Trap closure and prey retention in Venus flytrap (*Dionaea muscipula*)
temporarily reduces photosynthesis and stimulates respiration

Andrej Pavlovič*, Viktor Demko and Ján Hudák
Department of Plant Physiology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina B2, 842 15, Bratislava, Slovak Republic

Received: 10 August 2009 Returned for revision: 11 September 2009 Accepted: 5 October 2009 Published electronically: 3 November 2009

Background and Aims The carnivorous plant Venus flytrap (*Dionaea muscipula*) produces a rosette of leaves: each leaf is divided into a lower part called the lamina and an upper part, the trap, with sensory trigger hairs on the adaxial surface. The trap catches prey by very rapid closure, within a fraction of a second of the trigger hairs being touched twice. Generation of action potentials plays an important role in closure. Because electrical signals are involved in reduction of the photosynthetic rate in different plant species, we hypothesized that trap closure and subsequent movement of prey in the trap will result in transient downregulation of photosynthesis, thus representing the energetic costs of carnivory associated with an active trapping mechanism, which has not been previously described.

Methods Traps were enclosed in a gas exchange cuvette and the trigger hairs irritated with thin wire, thus simulating insect capture and retention. Respiration rate was measured in darkness ($R_D$). In the light, net photosynthetic rate ($A_N$), stomatal conductance ($g_i$) and intercellular CO2 concentration ($c_i$) were measured, combined with chlorophyll fluorescence imaging. Responses were monitored in the lamina and trap separately.

Key Results Irritation of trigger hairs resulted in decreased $A_N$ and increased $R_D$ not only immediately after trap closure but also during the subsequent period when prey retention was simulated in the closed trap. Stomatal conductance remained stable, indicating no stomatal limitation of $A_N$, so $c_i$ increased. At the same time, the effective quantum yield of photosystem II ($Φ_{PSII}$) decreased transiently. The response was confined mainly to the digestive zone of the trap and was not observed in the lamina. Stopping mechanical irritation resulted in recovery of $A_N$, $R_D$ and $Φ_{PSII}$.

Conclusions We put forward the first experimental evidence for energetic demands and carbon costs during insect trapping and retention in carnivorous plants, providing a new insight into the cost/benefit model of carnivory.

Key words: Action potential, carnivorous plant, cost/benefit model, chlorophyll fluorescence imaging, *Dionaea muscipula*, photosynthetic rate, respiration rate, Venus flytrap.

INTRODUCTION

Carnivorous plants have fascinated scientists for centuries, and the Venus flytrap (*Dionaea muscipula*) is one of the most spectacular due to the rapid movement of its trap. Charles Darwin was also fascinated by the Venus flytrap and called it ‘one of the most wonderful plants in the world’ (Darwin, 1875). Closure of the Venus flytrap is one of the fastest movements in the plant kingdom. The plant produces a rosette of leaves, each divided into two parts: the lower called the lamina and the upper the trap. The trap consists of two lobes, which close together forming an enclosed pocket. Juniper et al. (1989) described the trap as consisting of three zones. The first has 14–21 marginal teeth on each lobe, which interlock when the trap snaps. The second zone is a peripheral narrow band bearing small sessile glands, which secrete carbohydrates, presumably as a prey attractant. The third zone, the largest, is the whole central zone which is covered with digestive glands. Among these are bristles known as trigger hairs, usually three to a lobe. When an insect crawls along the venal surfaces and bumps into the three small trigger hairs, the trap snaps shut. Two touches of a trigger hair activate the trap which snaps in a fraction of second at room temperature. However, at higher temperature (35–40 °C) only one stimulus is required for trap closure (Brown and Sharp, 1910). Darwin suggested that an impulse must travel rapidly to enable the rapid response observed. In response to Darwin’s request, Burdon-Sanderson (1873) discovered that the impulse was electrical and resembled the signal of animal nerve and muscle. There is no doubt that action potentials play an indispensable role in rapid plant movements. The action potentials in *Dionaea* have been extensively studied (e.g. Burdon-Sanderson, 1873; Hodick and Sievers, 1986, 1988, 1989; Sibaoka, 1991; Krol et al., 2006; Volkov et al., 2008a). An electrical stimulus closes the trap without mechanical stimulation of the trigger hair, and repeated application of a lower voltage demonstrates the existence of electrical memory in *Dionaea* (Volkov et al., 2007, 2008a, b, c, 2009). However, the mechanism by which the trap shuts is poorly understood. The most frequent explanations are acid-induced cell wall loosening (Williams and Bennett, 1982) and rapid loss of turgor pressure (Batalin, 1877). Trap closure occurs via rapid changes in the curvature of each lobe rather than movement of the leaf as a whole. Recently Forterre et al. (2005) provided a comprehensive analysis of leaf geometry during closure of the trap. The driving force in closure is most probably the elastic...
energy accumulated due to the hydrostatic pressure differences between the upper and lower layers of the lobes. The electrical signals open the water pores between these layers to open and the water transfers from the upper to the lower layer. Aquaporins may play an important role in this process, because aquaporin inhibitors (e.g. HgCl₂) inhibit trap closure and ion channel inhibitors (e.g. lanthanum) reduce the amplitude of action potentials (Krol et al., 2006; Volkov et al., 2008b, c). After rapid closure secures the prey, chemical and mechanical stimuli from the struggling prey result in a slow closing process during which the whole trap is sealed into a tight pouch. Soft parts of insect bodies are broken down by enzymes and the digestive products are absorbed (Schnell, 2002). In this way D. muscipula growing in nutrient-poor habitats obtains up to 75% of its nitrogen from insects (Schulze et al., 2001).

