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FIELD GROWTH CHARACTERISTICS OF TWO AQUATIC CARNIVOROUS PLANTS, *ALDROVANDA VESICULOSA* AND *UTRICULARIA AUSTRALIS*

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Abstract: Basic growth characteristics of two species of free-floating submerged carnivorous plants, the very rare and stenotopic *Aldrovanda vesiculosa* and the very common and eurytopic *Utricularia australis*, were investigated in a 10/11-day field growth experiment within three nylon enclosures at two artificial *Aldrovanda* sites in the Třeboň region, S Bohemia, Czech Republic, at the peak of a growing season.

Growth of *Aldrovanda* was best at a meso-eutrophic site (biomass doubling time, T_2, 8.4–10.7 days, mean growth of new leaf whorls 0.96 whorls days^{-1}, 1.6 developed branches per shoot) and slower at an oligo-mesotrophic site (T_2 17.2–21.5 days, growth of whorls 1.01 whorls days^{-1}, 0.1–0.5 branches per shoot). Growth of *Utricularia* was similar at both sites (T_2 19.8–33.2 days or 9.1–16.8 days, growth of whorls 3.1 or 2.7 whorls days^{-1}, 1.5–2.1 or 0.8–1.4 developed branches per shoot at the former or latter site, respectively). Throughout the experiment, both species at the meso-eutrophic site allocated relatively more biomass to the production and growth of branches, than to that of new whorls. The results show that *Aldrovanda*, although usually considered as competitively weaker, can grow faster during the growing season peak than *Utricularia* due to frequent branching and the subsequent rapid growth and separation of daughter shoots. Very rapid growth of rootless aquatic carnivorous plants in nutrient-poor habitats allows the consideration of ecophysiological adaptations that enable the plants to gain limiting mineral nutrients. These adaptations include carnivory, efficient nutrient reutilization from senescent shoots, and very high affinity for mineral nutrient uptake from water. Comparison of growth rates of rare and stenotopic *A. vesiculosa* and very common and eurytopic *U. australis* shows that differences in their rarity do not seem to be based on differences of growth rate.

Keywords: *Aldrovanda* introduction, Czech Republic, Growth analysis, Photosynthetic CO_2 affinity, Shallow dystrophic waters, Water chemistry

INTRODUCTION

Aldrovanda vesiculosa L. (*Droseraceae*) and *Utricularia australis* R.BR. (*Lentibulariaceae*) are free-floating rootless submerged carnivorous plants growing commonly in the same shallow standing dystrophic waters (e.g., KAMIŃSKI 1987). While *Aldrovanda vesiculosa* is a very rare and critically endangered plant species throughout its European range (ADAMEC 1995a), *Utricularia australis* is one of the most common submerged plant species (CASPER & KRAUSCH 1981, TAYLOR 1989). Unlike *Aldrovanda*, which is considered to be rather stenotopic (ADAMEC 1995a, 1999), *Utricularia* behaves as a eurytopic species (ADAMEC, unpubl.).

Both species have a similar regular and modular structure composed of leaf whorls separated by internodes, and they propagate only by apical branching of the shoots. A high branching frequency indicates favourable growth conditions (KAMIŃSKI 1987, ADAMEC

1999, 2000). Adult *Aldrovanda* plants are usually only 8–15 cm long (KAMIŃSKI 1987, ADAMEC 1999), while *Utricularia* is much more robust and its usual length is 0.4–1 m (CASPER & KRAUSCH 1981, TAYLOR 1989). Both species have the same life form and growth strategy. Their most important common feature is their continuous apical growth during the growing season, with progressive aging and decomposition at the base. Rapid apical growth and shoot turnover are necessary in both species to enable rapid vegetative propagation over a relatively short growing season (FRIDAY 1989, ADAMEC 1999). *Aldrovanda* can produce 1–2 new leaf whorls a day under optimum conditions (ADAMEC 1995a, 2000). Data for *Utricularia australis* are not available, but a very similar species, *U. vulgaris*, is known to produce 1.4–2.8 leaf whorls a day over a growing season (FRIDAY 1989, 1992). Both *Aldrovanda* and *Utricularia* overwinter as turions (winter buds).

