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Soil fertilization enhances growth of the carnivorous plant *Genlisea violacea*

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Abstract: In a 116-d greenhouse growth experiment on a terrestrial carnivorous plant *Genlisea violacea* (Lentibulariaceae), mild fertilization of a peaty soil led to a 2.4 fold increase in total plant biomass as compared to the controls. Tissue P and K content in fertilized plants was significantly higher than that in the controls.

Key words: rootless carnivorous plant; Lentibulariaceae; soil enrichment; leaves; traps; tissue nutrient content

Introduction

Carnivorous plants of the genus *Genlisea* (Lentibulariaceae) are terrestrial, rootless species growing in wetlands in South America and Africa (Juniper et al. 1989; Reut 1993). *Genlisea* forms short stems with a rosette of small, photosynthetic, green leaves and subterranean white traps. The narrow, inverted Y-shaped chlorophyll-free traps up to 12 cm long are highly modified leaves. They function as "eel traps" and probably passively capture microscopic soil animals (e.g. protozoa; Barthlott et al. 1998; Płachno et al., 2005). The traps analogous to roots are submerged to very wet, nutrient-poor peaty soils. Though *Genlisea* is taxonomically closely related to *Utricularia*, exhibiting active water flow in traps, no water flow has been observed in *Genlisea* traps (Adamec 2003). Uptake of ^{35}S from labelled prey has been demonstrated in *Genlisea aurea* (Barthlott et al., 1998) but other processes of mineral nutrition have never been studied in *Genlisea*. Generally, mild mineral nutrient enrichment of nutrient-poor soils leads to a marked growth enhancement in terrestrial carnivorous plants (for the review see Adamec, 1997).

In this paper, the effect of soil fertilization on *G. violacea* growth was investigated in a greenhouse growth experiment. An emphasis was put on tissue nutrient contents and investment in carnivory.

Material and methods

A growth experiment was carried out on small plantlets of perennial *G. violacea* St.-Hil. (native to Itacambira, MG, NE Brazil) which were obtained from a vegetatively propagating culture growing in pots with fibrous peaty substrate in a greenhouse. The initial plantlets always consisted of two leaves 6–16 mm long and one trap 6–18 mm long. The initial length of the longest leaf and the trap was measured using a ruler. Leaves and traps of other 18 parallel plantlets were pooled and weighed for their mean initial dry mass (DM). On 31 May 2003, the plantlets were carefully planted to fibrous acid peat (Lithuanian peat moss, Klasmann, F.R.G.) in 6 × 6 × 6 cm plastic pots. During the growth experiment, twelve parallel pots with one plantlet in each representing the controls stood in distilled water (10–15 mm) on a shallow plastic plate. The same arrangement was used for twelve pots with plantlets for the nutrient-enriched variant. The pots standing on plastic plates were placed in a 0.8 m^2 white plastic container 0.3 m high in a naturally lit greenhouse (Adamec 2002). In the container, all pots with the plantlets had their position changed by rotation every week. To increase relative air humidity, the container was covered with a translucent foil. Daily temperatures at plant level fluctuated between 20 and 36 °C and relative air humidity between 60 and 90% during the day, and between 16 and 22 °C and 80 and 96% at night. The mean photosynthetically active radiation (PAR) irradiance at plant level was ∼ 19.5% of that in the open.

On 31 May 2003, 5 mL of the JKL 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; Adamec 2002) was applied evenly as drops on the top of the soil in each pot with the plantlets in the nutrient–enriched variant and the same soil fertilization was repeated on 15 June 2003. The same volume of distilled water was added to control pots. Thus, considering the pot area of 0.0036 m^2 the following dose of mineral nutrients was added totally to the peaty soil in the nutrient-enriched variant (in mg m^{-2}): N, 194.6; P, 63.6; K, 80.4; S, 36.5; Mg, 27.7; Ca, 111.3; Fe, 2.48. These N and P fertilization doses were about 1–2 orders of magnitude lower than those having been applied in field growth experiments on carnivorous plants (Adamec 1997). Water pH of the soil suspension was 3.67 and exchange pH (1 M KCl) 2.27 at the start of the experiment.

