H.M. Hanslin • P.S. Karlsson

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

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*

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*, *Barbara alpina*, *Salix reticulata*, *Saxifraga aizoides* and *Cetraria eucalyptus* 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 *Dispenzia 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 (FlAstar 5010, Teto, Höganas, 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 15N 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 15N-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 15N-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* flowers, 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 8x8 cm pots, placed in a greenhouse and tray-watered with tap water. These plants were then fed two 15N-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 15N-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.

For each species and site, 12–24 plants per reproductive status (flowering or non-flowering) were fed 15N-enriched *Drosophila* in.

**Table 1** Kjeldahl nitrogen (mg N g⁻¹ ± 1 SE, n=4) and pH (H₂O) of substrate at the various experimental sites

<table>
<thead>
<tr>
<th>Site</th>
<th>pH</th>
<th>Kjeldahl N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinguicula alpina</td>
<td>8.7</td>
<td>2.78 ± 0.44</td>
</tr>
<tr>
<td>Pinguicula-alpina</td>
<td>6.8</td>
<td>14.14 ± 0.41</td>
</tr>
<tr>
<td>Pinguicula-villosa</td>
<td>4.8</td>
<td>4.47 ± 0.39</td>
</tr>
<tr>
<td>Pinguicula vulgaris</td>
<td>4.8</td>
<td>2.98 ± 0.23</td>
</tr>
<tr>
<td>Pinguicula vulgaris</td>
<td>6.7</td>
<td>8.02 ± 0.12</td>
</tr>
<tr>
<td>Drosera rotundifolia</td>
<td>4.6</td>
<td>3.96 ± 0.55</td>
</tr>
</tbody>
</table>

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