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A comparison of photosynthetic and respiration rates in six aquatic carnivorous *Utricularia* species differing in morphology

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ABSTRACT

The rootless carnivorous plant genus *Utricularia* includes about 50 submerged aquatic or amphibious species. They usually grow in standing humic waters rich in CO_2 and are known to be strict photosynthetic CO_2 users. In this study, oxygen-based net photosynthetic (P_N) and dark respiration (RD) rates were measured in trap-free leaves of shoot segments from different aged sections of *Utricularia australis* and *U. vulgaris* and the photosynthetic CO_2 affinity was estimated in adult shoot segments. P_N and RD were compared in adult trap-free leaves in three species with linear shoots (*U. australis*, *U. vulgaris*, *U. purpurea*) and four populations of three rhizomatous/rosette species (*U. dichotoma*, *U. resupinata*, *U. volubilis*) under standard conditions (25 °C, 400 μmol m^{-2} s^{-1} PAR, 0.25 mM CO_2). In *U. australis* and *U. vulgaris* shoots, dry-weight based RD was highest in the youngest segments (174–184 mmol kg^{-1} h^{-1}) and gradually declined down to the progressively senescent segments (43–58 mmol kg^{-1} h^{-1}). In *U. vulgaris*, P_N increased from the shoot apex up to the 25th leaf nodes, while it was highest in the 3rd leaf nodes and decreased significantly down to the shoot bases in *U. australis*. Chlorophyll-based P_N rates along the shoots in both species were almost constant. Dry-weight based P_{Nmax} in *U. australis* was significantly greater than that in *U. vulgaris* (1634 ± 69 *vs.* 1077 ± 56 mmol kg^{-1} h^{-1}), while the CO_2 affinity (K_m) was opposite – 48 ± 10 *vs.* 21 ± 2 μM. Although the mean photosynthetic parameters for individual species usually differed considerably from each other between both subgroups and supported the view that the linear-shoot species have higher P_N rates than the other subgroup (732–1592 *vs.* 155–687 mmol kg^{-1}_{DW} h^{-1}), statistically significant difference between both subgroups was only found for chlorophyll *a*-based P_N. The differences in photosynthetic characteristics found between both morphological subgroups of *Utricularia* presumably reflect the differences in growth rates: the linear-shoot species with high P_N rates are known to grow very rapidly while those from the other subgroup with lower P_N grow slowly. The high P_N rates of the linear-shoot *Utricularia* species approach the upper limit of P_N reported for other aquatic non-carnivorous plants and are a prerequisite for their very rapid growth. Therefore, to attain such high P_N rates and rapid growth, these species demand high [CO_2] >0.15 mM in their habitats.

1. Introduction

The rootless carnivorous plant genus *Utricularia* L. (bladderwort, Lentibulariaceae) includes about 220 species which are subdivided into 35 generic sections (Taylor, 1989; Jobson et al., 2003). The majority of the species are wetland, terrestrial ones but about 50 are submerged aquatic or amphibious species belonging mainly to the *Utricularia*, *Pleiochasia*, *Lecticula*, *Avesicaria*, *Avesicarioides* and *Vesiculina* sections. The typical aquatic or amphibious species from the *Utricularia* and *Vesiculina* sections have a linear, modular and fairly regular shoot structure, consisting of nodes with dissected leaves reminiscent of whorls and thin cylindrical internodes (Friday, 1989; Taylor, 1989; Sattler and Rutishauser, 1990; Rutishauser, 1993). The aquatic or amphibious species from the other sections have rhizomatous shoot structures with flat, lanceolate or narrow cylindrical leaves growing in nodes (rarely as rosettes) from short filiform stems (Taylor, 1989). In this way, they are reminiscent of the terrestrial *Utricularia* species. In this paper, I shall use the term "leaf" for the dissected or flat organ with the prevailing photosynthetic function, growing in leaf nodes (or untrue whorls) in a plane perpendicular to the "stem" (stolon).

Aquatic *Utricularia* species usually grow in oligo-mesotrophic, humic (dystrophic) waters with a high concentration of free CO_2 commonly exceeding 0.1–0.2 mM and all aquatic species tested so far use only CO_2 for photosynthesis (Moeller, 1978; Adamec, 1997a, 2007, 2008a,b, 2009, 2011a, 2012; Adamec and Kovářová, 2006; Pagano and Titus, 2007; Adamec and Pásek, 2009). Generally, in 12

Abbreviations: DR, dark respiration rate; P_N, net photosynthetic rate; P_{Nmax}, maximum net photosynthetic rate; chl. *a*, chlorophyll *a*; DW, dry weight; FW, fresh weight; K_m, half-saturation constant.

