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Short communication

The comparison of mechanically stimulated and spontaneous firings in traps of aquatic carnivorous *Utricularia* species

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ABSTRACT

Firing and resetting of traps in aquatic *Utricularia* species are associated with water flows and trap volume changes. In this study, trap thickness was used as a measure of water flow and was monitored automatically using an electronic position sensor. Isolated traps from three aquatic *Utricularia* species were monitored over the course of 1–2 days to verify spontaneous firings (without any mechanical stimulation) and describe their basic characteristics. Isolated traps of three *Utricularia* species were initially fired by mechanical stimulation and allowed to naturally reset within a period of 24–48 h. Within this resting period, spontaneous firings were found in the traps of all species and in two trap age categories of *U. vulgaris*. The timing of spontaneous firings was found to be irregular. Spontaneous firings ranged between 0.29 and 2.4 during the 24-h resting period and the mean time between two spontaneous firings was highly variable within each species (319–891 min). There was no quantitative difference between spontaneous and mechanically stimulated firings of the traps. Spontaneous firings could explain how phytoplankton or detritus enters traps even when no prey species are present.

1. Introduction

The carnivorous angiosperm genus *Utricularia* L. (bladderwort, Lentibulariaceae) includes about 220 species. This rootless genus contains around 50 species of aquatic or amphibious plants which usually grow in standing, nutrient-poor humic waters (Taylor, 1989; Guisande et al., 2007). Small aquatic animals such as crustaceans, mites, nematodes, rotifers and protozoa, are captured by foliar traps on the plants (*e.g.*, Richards, 2001; Gordon and Pacheco, 2007). These discoid traps are hollow, water-filled bladders, typically 1–5 mm long with a wall thickness of two cells; they contain a variety of glands and trichomes on both the inner and outer surfaces, the function of which is still partially unresolved (Sydenham and Findlay, 1975; Sasago and Sibaoka, 1985a; Juniper et al., 1989). When set, a negative pressure of ~−15 to −17 kPa relative to the ambient medium is maintained within the trap (Sydenham and Findlay, 1973; Sasago and Sibaoka, 1985a). Trigger hairs are situated close to the trap door and when touched by a prey species the door opens and the creature is aspirated into the trap and the door closes again. This process is complete within 10–15 ms (Sydenham and Findlay, 1973). Immediately after firing, the pressure within the trap is equalized with the ambient medium, but the negative pressure is soon restored by the rapid removal of *ca.* 40% of water from the trap lumen until the original compressed shape is reached. This process usually lasts about 30 min, when the trap is ready to fire again (Sydenham and Findlay, 1973, 1975; Sasago and Sibaoka, 1985a). The trap lumen is completely sealed so once inside, prey and any other aspirated particles are unable to leave.

The processes associated with pumping water out of the *Utricularia* traps have been partly elucidated (Sydenham and Findlay, 1973, 1975; Sasago and Sibaoka, 1985a,b). In these studies, the authors measured trap thickness (*i.e.*, the distance between the two parallel walls) and quantified trap water pumping and pressure changes using simple methods based on piercing isolated traps with fine glass capillaries. The trap thickness, as an easily and accurately measured parameter, correlated closely with the magnitude of the negative pressure during trap resetting. The negative pressure within the traps attained its minimum, stable value as early as 25–30 min after firing, while their thickness decreased exponentially and water removal continued for a few hours (Sydenham and Findlay, 1973, 1975; Sasago and Sibaoka, 1985a). At any given time, trap thickness is therefore a better measure of the quantity of water pumped out of the trap than the internal trap pressure. This negative pressure inside the traps is decisive for further pumping out water so that the concept of a physiological negative pressure sensor in the traps appears valid (Sasago and Sibaoka, 1985a). The importance of using trap thickness as the only (and simplest) reliable method of measuring water flow is further highlighted by our inability to repeat the methods used in the four studies published

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in 1973–1985; methodical problems greatly affected the reliability of the results (Adamec, unpubl.).

