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Note

By which mechanism does prey capture enhance plant growth in aquatic carnivorous plants: Stimulation of shoot apex?

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With 2 tables

Abstract: Prey capture in rootless aquatic carnivorous plants usually leads to more rapid plant growth, especially to increasing apical shoot growth rate and branching. Yet, the mechanism of this growth effect is still unknown. In this paper, dark respiration (R_D) and tissue N and P content were estimated in young parts of shoot apices in three aquatic carnivorous plants, *Aldrovanda vesiculosa*, *Utricularia australis*, and *U. bremii*, grown with or without prey in a 12-d greenhouse growth experiment. Fed plants of all three species were significantly longer and had more mature leaf nodes on the main shoot than unfed plants. Similarly, the apical shoot growth rate of fed plants in all three species was significantly higher by 49–85 % than that of the unfed variants (day 6–12) and so also was shoot branching. In *A. vesiculosa* only, tissue N content both in apices and shoot segments of fed plants was significantly greater that in unfed plants. Both apical and shoot P content was significantly greater in fed plants of *A. vesiculosa* and *U. australis*, while the P contents were the same in *U. bremii*. Feeding on prey significantly increased R_D of shoot apices in *A. vesiculosa*, while the values for fed and unfed plants were exactly the same in the other two species. In conclusion, the more rapid growth due to feeding could hypothetically be caused by stimulating the cell division in the youngest parts of shoot apex due to a faster allocation of prey-derived N and P. The methods used in this study were not sensitive enough to prove this hypothesis although the results partly support it.

Key words: *Aldrovanda vesiculosa, Utricularia australis, U. bremii*, growth experiment, prey capture, shoot apex, dark respiration, tissue N and P content.

Introduction

Aquatic carnivorous plants comprise the species *Aldrovanda vesiculosa* L. (Droseraceae) and about 50 submerged or amphibious species of the genus *Utricularia* L. (Lentibulariaceae; Juniper et al. 1989, Taylor 1989). Rootless aquatic carnivorous plants usually grow in shallow standing dystrophic waters and growth can often be limited by a shortage of N and P, and also of K in these waters (for the review see Adamec 1997a, Ellison 2006, Guisande et al. 2007). All necessary nutrients are taken up through the shoots, either directly from water or from prey. The typical feature of most species of aquatic carnivorous plants is a linear shoot exhibiting a marked physiological polarity (Adamec 2000, 2008a, Sirová et al. 2010). Contrary to terrestrial carnivorous plants, most species of aquatic carnivorous plants exhibit very rapid apical shoot growth (1–4 leaf nodes/d) and a high relative growth rate (Friday 1989, Adamec 2000, 2002, 2008b, 2009,

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Adamec & Kovářová 2006). The very rapid growth of aquatic carnivorous plants in nutrient-poor habitats requires ecophysiological adaptations that enable the plants to gain the very limited supplies of mineral nutrients. The adaptations include prey capture, keeping trap commensals, efficient N and P re-utilization (recycling) from senescent shoots, and a very high affinity for nutrient uptake from water (Kamiński 1987a,b, Kosiba 1992a,b, Adamec 1997a, 2000, 2008a, 2009, Richards 2001, Englund & Harms 2003, Sirová et al. 2009, 2010).

Considering the ecological cost-benefit relationships, Givnish et al. (1984) hypothesized that carnivory in terrestrial species provides these plants with a greater mineral nutrient availability and may lead to increasing a plant's total rate of net photosynthesis (P_N) as a principal effect. This effect may either be due to an increased P_N per unit leaf biomass or an increased total leaf biomass that it can support. So far, the positive effect of carnivory on increased P_N has been confirmed only in pitcher plants of the genus *Sarracenia* (Farnsworth & Ellison 2008) and in *Nepenthes talangensis* (Pavlovič et al. 2009), but not in *Pinguicula* (Méndez & Karlsson 1999). Although prey capture in aquatic carnivorous plants is very important to attain a high growth rate (for the review see Adamec 1997a, 2000, 2008b, Englund & Harms 2003), the relationship between carnivory and P_N is still very ambiguous. Adamec (2008b) demonstrated a significant P_N increase due to prey capture only in young, mature shoot segments in *A. vesiculosa* but a simultaneous P_N decrease in *U. australis* which was accompanied with a significant decline of CO_2 affinity and chlorophyll-*a* content. Moreover, this different effect on P_N was associated with a significant decrease in foliar N and P content in mature shoot segments in prey-fed variants in both species (see also Adamec 2000).

