

## Respiration of turions and winter apices in aquatic carnivorous plants

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**Abstract:** Basic respiration characteristics were measured in turions of six aquatic plant species differing greatly in their ecological and overwintering characteristics both before and after overwintering, i.e., in dormant and non-dormant state: non-carnivorous *Hydrocharis morsus-ranae* and *Caldesia parnassifolia* and carnivorous *Aldrovanda vesiculosa*, *Utricularia australis*, *U. ochroleuca*, and *U. bremii*, and in non-dormant winter apices of three Australian (sub)tropical populations of *Aldrovanda* and of two temperate North American *Utricularia* species, *U. purpurea* and *U. radiata*. Respiration rate of autumnal (dormant) turions at 20°C ranged from 0.36 to 1.3  $\mu\text{mol O}_2 \text{ kg}^{-1}(\text{FM}) \text{ s}^{-1}$  and, except for *U. bremii*, increased by 11–114% after overwintering. However, this increase was statistically significant only in two species. Respiration  $Q_{10}$  in dormant turions ranged within 1.8–2.6 and within 2.3–3.4 in spring (non-dormant) turions. Turions of aquatic plants behave as typical storage, overwintering organs with low respiration rates. No relationship was found between respiration rate of turions and overwintering strategy. In spite of their low respiration rates, turions can usually survive only from one season to another, due to their limited reserves of respiratory substrates for long periods. Contrary to true turions, respiration rates in non-dormant winter apices both in Australian *Aldrovanda* populations and temperate *U. radiata* and *U. purpurea*, in sprouting turions, and growing shoot apices of *Aldrovanda* were high and ranged from 2.1 to 3.1  $\mu\text{mol kg}^{-1}(\text{FM}) \text{ s}^{-1}$ , which is comparable to that in aquatic plant leaves or shoots.

**Key words:** aquatic plants; dormant winter buds; non-dormant winter apices; overwintering; aerobic respiration; temperature quotient; cyanide-resistant respiration

**Abbreviations:**  $R_D$  – dark respiration rate, DM – dry mass, FM – fresh mass, SHAM – salicylhydroxamic acid,  $\text{CN}^-$ -R – cyanide-resistant respiration.

### Introduction

Turions (winter buds) are vegetative dormant organs produced by perennial aquatic plants as a response to unfavourable ecological conditions (Sculthorpe 1967; Bartley & Spence 1987). Turions are formed in subtropical to polar zones at the end of the growing season. They are modified shoot apices, formed by extreme condensation of very short modified leaves and serve as storage organs with high starch content (25–70% of DM; Winston & Gorham 1979; Ley et al. 1997; Adamec 1999, 2003a,b). Turions are frost resistant, but they usually overwinter and break their dormancy in warmer water at the bottom, often under anaerobic conditions. However, different aquatic plant species vary greatly in their ecological strategy of turion overwintering and depth of dormancy (Sculthorpe 1967; Bartley & Spence 1987; Adamec, 1999). Turions of free-floating aquatic species (e.g., *Hydrocharis*, *Utricularia*, *Aldrovanda*, *Spirodela*) usually germinate (sprout) at the water surface, while those of submerged rooted species (e.g., *Potamogeton*, *Caldesia*) at the bottom. Moreover, turions of free-floating aquatic plants have two different strategies of autumnal sinking and spring

floating (Adamec 1999): Turions of *Aldrovanda vesiculosa* and *Hydrocharis morsus-ranae* have developed an active mechanism of sinking and rising. In autumn, ripe turions break off the dying mother shoots at the water surface. After a few days, they sink gradually to the bottom. Over winter, the turions are partially submerged in the sediments. In the spring, they respond to the warming water and rise to the water surface within a few days (Adamec 1999, 2003a). Active sinking and rising occurs also in *Spirodela polyrhiza* turions (Newton et al. 1978). It has been suggested that sinking and rising of *Aldrovanda* turions is caused by variable gas volume in voluminous gas spaces in turion leaves (Adamec 1999, 2003a). Probably, the source of this gas comes from respiration or fermentation. On the other hand, turions of temperate aquatic *Utricularia* species are always less dense than water and are usually firmly connected to the mother shoots. After the mother shoots gradually decompose they become denser than water and drag the turions to the bottom. By early spring, the turions separate and float to the surface.

