



## Original papers

# The effect of soil nutrient status on prey utilization in four carnivorous plants

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**Summary.** The hypothesis that carnivorous plants are less responsive to prey at high soil nutrient levels than at lower levels (Givnish et al. 1984) is tested on four plant species (*Drosera rotundifolia*, *Pinguicula alpina*, *P. villosa* and *P. vulgaris*) from a subarctic environment. The response, measured in terms of seven characteristics (winter bud weight, winter bud nitrogen and phosphorus content, flowering frequency, total seed weight, seed number and weight per seed), was analysed. Although all species responded to prey supply the response varied depending on the characteristic and species concerned. In 5 cases (out of 28 tests) the hypothesis was supported, whereas in 1 case it was refuted, i.e. the response to prey was higher for plants supplied with soil nutrients. In the remaining three-quarters of the tests, responses to prey were not significantly different between the two nutrient levels. Thus, the hypothesis that the response to prey diminishes as soil nutrient availability increases was not supported by our findings. A modification of the model presented by Givnish et al. (1984) is therefore suggested. This modified model measures the cost of carnivory as loss in growth rate and assumes that responses to prey remain unchanged as the soil nutrient content increases. Although the distribution of carnivorous plants is still predicted to be limited mainly to wet and sunny but nutrient-poor sites, the modified model also allows for their occurrence in richer habitats, provided competition is low.

**Key words:** *Drosera* – *Pinguicula* – Subarctic – Growth – Reproduction

Based on the relative rarity of botanical carnivory and the fact that most carnivorous plants are restricted to a certain type of environment, Givnish et al. (1984) pre-

sented a cost/benefit model predicting the conditions under which the cost of trapping prey is exceeded by the benefits. According to this model, carnivorous plants should be restricted to environments with an abundant supply of water and light but poor in nutrients, i.e. where nutrient availability is the main limiting factor. In other environments the cost of producing traps would exceed the benefits gained from prey. The cost/benefit model is based on the assumption that a considerable cost is associated with the ability to trap and digest prey. Data on the costs of carnivory are scarce, however, and the only estimate that we are aware of was made by Pate (1986), where the carbon cost of secretions from *Drosera* tentacles was estimated to be 4–6% of the plant's total carbon budget.

Few empirical studies have attempted to determine how the benefits from trapped prey vary with soil resource availability. Experimental support for the cost/benefit model can be found in a study by Chandler and Anderson (1976), who showed that the effect of prey supplied to two Australian *Drosera* species diminished when the nitrogen supply to the soil increased (however, see below). Furthermore, *Utricularia gibba* showed no response to prey when grown on a complete nutrient medium (Sorenson and Jackson 1968). Some results indicate that the trapped prey provide more than just a supplementary source of soil nutrients. No sign of a diminishing response to prey supply was observed in *Pinguicula vulgaris* when the soil nutrient supply was increased (Aldenius et al. 1983). Chandler and Anderson (1976) obtained the largest response in *Drosera binata* when it was supplied with prey but not with soil nitrogen. Supplying both prey and soil nitrogen or soil nitrogen only resulted in smaller plants. In an experiment with *P. vulgaris*, in which nutrients were supplied through "artificial prey", i.e. agar-blocks differing in nutrient content, a complete nutrient supply in this form resulted in a 2–3 times larger increase in nitrogen and phosphorus pools as compared with plants receiving "prey" contain-

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ing nitrogen or phosphorus only (Karlsson and Carlsson 1984).

This study was designed to test how the effect of trapped prey varies with soil nutrient status for four species of carnivorous plants from the subarctic region of north Sweden. Two of the species, *Drosera rotundifolia* and *Pinguicula villosa*, grow in nutrient-poor bog habitats, whereas the other two species, *P. alpina* and *P. vulgaris*, are from relatively rich mineral soils. *D. rotundifolia* has long been known to benefit from prey (e.g. Darwin 1878; Kellermann and Raumer 1878). Among the *Pinguicula* species included, only *P. vulgaris* (Aldenius et al. 1983; Karlsson and Carlsson 1984) has been tested explicitly with regard to its ability to respond to trapped prey. All three *Pinguicula* species trap prey, although with different degrees of success (Karlsson et al. 1987). In contrast to most carnivorous plants, *P. alpina* and *P. vulgaris* are not restricted to nutrient-poor habitats. Both can be found on rich, calcareous, soils in northern Fennoscandia (cf. Karlsson 1986).

