DOI: 10.1007/s11099-011-0032-0 PHOTOSYNTHETICA 49 (2): 253-258, 2011

Photosynthetic characterization of Australian pitcher plant *Cephalotus follicularis*

A. PAVLOVIČ

Department of Plant Physiology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina B2, 842 15, Bratislava, Slovakia

Abstract

Australian carnivorous pitcher plant *Cephalotus follicularis* Labill. produces two types of leaves. During the spring time, the plant produces a foliage type of noncarnivorous leaf called lamina. Later, the second type of leaf is produced - carnivorous pitcher. Using simultaneous measurements of gas exchange and chlorophyll (Chl) fluorescence photosynthetic efficiency of these two distinct forms of leaves were compared. In addition stomatal density, an important component of gas exchange, and Chl concentration were also determined. Pitcher trap had lower net photosynthetic rate (P_N) in comparison to noncarnivorous lamina, whereas the rate of respiration (R_D) was not significantly different. This was in accordance with lower stomatal density and Chl concentration in the pitcher trap. On the other hand maximum quantum yield of PSII (F_v/F_m) and effective quantum yield of photochemical energy conversion in PSII (Φ_{PSII}) was not significantly different. Nonphotochemical quenching (NPQ) was significantly higher in the lamina at higher irradiance. These data are in accordance with hypothesis that changing the leaf shape in carnivorous plants to make it a better trap generally makes it less efficient at photosynthesis. However, the pitcher of *Cephalotus* had much higher P_N than it was expected from the data set of the genus *Nepenthes*. Because it is not possible to optimize for contrasting function such as photosynthesis and carnivory, it is hypothesized that *Cephalotus* pitchers are less elaborated for carnivorous function than the pitchers of *Nepenthes*.

Additional key words: carnivorous plants; *Cephalotus*; chlorophyll; chlorophyll fluorescence; pitcher plants; photosynthesis; respiration; stomatal density.

Introduction

Carnivorous plants grow in nutrient poor, sunny and wet habitats. In this environment the cost of producing traps is far exceeded by the benefits gained from prey capture (Givnish *et al*. 1984). Carnivorous plants have evolved six times independently and represent a good example of convergent evolution (Albert *et al*. 1992, Ellison and Goteli 2009). Their leaves are modified into the traps, which attract, capture and digest an animal prey. The diversity of trap forms includes the famous snap-trap Venus flytrap (*Dionaea muscipula*), sucking bladder-trap of bladderwort (*Utricularia*), fly-paper traps of, for example, sundew (*Drosera*) or butterwort (*Pinguicula*), and eel traps (*Genlisea*, *Sarracenia psittacina*) as well as pitfall-traps of pitcher plants (*Cephalotus*, *Darlingtonia*, *Heliamphora*, *Nepenthes*, *Sarracenia* and *Brocchinia*, Peroutka *et al*. 2008, Mithöfer 2011). Transformation of leaves into trapping organs seriously affects their photosynthetic efficiency (Givnish *et al*. 1984, Adamec 2006, Pavlovič *et al*. 2007, 2009, Karagatzides and Ellison 2009, Hájek and Adamec 2010). Some species have leaves that perform photosynthesis and prey capture simultaneously (*e.g*. *Pinguicula* and *Sarracenia*). Other species are heterophyllous, with different types of leaves specialized either for prey capture or photosynthesis (*e.g. Cephalotus* and *Utricularia*), or with only one part of the leaf specialized for photosynthesis and the other one for prey capture (*e.g. Nepenthes* and *Dionaea*, Peroutka *et al*. 2008). The extent, by which the P_N is reduced, may be

