Leaf absorption of mineral nutrients in carnivorous plants stimulates root nutrient uptake

Lubomír Adamec

Institute of Botany of the Academy of Sciences of the Czech Republic, Section of Plant Ecology, Dukelská 135, CZ-379 82 Třeboň, Czech Republic

Author for correspondence:
Lubomír Adamec
Tel: +420 333 721156
Fax: +420 333 721136
Email: adamec@butbn.cas.cz

Received: *18 January 2002*
Accepted: *1 March 2002*

Summary

- The mineral nutrition of terrestrial carnivorous plants was investigated under glasshouse conditions to elucidate ecophysiological adaptations of this plant group.
- In *Drosera capillaris* and *D. capensis*, absorption of N, P, K, and Mg from insects was relatively efficient (> 43%), whereas that of Ca was not. Carnivorous plants (*D. capensis*, *D. peltata*, *D. scorpioides*, and *Dionaea muscipula*) exhibited a high efficiency of re-utilization of N (70–82%), P (51–92%), and K (41–99%) from senescing leaves. Re-utilization of Mg was low or negative, and that of Ca highly negative.
- In a growth experiment, foliar nutrient supply led to markedly increased growth and nutrient accumulation in *D. capillaris*, *D. aliciae*, and *D. spathulata*. In all the three species tested it was demonstrated that leaf-supplied nutrients were accumulated in the plant biomass and even stimulated root nutrient uptake.
- These results suggest that the main physiological effect of leaf nutrient absorption from prey is a stimulation of root nutrient uptake.

Key words: terrestrial carnivorous plants, utilization of prey, mineral nutrient re-utilization, leaf nutrient supply, stimulation of root nutrient uptake.

© *New Phytologist* (2002) **155**: 89–100

Introduction

The majority of terrestrial carnivorous plants grow in bog and fen soils, in which they encounter persistent unfavourable conditions. The soils are usually wet or waterlogged, mostly acid, and usually poor in available mineral nutrients (N, P, K, Ca, Mg; Juniper *et al.*, 1989, Adamec, 1997a). Thus, carnivory in most terrestrial plants may be considered as an adaptation to all of these stress factors. The basic questions of mineral nutrition of carnivorous plants that have been raised by biologists in the last decades are related to the relative importance of foliar and root mineral nutrient uptake, the identification of the elements from prey bodies, the uptake of which is for plant growth, the relationship between the uptake of organic and mineral nutrients from prey, and the nature of interactions between the foliar and root uptake of mineral nutrients (Lüttge, 1983; Juniper *et al.*, 1989; Adamec, 1997a). However, our knowledge of the principal processes of mineral nutrition of carnivorous plants is still very fragmentary. On the basis of many glasshouse growth experiments, it has been concluded that terrestrial carnivorous plant species differ greatly in their ability to use soil or foliar mineral nutrient supply. Accordingly, carnivorous plants have been classed with three main ecophysiological groups (Adamec, 1997a). Plants in the group of 'nutrient requiring species' markedly increase their growth due to both soil and leaf nutrient supply and their root nutrient uptake may be stimulated by foliar uptake. Plants in the group of 'root-leaf nutrient competitors' grow better and accumulate more nutrients because of both root and leaf nutrient uptake. However, competition occurs between root and leaf nutrient uptake. Plants in the third group of 'nutrient modest species' have roots with a very low nutrient uptake capacity and rely on leaf nutrient uptake.

The aim of this present study is to elucidate the principal processes of mineral nutrition of some terrestrial carnivorous plant species under glasshouse conditions. The physiological efficiency of mineral nutrient uptake (N, P, K, Ca, Mg) from model prey (fruit flies, mosquitoes) was investigated in *Drosera capillaris* and *D. capensis* as a difference in nutrient content between intact and spent carcasses. The efficiency of the re-utilization of the nutrients from senescent leaves of *D. capensis*, *D. peltata*, *D. scorpioides*, and *Dionaea muscipula* was investigated as a comparison of tissue nutrient content in adult and

Table 1 Available nutrient content and pH values in soils used for growing carnivorous plants throughout the study

Soil type	Initial pH	NH_4^+-N	PO_4-P	K	Ca	Mg
		mg kg^{-1} (d. wt)				
(A) Conifer leaf mould (1999)	4.20	27	8.7	229	342	337
(B) Conifer leaf mould (2000)	4.38	151	4.7	267	720	484
(C) Acid fen soil (1999)	4.10	31	17	47	569	74
(D) Acid fen soil + sand (2000)	4.16	23	5.7	30	260	143

One mixed soil sample was analysed.

senescent leaves. A growth experiment was performed to reveal the effect of foliar mineral nutrient supply on root nutrient uptake in *Drosera capillaris*, *D. aliciae*, and *D. spathulata*. Thus, the hypothesis that foliar mineral nutrient supply can stimulate root nutrient uptake (Hanslin & Karlsson, 1996; Adamec, 1997a) was tested.

Materials and Methods

Mineral nutrient uptake from prey

The proportions of total N, P, K, Ca, and Mg absorbed from model prey were investigated in two perennial, evergreen sundew species, low erect *Drosera capensis* L. (native to South Africa) and rosette-leaved *D. capillaris* Poir. (America). Both species have a relatively high capacity for mineral nutrient uptake both by leaves and roots (Adamec, 1997a). The subadult *D. capensis* plants grown from root cuttings were 8–12 cm high, with 15–25 adult leaves, while adult *D. capillaris* plants grown from seeds had rosette diameters of 4.2–4.5 cm, with 15–17 adult leaves. Neither species flowered during this study. The plants were grown in plastic 10 × 10 × 10 cm pots in organic soils with *c.* 10% (v/v) of vermiculite; the *D. capensis* in conifer needle mould (see Table 1a) and *D. capillaris* in acid fen soil (Table 1c; Adamec *et al.*, 1992). The pots with the plants were placed in a 0.84-m^2 white polypropylene container 0.4 m high, filled with water to a depth of 2–3 cm. The insect-proof container was covered with a nylon net (mesh diameter 470 µm) and a neutral-density plastic foil to reduce irradiance. In this way, the plants were protected from overheating. In summer, the irradiance on the level of plants was 12–15% of that in an open area outdoors. The container with the plants was maintained in a naturally lit glasshouse. Daily temperatures at plant level fluctuated between 20 and 36°C and relative air humidity (RH) between 60 and 90% during the day, and between 16 and 22°C and 80–96% RH at night. This manner of cultivation and the summer microclimatic conditions were the same for all plants used throughout this study.

As a model prey, fruit flies *Drosophila melanogaster* and mosquitoes *Culex pipiens* were used. The former species is the one that has been most commonly used in similar studies

Table 2 Elemental content in standard prey (fruit flies, *Drosophilia melanogaster* and mosquito *Culex pipiens*)

Element	Prey	Content (µg per prey)	SE	*n*	% of d. wt of prey	SE
N	Fruit fly	18.8	0.8	8	6.3	0.3
P	″	2.6	0.2	8	0.88	0.06
K	″	2.7	0.1	8	0.89	0.03
Ca	″	0.16	0.01	8	0.05	0.002
Mg	″	0.30	0.01	8	0.10	0.004
N	Mosquito	65.9	11.4	5	4.1	0.7
P	″	28.7	2.7	4	1.8	0.2
K	″	13.1	1.1	4	0.81	0.07
Ca	″	17.0	1.8	4	1.0	0.01
Mg	″	6.2	0.1	4	0.38	0.004

Mean elemental content per one prey and in prey d. wt are shown. *n*, number of independent samples analysed.

