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Field Growth Analysis of *Utricularia stygia* and *U. intermedia* – Two Aquatic Carnivorous Plants with Dimorphic Shoots

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Summary

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A detailed 14-d growth experiment on two temperate aquatic *Utricularia* species with dimorphic shoots, *U. stygia* and *U. intermedia*, was conducted at two natural shallow dystrophic sites in S Bohemia, Czech Republic. Both sites were oligo- to slightly mesotrophic, and dissolved O_2 and free CO_2 concentrations were sufficient so as not to limit plant growth. Both species exhibited a similarly high apical growth rate of photosynthetic shoots (1.9–2.1 leaf node d^{-1}), as is reported in the literature for aquatic *Utricularia* species with monomorpic shoots. Moreover, the estimated doubling time for biomass of the two species (6.6–9.2 d) represents the absolute maximum growth rate ever estimated for an aquatic carnivorous plant (*Aldrovanda*, *Utricularia* spp.). These findings thus clearly support the ecophysiological concept that aquatic carnivorous plants differ greatly from their terrestrial counterparts in their very rapid growth.

Zusammenfassung

ADAMEC L. 2010. Field growth analysis of *Utricularia stygia* and *U. intermedia* – two aquatic carnivorous plants with dimorphic shoots. [Freilanduntersuchungen des Wachstums zweier Fleischfressender Wasserpflanzen mit dimorphen Sprossen *(Utricularia stygia* und *U. intermedia)*]. – Phyton (Horn, Austria) 49 (2): 241–251.

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Im dystropen Flachwasserstandort S Bohemia, Tschechische Republik, wurde ein vierzehn-tägiges Experiment an zwei in gemäßigt temperiertem Wasser lebenden Pflanzen mit dimorphen Sprossen, *U. stygia* und *U. intermedia*, durchgeführt. Beide Pflanzen leben in oligo- bis schwach mesotrophen Gewässern, die am Standort im Wasser gemessenen O_2 und CO_2 Konzentrationen sind für deren Wachstum nicht limitierend. Beide Arten zeigten ungefähr gleich große Wachstumsraten der photosynthetisch aktiven Sprosse (1,9–2,1 Blattknoten d^{-1}), wie es auch für *U.*-Arten mit monomorphen Sprossen in der Literatur angegeben wird. Darüber hinaus stellt die Zeit für die Verdoppelung der Biomasse der zwei Arten (6,6–9,2 d) die höchste Wachstumsrate dar, die je bei fleischfressenden Wasserpflanzen gefunden wurde (*Aldrovanda, Utricularia* spp.). Die Ergebnisse unterstützen das ökophysiologische Konzept, dass sich karnivore Wasserpflanzen grundsätzlich von ihren entsprechenden Ebenbildern am Land durch ihre sehr hohen Wachstumsraten unterscheiden.

Introduction

About 50 species of the carnivorous genus *Utricularia* L. (*Lentibulariaceae*) are aquatic (or amphibious) plants (TAYLOR 1989). Generally, rootless aquatic *Utricularia* species grow in shallow dystrophic waters in which their growth can often be limited by a shortage of not only inorganic N and P, but sometimes also K (for the review see ADAMEC 1997, ELLISON 2006, GUISANDE & al. 2007). On the other hand, the waters are usually very rich in free CO_2. These plants use their shoots to take up all necessary nutrients, either from the water or from captured prey. Most species have a linear, modular and fairly regular shoot structure, consisting of nodes with dissected leaves and cylindric internodes (TAYLOR 1989). They mostly propagate vegetatively via branching shoots. Contrary to terrestrial carnivorous plants, most aquatic *Utricularia* species exhibit very rapid apical shoot growth (1–4 leaf node d^{-1}) and a high relative growth rate (doubling time of biomass, T2, 9–33 d; FRIDAY 1989, PAGANO & TITUS 2004, ADAMEC & KOVÁŘOVÁ 2006, ADAMEC 2009, cf. ADAMEC 2002, 2008c, FARNSWORTH & ELLISON 2008). This very rapid growth in nutrient-poor habitats requires several ecophysiological adaptations, including a very high net photosynthetic rate of shoots, carnivory, efficient nutrient re-utilization (recycling) from senescent shoots, and a very high affinity for mineral nutrient uptake from ambient water (KOSIBA 1992a,b, ENGLUND & HARMS 2003, ADAMEC 2006, 2008a,b).