Aquatic *Utricularia* traps are usually inhabited by diverse communities of microorganisms as commensals which likely originate in the *Utricularia*-associated periphyton: *i.e.*, bacteria, algae, protists, and rotifers (*e.g.*, Mette et al., 2000; Richards, 2001; Sirová et al., 2003, 2009). In two *Utricularia* species, Sirová et al. (2009) found high concentrations of organic C, and mineral N and P in the filtered fluid collected from traps free from macroscopic prey. This suggests the existence of a microbial food-web inside the traps. Recent investigations have also confirmed a prolific occurrence of phytoplanktonic algae inside *Utricularia* traps, especially in nutrient-poor waters (Peroutka et al., 2008; Alkhalaf et al., 2009). Most algal cells found in the trap fluid were aspirated in from the ambient water, however, around 90% of those in the traps were dead (Peroutka et al., 2008). It is therefore evident that microscopic organisms (and also detritus) which are neither capable of triggering traps to fire nor reproducing once inside, get captured also without any macroscopic prey. This is most probably due to incidental, above-threshold mechanical irritation of the trigger hairs (*e.g.*, wind, animals). Most of these microscopic organisms likely die of anoxia in the trap fluid (Adamec, 2007), are decomposed and may serve as a nutrient source for *Utricularia*. It has been suggested that these commensal–trap interactions in *Utricularia* plants growing in nutrient-poor waters with low prey availability may be of greater nutritional importance to the plants than prey capture alone (Richards, 2001; Sirová et al., 2009). In support of this, Alkhalaf et al. (2009) determined phytoplankton occurrence in *U. vulgaris* and *U. australis* traps and preliminarily estimated that the nutritional use of phytoplankton could have a great ecological importance for the plants.

This concept of "vegetarian" nutrition in nutrient-poor waters has a major question to answer: how does a sufficient quantity of N and P in the form of microorganisms and/or detritus enter the traps from the ambient medium? Recently, using a high-speed camera, Marmottant et al. (2009) reported an occurrence of spontaneous and regular firing (without any mechanical irritation) in intact *Utricularia* traps. This may explain how phytoplankton or detritus enter the traps.

The aim of this work was to automatically monitor trap thickness as a measure of water flow in three aquatic *Utricularia* species. An electronic position sensor was used over a period of 1–2 days to verify spontaneous firings and describe their basic characteristics. Ecological and physiological consequences of such spontaneous firings for *Utricularia* are also discussed.

2. Materials and methods

2.1. Plant material

Adult plants of *U. vulgaris* L. (collected in the Czech Republic) and *U. inflata* Walt. (collected in New Jersey, USA) were grown outdoors in two plastic containers which simulated their natural conditions (area 2 m^2, 750 L for the former species, area 0.8 m^2, 300 L for the latter species; for details see Sirová et al., 2003; Adamec, 2008a). The plants were grown in tap water with a litter of robust *Carex* species used as a substrate. The pH of the cultivation media was ~7.0, dissolved oxygen concentration ranged from 0.15 to 0.30 mM and the free CO_2 concentration was 0.10–0.15 mM. From the concentrations of nutrients (range in μM: NO_3^-, 0–3; NH_4^+, 1–4; PO_4^{3-}, 0.3–0.6) and humic substances (range 4–10 mg L^{-1}), the water in these cultures was considered oligotrophic and humic (Sirová et al., 2003; Adamec, 2008a; Adamec et al., 2010). *U. reflexa* Oliver (collected in the Okavango Delta, Botswana) was grown in an indoor laboratory under natural light in 3 L aquaria and *Carex* litter was also used as a substrate. Small zooplankton species (mainly copepods and chydorids) were added weekly to all cultures to promote plant growth.

