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

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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

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photosynthetic efficiency (Benzing 1987). Finally, microhabitat requirements for prey trapping and photosynthesis can be incompatible. In *Pinguicula vallisnerifolia*, 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).

Photosynthesis in carnivorous plants vs other subarctic growth forms

Photosynthetic rate for the carnivorous plants was the lowest among all subarctic growth forms, compared either as P_a or as P_w (Table 2). Mean P_a for carnivorous plants was 10% of that for forbs and one third of that of hemiparasitic plants. When measured on a mass basis (P_w) the differences among growth forms were smaller. PNUE of carnivorous plants also ranged the lowest among the growth forms (Table 2), but the data base was smaller for PNUE than for P_a or P_w.

P_w increased with leaf nitrogen content in all the subarctic growth forms (Fig. 2). The rate of increase was similar in carnivorous plants to the other growth forms combined (Fig. 2). The elevation of the regression line was, however, significantly lower than that for non-carnivorous plants. Thus, at similar leaf N content carnivorous plants had a lower PNUE.

Photosynthesis and prey capture

Experimental manipulation of prey capture caused significant differences between treatments in leaf nitrogen concentration (Table 3). On a leaf area basis, leaf nitrogen content decreased in the order prey addition > control > prey removal (Table 3). However, these differences disappeared after Bonferroni correction (Table 3). We did not find significant differences in either P_a, R_a, P_w, R_w or PNUE between plants with prey added, prey removed or control (Table 3).

Photosynthesis in reproductive vs vegetative plants

In *P. alpina*, no significant difference in either P_a or respiration (R_a and R_w) was found between vegetative and reproductive (open flower) plants (Table 4). P_w and PNUE were significantly higher in reproductive plants (Table 4), although Bonferroni correction turns these differences non-significant (Table 4).

In *P. vulgaris*, no significant difference was found in P_a, P_w or PNUE between either vegetative plants, plants with flower buds or plants with open flowers (Table 4). However, vegetative plants showed a lower respiration than reproductive plants, both for R_a and for R_w (Table 4).

Discussion

Photosynthesis in subarctic carnivorous vs non-carnivorous plants

Photosynthetic rates for carnivorous plants reported in the present study agreed with values found by Small (1972) for the bog-living *Sarracenia purpurea* (29.7 nmol CO_2 g^{-1} s^{-1}), and with values given for other two aquatic carnivorous plants: *Aldrovanda vesiculosa* (27.5 nmol CO_2 g^{-1} s^{-1}, Adamec 1995) and *Utricularia macrorhiza* (range 2.4–20.0 nmol CO_2 g^{-1} s^{-1} in bladders, depending on position on leaf and population, Knight 1992). Thus, photosynthetic rates in carnivorous plants seem to be low, in general, although further studies will be necessary to establish the generality of this pattern.

Our results showed a lower photosynthetic performance in subarctic carnivorous plants compared with other non-carnivorous species (Table 2 and Fig. 2). Ranking of photosynthetic rates in subarctic growth forms (forbs, graminoids, deciduous shrubs, and evergreen shrubs, in a decreasing order) agreed with a previous review by Oberbauer and Oechel (1989) and with other general reviews on photosynthetic rates (Larcher 1995). Both hemiparasitic and carnivorous plants showed photosynthetic rates lower than those from other growth forms.

Photosynthetic capacity of carnivorous plants increased with leaf nitrogen content at a similar rate as for non-carnivorous plants, but the carnivorous plants

Table 1. Mean ± SD values of leaf area based (P_a, µmol CO_2 m^{-2} s^{-1}) and mass based (P_w, nmol CO_2 g^{-1} s^{-1}) photosynthetic rates, photosynthetic nitrogen use efficiency (PNUE, µmol CO_2 mol N^{-1} s^{-1}) and N content in four subarctic carnivorous plants. *F* value and significance of the ANOVA for interspecific comparison (data from Abisko for *P. vulgaris*) are also given. Means followed by different letters were different according a posteriori SNK test. ns = $P>0.05$; *** = $P<0.001$; **** = $P<0.0001$.