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aquatic *Utricularia* species with linear shoots (sections *Utricularia* and *Vesiculina*) growing in the field or semi-natural cultures, the CO_2 compensation point of photosynthesis fell within the range 1.2–13.6 μM (mean 3–5 μM) and was the same (mean 5.2 μM, range 2.5–8.8 μM) for these species growing *in vitro* (Moeller, 1978; Adamec, 1997a, 2008b, 2009, 2011a; Adamec and Kovářová, 2006; Pagano and Titus, 2007; Adamec and Pásek, 2009). Similar values of 1.5–10 μM are reported in many aquatic non-carnivorous plants (Maberly and Spence, 1983). All results show clearly that the CO_2 compensation point in aquatic *Utricularia* species is rather variable and adaptable.

The very rapid growth of most of aquatic *Utricularia* species with linear shoots, even in oligotrophic habitats, is associated with both a high apical shoot growth rate of 2–4 leaf nodes per day and frequent vegetative propagation by branching (Friday, 1989; Adamec, 2008b, 2009, 2010, 2011a,b, 2012; Ellison and Adamec, 2011). The rapid growth of aquatic *Utricularia* species requires several ecophysiological adaptations: high photosynthetic rate of shoots, prey capture, efficient nutrient re-utilization from senescent shoots and high nutrient uptake affinity from the ambient water (Richards, 2001; Adamec, 2008a,b, 2009, 2011a, 2012). Aquatic *Utricularia* species in their habitats may also face shortage of light (only 2–20% of incident PAR irradiance) and sometimes also free CO_2 (<0.02–0.05 mM; Adamec, 1997a, 2008a, 2009, 2012). Therefore, their net photosynthetic rate (P_N) in standing waters, like that of other submerged plants generally, is limited by unfavorable physical and chemical factors. They include a low diffusion rate of CO_2, variable $[CO_2]$ strongly dependent on pH and total alkalinity (TA) and a shortage of light (*e.g.*, Maberly and Madsen, 2002). Even though available data are limited, the maximum P_N (P_{Nmax}) of aquatic *Utricularia* with linear shoots (eight species, 40–148 mmol O_2 kg^{-1} (fresh weight) h^{-1} or 650–1860 mmol O_2 kg^{-1} (dry weight) h^{-1}) is usually comparable with the highest values of P_{Nmax} found in aquatic non-carnivorous species (*ca.* 300–1100 mmol O_2 $kg^{-1}{}_{DW}$ h^{-1}) or higher (*cf.* Moeller, 1978; Pokorný and Ondok, 1991; Madsen et al., 1993; Maberly and Madsen, 2002; Kahara and Vermaat, 2003; Adamec, 2006, 2008b, 2011a,c; Ellison and Adamec, 2011). Nevertheless, the P_N values in aquatic *Utricularia* shoots/leaves measured under natural habitat conditions or in natural water may be considerably lower (*U. vulgaris*: 120–380 mmol $kg^{-1}{}_{DW}$ h^{-1}, Draxler, 1973; *U. macrorhiza*: 70–500 mmol $kg^{-1}{}_{DW}$ h^{-1}, Knight, 1992).

Traps of aquatic *Utricularia* species are physiologically very active organs having high aerobic dark respiration rates (RD) and large photosynthetic and energetic (maintenance) costs (Knight, 1992; Adamec, 2006, 2011a). In six species, trap RD (90–153 mmol $kg^{-1}{}_{DW}$ h^{-1}) was 1.7–3.0 times greater than that in leaves on carnivorous or photosynthetic shoots, while trap P_{Nmax} (112–264 mmol $kg^{-1}{}_{DW}$ h^{-1}) was 7–10 times lower than that in photosynthetic leaves (Adamec, 2006). This very high RD:P_{Nmax} ratio in traps (50–140%) is not found in leaves (only 3.6–8.2%) and means that there are high maintenance costs but very low photosynthetic efficiency in traps. In spite of a steep physiological polarity along the shoots of aquatic *Utricularia* in tissue N and P content (Adamec, 2008a; and carbohydrate content in ecologically similar *Aldrovanda vesiculosa*; Adamec, 2000), the measurements of P_N and RD in *U. macrorhiza* shoot segments of different age from the apex to the senescent, trap-free segments showed a virtually constant P_N (DW- or chlorophyll-based) along the whole shoot (Knight, 1992).

