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Effects of supplementary feeding on growth and reproduction of three carnivorous plant species in a subarctic environment

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Summary

1 The effect of supplementary feeding on growth and reproduction of three carnivorous plants species was investigated over a 6-year period. *Pinguicula alpina*, *P. villosa* and *P. vulgaris* populations growing at two altitudes in a subarctic environment were fed with fruit flies (*Drosophila melanogaster*).

2 Fed plants increased in size relative to control plants during the first years. Subsequently a stable size difference between feeding levels was established. The weight of the over-wintering part was higher in fed plants than in control plants.

3 The flowering frequency (i.e. proportion of plants in a population carrying flowers) was also higher in the fed plants. The proportion of flowering plants increased in the feeding treatment compared to control plants during more-or-less the whole experimental feeding period (5–6 years). Seed production also increased slowly in response to feeding.

4 No feeding effect on nitrogen and phosphorus concentrations in seeds and over-wintering parts was found.

5 In most characteristics the high-altitude populations were less responsive than populations growing at low altitude. In the high-altitude population reproduction failed repeatedly, suggesting that seed output may be more dependent on abiotic factors than on resource availability in cold environments.

6 *Pinguicula villosa* and *P. vulgaris* used the new resources the same summer for increased leaf rosette growth and current reproduction, showing these species to be income breeders, while the third species (*P. alpina*) allocated a larger proportion to storage and future reproduction, characteristic of a capital breeder.

Keywords: capital breeder, carnivorous plant, income breeder, nutrients, *Pinguicula*, resource allocation

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Introduction

Carnivorous plants live predominantly in sunny, moist and, above all, nutrient-poor environments (Givnish *et al.* 1984). They have evolved the ability to trap, digest and utilize the nutrients in animals (mostly insects) (Darwin 1875; Heslop-Harrison 1978; Lüttge 1983; Givnish 1989; Juniper *et al.* 1989). It is well known that carnivorous plants respond to prey capture by increased growth and reproduction (e.g. Darwin 1878; Kellerman & Raumer 1878; Chandler & Anderson 1976; Aldenius *et al.* 1983). Most experiments on the benefits of prey capture have been performed under conditions in which the natural prey have been excluded (Aldenius *et al.* 1983; Wilson 1985; Gibson 1991; Karlsson *et al.* 1991; Krafft & Handel 1991; Chapin & Pastor 1995). Only rarely have feeding experiments been carried out *in situ* with the natural capture of prey as a 'background' condition (Thum 1988; Schulze & Schulze 1990; Karlsson & Pate 1992) and, to our knowledge, no such experiment has been extended over several years.

In situ experiments with supplementary feeding

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over several years may reveal important insights as to the benefits to plants of prey capture.

1 Whether carnivorous plants are efficient enough to satiate their requirements or would benefit from additional prey capture may vary with the habitat conditions of the plant. We expect that when nutrient availability limits plant performance, supplemental feeding will be beneficial. However, when environmental conditions other than nutrient availability limit plant performance, prey capture becomes less important, and this may be the case among high-altitude populations in the subarctic, where climate may restrict growth and reproduction more severely than nutrient acquisition.

2 If these plants benefit from supplementary feeding, how do they use these additional resources? Growth and reproduction could be increased in equal proportions, or the plants might favour one function over the other or storage might increase.

3 Does allocation to growth and reproduction respond to an increased resource level similarly over time, or do differences result in the relative allocations of additional resources varying over time? In arctic plants reproductive parts are often initiated one or more years before a reproductive event (Sørensen 1941) and a reproductive response to feeding may thus be hypothesized to show a longer time lag than a growth response. Furthermore, reproductive investment in an individual may be increased either by more frequent reproductive events (which is seen in an increased proportion of the population being reproductive in a given year) and/or a higher reproductive effort, or larger seed output, on the part of those individuals that produce seeds.

To answer these questions, we increased prey capture, and thus resource availability, by supplementary feeding for three *Pinguicula* species growing at two elevations in a subarctic area. We fed the plants with prey over 6 years and recorded plant size, flowering and seed production each year.

Materials and methods

PLANT MATERIAL

The genus *Pinguicula* is represented in northern Scandinavia by three species, *P. alpina* L., *P. villosa* L. and *P. vulgaris* L. All three are herbaceous, iteroparous geophytes with a simple morphology (Heide 1912; Slack 1979; Karlsson 1986). During late summer a winter resting bud (hibernaculum) is formed and this is the only somatic part that survives the winter (apart from the roots in *P. alpina*). All members of the genus are carnivorous, from which they are known benefit by increased growth (Aldenius *et al.* 1983; Karlsson *et al.* 1987, 1991; Thorén *et al.* 1996). However, species differ, for instance in morphology, phenology, reproductive system, habitat selection and allocation patterns (Karlsson 1986; Molau 1993), as well as in their success as carnivores (Karlsson *et al.* 1994). In natural populations only a fraction of the plants flower during a given year (Svensson *et al.* 1993). In the same area as this study was performed, the population half-life was found to be 1.9 years for *P. villosa* and 7.5 years for *P. alpina* and *P. vulgaris* (Svensson *et al.* 1993).