Action potentials occur in many plant species, including rapid leaf movements in ‘sensitive plants’ and, irrespective of rapid leaf movements, electrical signals also trigger physiological processes in plants which are not carnivorous or sensitive (reviewed by Fromm and Lautner, 2007). It has been well documented that electrical signals propagated in plants over long, as well as short, distances reduce photosynthesis. Thus, heat stimulation evokes electrical activity and decreases photosynthesis in adjacent leaves in different species (Koziolek et al., 2003; Lautner et al., 2005; Hlaváčková et al., 2006; Kaiser et al., 2006). This convincing evidence for a link between electrical signalling and photosynthesis in response to abiotic stress suggests that trap closure in Dionaea and the associated electrical signals will decrease photosynthesis. However, physiological effects in carnivorous plants in response to mechanical irritation have not been investigated. We hypothesized that trap closure and subsequent movement of prey in the trap (simulation of insect retention) will result in transient downregulation of photosynthesis. Because the rate of net photosynthesis (Aₙ) is a function of dark respiration (Rₒ) as well as of gross photosynthesis (Aₒ), we also measured the rate of Rₒ. Carbon dioxide fluxes were measured by gas exchange, and these were combined with chlorophyll fluorescence imaging to measure effective quantum yield of photosystem II (ΦPSII). This parameter measures the proportion of the light absorbed by chlorophylls associated with photosystem II that is used in photochemistry. Under laboratory conditions it can give a measure of the rate of linear electron transport and so an indication of overall photosynthesis (Maxwell and Johnson, 2000). Because photosynthesis and respiration are principal points in cost/benefit analysis of carnivorous plants (Ellison and Gotelli, 2009), we discuss our results with regard to the cost/benefit model of carnivory proposed by Givnish et al. (1984). We extended the classical interpretation of the model (carnivorous plants with constant low Aₙ in traps) by direct carbon costs associated with insect trapping and retention, which has not been previously described.

