

## Photosynthesis and dark respiration of leaves of terrestrial carnivorous plants

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**Abstract:** Using CO<sub>2</sub> gasometry, net photosynthetic ( $P_N$ ) and dark respiration rates ( $R_D$ ) were measured in leaves or traps of 12 terrestrial carnivorous plant species usually grown in the shade. Generally, mean maximum  $P_N$  (60 nmol CO<sub>2</sub> g<sup>-1</sup>(DM) s<sup>-1</sup> or 2.7 μmol m<sup>-2</sup> s<sup>-1</sup>) was low in comparison with that of vascular non-carnivorous plants but was slightly higher than that reported elsewhere for carnivorous plants. After light saturation, the facultatively heliophytic plants behaved as shade-adapted plants. Mean  $R_D$  in leaves and traps of all species reached about 50% of maximum  $P_N$  and represents the high photosynthetic (metabolic) cost of carnivory.

**Key words:** CO<sub>2</sub> gasometry; net photosynthetic rate; dark respiration rate; light photosynthetic curve; costs of carnivory

**Abbreviations:** CPs, carnivorous plants;  $P_N$ , net photosynthetic rate;  $P_{Nmax}$ , maximum net photosynthetic rate;  $P_{Gmax}$ , maximum gross photosynthetic rate;  $R_D$ , dark respiration rate; DM, dry mass; RH, relative air humidity; SLA, specific leaf area;  $I$ , irradiance;  $I_C$ , light compensation point of photosynthesis;  $I_S$ , light saturation point of photosynthesis;  $\alpha$ , maximum quantum efficiency of photosynthesis; PAR, photosynthetically active radiation.

### Introduction

About 600 species of terrestrial carnivorous plants (CPs) grow around the world, mostly in wet or waterlogged infertile soils in bogs and fens (Juniper et al. 1989). From a functional point of view, all CPs fulfil several principal criteria: they form traps of foliar origin, capture animal prey, release nutrients from prey carcasses, and utilize them for their growth and development. It is generally accepted that uptake of the mineral nutrients, nitrogen and phosphorus from prey by CP traps is of a principal importance, while uptake of organic carbon is not important (e.g., Juniper et al. 1989; Adamec 1997; Wakefield et al. 2005). One of the crucial ecophysiological questions associated with carnivory is how the mineral nutrients taken up from prey stimulate plant growth. It has been observed that these nutrients markedly stimulate mineral nutrient uptake by roots from nutrient-poor soils (for reviews see Adamec 1997, 2002). All CPs are green and fix CO<sub>2</sub> by photosynthesis. In addition, as postulated by Givnish et al. (1984) for cost–benefit relationships in CPs, carnivory should increase either specific (biomass- or leaf area-based) or total plant photosynthetic rate as a result of increasing foliar tissue nitrogen content. Nevertheless, this theory has not yet generally been confirmed (Méndez

& Karlsson 1999; Ellison & Farnsworth 2005; Wakefield et al. 2005; Farnsworth & Ellison 2008). Generally, the catching of prey does not increase tissue N content in CPs (see Adamec 1997). Furthermore, the theory of Knight (1992) says that net photosynthetic rate ( $P_N$ ) of carnivorous traps is lower than those of photosynthetic leaves but, on the contrary, trap dark respiration rate ( $R_D$ ) should be greater than that of leaves. The two processes and their ratio characterize the photosynthetic costs of carnivory. It may be concluded even from the limited available data that  $P_N$  of terrestrial CPs, based on unit leaf area or biomass, is several times lower than that in non-carnivorous plants (Small 1972; Méndez & Karlsson 1999; Ellison & Farnsworth 2005; Wakefield et al. 2005; Ellison 2006; Pavlovič et al. 2007; Farnsworth & Ellison 2008). As typical S-strategists (having slow growth, low competitive ability, high sensitivity to disturbance), terrestrial CPs grow slowly (Adamec 2002, 2008; Farnsworth & Ellison 2008) and this relatively low  $P_N$  in CPs corresponds to a low growth rate. Shipley (2006) has recently demonstrated for 614 woody or herbaceous species that their relative growth rate correlates strongly with biomass- or leaf area-based  $P_N$ . Thus, relatively low  $P_N$  may not be a limiting process for CP growth (*sensu* Shipley 2006) and nutrient (N) uptake from prey may not increase biomass- or leaf

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area-based  $P_N$  but could support preferentially other processes.