In aquatic plants, two dormancy states of turions have been distinguished (Winston & Gorham 1979; Bartley & Spence 1987; Adamec 2003a). In

the state of innate dormancy (autumn-winter), turions are held dormant by endogenous inhibitory phytohormones, while imposed dormancy (end of winter, spring) is maintained exogenously by low temperatures. Breaking imposed dormancy of turions is a prerequisite for turion sprouting. In contrast with true dormant turions, overwintering shoot apices in many aquatic species do not produce morphologically distinct winter buds and their dormancy is very weak or absent (i.e., quiescence; Bartley & Spence 1987). Although turions are crucial for survival of aquatic plants and their overwintering represents critical phase of the plants' seasonal cycle (Adamec 1999), very little has been known of their metabolism so far. Some studies, performed on *Spirodela* (Czopek 1964; Beer 1985) and *Aldrovanda* turions (Adamec 2003a), have shown that the FM-based dark respiration rate ( $R_D$ ) of turions is about 2–4 times lower than that of adult leaves or shoots. However, this relatively low  $R_D$  of turions is responsible for a marked decline of starch reserves over winter (Winston & Gorham 1979; Adamec 2003a).

Turions of free-floating, rootless aquatic carnivorous plants of the genera *Utricularia* and *Aldrovanda* are spherical or rhomboidal organs 1–20 mm in size (Sculthorpe 1967; Adamec 1999, 2003a). Some subtropical or temperate species of these genera produce non-dormant, quiescent shoot apices, denoted henceforth as “winter apices”. In these species, winter apices are firmly connected with mother shoots which usually do not decay over winter. The aim of this study was to compare basic respiration characteristics of turions of six aquatic plant species (see Fig. 1) differing greatly in their ecological and overwintering characteristics: Turions of non-carnivorous, free-floating *Hydrocharis morsus-ranae* L. (Hydrocharitaceae) sink and float actively and sprout on the water surface, while turions of rooted *Caldesia parnassifolia* L. (Alismataceae) sink actively and then sprout and root on the bottom. Turions of *Aldrovanda vesiculosa* L. (Droseraceae) sink and float actively and germinate on the water surface, while those of *Utricularia australis* R.Br., *U. ochroleuca* R.Hartm., and *U. bremii* Heer ex Kölliker (Lentibulariaceae) sink and float passively but usually germinate on the surface. Moreover,  $R_D$  of true dormant turions of these species is compared in this paper with the  $R_D$  of non-dormant winter apices of three (sub)tropical populations of *A. vesiculosa* from SE, N, and NW Australia (Adamec 2003b; Maldonado San Martín et al. 2003) and of two temperate North American *Utricularia* species, *U. purpurea* Walter and *U. radiata* Small. The following questions are raised: i) Are there differences in  $R_D$  between true dormant turions and non-dormant winter apices of aquatic plants? ii) Are there differences in  $R_D$  between autumnal (dormant) and spring (non-dormant) turions of aquatic plants? iii) Are there differences in  $R_D$  of turions between aquatic carnivorous and non-carnivorous plants? iv) Are there differences in  $R_D$  between turions with an active and passive way of sinking and rising? The following hypotheses were tested that  $R_D$  of turions can reflect ecological particulars rather on the level



Fig. 1. Turions of aquatic plants used for measurements of respiration rate. From the left: *Caldesia parnassifolia*, *Hydrocharis morsus-ranae*, *Aldrovanda vesiculosa*, *Utricularia ochroleuca*, *U. australis*, and *U. bremii*. Ticks indicate 1 mm.

of turions than adult plants (e.g., carnivory) and that the ability of overwintering apical organs to entry true dormancy is decisive for their  $R_D$ .

