OIKOS 86: 105–112. Copenhagen 1999

# Costs and benefits of carnivory in plants: insights from the photosynthetic performance of four carnivorous plants in a subarctic environment

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Méndez, M. and Karlsson, P. S. 1999. Costs and benefits of carnivory in plants: insights from the photosynthetic performance of four carnivorous plants in a subarctic environment. – Oikos 86: 105–112.

We measured photosynthetic performance in four subarctic carnivorous plants, *Pinguicula alpina*, *P. villosa*, *P. vulgaris* and *Drosera rotundifolia*, in order to test if there is a cost of combining photosynthetic and trapping devices into the same organ (leaves). We compared these data with published results on photosynthetic rates in subarctic non-carnivorous plants. In *P. vulgaris*, an experiment of prey addition and removal further tested the existence of a short-term benefit of increased nutrient gain from prey in terms of photosynthetic efficiency.
Leaf area-based photosynthetic rates ($P_a$) ranged 2.0–3.0 μmol $CO_2$ $m^{-2}$ $s^{-1}$, dry mass-based photosynthetic rates ($P_w$) 42–69 nmol $CO_2$ $g^{-1}$ $s^{-1}$, and photosynthetic nitrogen use efficiency (PNUE) 29–45 μmol $CO_2$ mol $N^{-1}$ $s^{-1}$. In general, $P_a$ and $P_w$ of carnivorous plants increased with leaf nitrogen content. When each species was analysed separately, those relationships were weak (*P. alpina* and *P. villosa*) or non-significant (*P. vulgaris* and *D. rotundifolia*). The photosynthetic rate of carnivorous plants was lower than that of other subarctic growth forms. In addition, $P_w$ for a given leaf nitrogen content was significantly lower in carnivorous plants than in non-carnivorous ones. No change in $P_a$, $P_w$ or PNUE occurred as a result of prey capture manipulation, but treatments differed only slightly in nutrient content. $P_w$ and PNUE showed a trend to be higher in reproductive *P. alpina* plants as compared to vegetative ones. In *P. vulgaris*, however, an increased leaf respiration was found in reproductive plants.

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Carnivory is considered a strategy to obtain nutrients in the nutrient-poor habitats where carnivorous plants usually appear (Givnish 1989). Benefits of carnivory derive from savings in metabolic assimilation of inorganic N (Pate 1986), and increased tissue nutrient content and growth (see Adamec 1997 for a review). Furthermore, prey capture may enhance survival (Zamora et al. 1997), competitive ability (Wilson 1985), vegetative multiplication (Thum 1988, Zamora et al. 1997) and sexual reproduction (Thum 1988, Karlsson et al. 1991, Karlsson and Pate 1992, Zamora et al. 1997). But carnivory is not prevalent among plants in general since it entails also costs that under some conditions may be larger than benefits (Benzing 1987).

Potential costs of carnivory include investment in prey trapping (Pate 1986) and luring devices (e.g. amino acid-rich nectar, Dress et al. 1997). Also, dual use of leaves for carbon and nutrient gain could decrease their

Accepted 26 September 1998

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ISSN 0030-1299
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photosynthetic efficiency (Benzing 1987). Finally, microhabitat requirements for prey trapping and photosynthesis can be incompatible. In *Pinguicula vallisneriifolia*, Zamora (1995) found that moist microhabitats, where prey were more abundant, were also shaded, thus likely decreasing photosynthetic performance. In addition to these considerations, there are some empirical indications of the existence of costs of the carnivorous habit. For instance, some species only produce the traps during favourable periods of the year (see Givnish et al. 1984 for a review) or vary their investment in carnivory as a function of the environment or conditions where they are growing (Knight and Frost 1991). In *Utricularia macrorhiza*, bladders were less efficient for photosynthesis than unmodified leaves (Knight 1992).

Givnish et al. (1984) developed a cost-benefit model for the evolution of carnivory, postulating three potential net benefits of carnivory in the – usually nutrient poor, sunny, moist – habitats where carnivorous plants live: (1) increased photosynthetic rates as result of prey-derived nutrient gain, (2) increased reproductive performance, or (3) partial replacement of autotrophy by heterotrophy as source of chemical energy. Givnish et al. (1984) considered the third benefit as very unlikely and reduced the second one to a product of increased photosynthetic rates. Thus, photosynthetic performance is central to any discussion of costs and benefits of carnivory. Nevertheless, besides the study by Knight (1992), information about photosynthetic performance of carnivorous plants is mostly lacking.

