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# Nitrogen uptake from prey and substrate as affected by prey capture level and plant reproductive status in four carnivorous plant species

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**Abstract** Uptake of nitrogen from prey and substrate and partitioning of prey-derived nitrogen were studied in the carnivorous plant species *Pinguicula alpina, P. villosa*, *P. vulgaris* and *Drosera rotundifolia* in a subarctic environment. Efficiency in nitrogen uptake from prey was evaluated by tracing $^{15}N$ from $^{15}N$-enriched *Drosophila* flies fed to the plants. The *in situ* uptake efficiency differed somewhat between species and ranged from 29 to 41% of prey N. This efficiency was not affected by different feeding levels or plant reproductive status (flowering or non-flowering). A test of the amount of N absorbed from prey caught on flower stalks of *Pinguicula villosa* and *P. vulgaris* showed that both species took up little of what was available in prey (2.5% or less). The uptake efficiency found in greenhouse grown plants was higher than in plants *in situ* (40–50% vs. 30–40% respectively). This could probably best be explained by the absence of rain and a higher temperature in the greenhouse. The prey-derived $^{15}N$ was traced to reproductive organs and winter buds. Non-flowering individuals allocated 58–97% of the N derived from prey to their winter buds. Flowering individuals allocated 17–43% of the N income from prey to reproduction, while 34–71% were allocated to buds. Root uptake of nitrogen was stimulated by increased prey capture. This increase in uptake of nitrogen from the substrate was larger than the potential direct uptake of nitrogen from captured prey.

**Key words** Carnivorous plants · Nitrogen uptake · $^{15}N$ · *Pinguicula* · *Drosera*

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## Introduction

From experimental feeding studies, it is well known that carnivorous plants benefit from the capture of prey (Aldenius et al. 1983; Thum 1988; Karlsson and Pate 1992). This benefit is generally believed to be an effect of mineral nutrient uptake from prey, mainly of nitrogen and phosphorus (Chandler and Anderson 1976; Aldenius et al. 1983; Karlsson and Carlsson 1984; Karlsson and Pate 1992). Although there are studies on natural prey capture in some carnivorous plants (Dixon et al. 1980; Watson et al. 1982; Thum 1986; Zamora 1990; Jaffe et al. 1992; Karlsson et al. 1994), few attempts have been made to quantify the relative contribution of nutrient uptake from prey to the nutrient pool in the plant. To our knowledge, there are only two studies quantifying the assimilation efficiency of nitrogen from prey. Dixon et al. (1980) found that 76% of prey nitrogen was assimilated by *Drosera erythrorhiza*, while Friday and Quarmby (1994) recovered 30% of applied $^{15}N$ in prey in *Utricularia vulgaris* 2 days after feeding. With the efficiency found, Dixon et al. (1980) calculated that prey capture could make up 11–17% of the seasonal nitrogen uptake of a plant and that 70% of applied $^{15}N$ was allocated to tubers at the end of the growing season. To estimate the importance of prey-derived nitrogen integrated over several seasons, an other approach was applied by Schulze et al. (1991). Using the $^{15}N$ natural abundance method, they found an on average *in situ* dependence on prey derived nitrogen of 50% in a range of Australian *Drosera* species, with a variation between growth forms.

This study evaluates the efficiency in uptake and assimilation of nitrogen from prey and the allocation of this nitrogen to winter buds and reproductive structures in four carnivorous plant species (*Pinguicula alpina, P. villosa*, *P. vulgaris* and *Drosera rotundifolia*) by tracing $^{15}N$ from artificially enriched prey. The impact of the reproductive status of the plant and the amount of prey captured on the uptake of N from prey is also evaluated. Finally, the root nitrogen uptake in reproductive and non-

reproductive plants under different feeding regimes is compared.