MATERIALS AND METHODS

Plant culture and experiments

Twenty 3- or 4-year-old Dionaea muscipula J. Ellis plants were grown under standard greenhouse conditions at a maximum daily irradiance of 1000 μmol m⁻² s⁻¹ PAR (photosynthetically active radiation), in a collection of carnivorous plants at the Department of Plant Physiology in Bratislava, in well-drained peat moss in plastic pots irrigated with distilled water. All experiments were performed on healthy leaves. Because the diameter of the cuvette window used in gas exchange measurements was 18 mm, the traps used in our experiments did not exceed this size. The laminae were longer than 50 mm, because the size of the cuvette head gasket plates was 45 mm. Leaves were cut near the base, without causing closure of traps, and the upper part of the leaf (trap) and thin wire (diameter approx. 0.1 mm) inside the needle from a syringe plugged with silicone grease were sealed into a leaf cuvette (PLC6, PP-systems, Hitchin, UK) which monitors the CO₂ and H₂O exchange. The bases of laminae were submerged in distilled water in Eppendorf tubes to prevent drying out. Movement of the wire in the empty, closed cuvette had no effect on CO₂ and H₂O exchange, confirming that the movements of thin wire had no effect on the gas-tight seal. After stabilization of conditions (leaf temperature 24 ± 1°C, ambient CO₂ concentration 380 μL L⁻¹, relative air humidity 60–65%), the trigger hairs of the trap were mechanically stimulated by manipulation of the wire protruding outside the cuvette. The wire was placed between the two trigger hairs inside the open trap, so just a very short movement (5 mm) was sufficient for trigger hair stimulation. Two of the six trigger hairs inside the trap were gently touched until the trap snapped: this is the ‘snap phase’ of the experiment. In the subsequent ‘prey struggle’ phase of the experiment the trigger hairs were repeatedly stimulated mechanically for 5 min with the wire inside the closed trap whilst it was enclosed in the cuvette. Both experiments were repeated on the lower part of the leaf (lamina), by enclosing only the lamina in the cuvette, with the trap protruding outside. The mechanical irritation was performed on the trap outside the cuvette, with the same wire. Both experiments were repeated under light as well as dark conditions. The experiments were repeated ten times for each experimental set-up with the same results. Because the trap of the Venus flytrap rapidly changes geometry after closure (Forterre et al., 2005), we wanted to exclude the possibility that reduced photosynthetic parameters are due to changes of light interception by traps. Therefore, we irritated only one trigger hair by one touch. One stimulus generates one electrical potential (Volkov et al., 2008a) and we expected that photosynthetic parameters would decrease without trap closure (trap geometry remained unchanged). This experiment was repeated ten times with the same results.

Gas exchange measurements

Gas exchange was measured using an infrared gas analyser with an automatic leaf cuvette (CIRAS-2 and PLC6; PP-Systems, Hitchin, UK). The rates of net photosynthesis (Aₙ), stomatal conductance (gₛ) and intercellular CO₂ concentration (c_i) were measured at a saturating irradiance of 1000 μmol m⁻² s⁻¹ PAR, leaf temperature 24 ± 1°C, ambient CO₂ concentration 380 μL L⁻¹, relative air humidity 60–65% and water vapour deficit 700–1000 Pa. The rate of respiration (Rₒ) was measured under the same conditions at
0 µmol m\(^{-2}\) s\(^{-1}\) PAR. Light was provided by blue and red light-emitting diodes (LEDs) using the Fluorcam FC-1000 LC (Photon Systems Instruments, Brno, Czech Republic) attached to the PLC6 cuvette. During illumination, the camera allowed movement of the wire and trap to be monitored inside the cuvette during irritation. The traps or laminae were kept in the cuvette for 5–10 min (until steady-state CO\(_2\) concentrations were reached) before the trap (inside or outside the cuvette) was stimulated. After stopping stimulation of the trap, gas exchange measurements continued for an additional 10 min. All parameters were recorded every 2 s. The area of the trap or lamina did not usually cover the entire cuvette area, therefore their areas were determined after the measurement from the recorded images, using the calibrated Fluorcam FC-1000 LC, and gas exchange rates per unit surface area of trap and lamina were calculated. Live prey could not be used in our experiments due to their respiration which would have affected gas exchange measurements.

**Chlorophyll fluorescence imaging**

Chlorophyll fluorescence imaging, measured by the Fluorcam FC-1000 LC attached to the PLC6 cuvette, was used to assess the spatiotemporal variations of \(\Phi_{\text{PSII}}\) by the saturation pulse method. The laminae and traps inside the cuvette were adapted for 5–10 min to 100 µmol m\(^{-2}\) s\(^{-1}\) PAR before the stimulation. Saturation pulses were given every 35 s (4000 µmol m\(^{-2}\) s\(^{-1}\) PAR, 800 ms duration) for determination of \(\Phi_{\text{PSII}}\). The three pulses were applied before the trap was stimulated. The fourth pulse followed 1–2 s after trigger hairs were irritated and then every 35 s for 10 min (‘snap phase’) or 15 min (‘prey struggle phase’). Effective quantum yield was calculated as \((F_m' - F_i)/F_m'\) (Maxwell and Johnson, 2000). The changes in \(\Phi_{\text{PSII}}\) were most pronounced at low light intensity (100 µmol m\(^{-2}\) s\(^{-1}\) PAR), when \(\Phi_{\text{PSII}}\) values are higher (more light absorbed by PSII is used for photochemistry) than at high light intensity; therefore, \(\Phi_{\text{PSII}}\) was not measured simultaneously with gas exchange at saturating irradiance.

