

Dark respiration and photosynthesis of dormant and sprouting turions of aquatic plants

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With 1 figure and 2 tables

Abstract: Turions are overwintering, dormant organs, produced by aquatic plants. In spring, aerobic dark respiration (R_D) and photosynthetic rates (P_N) were measured as criteria of metabolic activity and photosynthetic capacity in dormant turions of 7 temperate aquatic plant species. These rates were also measured in old, original turion segments and in the newly formed shoots of sprouting turions. Two non-carnivorous rooting species (*Caldesia parnassifolia*, *Hydrocharis morsus-ranae*) and 5 carnivorous rootless species (*Aldrovanda vesiculosa*, *Utricularia vulgaris*, *U. australis*, *U. stygia*, *U. bremii*) were studied. R_D values of dormant turions per unit fresh weight (range 1.1–5.4 mmol kg⁻¹_{FW} h⁻¹) were significantly lower (1.9–13 times) for all species, except *A. vesiculosa*, than those for old segments of sprouting turions (range 5.2–14 mmol kg⁻¹_{FW} h⁻¹). However, R_D and P_N values of old and newly formed turion segments in *U. australis* and *U. stygia* were similar. P_N values of dormant turions under optimum conditions were either very low or negative, while P_N values of old segments of sprouting turions of all species except *H. morsus-ranae* were very high (18–94 mmol kg⁻¹_{FW} h⁻¹). In a N- and P-free solution, turions of all species except *A. vesiculosa* formed distinct new organs after 6–20 days. In conclusion, the intensity of metabolism (both R_D and P_N) in sprouting turions reaches the level of adult shoots or leaves of the same species. Turions of aquatic plants also function as important storage organs for mineral nutrients (N, P, S and Mg) to ensure the growth of new organs.

Key words: Carnivorous and non-carnivorous plants, imposed dormancy, turion sprouting, aerobic respiration, photosynthetic rate, storage functions.

Introduction

Turions (winter buds) are vegetative dormant organs produced by perennial aquatic plants in response to unfavourable ecological conditions (Sculthorpe 1967, Bartley & Spence 1987). Turions are formed by extreme condensation of short, modified leaves in the shoot apex and are tough, sturdy organs. They form at the end of the growing season and can be spherical (*Utricularia*), rhomboid (*Aldrovanda*) or greatly enlarged (*Potamogeton* spp., *Caldesia*). Turions are

overwintering organs and are partly frost resistant protecting fragile plant shoots from freezing and decaying (Winston & Gorham 1979 a, Adamec 1999 a). They are also storage organs and, in autumn, they accumulate starch (9–70 % dry weight (DW)) and free sugars (in total 7–14 % DW, Winston & Gorham 1979 a, Kunii 1989, Ley et al. 1997, Adamec 2003 a,b, Weber & Noodén 2005). Turions of aquatic plants also act as storage organs for mineral nutrients (N, P) though this storage function (*sensu* Chapin et al. 1990) is presumably less distinct than that for carbohydrates (Adamec 2010).

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Turions of all aquatic plant species usually overwinter and break their innate dormancy at the bottom of their aquatic habitat in darkness and under hypoxic or anoxic conditions. Two distinct ecological strategies for their germination and sprouting may be distinguished (Sculthorpe 1967, Bartley & Spence 1987, Adamec 2008). Turions of free-floating aquatic genera (e.g., *Hydrocharis*, *Utricularia*, *Aldrovanda*, *Spirodela*) ripen at the water surface, overwinter at the bottom, then usually germinate and sprout at the water surface when the water warms. Those of aquatic rooted genera, however, (e.g., *Potamogeton*, *Caldesia*, *Myriophyllum*) ripen, germinate, sprout and root at the bottom in colder water and in shade. Moreover, turions of free-floating aquatic species differ considerably in the mechanism of autumnal sinking and spring floating (Newton et al. 1978, Adamec 1999 b, 2008): Turions of *Aldrovanda vesiculosa*, *Hydrocharis morsus-ranae*, and *Spirodela polyrhiza* have developed an active mechanism of sinking and rising. For *Aldrovanda*, this is caused by a variable release of gas from gas spaces in the turion leaves (Adamec 2003 a), while *Utricularia* turions are less dense than water and are dragged to the bottom by their decaying, denser mother shoots. In early spring, the turions separate and float to the surface (Adamec 1999 b). Rising of turions due to evolution of a gas in internal gas spaces (*Aldrovanda*, *Hydrocharis*) or on the external turion surface (*Spirodela*) is triggered by the increasing water temperature breaking the imposed dormancy (Newton et al. 1978, Adamec 1999 b, 2003 a).