STUDY SITES

The experiment was carried out near the Abisko Scientific Research Station, northern Sweden (68°21′N, 18°49′E). Two populations of each of *P. alpina* and *P. vulgaris* were chosen, one at low and one at high altitude. The low altitude population of each species was in a subalpine heath at approximately 400 m altitude in the Abisko valley, whereas the high altitude populations were in an alpine meadow at approximately 800 m altitude on Mount Njulla. The soils at the low altitude sites were drier and more subject to frost-heaving than at the higher altitude. The *P. alpina* populations grew on calcareous soils more subject to frost-heaving, while the *P. vulgaris* populations tended grow on more stable soils, ranging from ombrotrophic to calcareous. Since *P. villosa* is not found at high altitudes in this area, only one population, growing in a nutrient-poor *Sphagnum fuscum* (Schimp.) Klinggr. carpet at low altitude (approximately 400 m), was included in the study.

EXPERIMENTAL DESIGN

In early July 1989, 240 adult plants of each population were selected and randomly split into two groups (120 plants each) which were assigned to fed or unfed (control) treatments. Any plant equal in size to or larger than the smallest reproductive individual found was considered adult (Karlsson 1988). Our studied plants were thus larger and had a higher proportion of flowering individuals than the overall natural populations.

Each year from 1989 to 1994 the plants assigned to the feeding treatment received a period of supplementary feeding with fruit flies (*Drosophila melanogaster*) that had been killed by freezing. This consisted of two flies per plant per week, starting in mid-June for 4 weeks for *P. alpina* and *P. vulgaris* and for 2 weeks for *P. villosa*. This relatively short period of intensive feeding was chosen to mimic the natural pattern of prey capture (Karlsson *et al.* 1994). The mean dry weight of a *Drosophila* fly was approximately 200 μg and the total seasonal feeding supplement was thus 1600 μg for *P. alpina* and *P. vulgaris*, and 800 μg for *P. villosa*. These amounts correspond to an approximately five-, three- and 10-fold increase in captured mass per season for *P. alpina*, *P. vulgaris* and *P. villosa*, respectively (cf. Karlsson *et al.* 1994). The actual increase might have been lower due to prey-robbery by ants, which is common for other

Pinguicula species (Zamora 1990, 1995) and was observed to occur in Abisko in the course of the present study.

To study the effects of a reduced prey capture by reverting back to natural rates, feeding was discontinued in 1993 and 1994 for 20 plants in each of the *P. alpina* and *P. vulgaris* populations.

For each plant in the experimental populations, flowering was recorded and plant size was measured in late July each year when plants had reached their maximum size (c.f. Karlsson 1986). The number of leaves in the rosette multiplied by the length of the longest leaf served as an index of plant size or rosette size (Svensson *et al.* 1993). Each year seeds and seed capsules were harvested when the seeds were ripe, i.e. when the seed capsule turned brown. Twenty plants from each treatment in each population were harvested in 1993 and the rest in 1994. The somatic parts (winter resting buds, and roots for *P. alpina*) were collected when all leaves were dead in late September in 1993 and 1994. The seeds and winter resting buds were dried at 70 °C and weighed. Seeds and winter buds infected by fungi and seeds that contained no or little endosperm were excluded. A randomly chosen subset of the material (10 samples per group and part) was digested in sulphuric acid, and nitrogen and phosphorus content were determined using a flow analysis system (FIA-Star 5012 Analyser, Tecator, Höganäs, Sweden).

DATA ANALYSIS

The various plant response variables were analysed using four-way analysis of variance. The following four factors were included in the model: feeding, species, habitat type (high and low altitude) and year. When analysing the variation in plant rosette size a repeated measures design was used with year as the within-subject factor. The other factors were considered as fixed factors. When analysing reproductive characteristics (flowering frequency and seed production) year was considered as a standard fixed factor since the specific plant individuals that were reproductive varied between years. The analysis of flowering frequency was based on the proportion reproductive in each population, and since only one value per population and year was available three-way and higher interactions were suppressed. Since failed seed production in some populations during some years resulted in several empty cells in this data set, three-way and higher interactions were also suppressed.