(Adamec, 1997a). *D. melanogaster* (strain Oregon R) flies were cultured from the egg stage in a carbohydrate-rich medium. Adult flies (d. wt, *c.* 0.30 mg) were narcotized with ether and stored frozen at −15°C in a vial until used. The mosquitoes (d. wt *c.* 1.63 mg) were caught by a fine net in a forest, narcotized, and stored similarly. On 20 June 1999, two fruit flies were put on the centre of adult leaves of both *Drosera* species. The distance between the two flies on the same leaf was *c.* 10 mm in *D. capensis* and 2–3 mm in *D. capillaris*. This treatment was replicated for three adult leaves in each of 11 plants of both species, totalling six flies per plant. The tentacles and leaves surrounded the dead flies in a similar manner to that observed with live flies. After 15 days, the spent carcasses were carefully removed by fine forceps and put in mineralization glass flasks. One mosquito each was put on two adult leaves of each of seven *D. capensis* plants. The spent carcasses were removed and analysed after 22 days. The experiment on feeding *D. capillaris* on fruit flies was repeated on 11 June 2000. In this case, the plants were grown in a similar substrate but watered by distilled water (Table 1d). Thus, the tissue nutrient content in the leaves of these plants was somewhat lower than that in the 1999 season (cf. Table 2) and the relationship between the tissue nutrient content and nutrient absorption efficiency could be estimated.

Two flies were always used for analyses of N, two for P, and four for K, Ca, and Mg analyses, or one mosquito for each of the analyses. As a control, intact frozen flies and mosquitoes were analysed. Absorption of the nutrients from the prey was expressed as a difference in nutrient content between the intact and spent carcasses (Dixon *et al.*, 1980). Six to 10 parallel analyses of fruit flies and 4–5 of mosquitoes were performed on each plant species.

Mineral nutrient re-utilization

The proportions of N, P, K, Ca, and Mg re-utilized (recycled) from senescing leaves were studied in *Drosera capensis*, microstilt *D. scorpioides* Planch. (Australia), tuberous *D. peltata* Thunb. (Australia), and in erect-rosette Venus flytrap *Dionaea muscipula* Ell. (USA), and compared with tissue nutrient content in adult and senescent leaves. *D. peltata* was grown from tubers, *D. scorpioides* from *in vitro* cultured plants, while *Dionaea muscipula* was grown from plant cuttings. All these species have erect leaves which are usually not in contact with the soil. In June, a further 12 *D. capensis* plants, grown on conifer needle mould (Table 1a), were selected. They were of the same size as in a parallel study of nutrient uptake from prey. Three younger adult leaves of approximately the same age and size were selected from each plant. To obtain a measure of the relationship between the d. wt of adult and senescent leaves the selected leaves were tagged by a fine silicon ring on their petiole. The approximate 'leaf area' of the ribbon-like carnivorous part of leaf laminae with tentacles (i.e. traps) was estimated as a multiple of leaf length times leaf width. In each selected leaf, these parameters were measured by a plastic caliper; leaf length to the nearest 0.5 mm, and leaf width to the nearest 0.2 mm. In each plant, one selected and measured leaf was excised and its carnivorous lamina dried (80°C) and weighed. The plants with the tagged leaves were allowed to grow for further 2–3 months (by the end of September) until the complete senescence of leaf laminae took place. In order to prevent any contact of the senescent leaves with the soil in the pots, the senescing leaves were supported gently by a fine isolated wire. The brown colour of the leaf traps was the criterion for a complete leaf senescence. The leaf laminae were excised as soon as they had become fully senescent, dried and weighed. Linear correlation between the 'leaf area' of adult leaves and d. wt of senescent leaves was calculated. Tissue N, P, K, Mg, and Ca content in adult and senescent leaves was estimated in 7–13 parallel leaf samples.

The same experiment was performed with *Dionaea muscipula*. The subadult plants were grown in conifer needle mould with vermiculite watered by distilled water (Table 1b). The length and width of both lobes of the snapping traps were measured independently. Thus, the total 'leaf area' is the sum of 'leaf areas' of the both leaf lobes. All mineral nutrient analyses were repeated 9–10 times. A similar experiment was performed with *Drosera peltata* plants grown in a fen soil (Table 1d) and watered by distilled water. From 12 plants, leaf laminae of *c.* 50 adult (17th March) and *c.* 60 senescent leaves (27th April) were excised. All mineral nutrient analyses were performed four times. A preliminary experiment was also performed with adult *Drosera scorpioides* plants grown in a fen soil (Table 1d) and watered by distilled water. From 10 plants, leaf laminae of 12 adult and *c.* 40 senescent leaves were excised. Due to the small size of the leaves, only two parallel nutrient analyses were performed. For the calculation of nutrient re-utilization in this species and *D. peltata*, the decrease of d. wt of adult *D. capensis* leaves was used. No plants of any of the four species were allowed to flower during the experiment. It was only necessary to excise developing flower stalks in *D. capensis.*

Growth experiment

A growth experiment was performed on three perennial rosette *Drosera* species to reveal the efficiency of foliar mineral nutrient supply on root mineral nutrient uptake from soil (Adamec *et al.*, 1992). The seeds of *D. capillaris*, *D. aliciae* Hamet (South Africa), and *D. spathulata* Labill. (Australia) were sown on a fen soil with perlite in an insect-proof container in the glasshouse on 15th November 1999. On 27th April 2000, 90 homogeneous seedlings (rosette diameter *c.* 10–12 mm) of each of the three species were carefully selected. Eighty randomly selected seedlings of each species with intact root systems were planted in 16 10 × 10 × 10 cm plastic pots (five seedlings per pot) in a filamentous fen soil with *c.* 10% (v/v) of washed sand (Table 1d). Initial root length of the seedlings was measured. In 10 plants of each species, initial root and shoot d. wt (80°C) was measured. In each species, 20 seedlings in four pots represented controls or fertilized treatment for the growth experiment. For 5 d after the transplantation, all plants were sprayed gently with distilled water to reduce their transpiration. Every week from 3 May until 6 June 2000, one drop of a mineral nutrient solution (volume 2 µl) was placed onto each of the two largest leaves of all plants in the fertilized variant using an automatic micropipette. The same nutrient solution (in mM, NH_4NO_3 2.5; KH_2PO_4 0.74; $MgSO_4$ 0.41; $CaCl_2$ 1.0; $FeCl_3$ 0.016) was used as in the previous study (Adamec *et al.*, 1992). Every week from 15 June to 23 August, a further 3 µl drops of the solution were dropped in the same way. In *D. spathulata*, the plants were fertilized only until 26th July. The control plants were treated in the same way with the same volume of distilled water. Thus, during the whole growth experiment, 90 µl of the nutrient solution or distilled water was supplied to each *D. capillaris* and *D. aliciae* plant, while only 66 µl was supplied to each *D. spathulata* plant. In total, 6.44 µg N, 2.21 µg P, 2.32 µg K, 3.57 µg Ca, and 0.80 µg Mg was supplied to each fertilized *D. capillaris* and *D. aliciae* plant, while 73.3% of this amount was supplied to *D. spathulata* during the experiment.

In *D. capillaris* and *D. aliciae*, parallel sets of 20 seedlings in four pots were treated in the same way. At the end of the growth experiment, they were used for root respiration measurements. The 3-µl drops were checked by weighing and their true volume could be greater by 20–25%.

During the growth experiment in the glasshouse, all pots with the plants stood in distilled water in the same insect-proof plastic container as above, but its height was 30 cm and the irradiance on the level of plants was *c.* 19.5% of that in the open. In the container, all pots with the plants had their position changed by rotation regularly every week. *D. capillaris* and *D. aliciae* were grown for 125 d, to 30 August, while *D. spathulata* was grown for 95 d, to 31 July Longest leaf length (± 0.5 mm), number of live leaves, and occurrence of flower organs were estimated in all plants at 1-month intervals. At the end of the experiment, the plants were carefully released from the fen soil and their excised roots washed thoroughly with tap water until all attached soil particles were removed. Root length was measured with a plastic ruler. Roots, shoots, and reproductive organs at each stage of development were dried (80°C) and weighed to the nearest 0.01 mg. Dead parts of the organs were removed. Tissue N, P, K, Mg, and Ca content in roots, shoots and reproductive organs, both at the beginning and the end of the experiment, were estimated in 3–5 parallel samples from different pots. Several organs from one pot were usually pooled together. The efficiency of utilization of single leaf-supplied nutrients for their own accumulation in the final total plant biomass (i.e. stimulation of root nutrient uptake from soil) was calculated for each species as (F–C): S; where F, total nutrient content in the leaf-fertilized variant; C, total nutrient content in controls; S, total nutrient content supplied onto the leaves (Aldenius *et al.*, 1983; Adamec *et al.*, 1992; Hanslin & Karlsson, 1996; Adamec, 1997a). At the end of the growth experiment, oxygen-based respiration rate was measured in whole roots of the parallel *Drosera* plants as a criterion of their metabolic activity. For one measurement, roots of three plants (f. wt, 5–20 mg) were pooled. Respiration rate was measured in the 50 times diluted mineral nutrient solution, which was used in the growth experiment, in an 8-ml stirred thermostatted chamber at 22.0 ± 0.1°C and in darkness, using a Clark-type oxygen sensor (Labio, Prague, Czech Republic) and a pen recorder (Adamec, 1997b). Oxygen concentration during the measurements was 80–90% of saturation.