Two dormancy states and their hormonal patterns were described in detail for turions of Canadian *Utricularia macrorhiza* using bioassays (Winston & Gorham 1979 b). Turions enter a state of innate dormancy at the end of the summer, when their growth is blocked by endogenous factors in the turions and when ageing and dying of their mother shoots occurs. In this state, they cannot germinate even at high temperature. High levels of abscisic acid induce turion formation and low levels of free gibberellins, auxin and cytokinins occur in this state. Innate dormancy was only broken by the combination of short days and low temperatures at the end of October and the turions entered a state of imposed dormancy when turion germination depends only on higher temperature. This was characterized by a decreasing level of abscisic acid and increasing levels of gibberellins, auxin and cytokinins. When the imposed dormancy was broken by a temperature increase, the first turions germinated after two days. Low levels of abscisic acid and high levels of the other three stimulatory phytohormones were found during

this phase. The next stage in turion germination leads to the sprouting of new shoots and this occurs under sufficient temperature and light conditions. These two dormancy states were also described in *Aldrovanda vesiculosa* turions (Adamec 2003 a).

Turions are always green-coloured and are weakly capable of photosynthesis (Beer 1985, Adamec 2003 a); in *Aldrovanda* turions, the chlorophyll-*a* content is similar to that found in adult shoots (Adamec 2000). Although turions contain chlorophyll, their net photosynthetic rate (P_N), even under optimum conditions, is very low and commonly negative. P_N is reportedly dependent on turion size with small turions having positive P_N values (cf. Beer 1985, Adamec 2003 a). Photosynthesis or chlorophyll content are obviously not important for dormant turions, which contain much stored carbohydrate, but are important for sprouting turions which start producing new biomass. High chlorophyll content in turions may thus contribute to attaining high P_N in sprouting turions without the need for its *de novo* synthesis. This offers the plants a competitive advantage over annual species.

As in typical storage organs, the aerobic dark respiration rate (R_D) of dormant turions of 6 aquatic species was rather low when compared with R_D of shoots (leaves) of aquatic plants of the same or similar species (Adamec 2008) – around 30–75 % lower on a fresh weight (FW) basis (1.3–5.2 mmol kg⁻¹ h⁻¹) and 80–85 % lower per unit DW. For turions in the innate dormancy state, a high proportion of the total R_D was cyanide-resistant respiration (22–90 %) (Adamec 2008) indicating a low energy demand for these organs. Respiration Q_{10} values were usually higher in spring turions (imposed dormancy) when compared with the autumnal ones (innate dormancy) but no greater changes in R_D occurred. For *A. vesiculosa* turions in both innate and imposed dormancy states, the rate of anaerobic fermentation was only 1.5–7 % of the values for R_D and did not increase during the 2 days following the break of imposed dormancy (Adamec 2003 a). However, as turions usually overwinter under hypo- or anoxic conditions, the lower values of anaerobic fermentation and energy consumption are more realistic under natural conditions than the experimental aerobic values (Adamec 2008). In these turions, during the break of imposed dormancy, the R_D values were almost constant and the same was also true for the content of starch and free sugars (sucrose, glucose, fructose; Adamec 2003 a). Thus, all dormant turions and those just breaking imposed dormancy exhibit an R_D which is several times lower than that of shoots. However, R_D of sprouting *A. vesiculosa* turions

is high and comparable with that of shoots (Adamec 2008, cf. Czopek 1964).

All mineral nutrients allocated for the next season's plant growth are transferred by turions as these propagules are the only part of the plant that survives over winter. Turions overwintering at low temperatures probably need only a very low mineral nutrient level to ensure their maintenance function. Germinating and sprouting turions only enlarge internodes and use reserves of organic and mineral nutrients as, presumably, their leaves (which are modified to have storage function) are not able to take up mineral nutrients from the water until new roots or shoots are formed. The main mineral storage function of turions could thus be associated with supporting the growth of new roots or shoots in relatively cold water. Adamec (2010) has recently shown that for 12 aquatic plant species, the turion N and P content is moderately lower but the K, Ca and Mg is markedly lower than that in growing shoots/leaves of the same or similar species (cf. also Knight 1988, Adamec 2000). Yet, Adamec (2010) has assessed that theoretically, about 30 % of the total turion's N and about 50 % of the P content could be re-utilized, as if they were stored mineral nutrients, and facilitate the sprouting of new organs without a decrease in growth rate of the sprouting turions. In *Hydrocharis morsus-ranae* turions, a great deal of the total organic N was found in the form of arginine (Villanueva et al. 1985).

