prey
Parameter	+prey	–prey	+prey	–prey		
Initial shoot DW (mg)	4.45 ± 0.30	8.75 ± 0.60	–	–		
Final shoot DW (mg)	14.6 ± 0.45**	9.13 ± 0.31	37.8 ± 4.46$^{\text{ns}}$	45.1 ± 4.65	$^{\text{ns}}$	$^{\text{ns}}$
Initial shoot length (mm)	31.2 ± 0.79	30.2 ± 0.60	72.5 ± 1.94	76.5 ± 2.24	–	–
Final shoot length (mm)	122 ± 2.3**	92.6 ± 1.9	481 ± 19.2**	410 ± 17.1	***	$^{\text{ns}}$
Initial number of shoot nodes	6.10 ± 0.078	6.10 ± 0.058	15.0 ± 0.00	15.0 ± 0.00	–	–
Final number of shoot nodes	18.6 ± 0.16**	15.7 ± 0.16	58.9 ± 1.21**	55.2 ± 0.69	***	$^{\text{ns}}$
Final shoot branches	1.39 ± 0.12**	0.00	1.06 ± 0.19$^{\text{ns}}$	0.850 ± 0.167	***	***
ASGR: 22–26 June (days 0–4)	0.863 ± 0.046$^{\text{ns}}$	0.788 ± 0.039	4.10 ± 0.102$^{\text{ns}}$	3.91 ± 0.076	–	–
ASGR: 26–30 June (days 4–8)	1.33 ± 0.057**	0.813 ± 0.053	4.13 ± 0.276$^{\text{ns}}$	3.80 ± 0.195	–	–
ASGR: 30 June–3 July (days 8–11)	1.24 ± 0.093$^{\text{ns}}$	1.06 ± 0.092	3.67 ± 0.634$^{\text{ns}}$	3.12 ± 0.390	–	–
ASGR: 22 June–3 July (days 0–11)	1.13 ± 0.021**	0.871 ± 0.020	3.99 ± 0.110*	3.65 ± 0.063	–	–
Doubling time of biomass (d)	6.43	10.6	5.20	4.65	–	–
Initial investment in carnivory (% DW)	62.9 ± 1.03		13.8 ± 3.14		–	–
Final investment in carnivory (% DW)	52.9 ± 0.53$^{\text{ns}}$	52.3 ± 0.78	52.9 ± 1.47**	45.8 ± 0.19	***	**
Initial mean trap DW (μg)	60.7 ± 6.80		6.58 ± 1.04		–	–
Final mean trap DW (μg)	36.6 ± 1.31**	27.1 ± 0.76	13.9 ± 1.81$^{\text{ns}}$	11.5 ± 0.31	***	**
Final maximum trap length (mm)	3.71 ± 0.074**	3.14 ± 0.070	2.26 ± 0.085*	2.04 ± 0.057	***	*
Initial traps with prey (%)	18.5 ± 3.16		0.45 ± 0.45		–	–
Final traps with prey (%)	55.5 ± 6.98**	0.00	19.1 ± 2.10**	0.22 ± 0.22	***	**
Initial shoot N content (% DW)	1.70 ± 0.02		3.10 ± 0.15		–	–
Final shoot N content (% DW)	2.35 ± 0.15*	1.66 ± 0.17	1.44 ± 0.11**	0.981 ± 0.050	***	$^{\text{ns}}$
Initial shoot P content (% DW)	0.271 ± 0.006		0.592 ± 0.019		–	–
Final shoot P content (% DW)	0.320 ± 0.005**	0.184 ± 0.005	0.166 ± 0.003$^{\text{ns}}$	0.160 ± 0.006	***	***
Initial shoot K content (% DW)	2.96 ± 0.05		4.63 ± 0.09		–	–
Final shoot K content (% DW)	2.52 ± 0.08**	2.88 ± 0.05	4.84 ± 0.14**	4.14 ± 0.05	$^{\text{ns}}$	***
Initial shoot Mg content (% DW)	0.192 ± 0.006		0.482 ± 0.022		–	–
Final shoot Mg content (% DW)	0.177 ± 0.002$^{\text{ns}}$	0.173 ± 0.005	0.439 ± 0.009**	0.480 ± 0.006	**	**