Origin of the plant material

The plant material of *Dionaea muscipula*, *Drosera capensis*, *D. capillaris*, *D. peltata*, *D. aliciae*, and *D. spathulata* was provided from the carnivorous plant collection in the Institute of Botany at Třeboň, Czech Republic, *D. scorpioides* from a private collection at Ostrava, Czech Republic, and *D. capillaris* seeds from the Botanical Garden at Liberec, Czech Republic.

Chemical analyses

Values of pH in the soils were measured with a pH electrode in soil suspensions (1 g of soil f. wt + 4 ml of distilled water). Available mineral nutrient content in the soils was determined using an extracting solution (1.22 M sodium acetate and 0.52 M acetic acid, pH 4.80, 5 min) after Morgan and Wolf (Wolf, 1982). In soil extracts filtered through GF/C glass microfiber filters (Whatman, Maidstone, UK), NH_4 ± N and PO_4-P concentrations were determined colorimetrically by an automatic FIAstar 5010 Analyzer (Tecator, Höganäs, Sweden), while K, Ca, and Mg concentrations were estimated by atomic absorption flame spectrometry using an analyzer SpectrAA 640 (Varian Techtron, Melbourne, Australia). The nutrient solution used for leaf nutrient supply in the growth experiment was analyzed in the same way and its exact composition was: NH_4 ± N, 42.6 mg l^{-1}; NO_3^--N, 29.0 mg l^{-1}; PO_4-P, 24.6 mg l^{-1}; K^+, 25.8 mg l^{-1}; Ca^{2+}, 39.7 mg l^{-1}; Mg^{2+}, 8.86 mg l^{-1}. This composition was used for all calculations. NO_3^--N concentrations were also determined using the FIAstar 5010 Analyzer. NO_3^--N was determined using a Cd reductor and the sulphanilamide method, to form a diazo compound, with N-(1-naphtyl)-ethylenediamine dihydrochloride. NH_4 ± N was determined colorimetrically in an acid-base indicator, after alkalization of the sample and the diffusion of the released NH_3 through a gas-permeable membrane, and PO_4-P using the phosphomolybdate blue method (for all methods see Ruzicka & Hansen, 1981).

Mineral content of intact and spent fruit flies and mosquitoes was estimated in diluted mineralized samples. For N analyses, the carcasses were mineralized with 0.2 ml of 98% H_2SO_4 (190°C, 6 h), for P, with 0.15 ml of 60% $HClO_4$ (170°C, 3 h), and for K, Ca, and Mg analyses, with 0.15 ml of 65% of HNO_3 (140°C, 30 min). Dry plant biomass was mineralized in the same way in 12 ml mineralization flasks. When necessary, larger plant organs were ground in a mini-mortar. About 1.0–2.5 mg of d. wt was mineralized for N analyses, 1.5–4.0 mg for P, and 2.0–4.5 mg for cation analyses. N, P, and cation concentrations in the mineralizates were determined as above. Blank samples were used for all mineralization methods. Nutrient analyses always included plants from different pots.

Where possible all paired data were statistically evaluated by a two-tailed paired *t*-test. Since the biometric data for the groups of five plants within the same pots in the growth experiment are dependent on each other, means of four parallel pots were always taken into account. Other data were processed by one-way ANOVA (Tukey HSD test).

Results

The total mineral content in intact mosquitoes as model prey was about 3.5–109 times greater than that in fruit flies (Table 2). Per unit d. wt, mosquitoes were a richer source of

Table 3 Mineral nutrient absorption from standard prey (fruit flies, *Drosophila melanogaster* and mosquito *Culex pipiens*) by *Drosera capillaris* and *Drosera capensis*

Species	Nutrient	Prey	Content (μg per prey)	SE	*n*	Absorbed nutrient (%)
D. capillaris[a]	N	Fruit fly	9.4	0.6	7	50.3
″	P	″	0.28	0.04	6	89.5
″	K	″	0.36	0.07	6	86.5
″	Ca	″	0.25	0.04	6	–54.1
″	Mg	″	0.13	0.02	6	57.4
D. capillaris[b]	N	Fruit fly	7.2	0.5	10	61.6
″	P	″	0.093	0.010	9	96.5
″	K	″	1.1	0.2	10	59.8
″	Ca	″	0.18	0.02	10	–10.7
″	Mg	″	0.069	0.015	10	76.5
D. capensis	N	Fruit fly	10.8	0.8	7	42.9
″	P	″	0.22	0.06	7	91.6
″	K	″	0.095	0.019	6	96.4
″	Ca	″	0.49	0.05	6	–206
″	Mg	″	0.12	0.02	6	59.7
D. capensis	N	Mosquito	37.1	7.6	5	43.7
″	P	″	11.2	2.0	5	61.2
″	K	″	0.79	0.26	4	94.0
″	Ca	″	7.2	0.7	4	57.6
″	Mg	″	0.53	0.11	4	91.5

n, number of independent samples analysed. [a]plants with higher mineral nutrient content in leaves. [b] plants with lower mineral nutrient content in leaves. The negative sign indicates accumulation of the nutrient in the prey. Mean mineral nutrient content remaining in one digested prey and mean percentage of absorbed nutrient are shown.

Table 4 Tissue nutrient content in leaves of *Drosera capillaris* plants used in two experiments on nutrient absorption from fruit flies

Water for watering	N	P	K	Ca	Mg
			% d. wt		
Tap water	1.51–1.65	0.081–0.095	1.54–2.02	0.52–0.53	0.36–0.38
Distilled water	1.12–1.30	0.031–0.042	1.30–1.55	0.45–0.51	0.25–0.26

Duplicate values are always shown.

Ca and Mg than fruit flies. Absorption of N, P, K, and Mg from both prey species was relatively efficient (> 43%) in *D. capillaris* and *D. capensis*. However, neither species of *Drosera* could absorb Ca from fruit flies, only *D. capensis* could from calcium-rich mosquitoes (Table 3). In both plant species, 43–62% N, 61–97% P, 60–96% K, and 57–92% Mg were absorbed from the two prey species. With the exception of K, the efficiency of nutrient absorption from fruit flies was greater in the *D. capillaris* variant with lower tissue nutrient content than in that with greater content (cf. Table 4).

All four carnivorous species exhibited a high efficiency of N, P, and K re-utilization (recycling) from senescent leaves, whereas a considerable loss of Ca (–32 to –119% of the initial amount) or slight Mg re-utilization or loss to the leaves (33 to –75%; Table 5). The efficiency of re-utilization of N was 70–82%, P 51–92%, and of K 41–99%. Thus, K was the most efficiently re-utilized element from senescing leaves of all species except for *D. peltata*. As available Ca and Mg content in all soils used throughout the study was relatively high (Table 1) Ca and Mg plant tissue content was also relatively high. This fact could influence the patterns of Ca and Mg absorption from prey and re-utilization. The following linear correlation was obtained in adult *Drosera capensis* leaves between 'leaf area' (A) in mm^2 and d. wt. (mg) of leaf traps: A = 22.7 d. wt + 118.7 ($n = 12$; $r = 0.84$; $P < 0.01$), while A = 42.9 d. wt + 53.4 ($n = 16$; $r = 0.78$; $P < 0.01$) in senescent leaves. In *Dionaea muscipula*, the correlation was found in adult leaves: A = 17.5 d. wt + 70.4 ($n = 17$; $r = 0.93$; $P < 0.01$), while A = 21.8 d. wt + 95.8 ($n = 16$; $r = 0.94$; $P < 0.01$) in senescent leaves. Thus, before they senesced adult *Drosera capensis* leaves lost on average 30% of d. wt and *Dionaea muscipula* leaves 28%.