## Methods

The experiments were carried out at or near the Abisko Scientific Research Station, Northern Sweden (68° 21′ N, 18° 49′ E) during the summer of 1993, with a supplementary experiment in 1994. The four species investigated grow in different types of habitat (Karlsson 1986) and the experiments were accordingly carried out in different habitats for two of the species. The reproductive status (flowering or non-flowering) was recorded for each plant, because of the possibility that flowering plants act as larger sinks for nutrients, as indicated by the low somatic costs of reproduction in some of these species (Karlsson et al. 1990).

### Experimental sites

Experiments were carried out at one or two sites per species. Site 1 for *P. alpina* was located on the edge of a frost upheaval zone where *Tofieldia pusilla, Dryas octopetala, Bartsia alpina, Salix reticulata, Saxifraga aizoides and Cetraria cucullata* are the characteristic plants (nomenclature follows Lid and Lid 1994). At site 2, *P. alpina* grew on more stable soil with a dense moss cover. Along with the species present at site 1, *Betula nana, Bistorta vivipara, Rhododendron lapponicum, Andromeda polifolia, Arctostaphylos alpinus* and *Euphrasia* sp. were also common. *P. villosa* and *D. rotundifolia* grew on *Sphagnum* hummocks together with *Rubus chamaemorus, Betula nana, Vaccinium microcarpum, V. uliginosum, Empetrum hermaphroditum* and *Andromeda polifolia. P. vulgaris* was studied at two sites. The drier site 1 was dominated by bare ground with some lichens, *Tofieldia pusilla, Saxifraga aizoides* and *Diapensia lapponica*. Site 2 was a wet moss-covered locality with such species as *Tofieldia pusilla, Carex* spp., *Juncus arcticus, Andromeda polifolia* and liverworts. Substrate samples were taken from the upper 5 cm of the soil and analysed for pH (soil to water 1: 2 by volume), air dried and stored at 5°C until analysis for Kjeldahl-N. Kjeldahl analyses were carried out with acid digestion (Cu catalyst) of plant material and substrate, followed by flow injection analysis on ammonium (FIAstar 5010, Tecator, Höganäs, Sweden). The nitrogen content (Kjeldahl-N) and pH of the substrate at the respective sites are shown in Table 1.

### Efficiency in uptake and allocation patterns of prey-derived nitrogen

This experiment was carried out to determine the proportion of the prey nitrogen that is assimilated by the plant, and the allocation of this nitrogen to winter buds and reproductive parts. This was done by quantifying the transfer of $^{15}N$ from labelled *Drosophila* flies fed to the plants *in situ* at all the sites defined above, except *P. alpina* site 2, and in a greenhouse.

For each species and site, 12–24 plants per reproductive status (flowering or non-flowering) were fed $^{15}N$-enriched *Drosophila* in the field during their natural period of prey capture from mid June to late July. Each plant was fed one (*D. rotundifolia* and *P. villosa*) or two (*P. alpina* and *P. vulgaris*) flies throughout the experiment (feeding dates: 18–22 June and 10–15 July). In addition, eight non-flowering plants per species were fed both $^{15}N$-enriched flies and the same number of unlabelled flies. The extra feeding with unlabelled flies was done to test whether the amount of prey affects the nitrogen uptake efficiency. As most *Drosera* flowered, both feeding experiments for this species were only done on flowering plants.

To exclude factors that may affect N uptake efficiency *in situ*, such as cleptoparasitism, natural prey capture and rain, five flowering plants per species were dug up with parts of their natural substrate in late June, potted in 8×8 cm pots, placed in a greenhouse and tray-watered with tap water. These plants were then fed two $^{15}N$-enriched flies per plant over the experiment. Feeding was performed at the same time as for plants *in situ*. Ten plants of *P. villosa* and five of *P. vulgaris* were also fed $^{15}N$-enriched *Drosophila* on the flower stem in the greenhouse. Two flies per plant were placed halfway up the stem and a small piece of plastic film was placed around the stem to prevent them from falling onto the leaves. The daily maximum temperature in the greenhouse was 2–11°C higher than the air temperature outside.