Since one of the species, *P. villosa*, was not present at high altitude, we chose to include the two species present at both altitudes in the main model, while the responses of *P. villosa* were analysed separately in a two-way ANOVA model with feeding and year as factors. As for the analysis of the other species, rosette size was analysed using a repeated measures design.

Although the data did not show homogeneous variances, we obtained the same significance patterns when performing the tests using rank-transformed data (Conocer & Iman 1981) or permutation tests (Manly 1997). Thus we concluded that the GLM method used to compute the ANOVA in these cases was robust enough to provide reliable results despite the deviations from its assumptions. All statistical analysis were performed using the GLM procedure of SPSS 7.0 (SPSS Inc., Chicago, USA)

Results

SIZE OF LEAF ROSETTE AND WINTER RESTING BUD

Supplementary feeding caused an increase in plant size in all species (Fig. 1; feeding main effect Table 1). The effect on plant size was slightly more pronounced for *P. vulgaris* than for *P. alpina*, resulting in a feeding × species interaction (Table 1). The effect of feeding on plant size did not vary between altitudes. However, the effect of feeding changed with time and this interaction was due to the fact that fed plants successively increased in size relative to controls but only during the first 2 years (Fig. 1 and Table 1). Running the same model for only the years 1991–94 removed both the interaction effects, including feeding and year, that were significant in the full model (i.e. F × Y and F × S × A × Y) ($P \geqslant 0.271$; data not shown). Thus, by the third year (1991) a stable size difference had been established between fed and non-fed plants for both populations of the two species (Fig. 1). The effect of feeding on growth of *P. villosa* ($P = 0.013$) also showed an interaction between year and feeding ($P = 0.050$), but a stable size difference was reached after only one season. In a model including the years 1990–94 the interaction effect between feeding and year was non-significant ($P = 0.720$).

The dry weight of winter resting buds also increased in all species (Fig. 2; feeding main effects Table 1; for *P. villosa* $P = 0.011$). Significant differences were observed between feeding levels, species and altitudes (Table 1). Feeding had a larger effect on the winter resting bud of *P. alpina* than of *P. vulgaris*.

When the supplementary feeding was discontinued both rosettes and winter resting buds decreased in size for both species. The reduction in rosette size was larger for *P. alpina* than for *P. vulgaris* but the reduction in winter resting buds was larger for *P. vulgaris* than for *P. alpina*.

FLOWERING FREQUENCY AND SEED PRODUCTION

The feeding treatment caused, with one exception, an increase in flowering frequency (or prevented a decline in the case of *P. villosa*) (Fig. 3 and Table 2). This increase in flowering frequency was higher in *P. vul-*