In all three *Drosera* species, leaf nutrient supply resulted in marked growth enhancement (Fig. 1, Table 6). After 64 d, the fertilized variants of *D. capillaris* and *D. aliciae* differed statistically significantly (at least at $P < 0.05$) from the non-fertilized controls in length of the longest leaf and the number of live leaves (Fig. 1a,b). In *D. spathulata*, the only statistically

Table 5 Re-utilization of N, P, K, Ca, and Mg from senescing carnivorous plant leaves

Element	Content in adult leaves (% d. wt)	SE	n	Content in senescent leaves (% d. wt)	SE	n	Re-utilization (% of initial amount)
	Drosera capensis						
N	1.42	0.12	10	0.36	0.05	9	82.4 ± 3.5
P	0.12	0.01	9	0.014	0.003	7	92.2 ± 2.3
K	1.48	0.07	10	0.45	0.09	10	79.0 ± 4.9
Ca	0.46	0.04	10	1.23	0.14	13	−87.8 ± 59.1
Mg	0.24	0.01	10	0.43	0.03	13	−23.2 ± 14.1
	Drosera peltata						
N	1.70	0.13	4	0.54	0.06	4	77.8 ± 3.8
P	0.12	0.01	4	0.025	0.002	4	85.7 ± 1.7
K	1.17	0.05	4	1.00	0.14	4	40.7 ± 10.1
Ca	0.26	0.03	4	1.05	0.06	4	−187 ± 50
Mg	0.22	0.01	4	0.44	0.02	4	−44.6 ± 15.7
	Drosera scorpioides						
N	1.62	–	2	0.70	–	2	69.8
P	0.048	–	2	0.0088	–	2	87.2
K	2.56	–	2	0.088	–	2	97.6
Ca	0.34	–	2	0.63	–	2	−31.9
Mg	0.31	–	2	0.30	–	2	33.2
	Dionaea muscipula						
N	2.16	0.11	10	0.60	0.09	10	80.1 ± 3.7
P	0.21	0.01	10	0.15	0.02	9	50.6 ± 8.8
K	1.20	0.09	10	0.017	0.007	10	99.0 ± 0.4
Ca	0.34	0.04	10	1.05	0.06	10	−119 ± 66
Mg	0.19	0.01	10	0.47	0.03	10	−75.2 ± 19.4

Values of mean leaf tissue elemental content are shown for adult and senescent leaves. Percentage of re-utilized elements was corrected for the decrease in d. wt of senescent leaves by 30.0% of that of adult leaves in *Drosera capensis*, *D. peltata*, and *D. scorpioides*, and by 28.1% in *Dionaea muscipula*. A negative sign indicates accumulation of the nutrient in senescent leaves. Mean values ±1 SE are shown where possible; *n*, number of independent samples analysed.

significant difference was in leaf length after 64 d (Fig. 1c). At the end of the growth experiment after 125 d, the fertilized variants of *D. capillaris* and *D. aliciae* differed statistically significantly from the nonfertilized controls in root length, root d. wt, shoot d. wt, and total d. wt. However, in *D. spathulata* after 95 d, leaf nutrient supply led to a statistically significant increase only in total d. wt (Table 6). At the end of the experiment, the increase of total plant d. wt in the fertilized variant was 88% greater than in the controls in *D. capillaris*, 120% in *D. aliciae*, and 81% in *D. spathulata*. The relative growth rates (RGR) of the controls of all three species ranged from 0.010–0.013 d^{-1}, and from 0.014–0.018 d^{-1} in the variants. In the three *Drosera* species, no control plants flowered. Leaf nutrient supply enhanced flowering in *D. capillaris* and *D. spathulata.* Flowering attained 25% in *D. capillaris* and 85% in *D. spathulata*. The former species allocated on average *c.* 8% of the total plant d. wt to reproductive biomass, while the latter species allocated 26%.

Root and shoot N, P, K, Ca, and Mg tissue content per unit d. wt of the fertilized variants and the controls at the end of the growth experiment were compared (Tables 7 and 8). In all three *Drosera* species, the final root or shoot nutrient content in the fertilized variant ($n = 30$ cases) was statistically significantly greater than that in the controls in only three cases. No statistically significant difference was found in 25 cases, while the controls had statistically significantly greater tissue nutrient content than the fertilized variants in only two cases (shoot N content in *D. aliciae* and shoot Mg content in *D. capillaris*). Nutrient-fed plants of all three species contained 1.50–1.79 times more total N, 1.64–2.17 times more P, 1.56–2.15 times more K, 1.45–2.07 times more Ca, and 1.36–2.03 times more total Mg in their final biomass than control plants (Tables 7 and 8). A very high efficiency for the use of supplied mineral nutrients for nutrient accumulation in total plant biomass was found with the sole exception of P (Table 9). For the three species, the efficiency was 7.9–14 for N, 21–27 for K, 5.4–8.7 for Ca, and 6.4–13 for Mg, but only 0.67–0.87 for P. Oxygen-based respiration rate of roots of nutrient-fed plants of *D. capillaris* was 50% greater than that of the controls (at $P < 0.05$), while the opposite effect was found in *D. aliciae* (but $P > 0.05$; Table 10).

Discussion

It is generally accepted that mineral nutrients are the most important substances that carnivorous plants absorb from

Table 6 Results of growth experiment on Drosera seedlings in a glasshouse

Parameter	*D. capillaris*		*D. aliciae*		*D. spathulata*	
	Controls	Fertilized	Controls	Fertilized	Controls	Fertilized
Initial root length (cm)	5.06 ± 0.43		2.81 ± 0.26		4.20 ± 0.32	
Final root length (cm)	7.97 ± 0.30	9.47 ± 0.51*	4.65 ± 0.24	5.41 ± 0.14*	7.98 ± 0.70	8.56 ± 0.26^{ns}
Initial root d. wt (mg)	0.53		0.17		0.35	
Final root d. wt (mg)	1.34 ± 0.08	2.01 ± 0.13**	0.76 ± 0.15	1.62 ± 0.11**	1.05 ± 0.18	1.35 ± 0.11^{ns}
Initial shoot d. wt (mg)	1.52 ± 0.24		0.83 ± 0.08		1.24 ± 0.15	
Final shoot d. wt (mg)	5.84 ± 0.49	8.71 ± 0.53**	4.23 ± 0.24	8.14 ± 0.26**	4.39 ± 0.62	4.94 ± 0.19^{ns}
Final reproduct d. wt (mg)	0.00	0.95 ± 0.40	0.00	0.00	0.00	2.26 ± 0.37
Total initial plant d. wt (mg)	2.05		1.00		1.58	
Total final plant d. wt (mg)	7.18 ± 0.57	11.7 ± 1.06**	4.99 ± 0.39	9.76 ± 0.37**	5.44 ± 0.80	8.55 ± 0.67*
Final root : shoot ratio	0.23	0.21	0.18	0.20	0.24	0.19
Flowering (% of plants)	0.0	25	0.0	0.0	0.0	85
Relative growth rate (d^{-1})	0.0100	0.0139	0.0129	0.0182	0.0130	0.0178

The growth period lasted for 125 d for *D. capillaris* and *D. aliciae* and 95 d for *D. spathulata*. Drops of a nutrient solution were supplied onto the leaves of the plants denoted as fertilized. The reproductive d. wt includes all stages of flower and seed development. Mean values ±1 SE are shown where possible; $n = 4$ parallel pots. Statistically significant difference between control and fertilized plants is denoted for each species. Statistical significance: *, $P < 0.05$; **, $P < 0.01$; ns, nonsignificant.