Generally, prey capture in aquatic carnivorous plants leads to more rapid growth (expressed as apical shoot growth rate, relative growth rate, branching; e.g., Adamec 1997a) which, however, may not be followed by higher P_N per unit biomass in mature shoot segments but, on the contrary, leads to a significant decrease in tissue N and P content in both young and mature shoot segments (Adamec 2000, 2008b). More rapid growth might be attained by a greater allocation of newly fixed carbon to shoot growth processes than to trap production (*sensu* Adamec 2008a). As these characteristics of accelerated growth in aquatic carnivorous plants should be mediated by more rapid growth of the youngest parts of shoot apices, Adamec (2008b) postulated a hypothesis that N and P absorbed from prey supports preferentially essential growth processes such as cell division, DNA replication, and proteosynthesis in the youngest tissues in shoot apices. Therefore, an increased tissue N and P content as well as dark respiration rate (R_D) could also occur in the youngest tissues in shoot apices as a consequence of this increased metabolism in more rapidly growing plants. Generally, prey capture might finally also lead to a greater reproductive effort and greater turion size and better plant overwintering and survival.

The aim of this paper was to verify whether O_2-based R_D and tissue N and P content are increased due to prey capture in young parts of shoot apices in three aquatic carnivorous plant species, *A. vesiculosa*, *U. australis* R. Br., and *U. bremii* Heer ex Kölliker, grown in a greenhouse growth experiment. Growth characteristics of the plants were also investigated. The experimental species are free-floating submerged carnivorous plants growing in the same shallow dystrophic waters (e.g., Kamiński 1987a). They all have commonly been used in previous ecophysiological studies (Adamec 1997b, 2000, 2006, 2008a,b, 2009, Adamec & Kovářová 2006). While *A. vesiculosa* has snapping traps, those of *Utricularia* spp. represent suction traps (bladders) usually allowing to host a commensal community in the trap fluid (Richards 2001, Peroutka et al. 2008) in which a miniature food web could run (Sirová et al. 2009, 2010).

Material and methods

Growth experiment

Adult plants of *A. vesiculosa* (collected from E. Poland) were pre-cultivated outdoors in a 1 m^2 plastic container simulating natural conditions and adult plants of *U. bremii* (collected from N. Russia) similarly in a 0.8 m^2 plastic container (for details see Adamec 1997b). While subadult, 20–40 cm long plants of *U. australis* were freshly collected from a mesotrophic sand-pit (Branná, Třeboňsko Biosphere Reserve, Czech Republic). All three species could capture prey under these conditions. Before the experiment, the percentage of traps with macroscopic prey was about 46 % in 6^{th}–8^{th} mature leaf nodes in *A. vesiculosa*, 32 % in 12^{th} leaf nodes in *U. australis*, and 10 % in 10^{th}–12^{th} leaf nodes of *U. bremii*.

The growth experiment provided both data on g rowth characteristics of the species and experimental material for the subsequent measurement of R_D and tissue N and P content. The experiment on all species proceeded in one 0.8 m^2 white, plastic container, which stood in a naturally lit greenhouse with open lateral walls for cooling. The container (40 cm high) contained 280 l of tap water and 100 g dry weight (DW) of *Carex elata* litter as substrate. For 39 days preceding the experiment, the pre-soaked substrate allowed water in the container to mimic that of an oligo-mesotrophic and slightly dystrophic environment. On 9 June 2009, 24 relatively homogeneous plants of