U. stygia THOR (syn. *U. ochroleuca* HARTM. *s. lato*) and *U. intermedia* HAYNE are rare temperate aquatic plants with distinctly dimorphic shoots. They are differentiated in green photosynthetic (PS) shoots with at most only a few traps and in colourless carnivorous (CA) shoots with strongly reduced leaves bearing the dominant majority of traps (THOR 1988, ADAMEC 2007). In several natural populations of both species, ADAMEC 2007 has recently described the main water chemistry parameters in typical microhabitats in which both PS and CA shoots grow, and estimated important plant morphometric data including the structural investment in carnivory (i.e., the proportion of trap or CA shoot biomass to the total plant biomass). In both species, the proportion of CA shoots to the total plant biomass ranged from 40–59 % and differed significantly between sites suggesting an ecological regulation of this parameter (cf. BERN 1997, KIBRIYA & JONES 2007, ADAMEC 2008b). However, growth rate parameters have never been measured in these species.

In this paper, a detailed 14-d growth experiment on both *Utricularia* species was conducted at natural sites in S Bohemia, Czech Republic. An emphasis was focused on estimation of apical shoot growth rate (ASGR), doubling time of biomass, and investment in carnivory, to compare these parameters with those in aquatic *Utricularia* species with monomorphic shoots.

Abbreviations: DM – dry mass, PAR – photosynthetically active radiation, T_2 – doubling time of biomass, CA – carnivorous (shoot), PS – photosynthetic (shoot), ASGR – apical shoot growth rate, IC – investment in carnivory.

Material and Methods

Study Sites

U. intermedia and *U. stygia* are considered critically endangered (C1) among Czech flora, though *U. stygia* is not officially mentioned (HOLUB & PROCHÁZKA 2000). The Třeboň basin in S Bohemia is the centre of their recent distribution in the Czech Republic (PŁACHNO & ADAMEC 2007), and the 14-d growth experiment on both *Utricularia* species was conducted at one native site of each species in the Protected Landscape Area and Biosphere Reserve Třeboňsko, Czech Republic. Both sites have a character of shallow standing dystrophic waters and have never been protected as nature reserve.

The growth experiment on *U. stygia* was conducted in fen Lake Karštejn (49°08' N, 14°48' E; 420 m a.s.l.; see ADAMEC & KOVÁŘOVÁ 2006). This site originated as a ca. 4-ha complex of shallow dystrophic pools after peat extraction at the beginning of the 1980s and has been subject to slow hydroseral succession since then. In 2008, loose or denser stands of *U. stygia* covered hundreds of m^2 within shallow (5–10 cm) sedge-dominated stands. Within a typical and optimum microhabitat of *U. stygia,* a spot 3 x 3 m was selected and five microsites in this spot were labelled by a tag. The experimental spot was 3–10 cm deep and its total coverage was about 80%, with dominants of *Carex rostrata* (60% cover) and *C. lasiocarpa* (40% cover); the cover of *U. stygia* was about 10%.

The growth experiment on *U. intermedia* was conducted in a shallow peat bog situated in the littoral zone of the eutrophic Výtopa fishpond (48°59' N, 14°53' E; 440 m a.s.l.). In 2008, patchy loose stands of *U. intermedia* covered about 50 m^2 within shallow (5–10 cm) sedge- or reed-dominated stands. Within a typical and optimum microhabitat of *U. intermedia,* a spot 2 x 2 m was selected and five microsites in this spot were labelled by a tag. The spot was 5–12 cm deep and its total coverage was about 80%, dominated by *Carex lasiocarpa* (60% cover), *C. rostrata* (40% cover), and *Phragmites australis* (40 % cover); the cover of *U. intermedia* was about 10 %.