Received 13 February 2011, *accepted* 27 April 2011.
Tel: +421 2 60296640, e-mail: pavlovic@fns.uniba.sk
Abbreviations: F_0 – minimal fluorescence in dark-adapted state; F_m – maximal fluorescence in dark-adapted state; F'_m – maximal fluorescence in light-adapted state; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII; g_s – stomatal conductance; NPQ – nonphotochemical quenching; PAR – photosynthetic active radiation; P_N – net photosynthetic rate; P_{Nmax} – maximal net rate of photosynthesis at saturating irradiance; R_D – rate of respiration; Φ_{PSII} – effective quantum yield of photochemical energy conversion in PSII.
Acknowledgements: This work was supported by grant VEGA 1/0040/09.

dependent on this specialization. For example, despite morphological similarity, the pitchers of *Sarracenia* and *Darlingtonia* have significantly higher P_N than the pitchers of the genus *Nepenthes* with the lowest P_N in the pitchers (close to zero) among studied terrestrial carnivorous species (Ellison and Farnsworth 2005, Pavlovič *et al*. 2007, Karagatzides and Ellison 2009). It has been hypothesized that this discrepancy may be caused by the fact that *Sarracenia* has not additional organs for photosynthesis and the trap must function in both; photosynthesis and prey capture to achieve a positive carbon gain. On the other hand the pitcher of *Nepenthes* can rely on assimilates from the adjacent photosynthetically active lamina (Pavlovič *et al*. 2007). And indeed, recently it has been found that significant proportion of the newly fixed carbon is allocated to the trap of *Utricularia*, another genus with specialized leaves for prey capture as well as strong reduction of photosynthesis in them (Adamec 2006, Sirová *et al*. 2010).

Greater energetic cost in traps may increase respiration rate (R_D) in them, especially in traps with an active trapping mechanism like *Drosera*, *Dionaea* and *Utricularia* (Adamec 2006, Adamec 2010, Hájek and Adamec 2010, Pavlovič *et al*. 2010). Ion and water pumping during the resetting of *Utricularia* bladders is a process requiring high amounts of metabolic energy derived from respiration. And indeed R_D of bladders of six *Utricularia* species was 75–200% greater, than that in leaves (Adamec 2006). In the case of *D. muscipula* enhanced R_D is only transient as a result of generation of action potentials (Pavlovič *et al*. 2010, 2011). Electrical irritability may also explain seven times higher R_D in tentacles than in leaf lamina of *Drosera prolifera* (Adamec 2010). It seems that passive pitcher plants do not usually have higher R_D in their traps (Pavlovič *et al*. 2007, Adamec 2010).

Cephalotus is a monotypic genus from Southwest Australia with one endemic species: *C. follicularis*. It is a small, low growing terrestrial perennial carnivorous pitcher plant with the heterophyllous leaves differentiated into photosynthetic lamina and the pitcher trap (Lowrie 1998). Because photosynthetic performance in this unusual plant has never been studied before, gas exchange and Chl fluorescence were measured simultaneously in the lamina and pitcher trap separately. Stomatal density, an important component of gas exchange and Chl content were also determined. The results presented here indicate that despite morphological and functional differentiation of the leaves for photosynthesis (lamina) and prey capture (pitcher), the pitchers had higher photosynthetic efficiency than it was expected from the known data of the genus *Nepenthes*. Because the photosynthetic efficiency and degree of carnivory are inversely correlated, the degree of carnivory in *Cephalotus* in relation to other pitcher plants is discussed.

Materials and methods

Plant culture: The endemic carnivorous pitcher plant *Cephalotus follicularis* Labillardiére was grown under greenhouse condition at Department of Plant Physiology of Comenius University in Bratislava. Three-year-old, vegetatively propagated plants were used in experiments. They were grown in greenhouse in pots with peat as substrate irrigated with distilled water at a maximum daily irradiance of 1,000 μmol m^{-2} s^{-1} PAR, day/night temperature 20–30/15–20°C and high relative air humidity (70–80%). Because the diameter of the cuvette window used in gas exchange measurements was 18 mm, the pitchers and laminae used in the experiments did not exceed this size.