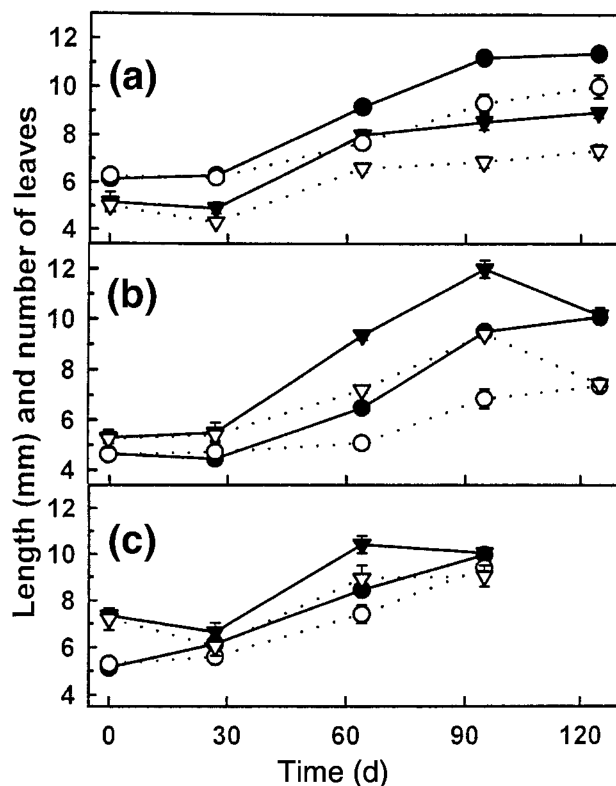


Fig. 1 Longest leaf length (circles) and number of live leaves (triangles) of *Drosera capillaris* (a), *Drosera aliciae* (b), and *Drosera spathulata* (c) during the growth experiment. Full symbols and full lines, plants fertilized with mineral nutrient solution onto the leaves; empty symbols and dotted lines, plants treated with drops of distilled water (controls). Mean values ±1 SE intervals are always shown; $n = 4$ parallel pots.

prey (Lüttge, 1983; Juniper *et al.*, 1989; Adamec, 1997a). The level of mineral macronutrients available to plants from the soil (N, P, K, Ca, Mg) is usually very low and is presumably the primary unfavourable ecological factor in most habitats of carnivorous plants. This nutrient limitation is overcome by carnivory. Furthermore, it has been verified repeatedly that a supply of a mineral nutrient solution alone when put onto the leaves of carnivorous plants can support the growth of carnivorous plants just as adequately as feeding on prey (Adamec, 1997a). For this reason considerable attention was paid in the present study to fluxes of N, P, K, Ca, and Mg in carnivorous plants.

Mineral nutrient uptake from prey

Knowledge of the efficiency of mineral nutrient absorption from prey is basic for assessing the proportion of the seasonal nutrient gain which can be met by carnivory (Dixon *et al.*, 1980; Watson *et al.*, 1982; Karlsson *et al.*, 1987; Karlsson, 1988; Thum, 1988; Karlsson *et al.*, 1994; Hanslin & Karlsson, 1996; Karlsson *et al.*, 1996; Zamora *et al.*, 1997). Hanslin & Karlsson (1996) found the ecological efficiency of N absorption from fruit flies in *Drosera rotundifolia* and three *Pinguicula* species in a subarctic environment to be only 29–42%, whereas it was 39–50% in a glasshouse.

The efficiency of N absorption (43–62%) from prey in the both *Drosera* species was considerably lower compared with the values for P (61–97%), K (60–96%), and Mg (57–92%; Table 3). However, Dixon *et al.* (1980) estimated a 76% efficiency of N absorption from fruit flies in the rhizomatous *D. erythrorhiza* when grown under glass. An unknown proportion of all mineral nutrients in insect carcasses will be unavailable for absorption by carnivorous plant traps since this part

Table 7 Plant tissue content of N and P at the start and the end of the growth experiment for *Drosera capillaris*, *Drosera aliciae* and *Drosera spathulata*

	D. capillaris		*D. aliciae*		*D. spathulata*	
Parameter	Controls	Fertilized	Controls	Fertilized	Controls	Fertilized
Initial root N content (% d. wt)	1.57		0.87		0.62	
Final root N content (% d. wt)	1.65 ± 0.14	1.47 ± 0.13^{ns}	2.06 ± 0.36	1.93 ± 0.26^{ns}	1.17 ± 0.10	1.51 ± 0.08*
Init. shoot N content (% d. wt)	2.11 ± 0.07		1.34		1.40 ± 0.14	
Final shoot N content (% d. wt)	1.63 ± 0.06	1.92 ± 0.07*	1.95 ± 0.10	1.45 ± 0.03**	1.59 ± 0.12	1.47 ± 0.07^{ns}
Reproduct. N content (% d. wt)	–	1.36 ± 0.35	–	–	–	1.33 ± 0.08
Total initial plant N (µg)	40.5		12.6		19.4	
Total final plant N (µg)	117 ± 12	210 ± 23*	98.1 ± 14.0	149 ± 14*	82.1 ± 12.0	123 ± 15^{ns}
Initial root P content (% d. wt)	0.019		0.031		0.034	
Final root P content (% d. wt)	0.017 ± 0.003	0.019 ± 0.001^{ns}	0.021 ± 0.001	0.029 ± 0.003*	0.018 ± 0.003	0.012 ± 0.002^{ns}
Init. shoot P content (% d. wt)	0.031 ± 0.001		0.033		0.043 ± 0.008	
Final shoot P content (% d. wt)	0.036 ± 0.001	0.037 ± 0.003^{ns}	0.035 ± 0.002	0.038 ± 0.003^{ns}	0.034 ± 0.002	0.034 ± 0.003^{ns}
Reproduct. P content (% d. wt)	–	0.023 ± 0.014	–	–	–	0.054 ± 0.001
Total initial plant P (µg)	0.57		0.33		0.65	
Total final plant P (µg)	2.33 ± 0.23	3.82 ± 0.58^{ns}	1.64 ± 0.21	3.56 ± 0.45**	1.68 ± 0.24	3.06 ± 0.47*

Mean values ±1 SE are shown where possible, n = 3–5. Statistically significant difference between control and fertilized plants is denoted for each species. Statistical significance: *, $P < 0.05$; **, $P < 0.01$; ns, nonsignificant.

Table 8 Plant tissue content of K, Ca, and Mg at the start and the end of the growth experiment for *Drosera capillaris*, *Drosera aliciae* and *Drosera spathulata*