In conclusion, very high P_N of shoots is typical for aquatic *Utricularia* species with linear shoots and rapid growth. It is also a prerequisite for this rapid growth as the rapid decay of senescent shoot segments causes a great and permanent loss of structural and non-structural carbohydrates together with the high maintenance costs of traps (Adamec, 2011a). However, photosynthetic and growth traits of aquatic (amphibious) rhizomatous *Utricularia* species from the *Pleiochasia* and *Lecticula* sections have never been studied. The aim of this study has been to compare P_N values (DW-, FW-, and chlorophyll *a*-based) in three species of aquatic *Utricularia* with homogeneous, linear shoots (*U. vulgaris*, *U. australis*, *U. purpurea*) with those in three aquatic/amphibious species with rhizomatous or rosette-shaped shoots (*U. dichotoma*, *U. resupinata*, *U. volubilis*). As opposed to rapid growth of the species from the first group (Adamec, 2011a), those from the second group grow rather slowly in cultures (Adamec, unpubl.). It is thus possible to test whether photosynthetic traits relate to growth traits within aquatic *Utricularia* species. For two species from the first group (*U. vulgaris*, *U. australis*), P_N and RD were measured as standard in trap-free leaves from the apex down to the senescent shoot basis, to estimate a photosynthetic shoot polarity and CO_2 uptake affinity (K_m) was estimated in mature shoot segments.

2. Materials and methods

2.1. Plant material

Measurements were performed in three aquatic *Utricularia* species with homogeneous, linear shoots (*U. vulgaris* L., *U. australis* R.Br. /both collected from the Czech Republic/ – section *Utricularia*, and *U. purpurea* Walt. /from Florida, USA/ – section *Vesiculina*) and in three aquatic/amphibious species with rhizomatous or rosette shoots (two distinct populations of *U. dichotoma* Labill. /collected from Newcastle, N.S.W., Australia, with robust leaves, and from Katoomba, N.S.W., Australia, with normal-sized leaves/, *U. volubilis* R.Br./rosette, from W.A., Australia/ – all of them section *Pleiochasia*, and *U. resupinata* Greene *ex* Bigelow /from Nicaragua/ – section *Lecticula*). *U. vulgaris* and *U. australis* were grown outdoors in two plastic containers (area 0.6–3 m^2, 200–2000 L) in which the water chemistry, light and temperature conditions were similar to natural conditions. *U. purpurea* and *U. volubilis* were grown in a naturally lit greenhouse in a 300 L plastic container. The plants in these cultures were grown in tap water and a litter of robust *Carex* species was used as a substrate. The pH of the cultivation media was 6.9–7.5, dissolved oxygen concentration ranged from 0.15 to 0.30 mM, total alkalinity from 0.6 to 0.9 mequiv. L^{-1} and the free CO_2 concentration was 0.08–0.20 mM (for all details, see Adamec, 1997b, 2008b). The water in these cultures was considered oligotrophic (in μg L^{-1}: NO_3^--N, 0–12; NH_4^+-N, 8–16; PO_4-P, 19–27) and humic. Both populations of *U. dichotoma* and *U. resupinata* were grown in the greenhouse as submerged plants in 3 L aquaria floating in the 300 L container and a mixture of peat with sand was used as the substrate. The pH of the cultivation media was 6.1–6.2. All outdoor and greenhouse cultures were partly shaded. Small zooplankton species were added weekly to most cultures to promote plant growth. Adult plants of all species were used for measurements from 18 July to 8 August.

2.2. Gas exchange measurements

For *U. vulgaris* and *U. australis*, RD and P_N were measured on 2–4 freshly collected leaves (from 1 to 2 plants) of five different ages (shoot segments) which were thoroughly stripped of mature traps. *U. vulgaris* plants were 55–70 cm long with 72–98 adult leaf nodes and *U. australis* were 60–80 cm long with 76–88 leaf nodes. They were very young, subapical leaves 5–8 mm long positioned just below the shoot apex bearing immature traps 0.5–1 mm large and adult leaves (without traps) from the 3rd, 10th, 25th and 50–60th adult leaf nodes. The leaves from the 3rd, 10th and 25th leaf nodes bore mature functional traps, while the leaves from the 50th to 60th leaf nodes were partly senescent and usually trap-free. Except for the youngest subapical leaves, all traps on all older leaves were thoroughly removed using two pairs of forceps as the trap P_N is very low and the trap proportion to the shoot biomass may be variable along shoots (Friday, 1989; Adamec, 2006, 2008a). In these two species, the dependence of P_N on $[CO_2]$ was also measured in trap-free leaves from the 10th leaf nodes. The measured leaves were exposed successively to new media with 0.02, 0.05, 0.10, 0.25, 0.50 and 1.00 mM free CO_2 prepared by bubbling with CO_2 according to pH (Helder, 1988). To compare photosynthetic traits in various species, RD and P_N were measured in 3–4 leaves (with traps removed) from the 2nd adult leaf nodes of *U. purpurea*, 2–7 mature leaves of *U. dichotoma* (of both populations), 14–18 mature leaves of *U. resupinata* (3–6 cm long), and 8–12 mature leaves (6–15 cm long) of *U. volubilis*. The leaves of *U. resupinata* were cut into 1.5–2 cm long segments. The large air spaces in these were filled with the experimental solution using negative pressure in a syringe before the measurements. After this treatment, only a minor part of fine intercellulars was not filled by water. *U. volubilis* leaves were cut to 2–3 cm segments. FW of measured leaves of all species was 5–46 mg.

