Competitive ability of three ecologically contrasting grass species at low nutrient supply in relation to theri maximal relative growth rate and tissue density

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Summary

1 Relative growth rates *(RGR)* of *Bromus erectus, Arrhenatherum elatius* and *Dactylis glomerata* were measured over periods of 1–2 months at high nutrient supply, at low nutrient supply and and at low nutrient supply with competition.

2 Rank order of the *RGR*s of the three species remained the same under all treatments, *D. glomerata* having the highest, *B. erectus* the lowest *RGR*. This indicates that short-term ability to compete for resources is directly related to maximal *RGR* and independent of the resource supply.

3 High *RGR* was correlated with low tissue density, which is known to be associated with short organ life span and fast nutrient losses.

4 We conclude that low tissue density is an important characteristic for the competitive ability in the short term, but leads in the long term to a competitive disadvantage, if nutrient availability is too low to sustain the losses.

Keywords: allocation, comparative plant ecology, dry/fresh weight ratio, resource acquisition

Introduction

Under productive conditions species with a high maximal relative growth rate (RGR$_{max}$) are competitively superior to more slowly growing species (Grime & Hunt 1975). High RGR$_{max}$ is usually associated with high leaf area ratio (Lambers & Poorter 1992), a trait which gives the plant a high assimilation capacity and is an advantage in competition for light.

In nutrient-poor habitats competition occurs mainly below-ground (Wilson & Tilman 1991). It has been claimed that species which are superior competitors for light are also superior in acquiring below-ground resources (Grime 1979). This view is supported by the fact that fast-growing species may have a high root length ratio as well as a high leaf area ratio, which is possible due to their low tissue density (Ryser & Lambers 1995). The low investment of dry matter per tissue volume enables a rapid build-up of organs and a fast expansion of leaves and roots. The large

amount of low-density tissue which can be produced with a certain amount of dry matter provides the plant simultaneously with a high acquisition capacity both for above- and below-ground resources. This may explain the higher growth rates attained by these species even at low nutrient supply (Poorter *et al.* 1995; Ryser & Lambers 1995).

The question arises, why do plants with low tissue density not dominate the vegetation on nutrient-poor sites? Do different factors influence nutrient acquisition in a competitive situation than if the plants grow alone? There is indeed evidence that the slow-growing species are better competitors under low nutrient supply (Tilman & Wedin 1991). However, other experiments show a constant competitive ranking of species regardless of the level of nutrient supply (Mahmoud & Grime 1976).

Differences in time-scale of observation might explain some of the disagreements about properties of a "good competitor". Experiments showing a competitive superiority of slow-growing species at low nutrient supply usually last more than one growing season, while shorter experiments tend result in superiority of the fast-growing species. We hypothesise that in the short term, i.e. during the first growing season, capacity to acquire nutrients mainly determines competitive ranking among the species, while the total nutrient balance including losses becomes more important in periods longer then one growing season. Species with a low tissue density grow during the first months faster than those with a high tissue density even at low nutrient supply (Ryser & Lambers 1995), but loose this initial advantage because of high nutrient losses due to the short life span of leaves and roots (Schläpfer & Ryser 1996; Ryser in press).

In the present experiment we tested the hypothesis that species, which at high nutrient supply attain the highest growth rates, are in the short-term better also in competing for nutrients at low supply level. In our experiments we used the same grass species as Schläpfer & Ryser (1996) did, in order to relate the results of our short-term experiment with the species' tissue turnover-rate in the field. As tissue density is an important trait both for *RGR* and organ turn-over, we paid special attention to its relevance for the competitive ability of the species.

Material and methods

The experiments were conducted with three grass species: *Arrhenatherum elatius* (L.) J. et C. Presl., *Bromus erectus* Huds. and *Dactylis glomerata* L. These species potentially dominate the vegetation of meadows, but differ in their nutrient requirements. *B. erectus* is characteristic in nutrient-poor meadows whereas *A. elatius* occurs as a dominant species in more nutrient-rich meadows with 2–3 cuts per year. *D. glomerata* is a highly productive grass on nutrient-rich sites but has a wide ecological range. Seed sizes for *A. elatius, B. erectus* and *D. glomerata* are 2.93 mg, 4.23 mg and 0.51 mg, respectively (Grime *et al.* 1988).