Species – Population	*n*	P_a	P_w	PNUE	N content (mmol m^{-2})	N content (mmol g^{-1})
Pinguicula alpina	20	3.0 ± 0.6 a	69.3 ± 14.1 a	45.4 ± 8.4 a	66.8 ± 12.5 a	1.5 ± 0.2 a
P. villosa	10	2.0 ± 0.4 b	41.8 ± 9.1 c	29.4 ± 5.0 b	69.2 ± 13.5 a	1.4 ± 0.2 a
P. vulgaris – Abisko	30	2.3 ± 0.9 b	56.7 ± 22.8 b	37.7 ± 15.8 b	61.4 ± 10.0 a	1.5 ± 0.2 a
P. vulgaris – Katterjåkk	8	2.0 ± 0.4	64.9 ± 13.2	39.9 ± 7.2	52.3 ± 8.3	1.6 ± 0.2
Drosera rotundifolia	10	2.1 ± 0.4 b	45.6 ± 10.4 bc	33.6 ± 8.0 b	65.2 ± 10.4 a	1.4 ± 0.3 a
ANOVA results:		$F_{3,66}$ = 8.456***[1]	$F_{3,66}$ = 9.860****[1]	$F_{3,66}$ = 7.821***[1]	$F_{3,66}$ = 1.614 ns	$F_{3,66}$ = 1.658 ns

[1] ANOVA performed using ranks.