Most studies on the effect of prey on carnivorous plants have focused on growth or on the size of the entire plant when close to its seasonal peak in biomass (however, cf. Thum 1988). Here, we measure the effect of prey on characteristics more closely related to plant fitness, i.e. the size and nutrient content of the two compartments of these species that survive from one season to another – the winter bud and seed.

## Methods

In early June ca. 250 specimens each of *Drosera rotundifolia* L., *Pinguicula alpina* L., *P. villosa* L. and *P. vulgaris* L. were dug up with a part of their original substrate and placed in plastic pots (ca. 8 × 8 × 8 cm). Other vascular plants occurring in the pots were removed. The pots were kept in trays with 24 pots of the same treatment in each tray. The trays were randomly distributed between two glasshouses. Once a week the trays were moved between and within the glasshouses.

All four species were grown on their original soil, *D. rotundifolia* and *P. villosa* on a *Sphagnum fuscum* substrate, and the other two species on a mineral soil (further details on soil and site characteristics are given in Karlsson 1986). The plants were randomly divided into six groups receiving different combinations of two levels of soil nutrient supply and three levels of prey supply according to a factorial design. The nutrient supply levels were: (1) tap water plus a complete nutrient solution with 0.05 mM of nitrogen (Rika, Weibulls, Landskrona, Sweden; cf. Karlsson and Nordell 1987 for the composition of the nutrient solution) and (2) tap water plus a complete nutrient solution with 5 mM of nitrogen. The nutrient solutions were poured into the trays (to ca. 4 cm depth), left for 24 h and then removed. This treatment was repeated at a weekly intervals. The nutrient solution reached the rhizosphere through capillary forces and diffusion: therefore, nutrient conditions may have differed between substrates. It was not possible, however, to grow all species on one standardized substrate.

Fruit flies, *Drosophila melanogaster*, were used as prey. Before feeding the plants the flies were killed by freezing them for 10–15 min at –15°C. The levels of prey supply were: (1) no prey, (2) 1 fly every 3rd week and 3) 1 fly every week. Because of its small size, *P. villosa* received less prey. For this species the intermediate prey supply was 1 fly every 4th week and the high prey supply was 1 fly every 2nd week.

Since "wild" plant material was used there was considerable

variation in size among the plants at the start of the experiment. To take this variation into account, the rosette size (i.e. length of longest leaf) was measured for each individual at the start of the experiment and used as a covariable in the statistical analysis.

All flowers were pollinated with a soft brush. Seed capsules were harvested successively as they ripened (turned brown and started to open), throughout August. The treatments were repeated until the end of August, by which time most plants had started to senesce. Once the annual plant parts had wilted, in late September, the winter buds were extracted from the soil. For *P. alpina* the perennial roots (cf. Karlsson 1986) were included in the "winter bud" fraction.

Winter buds and seeds were dried at 70 °C and weighed to the nearest 0.01 mg. Seed counts, including up to 10 plants per treatment, were made under a dissecting microscope. A subset of the material was digested in sulphuric acid, and the nitrogen and phosphorus contents were determined using a flow analysis system (FIA-Star, Tecator, Höganäs, Sweden). For small plants, material from two to three individuals was pooled to obtain at least 2 mg of seeds or 5 mg of buds for analysis. Ten bud samples per treatment were analysed, while the seed material was sufficient for 2–5 analyses per treatment. Owing to the low number of replicates and the large number of pooled samples, the total nutrient content of seeds was not calculated.

## Statistical analysis

The effects of soil nutrients and prey were analysed by analysis of variance, with initial plant size as a covariable, using SPSS/PC+ (SPSS Inc, Chicago). For analyses treating bud characteristics, whether or not the plants produced seeds (as a third dimension in the analysis of variance) was also taken into account. In this analysis the three-way interaction term was suppressed. Comparisons among species was made on data normalised by dividing each value by the mean for respective species. Winter bud weight and total content of nitrogen and phosphorus were log<sub>e</sub>-transformed before the analysis, i.e. it was assumed that growth responses were exponential. This transformation also removed differences in variance found among treatments for some of the species. To determine whether the response of flowering frequency to prey was independent of soil nutrient status a hierarchical log-linear analysis was used to test the "reproductive status × nutrient supply × prey supply" effect (SPSS/PC+). The hypothesis that the response to prey diminishes with increasing soil nutrient status can be statistically tested through the prey × nutrient supply interaction term in an analysis of variance. Three types of responses can be recognized using this analysis: (1) The interaction term is significant, with the response to prey being largest at the low nutrient supply level (hypothesis supported). (2) The interaction effect is significant, with the response to prey being largest at the high nutrient supply level (hypothesis rejected). (3) No significant interaction effect, i.e. the response to prey is similar at both nutrient supply levels (hypothesis apparently false, but experimental limitations, e.g. too few replicates or inappropriate treatment levels, could have affected the outcome).