	D. capillaris		*D. aliciae*		*D. spathulata*	
Parameter	Controls	Fertilized	Controls	Fertilized	Controls	Fertilized
Initial root K content (% d. wt)	0.52		–		0.72	
Final root K content (% d. wt)	0.33 ± 0.02	0.41 ± 0.03^{ns}	0.43 ± 0.06	0.52 ± 0.08^{ns}	0.63 ± 0.05	0.72 ± 0.03^{ns}
Init. shoot K content (% d. wt)	1.49 ± 0.13		1.27		1.40 ± 0.04	
Final shoot K content (% d. wt)	1.46 ± 0.09	1.54 ± 0.05^{ns}	1.22 ± 0.04	1.35 ± 0.07^{ns}	1.30 ± 0.08	1.39 ± 0.04^{ns}
Reprod. K content (% d. wt)	–	0.54 ± 0.08	–	–	–	0.94 ± 0.04
Total initial plant K (µg)	25.4		11.6		19.8	
Total final plant K (µg)	89.7 ± 10.7	148 ± 13*	54.9 ± 5.9	118 ± 12**	63.7 ± 8.5	99.6 ± 10.0*
Initial root Ca content (% d. wt)	0.54		–		0.39	
Final root Ca content (% d. wt)	0.48 ± 0.03	0.45 ± 0.03^{ns}	0.33 ± 0.02	0.30 ± 0.01^{ns}	0.44 ± 0.02	0.48 ± 0.02^{ns}
Init. shoot Ca content (% d. wt)	0.71 ± 0.08		0.76		0.79 ± 0.05	
Fin. shoot Ca content (% d. wt)	0.62 ± 0.03	0.57 ± 0.02^{ns}	0.63 ± 0.05	0.68 ± 0.03^{ns}	0.70 ± 0.03	0.75 ± 0.02^{ns}
Reprod. Ca content (% d. wt)	–	0.34 ± 0.01	–	–	–	0.47 ± 0.03
Total initial plant Ca (µg)	13.7		7.10		11.1	
Total final plant Ca (µg)	42.6 ± 4.6	61.9 ± 6.0*	29.1 ± 4.3	60.2 ± 5.3*	35.4 ± 4.0	54.1 ± 5.5*
Init. root Mg content (% d. wt)	0.062		–		0.045	
Final root Mg content (% d. wt)	0.057 ± 0.002	0.056 ± 0.003^{ns}	0.051 ± 0.001	0.061 ± 0.004^{ns}	0.042 ± 0.003	0.046 ± 0.001^{ns}
Init. shoot Mg content (% d. wt)	0.25 ± 0.02		0.34		0.27 ± 0.004	
Fin. shoot Mg content (% d. wt)	0.23 ± 0.01	0.19 ± 0.005**	0.23 ± 0.02	0.24 ± 0.01^{ns}	0.18 ± 0.01	0.19 ± 0.01^{ns}
Reprod. Mg content (% d. wt)	–	0.17 ± 0.03	–	–	–	0.20 ± 0.01
Total initial plant Mg (µg)	4.13		2.91		3.49	
Total final plant Mg (µg)	14.2 ± 1.4	19.3 ± 2.0^{ns}	10.1 ± 1.5	20.5 ± 1.8**	8.34 ± 1.01	4.5 ± 1.8*

Mean values ±1 SE are shown where possible, n = 3–5. Statistically significant difference between control and fertilized plants is denoted for each species. Statistical significance: *, $P < 0.05$; **, $P < 0.01$; ns, nonsignificant.

of the nutrient pool cannot be digested. Chitinous insect exoskeletons contain N as poly N-acetyl-glucose-amine and are not digested in the traps (Juniper *et al.*, 1989). It is also probable that various cultures of fruit flies differ from each other in the proportion of unavailable nutrient pools. Although Ca uptake from a solution was shown to occur in *Droseraceae* traps (Juniper *et al.*, 1989) no Ca was absorbed from fruit flies by either of the two *Drosera* species (Table 3). All plants used for this experiment had very high Ca leaf tissue content (Tables 4 and 5; cf. Adamec, 1997a), which could

Table 9 The efficiency of the use of mineral nutrients N, P, K, Ca, and Mg supplied onto *Drosera* leaves for accumulation of the mineral nutrients in total plant biomass, during the growth experiment

	Efficiency of use of added nutrients				
Species	N	P	K	Ca	Mg
D. capillaris	14.4 ± 5.4	0.67 ± 0.37	25.1 ± 10.2	5.4 ± 3.0	6.4 ± 4.3
D. aliciae	7.9 ± 4.3	0.87 ± 0.30	27.2 ± 7.7	8.7 ± 2.7	13.0 ± 4.1
D. spathulata	8.7 ± 5.7	0.85 ± 0.44	21.1 ± 10.9	7.1 ± 3.6	10.5 ± 4.8

The efficiency is defined as [total nutrient content in the fertilized plants *minus* total nutrient content in controls] divided by total nutrient content supplied onto the leaves. Mean values ±1 SE are shown; n = 3–5.

Table 10 Aerobic respiration rate of excised roots of *Drosera* plants

	Respiration rate (mmol kg^{-1} f. wt h^{-1})	
Species	Controls	Fertilized
D. capillaris	6.0 ± 0.6[a]	9.1 ± 1.2[b]
D. aliciae	12.5 ± 2.3[a]	9.8 ± 0.4[a]

Drosera plants were treated by drops of distilled water (controls) or nutrient solution (fertilized) onto their leaves for 4 months. The intervals ±1 SE are shown; n = 6. The same letter within single rows denotes no statistical significant difference at $P < 0.05$.

inhibit Ca absorption. But the finding of a 58% Ca absorption from Ca-rich mosquitoes (Ca content per d. wt *c.* 21 times greater than in fruit flies) by *D. capensis* leaves proves that Ca availability in prey is the principal factor that decides whether or not Ca is absorbed from a prey or secreted to it. Because Rost & Schauer (1977) found high concentrations of Ca (22 mM) and Mg (19 mM) but only 0.9 mM K in mucilage of resting *D. capensis* tentacles it is possible to assume that a high Ca and Mg concentration is also kept in mucilage during the digestion of prey and nutrient absorption. On the other hand, the low K concentration in mucilage could be associated with a very high K absorption efficiency (Table 3).

The efficiency of absorption of all mineral nutrients except K from fruit flies was 7–43% greater in *D. capillaris* plants with slightly lower leaf mineral content, when watered with distilled water, than when plants were watered with tap water (Tables 3 and 4). Presumably, this tap-water effect was caused by the higher level of leaf mineral content. However, more data are needed to prove this relationship. Hanslin & Karlsson (1996) found in *D. rotundifolia* and three *Pinguicula* species that N absorption efficiency from fruit flies depended neither on feeding quantity nor plant flowering. The period of fruit fly application used in the present study lasted for only 15 d (22 d for mosquitoes). It was only half the period used by Dixon *et al.* (1980) and Hanslin & Karlsson (1996). Nevertheless, due to the great efficiency of P and K absorption the period was sufficient. As suggested by the latter authors higher temperatures should accelerate prey digestion and nutrient absorption.

Mineral nutrient re-utilization

Efficiency of mineral nutrient re-utilization from senescent plant organs is an important ecophysiological characteristic which may indicate the degree of plant adaptation to soil nutrient availability and growth strategy (Aerts *et al.*, 1999). As proposed by Adamec (1997a) carnivorous plants, due to their relatively small root system, should re-utilize mineral nutrients more efficiently than accompanying noncarnivorous plants with a greater root system, as an adaptation to low soil mineral content. It is generally accepted that noncarnivorous plants are able to re-utilize N, P, and K from senescing leaves (shoots) relatively efficiently, but their Mg re-utilization is very low or zero and that of Ca highly negative (i.e. enrichment in Ca; Marschner, 1995). The pattern of mineral nutrient re-utilization was similar in all four *Droseraceae* species despite their different growth forms (Table 5). About 28–30 % of d. wt of adult traps was also re-utilized. The tissue content of N, P, K, and Mg in adult leaves of these species was comparable with the literature data for carnivorous plants (cf. Adamec, 1997a) but that of Ca (0.26–0.46% of d. wt) was 2–3 times greater.

In senescing leaf rosettes of tuberous *Drosera erythrorhiza* grown in a glasshouse, Pate & Dixon (1978) reported an efficient re-utilization of dry biomass (71%), P (88%), N (79%), Mg (63%), but a lesser re-utilization for K (56%), Zn (39%), and Ca (25%). However, nutrient re-utilization from senescing parental tubers was much more efficient (d. wt, 89%; P, 98%; N, 95%; Mg 83%; K 99%, Zn 99%), while Ca was accumulated (+56%) in the old tubers. Using ^{15}N distribution in this species in a glasshouse, Dixon *et al.* (1980) estimated a 94% re-utilization of N from leaf rosettes and even 99% from stems. Thus, efficiency of nutrient re-utilization may vary in different plant organs and possibly depends on nutrient tissue content and conditions of growth as found in noncarnivorous plants (Chapin & Shaver, 1989). In leaves of field-grown *Sarracenia purpurea*, Small (1972) estimated an efficiency of 56% for N re-utilization, 75% for P, and 89% for K. Hanslin & Karlsson (1996) supported the idea of efficient N re-utilization in *D. rotundifolia* and three *Pinguicula* species. Approximately 58–97% of prey-derived N (or applied onto the leaves as NH_4NO_3) was found in ripe winter buds in these field-grown species. However, efficiency of mineral