In this paper, aerobic R_D and P_N were measured in turions of 7 temperate aquatic plant species of different functional groups in the spring. R_D was used as a criterion of physiological and metabolic organ activity and P_N as a measure of photosynthetic organ capacity (e.g. Adamec 2005, 2006, 2008). The two non-carnivorous species form roots (*Caldesia parnassifolia*, *Hy-*

drocharis morsus-ranae) while the other 5 carnivorous species are rootless (*Aldrovanda vesiculosa*, *Utricularia vulgaris*, *U. australis*, *U. stygia*, *U. bremii*). Both R_D and P_N were compared in the spring for overwintered turions in the state of imposed dormancy (denoted henceforth as "dormant") and in sprouting turions (denoted as "sprouting"). Additionally, original old turion segments (denoted as "old") and newly sprouting shoot segments (denoted as "new") were studied. Thus, the aim was to determine at which phase of sprouting the turion becomes independent of its carbohydrate store and produces new biomass. Furthermore, as the turions were sprouting in a N- and P-free medium, all N and P contained in the newly sprouting shoot segments (leaves) had to be provided by the old turion segments. Photo documentation was provided to demonstrate the ability of turions to function as storage organs for N and P.

Material and methods

Plant material

Ripe turions of *Hydrocharis morsus-ranae* L. (Hydrocharitaceae; non-carnivorous, rooting free-floating) and *Aldrovanda vesiculosa* L. (Droseraceae; carnivorous, rootless submerged) were collected from two field sites in the Třeboň Basin Biosphere Reserve and Protected Landscape Area, S. Bohemia, Czech Republic (approx. 49° N, 14° 45' E) in October 2009. Ripe turions of another 5 aquatic species were collected from artificial cultures in 1–2.5 m² outdoor plastic containers at the Institute of Botany at Třeboň during the 2009 autumn from 28 September to 20 November (for details see Adamec 2010). They were: *Caldesia parnassifolia* L. (Alismataceae; non-carnivorous, bottom rooting, amphibious), and 4 carnivorous rootless submerged species: *Utricularia vulgaris* L. (Lentibulariaceae), *U. australis* R. Br., *U. stygia* Thor (syn. *U. ochroleuca* Hartm. s.l.), and *U. bremii* Heer (see Table 1). Ripe turions of all 7 species were washed with tap water and stored in filtered

Table 1. Size and FW of dormant or sprouting turions used for measurement of R_D and P_N . CP, *Caldesia parnassifolia*, HM, *Hydrocharis morsus-ranae*, AV, *Aldrovanda vesiculosa*, UV, *Utricularia vulgaris*, UA, *U. australis*, US, *U. stygia*, UB, *U. bremii*. The overwintered dormant turions were in the state of imposed dormancy. Time, time of turion sprouting at 20 °C. In sprouting turions, old turion segments were used for the measurements and, in UA and US, also newly sprouting organs were used.

Spec.	Dormant turions		Sprouting turions					
	Size (mm)	FW (mg)	Old segments			Newly sprouting organs		
			Time (d)	Size (mm)	FW (mg)	Time (d)	Size (mm)	FW (mg)
CP	11–14	61–85	8	~15	26–54	–	–	–
HM	7–8	80–139	6	15–20	45–108	–	–	–
AV	5–6	90–148	8	16–20	18–26	–	–	–
UV	10–12	135–214	4	40–50	32–108	–	–	–
UA	5–7	84–171	5	30–35	14–25	8	35–45	12–14
US	4–7	51–85	5	20–25	10–18	6–10	25–30	9–18
UB	3–4	90–147	6	8–12	24–40	–	–	–

cultivation media (from the outdoor culture of *U. vulgaris* and *U. stygia*) in a dark refrigerator at 2 to 3 °C over winter; the measurements were made at the beginning of April 2010. It was verified that the turions of all these species had been innately dormant in mid-November.

Gasometric measurements

Aerobic R_D and P_N of turions of the 7 species were measured both in dormant turions taken straight from the refrigerator and in old turion segments of sprouting turions. Turions were allowed to germinate and sprout in a growth chamber at 20 ± 1 °C with a 14 h photoperiod in a N- and P-free solution of 0.2 mM NaHCO_3 with 0.1 mM KCl and 0.05 mM CaCl_2 for 4–20 days. The solution was renewed every 3 days. Thus, the N, P, S and Mg content of the newly sprouting shoot segments or leaves was provided by the old turion segments. Before measurement, the two outermost membranous leaves of *Hydrocharis* and *Caldesia* turions were removed and dormant turions of *Hydrocharis* and *U. vulgaris* were halved longitudinally with a razor blade to ensure a better contact with the solution. Different numbers of turions (1–8) of each species were used to attain a sufficient response (see Table 1 for the size and fresh weight [FW] of dormant turions measured). Whole sprouting turions of *Caldesia*, *Hydrocharis* (without membranous leaves and roots) and *U. breinii* and old segments from the middle of sprouting turions of the other species were also used for the measurements (see Table 1 for the time of sprouting and the size of the sprouting turions). In *U. australis* and *U. stygia*, R_D and P_N were also measured in newly grown subapical shoot segments of sprouting turions (for 6–10 days, Table 1).