On 23 September 2003, after 116 days, the growth experiment was finished. Leaves and traps were counted and the longest organs were measured for each plant. Leaves and traps of individual plants were cleaned of the soil and

Table 1. Physiological parameters of 116-d growth experiment with *Genlisea violacea* in a greenhouse. The initial plants always consisted of two leaves and one young trap. Means of 12 plants (± SE) are shown where possible. The values of relative growth rate and doubling time of dry mater (DM) are based on total plant biomass. Statistically significant difference between the controls and fertilized variant (*t*-test), * – $P < 0.01$; NS – $P > 0.05$.

Parameter	Controls		Fertilized	
	Initial	Final	Initial	Final
Traps				
Longest trap length (mm)	11.3 ± 1.1	48.2 ± 3.4	12.4 ± 1.0^{NS}	67.6 ± 5.3*
Trap DM per plant (mg)	0.14	2.77 ± 0.29	0.14	6.27 ± 0.76*
Trap number per plant	1.00	4.75 ± 0.46	1.00	8.58 ± 1.15*
Leaves				
Longest leaf length (mm)	11.8 ± 0.9	10.2 ± 0.9	10.8 ± 1.0^{NS}	11.3 ± 1.0^{NS}
Leaf number per plant	2.00	5.75 ± 0.57	2.00	8.75 ± 0.83*
Leaf d.m. per plant (mg)	0.20	0.64 ± 0.07	0.20	1.94 ± 0.21*
Whole plants				
Total plant DM (mg)	0.34	3.41 ± 0.36	0.34	8.21 ± 0.97*
Leaf : trap DM ratio	1.43	0.234 ± 0.014	1.43	0.322 ± 0.025*
Leaf : trap number ratio	2.00	1.32 ± 0.19	2.00	1.20 ± 0.21^{NS}
Relative growth rate (d^{-1})	–	0.0199	–	0.0274
Doubling time of DM (d)	–	34.8	–	25.3

briefly rinsed with distilled water, blotted dry with a clean soft paper tissue, dried at 80 °C, and weighed to the nearest 0.01 mg. Tissue N, P, K, Ca, and Mg content in leaves and traps were estimated in four parallels consisting of 2–3 plants at the end of the experiment. Tissue nutrient content was also estimated in young adult leaves and traps at the start of the experiment to obtain initial values. Tissue nutrient content was estimated in mineralized samples using conventional methods (for all analytical details see Adamec 2002). Relative growth rate and doubling time were calculated from the increase of the total dry mass and increase in total plant nutrient amount was calculated from plant biomasses and tissue nutrient contents. All results were expressed as means ± SE and significant differences between the controls and the fertilized variant were evaluated by a two-tailed *t*-test.

Results and discussion

As follows from orientation soil analyses available nutrient content (Na acetate extraction), both in the control and fertilized soil 24 days after the second fertilization was within 177–212 mg kg^{-1} (DM) NH_4^+-N, 0.5 mg kg^{-1} NO_3^--N, 20–28 mg kg^{-1} PO_4-P, 38–45 mg kg^{-1} K, 807–984 mg kg^{-1} Ca, and 489–748 mg kg^{-1} Mg (data not shown), but the small addition of fertilizer was not evident for N. As compared to other peaty soils in which carnivorous plants grow naturally the peat used was relatively rich in macronutrients, especially in N, K, Ca, and Mg (Adamec 1997). Over the 116-d growth experiment, unfertilized control *G. violacea* plants increased their total dry matter 10.0 times, while the fertilized ones 24.1 times (Table 1). This difference was statistically significant at $P < 0.01$. It corresponded to doubling time of biomass of 34.8 and 25.3 d, respectively. Fertilized plants differed statistically significantly ($P < 0.01$) from control plants in final longest trap length (by 40%), trap DM per plant (by 126%), trap number per plant (by 81%), leaf number per plant (by 52%), and leaf DM per plant (by 203%). On the other hand, final longest leaf length was similar in control and fertilized plants and was about the same as in the initial plants. The final leaf : trap DM ratio was 0.23 in the controls and increased statistically significantly to 0.32 in fertilized plants. Generally, the small fertilization treatment increased the total plant biomass 2.4 times as compared to the controls and reduced significantly the proportion of subterranean traps which function as roots. Thus, the growth of *Genlisea* traps as investment in carnivory was regulated by mineral nutrient availability in peaty soils. The fertilization effect decreased the investment in carnivory and led rather to production of more traps rather than longer traps (Table 1).

