

Respiration and Photosynthesis of Bladders and Leaves of Aquatic *Utricularia* Species

L. Adamec

Institute of Botany of the Academy of Sciences of the Czech Republic, Section of Plant Ecology, Dukelská 135, 379 82 Třeboň, Czech Republic

Received: September 28, 2005; Accepted: August 10, 2006

Abstract: In aquatic species of carnivorous *Utricularia*, about 10–50% of the total biomass consists of bladders. *Utricularia* bladders are physiologically very active organs though their chlorophyll content may greatly be reduced. To specify energetic costs of carnivory, respiration (RD) and net photosynthetic rate (PN) were compared in bladders and leaves or shoot segments of six aquatic *Utricularia* species with differentiated (*U. ochroleuca*, *U. intermedia*, *U. floridana*) or non-differentiated shoots (*U. vulgaris*, *U. australis*, *U. breinii*) under optimum conditions (20 °C, [CO₂] 0.20 mM, 400 μmol m⁻² s⁻¹ PAR). RD of bladders of six *Utricularia* species (5.1–8.6 mmol kg⁻¹_{FW} h⁻¹) was 75–200% greater, than that in leaves in carnivorous or photosynthetic shoots (1.7–6.1 mmol kg⁻¹_{FW} h⁻¹). Within individual species, this difference was statistically significant at $p < 0.002$ – 0.01 . However, PN in photosynthetic leaves/shoots (40–117 mmol kg⁻¹_{FW} h⁻¹) exceeded that in bladders (5.2–14.7 mmol kg⁻¹_{FW} h⁻¹) 7–10 times. RD of empty bladders of *U. ochroleuca* was exactly the same as that in bladders containing prey. Though *Utricularia* bladders are essential for uptake of growth limiting mineral nutrients N and P from prey as the main benefit of carnivory, the current results support previous work showing that bladder function requires greater metabolic (maintenance) cost and very low photosynthetic efficiency (great RD:PN ratio).

Key words: Aerobic respiration, photosynthetic rate, bladders, leaves, photosynthetic and carnivorous shoots, cost-benefit relationships, aquatic carnivorous plants.

Abbreviations:

RD: respiration rate

PN: net photosynthetic rate

Introduction

Carnivorous plants face the problem of what proportion of their biomass should be invested in carnivory and maintenance of traps (Givnish et al., 1984; Knight and Frost, 1991;

Knight, 1992; Friday, 1992; Méndez and Karlsson, 1999; Guisande et al., 2000; Richards, 2001; Englund and Harms, 2003; Guisande et al., 2004; Ellison and Farnsworth, 2005). Generally, a greater proportion of traps can increase total success in trapping prey and subsequent uptake of mineral and organic substances as a benefit of carnivory, while also presenting greater costs. These costs are based on production of traps, their reduced photosynthetic rates, and on their metabolic maintenance (Givnish et al., 1984; Knight, 1992; Méndez and Karlsson, 1999; Ellison and Farnsworth, 2005). Previous studies have also shown that the proportion of trap biomass, when compared to the the total biomass, is under ecological control (Knight and Frost, 1991; Bern, 1997; Richards, 2001; Ellison and Gotelli, 2002; Englund and Harms, 2003; Guisande et al., 2004).

Within the genus *Utricularia* (Lentibulariaceae), about 50 of the 214 recognised species are submerged or amphibious aquatics, which most often produce shoots with a relatively regular, modular structure (Taylor, 1989). Their shoots are either homogeneous, undifferentiated (i.e., forming only one type of shoot) and green, bearing both leaves and bladders (e.g., *U. australis*, *U. vulgaris*, *U. purpurea*), or heterogeneous, differentiated (i.e., forming two types of shoot) into green photosynthetic shoots with few to no bladders, and usually pale carnivorous shoots with abundant bladders and reduced leaves (e.g., *U. intermedia*, *U. ochroleuca*, *U. floridana*; Thor, 1988; Taylor, 1989). In aquatic *Utricularia* species with homogeneous shoots, about 10–55% of the total plant biomass (DW) is formed by bladders (Friday, 1992; Knight, 1992; Richards, 2001; Englund and Harms, 2003). The bladder is a hollow utricle, mostly two cells thick, filled with water, and usually 1–4 mm long (Sydenham and Findlay, 1975; Juniper et al., 1989). Bladders contain abundant bifid and quadrifid glands in their lumen, and on trapdoors that are also surrounded by trigger hairs and other appendages. The fluid in the bladders exhibits high phosphatase activity, secreted by quadrifid glands (Sirová et al., 2003; Laakkonen et al., 2006). After firing, the bladder pumps out ions and water from the lumen until the original compressed shape is reached in about 30 min (Sydenham and Findlay, 1975). Generally, bladders of aquatic *Utricularia* species are physiologically very active, though their chlorophyll content may be greatly reduced. Moreover, mutations of the mitochondrially encoded cytochrome *c* oxidase in *Utricularia*, which could result in faster reaction kinetics of this enzyme, may be an adaptation for greater respiratory capacity