Simultaneous measurements of gas exchange and Chl fluorescence: Seven laminae and seven pitchers from five different plants were used for measurements. P_N and Chl fluorescence were measured simultaneously with a *CIRAS-2* (*PP-Systems*, Hitchin, UK) and a fluorcam *FC 1000-LC* (*Photon System Instruments*, Brno, Czech Republic) attached to the infrared gas analyzer. Prior to measurements, the plants were dark-adapted for 30 min. Thereafter the whole lamina or pitcher was enclosed in the leaf cuvette (*PLC6*, *PP-Systems*, Hitchin, UK). Once stabilization of CO_2 exchange was achieved, the rate of respiration (R_D) was measured for 5 min in the dark. Then Chl fluorescence was measured. Minimal fluorescence of dark-adapted state ($F_0 < 0.1$ μmol m^{-2} s^{-1} PAR, 5 s) and thereafter maximal fluorescence (F_m, 4,000 μmol m^{-2} s^{-1} PAR, 800 ms) were measured and F_v/F_m was calculated as $(F_m - F_0)/F_m$. Thereafter the saturation irradiance (1,600 μmol m^{-2} s^{-1} PAR) was applied for 15 min for adaptation, and light response curves were recorded. The light was provided by blue (λ = 455 nm) and red (λ = 620 nm) LED diodes. P_N was recorded at CO_2 concentration 360 μmol mol^{-1}, leaf temperature 23 ± 1°C and relative air humidity 65–70% The light intensity was decreased stepwise with irradiation periods of 3.5 min and subsequent saturation pulses (4,000 μmol m^{-2} s^{-1} PAR, 800 ms) for determination of maximal fluorescence in light-adapted state (F_m') were applied until 60 μmol m^{-2} s^{-1} PAR was reached. Light-response curves of P_N, Φ_{PSII}, and NPQ were recorded simultaneously. For calculation and definition of Chl fluorescence parameters *see* Maxwell and Johnson (2000) or Roháček (2002). After the measurements the leaf tissues were dried at 70°C for five days, then weighed and the P_N was calculated in nmol(CO_2) g^{-1}(DM) s^{-1}.

Chl extraction and quantification: Four laminae and four pitchers were removed from four plants. Half of the each lamina or pitcher was dried at 70°C for 5 days to

determine % of dry mass. Remaining parts of lamina or pitcher were ground in a mortar and pestle with small amount of sand and extracted with 80% (v/v) chilled acetone with $MgCO_3$ to avoid acidification and pheophytinisation of pigments as was recommended by Ritchie (2006). The samples were centrifuged at 8,000 × *g* for 5 min at 4°C. Chl (*a*+*b*) in supernatant were determined spectrophotometrically (*Jenway 6400, Krackeler Scientific*, London UK): Chl *a* at 663.2 nm, Chl *b* at 646.8 nm. Chl concentration was calculated according to Lichtenthaler (1987).

Determination of stomatal density: The stomatal densities were determined in three laminae and pitchers using a microrelief method. Epidermal impressions were prepared by coating the leaf surface (pitcher, adaxial and abaxial surface of lamina) with nail varnish, peeling off the dried layer of nail varnish using sticky tape and adhering onto a microscope slide. Three randomly chosen views of each slide were observed *via* an *Axioskop 2* plus microscope (*Zeiss,* Jena, Germany) and evaluated using Laboratory Universal Computer Image Analysis software (*Lucia G, ver. 4.80, Laboratory Imaging*, Prague, Czech Republic).

Statistical analysis: Prior to statistical tests, data were analysed for normality and homogeneity of variance. When nonhomogeneity was present, a *t*-test was employed with the appropriate corrected degrees of freedom. To evaluate the significance of the data between lamina and pitcher trap [P_N, F_v/F_m, Φ_{PSII}, NPQ, Chl (*a*+*b*)] on the same plant individual, two-tailed paired *t*-test was used (*Microsoft Excel*). One-way *ANOVA* followed by Least Significance Difference (LSD) test (*Statgraphics, Centurion XV*, Warrenton, Virginia,USA) was used to evaluate the differences in stomatal density.