captured prey (Table 1). Certain differences between both species also remained after the 11-day growth experiment as *Aldrovanda* captured prey more efficiently. Both treatments without prey captured almost no prey. The growth of *Aldrovanda* in the terms of DW was highly significantly supported by prey (by 60 %), while no significant effect of prey addition occurred in *Utricularia*. However, the main shoots of fed plants in both species were significantly ($P < 0.01$) longer and also had more mature leaf nodes than the unfed plants. Branching was markedly supported by prey only in *Aldrovanda* ($P < 0.001$), so that a highly significant species × prey interaction was found. Over the entire 11-day growth period, mean ASGR in fed plants was about 30 % greater in *Aldrovanda* (1.13 nodes d^{-1}; $P < 0.0001$), while only about 9 % in *Utricularia* (3.99 nodes d^{-1}; $P < 0.02$). In *Aldrovanda*, the positive effect of feeding on ASGR was significant ($P < 0.001$) as early as days 4 to 8. More rapid growth (DW) in fed *Aldrovanda* plants led to a marked shortening of T_2 (6.4 *vs.* 10.6 d), while in *Utricularia* these values were similar (5.2 *vs.* 4.7 d).

While feeding on prey significantly increased the structural investment in carnivory (trap proportion) in *Utricularia,* in *Aldrovanda* this parameter was virtually unaffected (Table 1). Yet, in the latter case, feeding led to a highly significant increase in mean trap DW and maximum trap length. In *Utricularia*, however, only maximum trap length was slightly ($P < 0.04$) increased due to feeding.

The total mean mineral N, P, K, and Mg amount in ostracods, which were the dominant prey species for *Aldrovanda,* was 2.74; 0.245; 3.08; and 1.14 μg prey^{-1}, respectively. *Eudiaptomus* sp., the dominant prey for

Table 2. Comparison of the mean total nutrient amount in experimental plants of both treatments at the start and the end of the 11-day growth experiment. The values are based on the data shown in Table 1. Model values of the nutrient amount which could be taken up from prey in the +prey variant (for details see text) are also shown. The values in parentheses denote the percentage of the increased nutrient amount within the +prey variant (*minus* that in the –prey variant) which was theoretically covered by the nutrient uptake from prey. Values > 100 % indicate that the efficiency of nutrient uptake from prey may have been lower than was assumed.

	Aldrovanda vesiculosa		*Utricularia australis*	
Parameter	+prey	–prey	+prey	–prey
Initial total shoot N amount (μg)	75.5		271	
Final total shoot N amount (μg)	342	151	544	442
N amount taken up from prey (μg)	139 (73 %)	0	187 (183 %)	0
Initial total shoot P amount (μg)	12.0		51.8	
Final total shoot P amount (μg)	46.6	16.8	62.7	72.3
P amount taken up from prey (μg)	14.7 (49 %)	0	31.4	0
Initial total shoot K amount (μg)	132		405	
Final total shoot K amount (μg)	368	262	1832	1868
K amount taken up from prey (μg)	185 (175 %)	0	336	0
Initial total shoot Mg amount (μg)	8.53		42.2	
Final total shoot Mg amount (μg)	25.8	15.8	166	216
Mg amount taken up from prey (μg)	68.3 (683 %)	0	0	58.8

Utricularia in this experiment, contained 0.785; 0.111; 1.19; and 0.208 μg prey^{-1} of N, P, K, and Mg, respectively. Mean tissue N content in the whole shoots was significantly higher by 42–47 % in fed plants of both species as compared to unfed plants (Table 1). Shoot P content, however, was markedly higher due to feeding (by 74 %; $P < 0.0002$) in *Aldrovanda* only, while it remained unchanged in *Utricularia*. There was a contrasting effect of feeding on shoot K content in the two species: a highly significant increase was observed in fed *Aldrovanda*, while *Utricularia* K content decreased compared to unfed plants. There was also a significant decrease of shoot Mg content due to feeding in *Utricularia*.