associated with the high energetic demands of bladder traps (Jobson et al., 2004; Laakkonen et al., 2006).

The demanding physiological function of *Utricularia* bladders may translate into higher energetic demands and thereby an increased respiration rate (RD). Knight (1992) showed that the RD of bladders was 10% greater than the RD of the same leaves in *U. macrorhiza* (mean about 6.9 vs. 6.3 mmol O₂ kg⁻¹_{FW} h⁻¹). On the other hand, she also demonstrated markedly lower net photosynthetic rate (PN) in bladders as compared to leaves. In younger shoot segments of *U. macrorhiza* collected from various sites, PN ranged from 3.8 to 27 mmol CO₂ kg⁻¹_{FW} h⁻¹ in bladders, while it was 6.7–50 mmol kg⁻¹_{FW} h⁻¹ in leaves. Thus, the PN in bladders reached only 41–67% of that in leaves. PN expressed per unit chlorophyll content was comparable in younger leaves and bladders but decreased markedly in older, more pigmented bladders. This is in agreement with Friday (1989), who found increased ageing and disintegration of *U. vulgaris* bladders as compared to leaves. Similarly, in snapping traps of an aquatic carnivorous plant, *Aldrovanda vesiculosa*, grown under optimum photosynthetic conditions, PN of traps per unit FW reached only 52% of that of apical shoot segments without traps (Adamec, 1997a). Generally, all these results clearly demonstrate the greater energetic demand of traps as compared to leaves in aquatic carnivorous plants and, simultaneously, lower photosynthetic efficiency of traps. However, these metabolic costs may be counterbalanced partly by direct uptake of organic substances from prey, which can be ecologically important in aquatic carnivorous plants (for review see Adamec, 1997b). To determine the metabolic costs of carnivory in *Utricularia*, RD and PN were compared in bladders and leaf filaments or shoots of six aquatic *Utricularia* species with differentiated or undifferentiated shoots.

Materials and Methods

Measurements were performed in three *Utricularia* species with undifferentiated green, photosynthetic shoots: *U. vulgaris* L., *U. australis* R. Br., and *U. breinii* Heer ex K lliker, and in three species with differentiated shoots: *U. ochroleuca* R. Hartm., *U. intermedia* Hayne, and *U. floridana* Nash. Species were grown outdoors in plastic containers filled with dystrophic water, with *Carex* litter used as the main substrate (Adamec, 1997a). However, *U. floridana* (origin from N Florida, USA) was grown in a 20-l aquarium in a greenhouse. *U. breinii* originated from Lake Onega, N Russia, and the other species originated from sites in the Czech Republic. Adult plants with fully developed bladders were used for measurements from 13 June to 11 August 2004.

For *U. vulgaris* and *U. australis*, RD and PN measurements were made using slightly pigmented bladders and green leaves deprived of bladders from the 6th–10th adult leaf whorl. In *U. breinii*, green bladders and 2 cm long shoot segments without bladders were also prepared from the same leaf whorls. In the other three species, RD was measured in bladders from mostly colourless carnivorous shoots taken from about 1.5–5 cm from the shoot apex and in shoot segments cut from the same zone of the shoots. In these three species, both RD and PN were measured in photosynthetic shoot segments deprived of bladders about 1.5–3.0 cm from the shoot apex. Generally, RD and PN was measured using 15–22 freshly excised bladders (1.5–3.5 mm long), devoid of prey and air bubbles (FW 13–35 mg),

and in 1–2 composite leaves or 2–3 shoot segments without bladders (FW 13–66 mg). To prevent the suction of air during rinsing, bladders were stimulated to fire prior to excision.