Results

Fig. 1 shows differences in the leaf types (lamina and pitcher) produced by *C. follicularis*. R_D did not differ significantly between lamina and pitcher (P=0.387, Fig. 2*A*, zero point on x-axis). The pitcher had significantly lower P_N in comparison to the lamina irrespective of light intensity. The shape of light-response curves of lamina and pitcher trap was similar. First, P_N increased almost linearly with increasing irradiance at irradiances less than about 200 μmol m^{-2} s^{-1} PAR and then reached saturation under an irradiance of about 700 μmol m^{-2} s^{-1} PAR. The P_{Nmax} of pitchers was about 60% that of the laminae at saturating irradiance (Fig. 2*A*). The stomatal conductance (g_s) was not evaluated, because the walls of the pitcher are wetted by digestive fluid what did not enable the correct determination of g_s. However, high g_s in the lamina indicated that stomata were open. On the other hand, Φ_{PSII} did not differ significantly between lamina and pitcher at any irradiance (Fig. 2*B*).

Fig. 1. Two types of leaves of *Cephalotus follicularis*: pitcher (*A*) and lamina (*B*).

At higher irradiances, NPQ was significantly higher in the lamina (Fig. 2*C*). Maximum quantum yield of PSII (F_v/F_m) was also not significantly different between leaf types. The lamina had F_v/F_m = 0.785 ± 0.01, the pitcher had F_v/F_m = 0.761 ± 0.02 (P=0.259, mean ± SE, n = 7). Fig. 3 shows spatial distribution of F_v/F_m and Φ_{PSII}. It is evident that the back lower side of the pitcher had lower F_v/F_m and Φ_{PSII} than the upper side exposed to sun. This may be caused by the fact that the back side of the pitcher usually lies buried in the ground and is etiolated. Chl concentration was significantly higher in the lamina [2.51 ± 0.05 mg g^{-1} (DM)] than in the trap [1.93 ± 0.12 mg g^{-1} (DM)], P=0.034, mean ± SE, n = 4).

Fig. 4 shows stomatal density on the external surface of pitcher (Fig. 4*A*), lower abaxial (Fig. 4*B*) and upper adaxial surface (Fig. 4*C*). The lamina had stomata on

upper as well as lower surface, however on the upper surface they were scarce (lower surface = 58.3 ± 1.7, upper surface = 3.3 ± 0.6, stomata mm^{-2}, P<0.001, n = 9). In general, stomatal density was higher on the lower surface of the lamina than on the external surface of the trap (11.5 ± 2.38 stomata mm^{-2}, P<0.001, n = 9). The number of stomata differs from each other (P<0.001, LSD test, n = 9).

Discussion

Carnivorous plants have usually low P_N in comparison to noncarnivorous plants. Values of P_{Nmax} determined for lamina and pitcher trap of *C. follicularis* are within the range as those published for numerous terrestrial carnivorous species (Ellison 2006). Although the P_N of the pitcher was significantly lower than in the lamina (Fig. 2*A*), we had expected much lower values in it. The P_N of the pitcher of different carnivorous *Nepenthes* species was near to zero, whereas *Nepenthes* lamina had photosynthetic activity comparable with other carnivorous species including *C. follicularis* (Pavlovič *et al.* 2007, 2009, Karagatzides and Ellison 2009). On the other hand, in 10 species of American pitcher plants of the genus *Sarracenia* P_N ranged between 29.4–72.0 nmol(CO_2) g^{-1}(DM) s^{-1} and in *Darlingtonia californica* P_N was 27.5 nmol(CO_2) g^{-1}(DM) s^{-1} (Ellison and Farnsworth 2005, Karagatzides and Ellison 2009, Bruzzese *et al.* 2010, Hájek and Adamec 2010). The P_{Nmax} of *Cephalotus* pitcher [27.3 ± 2.5 nmol(CO_2) g^{-1}(DM) s^{-1}] was only slightly lower than those in *Sarracenia* and very similar to *Darlingtonia* pitchers, however much higher than was found in pitchers of five *Nepenthes* taxa [–4.4–2.5 nmol(CO_2) g^{-1}(DM) s^{-1}] by Pavlovič *et al.* (2007, 2009) and Kargatzides and Ellison (2009). Also the P_N of *Utricularia* bladders was 7–10 times lower than in photosynthetic leaves. This indicates that the plants with two type of leaves or the part of leaf specialized either for photosynthesis or carnivory may have much lower P_N in their traps than species with one type of leaf which must both: photosynthesize and capture prey. Despite this morphological specialization of *Cephalotus* leaves, P_N in the pitcher is much closer to the species which forms only one type of leaf (*e.g. Darlingtonia*). Thus *Cephalotus* pitchers are probably much less dependent on assimilates produced by the lamina than for example *Utricularia* bladder or *Nepenthes* pitchers.