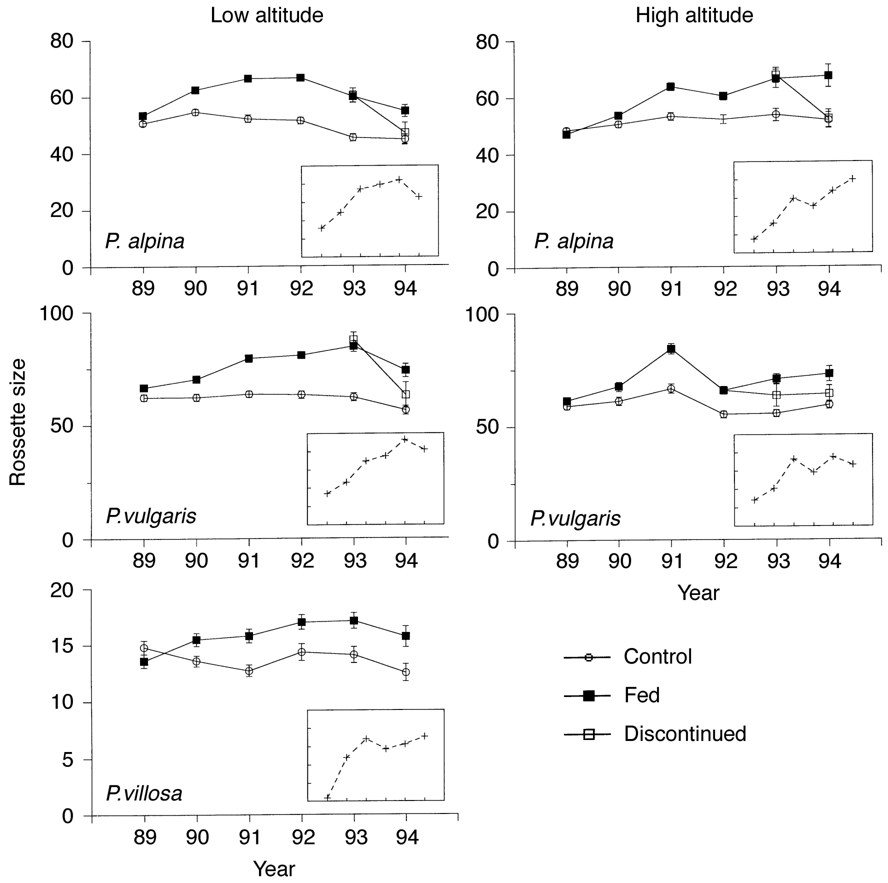

Fig. 1 Rosette size of low- and high-altitude populations of three *Pinguicula* species: plants supplied with supplementary feeding with prey, control plants receiving their natural prey capture only, and plants initially supplied with supplementary feeding but where the feeding was discontinued in 1993. Supplementary feeding was initiated in 1989. Rosette size was calculated as the number of leaves in the rosette multiplied by the length of the longest leaf. Error bars indicate the standard error of rosette size. Inset shows the relative effect of feeding on size (relative size = (fed – control)/control and axis range is from −0.1 to 0.4). The corresponding statistical analysis is shown in Table 1.

Table 1 The effect on rosette size, winter resting bud weight and seed output of feeding (Fed, Control), species (*P. alpina*, *P. vulgaris*), altitude (Low, High) and year (1989–94) using ANOVA. Mean values and standard error are shown in Figs 1, 2 and 4. Rosette size was analysed using a repeated measures ANOVA and degrees of freedom were 5 and 1440 for tests involving year and 1 and 288 for all others. Winter resting bud weight was analysed using a four-way ANOVA and degrees of freedom were 1 and 514 in all cases. Seed output was analysed using a four-way ANOVA and error degrees of freedom were 746. Due to no seed production in some cases (cf. Figure 4) all interactions higher then two-ways have been suppressed

	Rosette size	Winter resting bud	Seed output	
	P	*P*	d.f.	*P*
Feeding	< 0.001	< 0.001	1	< 0.001
Species	< 0.001	< 0.001	1	< 0.001
Altitude	0.037	< 0.001	1	< 0.001
Year	< 0.001	0.228	5	< 0.001
F × S	0.049	0.009	1	0.435
F × A	0.134	0.254	1	0.008
F × Y	< 0.001	0.703	5	< 0.001
S × A	< 0.071	0.747	1	< 0.001
S × Y	0.112	0.858	5	< 0.001
A × Y	< 0.001	0.523	4	< 0.001
F × S × A	0.726	0.661		
F × S × Y	0.745	0.889		
F × A × Y	0.249	0.665		
S × A × Y	< 0.001	0.046		
F × S × A × Y	0.036	0.259		