2.2. Measurement of trap thickness

As a measure of water flow and trap volume change, trap thickness was measured in isolated traps of the three *Utricularia* species. For *U. vulgaris*, either young, rose-coloured traps from the 5th–6th mature leaf node or old, dark pink traps from the 30th leaf node were used. The traps were fully functional and typically ~4.0 mm long, ~3.0 mm wide and the leaf nodes were counted from the plant apex. Rose-coloured traps of *U. inflata* were from the 4th mature leaf node (length *ca.* 2.9 mm, width *ca.* 2.2 mm) and may be considered young. Greenish, young traps of *U. reflexa* were from the 3rd–5th leaf nodes (length *ca.* 5.5 mm, width *ca.* 3.8 mm). The intact trap-bearing leaves were excised directly under water in the cultivation containers and trap firing was induced by shaking the leaves. They were then transferred to the laboratory and after washing the leaf in tap water, a trap was excised and carefully transferred to a 10 mL perspex chamber containing a solution composed of 0.1 mM KCl, 0.05 mM $CaCl_2$ and 0.2 mM $NaHCO_3$ of pH 7.3–7.4.

A freshly excised trap at the initial stage of resetting (2–5 min) and without any macroscopic animal prey or air bubbles, was carefully inserted into the holder between a fixed stainless steel plate and a mobile T-shaped plastic plate which acted as a clamping ring and was connected to the position sensor (Fig. 1). The trap was fixed such that the T-shaped plate slightly compressed around two-thirds of its length at the end opposite the trap door (see Sydenham and Findlay, 1975; Sasago and Sibaoka, 1985a). The position sensor was thus able to measure trap thickness changes very sensitively by avoiding the wider, trap door area as this has a more constant thickness. The trap was also fixed such that the trap door faced upwards, to enable easy experimental firing (Fig. 1) and the position sensor was fixed at an angle of about 45° so that the trap door was ~4 mm below the surface. The computer-interfaced position sensor was a miniature linear displacement transducer (model GH-UMS-0.5, Singer Instruments Ltd., Tirat Karmel, Israel). Essentially, this is an electrical coil equipped with a fine mobile core as a sensor; the mobile core being equipped with a very fine spring for trap fixation. The position sensor had a total sensing range of 2.0 mm with a 1 μm resolution; its long-term stability and reproducibility was 2–3 μm. It was estimated using a digital balance that the position sensor had pressed against the fixed trap by the force not

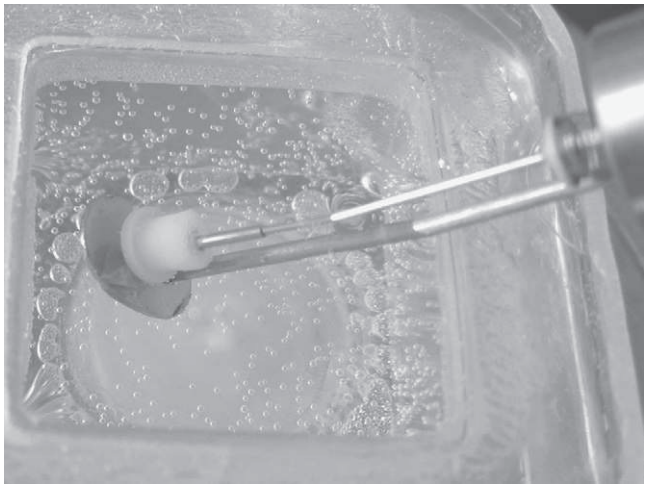

Fig. 1. A photo of a measurement of trap thickness changes in *Utricularia reflexa* using a linear position sensor. The trap is fixed in the sensor laterally.

exceeding about 4 mN (*i.e.*, equivalent to the weight of 0.4 g). There was no indication that such a small force adversely affected the native trap function during the measurements. Furthermore, the measured recordings with a fixed trap were very resistant to all kinds of mechanical shock. In most cases, trap thickness measurements were made at 1 min intervals and the chamber was partly covered by a perspex lid to minimise water evaporation.