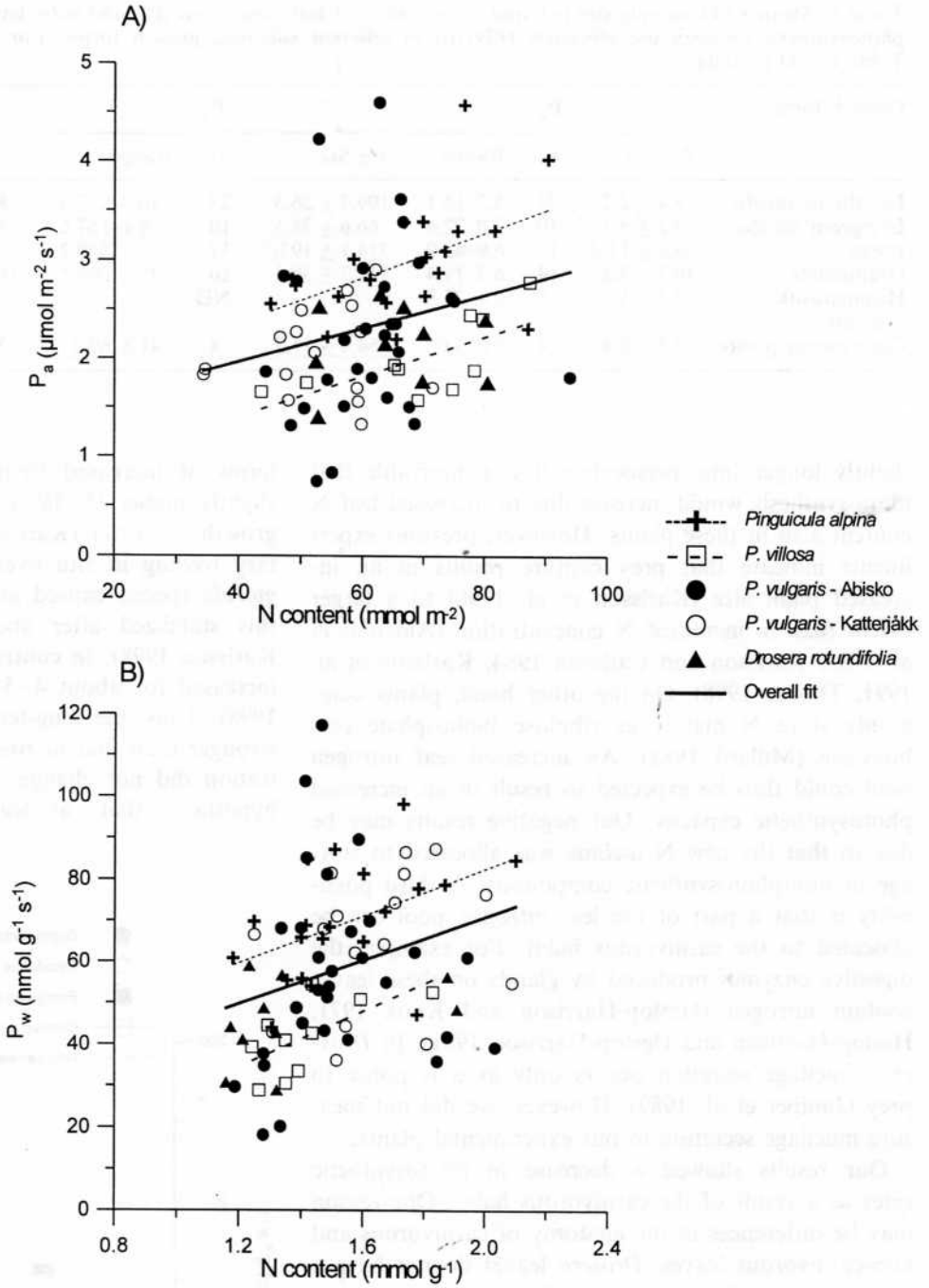

Fig. 1. Leaf area based (P_a) and mass based (P_w) photosynthetic rates in relation to leaf nitrogen content in four subarctic carnivorous plants. Regression lines are shown only for significant relationships. A) P_a: bold line, overall data ($R^2 = 0.08$, $F_{1,84} = 7.024$, $P < 0.01$); dotted line, *Pinguicula alpina* ($R^2 = 0.24$, $F_{1,18} = 5.613$, $P < 0.05$); dashed line, *P. villosa* ($R^2 = 0.47$, $F_{1,8} = 7.054$, $P < 0.05$). B) P_w: bold line, overall data ($R^2 = 0.10$, $F_{1,84} = 9.095$, $P < 0.01$); dotted line, *Pinguicula alpina* ($R^2 = 0.21$, $F_{1,18} = 4.836$, $P < 0.05$); dashed line, *P. villosa* ($R^2 = 0.43$, $F_{1,8} = 5.988$, $P < 0.05$).

studied had a lower nitrogen use efficiency. A positive correlation between nitrogen content and photosynthetic rate is considered general for plants (Field and Mooney 1986) and has been found in some other subarctic species (e.g. Karlsson and Nordell 1988, Karlsson 1994). The carnivorous plants studied, however, showed a weak or non-significant relationship between nitrogen content and photosynthesis. Knight (1992) found an increasing photosynthetic performance with nitrogen content in *Utricularia macrorhiza*, but nutrient use efficiency of this species was still lower than that of non-carnivorous plants.

Weiss (1980, quoted in Givnish et al. 1984), found a higher photosynthetic rate in *Sarracenia flava* as result of nutrient gain through carnivory. At the short time scale studied, we did not find any effect on photosynthetic rate from manipulated prey capture levels for *P. vulgaris*. One reason can be that increase in nitrogen content as a result of our manipulation was slight and only significant before Bonferroni correction (Table 3). This could reflect the need of a longer time to find a response to feeding. At a

Table 2. Mean ± SD, sample size (n), and range values of leaf area based (P_a) and mass based (P_w) photosynthetic rates and photosynthetic nitrogen use efficiency (PNUE) in different subarctic growth forms. For units of P_a, P_w and PNUE see Table 1. ND no data.

Growth form	P_a			P_w			PNUE		
	$\bar{x} \pm$ SD	n	Range	$\bar{x} \pm$ SD	n	Range	$\bar{x} \pm$ SD	n	Range
Deciduous shrubs	9.4 ± 2.2	21	5.2–15.1	109.3 ± 26.3	23	46.7–252.5	80.3 ± 18.6	17	37.1–141.4
Evergreen shrubs	9.2 ± 5.3	10	2.0–22.4	66.6 ± 38.5	10	6.1–157.6	87.1 ± 44.3	10	20.0–169.1
Forbs	23.0 ± 11.4	15	6.9–42.9	314.1 ± 193.7	17	107.3–568.2		ND	
Graminoids	10.7 ± 3.2	14	6.3–19.4	112.7 ± 30.1	10	25.2–208.3	109.5 ± 35.4	3	60.1–160.0
Hemiparasitic plants	7.3 ± 5.2	5	2.1–27.5		ND			ND	
Carnivorous plants	2.3 ± 0.4	4	2.0–3.0	54.4 ± 11.2	4	41.8–69.3	36.8 ± 6.0	4	29.4–39.9

slightly longer time perspective it is conceivable that photosynthesis would increase due to increased leaf N content also in these plants. However, previous experiments indicate that prey capture results in an increased plant size (Karlsson et al. 1996) to a larger extent than in increased N concentration (Aldenius et al. 1983, Karlsson and Carlsson 1984, Karlsson et al. 1991, Thorén 1998). On the other hand, plants commonly store N mainly as ribulose biphosphate carboxylase (Millard 1988). An increased leaf nitrogen pool could thus be expected to result in an increased photosynthetic capacity. Our negative results may be due to that the new N income was allocated to storage in non-photosynthetic compounds. A third possibility is that a part of the leaf nitrogen pool can be allocated to the carnivorous habit. For example, the digestive enzymes produced by glands on these leaves contain nitrogen (Heslop-Harrison and Knox 1971, Heslop-Harrison and Heslop-Harrison 1981). In *Drosera*, mucilage secretion occurs only as a response to prey (Juniper et al. 1989). However, we did not measure mucilage secretion in our experimental plants.