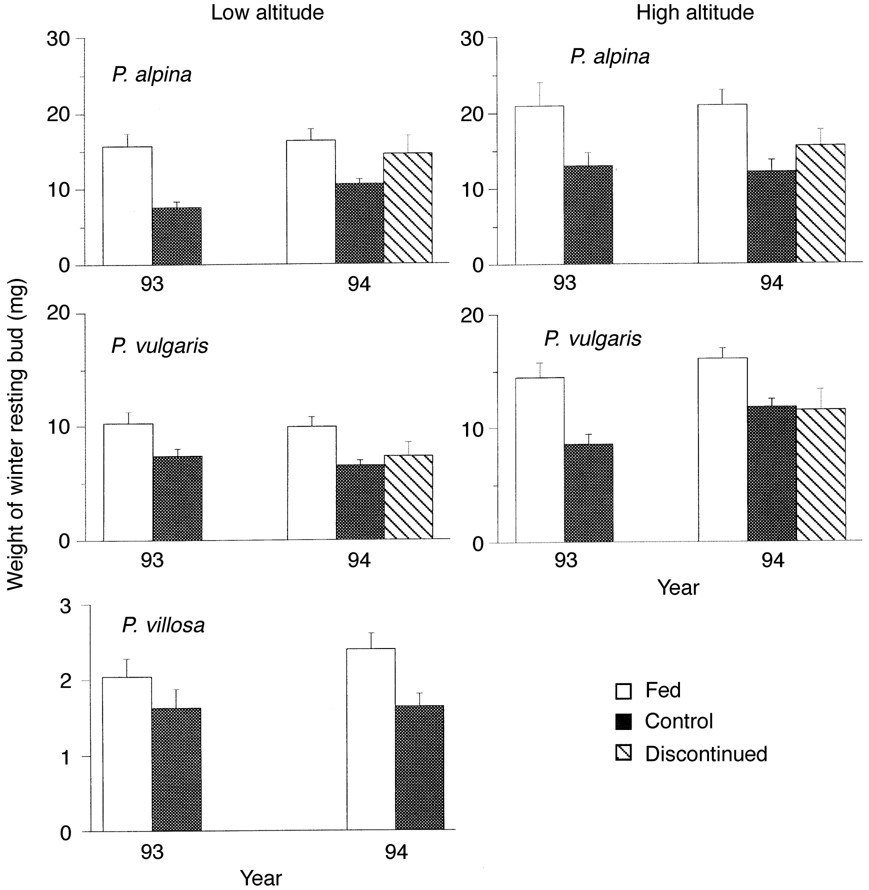

Fig. 2 Effect of feeding on weight of winter resting buds of low- and high-altitude populations of three *Pinguicula* species. The perennial roots of *P. alpina* are included in the weight of the winter resting bud. Supplementary feeding was initiated in 1989. Error bars indicate the standard error of the weight of winter resting bud. The corresponding statistical analysis is given in Table 1.

garis (where it was most marked at low altitude) than in *P. alpina*. The high-altitude *P. alpina* population, however, showed a relatively stable difference between feeding treatments over the duration of the experiment, suggesting that the higher reproductive frequency of fed, high-altitude *P. alpina* plants was an accidental effect of random assignment of the feeding treatment rather than an effect of the feeding itself. This lack of response in combination with a higher flowering frequency in fed plants is the major cause for several of the significant interaction effects. In 1992 all flowers in the *P. alpina* high altitude population died before opening (Fig. 3).

The feeding treatment caused an increase in seed weight per plant in the *P. vulgaris* low-altitude population and in both *P. alpina* populations, but neither the *P. vulgaris* high-altitude population nor the *P. villosa* population showed this response (Fig. 4 and Table 1; for *P. villosa* $P = 0.323$). The *P. vulgaris* high-altitude population failed to produce mature seeds during 3 of the 6 years of the study (Fig. 4). This was probably due to low temperatures at the end of the growing season.

NITROGEN AND PHOSPHORUS

Although there were large differences in nitrogen and phosphorus concentration between species and altitudes, concentrations in winter resting buds and seeds were unchanged by feeding (Tables 3 and 4; statistics not shown). The total nutrient pools in these compartments were proportional to their mass.

Discussion

We manipulated resource availability for three *Pinguicula* species and measured effects on growth and reproduction. All three species were limited by the amount of prey they captured. For all the species and populations there was an increase in growth, as indicated by rosette and winter resting bud size as well as reproduction, through an increase in flowering frequency and/or seed production. Nutrient concentrations of winter buds and seeds did not change as a result of feeding, suggesting that growth and reproduction increase in proportion to increased nutrient availability. Environmental factors such as