Seeds were collected in June–July 1993 in NW-Switzerland near Biberstein (AG) in a nutrient-poor limestone grassland at 600 m a.s.l., in which all three species co-occur. Standing crop of the meadow was 484 ± 20 g m^{-1} (mean $\pm$ 1SE) above-ground dry weight in late June 1994.

Two experiments were conducted. In the first experiment relative growth rate of the species under close to optimal conditions was measured. In the second experiment their competitive abilities were assessed under nutrient-poor conditions.

Both growth rate and competitive ability were studied in the context of tissue density. As a measure for tissue density dry/fresh

weight ratio was used. Assuming a close re-lationship between tissue volume and fresh weight (Garnier & Laurent 1994), the dry/fresh weight ratio reflects the specific weight, i.e. density, of the tissue.

MEASUREMENT OF THE RELATIVE GROWTH RATE AT CLOSE TO OPTIMAL CONDITIONS

After germination in a greenhouse, seedlings were planted in 0.75 l pots filled with nutri-ent-rich compost soil, one seedling per pot. The pots were large enough to prevent any size limitation during the experiment. Ten seedlings of each species were collected for initial dry weight measurement. Seedlings were planted on 30 August 1994. The plants were grown in a greenhouse in daylight sup-plemented by artificial illumination of 70–100 µmol $m^{-2}s^{-1}$ 12 h a day. Day and night temperatures were 20–30 °C and 15 °C, re-spectively. The plants were watered daily.

Ten plants of each species were harvested 21, 27 and 31 days after planting. Plants were separated into leaf blades, leaf sheaths (sub-sequently referred to as stem) and roots, and fresh weight and dry weight (after 24 hours at 75 °C) were measured.

COMPETITION EXPERIMENT

In this experiment plants were grown in 1.3 l pots (10 cm deep) filled with a 1:4 mixture of nutrient-rich compost soil and quartz-sand. Temperatures in the greenhouse were about 20 °C at day and 10–15 °C at night.

On 3 August 1994 five seedlings of D. glomerata were planted in a circular pattern in each pot. These plants provided competi-tion for the target plants and will be referred to as the neighbouring plants. Fast-growing D. glomerata was chosen as neighbouring plant species in order to have the pots rapidly filled by roots. 23 days later seedlings of the three studied species were planted as target

plants, one seedling in the middle of each pot. In the competition treatment the neighbour-ing plants were left intact, in the control treat-ment (without competition) above-ground parts of the neighbouring D. glomerata-plants were removed by cutting them at the soil-surface. Resprouting leaves were also re-moved. By this a similar nutrient status in the pots at the time of planting of the target plants was provided for control and for competition treatments, as until then in both treatments a similar amount of nutrient depletion due to plant growth had occurred.

Target plants were harvested 27 and 57 days after planting. Each harvest consisted of eight plants of each species and treatment. Only above-ground parts were removed, as the roots of the target plants could not be sep-arated from those of the neighbouring plants. Fresh weight of leaf blades and stems was measured at harvest, the dry weight after dry-ing for 24 hours at 75 °C.

DATA ANALYSIS

Relative growth rates were calculated using a linear regression after logarithmic transfor-mation of the dry weight data. In the first ex-periment interspecific differences in RGR were tested using the interaction factor in a two-way ANOVA on the effect of species and harvest on the total dry weight (SyStat 1992). Data on biomass allocation and tissue density were analysed with a one-way ANOVA using first harvest data, as the interspecific size dif-ferences were lowest at that time. In the sec-ond experiment data were analysed with a three-way ANOVA, testing the effect of species, competition and time of harvest on the biomass and tissue density.

Prior to analyses, logarithmic transforma-tion was conducted on all biomass data and arcsine-square root transformation on pro-portional data, i. e. allocation data and dry/ fresh weight ratios.