each species were shortened to a constant number of mature apical leaf nodes, all visible branches were excised, and the shortened apical shoot segments were used for the experiment. *A. vesiculosa* was shortened to 8 mature apical leaf nodes (shoot length 5.2–7.5 cm), *U. australis* to 20 leaf nodes (shoot length 14.2–21.5 cm), and *U. bremii* to 16 leaf nodes (shoot length 12.3–19.2 cm). In all plants, the internode between the second and third mature leaf nodes was tagged by a short piece of fine thread for measuring the apical shoot growth rate (see Adamec 2000, 2008b). Twelve randomly selected tagged plants of each species were put freely into the experimental container, in which they could capture prey (i.e., the variant with prey), while the other 12 plants were put in a floating plastic frame in the container. Each species was grown in a separate floating frame. The floating frame was 0.3 × 0.3 m by about 6 cm depth and mesh with a pore size of 150 µm was placed on the bottom; to exclude zooplankton but maintain free water exchange with the ambient water (i.e., the variant without prey; Adamec 2000, 2008b). Thus, although all plants within a certain variant were pseudoreplicates they grew in uniform conditions but those within frames were deprived of prey. Every other two days, the mesh on the floating frames was cleaned and washed by tap water. Fine zooplankton (copepods, ostracods, size 0.6–1.5 mm) was added repeatedly to the container to feed the control plants.

The irradiance (PAR) at plant level was about 40 % of that in the open area, which might be an optimum level for all species (Adamec 1997b, Adamec & Kovářová 2006). A submersible temperature data logger (Minikin T, EMS, Brno, Czech Rep.) monitored water temperature in the container at plant level. During the experimental growth period of 12 days (9–21 June), the mean water temperature at plant level was 19.4 °C (range of 14.0–24.7 °C, daily maximum 24.7 °C, daily minimum 18.0 °C, night maximum 21.1 °C, night minimum 14.0 °C). Basic water chemistry parameters were estimated in the cultivation water several times during the experiment (for the methods see Adamec 2000). The water was rather poor in main mineral nutrients (0–7 µg l^{-1} NO_3^--N; 19–23 µg l^{-1} NH_4^+-N; 20–33 µg l^{-1} PO_4-P). pH was 7.30–7.47, O_2 concentration about 80 % of the saturation, electrical conductivity 34.0–35.9 mS m^{-1}, total alkalinity 1.12–1.15 meq l^{-1}, and [CO_2] 0.09–0.13 mM. No significant difference in pH was measured between the frames and the ambient water in the container.

The apical shoot growth rate was measured in all plants as the position of the tag after 6 days of the experiment and again at the end of the experiment after other 6 days (21 June). At the end of the experiment, main shoot length, the number of mature leaf nodes, and the branching of shoots were estimated in all plants (Adamec 2000, 2008b). All plants continued their growth under the previous conditions for one further day (*A. vesiculosa, U. australis*) or two days (*U. bremii*) until R_D was measured.

Measurement of dark respiration and tissue nutrient content

In each species, R_D was compared in mature leaf nodes and in shoot apices. R_D was measured in the 5th mature leaf nodes of *A. vesiculosa*, in the 8th mature leaf nodes of *U. australis*, and in the 10th–11th mature leaf nodes of *U. bremii*. Fresh weight (FW) of this material from 1–2 plants was 5–16 mg. All traps were excised as their R_D greatly exceeds that of leaves/shoots (Adamec 2006) and their proportion might vary in individual samples. R_D was also measured in young parts of shoot apices from 1–2 plants (FW 2–16 mg). These shoot apices were 3–4 mm long in *A. vesiculosa*, 2.5–3 mm in *U. australis*, and 2–2.5 mm in *U. bremii*. R_D was measured in a solution of 1 mM $NaHCO_3$ with 0.1 mM KCl and 0.05 mM $CaCl_2$ (80–90 % O_2 saturation) in a 2.1-ml stirred chamber (kept at 25.0 ± 0.1 °C). A Clark-type oxygen sensor and a pen recorder (for details see Adamec 1997b) was used. R_D was measured in darkness for 15 min. FW was estimated in measured sampled, while dry weight (DW; 80 °C) was estimated in pooled samples. All measurements were repeated 6 times for a different plant material. R_D is expressed in mmol kg^{-1}_{FW} h^{-1}.