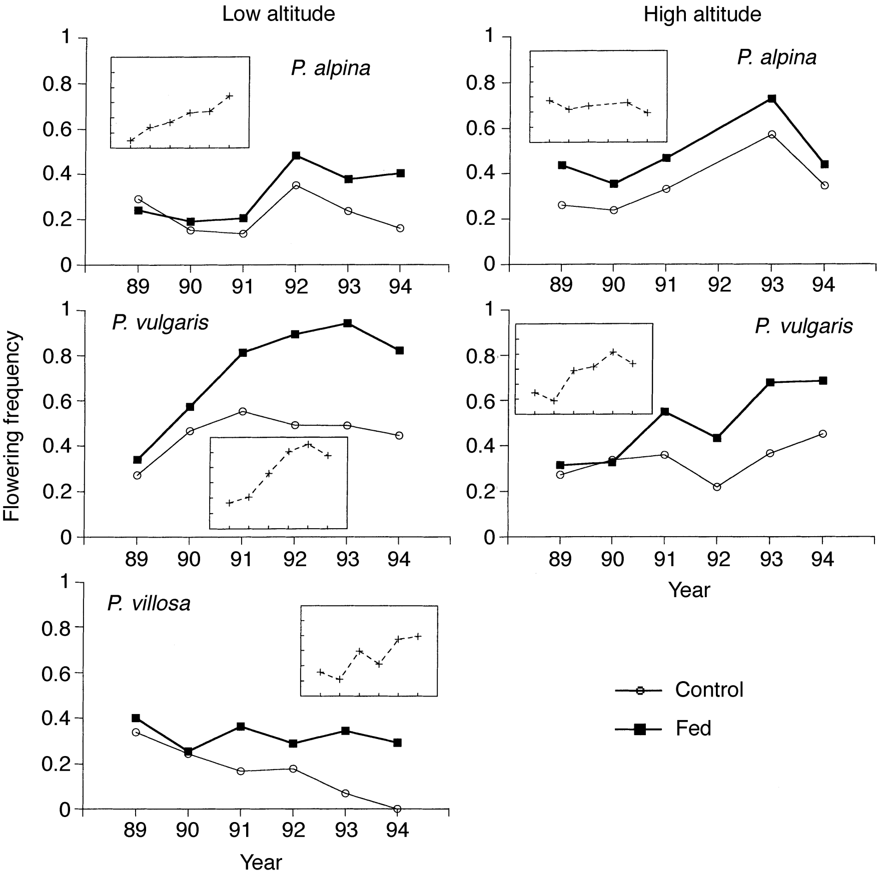

Fig. 3 Effect of feeding on flowering frequencies of low- and high-altitude populations of three *Pinguicula* species. No flowers were observed in the *P. alpina* high-altitude population in 1992, probably due to abiotic factors. Inset figure shows the relative effect of feeding on flowering frequency (relative flowering frequency = flowering frequency of fed minus that of control and axis range is from –0.1 to 0.5). The corresponding statistical analysis is shown in Table 2.

Table 2 The effect on flowering frequencies of feeding (Fed, Control), species (*P. alpina*, *P. villosa* and *P. vulgaris*), altitude (low and high) and year (1990–94) using ANOVA (values in Fig. 3). Error degrees of freedom are 5. Interactions higher than two-ways were suppressed

	d.f.	*P*
Feeding	1	< 0.001
Species	2	< 0.001
Altitude	1	0.067
Year	5	0.004
F × S	2	0.086
F × A	1	0.355
F × Y	5	0.047
S × A	1	< 0.001
S × Y	10	0.002
A × Y	5	< 0.001

water and light seem not to be limited in these species. A similar result with increased plant size but no increase in nutrient concentration has been found in other studies (e.g. Karlsson & Pate 1992; Thorén *et al.* 1996). Schulze & Schulze (1990) found an increase in nitrogen concentration, although it was relatively low compared with the increase in biomass. These carnivorous plants clearly benefit from additional prey capture, implying that their natural capture rate is not sufficient to fulfil their nutrient requirements. Previous *in situ* feeding experiments on carnivorous plants over a single season have found beneficial effects (Thum 1988; Schulze & Schulze 1990; Karlsson & Pate 1992), while Thum (1988) and Karlsson & Pate (1992) found an increase in reproduction. These two experiments were performed on *Drosera* species in warmer climates. The reproductive response to feeding is probably slower in the short, cool subarctic summer, although *Pinguicula* species may also be slower in their response than *Drosera*.

The *Pinguicula* species in this study differed in their responses to supplementary feeding (Table 5). At low altitude the rosette size increased relatively more in *P. vulgaris* than in *P. alpina*, although an opposite pattern was found for the winter resting bud. The winter bud of *P. alpina* (including the perennial roots of this species) was more responsive to feeding than that of *P. vulgaris* or *P. villosa*. Thus, *P. vulgaris* and *P. villosa* appear to preferentially allocate their new resources to increased rosette size, while *P. alpina* gives priority to allocation to roots and/or storage. This was confirmed when the supplementary feeding was discontinued, since the reduction in rosette size