Growth Experiment

At the start of the experiment on 25 May 2008, 30 homogeneously branched *U. stygia* plants were collected from the experimental location in fen Lake Karštejn. Their main PS shoot sprouting from the turion was about 10–12 cm long. All PS shoots were shortened to 8.0 cm and they bore 1–2 young CA shoots each. Ten plants were haphazardly selected for the estimation of initial dry mass (DM, 80 °C) for T_2 determination, total number of traps per plant, and the investment in carnivory (proportion of DM of CA shoots with all traps to the total plant DM). In the remaining 20 plants, the number of mature leaf nodes on the PS shoot and the number and length of CA shoots (branches) were estimated. For measuring the ASGR, the internode between the second and third mature leaf nodes was tagged carefully by a short piece of fine thread (FRIDAY 1989, ADAMEC & KOVÁŘOVÁ 2006, ADAMEC 2008a, 2009). Four randomly selected, tagged plants were placed carefully in each of the five labelled microsites, in an area of about 12 x 12 cm, and were allowed to continue their growth under natural conditions. On 25 May 2008, exactly the same procedures were also conducted with 30 experimental *U. intermedia* plants at the Výtopa fishpond but the shoot segments were shortened to 6.0 cm.

A submersible temperature datalogger (Minikin T, EMS, Brno, Czech Rep.) monitored water temperature at each experimental site at plant level during the whole experiment. At the start of the experiment, after 8 days, and at the end of the 14-d growth period (on 8 June 2008), basic water chemistry parameters were analyzed at plant level (1–2 cm deep) at all five microsites at both locations (Table 1; for the methods see ADAMEC 1999, 2007). An estimation of the level of water surface shading by emergent vegetation at different microsites was obtained by a submersible quantometric sensor (PAR; 400-700 nm) attached to a radiometer (PU 550, Meopta Přerov, Czech Rep.; ADAMEC 2007). The sensor was positioned about 1–2 mm below the water surface (PS shoot level). Readings are expressed as percentage of incident PAR in the adjacent open area.

At the end of the 14-d experiment, the length of the main PS shoots, the number of mature leaf nodes in main PS shoots, number of all PS and CA shoots (for the criteria see ADAMEC 2007), length of 1^{st}-order CA shoots, number of internodes between two successive branches on PS shoots, and the position of the tag on the PS shoots were estimated in all plants. Moreover, all traps on both PS and CA shoots were counted, pooled together, and weighed for DM (ADAMEC 2008a, 2009). Maximum trap size within each plant was estimated using a ruler to the nearest 0.5 mm. Both PS and CA shoots without traps were weighed for DM, for calculating two parameters of the structural investment in carnivory (IC). IC1 is defined as the proportion of trap DM to the total plant DM, while IC2 represents the proportion of DM of CA shoots with all traps to the total plant DM (see ADAMEC 2007). Total plant DM was also estimated. Suggesting an exponential pattern of growth, the doubling time of biomass was calculated from the initial and final values of the total plant DM as a reflection of relative growth rate (ADAMEC 1999, ADAMEC & KOVÁŘOVÁ 2006). The estimation of the percentage of traps with captured animal prey at the end of the experiment would be useful as an important ecological parameter. Since the most traps in both species were stained externally by dark-brown precipitates of humic acids and the majority of traps contained some dark-brown detritus, this estimate was not feasible. Instead, only a rough assessment of prey capture is available.

Table 1. Chemical and physical factors at experimental sites in the Třeboň basin, S Bohemia, Czech Republic where 14-d field-growth experiments on *Utricularia stygia* (fen Lake Karštejn) and *U. intermedia* (Výtopa fishpond) were conducted in 2008. Where possible mean ± SE interval is shown for 5 microsites; the range of values is shown in italics. G, electrical conductivity; TA, total alkalinity; HAT, sum of concentrations of humic acids and tannins; PAR, irradiance cca. 2 mm below the water surface in the % in open area.