Water temperature was relatively stable during the measurements and was within 25.0 ± 1.0 °C for young traps of *U. vulgaris*, 23.5 ± 1.0 °C for old *U. vulgaris* traps, 24.0 ± 0.5 °C for *U. inflata* and 21.0 ± 1.0 °C for *U. reflexa*, respectively. During the measurements, the temperature change was usually <1.2 °C and the traps were in natural dim daylight. As a control, and with the aid of a loupe, the fixed traps were stimulated to fire by mechanical irritation using a very fine, narrow brush which gently touched sensitive trigger hairs on the trap door (Sasago and Sibaoka, 1985a). The position of the fixed trap in the holder remained unchanged with mechanical irritation. Measurements of trap thickness were usually made according to the following schedule: 30 min after the insertion of a fired trap into the holder, the trap was again fired by mechanical irritation (denoted as time 0) and this step was usually repeated again after another 30 min. The trap was then allowed to rest for 24 h (or in few cases for 48 h) and spontaneous firings were recorded. After 24 h, the trap was further fired by mechanical irritation and the next 30 min of trap resetting were recorded. To compare trap firing and resetting due to prey capture with that caused by mechanical stimulation, young *U. vulgaris* traps were first fired mechanically and, after 30 min, about 30 living prey items (*Eudiaptomus* sp., ostracods) were carefully added to the chamber medium to enable natural firing. The number of prey items captured corresponded with the number of firings recorded by the sensor. To evaluate the plasticity of the trap wall structures, a 1-cm piece of nylon line (diameter 0.25 mm) was inserted into the trap door, to keep the intact trap permanently open. This was done after conventional 24-h measurements with young *U. vulgaris* and *U. reflexa* traps. Trap thickness was recorded during 1.5–3 h after nylon insertion but as the original trap position in the holder was usually changed due to this procedure, only subsequent relative values can be evaluated. After all measurements, trap length and width were estimated to the nearest 0.1 mm by measuring with a rule, again viewed under a loupe with 3 times magnification.

2.3. Evaluation of data and statistical analysis

Six to 15 parallel traps of the same age category, usually originating from different plants, were used for the measurements. The following parameters were evaluated from the recordings (*cf.* Sydenham and Findlay, 1975; Sasago and Sibaoka, 1985a): initial maximum (fired) trap thickness just after insertion into the holder; trap thickness before spontaneous firings; change of trap thickness due to mechanically stimulated firing after insertion, after 24 h, and during spontaneous firings; initial resetting rate after all types of firing over 10 min (expressed as trap thickness decrease between min 1 and 11) and over 30 min (min 0–min 30); frequency of spontaneous firings within the 24-h resting period with no mechanical irritation; and time between two spontaneous firings (and/or the time between the last mechanically stimulated firing and the first spontaneous firing). As the traps of the three *Utricularia* species differed greatly in their size it was not possible to compare trap thickness changes or resetting rates between the species, but only within each species (by 1-way ANOVA) for different phases of the experiments (firing after trap insertion, after 24-h resting period, spontaneous firings). Repeated measures design of ANOVA could not be used for evaluation of data as this step would lead to a substantial reduction of data. In that case, all measurements without any spontaneous firing would be discarded. Significant differences in the frequency of spontaneous firings and the time between two spontaneous firings between all species, and different trap ages of *U. vulgaris* were evaluated by 1-way ANOVA (Tukey HSD test for unequal *n*). Mean ± S.E. values are shown where possible.

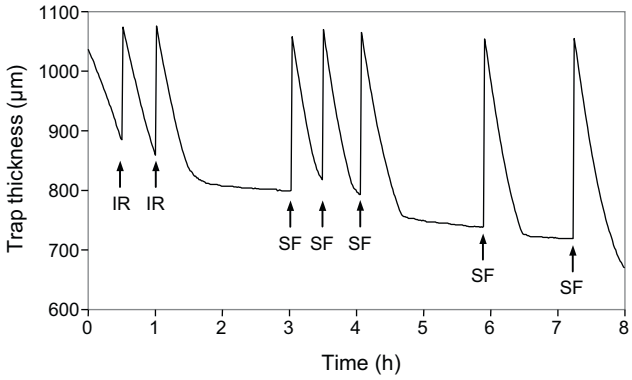

Fig. 2. Typical record of trap thickness changes in an isolated *Utricularia inflata* trap during firings and resettings. IR, firing by mechanical irritation; SF, spontaneous firing.