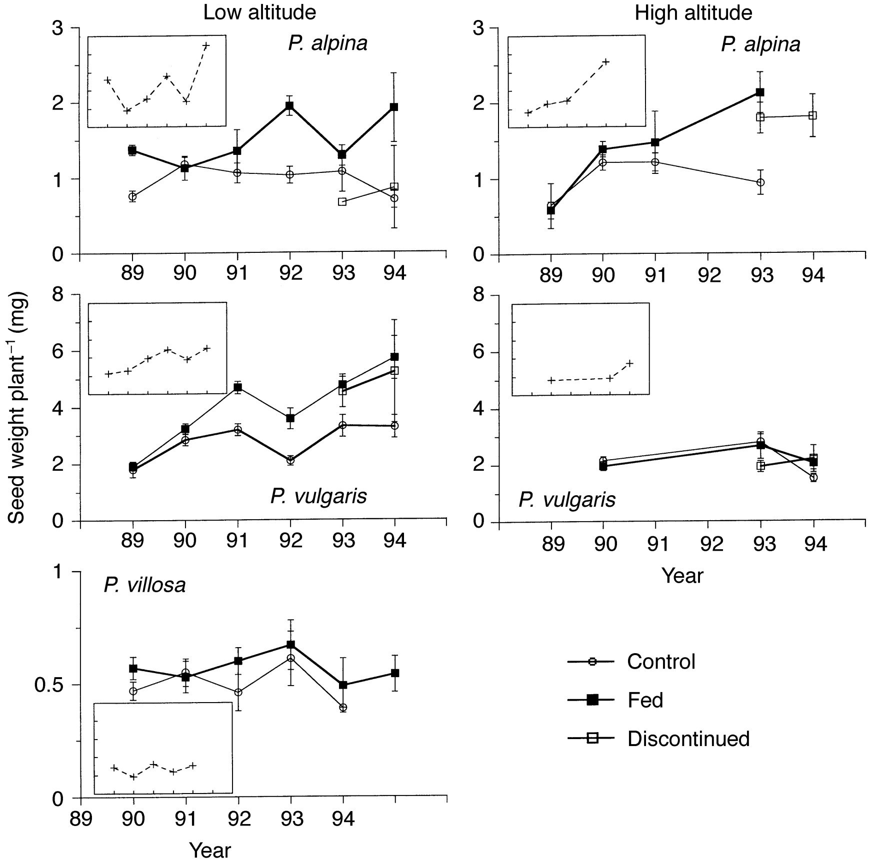

Fig. 4 The effect of feeding on seed weight per plant of low- and high-altitude populations of three *Pinguicula* species. Error bars indicate the standard error of the weight of seeds per plant. Inset figure shows the relative effect of feeding on seed weight per plant (relative seed weight = (fed – control)/control and axis range is from −0.5 to 2.0). The corresponding statistical analysis is shown in Table 1.

Table 3 Concentration of nitrogen (N) and phosphorus (P) (mg g^{-1}) in winter resting buds of fed, control and feeding-discontinued plants in *Pinguicula villosa, P. alpina* and *P. vulgaris* in low-altitude and high-altitude populations. The upper value is nitrogen and the lower value phosphorus. Mean values ± standard error

		1993		1994		
		Fed	Control	Fed	Control	Discontinued
P. villosa	N	26.9 ± 0.8	26.3 ± 1.4	25.4 ± 1.4	21.2 ± 0.8	–
	P	8.8 ± 1.1	10.7 ± 1.2	3.9 ± 0.2	3.5 ± 0.2	–
P. alpina						
Low	N	13.4 ± 0.7	12.6 ± 0.4	11.4 ± 0.4	9.9 ± 0.6	10.8 ± 0.7
	P	2.4 ± 0.4	2.4 ± 0.4	1.1 ± 0.1	0.9 ± 0.1	1.0 ± 0.1
P. alpina						
High	N	17.6 ± 0.9	17.8 ± 0.5	16.5 ± 0.8	17.6 ± 0.9	15.2 ± 1.1
	P	1.9 ± 0.2	1.8 ± 0.1	1.7 ± 0.1	1.4 ± 0.0	1.4 ± 0.1
P.vulgaris						
Low	N	22.2 ± 0.6	19.7 ± 0.8	21.0 ± 0.5	18.7 ± 0.9	19.3 ± 0.7
	P	5.7 ± 0.5	5.0 ± 0.4	3.7 ± 0.6	3.0 ± 0.2	3.1 ± 0.2
P.vulgaris						
High	N	17.4 ± 0.4	15.7 ± 0.9	21.8 ± 0.8	21.2 ± 0.9	21.1 ± 1.1
	P	1.4 ± 0.3	1.7 ± 0.3	2.2 ± 0.1	2.2 ± 0.1	2.0 ± 0.1

was larger for *P. alpina* than for *P. vulgaris*, whereas the reduction in winter resting bud was larger for *P. vulgaris*. Additional resources are to a large extent lost to *P. vulgaris* at the end of the growing season, whereas the gains from additional feeding diminish more slowly in *P. alpina*. It may be that the perennial root system in this species (Karlsson 1986) is an important characteristic that enables this behaviour.

Table 4 Concentration of nitrogen (N) and phosphorus (P) (mg g^{-1}) in seeds of fed, control and feeding-discontinued plants in *Pinguicula villosa, P. alpina* and *P. vulgaris* in low-altitude and high-altitude populations. The upper value is nitrogen and the lower value phosphorus. Missing values are due to no seed production and no standard error is due to single values. Mean values ± standard error