## Material and methods

### Plant material

Ripe turions of *Hydrocharis morsus-ranae* were collected from a sand-pit at Branná near Třeboň, S Bohemia, Czech Republic (48°59' N, 14°38' E), in mid-October 2003. Ripe turions of *Caldesia parnassifolia* (origin from Charlottenweiher near Schwandorf, Oberpfalz, FRG, 49°21' N, 12°09' E) were collected from an outdoor culture in the Institute of Botany at Třeboň in mid-September 2003. Unripe turions of *Aldrovanda vesiculosa* (origin from Lake Długie, E Poland, 51°26' N, 23°06' E) were collected from a fen pool near Ptačí blato fishpond in the Třeboň region (49°05' N, 14°41' E) in mid-October 2003 and were allowed to fully ripen in an outdoor culture (see Adamec 2003a). Ripe turions of *Utricularia australis* were collected from the same site. Ripe turions of *U. ochroleuca* (determined sensu stricto as *U. stygia* Thor; origin from Vizír fishpond, Třeboň region, 48°57' N, 14°50' E) and *U. bremii* (Lake Oniega, Kizhi island, Karelia, N. Russia, 61°55' N, 35°20' E) were collected from an outdoor culture at the beginning of November 2003. Ripe turions of all six species were washed using tap water and stored in darkness in filtered cultivation medium (from the outdoor culture of *Aldrovanda*) in a refrigerator at 3±1°C till the measurements. It was verified that the turions of all these species had been dormant in mid-November (20°C, 14 h light/10 h darkness, two weeks). Plants of *Aldrovanda* of three populations from SE (35°35' S, 150°09' E), N (12°31' S, 131°05' E), and NW Australia (14°50' S, 125°41' E) were grown outdoors in small aquaria (Adamec, 2003b) and formed non-dormant winter apices. Two weeks before  $R_D$  measurements (13–14 November 2003), water temperature fluctuated within 0–5°C in the aquaria. *U. purpurea* (from N Florida, USA, 29°26' N, 82°12' W) and *U. radiata* (from New Jersey, USA, 39°32' N, 74°37' W) were grown in small aquaria in a cold greenhouse and formed non-dormant winter apices (Fig. 2). Two weeks before  $R_D$  measurements (17 November 2003), water temperature ranged within 8–12°C in the aquaria. Sprouting turions of *Aldrovanda* (E Poland) 6–12 mm long were collected from an outdoor culture on 18 May 2004. They sprouted at 12–18°C for 9 days. Adult shoots of *Aldrovanda* from SE Australia were collected from an indoor aquarium (20–26°C). Generally, experimental turions or winter apices from cultures were derived from sev-

eral plants collected at natural sites. Plant material of each species was sampled from only one natural population or culture.

#### Measurement of respiration rates

Aerobic  $R_D$  of turions of the six species was measured both in mid-November 2003 (innate dormancy, dormant turions) and in mid-April 2004 (imposed dormancy, non-dormant turions).  $R_D$  of 2–10 turions (DM 34–280 mg) freshly taken out from a refrigerator was measured in a diluted mineral nutrient solution (pH ca. 4.7, 80–90% oxygen saturation) in a 5-ml stirred thermostatted chamber at  $4.0 \pm 0.1$  and  $20.0 \pm 0.1$  °C in darkness, using a Clark-type oxygen sensor and a pen recorder (for all details see Adamec 2005). For methodical reasons,  $R_D$  was measured about at oxygen saturation, while turions usually overwinter under hypoxia or even anoxia in the field or refrigerator. This discrepancy could lead to an overestimation of  $R_D$  as compared to a true one in the field. Different number of turions or winter apices of each species was used to attain a sufficient response. Before all measurements, the two outermost membranous leaves of *Hydrocharis* turions were removed, and the turions were halved longitudinally by a razor blade to ensure a better contact with the solution. The same two leaves were also removed from *Caldesia* turions. Bigger turions of all *Utricularia* species were halved transversally. The proportion of cyanide-resistant respiration ( $CN^-R$ ) as an estimate of the alternative oxidase pathway was measured at  $20.0 \pm 0.1$  °C in parallel dormant turions of the six species in mid-November.  $R_D$  was measured in the turions after a 3-h exposure ( $20 \pm 1$  °C, darkness, thoroughly shaken) to either 0.5 mM KCN, or 5 mM salicylhydroxamic acid (SHAM), or 0.5 mM KCN + 5 mM SHAM. The latter mixed solution is known to inhibit cyanide-resistant respiration (e.g., Kapulnik et al. 1992; Atkin et al. 1995; Millar et al. 1998). The inhibitors were added to the basic diluted mineral nutrient solution. Effective KCN and SHAM concentrations and exposure period used were chosen according to studies by Webb & Armstrong (1983) on pea roots and by Adamec (2005) on carnivorous plant roots.  $CN^-R$  was expressed in % of values for 0.5 mM KCN alone.