Due to optimization of ecological cost-benefit relationships, GIVNISH et al. (1984) suggested for terrestrial carnivorous plants that carnivory is beneficial only in sunny, moist, and nutrient-poor habitats. It is accepted that terrestrial carnivorous plants are S-strategists and their important ecological adaptation is slow growth (GIVNISH et al. 1984, ADAMEC 1997b, 2002). It is evident, however, that habitats of aquatic carnivorous plants do not fit the above category as these plants can often face not only shortage of mineral nutrients but primarily shortage of light and free CO_2 (e.g., ADAMEC 1995a,b, 1997a). These conditions are generally unfavourable for submerged plants in standing waters (POKORNÝ & ONDOK 1991). Although aquatic carnivorous plants are rootless they grow rapidly (PAGANO & TITUS 2004) and it is carnivory that markedly enhances their growth (for the review see ADAMEC 1997b).

Growth rate of aquatic carnivorous plants as a change in plant biomass has never been measured under field conditions. A comparison of growth rates of a stenotopic and eurytopic aquatic plant species, co-occurring natively in their habitats, could explain the different ecological status of such species. This study aimed to compare the basic growth characteristics of *Aldrovanda vesiculosa* and *Utricularia australis* during the peak of the growing season in a short-term field growth experiment within nylon mesh enclosures at two native, ecologically different *Utricularia* sites in the Třeboň region, S Bohemia, Czech Republic, where *Aldrovanda* had been introduced in the 1990s. Moreover, we compared these growth rates with literature data on these parameters in aquatic non-carnivorous plants. Chemical and physical parameters were measured in each enclosure as a base for the growth effects.

MATERIALS AND METHODS

A field growth experiment with *Aldrovanda vesiculosa* and *Utricularia australis* was carried out in two shallow dystrophic water bodies in the Protected Landscape Area and Biosphere Reserve Třeboňsko, Czech Republic, to which *Aldrovanda* had been introduced in the 1990s (ADAMEC & LEV 1999, ADAMEC, unpubl.). They were the Ptačí blato fishpond (PB; 49°05′ N, 14°41′ E; 434 m a.s.l.; ADAMEC 1999) and fen Lake Karštejn (KA; 49°08′ N, 14°48′ E; 420 m a.s.l.). Fen Lake Karštejn originated as a ca. 4-ha complex of shallow dystrophic pools after peat extraction at the beginning of 1980s and has been subject to slow hydroseral succession since then. In 2001, dense stands of over 500 shoot apices m^{-2} and

Table 1. Physical and vegetation characteristics of the microsites where enclosures were located in this study. [1)] – rooted in substrate.

	Microsite	Total water depth (cm)	Total coverage of vegetation (%)	Plant dominants and sub-dominants
Ptačí blato fishpond	PB1	39	10	*Typha angustifolia*, *Chara fragilis*[1)]
	PB2	32	50	*Phragmites australis*, *Potamogeton pusillus*[1)], *Chara fragilis*[1)]
	PB3	35	0	Water bloom of *Microcystis aeruginosa*, *Potamogeton pusillus*[1)], *Chara fragilis*[1)]
Fen Lake Karštejn	KA4	15–18	90	*Carex rostrata*
	KA5	17–21	60	*Carex rostrata*, *Phragmites australis*
	KA6	31–32	40	*Phragmites australis*, *Carex rostrata*

stable micropopulations exceeding 20,000 shoot apices occurred at both sites, while the density of native *U. australis* was about 4–40 shoot apices m^{-2}.

Three nylon mesh enclosures were placed in the northern-most dystrophic pool (denoted as PB1C in ADAMEC & LEV 1999) on the eastern shore of the Ptačí blato fishpond, and a further three were located in different vegetation communities in the central shallow pool of fen Lake Karštejn. The distance between individual enclosures at each site did not exceed 15 m. The microsites selected for individual enclosures represented distinct ecological habitats, characterized by different plant dominants, different total coverage of the dominants and, to a certain extent, by water depth (Table 1). They were representative of each site and *Aldrovanda* and *Utricularia* occurred in all of them. However, the microsites selected at PB did not correspond to those at KA. *Aldrovanda* occurred in very dense stands (60–100% cover) in some of them (PB1, KA4, KA5), but the density of *Utricularia* in all selected microsites was much lower (only 10–25% cover). The enclosures were bottomless and topless, one metre square and were made from a 33 cm wide band of 1.5 mm translucent nylon mesh (ADAMEC 1999). All enclosures rose about 10 cm above the water surface to prevent plant escape. The size of the enclosures was chosen to reduce the margin effect (shading) and possible species competition. After installation, just before the start of the experiment, all pre-existing *Aldrovanda* and *Utricularia* plants were removed from the enclosures.