The primary purpose of this paper was to test the hypothesis that there is a cost of carnivory in terms of a reduced photosynthetic performance of leaves combining both autotrophic function and traps in the same physical organ. Photosynthetic performance, estimated as leaf area and mass based maximum photosynthetic rates and as photosynthetic nitrogen use efficiency, in four subarctic carnivorous plants was compared with that of non-carnivorous subarctic plants belonging to different growth forms. In addition, we tested if there was a short-term benefit from prey capture in terms of an enhanced photosynthetic performance, as predicted by Givnish et al. (1984). Finally, we explored the capacity of intraspecific adjustment of photosynthetic rates according to the reproductive status. It has been suggested that reproductive plants could increase their photosynthetic rates and compensate for the cost associated to reproduction (Tuomi et al. 1983). But in carnivorous plants this kind of compensatory mechanism could be impaired if carnivory decreases photosynthetic performance. Instead, reproduction could entail higher metabolic costs and an increased respiration.

## Materials and methods

### Plant species and study area

We studied four carnivorous plant species, *Pinguicula alpina*, *P. villosa* and *P. vulgaris* (Lentibulariaceae) and *Drosera rotundifolia* (Droseraceae), in July 1996. Prey capture (Karlsson et al. 1987, 1994), benefits of carnivory (Aldenius et al. 1983, Karlsson and Carlsson 1984, Karlsson et al. 1991, Hanslin and Karlsson 1996), resource economy (Karlsson 1986, 1988), and somatic cost of reproduction (Karlsson et al. 1990, Thorén et al. 1996) have been previously studied in these species. They are all common at a sub-alpine heathland located in the surroundings of the Abisko Scientific Research Station (Swedish Lapland: 68° 21′ N, 18° 49′ E, 385 m above sea level [a.s.l.]). Each species occupies different microhabitats: *P. alpina* grows in limestone soils, *P. villosa* is an epiphyte on *Sphagnum* mosses, *P. vulgaris* grows in a range of microhabitats, from poor soils to rich limestone soils, and *D. rotundifolia* appears in bogs. For this study, both *P. alpina* and *P. vulgaris* were taken from "wet holes" among polygons. Additional samples for *P. vulgaris* were taken at a poor fen in Katterjåkk (68° 27′ N, 18° 10′ E, 540 m a.s.l.).

### Treatments

Samples of the four species were taken for the study of the photosynthetic performance. The sample size for each species ranged from 10 to 30 plants. For *P. alpina* and *P. vulgaris*, we recorded the reproductive status (i.e. vegetative or reproductive) of plants. Within reproductive plants of *P. vulgaris*, we considered two developmental stages: plants with a flower bud, and plants with an open flower. All reproductive plants of *P. alpina* were in the stage of open flower. For *P. villosa*, we analysed both reproductive and vegetative plants but because of the small sample size results are given for the pooled sample. All *D. rotundifolia* plants were non-reproductive at the time of the study.

To study the effect of prey trapping success on photosynthetic performance, we experimentally manipulated prey capture of *P. vulgaris* at Abisko. Prey addition treatment consisted of the addition, on three consecutive days, of two, two and one *Drosophila melanogaster* to 15 plants. Prey removal treatment consisted of the daily removal of all prey present on leaves of 15 plants. One week after the first prey addition, when prey apparently had been digested, all plants were collected and photosynthesis measured. All the plants used for this experiment were reproductive, with either flower buds or open flowers. Thus, reproductive *P. vulgaris* (flower bud and open flower pooled) of the main sample used to measure photosynthesis served as control for this experiment.

### Photosynthetic measurements

We excavated whole plants, with their surrounding soil, and brought them to the laboratory. Plants were processed the same day of collection, except plants from Katterjåkk, which were processed the day after collection.