The $^{15}N$-enriched flies were raised on 100 mg L-glutamic acid (98 atom% $^{15}N$, Sigma Chem. Company, St. Louis, USA) made up to c. 100 g with a standard *Drosophila* medium (Carolina Biological Supply Company, Burlington, USA) and water. This gave a $^{15}N$ enrichment in the flies of 2.75 atom% $^{15}N$. The flies were killed by freezing shortly before being fed to the plants, and where then placed under the curved leaf margins on *Pinguicula* species and on leaves with active secretion on *D. rotundifolia*.

To estimate the efficiency in uptake of nitrogen from prey, half of the plants ($n$ = 6–12 per species, habitat and reproductive status) were randomly selected and harvested near to maximum biomass (mid July for *P. villosa* and early August for the others), at least 7 days after the last supplementary feeding. *P. vulgaris, P. alpina* and *D. rotundifolia* plants in the greenhouse were harvested 1 week earlier than plants *in situ*. Seed capsules were harvested when ripe, the flower stalks being left to be harvested together with the winter-dormant buds, allowing for potential resorption of resources. Winter buds were harvested when all leaves had senesced. Some removal of supplied prey by ants and small spiders was observed at some sites. Flies removed within 2 h after feeding were replaced. No removal of *Drosophila* flies was observed after these 2 h, as confirmed by counting remaining prey carcases at the first harvest. All flowering individuals of *P. alpina* at site 1 aborted their flowers during the experiment, probably due to infection by a fungus, *Ustilago* sp. (Molau 1993). *D. rotundifolia* also failed to set seeds. Unmanipulated plants harvested near maximum biomass were used as references for the $^{15}N$ measurements in the *in situ* studies, and in the greenhouse studies greenhouse-grown plants deprived of prey were used as references.

As some of the allocation patterns observed were unexpectedly high, the allocation study was repeated in 1994. No $^{15}N$-labelled flies were available for this second allocation experiment and the plants were therefore fed with a $^{15}NH_4{}^{15}NO_3$ solution (0.5% with respect to N, 96 atom% $^{15}N$) directly on the leaves. Each plant was given a $^{15}N$ amount estimated to correspond to c. 20% of the total plant N. The label was divided into two feeding occasions at an interval of 2 weeks. On each occasion, one or two leaves (depending on plant size) were fed one drop each (c. 7 µl). Near maximum biomass in early August, half of the plants were harvested to ascertain for the amount of $^{15}N$ assimilated. The other half were harvested as reproductive organs and winter-dormant buds. Half of the *Pinguicula* plants were flowering, while only flowering plants of *D. rotundifolia* were included. In both studies prey carcasses were removed and plant materials were dried for 24 h at 70°C, milled and analysed for atom% $^{15}N$ (± 0.0002 atom%) and percent N (± 0.01%) with an ANCA-MS (Europe Scientific Ltd., Crewe, UK) by Waikato Stable Isotope Unit, Hamilton, New Zealand. For the smaller species and for reproductive organs and winter buds, individuals were lumped to yield enough nitrogen for analysis

**Table 1** Kjeldahl nitrogen (mg N $g^{-1}$ ± 1 SE, $n$=4) and pH ($H_2O$) of substrate at the various experimental sites

| Site | pH | Kjeldahl N |
|---|---|---|
| *Pinguicula alpina* 1 | 8.7 | 2.78 ± 0.44 |
| *Pinguicula-alpina* 2 | 6.8 | 14.14 ± 0.41 |
| *Pinguicula-villosa* | 4.8 | 4.47 ± 0.39 |
| *Pinguicula vulgaris* 1 | 4.8 | 2.98 ± 0.23 |
| *Pinguicula vulgaris* 2 | 6.7 | 8.02 ± 0.12 |
| *Drosera rotundifolia* | 4.6 | 3.96 ± 0.55 |

(0.5 mg N). Plants fed enriched *Drosophila* flies achieved a $^{15}N$ enrichment of 0.05–0.35 atom%, and the supply of enriched ammonium nitrate gave a $^{15}N$ enrichment in the plants of 10–25 atom%. Most enzymes discriminate against $^{15}N$ during nitrogen assimilation (Handley and Raven 1992), but as N is one of the most important limiting nutrients for these plants, discrimination against $^{15}N$ in uptake and assimilation was assumed to be negligible (Griffiths 1991). The $^{15}N$ loss was estimated as the difference between the amount $^{15}N$ found at peak biomass and the quantities found in reproductive parts and winter buds.