Measurements of RD and PN were performed in a solution of 1.2 mM NaHCO₃ with 0.05 mM KCl (80–90% oxygen saturation) in a 5-ml stirred chamber (kept constant at 20.0 ± 0.1 °C), using a Clark-type oxygen sensor and a pen recorder (for details see Adamec, 1997a, 2005). Initial pH of the solution was 7.14 and [CO₂] was 0.20 mM. After RD had been measured in darkness for 15–20 min, a light was switched on (halogen reflector, 400 μmol m⁻² s⁻¹ PAR) and PN was measured for 15–20 min. To investigate the effect of prey digestion on RD, comparisons were made for empty bladders of *U. ochroleuca* and those having been fed living ostracods (see Sirova et al., 2003; Laakkonen et al., 2006) 22–24 h before RD measurement. At the time of measurement, fed bladders contained 1–4 prey items (usually 1–2), which were observed to be dead but not digested. For comparison, RD measurements were also taken for 20 potential prey (~1.0 mm long ostracods and ~1.6 mm long *Diaptomus* sp. [Crustacea]) found living in the culture containers. FW was then determined for all leaves and bladders (the luminal fluid was pressed out from bladders), while DW (80 °C) was estimated in pooled samples. All measurements were repeated six times for the same conditions. RD and PN are expressed in mmol kg⁻¹_{FW} h⁻¹.

Results

RD of bladders for the six aquatic *Utricularia* species (5.1–8.6 mmol kg⁻¹_{FW} h⁻¹) was 75–200% greater, on a FW basis, than that in leaves in carnivorous or photosynthetic shoots (1.7–6.1 mmol kg⁻¹_{FW} h⁻¹; Table 1). Within species, this difference was statistically significant ($p < 0.002–0.01$; two-tailed t -test). For DW measurements, this difference was 70–225% as leaves usually contained a slightly higher proportion of DW in FW (3.9–11%) than bladders (4.1–6.0%) within the same type of shoots. Mean RD of bladders for the three species with undifferentiated shoots (7.69 ± 0.46 mmol kg⁻¹_{FW} h⁻¹) was significantly higher ($p < 0.05$) than that in the other three species with differentiated shoots (5.67 ± 0.55 mmol kg⁻¹_{FW} h⁻¹). In *U. ochroleuca*, *U. intermedia*, and *U. floridana*, having both types of shoots, RD of bladders (5.1–6.8 mmol kg⁻¹_{FW} h⁻¹; Table 1) was about 1.9–3.0-times higher than RD of carnivorous shoots alone (1.7–3.5 mmol kg⁻¹_{FW} h⁻¹), but was about the same as that of photosynthetic shoots (4.2–6.1 mmol kg⁻¹_{FW} h⁻¹). In the undifferentiated photosynthetic shoots of *U. vulgaris*, *U. australis* and *U. breinii*, RD of bladders was about 1.9–2.3-times higher than that of leaves/shoots on a FW basis and 2.9–3.2-times higher on a DW basis. However, PN on a FW basis in photosynthetic leaves/shoots (40–117 mmol kg⁻¹_{FW} h⁻¹) exceeded that in bladders (5.2–14.7 mmol kg⁻¹_{FW} h⁻¹) by 7–10-times and, on DW basis, by 4–6-times (Table 1). In three species with differentiated shoots, RD on a FW basis of photosynthetic shoots exceeded that of carnivorous shoots by 1.2–3.5-times. PN of colourless bladders and carnivorous shoots in *U. ochroleuca* and *U. intermedia* was zero (data not shown). RD in the empty control bladders of *U. ochroleuca* (5.15 ± 0.42 mmol kg⁻¹_{FW} h⁻¹) was exactly the same as that in fed bladders (5.09 ± 0.47 mmol kg⁻¹_{FW} h⁻¹). RD of ostracods as potential prey was 9.3 nmol prey⁻¹ h⁻¹ and of *Diaptomus* sp., 8.5 nmol prey⁻¹ h⁻¹.