The percentage of traps with any macroscopic prey in the experimental plants was estimated using a binocular loupe in the mature 6th–7th leaf nodes of *A. vesiculosa*, in the 10th–11th leaf nodes of *U. australis*, and in the 12th–14th leaf nodes of *U. bremii* (n = 5). In the same leaf nodes, maximum trap size (to the nearest 0.5 mm) was estimated using a ruler (Adamec 2009). Tissue N and P content was estimated after acid mineralisation in the 4th mature leaf nodes of *A. vesiculosa*, in the 7th leaf nodes of *U. australis*, in the 8th–10th leaf nodes of *U. bremii*, and in shoot apices which had been used for R_D measurements (for all analytical details, see Adamec 2002; n = 5). All traps were excised from the samples due to the different trap N and P content (Adamec 2008a) and presence of prey. Throughout the paper, the mean with standard error is shown. Differences between fed and unfed variants were evaluated by a two-tailed t-test.

Results

At the end of the growth experiment, traps of all three species without prey contained virtually no prey, while the control plants with prey had 30–73 % traps with captured prey in mature shoot segments (Table 1). Fed plants in all three species were significantly longer (by 19–45 %) and had more mature leaf nodes on the main shoot (by 21–30 %; $p < 0.01$) than unfed plants. Similarly, the apical shoot growth rate of fed control plants was by 16–36 % higher than that of the unfed variants in all three species as early as during the first half of the experiment (day 0–6), while this difference was more distinct (by 49–85 %) and highly significant in all species during the second half (day 6–12). A marked and significant difference in shoot branching was found between fed controls and unfed variants in all three species. Feeding on prey led to a significant increase in maximum trap size only in *U. australis*, with size exactly the same in the other two species (Table 1).

The proportion of DW to FW was greater in shoot apices than in mature shoot segments (Table 2). In all three species, the tissue N content in shoot apices was about 1.5–2 times greater than that of mature shoot segments and about 2–3 times greater for P content. However, in *A. vesiculosa*, tissue N content both in apices and shoot segments of control fed plants was

Table 1. Growth characteristics of *A. vesiculosa* (AV), *U. australis* (UA), and *U. bremii* (UB) grown with (+) or without prey (–) in a greenhouse for 12 days. ASGR, apical shoot growth rate, production of new mature nodes with leaves d^{-1}; ASGR values are shown for the 1st and 2nd half of the experiment. Traps with prey, % of traps with macroscopic prey estimated in mature 6th–7th leaf nodes in AV, 10th–11th nodes in UA, and in 12th–14th nodes in UB; n = 5–6. Means ± 1.SE are shown; n = 12. Statistically significant difference between fed and unfed variant within each species (two-tailed t-test): **, $p < 0.01$; *, $p < 0.05$; ns, $p > 0.05$.

Spec.	Prey	Shoot length (cm)	Mature leaf nodes	ASGR (node/d)		Branches ($plant^{-1}$)	Max. trap size (mm)	Traps with prey (%)
				day 0–6	day 6–12			
AV	+	12.7 ± 0.26**	16.7 ± 0.67**	0.59 ± 0.02ns	0.83 ± 0.06**	0.83 ± 0.17*	4.42 ± 0.08ns	72.9 ± 6.9
AV	–	10.7 ± 0.29	13.0 ± 0.28	0.51 ± 0.04	0.54 ± 0.05	0.25 ± 0.18	4.46 ± 0.11	0.0
UA	+	67.0 ± 2.6**	57.8 ± 0.37**	3.15 ± 0.06**	3.15 ± 0.13**	3.17 ± 0.30**	3.38 ± 0.07**	38.5 ± 5.0
UA	–	47.1 ± 1.4	47.8 ± 0.53	2.53 ± 0.05	2.11 ± 0.14	1.92 ± 0.23	2.60 ± 0.11	0.0
UB	+	36.0 ± 1.2**	41.9 ± 0.43**	1.92 ± 0.06**	2.40 ± 0.14**	2.42 ± 0.15**	2.33 ± 0.07ns	30.3 ± 11.5
UB	–	24.8 ± 1.1	32.2 ± 0.58	1.41 ± 0.05	1.30 ± 0.15	0.73 ± 0.19	2.29 ± 0.07	0.0

Table 2. Tissue N and P content and dark respiration (R_D) in shoot apices and mature shoot segments (traps excised) in *A. vesiculosa* (AV), *U. australis* (UA), and *U. bremii* (UB) having been grown with (+) or without prey (–) in a greenhouse for 12 days. The percentage of DW in FW is also shown. Means ± 1.SE are shown; n = 5–6. Statistically significant difference between fed and unfed variant for the same organ type within each species (two-tailed t-test): **, $p < 0.01$; *, $p < 0.05$; ns, $p > 0.05$.