Tissue nutrient content at the end of the experiment was statistically significantly ($P < 0.01$) greater in both traps and leaves only for P and K in the fertilized variant as compared with the controls but it was somewhat lower for Mg in traps (Table 2). Trap and leaf N content in control and fertilized *Genlisea* plants (1.4–1.6% DM) at the end of the experiment corresponded to that which has commonly been reported in many terrestrial carnivorous plants (Adamec 1997) and many wetland plant species (Dykyjová 1979). Very low trap and leaf P content in control plants (only 0.022–0.025% DM) and its marked increase by 80–90% as a result of fertilization mean that the growth of control *Genlisea* plants in the acid peat was P limited. In terrestrial carnivorous plants, shoot P content above 0.06% DM was usually found (Adamec 1997; Dykyjová 1979) but Adamec (2002) reported about the same low P content in roots and shoots in three *Drosera* species which grew in similar acid peat. Similarly as for P content, the trap and leaf K content in control *Genlisea* plants was very low (0.18–0.35% DM) and was nearly doubled in the fertilized variant (Table 2). Thus, the growth of control plants could be co-limited by P and K. Shoot K content may be as low as 0.25% DM in terrestrial carnivorous plants (Adamec 1997) as well as in

Table 2. Tissue content of N, P, K, Ca, and Mg (in % d.m.) at the start and the end of the growth experiment for *Genlisea violacea*. C – controls; FE – variant fertilized to the substrate. Means ± SE are shown, $n = 4$. Statistically significant difference between the controls and fertilized variant (t-test), * – $P < 0.01$; NS – $P > 0.05$.

Parameter	N		P		K		Ca		Mg	
	C	FE	C	FE	C	FE	C	FE	C	FE
Initial trap n.c.	0.90 ± 0.13		0.039 ± 0.004		1.30 ± 0.13		0.39 ± 0.01		1.41 ± 0.06	
Final trap n.c.	1.40±0.13	1.50^{NS}±0.10	0.025±0.002	0.046*±0.002	0.31±0.03	0.57*±0.04	0.37±0.01	0.34^{NS}±0.02	1.34±0.04	0.95*±0.07
Initial leaf n.c.	1.19 ± 0.33		0.045 ± 0.010		0.78 ± 0.11		0.30 ± 0.02		0.40 ± 0.05	
Final leaf n.c.	1.40±0.16	1.62^{NS}±0.05	0.022±0.000	0.041*±0.002	0.18±0.01	0.34*±0.04	0.33±0.04	0.24^{NS}±0.03	0.51±0.08	0.32^{NS}±0.05
Increase in total plant nutrient amount (μg)	44.1	122	0.69	3.56	6.44	38.7	11.2	24.8	37.5	62.9

n.c. – nutrient content

other wetland plants (Dykyjová 1979) but the common values in all these plants are much greater (0.6–2.5% DM). Slightly decreased trap and leaf Ca and Mg content in the fertilized variant as compared to the controls indicates that *Genlisea* growth was not limited by these nutrients. While both trap and leaf Ca content in *Genlisea* (0.24–0.37% DM.) was comparable with that found in terrestrial carnivorous and wetland non-carnivorous plants trap Mg content in *Genlisea* (1.34% DM in the controls, 0.95% DM in the fertilized variant) was about 3–5 times greater than it is common in carnivorous (Adamec 1997, 2002) and non-carnivorous wetland plants (Dykyjová 1979). On the basis of such a high trap Mg content, *G. violacea* can be considered as a plant species selectively accumulating Mg.

In summary, taking into account the biomass increase in *Genlisea* plants and their tissue nutrient content, the total nutrient accumulation in the fertilized variant rose comparatively to the controls 2.8 × for N, 5.2 × for P, 6.00 × for K, 2.2 × for Ca, and 1.7 × for Mg over the growth experiment (Table 2). These values indicate that both P and K co-limitation occurred in the controls. The increase in total biomass 2.4 times in the fertilized variant of *Genlisea* as compared to the controls was about the same over the experiment as it was reported for similar greenhouse growth experiments in rooted carnivorous plants (Adamec 1997).

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