Measurements of R_D and P_N were performed in a solution of 1 mM NaHCO_3 with 0.1 mM KCl (80–90 % oxygen saturation) in a 5-ml stirred chamber (thermostated at 20.0 ± 0.1 °C), using a Clark-type oxygen sensor and a pen recorder (for all details see Adamec 2003 a, 2005, 2006). The initial solution pH was 6.97 and the free CO_2 concentration was 0.25 mM. After R_D had been measured in darkness for 12–15 min, the chamber was illuminated (20 W halogen reflector, $400 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) and P_N was measured for 12–15 min. FW was then determined for all plant material used and DW (80 °C) was estimated in pooled samples. All measurements were repeated 6 times with different plant material. Means ± 1 SE are shown and R_D and P_N are expressed in $\text{mmol kg}^{-1} \text{FW h}^{-1}$. Within each species, statistically significant differences in R_D and P_N between dormant and sprouting turions (old vs. new segments) were evaluated by 1-way ANOVA. Sprouting turions were placed under water in a Petri dish and scanned using a desktop scanner to demonstrate the growth of new shoots facilitated by nutrients stored solely within the turions.

Results

In the dormant turions of all species except *C. parnassifolia*, there was a markedly greater proportion of DW to FW than in old segments of turions sprouting for 4–8 d (Table 2). R_D values of dormant turions per unit FW (range 1.1–5.4 $\text{mmol kg}^{-1} \text{FW h}^{-1}$) were significantly lower (1.9–13 times) in all species except *A. vesicu-*

Table 2. Aerobic dark respiration (R_D) and net photosynthetic rate (P_N) of turions of aquatic plants overwintered in a refrigerator at 2 to 3 °C in a state of imposed dormancy (dormant turions), in old segments of sprouting turions (at 20 °C for 4–8 days), or in new segments of sprouting turions. All measurements at 20.0 ± 0.1 °C; P_N at $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 0.25 mM CO_2 . R_D and P_N expressed in $\text{mmol O}_2 \text{kg}^{-1} \text{FW h}^{-1}$; DW, in % of FW. The negative sign for P_N denotes negative photosynthesis. Different letters for either R_D or P_N denote statistically significant difference at $p < 0.02$ (one-way ANOVA) within each species. Means ± 1 SE are shown; $n = 6$.

Species	Dormant turions			Sprouting turions (old segments)			Sprouting turions (new segments)		
	DW (%)	R_D	P_N	DW (%)	R_D	P_N	DW (%)	R_D	P_N
<i>Caldesia parnassifolia</i>	31.3	3.56 ^a ± 0.60	-1.61 ^a ± 0.43	32.7	6.63 ^b ± 0.85	17.6 ^b ± 2.4	–	–	–
<i>Hydrocharis morsus-ranae</i>	33.5	5.37 ^a ± 0.30	-1.70 ^a ± 0.41	21.2	10.1 ^b ± 0.5	8.77 ^b ± 0.67	–	–	–
<i>Aldrovanda vesiculosa</i>	18.8	4.47 ^a ± 0.19	-3.13 ^a ± 0.25	12.3	5.22 ^a ± 0.48	93.7 ^b ± 3.7	–	–	–
<i>Utricularia vulgaris</i>	18.4	2.12 ^a ± 0.21	2.57 ^a ± 0.28	10.9	7.14 ^b ± 0.32	42.3 ^b ± 2.8	–	–	–
<i>Utricularia australis</i>	37.0	1.06 ^a ± 0.06	0.46 ^a ± 0.15	25.0	14.0 ^b ± 0.8	52.3 ^b ± 1.6	14.4	12.7 ^b ± 0.4	67.0 ^c ± 3.6
<i>Utricularia stygia</i>	23.6	4.05 ^a ± 0.25	-2.78 ^a ± 0.31	13.5	10.8 ^b ± 0.5	70.3 ^b ± 2.8	7.3	10.7 ^b ± 1.3	76.6 ^b ± 4.9
<i>Utricularia breinii</i>	30.9	4.31 ^a ± 0.20	0.81 ^a ± 0.38	20.4	11.8 ^b ± 0.9	30.2 ^b ± 1.8	–	–	–
Mean per DW	–	13.8	–	–	52.8	303	–	117	757
Range per DW	–	2.9– 23.8	–	–	20.3– 80.0	41.4– 762	–	88.2– 147	465– 1049