The aim of the study was to measure  $P_N$  and  $R_D$  in leaves or traps of 12 terrestrial CP species grown in a culture, correlate them with each other, and compare the found values of  $P_N$  and  $R_D$  as photosynthetic costs of carnivory with those of leaves of non-carnivorous plants. Thus, we tested the hypothesis that the  $R_D:P_N$  ratio as a measure of the photosynthetic costs of carnivory is much greater in CP traps than that in leaves of non-carnivorous plants and that  $P_N$  in the latter plant group is generally much higher than that in CPs. As trap functioning in carnivorous plants requires greater energy consumption and lower  $P_N$  per unit biomass in traps than in leaves (Adamec 2006),  $R_D:P_N$  ratio was chosen as a criterion of the photosynthetic costs of carnivory in the present study (cf. Givnish 1988). Correlation between measured  $P_N$  values and slow growth of CPs as well as interspecific differences in photosynthetic parameters are discussed.

## Material and methods

### Cultivation of plants

Most plant materials (9 species) were provided from the indoor carnivorous plant collection in the Institute of Botany at Třeboň, Czech Republic. These plants were grown in a greenhouse under natural light in plastic pots in acidic peaty soils. The pots with the plants were placed in a 0.84 m<sup>2</sup> white plastic container 0.4 m high, filled with rain water to a depth of 2–3 cm (for details see Adamec 2002). The container was covered with a neutral-density plastic foil to reduce irradiance (and thus overheating) and increase relative air humidity (RH). With a few exceptions, the irradiance at plant level was ca. 10.3% of full sunlight. Thus, the greenhouse-raised plants could be considered to be shade acclimated. In summer, temperatures at plant level fluctuated between 20 and 36 °C and RH between 60–90% during the day, and between 16 and 22 °C and 80–96% RH at night. The following CP species used were grown in the greenhouse: *Sarracenia leucophylla* Raf. (its tall phyllodes grew above the container at ca. 13% sun), *Dionaea muscipula* Ell., *Drosera aliciae* Hamet, *D. binata* Labill., *D. capensis* L., *D. adelae* F.Muell. cv. Giant (only ca. 5.6% sun), *D. prolifera* C.T.White (“shade-acclimated” plants, only ca. 5.6% sun), *Pinguicula moranensis* H.B.K., and *Utricularia reniformis* A.S.Hil. “Sun-acclimated” plants of *D. prolifera* were grown in an aquarium at ca. 12–18% sun. *Drosophyllum lusitanicum* Link. and *Sarracenia purpurea* L. were grown in pots with peaty soils in full sunlight outdoors, while *Drosera rotundifolia* L. was grown at ca. 45% of full sun in *Sphagnum* hummocks in an artificial bog outdoors (Adamec 2005). Out of all species used, only *Utricularia reniformis* and *Sarracenia leucophylla* did not form traps on the measured leaves. All plant species used were allowed to catch natural prey but no extra feeding was applied. Yet the catch of prey was minimal both in greenhouse-grown and outdoor-grown plants. The amount of caught prey per unit biomass might be comparable with the minimum dose of prey applied by Farnsworth & Ellison (2008).

### Measurement of photosynthesis and dark respiration

$P_N$  and  $R_D$  were measured as CO<sub>2</sub> exchange using a LI-COR 6400 portable infra-red gas analyzer (LI-COR, Lincoln, NE,