For comparison with true, dormant turions,  $R_D$  was measured at  $20.0 \pm 0.1$  °C also in 3–6 non-dormant winter apices of *Aldrovanda* from SE, N, and NW Australia (length 4–6 mm, FM 20–44 mg), in 4–6 winter apices of *U. purpurea* (Fig. 2) and *U. radiata* (length 4–6 mm, FM 8–9 mg), in 5–6 sprouting turions of *Aldrovanda* (FM 100–200 mg), and in two apical shoot segments of *Aldrovanda* from SE Australia (length 3 cm, FM 80–130 mg). After  $R_D$  measurements, dry mass (DM; 80 °C) of the plant material was also estimated.  $R_D$  is expressed in  $\text{nmol kg}^{-1} \text{s}^{-1}$  per unit FM. All measurements were performed 6 times with a new plant material. Where possible all paired data were statistically evaluated by a two-tailed *t*-test. Other data were processed by one-way ANOVA (Tukey HSD test).

## Results

Dormant turions of the six species of aquatic plants had a high proportion of DM in FM (24–39%) which usually somewhat declined after 5 months of storing in a refrigerator (24–37%; Table 1). The values of  $R_D$  of dormant turions at 4 °C ranged within  $0.1$ – $0.3 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$  and within  $0.1$ – $0.3 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$  in non-dormant turions after overwintering. However,



Fig. 2. Winter shoot of *Utricularia purpurea* with non-dormant apex. Ticks indicate 1 mm.

the decline was statistically significant ( $P < 0.05$ ) only in *Aldrovanda* and *U. australis*.  $R_D$  of dormant turions at 20 °C varied within  $0.4$ – $1.3 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$  and, except for *U. bremii*, increased by 11–114% after overwintering (Table 1). However, this increase in  $R_D$  was statistically significant only in *Aldrovanda* and *U. ochroleuca*. Generally, the  $R_D$  of both dormant and non-dormant turions of the four carnivorous plant species at 20 °C was statistically significantly different only from that in *H. morsus-ranae*.  $Q_{10}$  (temperature quotient) of  $R_D$  in dormant turions ranged within 1.75–2.56 and increased by 2–69% (2.26–3.39) in non-dormant turions in the spring. However, this increase was statistically significant only in *Aldrovanda* and *U. australis*. KCN alone decreased  $R_D$  in three species, while it was without any effect in two species (Table 1). SHAM alone had usually no significant effect on  $R_D$  (data not shown) but KCN + SHAM decreased markedly  $R_D$ , demonstrating a great proportion of  $CN^-R$  (22–90 % of the value for KCN alone).

In contrast with low  $R_D$  in true turions,  $R_D$  in non-dormant winter apices both in Australian *Aldrovanda* populations and temperate *U. radiata* and *U. purpurea* were high and ranged from 2.1 to  $3.1 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$  (Table 2). Values of  $R_D$  of sprouting turions and growing shoot apices of *Aldrovanda* were of the same magnitude.

## Discussion

On FM basis, values of  $R_D$  of turions at 20 °C (Table 1) are about 1.5–4 times lower than those reported in growing shoots (leaves) of these or other aquatic species at the same temperature (range 0.5–8, most commonly  $0.8$ – $3.6 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$ ; cf. Draxler 1973; Maberly 1985; Madsen & Sand-Jensen 1987; Pokorný & Ondok 1991; Kahara & Vermaat 2003). In apical summer shoot segments of Polish *Aldrovanda*, Adamec (1997) measured  $R_D$   $2.5 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$ . However, the great difference in  $R_D$  between turions and growing shoots of aquatic plants is even amplified when  $R_D$  is expressed per unit DM (Table 1). DM-based  $R_D$ s at 20 °C were only  $1.5$ – $4.4 \mu\text{mol kg}^{-1}(\text{DM}) \text{s}^{-1}$  in dormant turions and  $1.3$ – $5.3 \mu\text{mol kg}^{-1}(\text{DM}) \text{s}^{-1}$  in non-dormant ones, while they were 5.3–80, and most commonly 8–28  $\mu\text{mol}$