Spec.	Prey	Organ	DW (% FW)	Tissue content (% DW)		R_D ($mmol/kg_{FW} \cdot h$)
				N	P	
AV	+	Apex	14.4	4.39 ± 0.11**	0.567 ± 0.012**	42.2 ± 2.3**
AV	–	Apex	11.4	2.63 ± 0.20	0.437 ± 0.006	32.7 ± 1.05
AV	+	Shoot	8.83	2.03 ± 0.09**	0.238 ± 0.016**	9.93 ± 0.64*
AV	–	Shoot	8.57	1.09 ± 0.04	0.138 ± 0.005	7.73 ± 0.55
UA	+	Apex	11.5	2.92 ± 0.15ns	0.437 ± 0.006**	27.1 ± 1.41ns
UA	–	Apex	21.1	2.39 ± 0.22	0.321 ± 0.006	27.0 ± 1.32
UA	+	Shoot	7.51	1.28 ± 0.06ns	0.146 ± 0.007**	9.83 ± 0.56*
UA	–	Shoot	7.77	1.34 ± 0.05	0.112 ± 0.002	7.51 ± 0.71
UB	+	Apex	11.4	2.59 ± 0.19ns	0.343 ± 0.033ns	27.0 ± 0.79ns
UB	–	Apex	12.5	3.38 ± 0.57	0.340 ± 0.016	27.5 ± 2.0
UB	+	Shoot	8.57	2.02 ± 0.14ns	0.185 ± 0.006ns	8.74 ± 0.93ns
UB	–	Shoot	7.59	1.78 ± 0.15	0.164 ± 0.007	8.18 ± 0.51

significantly greater than of unfed plants. The apical N content in *U. bremii* was not significantly higher in unfed plants. Both apical and shoot P content was significantly greater in prey-fed controls than in unfed variants in *A. vesiculosa* and *U. australis*, while the contents were the same in *U. bremii*. Feeding on prey significantly increased R_D of shoot apices in *A. vesiculosa*, while the values for fed and unfed plants were exactly the same in the other two species (Table 2). Furthermore, in *A. vesiculosa* and *U. australis*, R_D was also significantly increased (by 28–31 %) in the mature shoot segments of fed plants.

Discussion

In the present study, the growth of both *A. vesiculosa* and two *Utricularia* species was influenced positively by prey capture (Table 1). Due to much higher apical shoot growth rate in both *Utricularia* species than in *A. vesiculosa* however, the growth effect of prey feeding was usually somewhat greater and statistically more significant in the *Utricularia* species. Yet, the result for *A. vesiculosa* is quite consistent with the general conclusion that the growth of this species depends strongly and invariably on prey capture (Kamiński 1987b, Adamec 2000, 2008b, Adamec & Kovářová 2006, Adamec et al. 2010). On the other hand, growth effects of prey capture in various aquatic *Utricularia* species reported in the literature (Knight & Frost 1991, Kosiba 1992b, Englund & Harms 2003, Adamec 2008b, Adamec et al. 2010, this study) are rather variable and 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 in the ambient water, irradiance, temperature, initial shoot length) and may be species specific. Sometimes, the positive growth ef-

fect of prey capture on aquatic *Utricularia* may even be zero (Adamec et al. 2010). As the traps of various aquatic *Utricularia* species are permanently inhabited by commensal communities (Richards 2001, Peroutka et al. 2008, Sirová et al. 2009), Adamec et al. (2010) explained such an effect by mutualistic interactions between the commensals and traps. They could be of greater benefit for the plants grown in nutrient-poor waters with low prey availability. As a result of this microbial association, *Utricularia* plants might be far less sensitive to prey shortage or even absence.

