

PRODUCTION PROCESSES IN A GRASS *CALAMAGROSTIS* *EPIGEJOS* GROWN AT DIFFERENT SOIL NITROGEN SUPPLY

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Summary

The relative growth rate, allocation of biomass into leaves, pseudostems, roots and rhizomes, specific leaf area, net photosynthesis and respiration were measured in young plants of a perennial grass *Calamagrostis epigejos* growing in a substrate with a different amount of nitrate ions as the sole source of nitrogen. Both the metabolic and the morphogenetic processes were strongly influenced by varying nitrogen availability. The high relative growth rate of *C. epigejos* observed in fertile sites rich in mineral nitrogen is, therefore, caused not only by the better photosynthetic performance of leaves, but also by the more advantageous allocation of new biomass within a plant.

Keywords: growth, grass, nitrogen, biomass, photosynthesis, respiration.

Introduction

Calamagrostis epigejos is a perennial rhizomatous grass widely distributed over the whole of central and northern Europe. Rapid spreading of this grass has been observed recently from its typical habitats (mainly forest clearings) to some other disturbed site, and even to some infrequently mowed meadows. *C. epigejos* is in all cases regarded as a serious weed because its dense stands in colonized sites, after outcompeting more palatable grassland species, persist for many years. In forest clearings, stands of *C. epigejos* prevent spontaneous forest regeneration and also artificially planted tree seedling may be endangered by its presence.

The causes of the successful spreading of *C. epigejos* are not sufficiently

known. It is true that it possesses several traits of an invasive species (e.g., easy dissemination, vegetative spreading by long rhizomes). It is also well known, that its ecological distribution is remarkably broad, from water-logged littoral of fishponds to dry steppic grasslands, from deep shaded understory of coniferous forests to fully insolated clearings, and from oligotrophic sandy soils to eutrophic humus-rich habitats. The physiological characteristics and mechanisms underlying the observed adaptability and competitive ability are less known. The fast acclimatisation of *C. epigejos* to changes in the radiation environment was analyzed in our previous paper (Gloser & Glöser 1996). The present work has been focused on problems of mineral nutrition, particularly on the responses to mineral nitrogen availability in the substrate. It seems highly probable, that increasing the concentration of mineral nitrogen in grassland soils (due to accelerated mineralization of soil organic matter or by air-transported nitrogenous compounds) may contribute to the expansive spreading of *C. epigejos*.

Material and methods

Cultivation of plants and growth analysis

Plants of *Calamagrostis epigejos* (L.) Roth were grown from young tillers detached from terminal parts of rhizomes directly in the field (Babice near Brno). The tillers were planted singly in plastic containers (12 cm in diameter) with sand. The containers were placed in a garden under wooden frames covered by transparent polyethylene foil just for protection against rain. Half of the containers were watered regularly with Hoagland nutrient solution containing 15 mM nitrate (= high-N treatment). The second half of the containers were watered with a modified Hoagland solution containing only 1.5 mM nitrate (= low N-treatment).

The relative growth rate of plants was estimated by a destructive sampling

method. Five plants from each treatment were harvested at about 2-week intervals. The plants were washed free of sand and divided into roots, rhizomes, pseudostems (shoot base with leaf sheaths, further denoted as "stems"), and leaf blades (further denoted only as "leaves"). The relative growth rate (RGR) was calculated for paired plants using a classical approach the difference in \ln -transformed plant dry mass divided by the time interval of the two subsequent weighing. The other growth-analytical characteristics were: net assimilation rate (NAR, dry mass increment per projected leaf area unit), leaf weight ratio (LWR, dry mass of leaves per unit of whole plant dry mass), and leaf area ratio (LAR, projected leaf area per unit of whole plant dry mass). Specific leaf area (SLA, projected leaf area per unit of leaf dry mass) was estimated using segments cut from the central part of leaf blades.

Gas exchange measurements

Rates of net photosynthesis of leaves and dark respiration of all plant parts were calculated from measurements of CO_2 exchange. The apparatus used was an open type system with differential infra-red gas analyser, air-conditioned leaf chamber (Gloser 1970) and a mass flow meter. The air entering the assimilation chamber was prepared from CO_2 free air and pure CO_2 using gas mixing pumps. The pumps were also used for calibration of the analyser. Gasometric estimations of net photosynthetic rate were done on the youngest fully developed leaves at leaf temperatures of 20 °C. Light was supplied by a quartz iodine 1 kW lamp filtered by a 0.15 m layer of water.

Gasometric measurements of dark respiration were made both in intact leaves exposed in assimilation chamber (covered by a piece of dark cloth), and in detached plant parts (roots, rhizomes, stems, and leaves), placed in thermostatically controlled glass cuvettes (at 20 °C), and connected to the same gasometric system, as described above. To prevent any dessication of plant material during measurements, the dew point of air entering the cuvettes was

kept at the same temperature as the measured sample. No significant effect of detachment of plant organs on their respiration rate was found in preliminary experiments.

The apparent quantum yield of photosynthesis was calculated from the initial linear part of the irradiance response curves as the number of moles of CO₂ fixed per mole of incident photosynthetically active photons.

Results

As shown in Table 1, the biomass production in the experimental plants was much stimulated by the improved nitrogen availability in the substrate during the whole experiment. This is also expressed in much higher values of the relative growth rate (RGR, Table 2). Responses of individual organs were not the same. A high nitrogen concentration in the substrate stimulated growth mostly from aboveground parts and rhizomes, while the growth of roots was significantly inhibited. The root/shoot ratio was thus more than twice as high in plants from the low-N treatment.

Table 1 Changes in dry mass of the whole plants and their individual organs (roots, stems, leaves, and rhizomes, all in mg per plant) of Calamagrostis epigejos during their growth in substrate with 1.5 mM nitrate (Low-N) and with 15 mM nitrate (High-N). Mean values of five plants. Standard errors ranged from 5% to 10% of the means.