Calculation of the total nutrient amount in plants revealed that the fed plants of *Aldrovanda* contained much more N, P, K, and Mg at the end of the experiment than the unfed plants (Table 2). In *Utricularia*, however, only N content was higher in fed plants, whereas the total amount of P, K and Mg was greater in unfed plants. Theoretically, based on the model data, the amount of N taken up from prey could cover about 73 % of the total plant nutrient increase in fed *Aldrovanda* plants, and even 183 % in *Utricularia*. For *Aldrovanda*, about 49 % of P, but as much as 175 % of K and 683 % of Mg could also be recovered from prey, i.e., the entire increase in K and Mg amount.

Discussion

The presented growth experiment on two rootless, aquatic, carnivorous species was designed to determine detailed growth effects of prey addition and, moreover, to estimate a proportion of mineral nutrients (N, P, K, Mg) taken up from added prey to the total increased nutrient amount in the plants. This type of nutrient uptake growth experiment has commonly been performed in terrestrial carnivorous plants, either using a model prey (e.g., Hanslin & Karlsson 1996) or a defined mineral nutrient solution (e.g., Adamec 2002). Evidently, the growing shoots of both aquatic species could have taken up mineral nutrients for their rapid growth only from the ambient water or captured prey. Re-utilization of N and P from senescing shoot bases was unlikely, as the experiment started with greatly shortened shoots. Moreover, no loss of mineral nutrients from shoots to the ambient water is assumed, as the experiment was terminated before the basal shoot segments in both plant species died (Adamec 2008a). The difference in the total mineral nutrient amount between the fed and unfed plants at the end of the growth experiment was caused – either directly or indirectly – by the utilisation of mineral nutrients from prey. N, P, K, and Mg were investigated in this study as relatively efficient uptake of all of these nutrients has been shown for several *Drosera* species fed fruit flies (Dixon et al. 1980, Adamec 2002).

The results clearly show that the growth effect of prey feeding was different in both plant species (Table 1). In *Aldrovanda*, the high increase in DW due to feeding as the principal growth parameter, was consistently associated with a significantly greater plant size (shoot length, number of shoot nodes, branching, trap length, and trap DW) as well as with more rapid apical shoot growth. On the other hand, a non-significant decrease in shoot DW in fed *Utricularia* plants was counterbalanced by slightly longer plants (both shoot length and number of nodes), slightly greater branching and larger traps (both trap size and DW), and slightly greater ASGR. Thus, although the fed *Utricularia* plants were longer, they were weaker and thinner than the unfed ones. The marked positive growth effect of feeding in *Aldrovanda* clearly supports the general conclusion that the growth of this species depends strongly on prey capture (Kamiński 1987b, Adamec 2000, 2008b, Adamec & Kovářová 2006). However, the ambiguous growth effect in *Utricularia* in this study together with several data sets from the literature (Sorenson & Jackson 1968, Knight & Frost 1991, Kosiba 1992a, b, Jobson et al. 2000, Englund & Harms 2003, Adamec 2008b) support the view that growth responses to prey capture in aquatic *Utricularia* species can be modulated considerably by other ecological factors (e.g., CO_2 concentration, mineral nutrient level, irradiance, temperature) and be species specific. On the other hand, the positive growth responses are more common in terrestrial carnivorous plants (for the review, see Adamec 1997a).

It is possible that the principal difference in the growth response to prey between *Aldrovanda* and *Utricularia* was caused by different trap ecology in these genera. Due to its snapping traps, *Aldrovanda* cannot host commensal communities inside the traps, and directly utilises the captured animal prey. On the contrary, suction traps of various aquatic *Utricularia* species are permanently inhabited by commensal communities consisting mainly of bacteria and unicellular algae, but also rotifers and protozoa (e.g., Richards 2001, Peroutka et al. 2008, Sirová et al. 2009). Mutualistic, rather than predator–prey interactions have therefore been suggested to occur between *Utricularia* and the trap communities (Richards 2001). These interactions could be of greater benefit for the plants grown in nutrient-poor waters with low prey availability. Based on high concentrations of both organic carbon and mineral N and P in the fluid of aquatic *Utricularia* traps, Sirová et al. (2009) recently suggested an operation of a complex microbial food web inside the traps. However, the nutritional benefit of the commensal communities for the plants has not been assessed so far. The permanent operation of the food web could partly compensate for prey supply, thus making *Utricularia* plants far less sensitive to prey shortage or even absence in the presented growth experiment. Moreover, this food web operation could allow at least several aquatic *Utricularia* species (e.g., *U. australis*, *U. purpurea*, *U. foliosa*) to grow in ultraoligotrophic waters (sand-pits, lakes) without animal prey where other rootless higher aquatic plants cannot grow (Bern 1997, Richards 2001, Adamec 2009).