## Results

### Winter bud weight

For *Drosera*, *P. alpina* and *P. villosa* the level of prey supply explained more of the variation in winter bud weight than did nutrient supply, whereas *P. vulgaris* was more responsive to nutrient supply (Fig. 1, Table 1). The response to prey decreased with increasing nutrient supply in *Drosera* and *P. vulgaris* (Table 2), but not in the other two species.

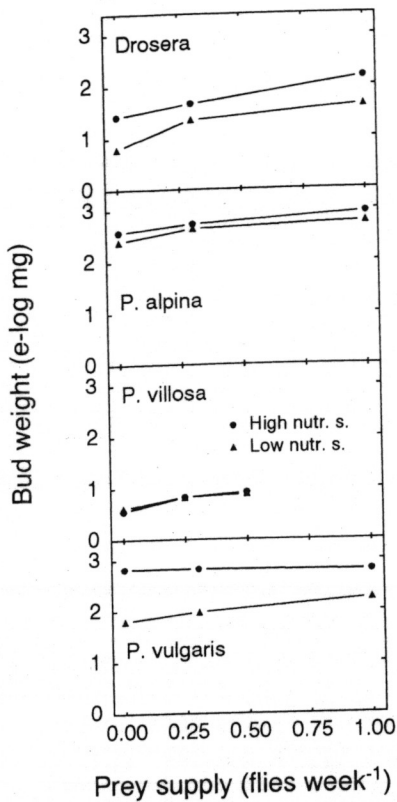


Fig. 1. Weight of the winter bud of four carnivorous plant species supplied with different levels of soil nutrients and prey. Circles and triangles denote high and low nutrient supply respectively.  $n = \text{ca. } 30$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions

#### Nitrogen and phosphorus concentrations in winter buds

In all four species, nitrogen concentration was highest in the high nutrient supply treatment (Fig. 2). For all species prey supply resulted in increased winter bud nitrogen concentrations in plants subjected to the low nutrient supply, but prey had no effect on plants given a high nutrient supply. Bud phosphorus concentrations varied more among species than nitrogen. In *Drosera*, regardless of the nutrient regime, phosphorus concentrations

increased with increasing prey supply. For all *Pinguicula* species the effect of nutrient supply, but not prey supply, was significant (Table 1). Phosphorus concentrations decreased with increasing soil nutrient supply in *P. vulgaris*, whereas they increased in *Drosera* and *P. villosa*.

#### Nitrogen and phosphorus contents of winter buds

Nitrogen and phosphorus pools increased with nutrient supply in all species except *P. alpina*, in which phosphorus content was independent of nutrient supply (Fig. 3). The effect of prey on pool sizes in *Drosera* and *P. vulgaris* was significantly smaller in the high-nutrient treatment than in the low nutrient treatment (Table 2). Nutrient pool size increased with prey supply in all species except for P content of *P. villosa* and *P. vulgaris*. No interaction effect between prey and nutrient supply was found for phosphorus content.

#### Seed production

Differences in flowering frequency were found among treatments for all species except *P. vulgaris* (Fig. 4). In *P. villosa* the proportion of flowering plants decreased with increasing prey supply. *Drosera* and *P. alpina* showed significant differences between nutrient levels, but the response patterns were more complicated and difficult to interpret.

Total seed weight per seed-producing *Drosera* plant increased with increasing prey supply, but was only weakly affected by nutrient supply (Fig. 5, Table 2). Among the *Pinguicula* species, the only significant effect found for total seed weight was that of prey supply for *P. vulgaris*.