		1993			1994		
		Fed	Control	Discontinued	Fed	Control	Discontinued
P. villosa	N	70.6±8.1	–	–	36.2±6.0	–	–
	P	12.4±1.6	–	–	10.1±1.7	–	–
P. alpina							
Low	N	38.1±4.5	59.2±9.9	–	35.7±1.1	39.2±3.9	23.9
	P	7.9±2.0	10.0±2.0	–	5.3±0.3	7.1±1.7	3.5
P. alpina							
High	N	33.0±2.5	39.5±2.9	34.5±1.5	–	–	31.2±0.8
	P	12.5±2.7	11.9±3.2	8.2±1.4	–	–	4.4±0.2
P.vulgaris							
Low	N	33.4±3.2	38.9±2.7	47.2±1.7	42.6±0.9	40.6±0.7	39.8
	P	5.4±0.4	6.2±0.6	7.3±0.7	7.3±0.3	6.6±0.1	6.3
P.vulgaris							
High	N	34.3±1.5	32.2±2.1	31.4±3.9	29.9±2.0	26.9±1.6	27.6±2.5
	P	8.2±1.6	8.6±2.1	6.3±0.6	4.7±0.4	5.2±0.5	4.7±0.3

Table 5 Relative effect of supplemental feeding (increase due to feeding as percentage of control). Values were calculated from means from 1993 and 1994 when the change due to feeding had presumably stabilized. Relative effect on flowering frequency was calculated as frequency for fed plants minus frequency for control plants

		Relative effect of supplemental feeding (increase due to feeding as percentage of control)			
Species	Altitude	Rosette size	Winter bud	Flower frequency	Seed weight
P. alpina	Low	27	82	19	96
	High	27	67	0*	127
P. vulgaris	Low	34	46	41	59
	High	26	52	27	15
P. villosa	Low	23	36	28	26

*For the feeding effect on flowering frequency for high-altitude *P. alpina* see the Results.

The species also differed markedly in the effects of supplementary feeding on reproduction. *Pinguicula alpina* showed a minor increase in flowering frequency but a major increase in seed production, whereas *P. vulgaris* showed a major increase in flowering frequency but seed production increased only in the low altitude population. Under natural conditions, *P. alpina* has the highest frequency of flowering among these three species (Svensson *et al.* 1993) although our results may differ from theirs because we selected plants of a minimum size rather than studying all plants in an area. *Pinguicula alpina* thus seems to have the strategy of flowering often, although the seed output of flowering individuals is strongly resource limited. The other two species flower less frequently and their more marked increase in flower production from supplementary feeding indicates that they have a higher resource economical threshold to begin flowering. Once flowering has begun, additional resources have a relatively small effect on seed set. In *P. vulgaris*, flower initiation does not seem to be resource dependent, since flower primordia can be found in almost all expanding buds in the early summer, although only a fraction of the plants ultimately flower (R. L. Eckstein and P. S. Karlsson, personal observations).

Pinguicula alpina can therefore be described as a capital breeder, relying mainly upon stored resources to begin reproduction (Stearns 1992; Jönsson 1997). On the other hand, *P. villosa* and *P. vulgaris* can be described as income breeders, were the decision whether to reproduce is based on current income. A capital breeder does not have to rely on the current year's 'income' and can therefore start to reproduce earlier and this may explain why *P. alpina* can flower earlier in the season than the other two species (Molau 1993). In environments with a short growing season, such as the high-altitude site in this study, an early start to reproduction lessens the risk of failing to produce mature seeds, as we found for *P. alpina* compared to *P. vulgaris* (Fig. 4). There is, however, a risk of flower loss early in the season due to abiotic factors, and of a lower pollination rate due to a lack of active pollinators (Molau 1993). If the risk of losing either flowers or seeds is high, selection might be expected to favour early reproduction as flowers alone represent a much smaller resource investment than both seeds and flowers.

Although populations at both altitudes increased in growth due to supplementary feeding, the response was somewhat more pronounced in the low- than in the high-altitude populations. Similarly, flowering frequency and seed weight increased more in the low-altitude population (Table 5). *Pinguicula alpina* is apparently better adapted to high altitude conditions. It starts flowering earlier than *P. vulgaris* (late June vs. early July; Molau 1993) and its seeds are usually ripe by the end of August, whereas *P. vulgaris* seeds have often not matured by mid-September when snow begins to fall (L. M. Thorén, personal observation). As we hypothesized, at higher altitudes or in colder environments, reproductive output seems more dependent on abiotic factors such as climate, than on resource availability. A longer or warmer growing season would give the seeds time to mature, and so a higher frequency of warmer growing seasons might be expected to lead to a higher reproductive output for *P. vulgaris* at high altitude.

A stable size difference was established between fed and non-fed plants after the first 1 or 2 years. Reproductive investment, however, increased more slowly and we cannot draw any firm conclusions as to whether the full effect on flowering frequency had been observed by the time the experiment was ended after six seasons. Therefore, it is not surprising that vegetation responses to experimental or global environment change may take a very long time to become apparent in the northern ecosystems (cf. Chapin *et al.* 1995).

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