Date	G	pH	TA	$[CO_2]$	$[O_2]$	HAT	NH_4-N	PO_4-P	PAR
	$\mu S.cm^{-1}$		$meq.l^{-1}$	mM	$mg.l^{-1}$		$\mu g.l^{-1}$		%
U. stygia									
25 MAY	158 ± 7	6.26	0.85	1.08 ± 0.09	7.5 ± 0.5	9.2	0.0	12.2	--
	135-175	*6.18-6.40*		*0.82-1.33*	*6.0-8.6*				
2 JUN	192 ± 4	6.28	0.94	1.00 ± 0.10	6.0 ± 0.5	14.1	--	--	--
	177-197	*6.22-6.43*		*0.75-1.22*	*4.4-7.0*				
8 JUN	160 ± 7	6.12	0.82	1.08 ± 0.12	--	13.1	0.0	21.1	40.1 ± 4.5
	133-170	*6.16-6.41*		*0.77-1.38*					*30.3-56.7*
U. intermedia									
25 MAY	113 ± 2	6.12	0.62	1.18 ± 0.09	4.6 ± 0.4	29.4	9.3	18.3	--
	106-118	*6.03-6.23*		*0.91-1.44*	*3.5-6.1*				
2 JUN	184 ± 3	6.12	1.04	1.75 ± 0.10	1.3 ± 0.1	44.6	--	--	--
	174-192	*6.06-6.19*		*1.52-2.03*	*1.1-1.6*				
8 JUN	139 ± 5	6.03	0.81	1.74 ± 0.14	--	37.6	0.0	46.8	27.9 ± 2.1
	127-155	*5.98-6.17*		*1.33-2.03*					*21.6-33.8*

During the experiment, many plants at both sites were damaged by trichopteran larvae. Damaged plants were discarded and, thus, only 17 *U. stygia* plants were evaluated at Karštejn, and only 13 *U. intermedia* plants at Výtopa. Due to this fact, the experimental block design could not be used and all final plants were pooled together at each site. All results were expressed as means ± SE. pH values were not transformed. Significant differences between both species were evaluated by a two-tailed t-test where needed.

Results

During the 14-d growth period in the *U. stygia* stand at Karštejn, the mean water temperature at plant level was 18.2 °C (range from 11.3 to 28.6 °C), while the mean daily minima was 14.6 °C and the mean daily maxima was 22.6 °C. Similarly, in the *U. intermedia* stand at Výtopa, the mean water temperature was 17.8 °C (range from 11.4 to 25.0 °C), while the mean daily minima was 14.8 °C and the mean daily maxima was 21.6 °C. The temperature regime at both sites was thus very similar, with the mean daily difference 7 to 8 °C. The slightly higher mean daily temperatures at Karštejn corresponded with greater values of irradiance (40 vs. 28%; Table 1). During the experiment, mean pH values at both sites were relatively stable and varied only within 0.16 of the pH unit. Based on total alkalinity, water at both sites can be considered medium soft. Mean free $[CO_2]$ at both sites was consistently higher than 1 mM. Dissolved $[O_2]$ was higher at Karštejn (4.4–8.6 mg l^{-1}) as compared to Výtopa (1.1–6.1 mg l^{-1}). The concentration of humic acids + tannins in the *U. intermedia* stand exceeded about three times that in the *U. stygia* stand. Water at both sites was very poor in main mineral nutrients. The concentration of NO_3–N was always below detection limit (data not shown) and the same applied for NH_4^+-N at Karštejn and partly for Výtopa (Table 1). The concentration of PO_4-P was 12–21 μg l^{-1} at Karštejn and about twofold at Výtopa.