Besides reduced P_N, *Cephalotus* pitcher shows other characteristics related to the carnivorous syndrome. The stomatal density is significantly lower in the pitchers than in the lamina (Fig. 3). The similar trend was also found in the pitchers of two *Nepenthes* species (Pavlovič *et al.* 2007). Chl concentration is also reduced, as was previously found in *Utricularia* bladders (Knight 1992) and *Nepenthes* pitchers (Pavlovič *et al.* 2007, 2009). However the Φ_{PSII}, which measures the proportion of the light absorbed by Chl associated with PSII that is used

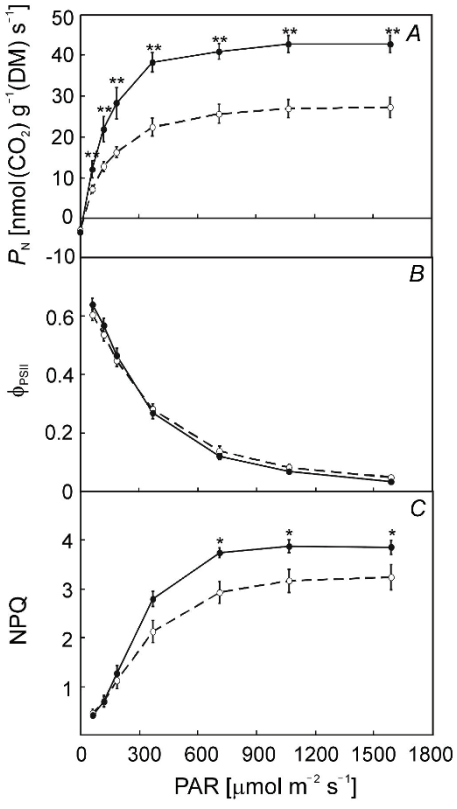

Fig. 2. Net photosynthetic rate (P_N, *A*), effective quantum yield of photochemical energy conversion in PSII (Φ_{PSII}, *B*) and nonphotochemical quenching (NPQ, *C*) in lamina (*close circle*) and pitcher trap (*open circle*) in response to irradiance, Mean ± SE, statistical differences between lamina and trap are denoted as * (P<0.05) and ** (P<0.01), two-tailed paired *t*-test, n = 7.

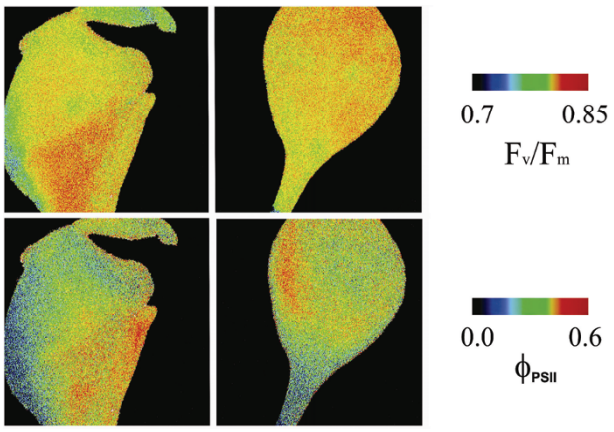

Fig. 3. Chlorophyll fluorescence imaging of leaf and trap of *Cephalotus follicularis*. Maximum quantum yield of PSII (F_v/F_m, *upper row*) and effective quantum yield of photochemical energy conversion in PSII at 200 μmol m^{-2} s^{-1} PAR (Φ_{PSII}, *lower row*).