Seventy homogeneous, unbranched *Aldrovanda* plants were collected from between the PB2 and PB3 enclosures and also between KA4 and KA5. All were shortened to 10 adult leaf whorls at PB (shoot lengths of 5.3–9.0 cm) and 12 at KA (6.5–8.9 cm), to reflect the generally larger plant size in the natural population at KA. This standard procedure essentially removed senescing shoot bases, leaving only young, metabolically active material. Similarly, 70 homogeneous *Utricularia* plants collected from the same two locations were shortened to 20 adult leaf whorls at PB (shoot lengths of 12.8–21.2 cm) and 25 at KA (16.1–25.5 cm). All visible shoot branches were excised. The number of adult leaf whorls on the main shoot was chosen as a principal measure of plant size and growth in both species, as shoot length itself is a very variable parameter that inadequately represents growth and fitness (FRIDAY 1989,

KOMIYA & SHIBATA 1998, ADAMEC 1999, 2000). To estimate growth rate in terms of the generation of new leaf whorls, the internode between the second and third adult whorls was tagged carefully by a short piece of fine thread using a pair of forceps (FRIDAY 1989, ADAMEC 2000, RICHARDS 2001). Young leaf whorls were counted as adult if they bore functional traps (i.e., if the traps were able to suck in air bubbles, or if they contained prey/detritus) and were spatially separated by a short internode from the apex. If they had an intermediate character, they were counted as 0.5 (ADAMEC 2000).

On 24 June 2001, 20 randomly selected, tagged plants of each species were introduced to each of the three enclosures at PB, and on 25 June 2001, this procedure was also carried out at KA. The mixed populations were subsequently studied for growth effects. Eight to ten of the remaining parallel plants of each species were dried at 80 °C to establish initial shoot mean dry weights. A further six to eight non-tagged parallel individuals of each species were placed in the PB3 and KA4 enclosures for subsequent estimation of photosynthetic CO_2 affinity. Total main shoot length, number of adult whorls on the main shoot, position of the tag, branching of shoots, and number of air shoots (in *Utricularia*) were recorded for all tagged *Aldrovanda* and *Utricularia* plants in all enclosures at time zero and then after 3, 7, and 10 days at PB and 3, 7, and 11 days at KA. When possible internodes between each branch were counted. Senescent, dead shoot bases were not measured. Shoot turgidity and light colour were the criteria for identifying living tissues in both species. The rate of leaf whorl senescence was estimated as the difference between the initial and final number of living whorls distal to the tag. At the conclusion of the experiment (4 or 6 July), plants were washed in tap water and big items of prey removed from traps (in *Aldrovanda*). After all measurements had been taken, the plants were dried (80 °C) and weighed. Biomass doubling time (T_2) was calculated from mean values of initial and final dry weight.

On each assessment occasion, the dissolved O_2 concentration, pH, conductivity, water temperature, and total alkalinity (TA) were measured in all enclosures. All measurements were taken 2 cm below the water surface. As water temperature in various enclosures at the sites was measured at different day times the results have only an orientation value. Twice during the measuring period (after 3 and 10 or 11 days), water samples were collected from all enclosures, filtered, and analyzed for macro-nutrients and humic acid concentration. For all analytical details see ADAMEC (1997a, 1999) and ADAMEC & LEV (1999). CO_2 concentration was calculated from total alkalinity and pH (HELDER 1988). An estimate of the level of shading by emergent vegetation was made using a submersible PAR sensor (ADAMEC 1997a, 1999). Readings are expressed as percentage of incident PAR penetrating to a water depth of 1 cm (submerged plant level). To relate the growth data to climatic factors, data on maximum, minimum and mean daily temperature and mean daily global radiation (i.e., sum of UV, PAR, and IR radiation; in MJ m^{-2}) were collected from a standard meteorological station in the Institute of Botany at Třeboň (about 12 and 19 km away from PB and KA, respectively).

Photosynthetic CO_2 affinity in parallel *Aldrovanda* and *Utricularia* plants from PB3 and KA4 enclosures was estimated using a simple final-pH method (ADAMEC 1997). 3 cm apical shoot segments of *Aldrovanda* or 6 cm ones of *Utricularia*, representing clean young segments, were placed in 10 ml glass test-tubes with 1.06 mmol l^{-1} $NaHCO_3$ + 0.1 mmol l^{-1} KCl (initial pH 7.91; ca. 9 ml of solution and ca. 1 ml of free air). The tubes were incubated at

Table 2. Water chemistry in enclosures at experimental sites at Ptačí blato fishpond (PB1–3) and Karštejn (KA 4–6) fen pools during the growth experiment. TA – total alkalinity; G – electrical conductivity; HAT – the sum of humic acids and tannins; PAR – % of incident (PAR) irradiance penetrating 1 cm below the water surface. Means of four values (together with the range) are shown for each microsite. For NH_4-N, PO_4-P, and HAT, means of two values and the ranges are shown. Means ± s.e. of the mean microsite values are shown under the group of microsites. SSD = statistically significant difference between the means of three microsites at the two sites using a *t*-test; d.f. = 4; *** – $P < 0.002$; ** – $P < 0.01$; * – $P < 0.05$; ns – non-significant at $P = 0.05$.