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Results

RELATIVE GROWTH RATE (RGR), BIOMASS ALLOCATION AND TISSUE DENSITY AT HIGH NUTRIENT SUPPLY

Dactylis glomerata had the highest *RGR* on the nutrient-rich compost soil, *Bromus erectus* the lowest (Table 1). Interspecific differences in *RGR*s were significant (species x harvest interaction, Table 2).

B. erectus had the highest biomass allocation to both leaf blades *(LWR)* and roots *(RWR)* (Table 3), and the lowest to stem *(SWR)*.

B. erectus had the highest dry/fresh weight ratio of leaf blades, stems and roots. For the above-ground parts this ratio was lowest in *D. glomerata* and for roots in *A. elatius* (Table 4).

Table 1. *Relative growth rate (regression coefficient ± 1SE), seedling dry weight (DW) at planting (day_0) and the range of mean plant dry weight used for the determination of RGR $(days_{21-31})$ on nutrient-rich substrate*

	RGR (day^{-1})	DW at day$_0$ (mg)	DW range (mg)
A. elatius	0.119 ± 0.011	8.1	83–283
B. erectus	0.082 ± 0.012	11.2	44–103
D. glomerata	0.146 ± 0.013	3.0	36–153

Table 2. *Two-way ANOVA results for above-ground dry weight (log transformed), testing the effect of species and harvest on nutrient-rich substrate*

	df	P	SS
Species	2	< 0.001	9.11
Harvest	2	< 0.001	20.72
Species x harvest	4	< 0.001	1.65
Residuals	82	–	6.02

Table 3. *Biomass allocation to leaf blades (LWR), leaf sheaths (SWR) and roots (RWR) on nutrient-rich substrate at day$_{21}$ after planting (mean ± 1SE); results of one-way ANOVA included (*, $P < 0.01$; **, $P < 0.01$; ***, $P < 0.001$)*

	LWR	SWR	RWR
A. elatius	0.578 ± 0.007	0.232 ± 0.006	0.190 ± 0.008
B. erectus	0.581 ± 0.006	0.173 ± 0.008	0.246 ± 0.012
D. glomerata	0.548 ± 0.009	0.240 ± 0.009	0.212 ± 0.011
	*	**	***

Table 4. *Dry/fresh weight ratio of leaf blades, leaf sheaths and roots on nutrient-rich substrate at day$_{21}$ after planting (mean ± 1SE); results of one-way ANOVA included*

	Leaf blades	Leaf sheaths	Roots
A. elatius	0.142 ± 0.002	0.107 ± 0.002	0.091 ± 0.001
B. erectus	0.156 ± 0.005	0.128 ± 0.005	0.127 ± 0.006
D. glomerata	0.135 ± 0.003	0.102 ± 0.003	0.100 ± 0.003
	***	***	***

COMPETITIVE ABILITY

Presence of the five neighbouring *D. glomerata* plants clearly reduced the growth of all target species (Fig. 1). *RGR* decreased due to competition by 70, 83 and 65% for *A. elatius, B. erectus* and *D. glomerata,* respectively. Ranking of the species was the same both with and without competition, and the same as on nutrient-rich soil without competition. Interspecific differences in *RGR* were significant (species x harvest interaction, Table 5). The relative reduction in *RGR* due to competition was highest for *B. erectus,* the lowest for *D. glomerata.* However, as plant size is an exponential function of *RGR,* relative reduction in plant size due to competition was highest in *D. glomerata* with the highest absolute values for *RGR.*
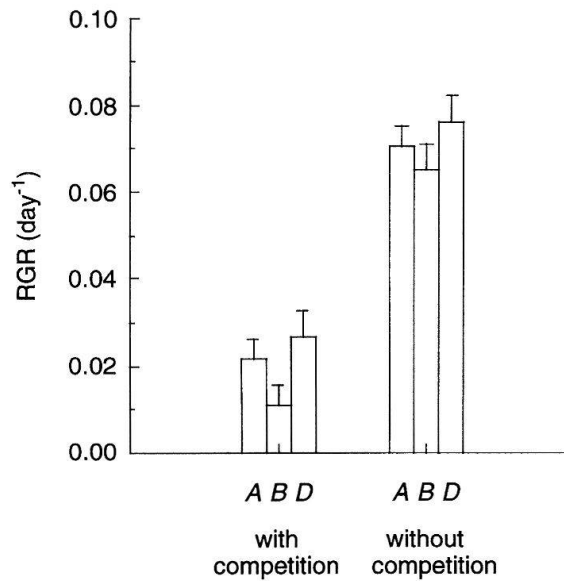