The shortened initial PS shoot segments of *U. stygia* contained about 22 mature leaf nodes, with CA branches that were on average 3.1 cm long containing about 18 traps. Their investment in carnivory (IC2) as the proportion of CA shoot (+traps) DM to the total plant DM was around 23% (Table 2). The initial PS shoots of *U. intermedia* contained about 20 mature leaf nodes, with CA branches on average only about 2.6 cm long and containing on average around 6 traps. The IC2 was only around 14%. At the end of the experiment, plants of both species had increased markedly in the size of their main PS shoots, and initiated up to two new short PS shoots on CA branches (Table 3). On average, there were 6.7 CA shoots in *U. stygia plants*, while 4.3 shoots in *U. intermedia* were produced. The mean length of 1st-order CA shoots was exactly the same in both species (6.7 cm), however the number of internodes between two successive CA

Table 2. Characteristics of 20 experimental *Utricularia stygia* (US) and *U. intermedia* (UI) plants at the beginning of the 14-d field-growth experiment. The plants consisted of apical photosynthetic (PS) shoot segments with 1–2 carnivorous (CA) shoots. Ten parallel plants were used for estimation of initial total shoot dry mass, trap number, and investment in carnivory (IC2, proportion of DM of CA shoot with all traps to the total plant biomass). Traps from PS shoots were added to CA shoots. Mean ± SE interval is shown.

Spec.	PS shoot length		No. of CA shoots	CA shoot length	Total trap No.	Total shoot DM	Invest. in carnivory (IC2)
	(cm)	(nodes)		(cm)		(mg)	(%)
US	8.0 ± 0.0	21.7 ± 0.7	1.55 ± 0.11	3.07±0.30	18.1 ± 1.6	6.86 ± 0.62	22.9 ± 2.2
UI	6.0 ± 0.0	20.3 ± 0.4	1.25 ± 0.10	2.55±0.31	5.80 ± 1.19	4.49 ± 0.31	13.9 ± 2.9

Table 3. Morphometric and growth characteristics of *Utricularia stygia* (US) and *U. intermedia* (UI) at the end of the 14-d field-growth experiment. PS, photosynthetic; CA, carnivorous; ASGR, apical shoot growth rate. Mean ± SE interval is shown for 17 US plants or 13 UI plants; range of values in italics. Statistically significant difference between the species (t-test); *** – P < 0.001; ** – P < 0.01; * – P < 0.05.

Spec.	Main PS shoot length		No. PS shoots	No. CA shoots	Length of 1st order CA shoots	Internodes between branches	Traps on PS shoots	Traps on CA shoots	Max. trap size	ASGR
	(cm)	(nodes)			(cm)				(mm)	node d^{-1}
	15.6	51.4	2.53	6.71	6.71	12.2***	7.88	46.8	3.56**	2.13*
US	± 0.49	± 1.09	± 0.12	± 0.37	± 0.33	± 0.24	± 0.73	± 3.14	± 0.10	± 0.058
	13.5-19.7	*45-61*	*2-3*	*4-9*	*0.6-10.3*	*9-16*	*3-13*	*30-70*	*3.0-4.0*	*1.71-2.43*
	12.1	47.7	2.00	4.31	6.67	17.7		36.2	4.08	1.91
UI	± 0.26	± 1.46	± 0.16	± 0.50	± 0.62	± 0.41	0.0	± 4.05	± 0.08	± 0.057
	10.5-13.0	*37-53*	*1-3*	*1-8*	*0.3-10.6*	*15-21*		*12-56*	*3.5-4.5*	*1.57-2.29*

Table 4. Biomass characteristics of *Utricularia stygia* (US) and *U. intermedia* (UI) at the end of the 14-d field-growth experiment. PS, photosynthetic; CA, carnivorous; IC1, investment in carnivory 1 (proportion of trap DM to total plant biomass); IC2, investment in carnivory 2 (proportion of DM of CA shoots with all traps to the total plant biomass). Mean ± SE interval is shown for 17 US plants or 13 UI plants; range of values in italics. Statistically significant difference between the species (t-test), * – $P < 0.001$; NS – $P > 0.05$.