Microsite	O_2 mg l^{-1}	pH	TA meq l^{-1}	CO_2 mmol l^{-1}	G µS cm^{-1}	NH_4-N µg l^{-1}	PO_4-P µg l^{-1}	HAT mg l^{-1}	PAR %
PB1	4.9 (2.2-10.4)	7.10 (7.04-7.28)	1.64 (1.51-1.74)	0.30 (0.20-0.36)	228 (207-248)	919 (822-1016)	22 (20-23)	18.7 (18.1-19.3)	25
PB2	6.3 (3.0-11.5)	7.04 (6.93-7.27)	1.51 (1.44-1.62)	0.33 (0.19-0.42)	219 (199-233)	584 (576-592)	21 (19-23)	21.3 (20.9-21.6)	33
PB3	7.0 (3.2-10.8)	7.06 (6.95-7.15)	1.48 (1.41-1.59)	0.32 (0.26-0.38)	231 (209-244)	573 (534-612)	22 (21-23)	21.6 (21.0-22.1)	45
Mean	**6.0±0.6**	**7.07**	**1.54±0.05**	**0.31±0.01**	**226±4**	**692±114**	**22±0.3**	**21±0.9**	**34±6**
KA4	11.4 (7.2-14.1)	6.97 (6.65-7.47)	0.74 (0.61-0.86)	0.19 (0.05-0.43)	180 (160-187)	74 (73-74)	8.5 (0-17)	10.4 (8.9-11.8)	16
KA5	11.1 (8.4-12.9)	6.93 (6.74-7.17)	0.84 (0.71-0.91)	0.24 (0.15-0.40)	203 (170-221)	86 (64-107)	16 (15-17)	9.0 (7.5-10.4)	27
KA6	10.0 (7.7-11.9)	7.08 (6.91-7.30)	0.96 (0.88-1.02)	0.19 (0.10-0.29)	221 (200-244)	92 (62-121)	7.5 (0-15)	7.8 (7.0-8.5)	26
Mean	**10.8±0.4**	**6.99**	**0.84±0.06**	**0.20±0.02**	**201±12**	**84±5**	**11±3**	**9.0±0.8**	**23±4**
SSD	**	**ns**	***	**	**ns**	**	*	***	**ns**

2 cm water depth at PB3 or KA4 with irradiance levels of 80–150 W m^{-2} PAR. After 5 h, a final pH was measured, and this indicated a corresponding CO_2 compensation concentration for photosynthesis. Six replicate measurements were taken for each species at both sites. At the end of the experiment, two randomly selected adult plants of both species were collected from each site close to the PB1 and KA4 enclosures to estimate the proportion of traps with prey. Using a binocular microscope, presence of any distinguishable prey in traps was estimated in whole shoots of *Aldrovanda* and in main shoot segments of the 6th to 20th adult leaf whorls of *Utricularia*.

The two sites (PB and KA) represent ecologically complex mosaics of several vegetation community types and, thus they contain local variations in both biotic and abiotic factors. Our aim was to study growth characteristics of the two species under a variety of local conditions. We selected three distinct microhabitats at each site but because the sites have somewhat different water chemistry, it is possible, in a sense, to regard the study as two groups of three replicates. In this way, water chemistry turns out to be a determining factor in plant performance. Plant growth parameters were measured several times during the experiment but between-enclosure statistical significance was tested only at the end of the experiment to avoid the time dependence of these data. However, statistical significance of leaf whorl production could be evaluated for consecutive measurements. Data were checked for normality and no transformation was used. Where possible the data were subjected to a one-way ANOVA (Tukey HSD-test) to find significant differences in measured parameters. At each site and within each species at the end of the experiment, the parameters (for single plants) as final dry weight, leaf whorls, shoot length, shoot branches, and air shoots were tested for significant differences between the three enclosures (as microsites). Mean values of leaf whorl production for each enclosure and experimental period were pooled ($n = 9$) to test for significant differences between sites and species. Values of biomass doubling time for single enclosures were pooled for each site ($n = 3$) to test for significant differences between sites and species. Some data sets were tested for statistical significance by a *t*-test for independent samples.