Treatment	Day	Whole plant	Roots	Stems	Leaves	Rhizomes
Low-N	41	1227	498	271	379	79
	51	1658	730	302	473	154
	63	2516	1096	423	637	379
	77	3610	1405	827	856	522
	90	4643	1578	866	1166	1034
High-N	41	1526	443	348	608	125
	51	2527	599	596	1008	323
	63	4691	953	1238	1708	792
	77	7194	1118	2121	2456	1500
	90	10020	1597	3174	2846	2402

Decomposition of RGR values into their components (NAR and LAR, see Table 2) revealed that both of them contributed to the variation in growth rate. Nevertheless, the predominant role of allocation of new biomass into the leaves (expressed in values of LAR and LWR) is quite clear. There were no significant changes in SLA at different nitrogen availability.

Table 2 Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR), root weight ratio (RWR), specific leaf area (SLA), root/shoot dry mass ratio (R/S) in plants of *Calamagrostis epigejos* grown in substrate with 1.5 mM nitrate (Low N) and with 15 mM nitrate (High-N). Mean values for the time interval from May 1 to June 6 (i.e., the 41st and the 63rd day of cultivation). Sensitivity of all parameters to the N-treatment (in relative values of the difference between treatments) is given in the last column.

Parameter	Unit	Low-N	High-N	Change (%)
RGR	[mg g ⁻¹ d ⁻¹]	32	51	59.3
NAR	[g m ⁻² d ⁻¹]	4.9	5.7	16.3
LAR	[m ² kg ⁻¹]	6.5	8.9	36.9
LWR	[kg kg ⁻¹]	0.28	0.38	35.7
SLA	[m ² kg ⁻¹]	23.0	23.3	1.3
R/S		0.85	0.41	-51.8

Photosynthetic and respiratory parameters of leaves of the experimental plants are summarized in Table 3. Maximum values of the net photosynthetic rate (at light saturation) were increased by about 70% in leaves of plants cultivated at the high nitrogen supply. Increased values of the apparent quantum yield, and also increased dark respiration rates (of all organs) were found in plants from the high-N treatment.

Discussion

Despite a very broad distribution and wide ecological level of *Calamagrostis epigejos*, striking differences in biomass production and in population dynamics were observed in contrasting habitats (e.g., Pyšek 1991). It

Table 3 Results of gasometric measurements of photosynthetic and respiratory parameters in plants of *Calamagrostis epigejos* grown in substrate with 1.5 mM nitrate (Low-N) and with 15 mM nitrate (High-N): maximum rate of net photosynthetic CO₂ uptake at light saturation and leaf temperature 20 °C ($P_{N\ max}$), apparent quantum yield of photosynthesis (F_{app}), and dark respiration rate of leaves, stems and roots at temperature 20 °C (R_D). Mean values from 5 plants, significance of differences between treatments was tested at $p = 0.05$.

Parameter	Unit	Low-N	High-N	Significance
$P_{N\ max}$ (area)	[$\mu\text{mol m}^{-2} \text{s}^{-1}$]	17.5	29.7	+
$P_{N\ max}$ (drymass)	[$\mu\text{mol kg}^{-1} \text{s}^{-1}$]	407.7	692.0	+
F_{app}	[mol mol^{-1}]	0.047	0.065	+
R_D leaves	[$\mu\text{mol kg}^{-1} \text{s}^{-1}$]	11.5	14.5	+
R_D stems	[$\mu\text{mol kg}^{-1} \text{s}^{-1}$]	15.1	18.1	+
R_D roots	[$\mu\text{mol kg}^{-1} \text{s}^{-1}$]	14.3	19.5	+
R_D rhizomes	[$\mu\text{mol kg}^{-1} \text{s}^{-1}$]	10.1	12.7	+

is nearly impossible to do causal analysis of variation in growth rate and productivity of plants directly in the field where several ecological factors are usually changing simultaneously. This is particularly true in the case of nutrient availability, which is limiting plant productivity in many natural environments. Complex interrelations exist among most of the nutrients in the soil and estimation of their specific importance for plant growth is very difficult. Experiments in controlled or semicontrolled conditions are indispensable for such a study.

In most cases, nitrogen availability has the decisive role in determining the growth rate of plants in their natural habitats (for review see Boot 1990, Pigott and Taylor 1964). Increased nitrogen input to nutrient-poor ecosystems results in a dramatic shift in species composition. Grasses belong to the most responsive species, but great interspecific differences exist among them (Bradshaw & al. 1964, Boot 1990).

The growth response of *C. epigejos* to increased nitrogen availability found in our experiments was of very similar magnitude to that reported for some other fast growing species (Boot 1990). In deeper analysis of the morphological and

functional characteristics which were determining the response, the RGR was factorized in its various components. The analysis showed, that the morphological components (LAR, LWR, but not SLA!) were much more important than changes in NAR, in spite of distinctly elevated values of specific net photosynthetic rate of leaves.

It should be mentioned, that our measurements of net photosynthesis were carried out on selected leaves having the best performance, and, therefore, they were not fully representative of the integral photosynthetic activity of the whole set of leaves of a plant. NAR is also a rather complex parameter, not simply dependent on photosynthetic activity of leaves only. Respiration losses of all organs, losses of organic compounds by root exudation and carbon content in the newly produced biomass contribute to its value as well.

We may conclude, that the high morphological adaptability of *C. epigejos*, which was found in our previous experiments as the most important trait determining its extraordinary capability to acclimatise to changes in radiation availability (Gloser and Glöser 1996) is also of key importance for the strong response of this species to increased nitrogen availability in the soil.

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