Spec.	PS shoot DM (mg)	CA shoot +trap DM (mg)	DM of traps (mg)	Total shoot DM (mg)	DM of one trap (µg)	IC1 (%)	IC2 (%)	Doubling time of biomass (d)
US	11.2 ± 0.90 *6.9-21.7*	8.48 ± 0.64 *5.2-13.9*	3.81 ± 0.30 *2.3-6.7*	19.7 ± 1.46 *12.7-35.6*	69.4* ± 3.93 *49-103*	19.7^{NS} ± 1.07 *13.9-28.2*	42.8^{NS} ± 1.28 *34.5-53.2*	9.21
UI	11.2 ± 0.55 *8.9-14.4*	8.14 ± 0.62 *5.9-10.9*	4.55 ± 0.40 *3.2-6.1*	19.4 ± 0.90 *15.1-23.6*	114 ± 6.8 *92-153*	23.3 ± 1.39 *16.7-29.8*	41.8 ± 1.04 *32.4-52.5*	6.64

branches on the main PS shoots in *U. stygia* (12.2 ± 0.2) was highly significantly lower than that in *U. intermedia* (17.7 ± 0.4). The mean ASGR in *U. stygia* (2.13 ± 0.06 node d^{-1}) was also significantly higher than in *U. intermedia* (1.91 ± 0.06). In *U. intermedia*, traps occurred only on CA shoots, while several traps occurred also on PS shoots in *U. stygia*.

The maximum trap size and DM for one trap were significantly greater in *U. intermedia* (Table 4). The values of IC1 in both species ranged from 20–23 %, and from 42–43 % in IC2, not providing a significant difference. Despite the initial variation in total shoot DM between both species the final DM was exactly the same, indicating a markedly higher growth rate in *U. intermedia* as compared to U. stygia (T_2 recorded at 6.64 d and 9.21 d, respectively). The inspection of traps showed that 25–35 % in both species had captured animal prey, while 50–60 % contained dark-brown detritus, potentially sucked in during plant manipulation (data not shown).

Discussion

According to water chemistry (Table 1), *U. stygia* habitat at Karštejn can be considered oligotrophic, while that of *U. intermedia* at Výtopa is slightly mesotrophic. Due to no or very low concentrations of mineral N at both sites, however, it is possible to assume that the growth of both *Utricularia* species could be limited more by N than P (although some organic N was present in the form of humic acids at both sites). It is also possible to assume that a great deal of N, P, and K necessary for plant growth was taken up from prey (ADAMEC 2008b). Though the water chemistry recorded in this study (2008) is similar to that found at these or similar sites during the last 8 years (cf. ADAMEC & KOVÁŘOVÁ 2006, ADAMEC 2007, 2008b), they do show variation most likely due to water level and quantity of precipitates. Generally, both at Karštejn and Výtopa in 2008, dissolved O_2 concentrations and free [CO_2] in the plant stands were so high that they enabled rapid plant growth.

The present growth experiment on two *Utricularia* species with dimorphic shoots was based on young, slightly shortened, subadult PS main shoots with around one month of growth from turion sprouting, however, growth continued under natural conditions. The young age of initial shoots explains why IC2 values (14–23%) were relatively low as compared to final shoots (42–43%; cf. Table 2 and 4) as when turions germinate they give rise to PS shoots without traps (ADAMEC 2007). Since the size of the initial shoots and therefore their DM differed greatly between both species (Table 1), the final values of plant size or DM cannot simply be compared. Although the final *U. stygia* PS shoots were somewhat longer, had more leaf nodes, and branched markedly more than in *U. intermedia*, the latter species had more robust PS and CA shoots. The present results confirmed previous findings (ADAMEC 2007) that the initiation of new CA branches on the main PS shoot was more frequent in *U. stygia* (Table 3).