Efficiency in uptake of nitrogen from prey was calculated as the $^{15}N$ uptake from prey (as the difference between fed and unfed plants) divided by the total $^{15}N$ in prey, according to the formula:

$$\text{Efficiency} = 100 \times [NC_{SAMPLE} \times (\text{Atom\%}^{15}N_{SAMPLE} - \text{Atom\%}^{15}N_{REFERENCE})] / [\text{No. of flies} \times NC_{PREY} \times \text{Atom\%}^{15}N_{PREY}] \quad (1)$$

where $NC_{SAMPLE}$ and $NC_{PREY}$ stands for nitrogen content (mg) of the plant sample and one *Drosophila* fly respectively. Amount of nitrogen derived from prey per plant was calculated as the $^{15}N$ uptake from prey divided by the atom%$^{15}N$ in prey:

$$\text{Nitrogen from prey} = [NC_{SAMPLE} \times (\text{Atom\%}^{15}N_{SAMPLE} - \text{Atom\%}^{15}N_{REFERENCE})] / [100 \times \text{No. of plants per sample} \times \text{Atom\%}^{15}N_{PREY}] \quad (2)$$

where abbreviations and subscript are as in Eq. 1.

Differences in uptake between species and between groups (flowering, non-flowering and extra-fed) within species, were evaluated by a Kruskal-Wallis one-way ANOVA and differences between greenhouse-grown plants and plants *in situ* were analysed with a ranked two-way ANOVA with species and location (*in situ* or greenhouse) as factors.

### Uptake of nitrogen from substrate

To estimate the effect of prey capture on uptake of N from the soil, plants of *P. alpina*, *P. vulgaris*, *P. villosa* and *Drosera rotundifolia* were fed *Drosophila* flies in addition to natural prey caught by the plants *in situ*. Plants were randomly distributed among three treatments: (1) an initial harvest, (2) a control set receiving no supplementary feeding, and (3) plants fed 1–2 extra *Drosophila* flies at c. weekly intervals (*P. villosa* obtained 2, *D. rotundifolia* 3, *P. alpina* 6 and *P. vulgaris* 8 flies per plant over the experiment). A total of 12–16 plants per species were allocated to each treatment. The initial harvest was performed at the time of the first feeding (mid to late June), while the other two groups were harvested 4–6 weeks later, near seasonal maximum biomass. Plant material was dried for 24 h at 70°C and analysed individually for Kjeldahl-N as described above.

Natural prey capture was estimated for each species by counting and mapping prey on plants growing nearby (cf. Karlsson et al. 1994) and together with results on efficiency in uptake, a nitrogen budget was constructed for the two treatments (fed and unfed). Uptake of N from the substrate was calculated by subtracting mean estimates of uptake of N from prey and mean N content at the initial harvest from plant N content at the final harvest in each treatment. As prey capture was not estimated for *D. rotundifolia*, a capture of 400 µg prey (dry weight) per plant and season was assumed, with an SE equal to the mean SE for the other three species (68 µg). These estimates are close to those found by Thum (1989) of 0.47 mg prey capture (SD = 0.60) in this species. Loss of nitrogen was assumed to be equal between treatments during the experiment. To test for differences in uptake, an ANOVA on $\log_{10}$ transformed data was applied with three factors: species, treatment and reproductive status.