Our results showed a decrease in photosynthetic rates as a result of the carnivorous habit. One reason may be differences in the anatomy of carnivorous and non-carnivorous leaves. *Drosera* leaves do not have a palisade layer (Juniper et al. 1989). A more compact morphology probably results in lower mesophyll conductance and thus lower photosynthetic rates. To our knowledge, such information on leaf anatomy is not available for *Pinguicula*.

Givnish et al. (1984) proposed that a potential benefit of carnivory could come primarily from higher photosynthetic rates due to an increase in nitrogen uptake from prey. They considered increased reproduction just a secondary consequence of increased photosynthesis. But since the photosynthetic production per unit leaf N in carnivorous plants was about 50% of that in non-carnivorous ones, it seems like the carnivorous habit does not pay off in leaf carbon-economy terms only. In comparison, the benefit in terms of increased frequency of seed production is slightly higher (5–48%) than the benefit in terms of growth (3–29%) (Karlsson et al. 1996). Supplementary feeding in situ over several years of three *Pinguicula* species caused an increase in rosette size, but this stabilized after about two years (Thorén and Karlsson 1998). In contrast, the reproductive response increased for about 4–5 years (Thorén and Karlsson 1998). Thus, the long-term reproductive response was stronger than that of rosette size while leaf N concentration did not change at all. Thus, we propose the hypothesis that, at least for the studied subarc-

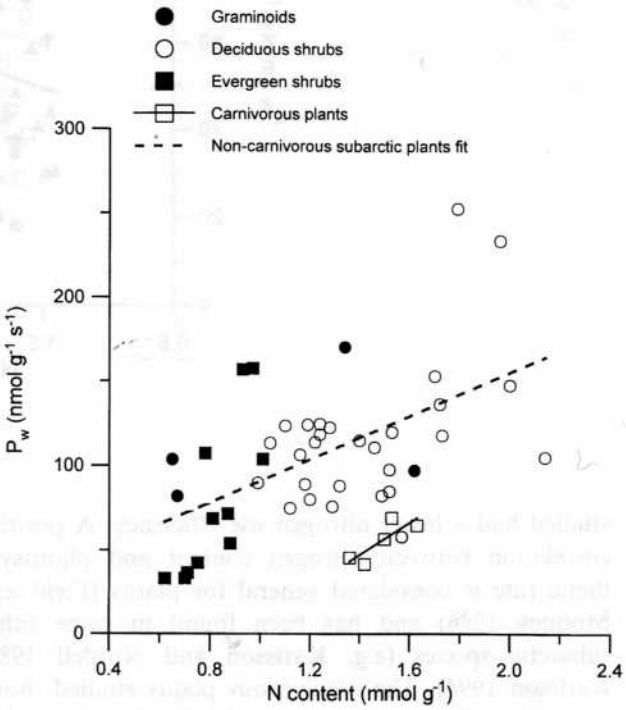

Fig. 2. Mass based (P_w) photosynthetic rates in several subarctic species in relation to their leaf nitrogen content. The lines for non-carnivorous ($y = 63.97x + 27.07$; $R^2 = 0.31$) and for carnivorous plants ($y = 95.81x - 86.91$; $R^2 = 0.70$) had similar slopes ($F_{1,44} = 0.03$, $P = 0.859$) but different intercepts according to ANCOVA ($F_{1,45} = 14.34$, $P < 0.001$).

Table 3. Mean ± SD values of nutrient content, leaf area based (P_a) and mass based (P_w) photosynthetic rates and respiration (R_a and R_w, respectively) and PNUE in plants of *Pinguicula vulgaris* from Abisko with different prey capture. *F* value and significance of the ANOVA are also given. Means followed by different letters were different according to a posteriori SNK tests. ns = $P>0.05$; * = $P<0.05$ (probability values within brackets indicate non-significant results after Bonferroni correction).