The ASGR values found in both species (1.9–2.1 node d^{-1}; Table 3) at relatively high water temperatures are comparable with those reported in several aquatic *Utricularia* species with monomorphic shoots: up to 2.8 node d^{-1} in field-grown *U. vulgaris* in England (FRIDAY 1989), 0.9–1.2 node d^{-1} in *U. australis* grown outdoors in a container (ADAMEC 2008a), and 2.7–3.5 node d^{-1} (ADAMEC & KOVÁŘOVÁ 2006) or 2.5–4.2 node d^{-1} for field-grown *U. australis* in the Czech Republic (ADAMEC 2009). Yet, the ASGR of field-grown *U. purpurea* in Florida was only 0.25 node d^{-1} suggesting that this species grows exceptionally slowly (RICHARDS 2001). In harmony with the rapid apical shoot growth found, both *Utricularia* species exhibited also very rapid production of new biomass so that T_2 values – as a measure of relative growth rate – ranged only from 6.6 d in *U. intermedia* to 9.2 d in *U. stygia* (Table 4). Although available T_2 values are very scarce for field-grown aquatic carnivorous plants, the values for *U. intermedia* and *U. stygia* represent the most rapid growth ever found for aquatic carnivorous plants. ADAMEC & KOVÁŘOVÁ 2006 reported T_2 values between 9.1–33.2 d for *U. australis* and 8.4–21.5 d for *Aldrovanda vesiculosa* growing in two dystrophic waters including Karštejn. Similarly, ADAMEC 1999 estimated T_2 values for *A. vesiculosa* at several favourable shallow sites in the Czech Republic to range from 12.9–25.8 d. However, very rapid apical shoot growth in aquatic *Utricularia* species may not correlate strictly with high relative growth rate as found for *U. australis* grown in oligotrophic sand-pits (ADAMEC 2009).

Both types of IC, estimated in *U. stygia* and *U. intermedia* at the end of the growth experiment (Table 4), were similar to those estimated in natural populations of these species (cf. ADAMEC 2007). Moreover, these species allocated to traps or CA shoots with all traps on average similarly as aquatic

Utricularia species with monomorphic shoots to traps (cf. Knight & Frost 1991, Friday 1992, Richards 2001, Englund & Harms 2003, Porembski & al. 2006, Adamec 2008b, 2009). *Utricularia* traps represent very high metabolic (energetic) cost due to their high respiration rate (Adamec 2006), yet, this metabolic cost has been found to be around the same for species with dimorphic or monomorphic shoots: 60–68% of the total plant respiration for *U. intermedia* and *U. stygia* CA shoots with all traps, and 67% for *U. australis* traps (Adamec 2006, 2007). If so, success of prey capture as the main function of CA shoots should be taken into account, judging the ecological benefit of differentiated CA shoots which bear the dominant majority of traps. Evidently, in very shallow, strongly dystrophic waters with a relatively deep layer of anoxic, partly decomposed, nutrient-poor organic substrate (Adamec 2007), the aquatic *Utricularia* species with distinctly differentiated shoots can ecologically dominate over the "pelagic" species with monomorphic shoots. Even though a great availability of prey in such anoxic substrates is doubtful, shortage of animal prey may be compensated for by a great availability of detritus as shown in this study.

In conclusion, a knowledge of both growth rates, biometric characteristics, and nutrient relations is essential in understanding the 'cost-benefit relationships' involved in the utilization of resources by aquatic carnivorous plants. In this study, two temperate aquatic *Utricularia* species with dimorphic shoots exhibited a similarly high apical growth rate of PS shoots as it is reported in the literature for aquatic species with monomorpic shoots. Moreover, the estimated doubling time for biomass of the two species (6.6–9.2 d) represents the absolute maximum growth rate ever estimated for an aquatic carnivorous plant (*Aldrovanda, Utricularia* spp.). These findings thus clearly support the ecophysiological concept that aquatic carnivorous plants differ greatly from their terrestrial counterparts in their very rapid growth.