## Results

### Efficiency in uptake and allocation patterns of prey-derived nitrogen

*P. vulgaris* had higher nitrogen uptake efficiency *in situ* (41%) than the other species (29–35%, Fig. 1, $P < 0.05$ for a nonparametric multiple comparison test (Zar 1984) between *P. vulgaris* and any of the other species). The N uptake efficiency was consistently higher (7–20%) for plants in the greenhouse than those *in situ* (Fig. 1, Table 2), while no effects of reproductive status or feeding level ($P = 0.08$ for *P. villosa* and $P > 0.4$ for the other species) were found. Uptake of N from prey fed on the flower stalk in *P. villosa* and *P. vulgaris* ranged from 1 to 2.5% of applied N.

For non-reproductive plants 58–97% of the prey-derived $^{15}N$ were recovered in the winter buds. The highest loss was found for *P. villosa* (42%), *P. vulgaris* and *Drosera rotundifolia* had intermediate losses (13–27%), while *P. alpina* individuals lost 3–27% of the $^{15}N$ pool (Table 3). For reproductive plants, the $^{15}N$ allocation to winter buds was lower, 34–71%, another 17–43% were recovered in reproductive parts. Reproductive individuals lost 2–34% of the prey-derived $^{15}N$.

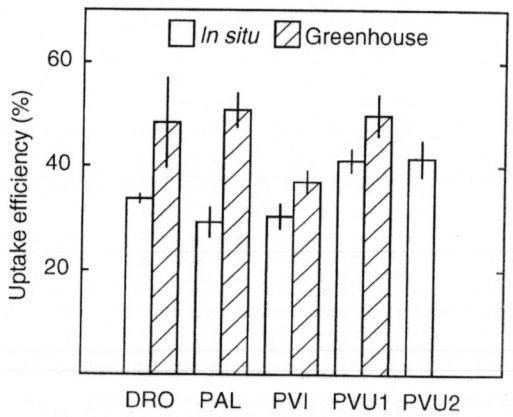


**Fig. 1** Efficiency in uptake of N from prey (mean values ± 1 SE) in four carnivorous plant species: *Drosera rotundifolia* (*DRO*), *Pinguicula alpina* (*PAL*), *P. villosa* (*PVI*) and *P. vulgaris* (*PVU*). The efficiency was calculated as the percentage of N available in prey assimilated by the plants as evaluated by tracing $^{15}N$ from prey. Experiments were carried out both *in situ* and in a greenhouse. *P. vulgaris* was manipulated at two sites *in situ*. Statistical analyses are shown in Table 2

**Table 2** Difference in uptake of N from prey in three *Pinguicula* and one *Drosera* species grown in the field and in a greenhouse as evaluated by a ranked two-way ANOVA. $R^2$ (adj.) = 0.502; mean values are shown in Fig. 1

| Source of variation | *F* | *df* | *P* |
|---|---|---|---|
| Species | 3.43 | 3 | 0.028 |
| Place of treatment | 22.69 | 1 | 0.000 |
| Species×place of treatment | 1.56 | 3 | 0.216 |

**Table 3** Partitioning of prey-derived nitrogen between reproductive organs (flower stalk, capsule and seeds), winter buds and loss (%± 1 SE) in different *Drosera* and *Pinguicula* species evaluated by tracing $^{15}N$ from enriched prey in 1993 (method 1) and application of $^{15}NH_4{}^{15}NO_3$ to the leaves in 1994 (method 2). *P. vulgaris* was studied at two sites (*n*=3–4, *nd*=not determined)