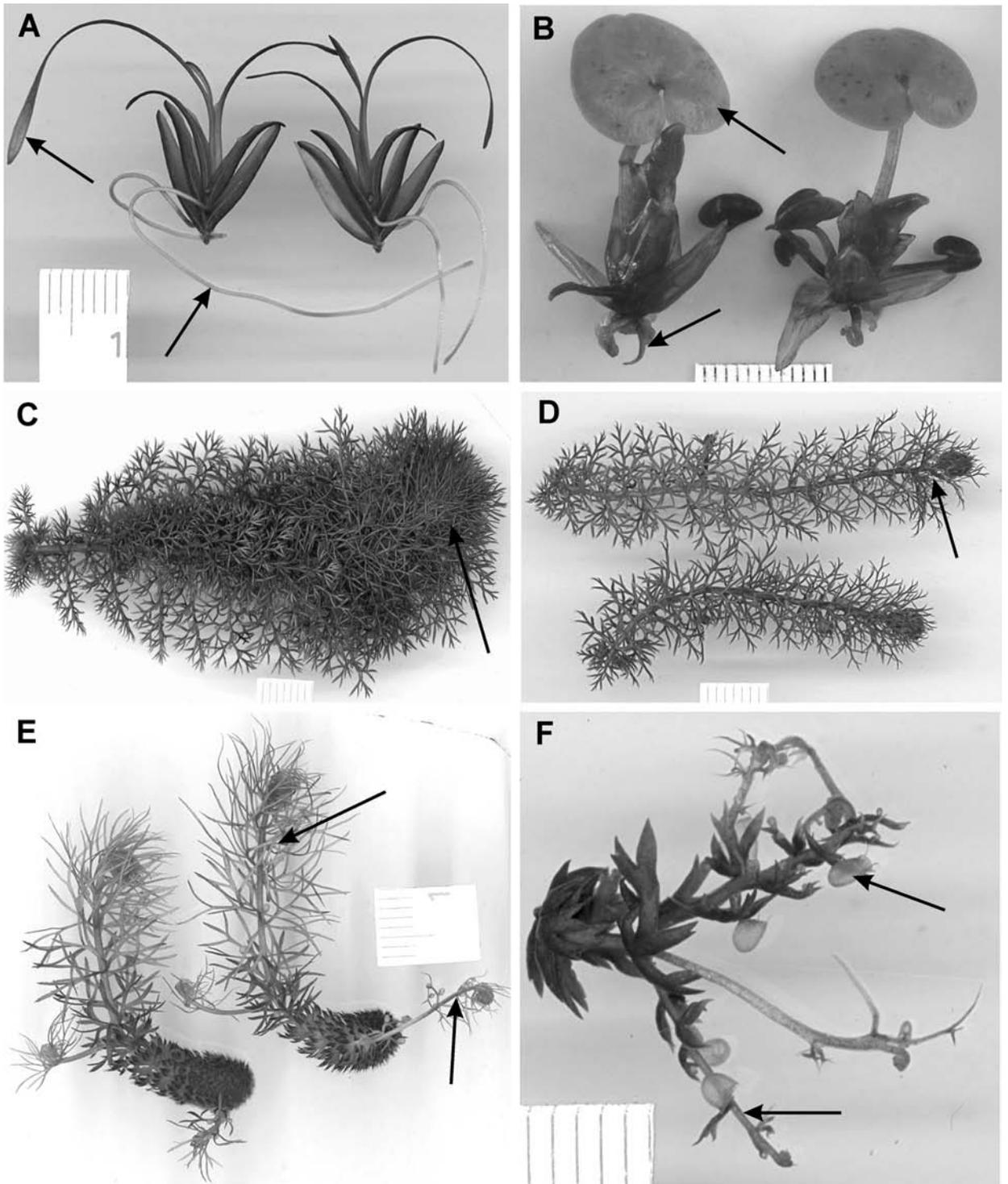


Fig. 1. Turions sprouting at 20 °C in a N- and P-free medium. **A**, *Caldesia parnassifolia* (20 d), **B**, *Hydrocharis morsus-ranae* (9 d), **C**, *Utricularia vulgaris* (10 d), **D**, *U. australis* (8 d), **E**, *U. stygia* (10 d), **F**, *U. breinii* (15 d). Arrows indicate the newly sprouting organs. Ticks in the scale, 1 mm

losa than those in old segments of sprouting turions (range 5.2–14 mmol kg⁻¹ FW h⁻¹). However, R_D values of old and newly formed turion segments in *U. australis* and *U. stygia* were similar. P_N values of dormant