Fig. 1. *Relative growth rate of the above-ground parts with and without competition on nutrient-poor substrate. (A,* A. elatius; *B,* B. erectus; *D,* D. glomerata; *regression coefficient ± 1SE).*

Table 5. *Three-way ANOVA results for above-ground dry weight (log transformed) and dry/fresh weight ratios of leaves and stems (arcsine transformed), testing the effects of species, competition and harvest*

	df	Dry weight P	SS	DW/FW leaves P	SS	DW/FW stems P	SS
Species	2	< 0.001	5.29	< 0.001	0.124	< 0.001	0.067
Competition	1	< 0.001	113.94	< 0.001	0.192	< 0.001	0.067
Harvest	1	< 0.001	43.97	< 0.001	0.046	< 0.001	0.071
Species x competition	2	< 0.001	1.85	< 0.001	0.026	< 0.001	0.022
Species x harvest	2	0.038	0.66	0.721	0.001	0.228	0.004
Comp x harvest	1	< 0.001	13.73	0.157	0.004	0.001	0.015
Spec x comp x harv	2	0.864	0.03	0.247	0.006	0.376	0.003
Residuals	83		8.02		0.164		0.116

B. erectus had the largest seeds. In the competition treatment this difference in initial weight remained throughout the experiment. Dry weight of the above-ground parts was highest for *B. erectus* (Table 6), although dry weight increase was relatively larger for the other species. The absolute increase in dry weight at the two harvests was similar for *D. glomerata* and *B. erectus* (6.3 g in competition treatment, 151–155 g in control treatment for both species). *A. elatius* had a

slightly lower absolute increase in biomass in the competition treatment (5.6 g) but a higher one in the control treatment (199 g).

Above-ground dry weight of the neighbouring plants was not significantly influenced by the species of target plants.

Dry/fresh weight ratio of leaf blades and stems was highest for *B. erectus* (Fig. 2). Interspecific differences were significantly increased by competition (species x competition interaction, Table 5). *B. erectus* re-

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Table 6. Above-ground dry weight in mg (mean ± 1SE) of the target plants with and without competition on nutrient-poor substrate, and the total dry weight of the five neighbouring D. glomerata *plants per pot in the competition treatment*