| Species | Method | Non-reproductive plants | | Reproductive plants | | |
|---|---|---|---|---|---|---|
| | | Bud | Loss | Bud | Reproduction | Loss |
| *P. alpina*[a] | 1 | 97.4 ± 0.4 | 2.6 ± 1.1 | nd | nd | nd |
| | 2 | 72.5 ± 10.0 | 27.5 ± 10.0 | 61.4 ± 10.7 | 17.3 ± 1.5 | 21.3 ± 10.8 |
| *P. villosa* | 1 | 58.0 ± 0.3 | 42.0 ± 0.4 | 45.6 ± 0.6 | 19.8 ± 0.2 | 34.6 ± 0.7 |
| *P. vulgaris* site 1 | 1 | 73.3 ± 0.3 | 26.7 ± 1.1 | 45.5 ± 0.3 | 27.4 ± 0.3 | 27.1 ± 0.4 |
| | 2 | 86.8 ± 8.7 | 13.2 ± 8.7 | 48.4 ± 6.3 | 43.5 ± 4.5 | 8.2 ± 7.8 |
| *P. vulgaris* site 2 | 1 | 78.6 ± 1.1 | 21.4 ± 4.2 | 34.0 ± 0.5 | 32.8 ± 0.4 | 33.2 ± 0.6 |
| *D. rotundifolia*[b] | 1 | 81.0 ± 0.2 | 19.0 ± 0.4 | 71.0 ± 0.5 | 17.3 ± 0.2 | 11.7 ± 0.5 |
| | 2 | nd | nd | 56.6 ± 8.1 | 41.3 ± 5.7 | 2.2 ± 9.9 |

[a] The perennial roots of *P. alpina* are included in the bud fraction
[b] *D. rotundifolia* failed to set seeds in 1993

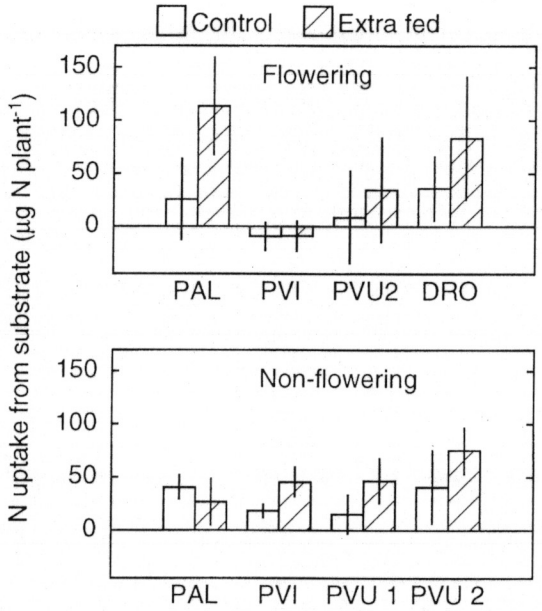


**Fig. 2** Uptake of N from substrate (mean values ± 1 SE) at different levels of prey capture in flowering (*upper*) and non-flowering (*lower*) plants of *Pinguicula alpina* (*PAL*), *P. villosa* (*PVI*), *P. vulgaris* (*PVU*) and *Drosera rotundifolia* (*DRO*) *in situ*. *P. vulgaris* was manipulated in two different habitats. Control plants caught only natural prey, while extra-fed plants received additional prey as *Drosophila* flies. Statistical analyses are shown in Table 4

### Uptake of nitrogen from substrate

Estimates of uptake of nitrogen from soil ranged from –10 to 113 µg N per plant (Fig. 2). In both treatments of *D. rotundifolia* and one treatment of *P. vulgaris* site 1 there was only one observation of non-flowering plants. These species were therefore not included in the statistical analysis. A significant effect was found for feeding level (Table 4), and extra-fed plants acquired more nitrogen from the substrate than control plants in all species, except non-flowering plants of *P. alpina* (Fig. 2). No significant effects of reproductive status or species on the uptake of N from substrate were found, but a species × reproductive status interaction was found (Table 4).