Table 1 RD and PN of bladders and leaves (or shoot segments) in green photosynthetic or colourless carnivorous shoots in six aquatic *Utricularia* species, in $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; DW as % of FW is also shown. Mean \pm SE interval is always shown; $n = 6$. At the bottom of the table, mean values per DW in $\text{mmol kg}^{-1}_{\text{DW}} \text{h}^{-1}$ and the range of values are shown for 3–6 species

| Species | Carnivorous shoots | | | | Photosynthetic shoots | | | | | |
|----------------------|--------------------|-----------------|--------|-----------------|-----------------------|-----------------|-----------------|--------|-----------------|-----------------|
| | Traps | | Leaves | | Traps | | | Leaves | | |
| | DW | RD | DW | RD | DW | RD | PN | DW | RD | PN |
| <i>U. vulgaris</i> | – | – | – | – | 5.57 | 7.49 \pm 0.21 | 14.7 \pm 0.64 | 8.84 | 3.94 \pm 0.36 | 96.9 \pm 5.2 |
| <i>U. australis</i> | – | – | – | – | 5.97 | 8.56 \pm 0.35 | 9.03 \pm 1.22 | 11.0 | 4.86 \pm 0.23 | 86.5 \pm 10.1 |
| <i>U. bremii</i> | – | – | – | – | 4.69 | 7.02 \pm 0.45 | 5.24 \pm 0.51 | 6.01 | 3.07 \pm 0.36 | 40.0 \pm 6.6 |
| <i>U. ochroleuca</i> | 4.10 | 5.15 \pm 0.42 | 4.46 | 1.73 \pm 0.17 | – | – | – | 6.47 | 6.06 \pm 0.40 | 111 \pm 5.6 |
| <i>U. intermedia</i> | 4.42 | 6.77 \pm 0.57 | 3.90 | 3.48 \pm 0.34 | – | – | – | 6.29 | 4.24 \pm 0.56 | 117 \pm 13.1 |
| <i>U. floridana</i> | 5.68 | 5.09 \pm 0.33 | 8.18 | 2.65 \pm 0.29 | – | – | – | 10.3 | 5.47 \pm 0.70 | 66.4 \pm 3.9 |
| Mean per DW | – | 123 | – | 53.5 | – | 142 | 176 | – | 59.0 | 1 128 |
| Range per DW | – | 90–153 | – | 32–89 | – | 134–150 | 112–264 | – | 44–94 | 645–1 860 |

Discussion

RD values, both on a FW and DW basis, determined for photosynthetic leaves/shoots in six aquatic *Utricularia* species (3.1–6.1 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$ or 44–94 $\text{mmol kg}^{-1}_{\text{DW}} \text{h}^{-1}$; Table 1) are similar to or somewhat lower than those published for numerous species of aquatic plants. For leaves or shoots of aquatic non-carnivorous plants, reported RD values at 20°C are usually within 3–30 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$ or 30–300 $\text{mmol kg}^{-1}_{\text{DW}} \text{h}^{-1}$ (e.g., Maberly, 1985; Madsen and Sand-Jensen, 1987; Pokorný and Ondok, 1991; Kahara and Vermaat, 2003). Moreover, the values of both RD and PN found in photosynthetic leaves/shoots in this study are similar to those measured for apical shoot segments of *U. vulgaris* in the field (RD, 5.6 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; PN, 25–38 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; Draxler, 1973) and in the laboratory (RD, 1.9–5.6 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; Pokorný and Ondok (1991), or in leaves without bladders in *U. macrorhiza* (RD, 3.9–6.3 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; PN, 6.7–50 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; Knight, 1992). The current results show that photosynthetic efficiency of leaves/shoots was very high in all six aquatic *Utricularia* species (Table 1; PN, 40–117 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$). Although PN was measured under favourable conditions in this study (400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, 0.20 mM CO_2), the $[\text{CO}_2]$ applied was below the limit for maximum PN. If the maximum PN for many aquatic plant species usually reaches only 30–110 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$ (for review see Pokorný and Ondok, 1991), it indicates that PN (on FW basis) found for photosynthetic leaves/shoots in aquatic *Utricularia* approach an absolute upper limit of PN reported for other aquatic plants. As PN of the aquatic carnivorous plant *Aldrovanda vesiculosa*, which frequently co-occurs with the *Utricularia* species used in this study, is also very high under similar photosynthetic conditions (ca. 70–90 $\text{mmol kg}^{-1}_{\text{FW}} \text{h}^{-1}$; Adamec, 1997a), it is reasonable to conclude that very high PN of photosynthetic shoots is a typical characteristic for aquatic carnivorous plants with very rapid growth and may be a prerequisite for this rapid growth (see Adamec, 1997a). On the other hand, lower RD in colourless carnivorous shoots, as compared to photosynthetic shoots (Table 1), reflects the fact that the former organs are greatly reduced and that their role is confined to bearing bladders and transporting nutrients.