turions under optimum conditions were very low and comparable with the R_D values only in *U. vulgaris*, *U. australis* and *U. breinii*. P_N values of dormant turions were negative in the other species (Table 2). P_N values

of old segments of sprouting turions of all species except *H. morsus-ranae* were, however, relatively very high ($18\text{--}94\text{ mmol kg}_{\text{FW}}^{-1}\text{ h}^{-1}$) and greatly exceeded the R_{D} values; in *H. morsus-ranae* both values were similar. P_{N} values for new subapical shoot segments of sprouting turions were significantly higher than those in old segments only in *U. australis*. The proportion of DW to FW was markedly lower in the new shoot segments of both *U. australis* and *U. stygia*. The differences in R_{D} between dormant and sprouting turions and the differences in R_{D} and P_{N} between old and newly formed shoot segments can be clearly seen when they are expressed per unit DW (Table 2).

With the exception of sprouting turions of *A. vesiculosa*, turions of all the other 6 species of aquatic plants kept in the N- and P-free solution formed new organs within 6–20 days (Fig. 1). Sprouting turions of *C. parnassifolia* and *H. morsus-ranae* formed new roots and leaves (Fig. 1 A,B). Sprouting turions of *U. vulgaris* and *U. australis* formed new shoot apices with young leaf nodes (Fig. 1 C, D), while turions of *U. stygia* and *U. breinii* additionally produced young carnivorous shoots or branches with functional traps (Fig. 1 E, F).

Discussion

The measurement of aerobic R_{D} in dormant, spring turions of 7 aquatic plant species (Table 2) has fully confirmed the previously reported findings for both innate and imposed dormancy states. It has been confirmed that they behave as typical overwintering storage organs (Adamec 2003 a, 2008) and that their R_{D} values are very low when compared with the reported values for growing shoots or leaves in the same or similar aquatic species at the same temperature (for the comparison and references see Adamec 2008). Although the R_{D} values of some species studied here differed from each other by up to 2.5–5 times, it is not clear which ecological traits are responsible for this; statistical analysis is not feasible because of the low number of species studied. The differences seem to be rather species-specific. Within the plant species measured, the highest R_{D} of dormant turions at 20 °C was always in *H. morsus-ranae* and *A. vesiculosa*, while the lowest was in *U. australis* (Table 2; cf. Adamec 2008). Adamec (2008) explained these results as being due to the thermophilous character of *H. morsus-ranae* and *A. vesiculosa* summer shoots and to actively sinking and floating turions in both species. Higher R_{D} in these turions will presumably lead to a faster evolution of

gas in the leaf lacunae of turions and faster turion floating. Dormant turions of *U. australis* have a very low R_{D} value but their sprouting turions have the highest measured value. This might reflect the very long lifespan of their overwintering turions (Adamec 2008) and the very rapid apical shoot growth (Adamec 2009, Adamec et al. 2010). The aerobic R_{D} values measured in dormant turions at 20 °C represent only the theoretical maximum values of respiration as most turions overwinter under stagnant conditions and are buried in the anoxic bottom sediment (Adamec 1999 a,b) where only anaerobic fermentation can occur (see Adamec 2003 a, 2008). Similarly, P_{N} values of dormant turions, even under optimum conditions, were consistently either very low or negative (Table 2). It may be concluded that the ecological importance of photosynthesis in dormant turions is negligible.

Turions sprouting in warm water for 4–8 days increased their FW-based R_{D} values in old, original turion segments by 1.2–13 times when compared with dormant turions. The increase per unit DW even reached 1.8–19 times (Table 2). This means that the sprouting turions usually have much more efficient respiration apparatus in their old tissues than dormant turions, regardless of the water content (cf. Adamec 2008). Similarly, Simola et al. (1985) found gradual and marked metabolic changes in the composition of fatty acids in glycolipids during 6 days of *U. vulgaris* turion germination. Only minor changes were found in the glycolipid classes but the proportion of unsaturated/saturated fatty acids in the glycolipids gradually increased in the turions during germination. Moreover, both R_{D} and P_{N} values of old segments in sprouting turions (except for P_{N} in *C. parnassifolia* and *H. morsus-ranae*) were comparable with those commonly found in growing shoots/leaves of aquatic plants (cf. Adamec 2006, 2008). There was almost no significant difference in FW-based R_{D} and P_{N} values between old and newly formed organs in sprouting turions but both parameters per unit DW were markedly higher (mean 2.2–2.5 times) in the new organs in two *Utricularia* species (Table 2). This again demonstrates a much more efficient respiration and photosynthetic apparatus in newly growing organs. Winston & Gorham (1979 a) reported that the R_{D} of 2–3 week sprouting turions of *U. vulgaris* increased exponentially with increasing temperature between 5 to 35 °C. Sprouting turions (8 d) of *C. parnassifolia* were only spread and opened (Fig. 1 A) but the character of their turion leaves with the high proportion of DW was unchanged. This amphibious species prefers terrestrial photosynthesis in its adult natant or emergent foliage. The very low P_{N} in sprouting *H. morsus-*