**Table 4** Effect of species, reproductive status and feeding level on uptake of N from soil, evaluated by ANOVA on $\log_{10}$ transformed data. $R^2$ (adj.)=0.21. Mean values are shown in Fig. 2

| Source of variation | *F* | *P* |
|---|---|---|
| Species | 2.47 | 0.092 |
| Reproductive status | 2.13 | 0.149 |
| Feeding level | 4.91 | 0.030 |
| Species×reproductive status | 3.27 | 0.044 |
| Species×prey capture | 0.46 | 0.635 |
| Reproductive status×prey capture | 1.10 | 0.298 |
| 3-Way interaction | 1.59 | 0.211 |

## Discussion

### Efficiency in uptake and allocation of prey-derived N

Less than half (29–42%) of the nitrogen present in the *Drosophila* flies was exploited by these species (Fig. 1). These efficiencies are about half that found for uptake from *Drosophila* flies in *Drosera erythrorhiza* (76%, Dixon et al. 1980). The uptake efficiency from natural prey *in situ* may be higher than the uptake from *Drosophila* flies since Collembola and most other natural prey are considerably smaller, which may permit more complete digestion and assimilation of nutrients. For small prey, usually the only remains of trapped prey are almost transparent exoskeletons (authors' personal observations).

All species had higher uptake efficiencies in the greenhouse than *in situ*. Two factors that may cause this difference are rain and temperature. After rain, natural prey may be lost from the most exposed leaves of *P. alpina* and *P. vulgaris*. Heavy rainfall is however, rare in the study area (Karlsson et al. 1987), but moderate rainfall may also cause loss of nutrients. Temperature-dependent enzyme activity may also give increased uptake in green-

**Table 5** Uptake of nitrogen from prey and substrate (μg plant$^{-1}$ ) in reproductive (*F*) and vegetative (*NF*) plants of *Pinguicula alpina* (*PAL*), *P. villosa* (*PVI*) and *P. vulgaris* (*PVU*), compared with the turnover of nitrogen (μg plant$^{-1}$season$^{-1}$, from Karlsson et al. 1994) and the additional uptake of nitrogen from substrate with increased prey capture (cf. Fig. 2). *P. vulgaris* was studied at two sites (*nd*=not determined)

| Species | | N uptake from | | N uptake from substrate due to extra feeding | | Sum N from prey and extra N from Substrate | N turnover per season |
|---|---|---|---|---|---|---|---|
| | | Natural prey | Substrate | Per plant | Per μg N from extra fed prey | | |
| PAL | F | 6.3 | 31.8 | 116.2 | 4.1 | 122.5 | 182.1 |
| | NF | 4.1 | 44.5 | 14.6 | 0.5 | 18.7 | 112.1 |
| PVI | F | 1.5 | (–8) | 10.3 | 1.0 | 11.8 | 61.6 |
| | NF | 1.6 | 19.8 | 37.1 | 3.8 | 38.7 | 28.0 |
| PVU 1 | F | 28.5 | 137.6 | nd | nd | nd | 224.2 |
| | NF | 7.4 | 22.5 | 84.5 | 1.6 | 91.9 | 102.3 |
| PVU 2 | F | 7.3 | 15.8 | 79.6 | 1.5 | 86.9 | (224.2) |
| | NF | 6.0 | 46.7 | 87.6 | 1.6 | 93.6 | (102.3) |

house plants. Since absorption of fluids from prey in *Pinguicula* starts within 2 h (Heslop-Harrison and Knox 1971), replacing robbed prey within 1–2 h probably does not result in overestimation of the uptake efficiency.

Under greenhouse conditions, *Drosera*, *P. alpina* and *P. vulgaris* had similar N uptake efficiencies, while *in situ P. vulgaris* had a significantly higher uptake than the other species. Thus the factors reducing N assimilation *in situ* seem to affect *P. vulgaris* less than the other species.

Uptake of N from prey did not seem to be affected by sink or source sizes as there was no difference between flowering and non-flowering individuals (varying sink strength) or between feeding levels (varying source sizes). The low efficiency in uptake from prey fed on the flower stalk is probably due to the small area and low number of glands in contact with prey, due to the curved surface of the stalk. Stalked glands are longer on flower stalks than on leaves in *P. villosa* (0.39 ± 0.02 mm vs. 0.21 ± 0.04 mm (± 1 SE, $n = 4$), but shorter in *P. vulgaris* [0.12 ± 0.01 mm vs. 0.19 ± 0.01 mm (± 1 SE, $n = 3$, H.M. Hanslin unpublished work)]. This may explain the low efficiency in *P. villosa* as little contact is established between prey and sessile glands on the flower stalks, but it does not explain the low efficiency in *P. vulgaris*.