USA) equipped with a standard 6-cm<sup>2</sup> leaf chamber. If possible, one intact leaf of a plant growing in a pot was fixed in the chamber or 1–4 freshly excised leaves or traps (or segments of these) were used for gasometric measurements. In *S. purpurea* pitchers, both a wing (keel) 2.5–3 cm wide and an adjacent pitcher wall (tube) about 1–5 cm below the peristome, and in *Dionaea muscipula*, both an opened trap and its petiole were used separately for the measurements. In all species, fully expanded young to medium-aged leaves were used. All material used was deprived of captured prey. During the measurements, the excised leaf or trap material extending into the chamber was moistened laterally by a wet soft paper tissue. Vapour pressure deficit in the sample cell ranged between 0.7–1.3 kPa (based on the leaf temperature). An automatic regime with pre-set PAR values of 1200, 400, 150, 50, 20, and 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of red monochromatic light was chosen for estimation of light curves of photosynthesis and dark respiration at 380 ppm CO<sub>2</sub> at a leaf temperature of  $23 \pm 1$  °C and air flow rate of 300  $\mu\text{mol s}^{-1}$ . One complete measurement on one object lasted for about 10–12 min. Due to both laterally moistening the excised leaf and the preferential application of the highest PAR values, we believe that leaf excision had a negligible effect on the measured  $P_N$  and  $R_D$  values. After measurements, leaf or trap material having been fixed in the chamber was excised, stored in humid air, scanned for estimation of the measured area, and dried at 80 °C for dry mass (DM). Thus, a relationship between leaf or trap area and DM (specific leaf area, SLA) is available for all species. Results of  $P_N$  are expressed standardly both in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  per unit DW and  $R_D$  in  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  per unit DW. Five replicates on material from different leaves of different plants were obtained for each species. We estimated the maximum quantum efficiency of photosynthesis ( $\alpha$ ) as a slope of the linear part of the light curve between PAR of 0 and 20  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ . We applied an asymptotic exponential model to fit the light curve:  $P_N = P_{G\text{max}}(1 - \exp(-\alpha I/P_{G\text{max}})) - R_D$ , where  $P_{G\text{max}}$  is the asymptotic maximum rate of light-saturated gross photosynthesis, and  $I$  is PAR irradiance (Thornley 1976). The determination coefficients  $r^2$  were  $> 0.96$  in all light curve fits. Light compensation ( $I_C$ ) and saturation ( $I_S$ ) points of photosynthesis were calculated from the model;  $I_S$  was defined as the irradiance where the  $P_N + R_D$  reached 95% of  $P_{G\text{max}}$ . Due to shortage of plants, neither tissue N nor chlorophyll content was determined in leaves of measured plants.

We applied principal component analysis (PCA) using Canoco for Windows 4.5 (Lepš & Šmilauer 2003) to show the correlations between the parameters of photosynthetic parameters ( $I_S$ ,  $I_C$ ,  $P_{N\text{max}}$ ,  $R_D$ ), SLA, and their relationships to CP species. The data of parameters were centred and standardized in order to make the variables comparable. To quantify the relationship between pairs of parameters, linear correlations were performed.

## Results

In our 12 CP species measured, the mean  $P_{N\text{max}}$  value was 60 and  $P_{N\text{max}}$  reached as much as 153  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  in *Drosera capensis* (Table 1). Out of the CP species measured, the highest leaf-area based  $P_{N\text{max}}$  values were in both *Sarracenia* species and *Drosophyllum*, while the lowest ones were in *P. moranensis*, *Drosera aliciae*, *D. prolifera*, and *U. reniformis*. Low

Table 1. Basic photosynthetic characteristics of carnivorous plants. Means  $\pm$  1 s.e. intervals are shown;  $n = 5$ . See Material and methods for explanation of the parameters.