RESULTS

Water chemistry parameters did not differ significantly within each group of enclosures (one-way ANOVA), but there was a statistically significant difference (*t*-test, $P < 0.05$) between the means of the two sites for O_2 concentration, TA, CO_2 concentration, NH_4-N, PO_4-P, and humic acid (+tannin) concentration (Table 2). Daily oxygen concentrations exceeded 2 mg l^{-1} in all enclosures at the time of measurement. However, the O_2 concentrations in PB enclosures (2–10 mg l^{-1}) were much more variable than at KA, suggesting greater diurnal fluctuations. Oxygen concentration was also measured at the sediment interface at each site and this was consistently less than 0.1 mg l^{-1} (data not shown). Mean pH values were about 7.0 at both sites (Table 2). Mean CO_2 concentration was 0.31 mmol l^{-1} at PB, and 0.20 mmol l^{-1} at KA, although KA minima sometimes fell below 0.10 mmol l^{-1}. NH_4^+ dominated mineral nitrogen at both sites (Table 2) and NO_3^- was not detected. Mean PO_4-P concentration at PB was twice that at KA. Humic acid and tannin concentrations were consistently higher at PB. On average, emergent vegetation cast about

Table 3. Results of field growth experiment with *Aldrovanda vesiculosa* and *Utricularia australis* in enclosures at Ptačí blato (PB1–3) and Karštejn (KA 4–6). The experiment lasted for 10 days at PB and 11 days at KA. Mean initial and final plant dry weights ± s.e. are shown. T_2 = biomass doubling time. For the final dry weights (DW), the same letters for each species at a particular microsite denote no statistically significant difference within the site at $P < 0.05$. For T_2, the same letters for the three averaged enclosures at each site denote no statistically significant difference between the sites and species at $P < 0.05$. Initial DW – n = 8–10; final DW – n = 16–20; T_2 – n = 1.

Species	Microsite	Initial DW (mg)	Final DW (days)	T_2
Aldrovanda vesiculosa	PB1	18.7±1.6	35.8 ± 1.5[a]	10.7
	PB2	18.7±1.6	42.1 ± 2.0[b]	8.5[a]
	PB3	18.7±1.6	42.5 ± 1.5[b]	8.4
	KA4	24.9 ± 1.3	35.4 ± 1.5[a]	21.5
	KA5	24.9 ± 1.3	36.5 ± 1.6[a]	19.8[b]
	KA6	24.9 ± 1.3	38.8 ± 1.9[a]	17.2
Utricularia australis	PB1	119.4 ± 13.6	169.5 ± 18.5[a]	19.8
	PB2	119.4 ± 13.6	165.1 ± 17.0[a]	21.4[b]
	PB3	119.4 ± 13.6	144.2 ± 11.9[a]	33.2
	KA4	64.6 ± 6.1	101.9 ± 5.5[a]	16.8
	KA5	64.6 ± 6.1	111.0 ± 12.4[ab]	14.1[b]
	KA6	64.6 ± 6.1	149.3 ± 12.8[b]	9.1

30% more shade at KA than at PB. During the experiment, the mean daily air temperature in the region ranged between 14–22.5 °C, while the maximum was between 22.5–32.5 °C and the minimum between 5.5–14 °C (data now shown). The highest water surface temperatures, measured at different day times, ranged from 24.8 °C (PB) to 30.0 °C (KA).

Growth rates (expressed as biomass doubling time, T_2) of *Aldrovanda* were greatest at PB2 and PB3 (8.5 days), 20% lower at PB1, and lowest (17.2–21.5 days) in the KA enclosures (Table 3). The mean growth rate of *Aldrovanda* for the three enclosures at PB was significantly greater than for those at KA (one-way ANOVA, $F_4 = 49.9$, $P < 0.002$) and also greater than for *Utricularia* at PB (T_2 24.8 days, $F_4 = 13.2$, $P < 0.022$). Biomass increase of *Utricularia* at KA6 was significantly greater compared with the same species at KA4 (Table 3). *Aldrovanda* in all PB enclosures approached its equilibrium (maximum) number of adult leaf whorls (15.0–16.5) on the main shoot as early as after 7–10 days from establishing the experiment, while whorl numbers were still increasing at KA even after 11 days (17.9–19.2 whorls; data not shown). Similar patterns emerged with shoot length measurements (data not shown, see Table 4). Linear *Aldrovanda* shoots started branching as early as 3 days at both sites but throughout the experiment the branching rate was 3–10 times greater in all enclosures at PB than it was at KA (Fig. 1, Table 4).