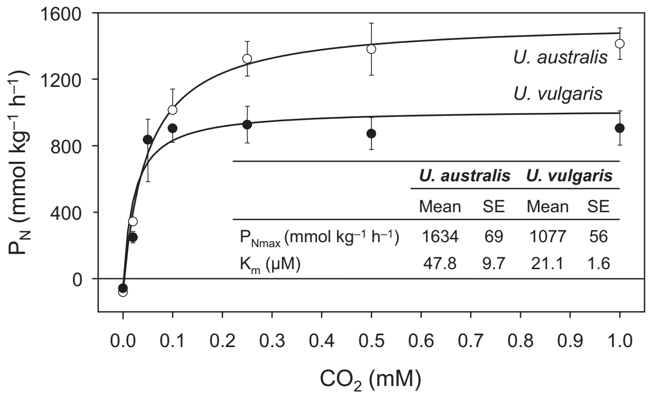
Generally for all measurements, RD and P_N were measured in a solution of 1 mM $NaHCO_3$ with 0.1 mM KCl (*ca.* 90% O_2 saturation) in a 4.2- or 5.3-mL stirred chamber kept at 25.0 ± 0.1 °C. A Clark-type oxygen sensor and a pen recorder (for details see Adamec, 1997b, 2006) was used. Free $[CO_2]$ of 0.25 mM was used as standard where possible. This $[CO_2]$ was chosen as it has been used commonly in many similar studies (*cf.* Adamec, 1997b, 2006, 2008b, 2011c), it often occurs in natural habitats and presumably approaches that for achieving the P_{Nmax}. After RD had been measured in darkness for 12–15 min, a light was switched on (halogen reflector, 400 μmol m^{-2} s^{-1} PAR) and P_N was measured for 12–15 min. FW was then estimated for all measured leaves and chlorophyll *a* content was determined (Pechar, 1987) after the measurements of shoot polarity in *U. vulgaris* and *U. australis* and the comparative interspecific measurements. DW (80 °C) was estimated in parallel foliar samples. All measurements were repeated six times under the same conditions using material from different plants. RD and P_N are expressed in mmol $kg^{-1}{}_{DW}$ h^{-1} as standard.

2.3. Statistical treatment

The plot of P_N against $[CO_2]$ for single measurements was fitted by a nonlinear regression. The Michaelis-Menten model, modified to include DR, was used to fit the data to obtain K_m and P_{Nmax} parameters. The statistically significant differences in these parameters between *U. vulgaris* and *U. australis* were tested using a two-tailed *t*-test. In these species, 1-way ANOVA was used to find significant differences in RD and photosynthetic parameters between the neighboring shoot segments to prove the physiological polarity along the shoots. Significant differences in RD and photosynthetic parameters within the three species with linear shoots, as well as within the three species with rhizomatous shoots, were found using 1-way ANOVA. Two-way ANOVA was used to find significant differences between these two morphological *Utricularia* groups. Species, nested within a morphological group, were chosen as a factor with random effect. Significant correlations between RD and P_N were sought using linear regressions of the data. All statistical analyses were performed using STATISTICA v. 10 (StatSoft, USA). Throughout the paper, means ± 1 SE are shown.

3. Results

In *U. australis* and *U. vulgaris* trap-free leaves from the 10th adult leaf nodes, the plot of P_N against $[CO_2]$, modified to include DR, corresponded to the Michaelis–Menten model (Fig. 1; coefficient of determination for pooled data 0.92 and 0.85, respectively).



	U. australis		U. vulgaris	
	Mean	SE	Mean	SE
P_{Nmax} (mmol kg^{-1} h^{-1})	1634	69	1077	56
K_m (μM)	47.8	9.7	21.1	1.6

Fig. 1. P_N rates (DW-based) in trap-free leaves from the 10th adult leaf nodes of *U. australis* and *U. vulgaris* as dependent on CO_2 concentration. Pooled data were fitted by the Michaelis–Menten model including RD. The negative values at zero $[CO_2]$ denote RD. Means ± SE intervals are shown; $n = 6$. P_{Nmax}, calculated maximum net photosynthetic rate; K_m, half-saturation constant.