3. Results

Isolated traps of all three tested *Utricularia* species could be fired by mechanical irritation and reset completely within a 24–48 h period. After trap insertion, mechanical irritation of traps led to a quick increase of mean trap thickness by 195–240 μm followed by much slower resetting (61–89 μm in the initial 10 min or 155–223 μm in 30 min) (Fig. 2, Table 1). After the resting period of 24 h, firing by mechanical stimulation increased the mean trap thickness by 288–373 μm and the resetting rates were not significantly different from those after initial trap insertion within each species. All these trap thickness changes were significantly lower in old traps of *U. vulgaris* than in young traps. Firing after the 24-h resting period increased the trap thickness by 22–32% of the initial maximum trap thickness, with the greatest increase occurring in *U. inflata* and the smallest in *U. reflexa*. Within the 24-h resting period, spontaneous firings were found in traps of all species and in both trap age categories of *U. vulgaris*, but their distribution in time was very irregular (Fig. 2). Within each plant species or trap age category, no significant difference in the trap thickness increase due to spontaneous firing was found when compared with firings stimulated mechanically after the 24-h resting period (Table 1). Traps of different species fired spontaneously on average 0.29–2.4 times within the 24-h resting period. There were, however, great differences in the frequency of spontaneous firing among individual traps (from 0 up to 6) but a significant difference was found only between old traps of *U. vulgaris* and *U. inflata*. Additionally, the time between two spontaneous firings was variable within each species (mean 891 min in young traps of *U. vulgaris*, range 80–1989 min; mean 838 min in old traps of *U. vulgaris*, range 72–2118 min; mean 319 min in *U. inflata*, range 28–1436 min; mean 559 min in *U. reflexa*, range 88–1430 min). Within each species or trap age category, resetting rates of traps after spontaneous firings did not differ significantly from those recorded after mechanical stimulation. There is no quantitative difference between spontaneous and mechanically stimulated trap firing.

In young traps of *U. vulgaris*, trap thickness increase and resetting rates were not significantly different between zooplankton prey capture and mechanical stimulation (data not shown). After young traps of *U. vulgaris* had been opened permanently by a piece of nylon line a logarithmic-type increase in trap thickness over time was recorded for 3 h (data not shown). Trap thickness increased on

Table 1
Thickness changes of separated *Utricularia* traps during trap firing (stimulated by mechanical irritation or induced spontaneously) or trap resetting during the 24-h resting period.

Initial max. trap thickness (μm)	Trap thickness increase (μm) during firing within			Resetting rate (μm) after firing during						Spontaneous firing		
	INS	24 h	SF	10 min within			30 min within			Trap thickness before SF (μm)	Frequency per 24 h	Time between SFs (min)
				INS	24 h	SF	INS	24 h	SF			
(A) *U. vulgaris* young traps												
1225	240	373[a]	319[a]	88.8[a]	79.0[ab]	65.3[b]	223[a]	203[ab]	165[b]	754	[AB]1.00	[A]891
±34	±12	±17	±21	±6.9	±3.7	±4.9	±15	±13	±10	±22	±0.46	±202
(10)	(17)	(6)	(13)	(13)	(7)	(12)	(13)	(5)	(12)	(12)	(8)	(13)
(B) *U. vulgaris* old traps												
1148	197	288[a]	297[a]	67.5[a]	56.8[a]	57.4[a]	173[a]	139[a]	141[a]	808	[A]0.29	[AB]838
±25	±17	±2.2	±17	±6.1	±5.6	±2.9	±13	±5.6	±8.6	±29	±0.18	±254
(6)	(9)	(5)	(9)	(8)	(4)	(9)	(8)	(3)	(9)	(9)	(7)	(9)
(C) *U. inflata* young traps												
978	195	316[a]	322[a]	78.3[a]	80.0[ab]	111[b]	207[a]	201[ab]	265[b]	658	[B]2.43	[B]319
±30	±18	±65	±19	±7.6	–	±5.1	±20	–	±9.4	±40	±0.72	±100
(7)	(11)	(3)	(19)	(11)	(2)	(18)	(11)	(2)	(18)	(20)	(7)	(20)
(D) *U. reflexa* young traps												
1635	208	356[a]	354[a]	61.0[a]	52.4[a]	56.4[a]	155[a]	145[a]	159[a]	1205	[AB]1.47	[AB]559
±34	±11	±26	±13	±2.7	±3.6	±3.7	±6.2	±11	±4.2	±35	±0.35	±91
(15)	(18)	(10)	(24)	(10)	(5)	(13)	(10)	(4)	(12)	(13)	(15)	(24)