In all PB enclosures, *Utricularia* nearly approached its equilibrium number of leaf whorls and its usual adult size after 10 days, but at KA shoots were still extending after 11 days (Table 4). The branching rate of main shoots of *Utricularia* at PB was consistently up to twice as fast as compared to KA (Fig. 1). At PB, by the end of the experiment, there were only on average 5.3 internodes (n = 35; s.e. = 0.2; range 2–7) between each *Aldrovanda* branch on the main shoot, but *Utricularia* plants had 14.5 internodes (n = 32; s.e. = 1.2; range 3–28) at PB and 15.1 (n = 12; s.e. = 1.7; range 7–28) at KA. By final sampling, on average 11.2 old

Table 4. Statistical significance of parameters within sites (three enclosures per site, 20 plants per enclosure) at the end of the field growth experiment with *Aldrovanda vesiculo*sa and *Utricularia australis* at Ptačí blato (PB; 10 days) or Karštejn sites (KA; 11 days). Means ± s.e. of mean values for three enclosures are also shown.

Species	Site	Parameter	*P*	*F*	d.f.	Mean ± s.e.
A. vesiculosa	PB	Final DW (mg)	0.009	5.07	2,57	40.1 ± 2.2
	KA	Final DW (mg)	0.288	1.27	2,57	36.9 ± 1.0
	PB	Leaf whorls	0.009	5.14	2,56	15.6 ± 0.5
	KA	Leaf whorls	0.004	6.05	2,57	18.9 ± 0.4
	PB	Shoot length (cm)	0.0002	10.3	2,56	9.92 ± 0.77
	KA	Shoot length (cm)	0.001	8.46	2,57	10.6 ± 0.5
	PB	Shoot branches	0.482	0.74	2,56	1.63 ± 0.06
	KA	Shoot branches	0.068	2.81	2,57	0.27 ± 0.10
U. australis	PB	Final DW (mg)	0.495	0.71	2,57	159.6 ± 7.8
	KA	Final DW (mg)	0.011	4.93	2,47	120.7 ± 14.5
	PB	Leaf whorls	0.0497	3.17	2,55	39.8 ± 1.1
	KA	Leaf whorls	0.0003	9.53	2,47	53.9 ± 1.5
	PB	Shoot length (cm)	0.109	2.31	2,55	29.9 ± 1.2
	KA	Shoot length (cm)	0.001	8.84	2,47	37.9 ± 2.3
	PB	Shoot branches	0.007	5.45	2,55	1.73 ± 0.19
	KA	Shoot branches	0.020	4.23	2,47	1.13 ± 0.19
	PB	Air shoots	0.316	1.18	2,55	2.12 ± 0.11
	KA	Air shoots	0.0004	9.07	2,47	1.50 ± 0.49

Utricularia internodes were decomposed at PB, but only 3.2 at KA. In contrast, *Aldrovanda* had only 4.1 decomposed internodes at PB and 4.3 at KA.

Neither species showed significant growth differences in leaf whorl production between sites ($P < 0.05$), but overall *Utricularia* was consistently about three times more prolific than *Aldrovanda* (Fig. 2), and this distinction was statistically highly significant ($P < 0.0001$). Linear correlation between averaged maximum, minimum, and mean daily air temperatures or mean daily global radiation on the one hand, and whorl production rates on the other (pooled for each species at both sites, $n = 18$, correlated with three averaged temperatures for the measuring periods), was statistically significant ($P < 0.04$) for maximum and mean air temperatures in respect of both species and even highly statistically significant ($P < 0.01$) for *Aldrovanda*. *Utricularia* developed air shoots at both sites and the mean numbers by the end of the experiment were 1.9–2.3 in the PB enclosures and 0.56–2.2 at KA ones (see Table 4). An examination of two *Aldrovanda* plants showed that about 8% of traps caught prey at PB, but only about 5% at KA. Two evaluated *Utricularia* plants revealed that about 2–4% of traps contained prey at PB, while only about 1–2% at KA (data not shown) did.

At PB3, *Aldrovanda* had a photosynthetic CO_2 affinity of 4.6 μmol l^{-1} – about twice that of *Utricularia* (Table 5). Species performance was similar (about 12 μmol l^{-1}) at KA, so there appears to be a difference in site performance.