P_{Nmax} in *U. australis* was significantly greater ($p < 0.002$, $t = 5.24$) than that in *U. vulgaris* (1634 ± 69 *vs.* 1077 ± 56 mmol $kg^{-1}{}_{DW}$ h^{-1}), while the CO_2 affinity (K_m) was opposite: 48 ± 10 *vs.* 21 ± 2 μM ($p < 0.05$, $t = 2.72$). In both species, P_{Nmax} was attained at only about 0.25 mM CO_2. As it follows from the comparison of photosynthetic traits in trap-free leaves along the shoots, chlorophyll *a* content in all tested shoot segments in *U. australis* exceeded that in *U. vulgaris* by 1.8–2.7 times (Table 1). RD values were comparable in both species. In both species, RD was the highest in the youngest, subapical segment and gradually declined down to the progressively senescent segments. Yet RD in the old, trap-free shoot segments (50–60th leaf nodes) was the same as that in the 25th leaf nodes with still fully functional leaves and traps. The course of DW-based P_N along the shoots was different in both species: in *U. vulgaris*, P_N increased from the shoot apex up to the 25th leaf node, while it was the highest in the 3rd leaf nodes and decreased significantly down to the shoot bases in *U. australis*. The same pattern held also for FW-based P_N (data not shown). The course of chlorophyll-based P_N along the shoots was similar in both species, more or less constant along the adult shoot segments, although there was a highly significant decline of chlorophyll *a* content in the senescent segments. The values were similar in both species. The RD:P_N ratio as a measure of photosynthetic efficiency was significantly ($p < 0.01$, $F_{4,25} > 15.2$) the highest in the subapical leaves and declined to the 25th leaf nodes in both species but the photosynthetic efficiency was significantly better in *U. australis* (Table 1).

From the comparison of photosynthetic traits between three aquatic *Utricularia* species with linear shoots, *U. australis* had significantly ($p < 0.05$, $F_{2,11} > 45.9$) the highest chl. *a* content and the DW- and FW-based P_N rates, while the chl. *a*-based P_N rates were comparable (Table 2). This species also had the highest photosynthetic efficiency. Generally, within this subgroup of three species, P_N ranged between 732–1592 mmol $kg^{-1}{}_{DW}$ h^{-1}, 61–145 mmol $kg^{-1}{}_{FW}$ h^{-1}, or 194–235 mmol g^{-1} chl. *a* h^{-1}. Within the subgroup of three aquatic *Utricularia* species with rhizomatous or rosette shoots, chl. *a* content in leaves ranged between 4.8–13.0 g $kg^{-1}{}_{DW}$ and was the highest in robust *U. dichotoma* from Newcastle, N.S.W. (Table 2). Within this subgroup, P_N ranged between 155–687 mmol $kg^{-1}{}_{DW}$ h^{-1}, 5.7–63 mmol $kg^{-1}{}_{FW}$ h^{-1}, or 28–79 mmol g^{-1} chl. *a* h^{-1}. The species with the lowest P_N rates and efficiency were *U. resupinata* and the robust *U. dichotoma* (Newcastle), while the rosette species *U. volubilis* and rhizomatous *U. dichotoma* from Katoomba, N.S.W., had the highest P_N rates and efficiency. Due to distinctly different DW proportion between both subgroups, the comparison of FW-based P_N or RD rates does not

Table 1
Oxygen-based RD and P_N rates of trap-free leaves of *Utricularia vulgaris* and *U. australis* of different age.

Leaf age (adult nodes)	*Utricularia vulgaris*						*Utricularia australis*					
	DW (% FW)	Chl. *a* ($g\,kg^{-1}{}_{DW}$)	RD_{DW} ($mmol\,kg^{-1}\,h^{-1}$)	P_{NDW} ($mmol\,kg^{-1}\,h^{-1}$)	P_{Nchl}	RD/P_N	DW (% FW)	Chl. *a* ($g\,kg^{-1}{}_{DW}$)	RD_{DW} ($mmol\,kg^{-1}\,h^{-1}$)	P_{NDW} ($mmol\,kg^{-1}\,h^{-1}$)	P_{Nchl}	RD/P_N
Apex	8.75	2.23 ± 0.12	184** ± 8.3	362** ± 9.4	155 ± 5.6	0.521** ± 0.044	8.37	6.10* ± 0.37	174* ± 27	1158** ± 56	191** ± 5.6	0.155** ± 0.026
3rd	10.3	3.33 ± 0.06	86.9 ± 8.0	739 ± 36	222 ± 11	0.119 ± 0.011	8.53	7.46 ± 0.25	103 ± 13	1855 ± 62	248 ± 4.7	0.056 ± 0.008
10th	10.7	3.39 ± 0.16	65.4 ± 9.9	732 ± 78	216 ± 23	0.109 ± 0.039	9.09	6.78 ± 0.07	59.9 ± 5.9	1592* ± 67	235 ± 10	0.038 ± 0.003
25th	10.8	3.88** ± 0.32	44.2 ± 5.7	845* ± 81	218 ± 18	0.052 ± 0.010	8.38	7.09** ± 0.27	53.5 ± 3.5	1451** ± 63	205 ± 9.8	0.037 ± 0.004
50–60th	10.9	2.39 ± 0.41	42.5 ± 4.0	538 ± 76	227 ± 23	0.084 ± 0.009	7.24	5.38 ± 0.41	58.1 ± 4.6	1119 ± 69	209 ± 14	0.053 ± 0.005