Species and measured organ	$P_{Nmax}$ $\mu\text{mol m}^{-2} \text{ s}^{-1}$	$P_{Nmax}$ $\text{nmol g}^{-1} \text{ s}^{-1}$	$R_D$ $\text{nmol g}^{-1} \text{ s}^{-1}$	$R_D$ % of $P_{Nmax}$	$\alpha$ $\text{mol mol}^{-1}$	$I_C$ $\mu\text{mol m}^{-2} \text{ s}^{-1}$	$I_S$ $\mu\text{mol m}^{-2} \text{ s}^{-1}$	SLA $\text{m}^2 \text{ g}^{-1}$
<i>Dionaea muscipula</i> petioles	4.03 $\pm$ 0.38	90 $\pm$ 9	8.2 $\pm$ 1.8	8.8 $\pm$ 1.6	0.059 $\pm$ 0.007	6.2 $\pm$ 1.1	231 $\pm$ 24	0.0223
<i>Dionaea muscipula</i> traps	3.04 $\pm$ 0.20	52 $\pm$ 3	6.8 $\pm$ 0.6	13.1 $\pm$ 0.3	0.057 $\pm$ 0.004	7.5 $\pm$ 0.3	182 $\pm$ 5	0.0171
<i>Drosera adelae</i> leaves	1.35 $\pm$ 0.05	64 $\pm$ 2	6.1 $\pm$ 0.3	9.5 $\pm$ 0.5	0.038 $\pm$ 0.003	3.6 $\pm$ 0.1	119 $\pm$ 7	0.0477
<i>Drosera aliciae</i> leaves	0.70 $\pm$ 0.24	22 $\pm$ 8	14.1 $\pm$ 1.5	88.8 $\pm$ 23.3	0.025 $\pm$ 0.003	24.7 $\pm$ 3.0	140 $\pm$ 28	0.0313
<i>Drosera binata</i> leaves	1.97 $\pm$ 0.18	47 $\pm$ 4	32.4 $\pm$ 1.7	72.0 $\pm$ 8.7	0.055 $\pm$ 0.004	32.1 $\pm$ 1.6	186 $\pm$ 21	0.0239
<i>Drosera capensis</i> leaves	3.42 $\pm$ 0.19	153 $\pm$ 9	44.5 $\pm$ 5.7	29.9 $\pm$ 4.8	0.064 $\pm$ 0.005	17.6 $\pm$ 1.8	212 $\pm$ 21	0.0447
<i>Drosera rotundifolia</i> leaves	1.56 $\pm$ 0.29	47 $\pm$ 9	34.8 $\pm$ 3.1	88.7 $\pm$ 22.5	0.045 $\pm$ 0.003	35.6 $\pm$ 5.1	182 $\pm$ 21	0.0302
<i>Drosera prolifera</i> shade-plant leaves	1.20 $\pm$ 0.22	36 $\pm$ 7	8.5 $\pm$ 0.6	27.1 $\pm$ 5.3	0.032 $\pm$ 0.001	9.9 $\pm$ 0.8	138 $\pm$ 21	0.0303
<i>Drosera prolifera</i> sun-plant leaves	1.17 $\pm$ 0.24	36 $\pm$ 8	14.3 $\pm$ 1.0	50.2 $\pm$ 13.6	0.029 $\pm$ 0.002	19.4 $\pm$ 2.0	168 $\pm$ 26	0.0311
<i>Drosophyllum lusitanicum</i> leaves	5.07 $\pm$ 0.40	56 $\pm$ 4	41.4 $\pm$ 1.3	76.5 $\pm$ 6.8	0.073 $\pm$ 0.001	68.5 $\pm$ 3.6	367 $\pm$ 22	0.0110
<i>Pinguicula moranensis</i> leaves	0.48 $\pm$ 0.07	17 $\pm$ 3	25.4 $\pm$ 1.8	162.2 $\pm$ 25.9	0.038 $\pm$ 0.002	29.2 $\pm$ 2.0	94 $\pm$ 3	0.0360
<i>Sarracenia leucophylla</i> phyllodes	5.32 $\pm$ 0.22	72 $\pm$ 3	11.1 $\pm$ 1.0	15.8 $\pm$ 0.9	0.065 $\pm$ 0.003	14.1 $\pm$ 1.5	286 $\pm$ 23	0.0132
<i>Sarracenia purpurea</i> pitcher wings	5.26 $\pm$ 0.46	64 $\pm$ 6	9.5 $\pm$ 1.1	14.7 $\pm$ 1.1	0.059 $\pm$ 0.003	14.0 $\pm$ 1.4	307 $\pm$ 25	0.0122
<i>Sarracenia purpurea</i> pitcher walls	3.97 $\pm$ 0.22	58 $\pm$ 3	12.6 $\pm$ 0.9	22.1 $\pm$ 1.7	0.060 $\pm$ 0.002	16.1 $\pm$ 1.1	242 $\pm$ 13	0.0145
<i>Utricularia reniformis</i> leaves	1.14 $\pm$ 0.20	81 $\pm$ 15	30.0 $\pm$ 2.8	41.9 $\pm$ 8.5	0.041 $\pm$ 0.004	12.4 $\pm$ 1.6	112 $\pm$ 8	0.0713