**RESULTS**

Stimulation of trigger hairs and subsequent trap closure very rapidly decreased the rate of net photosynthesis \((A_N)\) of traps to nearly zero. Then \(A_N\) started to recover, reaching the rate before mechanical stimulation within 10 min. In contrast, no inhibition of \(A_N\) was observed in the laminae (Fig. 1A). Rapid inhibition of \(A_N\) in traps resulted in a transient increase in the intercellular CO\(_2\) concentration (Fig. 1B). Stomatal conductance \((g_s)\) was not affected, either in the traps or in the laminae, indicating the absence of stomatal movements (Fig. 1C). There was a decrease in \(\Phi_{\text{PSII}}\) in traps but not in laminae (Figs 1D, and 2A, B). The rapid changes of \(\Phi_{\text{PSII}}\) are not related to the changes in trap geometry caused by closing, because inhibition of \(\Phi_{\text{PSII}}\) also occurred in traps that did not snap after single trigger hair stimulation. This type of experiment revealed that the inhibition of \(\Phi_{\text{PSII}}\) is confined mainly to the abaxial side of the trap (Fig. 3). The recovery of \(\Phi_{\text{PSII}}\) was not entirely completed within 10 min although the values are only slightly lower (about 0·04) than before stimulation (Figs 1D, 2A and 3). The inhibition of \(\Phi_{\text{PSII}}\) was not as great as inhibition of \(A_N\), suggesting that \(R_D\) may be transiently enhanced during irritation, because \(A_N\) is a function of \(R_D\) as well as of gross photosynthesis \((A_G)\). We repeated the experiments in the dark. Stimulation of trigger hairs resulted in transient efflux of carbon dioxide from traps but not from laminae (Fig. 4). The recovery of \(R_D\)
was completed within 10 min. Similar to the experiments in the light, $c_i$ transiently increased in the traps and stomatal conductance was not affected (data not shown).

After rapid closure secures the prey, mechanical stimulation of the trigger hairs due to its struggling continues until the prey is exhausted or dead. Therefore, we continuously measured gas exchange and chlorophyll fluorescence with mechanical irritation of traps for 5 min: the trigger hairs on the inner surface were touched by the wire, thus simulating the struggling of prey. Repeated mechanical irritation of trigger hairs resulted in a rapid decline of $A_N$ in traps, to below the CO$_2$ compensation point, so that negative values occurred compared with the ‘snap phase’ experiment. However, with prolonged stimulation, the suppression of $A_N$ slightly decreased.

Again, no inhibition of $A_N$ was found in the laminae (Fig. 5A). Similar to ‘snap phase’ experiments, $g_s$ was not affected and $c_i$ transiently increased (data not shown). $\phi_{PSII}$ dropped and the recovery started in parallel with $A_N$ after stimulation (Fig. 5B). The decrease of $\phi_{PSII}$ in both experiments was due to the decrease of maximum fluorescence ($F_{m}'$) as well as to an increase of steady-state fluorescence ($F_s$) in the light-adapted state. Chlorophyll fluorescence showed a substantial decrease of $\phi_{PSII}$ in traps but not in laminae. The strongest inhibition of $\phi_{PSII}$ in traps occurred in the third zone covered with digestive glands. Reduction of $\phi_{PSII}$ in the midrib as well as in the first zone with marginal teeth and in the second zone with nectar glands was negligible (Fig. 6A, B). The experiment was repeated in the dark,
confirming that both inhibition of the light reactions of photosynthesis and increased $R_D$ contribute to the rapid efflux of CO$_2$ from traps during prey retention. The most rapid efflux of CO$_2$ was during the first seconds of stimulation. Prolonged mechanical stimulation decreased the efflux of CO$_2$. The recovery of $R_D$ was also completed within 10 min., similarly to ‘snap phase’ trap experiments (Fig. 5C).