In summary, the current results (Table 1) demonstrate that, within the same shoot bearing bladders, RD of bladders (both on a FW and DW basis) is about 1.7–3.3-times higher than that of leaves/shoots. However, Knight (1992) found that the RD of bladders in *U. macrorhiza* was, on average, only about 10% higher, as compared to leaves but she did not state either the experimental temperature or $[\text{CO}_2]$, in the case of her photosynthetic measurements. The relatively high RD observed for *Utricularia* bladders is probably associated with their demanding physiological function, i.e., relating to ion and water pumping (Sydenham and Findlay, 1975) and digestion of prey (Sirová et al., 2003; Laakkonen et al., 2006). At an anatomical level, this physiological activity is associated with a high density of several kinds of glands or hairs (Juniper et al., 1989). As demonstrated by Sydenham and Findlay (1975), ion and water pumping during the resetting of *Utricularia* bladders is a process requiring high amounts of metabolic energy derived from aerobic respiration, and is prevented by respiration inhibitors or low temperatures. In the present study, traps were in a post-firing state and were therefore probably pumping water. Thus, it is possible to assume that their RD in this state was much higher than that in their unfired resting state.

PN in *U. australis* bladders has been shown to decrease with age (Adamec, 1995), despite a constant RD in the same bladders. However, PN of bladders in *U. macrorhiza*, having been measured presumably at low $[\text{CO}_2]$ in collected natural lake waters, was as much as 41–67% of that of leaves (Knight, 1992), while it reached only 10–15% of that of leaves in three *Utricularia* species in the present study at optimum $[\text{CO}_2]$ 0.20 mM (Table 1). This discrepancy suggests a markedly different photosynthetic CO_2 affinity for bladders and leaves/shoots: it may be that the CO_2 affinity of bladders is much greater than that of leaves/shoots.

It is not clear to what extent gas exchange (RD and PN) on the level of intact bladders is influenced by the occurrence of commensal organisms. Algal cells can colonize the lumen of bladders in aquatic *Utricularia* species (e.g., Richards, 2001; Sirová et al., 2003; Laakkonen et al., 2006) and numbers of *Euglena* and bacterial cells usually increase with the ageing of bladders (Sirová, unpubl.). Thus, the respiration or photosynthetic activity of this commensal community should influence the gas

exchange of bladders alone (Richards, 2001). However, the extent of such an influence is not known. It is possible that any gas exchange within the luminal fluid was gradually transferred to the stirred medium outside the bladders. However, work by Adamec (1995) on *U. australis* bladders with or without living prey did not support this assumption. In the present study, RD of *U. ochroleuca* bladders with or without dead prey was strictly the same, and RD of potential zooplankton prey of about 9 nmol prey⁻¹ h⁻¹ was measured. This value is comparable with those stated in literature on zooplankton respiration (within 1.2–50 nmol animal⁻¹ h⁻¹; Jørgensen, 1979, pp. 250–252) and corresponds to the mean RD of one bladder found in six *Utricularia* species in this study (10.1, range 3.4–26.5 nmol bladder⁻¹ h⁻¹). Thus, RD of a bladder with one living prey should theoretically double as compared to the same empty bladder. A direct measurement of [O₂] in the fluid inside empty bladders using an O₂ microsensor has recently been shown to be zero [O₂] (Adamec, unpubl.).