values of maximum quantum efficiency of photosynthesis ( $\alpha$ ) in some species indicated either a stress to the photosynthetic apparatus or a low chlorophyll content (Table 1; *Drosera adelae*, *D. aliciae*, *D. prolifera*, *D. rotundifolia*, *P. moranensis*, *U. reniformis*). Low  $\alpha$  led to a decrease of the leaf area-based  $P_{Gmax}$  ( $r = 0.90$ ,  $p < 0.0001$ ,  $n = 15$ ), which also closely inversely correlated with SLA ( $r = -0.65$ ,  $p = 0.008$ ) indicating that thin leaves with large SLA have low  $\alpha$ , i.e., low ability to utilize even weak PAR irradiance ( $r = -0.50$ ,  $p = 0.056$ ). *Drosera prolifera* is a typical shade-adapted species of the tropical forest understorey. Plants grown at about 15% of full sun reached the same  $P_{Gmax}$  as those at 5.6%, probably because of the light-induced stress, indicated by low  $\alpha$ . This may indicate that *D. prolifera* was not well acclimated to 15% of full sun. On the other hand, only *Drosophyllum* grown at full sun behaved as a typical sun plant ( $I_C$  69 and  $I_S$  367  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ).

The mean  $R_D$  in leaves and traps of all 12 CP species was  $20.0 \pm 1.7 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  (i.e.,  $0.82 \pm 0.10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and ranged between 6.1 and 44  $\text{nmol g}^{-1} \text{ s}^{-1}$  (Table 1). Focusing only on traps, the mean  $R_D$  was  $22.0 \pm 4.3 \text{ nmol g}^{-1} \text{ s}^{-1}$  ( $\pm 1.0 \text{ se}$ ,  $n = 11$ ). The highest DM-based  $R_D$  values were in three heliophilous *Drosera* species, in *Drosophyllum*, *P. moranensis*, and *U. reniformis*, while the lowest ones were in *D. adelae*, shade-acclimated *D. prolifera*, *Dionaea muscipula*, and both *Sarracenia* species. The mean proportion of  $R_D$  to  $P_{Nmax}$  in our CP species was 48% (Table 1; the proportion is the same when expressed on the DM or leaf-area basis). In four species, it even ranged from 80–162%.

## Discussion

### $P_{Nmax}$ and its limitations

Generally in all measured plants, maximum rates of leaf-area and DM-based net photosynthesis (Table 1) were relatively low in comparison with those in vascular non-carnivorous plants, but, on the other hand,

were relatively high within those known in CPs (Ellison 2006). The author reported in his literature search that an average leaf DM-based net photosynthetic rate ( $P_{Nmax}$ ) of 15 carnivorous plant species was 34  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  and did not exceed 100  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ . Similarly, Farnsworth & Ellison (2008) have recently found mean values of 39  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  in intact pitchers in 10 *Sarracenia* species and Pavlovič et al. (2007) mean values of 24–42  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  in leaf laminae of two *Nepenthes* species. The mean  $P_{Nmax}$  values in our results are comparable with those reported for leaves of woodland plants, mostly trees and shrubs, from the GlopNet data base (Wright et al. 2004), but are about twice as low than those reported for leaves of temperate and tropical plants, three times lower than those in grasslands, and four times lower than those in alpine plants. These relationships also hold on the leaf-area basis (Table 1; cf. Givnish 1988).