For non-flowering *P. alpina* plants in 1993 and flowering *D. rotundifolia* in 1994, the loss of prey-derived N was found to be exceptionally low. The sites are poor in nitrogen (Table 1), which may partly explain this efficient recycling. The loss of total N was, however, in the range of 15–20%.

Relative reproductive allocation of $^{15}$N (reproductive allocation divided by the sum of allocation to reproduction and buds) in this study was close to the results of Karlsson et al. (1990, their *RE*), except for *P. villosa*. In this study, *P. villosa* had a relative reproductive allocation (RRA) of prey-derived N of 30%, while Karlsson et al. (1990) found an RRA of 52–69% of the N pool. Reproduction in this early-flowering species (Molau 1993) therefore seems to be predominantly supported by old N reserves or soil-derived N, while the new prey-derived N is to a larger extent allocated to the winter bud. These carnivorous plants lost on average 22% of their seasonal N incomes from prey through leaf and root turnover; flowering individuals lost another 28% in reproduction. The total turnover of prey-derived N was on average 48% in reproductive plants and 22% in non-reproductive plants. The turnover of prey-derived N was 0–28% lower than that of the N pool in the same species (Karlsson 1988). No clear pattern in the allocation result could be traced to the difference between the two methods. The differences in allocation between 1993 and 1994 are as likely to be a result of variation between sites and seasons.

## Uptake of nitrogen from substrate

In view of the knowledge on natural prey capture and nitrogen turnover (Karlsson et al. 1994) and the uptake efficiency of nitrogen from prey found in this study, it is clear that the direct benefit from prey capture is small relative to the pool and turnover of nitrogen in these species. With a nitrogen concentration in prey of 10% (H.M. Hanslin and P.S. Karlsson unpublished work), uptake of nitrogen from prey was on average only 2–13% of the N turnover (Table 5). However, when the additional increase in uptake of N from the substrate is also taken into concideration, the benefit increases. Increased prey capture induced a nitrogen uptake (direct prey derived + additional soil derived) corresponding to between 17% of the nitrogen turnover in non-flowering *P. alpina* and 138% in non-flowering *P. villosa*. Flowering individuals of *P. villosa* seemed to experience a loss of N. This is probably not true and may be due to a random predominance of large individuals in the initial harvest. As found by Karlsson et al. (1994), there is a large variation in prey capture between individuals, and the variation in nutritional benefits from the capture of prey is expected to be correspondingly large. Root uptake of nitrogen was thus apparently enhanced by increased prey capture (Fig. 2, Table 4). Indications of such an effect have pre-

viously been found for *P. vulgaris*. Aldenius et al. (1983) found that when *P. vulgaris* was fed prey, the increase in N content in the plant was larger than the N content of the prey. Similarly, when artificial prey (agar blocks) were fed to *P. vulgaris* (Karlsson and Carlsson 1984), the interaction effect of a complete set of nutrients in the blocks (the N × P × micronutrient interaction in Table 3 in Karlsson and Carlsson 1984) was twice as large as the effect of supplying nitrogen. A similar pattern was also found for phosphorus. The stimulation effect is thus not restricted to nitrogen alone and seems to depend on the combined supply of N, P and some other elements (Karlsson and Carlsson 1984). Furthermore, the stimulation effect from prey does not seem to be associated with nutrient deficiences in the soil; in the experiment by Aldenius et al. (1983) the stimulation effect appeared to be larger for plants that benefited from a relatively high addition of fertiliser to the soil compared with plants grown in natural soil. We do not know the mechanism behind this effect, but one possibility is that root uptake efficiency (nutrient uptake per root unit) increases after feeding. Another is that prey capture stimulates root growth and thus increases the plant uptake capacity.

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