ranae turions (6 d) may occur because this free-floating species relies on terrestrial photosynthesis in its adult floating leaves (Fig. 1 B). In conclusion, P_N in both old and newly produced organs of sprouting turions of all submerged species is high when compared with that of adult shoots of the same species. This is ecologically very important for the new rapid growth of sprouting turions and the rapid production of standing biomass at the beginning of the growing season.

Another aim of the present study was to show that turions of aquatic plants also function as storage organs for mineral nutrients. Of the 7 tested species, turions of 6 species sprouting in a medium free from N, P, S and Mg for 6–20 d were able to form new organs – roots, leaves (*C. parnassifolia*, *H. morsus-ranae*) or leafy apical shoot segments with traps (all *Utricularia* species; Fig. 1). It is, however, not possible to distinguish precisely an exact boundary in sprouting turions between the old, original organs and the newly formed ones. Yet in the turions of the 6 species (Fig. 1) sprouting in the nutrient deficient medium, new organs were produced and their total amount of N, P, S and Mg was allocated from the original tissues of the turions. This suggests that turions generally function as storage organs for mineral nutrients for the production of new organs (roots, leafy shoots, traps; after Chapin et al. 1990) which then attain the ability to take up mineral nutrients from the medium. Quite different regulation occurs in *Spirodela polyrhiza* turions the germination of which depends strictly on the presence of N, P and Ca in the water (Appenroth et al. 1990). The situation is unclear in sprouting *A. vesiculosa* turions (data not shown) which did not grow new organs in the deficient medium. As the adult shoot growth of this species is highly dependent on prey capture (when compared to *Utricularia* spp.; Adamec et al. 2010), it is possible that its sprouting turions are more dependent on mineral nutrient uptake from the water for the production of new organs than the other species studied.

Based on tissue nutrient content in both dormant turions and growing shoots/leaves of 12 aquatic plant species and the proportion of DW to FW in the biomass, Adamec (2010) estimated that, theoretically, at least 30 % of the total turion's N and 50 % of the total P amount could be allocated to newly sprouting organs. Based on the relative proportion of newly sprouting organs to the total turion size (Fig. 1), it can be assumed that around 25–60 % of the total FW of the sprouting turions are newly sprouting organs and, thus, the quantity of N and P in these new organs is around 25–60 % of the total turion's amount. This amount of N, P, S and Mg, which can be allocated as

stored mineral nutrients, is sufficient for production of new organs (roots, leaves, traps) which can take up mineral nutrients from the sediment, free water column or animal prey. It can be assumed that the old segments of sprouting turions, which represent storage organs, have very limited uptake affinity for mineral nutrients in the ambient water. The analogous situation is with functional traps of aquatic carnivorous plants. Although very small, non-functional rudiments of traps are present in turions in both *A. vesiculosa* and *Utricularia* spp., the functional traps appear only in newly sprouting apical shoot segments (Fig. 1 E, F).

In conclusion, dormant turions of aquatic plants as storage organs exhibit a very low intensity of metabolism (R_D) and their P_N is negligible even under optimum ecological conditions. In sprouting turions, the DW to FW ratio decreases gradually and the intensity of metabolism (both R_D and P_N) increases up to the level of growing adult shoots or leaves of the same or similar species. Per unit DW, the intensity of metabolism is 2.2–2.5 times greater in newly sprouting organs than that in old turion segments. In a nutrient-deficient medium, turions of most species tested were able to produce newly sprouting organs as a result of mineral nutrients (N, P, S and Mg) stored in the dormant turion. This demonstrates that turions of aquatic plants also function as important storage organs for mineral nutrients.