DISCUSSION

At the end of the experiment, the marked difference in *Utricularia* size and total whorls between sites (Table 4) can be explained by a higher death rate of old internodes at PB. Although the mean shoot extension rate (new whorls $days^{-1}$) of *Utricularia* was about three

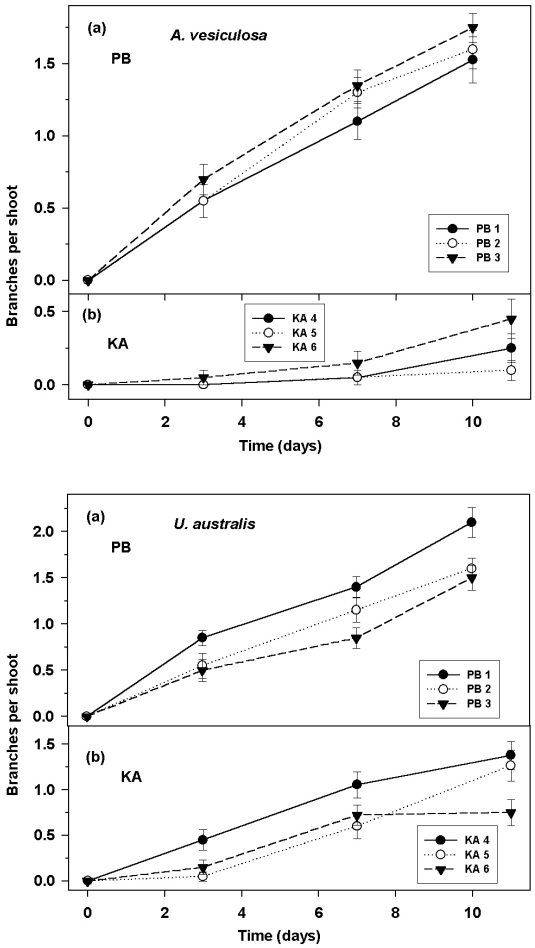

Fig. 1. The number of branches per shoot of *Aldrovanda vesiculosa* (n = 18–20) and *Utricularia australis* (n = 16–20) produced in each enclosure during the growth experiment. (a) – PB, Ptačí blato (24 June–4 July); (b) – KA, Karštejn (25 June–6 July). For each enclosure, means ± s.e. are shown.

times higher than of *Aldrovanda* at both sites (cf. Fig. 2, Table 4), *Aldrovanda* was still able to match, and sometimes exceed, the rate of biomass accumulation in *Utricularia* plants (Table 3). This apparent anomaly arises through differences in growth strategies, particularly branching, between the two species. The internode number between successive branches suggests that the rate of branch production (4.7–5.5 days between branches) is similar for both species, and the difference between both species lies in the rates at which these branches mature and separate from the mother plant as a vegetative propagule. *Aldrovanda* branches mature and separate rapidly and regularly (ADAMEC 1999), but *Utricularia* vegetative reproduction appears to be considerably slower. It follows from the results (Figs. 1 and 2) that certain competitive processes take place between the production of new whorls and branches

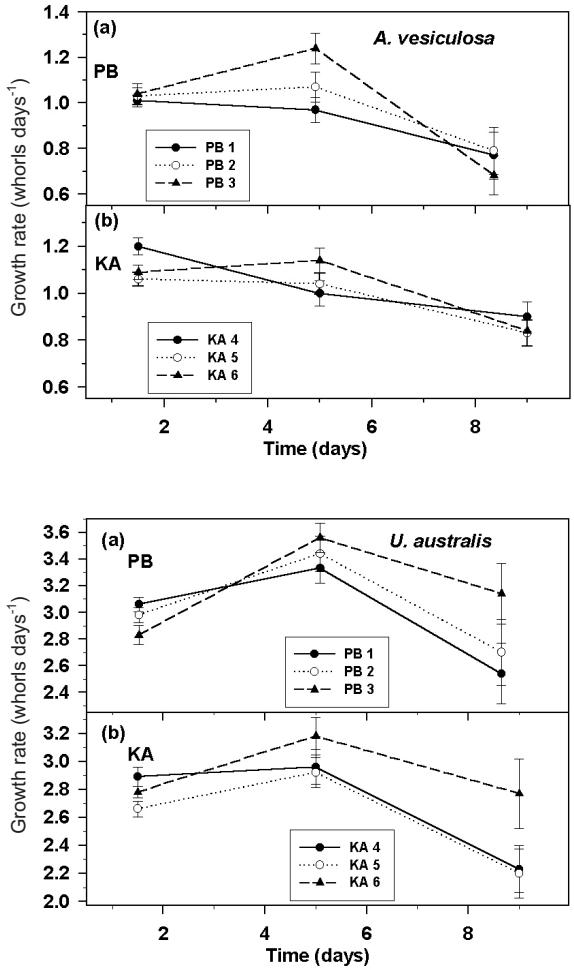

Fig. 2. The growth rate as the production of new leaf whorls days^{-1} in *Aldrovanda vesiculosa* (n = 18–20) and *Utricularia australis* (n = 16–20) in each enclosure during the growth experiment. (a) – PB, Ptačí blato (24 June–4 July); (b) – KA, Karštejn (25 June–6 July). For each enclosure, means ± s.e. are shown.