Table 11 Total root uptake of mineral nutrients in three *Drosera* species in the growth experiment in the fertilized variant, expressed as percentage of the controls, and theoretical root uptake rates of mineral nutrients in the fertilized variant

Species	Total root uptake (% of controls)					Root uptake rate (% of controls)					Root d. wt (%)	Root length (%)
	N	P	K	Ca	Mg	N	P	K	Ca	Mg		
D. capillaris	213	53	187	154	143	157	43	138	115	106	150	119
D. aliciae	152	78	240	225	234	86	40	125	117	121	213	116
D. spathulata	158	77	182	166	215	127	63	147	137	177	129	109
Mean	174	69	203	182	197	123	49	137	123	135	164	115

The uptake rates are calculated as the increase in total nutrient content *minus* the content supplied onto the leaves, related to mean root d. wt. ([initial d. wt + final d. wt]: 2), and expressed as percentage of the controls. The values of final root d. wt and root length of the fertilized variant, both as percentage of the controls, are also shown for comparison. Mean values for the three species are always shown. All values are based on mean values in Tables 6–8.

nutrient re-utilization might differ considerably in the case of nutrient translocation to other growing young leaves during the growing season and/or in evergreening species, or to dormant winter buds (or aestivating tubers; *sensu* Marschner, 1995).

Aerts *et al.* (1999) summarized data on N and P re-utilization from senescent leaves of plants growing in temperate bogs and fens, that is habitats of many carnivorous plant species. Although the mean N and P tissue content in the leaves of noncarnivorous bog and fen species was comparable with that of carnivorous plants (cf. Juniper *et al.*, 1989; Adamec, 1997a) the mean efficiency of N re-utilization from senescent leaves of carnivorous plants of *c.* 70–75% is *c.* 25% greater than that in the bog and fen species; in the case of P, the mean of *c.* 75–80% is greater by *c.* 20–25%.

Effect of leaf nutrient supply on growth

The design of the growth experiment with three *Drosera* species made it possible to test the effect of foliar mineral nutrition on mineral uptake by roots. This experiment partly repeated one that was performed under less accurately controlled conditions (Adamec *et al.*, 1992). *D. capillaris* and *D. aliciae* belong to the group of 'nutrient-requiring species' and can markedly enhance their growth as a result of both leaf and root nutrient supply (Adamec, 1997a). Such information is not available for *D. spathulata*. The mineral nutrient solution used for the leaf nutrient supply contained mineral elements at ratios that corresponded to their content in plant tissues rather than in insects. The total amount of N supplied to one plant during the 125-d experiment was equal to *c.* 34% of total N in one fruit fly, 85% of total P and K, while 2250% of total Ca and 270% of Mg.

Judging from the length of the longest leaf and number of live leaves, the growth of the all the *Drosera* species was zero during the first month (Fig. 1), possibly due to a transplantation effect. The marked reduction in the number of leaves in *D. aliciae* during the last month could be caused by a higher sensitivity of this species to high temperatures or to low RH. Leaf nutrient supply led to increased growth rates in all three *Drosera* species over the experiment so that the increase of total plant biomass in the fertilized variants was 81–120% greater than that in the controls (Table 6). Leaf nutrient supply slightly decreased the root : shoot ratio of d. wt in *D. capillaris* and *D. spathulata* but not in *D. aliciae*. By contrast in an analogous study (Adamec *et al.*, 1992), roots of leaf-fertilized variants were 2.0–2.5 times longer than in the controls, while in the present study, they were longer by only 9–19% (Tables 6 and 11). Leaf nutrient supply also markedly supported flowering in *D. capillaris* and *D. spathulata*, while the control plants did not flower at all. Thum (1988) explained a similar result in insect-fed *D. rotundifolia* as faster reaching a minimum plant size necessary for flowering.

The tissue content of N, K, and Mg in the biomass of the three *Drosera* species (Tables 7 and 8) lay well within a usual range published for carnivorous plants (Juniper *et al.*, 1989; Adamec, 1997a). However, in the all species, the P tissue content both in roots, shoots and reproductive biomass was very low (0.012–0.054% of d. wt) indicating that the plant growth could be P limited. The P content in roots was about half that found in shoots. This might suggest that a part of root biomass (primary cortex in basal zone) was senescent in all the species. Very low P tissue content in the experimental plants could reflect very low available P content in the fen soil used (Table 1d). However, the leaf nutrient supply increased P tissue content in neither roots nor shoots, except in *D. aliciae* roots (Table 7), but plant growth was nevertheless enhanced. As a result of a high available Ca soil content, Ca tissue content in both roots (0.30–0.48% of d. wt; Table 8) and shoots (0.57–0.75% of d. wt) in the three species was 3–5 times greater than it was usually estimated to be in carnivorous plants (cf. Juniper *et al.*, 1989; Adamec, 1997a).

The leaf supply of relatively small amounts of mineral nutrients onto the leaves, as a substitution for prey-derived nutrients, led to increased N, P, K, Ca, and Mg accumulation in the total biomass of 1.4–2.2 times greater compared with the controls (Tables 7 and 8). Except for P, it is evident that a dominant proportion of these accumulated nutrients (*c.* 77–96%) had to be taken up from the soil by roots. The theoretical

efficiency of the use of single supplied mineral nutrients for their own increased accumulation in total plant biomass ranged from 5.4–27.2 for N, K, Ca, and Mg, but only 0.67–0.85 for P (Table 9). The very low efficiency of P use (cf. Adamec *et al.*, 1992) raises the question of whether the supplied phosphate was really taken up by leaves or whether the soil P content was extremely low for plant growth. The highest values were usually estimated in *D. aliciae*, due to its low initial biomass and high growth rate. Thus, the leaf-supplied mineral nutrients stimulated roots in an unknown way to take up extra mineral nutrients from the soil. So far, this phenomenon has been found in several temperate or (sub)tropical *Drosera* and *Pinguicula* species under various experimental conditions (Oosterhuis, 1927; Pate & Dixon, 1978; Aldenius *et al.*, 1983; Karlsson & Carlsson, 1984; Adamec *et al.*, 1992; Hanslin & Karlsson, 1996). In the latter field study, feeding of three *Pinguicula* species on prey in addition to natural catch of prey led to increased growth and N accumulation in the biomass. About 20–67% (mean 39%) of the increased N amount was estimated to be absorbed directly from the additional prey, while the remaining part (33–80%; mean 61%) was taken up by roots, as a result of root stimulation. Thus, on an ecological basis, natural catch of prey could *directly* provide only a minor part of N (2–40%) from the total seasonal N turnover (or gain) but the remaining part was *indirectly* provided as stimulation of N root uptake (Karlsson *et al.*, 1994; Hanslin & Karlsson, 1996). It is highly probable that these relations held also for P uptake. Recently, Osaki *et al.* (1997) have hypothesized the mechanism of root-shoot signalling of N nutrition in plants.

It follows from studies on *Pinguicula vulgaris* that the stimulation effect on roots was caused only by a combined leaf supply of N + P + microelements and occurred mainly in a nutrient-rich soil (Aldenius *et al.*, 1983; Karlsson & Carlsson, 1984). As hypothesized by Adamec *et al.* (1992) and Hanslin & Karlsson (1996) the stimulation of total root nutrient uptake could be caused by a higher efficiency of root uptake (i.e. higher uptake rate per unit root biomass) or bigger roots. In the present study, the measurement of respiration rate of whole roots, as a criterion of root metabolic activity, has given ambiguous results (Table 10). As shown in Tables 7 and 8, about 1.4–2.4 times (mean 1.7–2.0) more total N, K, Ca, and Mg was taken up by roots of leaf-fertilized plants compared with the controls (Table 11). However, when a theoretical mean root uptake rate (per unit mean root d. wt) is taken into account it reached only 86–177% (mean 123–137%) of the controls (Table 11). The increase in total N, K, Ca, and Mg in the leaf-fertilized variants corresponded much better to relative increase in root d. wt (mean 164%) than to root length (mean 115%; Table 11). Thus, the effect of the leaf nutrient supply on mineral nutrient uptake by roots in the three *Drosera* species could be caused mainly (*c.* 70–85% of the effect) by increased root biomass, while only to a lesser extent by increased root uptake rate (*c.* 15–30% of the effect) or increased root length (*c.* 17%). As only youngest parts of roots are usually active in mineral ion uptake (e.g. Marschner, 1995) it might be assumed that the active zone of roots in the leaf-fertilized variants is longer than that in the controls. As a much lower proportion of seasonal turnover of K, Ca, and Mg is absorbed from natural catch of prey in carnivorous plants than in the case of N and P (Watson *et al.*, 1982; Karlsson, 1988) the stimulation effect on roots should be greater for K, Ca, and Mg than for N and P. Otherwise, the growth enhancement due to carnivory would be limited by shortage of K, Ca, and Mg.