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References

- Adamec, L., 1999 a: Seasonal growth dynamics and overwintering of the aquatic carnivorous plant *Aldrovanda vesiculosa* at experimental field sites. – *Folia Geobot.* **34**: 287–297.
- Adamec, L., 1999 b: Turion overwintering of aquatic carnivorous plants. – *Carniv. Plant. Newslett.* **28**: 19–24.
- Adamec, L., 2000: Rootless aquatic plant *Aldrovanda vesiculosa*: physiological polarity, mineral nutrition, and importance of carnivory. – *Biol. Plant.* **43**: 113–119.
- Adamec, L., 2003 a: Ecophysiological characterization of dormancy states in turions of the aquatic carnivorous plant *Aldrovanda vesiculosa*. – *Biol. Plant.* **47**: 395–402.
- Adamec, L., 2003 b: Ecophysiological comparison of green Polish and red Australian plants of *Aldrovanda vesiculosa*. – *Carniflora Aust.* **1**: 4–17.
- Adamec, L., 2005: Ecophysiological characterization of carnivorous plant roots: oxygen fluxes, respiration, and water exudation. – *Biol. Plant.* **49**: 247–255.

- Adamec, L., 2006: Respiration and photosynthesis of bladders and leaves of aquatic *Utricularia* species. – *Plant Biol.* **8**: 765–769.
- Adamec, L., 2008: Respiration of turions and winter apices in aquatic carnivorous plants. – *Biologia* **63**: 515–520.
- Adamec, L., 2009: Photosynthetic CO₂ affinity of the aquatic carnivorous plant *Utricularia australis* (Lentibulariaceae) and its investment in carnivory. – *Ecol. Res.* **24**: 327–333.
- Adamec, L., 2010: Tissue mineral nutrient content in turions of aquatic plants: does it represent a storage function? – *Fundam. Appl. Limnol.* **176**: 145–151.
- Adamec, L., Sirová, D. & Vrba, J., 2010: Contrasting growth effects of prey capture in two carnivorous plant species. – *Fundam. Appl. Limnol.* **176**: 153–160.
- Appenroth, K. J., Klinger, R., Wetzker, R. & Augsten, H., 1990: Photophysiology of turion germination in *Spirodela polyrhiza* (L.) Schleiden. IV. Importance of calcium and calmodulin. – *Biochem. Physiol. Pflanzen* **186**: 209–219.
- Bartley, M. R. & Spence, D. H. N., 1987: Dormancy and propagation in helophytes and hydrophytes. – *Archiv Hydrobiol., Beih. Adv. Limnol.* **27**: 139–155.
- Beer, S., 1985: Effects of CO₂ and O₂ on the photosynthetic O₂ evolution of *Spirodela polyrhiza* turions. – *Plant Physiol.* **79**: 199–201.
- Chapin, F. S. III, Schulze, E. D. & Mooney, H. A., 1990: The ecology and economics of storage in plants. – *Ann. Rev. Ecol. Syst.* **21**: 423–447.
- Czopek, M., 1964: The course of photosynthesis and respiration in germinating turions of *Spirodela polyrhiza*. – *Bull. Acad. Pol. Sci., Sér. Sci. biol.* **12**: 463–469.
- Knight, S. E., 1988: The Ecophysiological Significance of Carnivory in *Utricularia vulgaris*. – Ph.D. thesis, Univ. Wisconsin, Madison, USA.
- Kunii, H., 1989: Continuous growth and clump maintenance of *Potamogeton crispus* L. in Narutoh river, Japan. – *Aquat. Bot.* **33**: 13–26.
- Ley, S., Dölger, K. & Appenroth, K. J., 1997: Carbohydrate metabolism as a possible physiological modulator of dormancy in turions of *Spirodela polyrhiza* (L.) Schleiden. – *Plant Sci.* **129**: 1–7.
- Newton, R. J., Shelton, D. R., Disharoon, S. & Duffey, J. E., 1978: Turion formation and germination in *Spirodela polyrhiza*. – *Amer. J. Bot.* **65**: 421–428.
- Sculthorpe, C. D., 1967: *The Biology of Aquatic Vascular Plants*. – Edward Arnold, London.
- Simola, L. K., Koskimies-Soininen, K. & Tomell, M., 1985: Glycolipids of turions and leaves of *Utricularia vulgaris* at different stages of development. – *Physiol. Plant.* **65**: 23–26.
- Villanueva, V. R., Simola, L. K. & Mardon, M., 1985: Polyamines in turions and young plants of *Hydrocharis morsus-ranae* and *Utricularia intermedia*. – *Phytochemistry* **24**: 171–172.
- Weber, J. A. & Noodén, L. D., 2005: The causes of sinking and floating in turions of *Myriophyllum verticillatum*. – *Aquat. Bot.* **83**: 219–226.
- Winston, R. D. & Gorham, P. R., 1979 a: Turions and dormancy states in *Utricularia vulgaris*. – *Can. J. Bot.* **57**: 2740–2749.
- Winston, R. D. & Gorham, P. R., 1979 b: Roles of endogenous and exogenous growth regulators in dormancy of *Utricularia vulgaris*. – *Can. J. Bot.* **57**: 2750–2759.