Traps were fired mechanically both 30 min after trap insertion (INS) and 24 h afterwards (24 h); spontaneous firing was associated with no type of trap irritation. Frequency of spontaneous firings (SFs) is shown for the period of 24 h but the time of the occurrence of spontaneous firing from the last firing or between two subsequent spontaneous firings is shown for the resting period of 24–48 h. Means ± S.E. intervals and number of items (in parentheses) are shown. Different letters (right side of the columns) within each plant species for the same parameters of resetting rate (either 10 min or 30 min) after trap insertion, 24-h exposure, and after spontaneous firing, and firing trap thickness changes after the 24-h resting period and spontaneous firing denote statistically significant difference at $P < 0.05$ (1-way ANOVA). Different capital letters (left side of the columns) between four species for the frequency per 24 h and the time between SFs denote statistically significant difference at $P < 0.05$ (1-way ANOVA).

average by 83 ± 11 μm (S.E., $n = 4$) after 30 min, by 93 ± 7 μm after 1 h, and only by 110 ± 5 μm after 3 h.

4. Discussion

The position sensor used has been shown to be both suitably reliable and sensitive to monitor short and long-term changes in *Utricularia* trap thickness caused by water flow due to trap firing and resetting. Moreover, excised young traps of all three *Utricularia* species were able to both fire and reset in the chamber even after 48 h. Within all three species and both trap age categories, the rates of trap resetting, which are energetically demanding, were not significantly different between freshly inserted traps and those triggered after 24 h (Table 1). This character of relative long-term, normal trap functioning behaviour, in spite of high energetic requirements (Adamec, 2006, 2007), supports the established view that *Utricularia* traps are rather autonomous organs (Sirová et al., 2003; Adamec et al., 2010).

In general, the recorded patterns of trap thickness changes during firing and subsequent trap resetting were identical to those described by Sydenham and Findlay (1973, 1975) in *Utricularia* sp. (probably *U. australis*) and Sasago and Sibaoka (1985a) in *U. vulgaris*. In summary, a quick initial trap thickness increase by 288–373 μm, followed by a slow, negative-exponential thickness decrease lasting for at least 6–10 h (Fig. 2, Table 1) was observed. After this, further thickness changes were usually negligible. As per the studies by Sydenham and Findlay (1973, 1975) and Sasago and Sibaoka (1985a) there was a distinct discrepancy between the time-course of the pressure changes within the traps and that of trap thickness; the former attained a stable value within 25–30 min while the latter continued to decrease for at least 3 h. The time-course of the internal trap pressure does not correlate exactly with trap thickness change and/or water flow. After 25–30 min, when the trap is ready to fire again, further water flow does not lead to a decrease in the minimum, stable pressure. This is likely due to the special mechanical properties of the trap walls.