Table 1.  $R_D$  of autumnal dormant turions (5–18 Nov.) and non-dormant spring turions (20–23 Apr.) after overwintering at  $3 \pm 1^\circ\text{C}$  in darkness.  $\text{CN}^-$ -R, proportion of cyanide-resistant respiration in % of values for 0.5 mM KCN. Means  $\pm$  1.S.E intervals are shown;  $n = 6$ . Statistical significance (two-tailed  $t$ -test) of the differences between the pairs of values for autumnal and spring turions is stated in the lower part of the table (on the left side of columns) and that between the pairs of values for  $20^\circ\text{C}$  controls and 0.5 mM KCN is stated in the upper part of the table. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; ns, non-significant difference at  $P > 0.05$ . The same letters (on the right side of columns) denote no statistically significant difference between the species at the given temperature;  $P < 0.05$  (one-way ANOVA, Tukey HSD test).

Species	DM (% FM)	Respiration rate ( $\text{nmol kg}^{-1}(\text{FM}) \text{ s}^{-1}$ )			0.5 mM KCN	$\text{CN}^-$ -R (%)
		$Q_{10}$	Controls ( $4^\circ\text{C}$ )	Controls ( $20^\circ\text{C}$ )		
Autumnal dormant turions (5–18 Nov.)						
<i>Hydrocharis morsus-r.</i>	29.3	$2.56 \pm 0.12^a$	$292 \pm 19^a$	$1289 \pm 44^a$	$325 \pm 19^{**}$	64.3
<i>Caldesia parnassifolia</i>	39.0	$1.94 \pm 0.13^{ab}$	$286 \pm 30^a$	$806 \pm 77^b$	$594 \pm 50^*$	22.0
<i>Aldrovanda vesiculosa</i>	24.1	$1.75 \pm 0.07^b$	$294 \pm 22^a$	$706 \pm 19^b$	$492 \pm 25^{**}$	50.2
<i>Utricularia australis</i>	35.8	$2.01 \pm 0.18^{ab}$	$117 \pm 6^b$	$358 \pm 56^c$	$336 \pm 22^{\text{ns}}$	71.3
<i>Utricularia ochroleuca</i>	28.8	$2.30 \pm 0.22^{ab}$	$125 \pm 19^b$	$428 \pm 17^c$	$547 \pm 17^{**}$	80.6
<i>Utricularia bremii</i>	28.0	$2.55 \pm 0.23^a$	$150 \pm 17^b$	$622 \pm 17^b$	$617 \pm 19^{\text{ns}}$	90.0
Spring non-dormant turions (20–23 Apr.)						
<i>Hydrocharis morsus-r.</i>	27.3	$^{\text{ns}}2.71 \pm 0.12^{ab}$	$^{\text{ns}}294 \pm 17^a$	$^{\text{ns}}1436 \pm 61^a$	–	–
<i>Caldesia parnassifolia</i>	31.9	$^{\text{ns}}2.26 \pm 0.13^a$	$^{\text{ns}}250 \pm 17^{ab}$	$^{\text{ns}}900 \pm 39^b$	–	–
<i>Aldrovanda vesiculosa</i>	21.9	$^{**}2.94 \pm 0.14^{bc}$	$^{**}197 \pm 14^{bd}$	$^{**}1006 \pm 58^b$	–	–
<i>Utricularia australis</i>	37.3	$^{**}3.39 \pm 0.15^c$	$^{**}69 \pm 6^c$	$^{\text{ns}}481 \pm 22^c$	–	–
<i>Utricularia ochroleuca</i>	23.5	$^{\text{ns}}2.93 \pm 0.18^{bc}$	$^{\text{ns}}172 \pm 22^d$	$^{**}917 \pm 36^b$	–	–
<i>Utricularia bremii</i>	27.1	$^{\text{ns}}2.59 \pm 0.07^{ab}$	$^{\text{ns}}133 \pm 17^{cd}$	$^{\text{ns}}603 \pm 61^c$	–	–