We carried out photosynthetic measurements in the laboratory using an infrared gas analyser (IRGA; Series 225 Gas Analyser, ADC, Hoddesdon, England) measuring system with three cuvettes (Sveinbjörsson 1983). Thus, three samples could be analysed simultaneously, obtaining one reading for each of the cuvettes every 5 min. Just before measurement, we detached several leaves of the same plant, depending on species and plant size (see below), and immediately put them into a small water container and sealed with plasticine. The container with its mounted leaves was then placed inside a cuvette. We randomized samples among cuvettes. Photosynthetic active radiation was 750 $\mu E\ m^{-2}\ s^{-1}$ and light was supplied by a daylight lamp (Power Star HQI-TS 400 W/D, Osram, Germany) from above and filtered through 2 cm water above the cuvettes. After 10 min for stabilization, we took 5 measurements and calculated their mean. After this, we switched the light off, covered the cuvettes with aluminium foil, left them 10 min for stabilization, and took 5 additional measurements in order to estimate dark-respiration. Leaf temperature in the cuvettes was ca 18°C. The number of leaves used for each measurement varied depending on plant size. For *P. alpina* and *P. vulgaris* we used 2–4 leaves per sample, for *Drosera rotundifolia* we used 5–6 leaves. In all cases, the youngest leaf and successively older leaves were chosen until we got enough material. Leaves of *P. vulgaris* from Katterjåkk were bigger and they afforded us to make two measurements per plant (2 leaves per measurement). Due to the small size of *P. villosa*, we used 3–5 plants per sample. We measured projected leaf area using an area meter (Digital Image Analysis System, Delta-T Devices Ltd., England). Dry mass to the nearest 0.1 mg was obtained after oven-drying samples at 70°C for a week. We obtained nitrogen content, after digestion with sulphuric acid, using a flow analysis system (FIA-Star 5012 Analyzer, Tecator, Höganäs, Sweden). Photosynthetic rates and respiration were calculated in leaf area units ($P_a$, $R_a$, as $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and mass based units ($P_w$, $R_w$, as $nmol\ CO_2\ g^{-1}\ s^{-1}$), and photosynthetic nitrogen use efficiency (PNUE) as $\mu mol\ CO_2\ mol\ N^{-1}\ s^{-1}$.

### Bibliographic review

We compared our data on photosynthetic rates of the four carnivorous plants with published data of non-carnivorous subarctic plants, including hemiparasites. We excluded data obtained using the $^{14}C$-method because they may not be comparable with those obtained by the IRGA-method (Karlsson and Sveinbjörnsson 1981). When data on SLA or N content were provided, we used them to obtain $P_a$, $P_w$ and PNUE, respectively. These data were grouped by growth form (deciduous shrubs, evergreen shrubs, forbs, graminoids, or hemiparasitic plants). In the Results section only means will be shown. The complete list of data is available on request to the authors.

### Statistical analyses

We performed all statistical analyses using SPSS-PC +. We tested normality and homoscedasticity previously to ANOVA and a posteriori Student-Newman-Keuls (SNK) tests. Heteroscedastic variables were log-transformed. When homoscedasticity was not achieved after logarithmic or square root transformations, we performed ANOVA on ranks (Potvin and Roff 1993). When we made more than one comparison using the same analytical model, we applied table-wide sequential Bonferroni corrections (Rice 1989) to prevent type I error.

Because of the unbalanced sample size of different growth forms, we did not directly compare photosynthetic performance of carnivorous vs non-carnivorous subarctic plants. Instead, we used ANCOVA to test the homogeneity of slopes and intercepts of the relationship between $P_w$ and N concentration for carnivorous vs non-carnivorous plants. We chose $P_w$ because more data using this unit were available in the bibliography.

## Results

### Photosynthesis in carnivorous plants

The interspecific comparison (data from Abisko) showed significant differences between species in $P_a$ and PNUE (Table 1). *P. alpina* had higher $P_a$ and PNUE than the other three species (Table 1). *P. alpina* also ranged the highest in terms of $P_w$, followed by *P. vulgaris*, *D. rotundifolia* and *P. villosa* (Table 1). Leaf N concentration did not vary significantly among species (Table 1). For *P. vulgaris*, we did not find differences between the two populations compared in either $P_a$, $P_w$ or PNUE ($P > 0.05$). Significant differences in nitrogen content on a leaf area basis ($P < 0.05$, cf. Table 1) disappeared after Bonferroni correction.

For the whole data set and for *P. alpina* and *P. villosa*, both $P_a$ and $P_w$ increased with leaf nitrogen content (Fig. 1). Photosynthetic performance in *P. vulgaris* and *D. rotundifolia* did not show any significant relationship with leaf nitrogen content (Fig. 1).