In *Drosera prolifera*, the higher  $R_D$ ,  $I_C$  and  $I_S$  are consistent with the sun and shade plant adaptation concept (Givnish 1988). Most of the CPs we used were acclimated to low irradiance (usually 10% of full sun, i.e., up to 190  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) although they are considered facultative heliophytes (Givnish et al. 1984; Juniper et al. 1989). This irradiance corresponds with the relatively low values of light saturation (only below about 210  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) found in these greenhouse-raised plants. Thus, according to the photosynthetic light curves, most CP species behaved as typical shade plants. Moreover, in *Drosera binata* and *D. adelae*, a slight photoinhibition was found above 400  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  (data not shown). Sun leaves of *Drosophyllum lusitanicum* utilized high irradiance best of all species, while the other sun-acclimated species lacked the characteristics of such plants: leaves of *Drosera rotundifolia* grown at 45% of full sun were light-saturated already at 182  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ . Also, phyllodes of *S. leucophylla* and pitchers of *S. purpurea*, grown in contrasting light environments (13% and 100% of full sun, respectively), had similar  $I_S$ . *Dionaea muscipula*, *Drosera*

*adelae*, *D. prolifera* shade plants, and *U. reniformis* had  $I_C$  values below  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$  and, in this respect, behaved as typical shade-acclimated species (Table 1). For *Dionaea muscipula*, which behaves as heliophyte at natural sites (e.g., Juniper et al. 1989), such a photosynthetic characteristic can be rather surprising. Nevertheless, this characteristic is in line with the species' ability to be grown successfully even at low irradiances (Adamec, unpublished data). Generally, a partly shade-acclimated characteristic of some CP species considered as facultative heliophytes (*Dionaea muscipula*, *Drosera aliciae*, *D. capensis*, *D. binata*, *S. purpurea*), following from our study, shows a great ecophysiological plasticity of these species. In conclusion, no clear phylogenetic relationships of  $P_{N\text{max}}$  follow from this study. Rather, the differences in  $P_{N\text{max}}$  are attributable only to sun or shade adaptation of the species (e.g., *Dionaea muscipula* vs. *Pinguicula moranensis*).

#### $R_D$ and its proportion to $P_{N\text{max}}$

The mean  $R_D$  values in leaves and traps of CPs in Table 1 were about by one-third lower than those reported by Loveys et al. (2003) for leaves of 16 plant species of all functional groups (mean about 35, range 15–100  $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$ ) at  $23^\circ\text{C}$ , but were slightly higher than those reported for leaves of 32 plant species (mean about  $0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) by Givnish (1988). In our four CP species with very high  $R_D:P_{N\text{max}}$  ratio (except for *D. aliciae*), senescence of carnivorous leaves occurs at the end of the growing season and it might be a reason for their relatively low  $P_{N\text{max}}$ . Nevertheless, the measured leaves were not senescent. The proportion was similarly high (50–140%) in metabolically very active traps of three aquatic *Utricularia* species (Adamec 2006). This sharply contrasts with only about 7% reported in sun and shade non-CPs (Givnish 1988), about 11% reported in 166 temperate and tropical plant species, and 17% in 93 woodland species (the GlopNet data base, Wright et al. 2004). Also, SLA was clearly the highest in CPs ( $0.029 \text{m}^2 \text{g}^{-1}$ ) in comparison with the temperate and tropical species ( $0.012 \text{m}^2 \text{g}^{-1}$ ) and particularly woodland species ( $0.006 \text{m}^2 \text{g}^{-1}$ ).

However, the weak correlation between leaf area-based  $P_{N\text{max}}$  and  $R_D$  ( $r = 0.45$ ,  $p = 0.09$ ,  $n = 15$ ) in our results was overestimated by an extreme outlying value in *Drosophyllum* ( $r = 0.28$ ,  $p = 0.34$ , when *Drosophyllum* is excluded). The correlation between DM-based  $P_{N\text{max}}$  and  $R_D$  was similar ( $r = 0.33$ ,  $p = 0.24$ ) for all species and, after exclusion of the outlying *D. capensis*, the parameters became uncorrelated ( $r = -0.14$ ,  $p = 0.64$ ). One of the reasons for this discrepancy between  $P_{N\text{max}}$  and  $R_D$  could be the morphology and complexity of traps – greater trap complexity (e.g., in Droseraceae) should be associated with a greater  $R_D$  and a lesser  $P_{N\text{max}}$  as a metabolic cost of carnivory. Therefore, the  $R_D:P_{N\text{max}}$  ratio forms a long gradient in CPs. As high  $R_D:P_{N\text{max}}$  ratio was also reported for leaves of two European *Pinguicula* species (13–44%; Méndez & Karlsson 1999) and for leaf laminae of two *Nepenthes* species (15–33%; Pavlovič et al. 2007), this