The aim of this study was to determine whether the observable growth effect of prey capture might be caused by a stimulation of R_D and an increase of the tissue N and P content in young parts of shoot apices as it was suggested by Adamec (2008b). The parts of shoot apices selected were as young and small as possible for these measurements. In *A. vesiculosa* and *U. australis*, they represented very young, immature tissues, while in very small shoot apices of *U. bremii*, they represented the whole shoot apex with immature traps. In *A. vesiculosa* only, prey capture led to both significantly increasing shoot apex N and P content and R_D, while only the apex P content was increased in *U. australis* (Table 2). Arrigo (2005) argues that high tissue N content (mainly enzymes), but not P content, is necessary in mature plant tissues for an increased metabolism in association with the utilization of light and mineral nutrients, whereas both high tissue N and P content (mainly enzymes and RNAs) are necessary for rapid metabolism including the processes of cell division and growth. Exactly, the latter case occurs in shoot apices. The meristematic and division zone of shoot apex, which is responsible for cell divisions and initiation of new leaves and branches and thus for the apical shoot growth rate and branching in aquatic carnivorous plants used in this study, may be much shorter than were in fact the shoot apices (cf. Rutishauser 1993). Thus, the relative difference in the proportion of the meristematic and division zone to the total shoot apex biomass used between the more robust *U. australis* and the tiny *U. bremii* could explain the differences in tissue N and P in shoot apices found between these species (Table 2). However, R_D as criterion of aerobic energy metabolism in shoot apices in both *Utricularia* species was exactly the same regardless of prey capture and, thus, did not correlate with tissue N and P content. Unlike the similar studies (Adamec 2000, 2008b), in which prey capture led to a small or even significant decrease in tissue N and P content in young or mature shoot segments in *A. vesiculosa* and *U. australis*, this was not the case in this study. This variable response to prey capture shows that tissue N and P content in itself is not a reliable measure of N and P uptake from prey (see also Adamec 1997a).

At least in aquatic *Utricularia* species, the positive growth effect of prey capture may not be associated with increasing photosynthetic rate of mature shoot segments per unit biomass (Adamec 2008b). Therefore, the effect could be caused by stimulating the cell division in the youngest parts of shoot apex due to a faster allocation of prey-derived N and P. To reach very high apical shoot growth rate (1–4 nodes/d) in aquatic carnivorous plants, cell divisions and initiations of leaf primordia within shoot apex must be very rapid. It is possible to assume that any stimulation of this crucial, growth-rate limiting process shall result in more rapid apical shoot growth as well as branching.

In conclusion, the methods used in this study were not sensitive enough to prove this hypothesis although the results partly support it. It is evident that future studies should investigate selectively the youngest zones of shoot apex using topographically very detailed methods (e.g., X-ray nutrient microanalysis, microautoradiography of labelled RNA or DNA precursors, mitotic index, etc.). These studies should also be combined with a detailed anatomical structure of shoot apex of aquatic carnivorous plants.

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References

Adamec, L., 1997a: Mineral nutrition of carnivorous plants: A review. – Bot. Rev. **63**: 273–299.

Adamec, L., 1997b: Photosynthetic characteristics of the aquatic carnivorous plant *Aldrovanda vesiculosa*. – Aquat. Bot. **59**: 297–306.

Adamec, L., 2000: Rootless aquatic plant *Aldrovanda vesiculosa*: physiological polarity, mineral nutrition, and importance of carnivory. – Biol. Plant. **43**: 113–119.

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., 2008a: Mineral nutrient relations in the aquatic carnivorous plant *Utricularia australis* and its investment in carnivory. – Fundam. Appl. Limnol. **171**: 175–183.

Adamec, L., 2008b: The influence of prey capture on photosynthetic rate in two aquatic carnivorous plant species. – Aquat. Bot. **89**: 66–70.

Adamec, L., 2009: Photosynthetic CO_2 affinity of the aquatic carnivorous plant *Utricularia australis* (Lentibulariaceae) and its investment in carnivory. – Ecol. Res. **24**: 327–333.