in both species. Shoot growth (extension) rates recorded in the present paper (Fig. 2) are comparable with other published values for *Aldrovanda* or *Utricularia vulgaris* (FRIDAY 1989, 1992, KOMIYA & SHIBATA 1998, ADAMEC 2000).

The considerable variation in biomass doubling times between enclosures (*Aldrovanda* 8.4–21.5 days, *Utricularia* 9.1–33.2 days; Table 3) could still be partly due to differences between initial plant biomasses. However, a more plausible explanation involves variation in the death rates of the old internodes. As noted above, *Utricularia* at site PB has an apparently low relative growth rate, although it maintains a high rate of shoot extension and branch formation. Comparable values of T_2 for the total number of shoot apices (as a measure of shoot biomass) within 12.9–23.0 days were also found in field-grown *Aldrovanda* in a warm

Table 5. Photosynthetic CO_2 compensation concentration (CC) of *A. vesiculosa* and *U. australis* apical shoot segments measured under field conditions. Means ± s.e. of six parallel estimations are shown. The different letters denote statistically significant differences at $P < 0.05$.

Species	Site	CO_2 CC (μM)
A. vesiculosa	PB3	4.6 ± 0.4a
	KA4	11.4 ± 0.5b
U. australis	PB3	9.8 ± 1.0b
	KA4	13.2 ± 1.0b

summer period (ADAMEC 1999, ADAMEC & LEV 1999) and T_2 values of 12.8 days for dry weight increase in an outdoor growth experiment (ADAMEC 2000). Similar data (12.4–23.1 days) have been found for shoot segments of *U. vulgaris* grown in a greenhouse (PAGANO & TITUS 2004). Also, comparable values of T_2 between 6.4–34.7 days were recorded by NIELSEN & SAND-JENSEN (1991) for aboveground biomass in 12 rooted species of submerged or amphibious plants in a laboratory-growth experiment. Finally, photosynthetic CO_2 affinity of *Aldrovanda* and *Utricularia* (4.6–13 μmol l^{-1}; Table 5) is similar to that in other aquatic non-carnivorous plants (mostly 3–10 μmol l^{-1}; MABERLY & SPENCE 1983) and should not limit the rapid plant growth at the sites.

Concentrations of mineralized N and P (Table 2) at PB suggest that the water is meso-eutrophic, while at KA it is oligo-mesotrophic. Since 1995 (cf. ADAMEC & LEV 1999), PO_4-P concentration had doubled by 2001 and NH_4-N had increased by about 70 times. There was also a cyanobacterial bloom (*Microcystis* sp.) in 2001, due presumably to an open connection to an adjacent hypertrophic fishpond. So the growth of both plant species, and maybe also invertebrate prey availability, at KA may have been limited by the lower PO_4-P and NH_4-N concentrations. Certainly, growth rates do not seem to have been limited at either site by oxygen availability, because nowhere did these fall below 2.2 mg l^{-1} (Table 2; and cf. ADAMEC 1997, 1999). However, growth rates may be partly limited at KA by the lower CO_2 concentration there, as both *Aldrovanda* and *Utricularia* plants are strict CO_2 users (Table 2; ADAMEC 1995b, 1997a,b).

CONCLUSIONS

Two species of free-floating, rootless aquatic carnivorous plants under study are characterized by the same rapid growth as in rooted aquatic non-carnivorous plants. Because rootless aquatic carnivorous plants cannot take up mineral nutrients from nutrient-rich sediments their high growth rate gives evidence that they use other ecophysiological adaptations to gain mineral nutrients for their rapid growth. It can be carnivory (ADAMEC 1997b), very efficient nutrient reutilization from senescent shoots (ADAMEC 2000), and very high affinity for nutrient uptake from water. As it follows from the comparison of growth rates of rare and stenotopic *A. vesiculosa* and very common and eurytopic *U. australis* the reasons for their different ecological characteristics apparently are not based on the differences of growth rate.

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