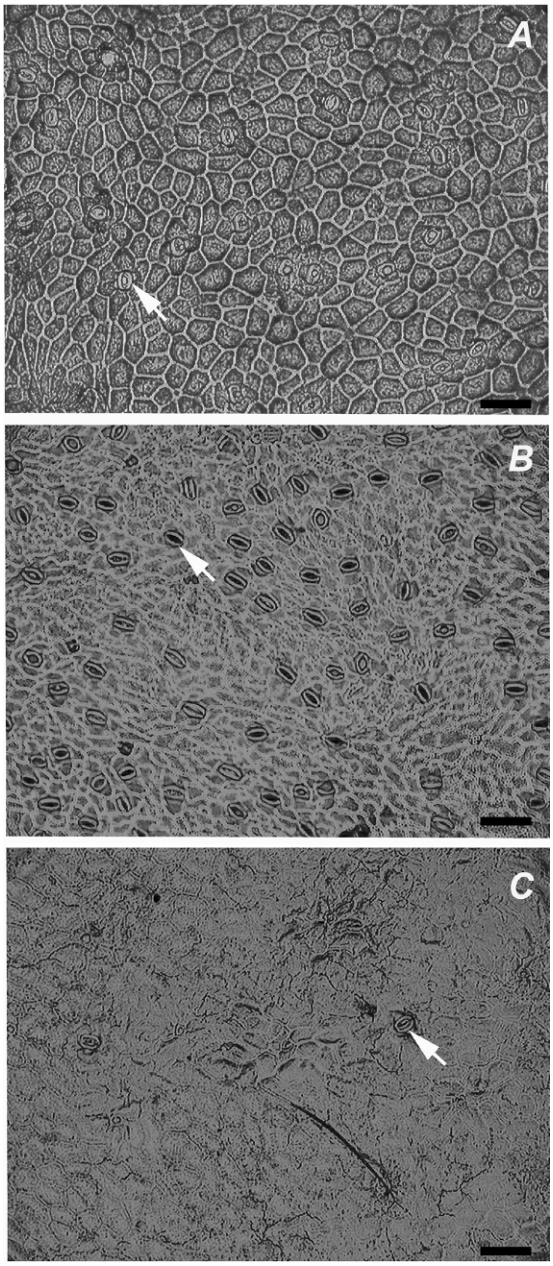

Fig. 4. Stomata (*arrows*) on external surface of pitcher (*A*), lower abaxial (*B*) and upper adaxial lamina surface (*C)* of *C. follicularis*. *Bars* = 100 μm.

in photochemistry, is not significantly different between lamina and pitcher trap. This is in contrast with the pitcher plant of the genus *Nepenthes* with significantly lower F_v/F_m and Φ_{PSII} in the pitcher. This indicates that efficiency of PSII photochemistry in *Cephalotus* pitcher is high, comparable with lamina. Because CO_2 fixation and Φ_{PSII} can correlate very well, the discrepancies can be caused by the changes in relative rates of CO_2 fixation and competing processes such as photorespiration, nitrogen metabolism and Mehler reaction (Maxwell and Johnson 2000). In the case of *Cephalotus* pitchers, unequal light interception caused by three-dimensional structure of the pitchers may also contribute to this discrepancy.

It seems that the pitchers of *Nepenthes* are better adapted for carnivorous than for assimilation function in comparison to the pitchers of *Cephalotus*. And indeed, some data indicate that *Cephalotus* pitchers represent an intermediate stage in the development of the pitchers, falling between *Heliamphora* and *Nepenthes* (Juniper *et al*. 1989).