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Recensio

SMITH Nathan, MORI Scott A., HENDERSON Andrew, STEVENSON Dennis Wm. & HEALD Scott V. (eds.) 2004. Flowering Plants of the Neotropics. – Lex. 8°, 594 Seiten, 1 Karte, 258 Abbildungen + 64 Tafeln mit 308 Farbphotos; geb. – Princeton University Press, Princeton and Oxford. – € 51.95. – ISBN 0-691-11694-6.

Ein wunderbares, prächtiges, informatives, didaktisch gutes und – bis auf Format und Gewicht – ein sehr praktisches Buch, das nur Begeisterung auslösen kann!

Das Buch gewährt eine ausgezeichnete Übersicht über die neotropische Diversität der Blütenpflanzen, indem 277 Familien in ABC-Folge nach einem einheitlichen Schema abgehandelt und durch meist eine, gelegentlich auch zwei oder drei Abbildung(en) von Vertretern der betreffenden Familie illustriert sind. Die Abbildungen sind gute, klare Strichzeichnungen, die neben dem Habitus auch viele Details (Blüte, Frucht, vegetative Merkmale etc.) zeigen. Die Familienbeschreibungen wurden von jeweiligen Kennern oder Spezialisten verfaßt, 150 Autoren haben sich an dem Werk beteiligt. Allein so viele Bearbeiter unter einen Hut zu bringen, ist schon eine bewundernswerte Leistung.

Der Aufbau der Beiträge folgt jeweils folgenden 8 Abschnitten:

1. Einige hervorstechende, zur Identifizierung der Familie geeignete Merkmale.
2. Zahl der Gattungen und Arten weltweit und in der Neotropis.
3. Verbreitung und Standort.
4. Familiensystematik und Familiengliederung. Das Buch folgt im allgemeinen den Systemen von CRONQUIST 1981 und DAHLGREN & al. 1985; Abweichungen sind diskutiert und in Appendix 1–4 (p. 529–534) dargestellt.
5. Eigenschaften der Familie gibt umfassende Beschreibungen vegetativer, Blüten-, Frucht- und Samenmerkmale.
6. Naturgeschichte bringt Hinweise auf Bestäubung und Ausbreitung.
7. Wirtschaftliche Nutzung.
8. Literatur. Den Abschluß jeder Familienbeschreibung bildet eine Liste der wichtigsten, speziell für die jeweilige Familie weiterführenden Literatur.

Das Tüpfchen auf dem i sind die durchwegs hervorragenden Farbphotos von Blüten oder Früchten. Auf p. 497–521 findet sich ein umfangreiches Glossar mit zwei Seiten Abbildungen. Hier möchte der Rezensent nur buzz pollination herausgreifen und zum wiederholten Male [z. B. in Phyton 45(2): 219, 2005] darauf hinweisen (was andere Autoren auch taten), daß es richtig buzz collection heißen muß, weil das Buzzing für das aktive Pollensammeln durch die Bienen, nicht aber für die Bestäubung wesentlich ist. Außerdem wird man nicht umhin können, die Synonyme vibratory pollen collection und sonication auch anzugeben. Eine Literaturliste folgt auf p. 525–527. Appendix 5 (p. 535–562) ist ein zu den Familien führender Bestimmungsschlüssel und der Index auf p. 563–594 schließt den Band ab.

Der vorliegende Band geht über MAAS & WESTRA 1998, Neotropical Plant Families sowie GENTRY 1993, A Field Guide to the Families and Genera of Woody Plants of Northwest South America weit hinaus. Letzterer ist wegen der Gattungsschlüssel sicher als Ergänzung zum vorliegenden Band gut brauchbar. Der Rezensent versucht gewissenhaft, Übertreibungen und Floskeln zu vermeiden; im vorliegenden Falle möchte er aber doch aus Überzeugung sagen, daß Flowering Plants of the Neotropics für jeden – vom Studierenden bis zum Systematik-Professor – ein Gewinn sein wird.

H. TEPPNER