Table 2.  $R_D$  [ $\mu\text{mol kg}^{-1}(\text{FM}) \text{ s}^{-1}$ ] of non-dormant winter apices of three Australian populations of *A. vesiculosa* and those of *U. radiata* and *U. purpurea*, 3-cm apical segments of growing shoots of SE Australian *A. vesiculosa*, and of 6–12-mm sprouting turions from E Poland. All measurements were conducted at  $20^\circ\text{C}$ . Means  $\pm$  1.S.E are shown;  $n = 6$ . For *A. vesiculosa*, the same letters denote no statistically significant difference;  $P < 0.05$  ( $F_{4,25} = 9.76$ ;  $P = 0.00007$ ; one-way ANOVA, Tukey HSD test).

Aldrovanda vesiculosa			Utricularia sp.			
Non-dormant Australian winter apices			Shoots	Spr. tur.	Non-dormant winter apices	
NW	N	SE	SE Austr.	E Poland	<i>U. radiata</i>	<i>U. purpurea</i>
$2.5 \pm 0.1^{ab}$	$2.7 \pm 0.1^{ac}$	$2.3 \pm 0.1^{ab}$	$2.2 \pm 0.1^b$	$3.0 \pm 0.1^c$	$3.1 \pm 0.2$	$2.1 \pm 0.2$

$\text{kg}^{-1}(\text{DM}) \text{ s}^{-1}$ , in aquatic plant shoots (Draxler 1973; Maberly 1985; Madsen & Sand-Jensen 1987; Pokorný & Ondok 1991; Adamec 1997; Kahara & Vermaat 2003).

On the other hand,  $R_D$  of non-dormant winter apices was similar to that reported above for aquatic plant shoots, on both FM (Table 2) and DM basis [ $10$ – $24 \mu\text{mol kg}^{-1}(\text{DM}) \text{ s}^{-1}$ ]. In these non-dormant winter apices, the proportion of DM was 21–26% of FM in *Aldrovanda* and 17.1 and 8.7% in *U. radiata* and *U. purpurea*, respectively. Though  $R_D$  of winter apices of the three (sub)tropical *Aldrovanda* populations is relatively high (Table 2) they evidently function as storage organs as their autumnal starch (45–53% DM) and sugar content (13% DM) is usually even higher than that in dormant Polish *Aldrovanda* turions (starch 23–32% DM, free sugars 13–15% DM; cf. Adamec 2003a,b). The hypothesis that the dormancy of overwintering apical organs is decisive for their  $R_D$  was clearly confirmed (cf. Tables 1 and 2).

$Q_{10}$  values found in turions (Table 1) are comparable with those reported for leaves of dozens of terrestrial herb or tree species (Atkin & Tjoelker 2003; Loveys et al. 2003) and *Fontinalis* shoots (Maberly 1985). However, a great variation of both  $R_D$  and  $Q_{10}$  values for different batches of turions of *Aldrovanda* and *U. aus-*

*tralis* at the same developmental state follows from the comparison of the data in Table 1 with those published by Adamec (2003a). One of the reasons for this variation might be rather different starch and sugar content in different turion batches. Greater differences between the six species exist on the level of  $R_D$  (both at 4 and  $20^\circ\text{C}$ ) than  $Q_{10}$  (Table 1). Although some species studied here differed in their  $R_D$  values up to 2.5–4 times from each other, both at 4 and  $20^\circ\text{C}$ , it is not clear which ecological features of these species are responsible for; statistical analysis is not feasible for the low number of species. The same conclusion was also made by Loveys et al. (2003) who did not find any correlations between foliar respiration  $Q_{10}$  and some physiological traits as plant growth rate, leaf sugar or nitrogen content in herbs. In both dormancy states and at both temperatures, relatively high  $R_D$  was found in *Hydrocharis*, *Aldrovanda*, and *Caldesia* (Table 1). All these species are considered to be thermophilous as to their summer growth requirements (e.g., Adamec 1997). Moreover, the first two species form turions with actively sinking and floating. It is expected that higher  $R_D$  in *Hydrocharis* and *Aldrovanda* turions will cause a faster evolution of gas in the leaf lacunae of turions and faster turion floating (Adamec 2003a). Yet, nei-