Although firing in itself is a purely mechanical process, there are indications for the existence of an excitatory step in the sensitive trigger hairs and the trap door (Sydenham and Findlay, 1973). In this study, 1 weak touch of the fine brush on the trigger hairs usually triggered the trap to fire after the 30 min intervals but in many cases, 2–6 repeated touches at about 1 s intervals were necessary to fire the trap.

In all three *Utricularia* species, repeated and reproducible firings were recorded during the 24-h resting period when all other plausible methods of trap irritation (mechanical shock, water movement in the chamber, presence of zooplankton, light/dark transition, *etc.*) were excluded (Fig. 2). The presence of such firings did not depend on the time of day or the irradiance. It is therefore believed that such firings are spontaneous and not stimulated by any other means. The spontaneous firings and the trap resetting rates agreed quantitatively with those stimulated mechanically after the 24-h resting period (Table 1). The occurrence of spontaneous firings was very irregular and the time period between two spontaneous firings in individual traps in all three species and in both age categories in *U. vulgaris* varied by 16–50 times. Moreover, 0–71% of traps within each species did not exhibit any spontaneous firing for the 24-h resting period. In comparison, Marmottant et al. (2009) have recently reported a regular occurrence of spontaneous firings in *Utricularia* sp. traps after about 5 h. The present results show that spontaneous firings occurred when the reset traps in all species were greatly narrowed; their mean thickness before each spontaneous firing was by 320–471 μm lower than the initial maximum trap thickness after trap insertion. Moreover, except for *U. inflata*, this trap narrowing was considerably greater than the trap thickness increase due to spontaneous firings (mean 297–354 μm). It is probable that a spontaneous firing occurs when the negative pressure inside the reset traps is minimal (*i.e.*, trap thickness is minimal, too) and the trap door is no longer able to withstand the ambient water pressure. Thus, spontaneous firing might function as a 'safety valve' when the magnitude of negative pressure is critical for the integrity of the trap door. Evidently, the magnitude of negative pressure inside the trap is the principal factor regulating processes associated with trap resetting (Sasago and Sibaoka, 1985a) and also spontaneous firings. It is also shown from our measurements that the trap thickness may not return to the same initial values as a result of firings (*see* Fig. 2), but may be somewhat lower. Sydenham and Findlay (1973) and Sasago and Sibaoka (1985a) also measured a relative negative pressure just after trap firing which did not equilibrate exactly to ambient. Traps do not aspirate in all water during the firing process to equalize the internal and ambient pressures. The behaviour of permanently open traps may indicate a great contribution of trap wall plasticity on biomechanical trap properties during firing and resetting.

In nutrient-poor waters with poor prey abundance, the nutritional gain of carnivory can be minimal (Richards, 2001; Adamec, 2008b; Peroutka et al., 2008; Sirová et al., 2009). Under such conditions, commensal–trap interactions in *Utricularia* could be of a greater nutritional importance for the plants than prey capture alone. However, for the possible trap uptake of growth-limiting N and P by the activity of the microbial food-web, it is essential that the traps are able to draw in as much particulate matter (phytoplankton, detritus) as possible. If the traps are not exclusively fired as a result of mechanical stimulation, but can also do so spontaneously after several hours, a much greater amount of digestable particles would be available as a potential nutrient source. The increased uptake of growth-limiting N and P for ecological benefit is counterbalanced by the energy cost of spontaneous trap firing. As the net photosynthetic rate of aquatic *Utricularia* shoots is extremely high (Adamec, 2006) the plants are capable of covering this energy demand of traps. Recent preliminary investigations of Alkhalaf et al. (2009) on two aquatic *Utricularia* species estimated the importance of nutrient uptake from phytoplankton. Moreover, if the "vegetarian" or detritivorous way of nutrition dominates over true carnivory in aquatic *Utricularia* species growing in waters with low prey availability, it allows one to hypothesize that the primary trap function in aquatic *Utricularia* species in the process of trap evolution was to draw in phytoplankton and detritus from the ambient water. The traps may have adapted to capture mobile animal prey in more fertile waters as a secondary function.

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