Conclusions

It is evident that two types of efficiencies of nutrient absorption from prey may be distinguished in carnivorous plants. Under glasshouse conditions, the efficiencies found (Dixon *et al.*, 1980; Hanslin & Karlsson, 1996) may be referred to as *physiological* as they represent the potential digestive and absorptive capacity of plants. Whereas, under field conditions, due to washing away of released nutrients and prey by rain, the *ecological* efficiency of nutrient absorption from nonrobbed prey may be considerably lower. Carnivorous plants re-utilize N, P, and K from their senescing shoots much more efficiently than do accompanying noncarnivorous plant species growing in the same habitats. Such an ecophysiological trait represents an important plant adaptation to combined unfavourable soil conditions along with catching of prey. However, in spite of growing in Ca-poor soils, carnivorous plants did not develop a special physiological mechanism to re-utilize Ca. They lose great amounts of Ca in senescent biomass. The absence of clear relationships between the tissue content of mineral nutrients and leaf nutrient supply (Tables 7 and 8) supports the view that mineral nutrient tissue content alone may not reflect an enhanced nutrient uptake from carnivory or soil nutrient supply in carnivorous plants (Adamec, 1997a).

The main nutritional benefit from carnivory may be based on increased root uptake of mineral nutrients from soils. Since the prevailing amount of mineral nutrients in carnivorous plants is gained by roots, the activity of which is stimulated by leaf nutrient absorption from prey, knowledge of their adaptations and functions is crucial for understanding mineral nutrition of carnivorous plants.

Acknowledgements

This study was funded by the Grant Agency of the Academy of Sciences of the Czech Republic (Project No. A6005909) and partly by the Research Programme of the Academy of Sciences of the Czech Republic (No. AV0Z6005908). Thanks are due to Mrs H. Strusková, Mrs M. Sergejevová, and Dr J. Bastl for skilful chemical analyses, Miss I. Pípalová, Mrs E. Zabilková, and Mrs H. Brabcová for technical assistance,

and Mrs J. Kollárová for cultivation of fruit flies. Thanks are also due to Mr K. Pásek, Drs M. Studnička, and V. Rybka for providing experimental plant material. I am grateful to Prof. R. M. M. Crawford for critically reading the manuscript and correction of the language.

References

Adamec L. 1997a. Mineral nutrition of carnivorous plants: A review. *Botanical Review* **63**: 273–299.

Adamec L. 1997b. Photosynthetic characteristics of the aquatic carnivorous plant *Aldrovanda vesiculosa*. *Aquatic Botany* **59**: 297–306.

Adamec L, Dušáková K, Jonáčková M. 1992. Growth effects of mineral nutrients applied to the substrate or onto the leaves in four carnivorous plant species. *Carnivorous Plant Newsletter* **21**: 18–24.

Aerts R, Verhoeven JTA, Whigham DF. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* **80**: 2170–2181.

Aldenius J, Carlsson B, Karlsson S. 1983. Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. *New Phytologist* **93**: 53–59.

Chapin FS III, Shaver GR. 1989. Differences in growth and nutrient use among arctic plant growth forms. *Functional Ecology* **3**: 73–80.

Dixon KW, Pate JS, Bailey WJ. 1980. Nitrogen nutrition of the tuberous sundew *Drosera erythrorhiza* Lindl. with species reference to catch of arthropod fauna by its glandular leaves. *Australian Journal of Botany* **28**: 283–297.

Hanslin HM, Karlsson PS. 1996. Nitrogen uptake from prey and substrate as affected by prey capture level and plant reproductive status in four carnivorous plant species. *Oecologia* **106**: 370–375.

Juniper BR, Robins RJ, Joel DM. 1989. *Carnivorous plants*. London, UK: Academic Press.

Karlsson PS. 1988. Seasonal patterns of nitrogen, phosphorus and potassium utilization by three *Pinguicula* species. *Functional Ecology* **2**: 203–209.

Karlsson PS, Carlsson B. 1984. Why does *Pinguicula vulgaris* L. trap insects? *New Phytologist* **97**: 25–30.

Karlsson PS, Nordell KO, Eirefelt S, Svensson A. 1987. Trapping efficiency of three carnivorous *Pinguicula* species. *Oecologia* **73**: 518–521.

Karlsson PS, Svensson BM, Carlsson BÅ. 1996. The significance of carnivory for three *Pinguicula* species in a subarctic environment. *Ecological Bulletins* **45**: 115–120.

Karlsson PS, Thorén LM, Hanslin HM. 1994. Prey capture by three *Pinguicula* species in a subarctic environment. *Oecologia* **99**: 188–193.

Lüttge U. 1983. Ecophysiology of carnivorous plants. In: Lange OL, Nobel PS, Osmond CB, Ziegler H, eds. *Encyclopedia of plant physiology. New Series, Vol. 12C*. Berlin, Germany: Springer-Verlag, 489–517.

Marschner H. 1995. *Mineral nutrition of higher plants*. London, UK: Academic Press.

Oosterhuis J. 1927. *Over de invloed van insectenvoeding op* Drosera. PhD thesis, University of Groningen, The Netherlands.

Osaki M, Shinano T, Matsumoto M, Zheng TG, Tadano T. 1997. A root–shoot interaction hypothesis for high productivity of field crops. *Soil Science and Plant Nutrition* **43**: 1079–1084.

Pate JS, Dixon KW. 1978. Mineral nutrition of *Drosera erythrorhiza* Lindl. with special reference to its tuberous habit. *Australian Journal of Botany* **26**: 455–464.

Rost K, Schauer R. 1977. Physical and chemical properties of the mucin secreted by *Drosera capensis*. *Phytochemistry* **16**: 1365–1368.

Ruzicka J, Hansen EH. 1981. *Flow injection analysis*. New York, USA: J. Wiley & Sons.

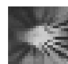
Small E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany* **50**: 2227–2233.

Thum M. 1988. The significance of carnivory for the fitness of *Drosera* in its natural habitat. 1. The reactions of *Drosera intermedia* and *D. rotundifolia* to supplementary feeding. *Oecologia* **75**: 472–480.

Watson AP, Matthiessen JN, Springett BP. 1982. Arthropod associates and macronutrient status of the red-ind sundew (*Drosera erythrorhiza* Lindl.). *Australian Journal of Ecology* **7**: 13–22.

Wolf B. 1982. An improved universal extracting solution and its use for diagnosing in soil fertility. *Communications of Soil Scientific Plant Analytics* **13**: 1005–1033.

Zamora R, Gómez JM, Hódar JA. 1997. Responses of a carnivorous plant to prey and inorganic nutrients in a Mediterranean environment. *Oecologia* **111**: 443–451.



About *New Phytologist*

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science. Regular papers, Letters, Research reviews, Rapid reports and Methods papers are encouraged. Complete information is available at **www.newphytologist.com**
- All the following are **free** – essential colour costs, 100 offprints for each article, online summaries and ToC alerts (go to the website and click on Synergy)
- You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £83 in Europe/$133 in the USA & Canada for the online edition (go to the website and click on Subscriptions)
- If you have any questions, do get in touch with Central Office (**newphytol@lancaster.ac.uk**; tel +44 1524 594691) or, for a local contact in North America, the USA Office (**newphytol@ornl.gov**; tel 865 576 5251)