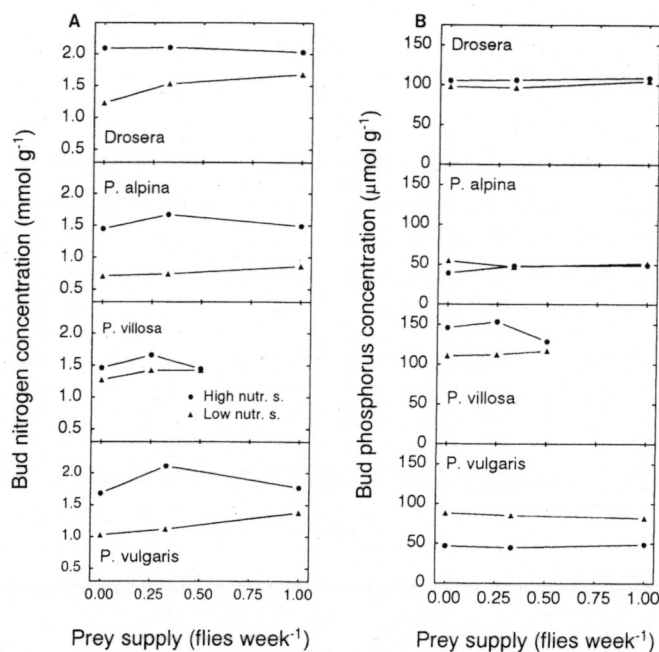
In *Drosera* the average weight per seed increased as the nutrient supply or the prey supply increased (Fig. 6) with the response to prey being highest for plants given the high nutrient supply. For *P. vulgaris* seed weight increased with increasing prey supply at the low-nutrient supply level, whereas the reverse was true for plants

Table 1. Significance levels of main effects of nutrient (N) and prey (P) supply. The number in brackets after each characteristic refers to the figure where the corresponding data are shown. DR: *Drosera rotundifolia*, AL: *Pinguicula alpina*, VI: *P. villosa* and VU: *P. vulgaris*

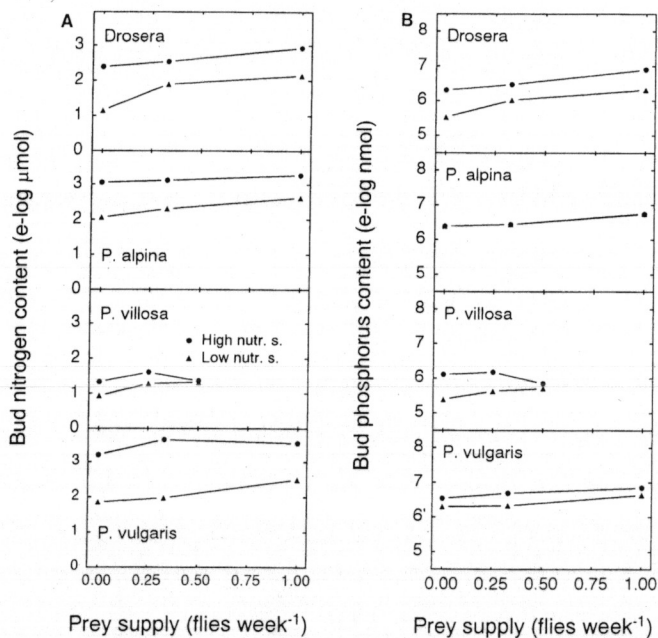
Characteristic	Species							
	DR		AL		VI		VU	
	N	P	N	P	N	P	N	P
But wt (1) <sup>a</sup>	<0.01	<0.01	<0.01	<0.01	>0.3	0.06	<0.01	<0.01
Bud N-conc. (2)	<0.01	<0.01	<0.01	0.16	<0.01	0.01	<0.01	<0.01
Bud P-conc (2)	<0.01	<0.01	0.04	0.19	<0.01	>0.3	<0.01	>0.3
Bud N pool (3) <sup>a</sup>	<0.01	<0.01	<0.01	<0.01	0.32	0.02	<0.01	<0.01
Bud P pool (3) <sup>a</sup>	<0.01	<0.01	>0.3	<0.01	<0.01	0.28	<0.03	0.14
Flowering freq. (4)	<0.01	>0.3	>0.3	>0.3	0.06	>0.3	0.12	>0.3
Total seed wt (5)	0.11	<0.01	>0.3	>0.3	>0.3	>0.3	0.04	>0.3
Seed wt (6)	<0.01	<0.01	0.28	>0.3	>0.3	0.17	<0.01	0.19
Seed number (7)	<0.01	0.10	>0.3	>0.3	>0.3	>0.3	>0.3	>0.3