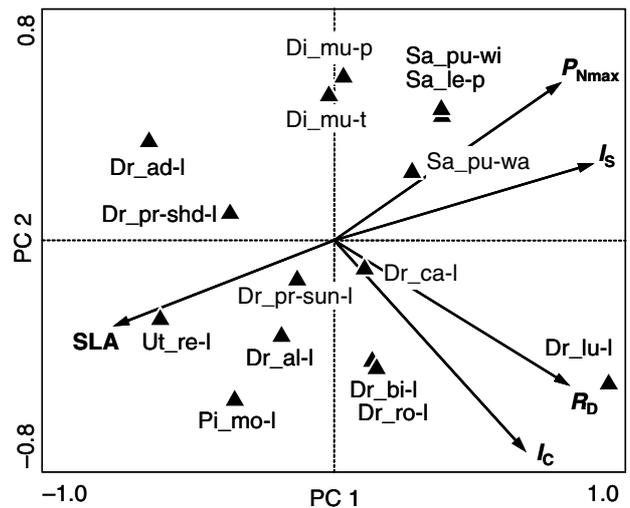


Fig. 1. PCA ordination diagram displaying correlations between photosynthetic leaf traits in CPs (data taken from Table 1). Centroids (triangles) of plant species are projected onto these correlations. Relative values of species for a trait can be estimated by a perpendicular projection of the centroid onto the trait arrow. Photosynthetic parameters were measured on leaves and the discrimination between leaves and traps is specified; l – leaves; p – petioles; t – traps; wi – pitcher wing; wa – pitcher wall. For the explanation of photosynthetic parameters (based on leaf DM) see the text. Underlined letters explain species' names abbreviations: *Dionaea muscipula*, *Drosera adelae*, *D. aliciae*, *D. binata*, *D. capensis*, *D. rotundifolia*, *D. prolifera*, *Drosophyllum lusitanicum*, *Pinguicula moranensis*, *Sarracenia leucophylla*, *S. purpurea*, *Utricularia reniformis*. Sun – sun acclimated plants; shd – shade acclimated plants.

leaf trait may be accepted as typical for CPs (see also Adamec 2006).

The PCA (Fig. 1) revealed correlations between DW-based parameters of the light curves and relationships between the CPs and the parameters. The first PC axis, which explained 56% of the total variation, represents all the parameters, while the second axis (20%) represents mainly  $I_C$  and  $P_N$ . The third axis (16%; not shown) is controlled by SLA (its score on the third axis was 0.59). Species' centroids in the PCA diagram are allocated over all the four quadrants characterizing the species as those with relatively (i) high  $P_{N\text{max}}$  and low  $R_D$  (upper right PCA quadrant;  $R_D:P_{N\text{max}}$  ratio is about 9–15% in *Dionaea* and *Sarracenia* which are approaching to non-CPs), (ii) high  $P_{N\text{max}}$  and high  $R_D$  (lower right; represented by *Drosophyllum*), (iii) low  $P_{N\text{max}}$  and high  $R_D$  (lower left), and (iv) low  $P_{N\text{max}}$  and low  $R_D$  (upper left). Thus  $R_D:P_{N\text{max}}$  ratio corresponds to the second PC axis. The light compensation point correlated with  $R_D$  ( $r = 0.70$ ,  $p = 0.001$ ) and similarly  $I_S$  with  $P_{N\text{max}}$  ( $r = 0.93$ ,  $p < 0.0001$  but  $r = 0.28$ ,  $p = 0.31$  when  $P_{N\text{max}}$  was expressed on DM basis), reflecting the typical light acclimation characteristics.