To be ecologically advantageous, the benefit of bladders should at least equal or exceed their costs (sensu Givnish et al., 1984). Investment in bladders and the associated high maintenance and/or metabolic costs (high RD:PN ratio) should result in shortages of organic substances (sugars) and, thus, a decrease in growth (Knight, 1992). Generally, as in other submerged aquatic plants, *Utricularia*'s PN depends strongly on CO₂ and light availability: key factors that are often limited by prevailing environmental conditions (Pokorný and Ondok, 1991). As shown by Adamec (1999), prey capture in aquatic *Aldrovanda* could partly compensate for the strict CO₂ limitation in water, and the same could occur in aquatic carnivorous plants growing in deep shade. This feature of the cost-benefit relationships in carnivorous plants has been ignored in models (Givnish et al., 1984; Knight, 1992). Due to very efficient re-utilization of N and P from senescent shoots of aquatic carnivorous plants (Adamec, 2000; Adamec, unpubl.), the loss of N and P from old shoots (including traps) may be very low, while that of organic carbon may not (Adamec, 2000). Thus, the main metabolic cost of carnivory in aquatic carnivorous plants is probably the expenditure on organic carbon for trap production and maintenance costs (greater RD, enzyme production) for trap functioning.

Concerning the benefits of carnivory in aquatic carnivorous plants, the direct uptake of organic carbon from prey may be crucial under strong CO₂ or light limitation, and marginal under optimum conditions. An increase in PN as a result of carnivory, as suggested by Givnish et al. (1984), has never been verified in aquatic carnivorous plants. However, this theory is contradicted by the lower tissue N and P content found in *Aldrovanda* shoots capturing prey (Adamec, 2000). Thus, the main metabolic benefit derived by catching prey in aquatic carnivorous plants is the uptake of the growth-limiting mineral nutrients, N and P (Friday and Quarmby, 1994).

Acknowledgements

This study was supported partly by the Research Programmes of the Academy of Sciences of the Czech Republic (Nos. AV0Z6005908, AV0Z60050516, and KSK6005114). Sincere thanks are due to Prof. Douglas W. Darnowski for correcting the English. Thanks are also due to an anonymous reviewer for correcting the manuscript and for valuable comments.

References

- Adamec, L. (1995) Oxygen budget in the traps of *Utricularia australis*. Carnivorous Plant Newsletter 24, 42–45.
- Adamec, L. (1997a) Photosynthetic characteristics of the aquatic carnivorous plant *Aldrovanda vesiculosa*. Aquatic Botany 59, 297–306.
- Adamec, L. (1997b) Mineral nutrition of carnivorous plants: a review. Botanical Review 63, 273–299.
- Adamec, L. (1999) Seasonal growth dynamics and overwintering of the aquatic carnivorous plant *Aldrovanda vesiculosa* at experimental field sites. Folia Geobotanica 34, 287–297.
- Adamec, L. (2000) Rootless aquatic plant *Aldrovanda vesiculosa*: physiological polarity, mineral nutrition, and importance of carnivory. Biologia Plantarum 43, 113–119.
- Adamec, L. (2005) Ecophysiological characterization of carnivorous plant roots: oxygen fluxes, respiration, and water exudation. Biologia Plantarum 49, 247–255.
- Bern, A. L. (1997) Studies on nitrogen and phosphorus uptake by the carnivorous bladderwort *Utricularia foliosa* L. in South Florida wetlands. MSc Thesis, Florida International University, Miami, p. 92.
- Draxler, G. (1973) Gaswechselformung an *Utricularia vulgaris*. In Ökosystemforschung (Ellenberg, H., ed.), Berlin, Heidelberg, New York: Springer-Verlag, pp. 103–107.
- Ellison, A. M. and Farnsworth, E. J. (2005) The cost of carnivory for *Darlingtonia californica* (Sarraceniaceae): evidence from relationships among leaf traits. American Journal of Botany 92, 1085–1093.
- Ellison, A. M. and Gotelli, N. J. (2002) Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*. Proceedings of the National Academy of Sciences of the USA 99, 4409–4412.
- Englund, G. and Harms, S. (2003) Effects of light and microcrustacean prey on growth and investment in carnivory in *Utricularia vulgaris*. Freshwater Biology 48, 786–794.
- Friday, L. E. (1989) Rapid turnover of traps in *Utricularia vulgaris* L. Oecologia 80, 272–277.
- Friday, L. E. (1992) Measuring investment in carnivory: seasonal and individual variation in trap number and biomass in *Utricularia vulgaris* L. New Phytologist 121, 439–445.
- Friday, L. E. and Quarmby, C. (1994) Uptake and translocation of prey-derived ¹⁵N and ³²P in *Utricularia vulgaris* L. New Phytologist 126, 273–281.
- 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. The American Naturalist 124, 479–497.
- Guisande, C., Andrade, C., Granado-Lorencio, C., Duque, S. R., and Núñez-Avellaneda, M. (2000) Effects of zooplankton and conductivity on tropical *Utricularia foliosa* investment in carnivory. Aquatic Ecology 34, 137–142.
- Guisande, C., Aranguren, N., Andrade-Sossa, C., Prat, N., Granado-Lorencio, C., Barrios, M. L., Bolívar, A., Núñez-Avellaneda, M., and Duque, S. R. (2004) Relative balance of the cost and benefit associated with carnivory in the tropical *Utricularia foliosa*. Aquatic Botany 80, 271–282.
- Jobson, R. W., Nielsen, R., Laakkonen, L., Wikström M., and Albert, V. A. (2004) Adaptive evolution of cytochrome c oxidase: infrastructure for a carnivorous plant radiation. Proceedings of the National Academy of Sciences of the USA 101, 18064–18068.
- Jørgensen, S. E. (ed.) (1979) Handbook of Environmental Data and Ecological Parameters. Copenhagen: ISEM.
- Juniper, B. E., Robins, R. J., and Joel, D. M. (1989) The Carnivorous Plants. London: Academic Press Ltd.