For example, *Nepenthes* and *Cephalotus* produce their own digestive enzymes; in Sarraceniaceae (including the genera *Darlingtonia*, *Heliamphora* and *Sarracenia*) the enzyme production is dubious and improbable and relies on the metabolic activity of inquilines (Jaffe *et al*. 1992, Adlassnig *et al*. 2011). However the digestive fluid of *Cephalotus* contains 5 times lower amount of acid proteinase than fluid samples from *Nepenthes alata* (Takahashi *et al*. 2009). *Nepenthes mirabilis*, *N. albo-marginata*, and *N. rafflesiana* obtained 61.5, 53.8, and 61.8% of nitrogen from prey, respectively; *C. follicularis* only 26% (Schulze *et al*. 1997, Moran *et al*. 2001). On the other hand, *C. follicularis* take up much more trace elements like iron, manganese and pottasium in comparison to *Sarracenia purpurea* and *Heliamphora nutans* (Adlassnig *et al*. 2009). Because there must be trade-offs, it appears that it is not possible to maximize for photosynthetic and carnivorous function in the same type of leaf (Karagatzides and Ellison 2009). It seems that the extent by which the photosynthesis is reduced correlates with the ability of the leaf to be carnivorous. In this respect, the pitcher plants of the genus *Nepenthes* are the best adapted to the carnivorous "lifestyle" among pitcher plants.

References

Adamec, L.: Respiration and photosynthesis of bladders and leaves of aquatic *Utricularia* species. – Plant Biol. **8**: 765-769, 2006.

Adamec, L.: Dark respiration of leaves and traps of terrestrial carnivorous plants: are there greater energetic costs in traps? – Centr. Eur. J. Biol. **5**: 121-124, 2010.

Adlassnig, W., Peroutka, M., Lendl, T.: Traps of carnivorous pitcher plants as habitat: composition of the fluid, biodiversity and mutualistic activities. – Ann. Bot. **107**: 181-194, 2011.

Adlassnig, W., Steinhauser, G., Peroutka, M., Musilek, A., Sterba, J.H., Lichtscheidl, I.K., Bichler M.: Expanding the menu for carnivorous plants: Uptake of potassium, iron and manganese by carnivorous pitcher plants. – Appl. Radiat. Isotopes **67**: 2117-2122, 2009.

Albert, V.A., Williams, S.E., Chase, M.W.: Carnivorous plants: Phylogeny and structural evolution. – Science **257**: 1491-1495, 1992.

Bruzzese, B.M., Bowler, R., Massicotte, H.B., Fredeen, A.L.: Photosynthetic light-response in three carnivorous plant species: *Drosera rotundifolia*, *D. capensis* and *Sarracenia*