**DISCUSSION**

The results show unequivocally that stimulation of trigger hairs in *D. muscipula* rapidly decreased $A_N$ in traps but not in laminae (Fig. 1A), and chlorophyll fluorescence imaging also showed a decrease of $\Phi_{PSII}$ in traps, but not in the laminae (Fig. 2A, B). Therefore, light, as well as dark, reactions of photosynthesis were inhibited during trap closure. We are convinced that reduction of photosynthesis in the Venus flytrap is due to irritation of trigger hairs which generate electrical signals and is independent of trap closure: ‘single hair irritation’ and the ‘prey struggle phase’ of the experiment also resulted in reduction of photosynthesis (Figs 3, 5A, B and 6A). Action potentials in *Dionaea* have been extensively studied (Burdon-Sanderson, 1873; Hodick and Sievers, 1988; Hodick and Sievers, 1989; Sibaoka, 1991; Krol et al., 2006; Volkov et al., 2007). Action potentials propagate from mechano-sensitive trigger hairs of the lobe to the midrib in the traps. Volkov et al. (2007, 2008a) concluded that action potential signalling in *Dionaea* is limited to the traps and is not propagated to the laminae. Only graded potentials with very low amplitude were detected 2 min after the trap closing in laminae, and these electrical signals have no effect on $A_N$, $R_D$ or $\Phi_{PSII}$ in laminae (Figs 1, 2 and 4–6). A graded potential is a wave of electrical excitation that appears as a result of short-lived depolarization or hyperpolarization of an area of the plasma membrane in conductive bundles of plants. Graded potentials become weaker as they travel along conductive bundles in plants, whereas action potentials remain the same strength as they travel. Inhibitory effects of electrical signals on photosynthesis have been documented in different plant species (Fromm and Eschrich, 1993; Koziolek et al., 2003; Lautner et al., 2005; Bulychev and Kamzolkina, 2006; Hlaváčková et al., 2006; Kaiser and Grams, 2006). However, the mechanisms causing photosynthetic limitation by electrical signals are poorly understood.

Subcellular alterations in ion fluxes may be involved (Lautner et al., 2005). In most studies, the response was induced by heat stimulation, and photosynthesis was measured in neighbouring leaves. In the case of the sensitive plant *Mimosa pudica*, reduction of net CO$_2$ exchange and $\Phi_{PSII}$ in a neighbouring leaf is much stronger than observed in other plant species, and stomatal conductance rapidly increases during the first 2 min after heat stimulation, and subsequently declines to approximately half of the initial value before heat stimulation (Koziolek et al., 2003; Kaiser and Grams, 2006). A rapid decline in stomatal conductance and photosynthesis in neighbouring leaves after heat stimulation also occurs in tobacco (Hlaváčková et al., 2006). In our experiment with *Dionaea*, no reactions of stomata after mechanical stimulation were observed; therefore, we can exclude stomatal limitation of photosynthesis (Fig. 1C). Moreover, rapid efflux of CO$_2$
in the dark indicates a transient increase of \( R_D \) (Fig. 4). Therefore, it seems unlikely that changes in light and dark reactions of photosynthesis alone can explain the rapid decline of \( A_N \). A transient increase in \( R_D \) after an electrical and damaging stimulus was found in the liverwort *Conocephalum conicum* (Dzubinska et al., 1989). In addition, significant amounts of ATP are hydrolysed in the midrib of *D. muscipula* during trap closure (Jaffe, 1973). Williams and Bennett (1982) confirmed that during the closure about 29% of the cellular ATP is lost; this is used for rapid transport of hydrogen and water, resulting in changes in turgor pressure and subsequent closure of the trap. However, data presented here indicate that enhanced \( R_D \) is not only associated with the energy needed for trap closure, because increased \( R_D \) also occurred during repeated mechanical irritation of trigger hairs in closed traps (Fig. 5C).