RD and P_N are expressed per unit DW, P_N also per unit chlorophyll *a* in $mmol\,g^{-1}$ chl. *a* h^{-1}. Percent of DW in FW and chlorophyll *a* content per DW are also shown. Means ± SE intervals are shown; $n = 6$. The asterisks denote statistically significant difference between the given and the next shoot segment (*$p < 0.05$; **$p < 0.01$; 1-way ANOVA).

reveal much. On the DW basis, RD in the linear-shoot species ranged between 55–65 $mmol\,kg^{-1}\,h^{-1}$ and was the same as that in the latter subgroup (35–84 $mmol\,kg^{-1}\,h^{-1}$). The mean values of photosynthetic parameters for individual species usually differed considerably between both subgroups from each other and this supported the view that the linear-shoot species have higher P_N rates than the other subgroup. Statistically significant differences between both subgroups were, however, only found for chl. *a*-based P_N ($p < 0.0006$, $F_{1,35} = 59.6$). The DW- and FW-based P_N rates were only weakly different from each other ($p < 0.057$–0.063; Table 2). The linear regression of FW-based P_N and RD revealed a statistically significant correlation only for all species ($P_N = 26.1 + 8.28$ RD; $n = 36$, $r^2 = 0.132$, $p = 0.029$) and the rhizomatous/rosette species ($P_N = -3.70 + 10.0$ RD; $n = 18$, $r^2 = 0.309$, $p = 0.016$), but not for the linear-shoot species (data not shown).

4. Discussion

In this study, photosynthetic traits were compared in three aquatic *Utricularia* species with linear shoots which have often been used for ecophysiological and photosynthetic research (*e.g.*, Moeller, 1978, 1980; Friday, 1989; Richards, 2001; Adamec, 2006, 2008a,b, 2009, 2011a,c; Adamec and Kovářová, 2006; Pagano and Titus, 2007; Adamec and Pásek, 2009), while the other species with rhizomatous or rosette shoots – *U. dichotoma*, *U. resupinata* and *U. volubilis* – have never been studied in this respect and their ecophysiology is quite unknown. The linear-shoot species *U. australis* and *U. vulgaris* from the section *Utricularia* are known for rapid apical growth with a high relative growth rate (0.9–4.2 leaf nodes d^{-1}; Friday, 1989; Adamec and Kovářová, 2006; Adamec, 2008b, 2009, 2011a), while *U. purpurea* (section *Vesiculina*) grows much slower (0.25 leaf nodes d^{-1}; Richards, 2001; see also Moeller, 1980). Although a close correlation between the relative growth rate and the DW- or leaf area-based P_{Nmax} generally holds for terrestrial plants (Shipley, 2006), it has not been found within the subgroup of three aquatic *Utricularia* species (Table 2). P_N values of slowly growing *U. purpurea* were similar to those of rapidly growing *U. vulgaris* and the same held for the RD:P_N ratio. The former species may invest more photosynthates either to trap exudation (*cf.* Sirová et al., 2009, 2010) or to the thick gellous slime covering its shoots.

In both *U. vulgaris* and *U. australis*, P_N measurements in trap-free leaves in shoot segments of different age revealed relatively high P_N values in the oldest (50–60th) segments. This corresponded to the significantly decreased chl. *a* content (Table 1); the FW-based P_N rates reached about 51–64% of the maximum P_N in younger segments, while the chl. *a*-based P_N rates were nearly constant. A similar pattern of chl. *a* content and chl. *a*-based P_N was also found in shoot segments of different age of *U. macrorhiza* (Knight, 1992; very relative to *U. vulgaris*). It is thus possible to conclude that aquatic *Utricularia* species from the generic *Utricularia* section with linear, homogeneous shoots and rapid apical growth dispose of high P_N rates even in very old, trap-free shoot segments. This contributes to covering both great photosynthetic and energetic (maintenance) costs associated with production and activity of traps (Knight, 1992; Adamec, 2006, 2011a; Sirová et al., 2010, 2011; Borovec et al., 2012) and requirements associated with rapid growth (allocation of carbohydrates to new biomass, great loss of biomass in basal decaying shoot segments; see Adamec, 1997b for similar *A. vesiculosa*). As recently shown by Borovec et al. (2012) exudation of organic matter into traps to support commensal communities depends on the photosynthetic conditions of *Utricularia* plants.

Some ecological differences between *U. vulgaris* and *U. australis* clearly follow from the present results. In all shoot segments from

Table 2
Oxygen-based RD and P_N rates of adult trap-free leaves of 6 aquatic *Utricularia* species.