ther thermophily of the species tested, nor the way of sinking and floating of turions nor carnivory can be correlated with the  $R_D$  values of turions. It is possible that the magnitude of  $R_D$  of turions in different species at higher temperatures (12–20°C) reflects also typical species' requirements for optimum temperature for turion sprouting (i.e., phenology of turion sprouting) or the rate of subsequent sprouting which is very energy demanding (Table 2; Czopek 1964). For example, at common sites, *U. australis* (cold-tolerant species) turions usually sprout in colder water a few weeks earlier than *Aldrovanda* turions, as a typical thermophilous species (Adamec unpubl.). Similarly, a statistically significant increase in  $R_D$  of turions at 20°C was found only in two species after overwintering (*A. vesiculosa* and *U. ochroleuca*; Tab. 1) and, thus, its ecophysiological consequence is unclear.

A question may be put whether a measurement of aerobic respiration of turions at 4°C and oxygen saturation reflects a true aerobic respiration and/or anaerobic fermentation rate which occur in the field or a refrigerator over winter. In *Aldrovanda* turions, detailed data on starch and sugar content before and after overwintering are available (Adamec 2003a) and they allow to compare the decline of starch and sugar content over winter with the  $R_D$  at 4°C measured here (Table 1). During five months of overwintering in a refrigerator at 4°C, *Aldrovanda* turions reduced their total starch and non-structural sugar content from about 45% DM to about 22% DM (Adamec 2003a). Assuming oxidative respiration of starch, the main energy substrate, and the mean proportion of turion DM in FM to be 23%, then the mean measured  $R_D$  of *Aldrovanda* turions at 4°C [ $0.25 \mu\text{mol kg}^{-1}(\text{FM}) \text{s}^{-1}$ ; Table 1] is about 3.26 times higher than it follows from the decline of starch and sugar content (as the true consumption rate of respiratory substrates) over winter. Furthermore, assuming the measured  $R_D$  of *Aldrovanda* turions at 4°C, all respiratory starch and sugar reserves (ca. 45% DM) could be consumed theoretically after only 90 days. Thus, under the conditions of partial or total anoxia in a refrigerator or in the field, the true aerobic  $R_D$  or anaerobic fermentation rate of the turions is much lower. This was confirmed in *Aldrovanda* turions at 20°C, the anaerobic fermentation rate of which was only 1.5–7% of their aerobic  $R_D$  (Adamec 2003a). It is therefore possible to consider the measured aerobic  $R_D$  of turions as a potential maximum  $R_D$  at the temperature given. Yet, the measured aerobic  $R_D$ 's in turions reflect the true respiratory consumption of starch and sugars in a certain way as the life-span of *Aldrovanda* turions with relatively high  $R_D$ , kept in a refrigerator at 3–4°C, is only at maximum 8–9 months, in contrast to at least 10–15 months for *U. australis*, *U. ochroleuca*, and *U. bremii* turions with low  $R_D$  (cf. Table 1; Adamec unpubl.).

In conclusion, true dormant turions of aquatic plants behave as typical storage, overwintering organs with low intensity of metabolism. Their  $R_D$  per unit biomass is several times lower than that of adult leaves or shoots of the same species, whereas  $R_D$  of non-

dormant winter apices of some aquatic species is comparable with that in adult leaves or shoots of aquatic plants. No clear relationship was found between  $R_D$  of turions and turion overwintering strategy. Thus, the differences found in  $R_D$  of turions are rather species-specific. Terminologically, the term *turion* should only be reserved for morphologically distinct organs which can enter the true dormancy. In spite of low  $R_D$  of turions, their reserves of respiratory substrates are limited and turions in the field can survive only from one season to another. Greater attention should be paid to turion overwintering under natural field conditions.