Adamec, L. & Kovářová, M.: 2006: Field growth characteristics of two aquatic carnivorous plants, *Aldrovanda vesiculosa* and *Utricularia australis.* – Folia Geobot. **41**: 395–406.

Adamec, L., Sirová, D. & Vrba, J., 2010: Contrasting growth effects of prey capture in two aquatic carnivorous plant species. – Fundam. Appl. Limnol. **176**: 153–160.

Arrigo, K. R., 2005: Marine microorganisms and global nutrient cycles. – Nature **437**: 349–355.

Ellison, A. M., 2006: Nutrient limitation and stoichiometry of carnivorous plants. – Plant Biol. **8**: 740–747.

Englund, G. & Harms, S., 2003: Effects of light and microcrustacean prey on growth and investment in carnivory in *Utricularia vulgaris*. – Freshwat. Biol. **48**: 786–794.

Farnsworth, E. J. & 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.

Friday, L. E., 1989: Rapid turnover of traps in *Utricularia vulgaris* L. – Oecologia **80**: 272–277.

Givnish, T. J., Burkhardt, E. L., Happel, R. E. & 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. – Amer. Nat. **124**: 479–497.

Guisande, C., Granado-Lorencio, C., Andrade-Sossa, C. & Duque, S. R., 2007: Bladderworts. – Funct. Plant Sci. Biotechnol. **1**: 58–68.

Juniper, B. E., Robins, R. J. & Joel, D. M., 1989: The Carnivorous Plants. – Academic Press Ltd, London.

Kamiński, R., 1987a: Studies on the ecology of *Aldrovanda vesiculosa* L. I. Ecological differentiation of *A. vesiculosa* population under the influence of chemical factors in the habitat. – Ekol. Pol. **35**: 559–590.

Kamiński, R., 1987b: Studies on the ecology of *Aldrovanda vesiculosa* L. II. Organic substances, physical and biotic factors and the growth and development of *A. vesiculosa.* – Ekol. Pol. **35**: 591–609.

Knight, S. E. & Frost, T. M., 1991: Bladder control in *Utricularia macrorhiza*: lake-specific variation in plant investment in carnivory. – Ecology **72**: 728–734.

Kosiba, P., 1992a: Studies on the ecology of *Utricularia vulgaris* L. I. Ecological differentiation of *Utricularia vulgaris* L. population affected by chemical factors of the habitat. – Ekol. Pol. **40**: 147–192.

Kosiba, P., 1992b: Studies on the ecology of *Utricularia vulgaris* L. II. Physical, chemical and biotic factors and the growth of *Utricularia vulgaris* L. in cultures *in vitro*. – Ekol. Pol. **40**: 193–212.

Méndez, M. & 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., Singerová, L., Demko, V. & Hudák, J., 2009: Feeding enhances photosynthetic efficiency in the carnivorous pitcher plant *Nepenthes talangensis*. – Ann. Bot. **104**: 307–314.

Peroutka, M., Adlassnig, W., Volgger, M., Lendl, T., Url, W. G. & Lichtscheidl, I. K., 2008: *Utricularia*: a vegetarian carnivorous plant? Algae as prey of bladderwort in oligotrophic bogs. – Plant Ecol. **199**: 153–162.

Richards, J. H., 2001: Bladder function in *Utricularia purpurea* (Lentibulariaceae): is carnivory important? – Amer. J. Bot. **88**: 170–176.

Rutishauser, R., 1993: The developmental plasticity of *Utricularia aurea* (Lentibulariaceae) and its floats. – Aquat. Bot. **45**: 119–143.

Sirová, D., Borovec, J., Černá, B., Rejmánková, E., Adamec, L. &, Vrba, J., 2009: Microbial community development in the traps of aquatic *Utricularia* species. – Aquat. Bot. **90**: 129–136.

Sirová, D., Borovec, J., Šantrůčková, H., Šantrůček, J., Vrba, J. & Adamec, L., 2010: *Utricularia* carnivory revisited: Plants supply photosynthetic carbon to traps. – J. Exp. Bot. (in press).

Taylor, P., 1989: The Genus *Utricularia*: A Taxonomic Monograph. – Kew Bulletin, Additional Series, XIV.

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