Species	DW (% DW)	Chl. *a* ($g\,kg^{-1}{}_{DW}$)	RD_{DW} ($mmol\,kg^{-1}\,h^{-1}$)	P_{NDW}	P_{NFW}	P_{Nchl} ($mmol\,g^{-1}$ chl. h^{-1})	RD/P_N
U. australis	9.09	6.78 ± 0.07a	59.9 ± 5.9a	1592 ± 67a	145 ± 6.1a	235 ± 10a	0.038 ± 0.003a
U. vulgaris	10.7	3.39 ± 0.16b	65.4 ± 9.9a	732 ± 78b	78.4 ± 8.4b	216 ± 23a	0.109 ± 0.040a
U. purpurea	7.36	4.30 ± 0.29c	55.1 ± 7.6a	835 ± 60c	61.4 ± 4.4c	194 ± 7.0a	0.070 ± 0.012a
U. dichotoma[a]	5.73	13.0 ± 0.28a	82.7 ± 6.1a	359 ± 31a	20.6 ± 1.8a	27.8 ± 2.7a	0.241 ± 0.048ab
U. dichotoma[b]	5.31	10.0 ± 0.69b	83.7 ± 6.2a	687 ± 68b	36.5 ± 3.6b	70.4 ± 9.1b	0.130 ± 0.011ac
U. resupinata	3.65	4.37 ± 0.40c	44.1 ± 4.7b	155 ± 14c	5.65 ± 0.51c	36.8 ± 4.6a	0.283 ± 0.058b
U. volubilis	12.4	6.45 ± 0.21d	35.1 ± 2.0b	509 ± 46a	62.9 ± 5.7d	78.9 ± 6.5b	0.071 ± 0.006c
$F_{1,35}$	–	2.13	2.47	5.65	6.08	59.6	3.41
p	–	0.20	0.18	0.063	0.057	0.0006	0.12

[a] Robust *U. dichotoma* from Newcastle, N.S.W.
[b] *U. dichotoma* population from Katoomba near Sydney, N.S.W.
RD and P_N are expressed per unit DW, P_N also per unit FW and chlorophyll *a* in mmol g^{-1} chl. *a* h^{-1}. *U. resupinata* leaves were infilled by water. Percent of DW in FW and chlorophyll *a* content per unit DW are also shown. Means ± SE intervals are shown; $n = 6$. The species with linear shoots are separated by a dotted line from the species with stoloniferous or rosette shoots. At the bottom, significant difference between both subgroups is shown (nested-design of ANOVA). The different letters within each plant subgroup denote statistically significant differences between species ($p < 0.05$; 1-way ANOVA).

the same position and of similar age, FW-and DW-based P_N values were significantly higher in *U. australis* (Table 1) and also the P_{Nmax} in adult shoot segments was 41% higher than that in *U. vulgaris* (Fig. 1). In both species, the P_N rate at the standard [CO_2] of 0.25 mM approached the P_{Nmax}. On the other hand, CO_2 affinity in *U. australis* was about twice as low as in *U. vulgaris*. Higher P_{Nmax} and the photosynthetic efficiency in *U. australis* confirm its higher apical shoot growth rate when compared with *U. vulgaris* (*cf.* Friday, 1989; Adamec, 2008b, 2009, 2011a; Adamec and Kovářová, 2006). However, the much lower CO_2 affinity in *U. australis* suggests that this species is primarily adapted to much higher CO_2 concentrations (and to much lower pH values) in the water (commonly peatbogs) than *U. vulgaris*, which prefers hard and slightly alkaline waters with lower [CO_2] (Adamec, 1997a, 2008a, 2009).

Generally, the three *Utricularia* species with rhizomatous or rosette shoots used in this study resemble typical terrestrial *Utricularia* species as they have similarly elongated, flat or tubular leaves 0.4–4 mm wide with a relatively low surface:volume ratio, as opposed to the linear-shoot species with fine filamentous leaves (Taylor, 1989). All three species grow slowly in cultures (Adamec, unpubl.). Moreover, *U. dichotoma* and *U. resupinata* grow in very shallow waters and may be considered true amphibious species (Taylor, 1989). Both populations of *U. dichotoma* had a significantly higher chl. *a* content in leaves than the other two species from the subgroup, while that in *U. resupinata* and *U. volubilis* was comparable with those in the linear-shoot species (Table 2). Overall, the DW- and chl. *a*-based P_N values and also the photosynthetic efficiency were somewhat higher in the linear-shoot species than in those from the other subgroup but, due to the small number of species studied and the relatively high variance of the results, the difference was significant only in chl. *a*-based P_N. Similarly, the comparison of photosynthetic traits between two functional subgroups of aquatic *Utricularia* species shows that some photosynthetic parameters clearly overlap between both subgroups thus forming a rather gradual transition of these parameters between the subgroups than a qualitative, sharp distinction. Within all (including the rhizomatous/rosette) species used, the discovered correlation between higher P_N rates and higher RD rates in trap-free leaves suggests a generally higher metabolic activity in leaves in some species. The linear-shoot species used in this study are known to have a relatively high proportion of traps to the total plant biomass as an investment in carnivory (4–62%; Friday, 1989; Adamec, 2008a, 2009). In the rhizomatous species used, an unknown but significant biomass proportion contains subterranean pale rhizomes or rhizoids as non-photosynthetic organs (Taylor, 1989).