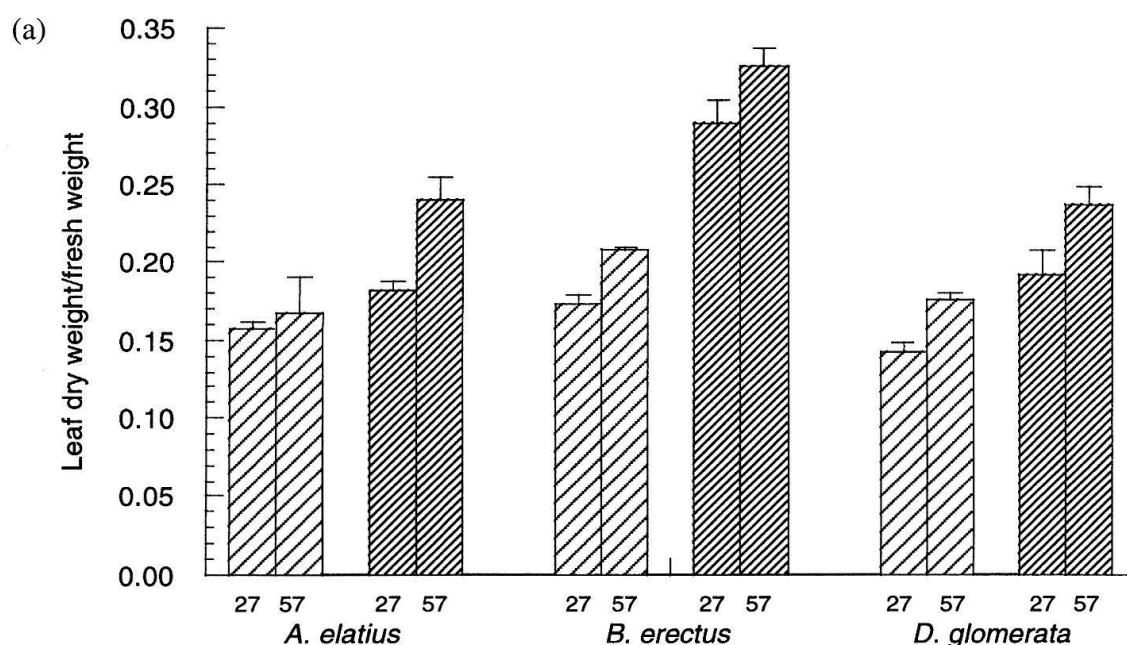|	Without competition		With competition	
	day_{27}	day_{57}	day_{27}	day_{57}
Target plants				
A. elatius	26.85 ± 2.43	226.14 ± 21.73	6.21 ± 0.67	11.77 ± 1.00
B. erectus	26.92 ± 4.11	177.87 ± 12.76	9.09 ± 0.85	12.73 ± 1.17
D. glomerata	19.10 ± 3.39	174.50 ± 12.05	3.37 ± 0.45	7.01 ± 1.00
Neighbouring plants (5)				
D. glomerata	–	–	609 ± 50	1157 ± 67

Fig. 2. *Dry/fresh weight ratio of leaf blades (a) and leaf sheaths (b) of the target plants 27 and 57 days after planting in control (light shade) and in competition (deep shade) treatments (mean ± 1SE).*

sponded strongest by increasing this ratio in the competition treatment by about 60% compared to the control.

RELATIONSHIP BETWEEN TISSUE DENSITY AND *RGR*

There was a significant positive correlation between *RGR* and and the reciprocal value of tissue density, fresh/dry weight ratio, across all species and treatments (Fig. 3). This rela-

tionship was approximatively linear after a logarithmic transformation of the *RGR*-values.