<sup>a</sup> log<sub>e</sub>-transformed data



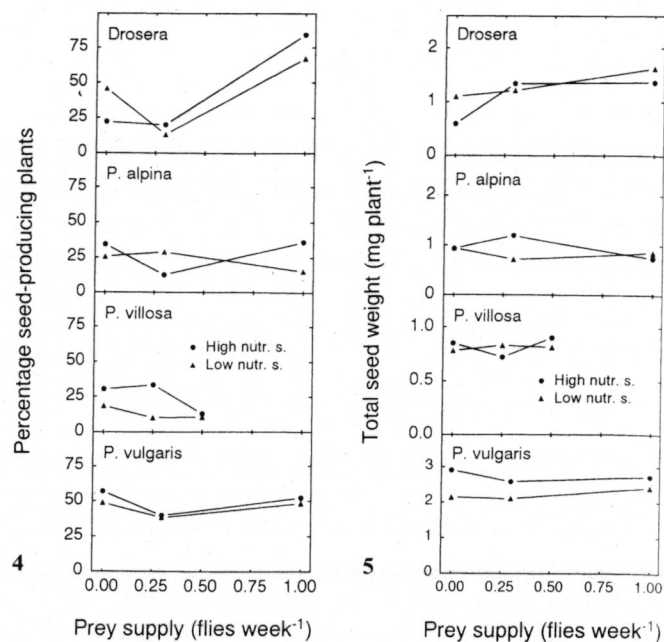


**Fig. 2A, B.** Winter bud nitrogen and phosphorus concentrations in four carnivorous plant species supplied with different levels of soil nutrients and prey.  $n = \text{ca. } 30$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions



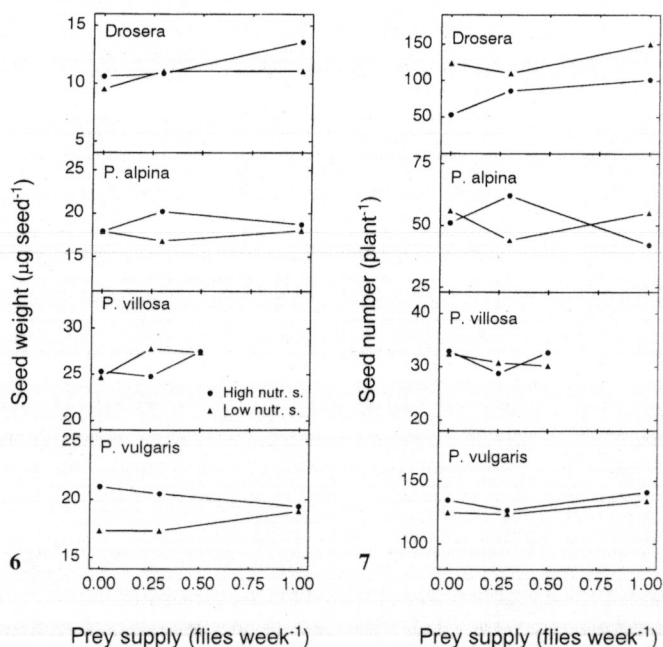
**Fig. 3A, B.** Nitrogen and phosphorus contents of winter buds of four carnivorous plant species supplied with different levels of soil nutrients and prey.  $n = \text{ca. } 30$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions

grown at the high-nutrient supply level. No significant differences in seed weight or seed number were found for *P. alpina* or *P. villosa* (Figs. 6 and 7, Table 1). The number of seeds produced per flowering plant of *Drosera* decreased with nutrient supply and increased with prey supply.



**Fig. 4.** Frequency of seed-producing specimens of four carnivorous plant species supplied with different levels of soil nutrients and prey.  $n = \text{ca. } 30$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions

**Fig. 5.** Seed weight per seed-producing specimens of four carnivorous plant species supplied with different levels of soil nutrients and prey.  $n = 5-25$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions



**Fig. 6.** Average weight per seed of four carnivorous plant species supplied with different levels of soil nutrients and prey.  $n = 5-10$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions

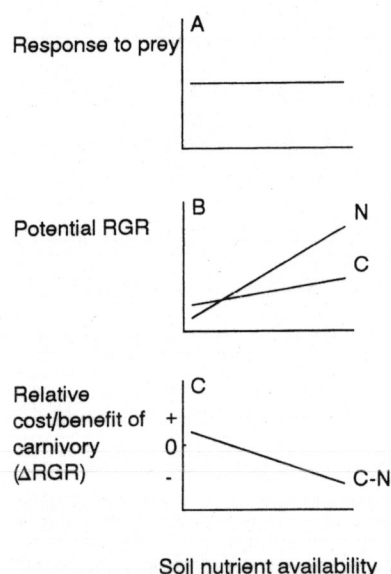
**Fig. 7.** Number of seeds per plant in relation to nutrient and prey supplies for each of four carnivorous plant species.  $n = 5-10$  per treatment. For significance levels see Table 1 for main effects and Table 2 for prey  $\times$  nutrient interactions



**Table 2.** Significance of interaction effects between prey and nutrient supply ( $N \times P$ ) and the interaction effect between species and treatments ( $S \times N \times P$ ). The test was made using analysis of variance, or for flowering frequency, hierarchical log-linear models (see Methods). The number in brackets after each characteristic refers to the figure where the corresponding data are shown.  $-$ : interaction effects where the effect of prey decreases with increasing soil nutrient supply,  $+$ : interaction effects where the effect of prey increases with increasing soil nutrient supply; numbers indicate probability level. NS: no significant interaction effect ( $P > 0.05$ ),  $?$ : significant interaction effect with a complicated response pattern difficult to interpret in relation to the hypothesis. DR: *Drosera rotundifolia*, AL: *Pinguicula alpina*, VI: *P. villosa* and VU: *P. vulgaris*

Characteristic	Species				All	
	DR	AL	VI	VU	$N \times P$	$S \times N \times P$
But wt (1) <sup>1</sup>	-0.03	NS	NS	-0.02	NS	NS
Bud N pool (3) <sup>1</sup>	-0.01	NS	NS	-0.05	NS	NS
Bud P pool (3) <sup>1</sup>	NS	NS	NS	NS	NS	NS
Flowering freq. (4)	? < 0.01	? 0.03	NS	NS		
Total seed wt (5)	NS	NS	NS	NS	NS	NS
Seed wt (6)	+ 0.04	NS	NS	-0.01	NS	0.01
Seed number (7)	NS	NS	NS	NS	NS	NS
Interaction summary					Sum	
negative	2	0	0	3	5	
no difference	3	6	7	4	20	
positive	1	0	0	0	1	

<sup>1</sup>  $\log_e$ -transformed data



**Fig. 8.** A cost/benefit analysis of carnivory where cost is expressed as loss in growth rate (RGR). **A** Assume a carnivorous plant (*C*) in which the gain from carnivory is independent of soil nutrient supply. **B** Owing to the cost of carnivory (production of glands, enzymes, loss of leaf photosynthetic efficiency etc), the carnivorous plant cannot increase its growth to the same degree as a similar non-carnivorous plant (*N*). **C** Thus, the growth rate of the carnivorous plant relative to that of the non-carnivorous ones (*C-N*) decreases with increasing soil nutrient availability

#### Comparisons among species

For all characteristics studied significant differences were found among species in responses to nutrient and prey supply (i.e. species  $\times$  nutrient supply and species  $\times$  prey supply interactions, not shown).

#### Discussion

All four species included in the experiment were able to utilize prey to increase the weight of their winter bud. Concerning the seed characteristics measured, however, only *Drosera* showed any response to prey. This apparent lack of response by the other species may have been due to the design of the experiment, with the treatments lasting for one season only. In the subarctic environment reproductive characteristics may be determined before the start of the actual flowering period (Sørensen 1941). In a more southern environment, Thum (1988) reported that several reproductive characteristics of *D. rotundifolia* were significantly enhanced by supplying prey for one season. Because large *Pinguicula* plants have a higher probability of flowering than smaller ones (B.M. Svensson, B.Å. Carlsson, P.S. Karlsson and K.O. Nordell, in prep.), an increase in the amount of resources stored in the winter buds probably results in a subsequent increase in seed production.