	Control ($n=20$)	Prey added ($n=15$)	Prey removed ($n=15$)	ANOVA results
N content (mmol m^{-2})	61.5 ± 11.2 ab	64.7 ± 9.9 a	54.5 ± 9.2 b	$F_{2,47}=3.886$ (*)
N content (mmol g^{-1})	1.5 ± 0.2 a	1.6 ± 0.2 a	1.4 ± 0.2 b	$F_{2,47}=4.437$ (*)
P_a (μmol CO_2 m^{-2} s^{-1})	2.2 ± 1.0	2.2 ± 0.4	2.2 ± 0.6	$F_{2,47}=0.174$ ns [1]
R_a (μmol CO_2 m^{-2} s^{-1})	0.7 ± 0.4	1.0 ± 0.4	0.8 ± 0.3	$F_{2,47}=2.657$ ns
P_w (nmol CO_2 g^{-1} s^{-1})	55.0 ± 25.1	52.1 ± 10.0	55.6 ± 16.9	$F_{2,47}=2.240$ ns [1]
R_w (nmol CO_2 g^{-1} s^{-1})	17.3 ± 6.4	23.1 ± 8.2	19.2 ± 8.1	$F_{2,47}=2.641$ ns
PNUE (μmol CO_2 mol N^{-1} s^{-1})	36.6 ± 17.9	34.0 ± 6.8	40.9 ± 10.0	$F_{2,47}=0.120$ ns [1]

[1] ANOVA performed on ranks.

Table 4. Mean ± SD ($n=10$ in all cases) values of leaf area based (P_a) and mass based (P_w) photosynthetic rates and respiration (R_a and R_w, respectively) in vegetative and reproductive plants of *Pinguicula alpina* and *P. vulgaris*. For units see Table 3. *F* value and significance of ANOVA are also given. For *P. vulgaris*, means followed by different letters were different according to a posteriori SNK tests. ns = $P>0.05$; * = $P<0.05$; ** = $P<0.01$ (probability values within brackets indicate non-significant results after Bonferroni correction).

	Pinguicula alpina			*Pinguicula vulgaris*			
	Vegetative	Open flower	ANOVA results	Vegetative	Flower bud	Open flower	ANOVA results
P_a	3.0 ± 0.6	3.0 ± 0.6	$F_{1,18}=0.000$ ns	2.4 ± 0.7 a	2.2 ± 1.2 a	2.2 ± 0.9 a	$F_{2,27}=0.208$ ns
R_a	0.4 ± 0.3	0.4 ± 0.4	$F_{1,18}=0.184$ ns	0.4 ± 0.2 a	0.8 ± 0.2 b	0.6 ± 0.4 b	$F_{2,27}=6.792$ ** [1]
P_w	61.9 ± 11.7	76.7 ± 12.9	$F_{1,18}=7.203$ (*)	60.1 ± 18.0 a	49.2 ± 24.5 a	60.8 ± 25.5 a	$F_{2,27}=0.803$ ns
R_w	9.8 ± 4.7	9.8 ± 7.9	$F_{1,18}=0.000$ ns	9.0 ± 3.6 a	17.4 ± 4.3 b	17.2 ± 8.3 b	$F_{2,27}=8.003$ ** [1]
PNUE	41.2 ± 7.1	49.6 ± 7.8	$F_{1,18}=6.195$ (*)	39.9 ± 10.9 a	34.2 ± 17.8 a	39.0 ± 18.7 a	$F_{2,27}=0.366$ ns

[1] Log-transformed data for analysis

tic species of carnivorous plants, the benefit from prey capture is larger in terms of reproduction than in terms of carbon incomes.

Plants have developed the whole way from autotrophy trough hemiparasitism to parasitism, with respect to carbon and mineral nutrition (Press 1995). In the same way, carnivorous plants have developed a varying dependence on animal prey concerning mineral nutrition (Adamec 1997). If their photosynthetic efficiency has decreased as a result of this, why not rely also on prey for carbon gain and become heterotrophic? It is known that some carnivorous plants take carbon from prey (Adamec 1997). Although benefits from this income were downplayed by Givnish et al. (1984), quantitative studies should consider how carbon gain from prey affect cost-benefit of carnivory and a decreased photosynthetic ability.

Photosynthetic performance and reproduction

It has been found that somatic cost of reproduction in some *Pinguicula* species is less than expected from their reproductive investment (Karlsson et al. 1990). Despite low photosynthetic rates found in the four carnivorous plants studied, at least *P. alpina* showed a trend to increase its photosynthetic capacity when reproducing. This could help this species to partially compensate for the cost of reproduction. In contrast, reproductive *P. vulgaris* showed an increased respiration rate and did not show any evidence of photosynthetic compensation for the reproductive cost. These results are consistent with the higher cost of reproduction found in *P. vulgaris* compared with *P. alpina* (Karlsson et al. 1990).

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