A certain difference between both species was also found in the final proportion of trap DW to the total DW of the shoot segment (Table 1). *Aldrovanda* is known as a species with more or less constant number of traps on the leaf nodes (whorls, Kamiński 1987a), while the number of traps, their size, as well as their biomass proportion are highly variable in *U. australis* (Adamec 2008a, 2009) and related aquatic *Utricularia* species (e.g., Knight & Frost 1991, Friday 1992, Englund & Harms 2003, Guisande et al. 2004). In *Aldrovanda*, the final structural investment in carnivory was quite unaffected by feeding. In *Utricularia*, however, in contrast to the markedly elevated shoot N content (see Adamec 2008a), feeding led to a highly significant increase in the investment in carnivory. This increase may also have contributed to the slower growth of the fed variant. Yet, the level of prey capture in mature traps (19 % traps with prey) was still relatively high compared to the natural prey capture (cf. Adamec & Kovářová 2006, Adamec 2008a, b, 2009). In any case, the proportion of mature traps with captured prey should be estimated in all studies dealing with growth ecophysiology of aquatic carnivorous plants.

The estimated total amount of N, P, K, and Mg in *Aldrovanda* shoots with prey at the end of the experiment always greatly surpassed that in unfed plants (by 40–177 %, Table 2). However, this relationship correlated only with the increased value of shoot N and P content; shoot Mg content was the same in both variants, while shoot K content slightly declined in fed plants. In *Utricularia*, only the total N amount in the shoots of fed plants was greater (by 23 %) than that in unfed plants and correlated with the significantly greater shoot N content. This fact together with low shoot N content in unfed plants and very low NH_4^+ concentration in the ambient water suggests that the unfed plants were partly N limited. Overall, the shoot N and P contents are similar to those found in the same species in similar studies (cf. Adamec 2000, 2008b).

Another task was to estimate the proportion of mineral nutrients from prey covering the increased consumption in the fed variants. According to the model used, one *Aldrovanda* shoot captured on average 66.6 ostracods and one *Utricularia* 314 diaptomids over the experiment. In both species, these amounts of captured prey represented a good deal (49–683 %, Table 2) of the increase in mineral nutrients (i.e., the total amount in fed *minus* that in unfed plants) as a result of growth, even though this nutrient budget was less accurate in *Utricularia* due to greater variation of DW. Theoretically, it means that fed *Aldrovanda* plants covered 73 % of their increased N consumption from prey and the remaining 27 % from the ambient water, or 49 % and 51 % of their P consumption, respectively. In contrast, they could cover all their increased K and Mg consumption from prey; the same also applies to N uptake in *Utricularia*. Comparing the initial and final total nutrient amount in shoots of fed plants, *Aldrovanda* could cover about 52 % of N, 42 % of P, 78 % of K, and 100 % of Mg of its total growth consumption from prey, while fed *Utricularia* only 68 % of N. Similarly, Knight (1988) estimated that field-grown *U. macrorhiza* could compensate up to 75 % of its seasonal N gain from prey.

It has been found that the main physiological effect of prey capture by traps in terrestrial carnivorous plants is based on a marked stimulation of mineral nutrient uptake by roots (Hanslin & Karlsson 1996, Adamec 1997, 2002). In this context, an analogous effect could also be expected in rootless aquatic carnivorous plants: prey capture by traps could stimulate shoots to take up growth limiting mineral nutrients from the ambient water more efficiently (by higher affinity or uptake rate). Although the total N and P amount in fed *Aldrovanda* plants was considerably greater (compared to unfed plants) than could have been taken up from prey (Table 2), it did not prove the occurrence of this stimulation mechanism. Instead, the data for *Utricularia* show a gentle growth retardation associated with a slight inhibition of mineral nutrient uptake (except for N) from the water due to prey capture. This growth effect of feeding might be associated with a significant decrease in net photosynthetic rate in this species (Adamec 2008b). However, the possible occurrence of the stimulation mechanism in fed plants should be tested further by direct measurements of mineral nutrient uptake rate from the ambient water.

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