- Kahara, S. N. and Vermaat, J. E. (2003) The effect of alkalinity on photosynthesis-light curves and inorganic carbon extraction capacity of freshwater macrophytes. *Aquatic Botany* 75, 217–227.
- Knight, S. E. (1992) Costs of carnivory in the common bladderwort, *Utricularia macrorhiza*. *Oecologia* 89, 348–355.
- Knight, S. E. and Frost, T. M. (1991) Bladder control in *Utricularia macrorhiza*: lake-specific variation in plant investment in carnivory. *Ecology* 72, 728–734.
- Laakkonen, L., Jobson, R. W., and Albert, V. A. (2006) A new model for the evolution of carnivory in the bladderwort plant (*Utricularia*): adaptive changes in cytochrome *c* oxidase (COX) provide respiratory power. *Plant Biology* 8, 758–764.
- Maberly, S. C. (1985) Photosynthesis by *Fontinalis antipyretica*. I. Interaction between photon irradiance, concentration of carbon dioxide and temperature. *New Phytologist* 100, 127–140.
- Madsen, T. V. and Sand-Jensen, K. (1987) Photosynthetic capacity, bicarbonate affinity and growth of *Elodea canadensis* exposed to different concentrations of inorganic carbon. *Oikos* 50, 176–182.
- 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.
- Pokorný, J. and Ondok, J. P. (1991) *Macrophyte Photosynthesis and Aquatic Environment*. Prague: Academia.
- Richards, J. H. (2001) Bladder function in *Utricularia purpurea* (Lentibulariaceae): is carnivory important? *American Journal of Botany* 88, 170–176.
- Sirová, D., Adamec, L., and Vrba, J. (2003) Enzymatic activities in traps of four aquatic species of the carnivorous genus *Utricularia*. *New Phytologist* 159, 669–675.
- Sydenham, P. H. and Findlay, G. P. (1975) Transport of solutes and water by resetting bladders of *Utricularia*. *Australian Journal of Plant Physiology* 2, 335–351.
- Taylor, P. (1989) *The Genus Utricularia – A Taxonomic Monograph*. Kew Bulletin Additional Series XIV. London: HMSO.
- Thor, G. (1988) The genus *Utricularia* in the Nordic countries, with special emphasis on *U. stygia* and *U. ochroleuca*. *Nordic Journal of Botany* 8, 213–225.

L. Adamec

Institute of Botany of the Academy of Sciences
of the Czech Republic
Section of Plant Ecology
Dukelská 135
379 82 Třeboň
Czech Republic

E-mail: adamec@butbn.cas.cz

Guest Editor: S. Porembski