The increase in winter bud size due to prey supply was largest for the two bog species, with the highest levels of prey supply leading to increases in the winter bud weights of *D. rotundifolia* and *P. villosa* of up to 50–100%. The two species from mineral soils, *P. alpina* and *P. vulgaris*, showed smaller increases (0–25%). These comparisons were made using  $\log_e$  transformed data, i.e. assuming exponential growth. If non-transformed data had been used in the statistical analysis four of the “negative interactions” in Table 2 would turn out differently. Two of these would change to non-significant (*Drosera* N pool and *P. vulgaris* bud weight), and the other two would change to “positive” (*Drosera* bud weight and *P. vulgaris* N pool). The total number of “negative” interaction effects would thus decrease to 1, while 3 cases would be “positive” and 22 non-significant with 2 in-

teraction effects significant but complex and difficult to interpret (Table 2).

No relationship between the nutrient status of the original habitat and the ability of these species to respond to nutrients was found, although plants from fertile habitats are commonly more responsive to increases in nutrient supply than plants from nutrient-poor habitats (Chapin 1980). The winter bud weight of one bog species (*Drosera*) and one mineral-soil species (*P. vulgaris*) showed a marked response to soil nutrient supply, whereas no such response was observed in the other two species. It should be noted that *P. alpina*, which grows on the most nutrient-rich substrate and has the largest root system of the *Pinguicula* species (Karlsson 1986), did not gain any additional phosphorus from the increase in soil nutrient supply (Fig. 3). Furthermore, its growth response to an increase in nutrient supply (Fig. 1) was relatively small despite a relatively large gain in nitrogen. The small response may be related to the high pH of the substrate on the *P. alpina* sites (Karlsson 1986), where phosphorus to a large extent is insoluble (cf. Jonasson and Sköld 1983; Jonasson 1986). Prey may thus be the major source of phosphorus in this species. The low phosphorus concentrations in the winter buds (Fig. 2) indicate the phosphorus could be an important limiting factor for *P. alpina*. Differences in soil quality could also explain why our findings differ from those of Aldenius et al. (1983) with regard to the response of *P. vulgaris* to prey in relation to soil nutrient supply. The *P. vulgaris* plants used by Aldenius et al. (1983), which showed no signs of a diminishing response to prey as the soil nutrient content was increased, originated from a site with a relatively high pH (ca. 5.7), whereas in our study this species grew in a more acidic soil (pH ca. 3.9). Apparently, *P. vulgaris* plants grown at low nutrient supply levels were not limited by phosphorus, since the concentration of this element decreased when the plants were supplied with a more concentrated nutrient solution.

Although the two bog species were more responsive to prey supply than the two species from mineral soils, the intraspecific responses to manipulations of soil nutrient and prey supplies show that the pattern is more complex. In one-fifth of the comparisons the response to prey decreased when soil nutrient availability was increased, supporting the hypothesis of Givnish et al. (1984). In most cases soil nutrient levels did not have any significant effect on the response to prey (Table 2). Although the lack of interaction in the majority of the tests could have been due to experimental limitations, this finding indicates that the plants respond to prey even when supplied with soil nutrients at relatively high concentrations. Since soil nutrient status is a very complex characteristic the plants in our experiment may even have experienced deficiencies of certain nutrients at the high nutrient supply. It is apparent that the effect of soil nutrient supply on response to prey supply varied among the four species studied, as well as among the characteristics measured.

The cost/benefit model presented by Givnish et al. (1984) predicts that carnivorous plants should be restricted to nutrient-poor habitats owing to the high costs

associated with carnivory. The currency that is optimized in their model is photosynthetic income. The net profit, i.e. photosynthetic income minus the costs of trapping prey, is predicted to decrease with increasing soil nutrient availability. This experiment does not provide any support for the model. The response to prey seems to be independent of soil nutrient status, with differences in response patterns occurring among plant characteristics and species. It should be possible, however, to modify the model so that it applies to a situation where response to prey is independent of soil nutrient status. We suggest, therefore, that the cost of carnivory should be expressed as a reduction in potential growth rate, using similar non-carnivorous plant species as a reference (cf. Grime 1979; Fagerström 1989). Although it would still be assumed that the carnivorous habit reduces the potential growth rate of these plants, the response to prey would be considered to be independent of soil nutrient status (Fig. 8A). Owing to the cost of carnivory these plants cannot increase their growth rate to the same degree as other coexisting species in response to an increase in soil nutrient availability (Fig. 8B). The competitive ability, in terms of relative growth rate, thus decreases compared to similar non-carnivorous plants as the soil nutrient status improves (Fig. 8C). With this modification the model will allow for the occurrence of carnivorous plants on rich soils, such as *Pinguicula alpina*, provided that few non-carnivorous competitors are present.

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