In this study, a relatively high CO_2 affinity was found in *U. vulgaris* and *U. australis* trap-free leaves (K_m 21 and 48 μM; Fig. 1). However, in carnivorous *A. vesiculosa*, which commonly accompanies both species, K_m was 165 μM (Adamec, 1997b) and in *U. purpurea* shoots collected from natural sites in the USA, CO_2 affinity was even markedly lower (K_m about 1.0–1.7 mM; Moeller, 1978). The CO_2 compensation points of photosynthesis found for 12 linear-shoot aquatic *Utricularia* species at many field sites or in nearly natural cultures or experiments are, however, consistently within a relatively narrow range of 1.2–13.6 μM (Moeller, 1978; Adamec, 1997a, 2008b, 2009, 2011a; Adamec and Kovářová, 2006; Pagano and Titus, 2007; Adamec and Pásek, 2009) and resemble those commonly reported in aquatic plants (Maberly and Spence, 1983; Sand-Jensen and Frost-Christensen, 1999).

The P_{Nmax} approaching values measured under standard laboratory conditions for three linear-shoot *Utricularia* species (Table 2) are the same or much higher than those reported by various authors for leaves or shoots for 8 aquatic *Utricularia* species with linear shoots (range *ca.* 8–148 mmol $kg^{-1}{}_{FW}\,h^{-1}$ or 80–1860 mmol $kg^{-1}{}_{DW}\,h^{-1}$; Draxler, 1973; Moeller, 1978; Knight, 1992; Adamec, 2006, 2011a). Besides, high P_N values of 150–1050 mmol $kg^{-1}{}_{DW}\,h^{-1}$ were also found in old or new segments of sprouting turions of 4 aquatic *Utricularia* species (Adamec, 2011c). Chlorophyll *a* content found in both subgroups of aquatic *Utricularia* (3.4–13 g $kg^{-1}{}_{DW}$; Table 2) is also the same or comparable to that reported for *U. vulgaris* and *U. macrorhiza* shoots (2–12 g $kg^{-1}{}_{DW}$; Maier, 1973; Knight, 1992) and/or for many aquatic plants (3–18 g $kg^{-1}{}_{DW}$; Madsen et al., 1993; Adamec, 2000; Kahara and Vermaat, 2003). Overall, if the P_{Nmax} of the majority of aquatic plant species usually reaches only about 300–1100 mmol $kg^{-1}{}_{DW}\,h^{-1}$ or 30–110 mmol $kg^{-1}{}_{FW}\,h^{-1}$ (for review see Pokorný and Ondok, 1991; Madsen et al., 1993; Maberly and Madsen, 2002; Kahara and Vermaat, 2003), it indicates that P_N values (both on DW, FW and chlorophyll basis) found in many aquatic *Utricularia* species with linear shoots approach an upper limit of P_{Nmax} reported for all other aquatic plants (*cf.* also Maberly, 1985).

In conclusion, aquatic *Utricularia* species usually grow in waters with high CO_2 concentrations (>0.15 mM; Adamec, 2007, 2008a, 2011a) and under sufficient light and temperature habitat conditions, their P_N rates can be very high and approach the P_{Nmax}. The crucial importance of [CO_2] for attaining high grow rate was proven for 4 aquatic *Utricularia* species in which an increase in [CO_2] in growth experiments led to a marked and significant increase in their relative growth rate (McDermott and Darnowski, 2002; Pagano and Titus, 2004, 2007); the same effect commonly also occurs in other aquatic non-carnivorous plants (*e.g.*, Sand-Jensen and Frost-Christensen, 1999; Pagano and Titus, 2004, 2007). The same ecological strategy – growth dependence on CO_2-rich waters

– occurs also in the rooted floating macrophyte *Stratiotes aloides* (Nielsen and Borum, 2008), which often accompanies *Utricularia* stands. Moreover, relatively high P_N is also kept in senescent shoot segments of *Utricularia*. Very high P_N of (photosynthetic) shoots of rapidly growing *Utricularia* species with linear shoots is therefore a prerequisite for this rapid growth. On the other hand, aquatic or amphibious *Utricularia* species with rhizomatous/rosette shoots do not require high P_N rates for their slow growth. As a result of their growing in very shallow waters as amphibious species, they can also take up atmospheric CO_2 by their aerial leaves when they emerge.

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