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### References

- Adamec L. 1997. Photosynthetic characteristics of the aquatic carnivorous plant *Aldrovanda vesiculosa*. *Aquat. Bot.* **59**: 297–306.
- Adamec L. 1999. Turion overwintering of aquatic carnivorous plants. *Carniv. Plant Newsl.* **28**: 19–24.
- Adamec L. 2003a. Ecophysiological characterization of dormancy states in turions of the aquatic carnivorous plant *Aldrovanda vesiculosa*. *Biol. Plant.* **47**: 395–402.
- Adamec L. 2003b. 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.
- Atkin O.K. & Tjoelker M.G. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plant Sci.* **8**: 343–351.
- Atkin O.K., Villar R. & Lambers H. 1995. Partitioning of electrons between the cytochrome and alternative pathways in intact roots. *Plant Physiol.* **108**: 1179–1183.
- Bartley M.R. & Spence D.H.N. 1987. Dormancy and propagation in helophytes and hydrophytes. *Archiv Hydrobiol. (Beih.)* **27**: 139–155.
- Beer S. 1985. Effects of CO<sub>2</sub> and O<sub>2</sub> on the photosynthetic O<sub>2</sub> evolution of *Spirodela polyrrhiza* turions. *Plant Physiol.* **79**: 199–201.
- Czopek M. 1964. The course of photosynthesis and respiration in germinating turions of *Spirodela polyrrhiza*. *Bull. L'Acad. Pol. Sci., Sér. Sci. biol.* **12**: 463–469.
- Draxler G. 1973. Gaswechselformungen an *Utricularia vulgaris*, pp. 103–107. In: Ellenberg H. (ed.), *Ökosystemforschung*, Springer-Verlag, Berlin, Heidelberg, New York.
- Kahara S.N. & Vermaat J.E. 2003. The effect of alkalinity on photosynthesis-light curves and inorganic carbon extraction capacity of freshwater macrophytes. *Aquat. Bot.* **75**: 217–227.
- Kapulnik Y., Yalpani N. & Raskin I. 1992. Salicylic acid induces cyanide-resistant respiration in tobacco cell-suspension cultures. *Plant Physiol.* **100**: 1921–1926.
- Ley S., Dölger K. & Appenroth K.J. 1997. Carbohydrate metabolism as a possible physiological modulator of dormancy in turions of *Spirodela polyrrhiza* (L.) Schleiden. *Plant Sci.* **129**: 1–7.
- Loveys B.R., Atkinson L.J., Sherlock D.J., Roberts R.L., Fitter A.H. & Atkin O.K. 2003. Thermal acclimation of leaf and root

- respiration: an investigation comparing inherently fast- and slow-growing plant species. *Glob. Change Biol.* **9**: 895–910.
- Maberly S.C. 1985. Photosynthesis by *Fontinalis antipyretica*. I. Interaction between photon irradiance, concentration of carbon dioxide and temperature. *New Phytol.* **100**: 127–140.
- Madsen T.V. & Sand-Jensen K. 1987. Photosynthetic capacity, bicarbonate affinity and growth of *Elodea canadensis* exposed to different concentrations of inorganic carbon. *Oikos* **50**: 176–182.
- Maldonado San Martín A.P., Adamec L., Suda J., Mes T.H.M. & Štorchová H. 2003. Genetic variation within the endangered species *Aldrovanda vesiculosa* (Droseraceae) as revealed by RAPD analysis. *Aquat. Bot.* **75**: 159–172.
- Millar A.H., Atkin O.K., Menz R.I., Henry B., Farquhar G. & Day D.A. 1998. Analysis of respiratory chain regulation in roots of soybean seedlings. *Plant Physiol.* **117**: 1083–1093.
- 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.
- Pokorný J. & Ondok J.P. 1991. Macrophyte photosynthesis and aquatic environment. Academia, Prague, 117 pp.
- Sculthorpe C.D. 1967. The biology of aquatic vascular plants. Edward Arnold, London, 684 pp.
- Webb T. & Armstrong W. 1983. Effects of KCN and salicylhydroxamic acid on the root respiration of pea seedlings. *Plant Physiol.* **72**: 280–286.
- Winston R.D. & Gorham P.R. 1979. Turions and dormancy states in *Utricularia vulgaris*. *Can. J. Bot.* **57**: 2740–2749.

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