The cost/benefit model of carnivory proposed by Givnish et al. (1984) predicts that carnivorous plants grow in nutrient-poor, but sunny and wet habitats, because only in this environment would the cost of producing traps be lower than the benefits gained from prey. Benefit from carnivory in term of increased \( A_N \) as a result of increased mineral absorption from prey, was confirmed only recently (Farnsworth and Ellison, 2008; Pavlovicˇ et al., 2009). In addition, costs represent energy devoted to carnivory in term of lures and digestive enzymes as well as lower \( A_S \) in traps, relative to non-carnivorous organs (reviewed by Ellison and Gotelli, 2001; Ellison, 2006; Ellison and Gotelli, 2009). Several authors also include in the costs increased \( R_D \) of carnivorous organs (Knight, 1992; Adamec, 2006). Laakkonen et al. (2006) modified the model of Givnish et al. (1984) by replacing photosynthetic with respiratory costs in *Utricularia*, because \( R_D \) in *Utricularia* bladders was 75–200% greater than that in the leaves (Adamec, 2006). Adamec (2006) suggested that bladders were probably in a post-firing state and pumping water. As demonstrated by Sydenham and Findlay (1975), ion and water pumping during the resetting of *Utricularia* bladders is a process requiring considerable energy, derived from respiration. However, there are no direct measurements of CO2 exchange in relation to resetting of bladders or trapping prey. The costs of carnivory have been assessed much less frequently than the benefits, because measuring energy lost is more difficult than measuring the benefits (Ellison and Gotelli, 2009). Until now, studies assessing the costs of carnivory have usually been confined to measurements of \( A_N \) and \( R_D \) in carnivorous traps vs. non-carnivorous leaves (Knight, 1992; Ellison and Gotelli, 2002; Adamec, 2006; Pavlovicˇ et al., 2007; Karagatzides and Ellison, 2009; Hájek and Adamec, 2010), to the construction costs and payback times for carnivorous organs (Osunkoya et al., 2007; Osunkoya et al., 2008; Karagatzides and Ellison, 2009) or to the carbon costs of sticky mucilage secretion by glands (Thorén et al., 2003). Taking into account the classical interpretation of the cost/benefit model, Ellison and Gotelli (2009) suggest that the *Dionaea* trap is an inexpensive structure. Our results demonstrate that rapid movement of traps is costly. Moreover, struggling prey closed inside the trap mechanically stimulate trigger hairs,
generating electrical signals which further inhibit \( A_N \) and \( \Phi_{\text{PSII}} \), and stimulate \( R_D \) (Fig. 5). That entrapped prey stimulate the trigger hairs and result in generation of action potentials was shown by Affolter and Olivo (1975). Lichtner and Williams (1977) elicited action potentials in traps for \( > 5 \) h using nylon bristles. This indicates that inhibition and stimulation of \( A_N \) and \( R_D \), respectively, may continue until the prey enclosed in the trap stops moving and may represent substantial carbon costs, especially at night or at low light intensities, when \( A_N \) is limited. Thus the prevailing cost/benefit model of carnivory requires modification to include photosynthetic responses directly associated with prey capture and retention (Fig. 7).

Darwin (1875) observed that small gaps between marginal teeth after rapid closure of the lobes of the leaf to form the trap allow small prey to escape from traps. This could be an adaptive trait, saving energy, because small prey do not provide sufficient amounts of nutrients to benefit the plant in terms of increased \( A_N \) and to outweigh the costs associated with retention of prey in a closed trap (decreased \( A_N \) + increased \( R_D \)). Gibson and Waller (2009) hypothesize that snap-traps evolved from ‘flypaper’ (sticky) traps to capture and digest larger prey efficiently, which brings greater benefit. The classical cost/benefit model considers a constant rate of \( \text{CO}_2 \) exchange with no direct photosynthetic costs increase due to insect trapping and retention. Benefit from prey enclosed in the trap stops moving and may represent substantial carbon costs, especially at night or at low light intensities, when \( A_N \) is limited. Thus the prevailing cost/benefit model of carnivory requires modification to include photosynthetic responses directly associated with prey capture and retention (Fig. 7).

In conclusion, we showed for the first time that irradiation of trigger hairs, which is usually associated with prey capture and retention in the carnivorous plant \( D. \text{muscipula} \), resulted in rapid downregulation of photosynthesis and stimulation of respiration probably via electrical signals. The limitation of photosynthesis was not associated with a decrease in stomatal conductance, but was due to the decrease of utilization of absorbed light energy by chlorophylls for photochemistry or by a decrease in activity of enzymes of the Calvin cycle, which affect \( \Phi_{\text{PSII}} \) by a feedback mechanism. We modified the classical interpretation of the cost/benefit model of carnivory by including the \( \text{CO}_2 \) costs directly associated with prey capture and retention. Further studies are required to assess the direct costs associated with prey capture and retention and their effect on the daily carbon gains in carnivorous plants.

ACKNOWLEDGEMENTS

This work was supported by grant VEGA 1/0040/09 from the Scientific Grant Agency of the Ministry of Education of the Slovak Republic.

LITERATURE CITED