#### The photosynthetic cost and benefit of carnivory

In *Dionaea* and *S. purpurea*, leaf area-based  $P_{N\text{max}}$  values in the photosynthetic parts of leaves (petiole or pitcher wing) were higher by 25% as compared to those in traps ( $p = 0.0037$ , two-way ANOVA); the values of

$R_D$  were ambiguous (Table 1). However, in line with the theory of Knight (1992), the  $R_D:P_{N_{\max}}$  ratio was higher in traps of both species ( $p = 0.0003$ ). This parameter, as a sensitive criterion of photosynthetic productivity of leaves, was dramatically different in leaf laminae and pitchers of two *Nepenthes* species in which  $P_{N_{\max}}$  of pitchers was even zero or slightly negative (Pavlovič et al. 2007). These data support the classic theory of Knight (1992) on the photosynthetic cost of carnivory that parts of leaves functioning as traps are photosynthetically less efficient than the adjacent, flat leaf laminae functioning only photosynthetically. They also confirm this theory in the other point that the respiratory (metabolic) cost of traps is greater than of leaf laminae. Pavlovič et al. (2007) has recently found for *Nepenthes* pitchers a cluster of characters which explain reduced  $P_{N_{\max}}$  and are associated with carnivory: replacement of chlorophyll-containing cells with digestive glands, low tissue chlorophyll and N content, compact mesophyll with a small proportion of intercellular spaces, absence of palisade parenchyma, and low stomatal density.

In spite of reduced  $P_{N_{\max}}$  of traps in CPs, it is not obvious why leaf laminae (without traps, i.e., phyllode, pitcher wing, petiole) of terrestrial, sun-adapted CPs reach only  $P_{N_{\max}}$  values which are 2–4 times lower than in non-CPs (Wright et al. 2004, Ellison 2006). One of the reasons is relatively low foliar tissue N and P content when compared to functional groups of non-CPs (Ellison 2006). It has recently been found for different pitcher plants (*Darlingtonia californica*, Ellison & Farnsworth 2005; *Nepenthes alata* and *N. mirabilis*, Pavlovič et al. 2007; 10 *Sarracenia* species, Farnsworth & Ellison 2008) that  $P_{N_{\max}}$  of pitchers or flat leaves correlates positively with their tissue N content. Moreover, in most of the *Sarracenia* species, feeding on prey led simultaneously to a significant increase of leaf tissue N content,  $P_{N_{\max}}$  of pitchers per unit DM and, also, of relative growth rate (Farnsworth & Ellison 2008). Although a significant correlation also was found between  $P_{N_{\max}}$  of leaves and foliar tissue N content in some subarctic CP species, the natural catch of prey or extra feeding on prey did not increase  $P_{N_{\max}}$  in *Pinguicula vulgaris* (Méndez & Karlsson 1999). It seems, therefore, that at least in several CP species, uptake of mineral nutrients from prey can also increase  $P_{N_{\max}}$  of mature leaves due to elevated tissue N (or also P and K) content in leaves. Generally, however, the relationship between catching of prey and tissue mineral nutrient content in CPs is rather ambiguous (Adamec 1997, 2002).

In conclusion we can state that slow growth of terrestrial CPs is accepted as a typical ecological trait, though exact data on relative growth rates are available only for several species of *Drosera* (Adamec 2002), *Sarracenia* (Farnsworth & Ellison 2008), and for *Genlisea violacea* (Adamec 2008). Since relative growth rate of terrestrial plants generally correlates significantly with  $P_{N_{\max}}$  values (Shipley 2006) it is possible to conclude that low  $P_{N_{\max}}$  values, commonly measured in terres-

trial CPs, are a typical attribute and a physiological consequence of this slow growth in S-strategists. Relatively low foliar tissue N and P content in CPs is usually below the critical content for growth (Ellison 2006). It is therefore probable that the growth rate of terrestrial CPs is much more limited by shortages of mineral nutrients (N, P, K) in rapidly growing juvenile tissues (apical meristems and differentiating tissues) for growth processes like cell division, DNA replication and transcription, protein synthesis, etc., than in mature leaves for photosynthesis. If such growth processes in juvenile tissues are preferentially stimulated by prey-derived nutrients, young leaves and traps are produced faster as a prerequisite for more rapid growth of the whole plant. Thus, no specific increase of  $P_N$  per unit DM needs to occur yet the total plant  $P_N$  will increase (see Givnish et al. 1984). Consideration of growth rate in any eco-physiological study on CPs seems to be indispensable (Farnsworth & Ellison 2008).

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