leucophylla. – Photosynthetica **48**: 103-109, 2010.
Ellison, A.M.: Nutrient limitation and stoichiometry of carnivorous plants. – Plant Biol. **8:** 740-747, 2006.
Ellison, A.M., Farnsworth, E.J.: The cost of carnivory for *Darlingtonia californica* (Sarraceniaceae): Evidence from relationships among leaf traits. – Amer. J. Bot. **92**: 1085-1093, 2005.
Ellison, A.M., Gotelli, N.J.: Energetics and the evolution of carnivorous plants—Darwin's 'most wonderful plants in the world'. – J. Exp. Bot. **60**: 19-42, 2009.
Givnish, T.J., Burkhardt, E.L., Happel, R.E., Weintraub, J.D.: Carnivory in the bromeliad *Brocchinia reducta* with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient poor habitats. – Amer. Natur. **124**: 479-497, 1984.
Hájek, T., Adamec, L.: Photosynthesis and dark respiration of leaves of terrestrial carnivorous plants. – Biologia **65:** 69-74, 2010.
Jaffe, K., Michalangeli, F., Gonzales, J.M., Miras, B., Ruiz, M.C.: Carnivory in pitcher plants of the genus *Heliamphora* (Sarraceniaceae). – New Phytol. **122**: 733-744, 1992.
Juniper, B.E., Robins, R.J., Joel, D.M.: The Carnivorous Plants. – Academic Press, London 1989.
Karagatzides, J.D., Ellison, A.M.: Construction costs, payback times and the leaf economics of carnivorous plants. – Amer. J. Bot. **96**: 1612-1619, 2009.
Knight, S.E.: Costs of carnivory in the common bladderwort, *Utricularia macrorhiza*. – Oecologia **89**: 348-355, 1992.
Lichtenthaler, H.K.: Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. – Methods Enzymol. **148**: 350-382, 1987.
Lowrie, A.: Carnivorous Plants of Australia. – Vol. 3., Univ. Western Australia Press, Perth 1998.
Maxwell, K., Johnson, G.N. Chlorophyll fluorescence—a practical guide. – J. Exp. Bot **51**: 659-668, 2000.
Mithöfer, A.: Carnivorous pitcher plants: insights in an old topic. – Phytochemistry: 2011, (In press.) doi:10.1016/j.phytochem.2010.11.024
Moran, J.A., Merbach, M.A., Livingstone, N.J., Clarke, C.M., Booth, W.E. Termite prey specialization in the pitcher plant *Nepenthes albomarginata*—Evidence from stable isotope analysis. – Ann. Bot. **88**: 307-311, 2001.
Pavlovič, A., Demko, V., Hudák, J.: Trap closure and prey retention in Venus flytrap (*Dionaea muscipula*) temporarily reduces photosynthesis and stimulates respiration. – Ann. Bot. **105**: 37-44, 2010.
Pavlovič, A., Masarovičová, E., Hudák, J.: Carnivorous syndrome in Asian pitcher plants of the genus *Nepenthes*. – Ann. Bot. **100**: 527-536, 2007.
Pavlovič, A., Singerová, L., Demko, V., Hudák, J.: Feeding enhances photosynthetic efficiency in the carnivorous pitcher plant *Nepenthes talangensis.* – Ann. Bot. **104**: 307-314, 2009.
Pavlovič, A., Slováková, Ľ., Pandolfi, C., Mancuso, S.: On the mechanism underlying photosynthetic limitation upon trigger hair irritation in the carnivorous plant Venus flytrap (*Dionaea muscipula* Ellis). – J. Exp. Bot. **62**: 1991-2000, 2011.
Peroutka, M., Adlassnig, W., Lendl, T., Pranjič, K., Lichtscheidl, I.K.: Functional biology of carnivorous plants. – In: Floriculture, Ornamental and Plant Biotechnology **V**: 266-286, Global Sci. Books, London 2008.
Ritchie, R.J.: Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. – Photosynth. Res. **89**: 27-41, 2006.
Roháček, K.: Chlorophyll fluorescence parameters: the definitions, photosynthetic meaning and mutual relationship. – Photosynthetica **40**: 13-29, 2002.
Schulze, W., Schulze, E.D., Pate, J.S., Gillinson, A.N.: The nitrogen supply from soils and insects during growth of the pitcher plants *Nepenthes mirabilis*, *Cephalotus follicularis* and *Darlingtonia californica.* – Oecologia **112**: 464-471, 1997.
Sirová, D., Borovec, J., Šantrůčková, H., Šantrůček, J., Vrba, J., Adamec, L.: *Utricularia* carnivory revisited: plants supply photosynthetic carbon to traps. – J. Exp. Bot. **61:** 99-103, 2010.
Takahashii, K., Matsumoto, K., Nishii, W., Muramatsu, M., Kubota, K.: Comparative studies on the acid proteinase activities in the digestive fluids of *Nepenthes*, *Cephalotus*, *Dionaea* and *Drosera*. – Carniv. Plant Newslett. **38**: 75-82, 2009.