Discussion

There is no general agreement about the characteristics of a competitively superior plant species under different environmental conditions (Grace 1990). We argue, that one of the reasons for this is that the competitive
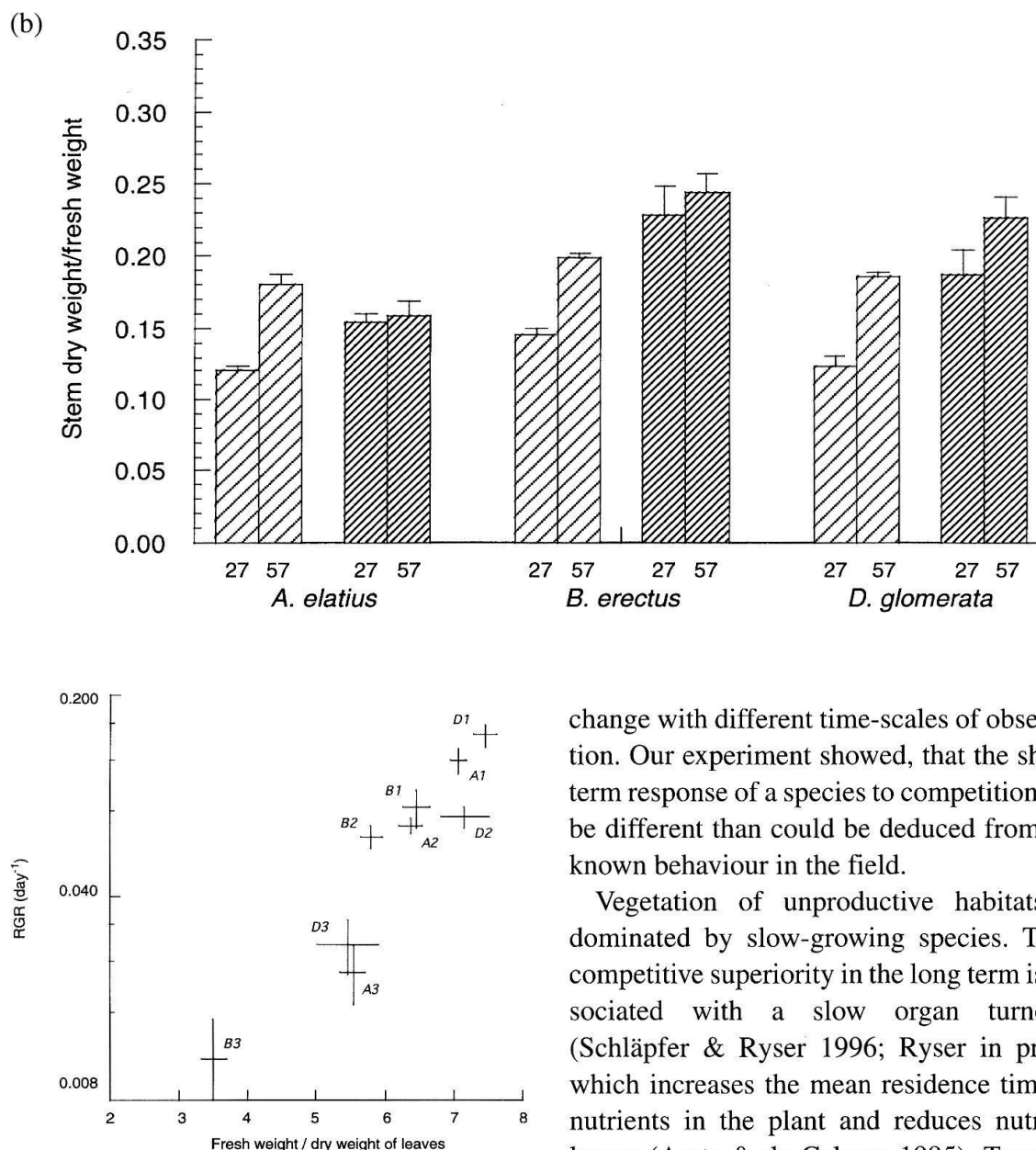
(b)

Fig. 3. Relative growth rate (log scale) of A. elatius *(A),* B. erectus *(B) and* D. glomerata *(D) at high nutrient supply without comptetion (1), at low nutrient supply without competition (2) and at low nutrient supply with competition (3) plotted against the fresh/dry weight ratio of leaf blades. Linear regression:* $r^2 = 0.878$, $P < 0.001$. *Error bars indicate two standard errors.*

ability of a species, i.e. its performance growing together with other species relatively to its performance when growing alone, may

change with different time-scales of observation. Our experiment showed, that the short-term response of a species to competition can be different than could be deduced from the known behaviour in the field.

Vegetation of unproductive habitats is dominated by slow-growing species. Their competitive superiority in the long term is associated with a slow organ turnover (Schläpfer & Ryser 1996; Ryser in press) which increases the mean residence time of nutrients in the plant and reduces nutrient losses (Aerts & de Caluwe 1995). Together with the low mineralisation rate of litter of these species (Wedin & Pastor 1993), the long mean residence time of nutrients leads to a lower nutrient availability in the soil than beneath fast-growing species with rapidly decomposing litter (Tilman & Wedin 1991).

However, the present experiment shows that fast-growing species grow in the short term faster than species of nutrient-poor sites, also at low nutrient supply level and even under strong competition. There was a remarkable stability in the rank-order of

*RGR*s of the studied species under different conditions: at high nutrient supply, low nutrient supply and low nutrient supply with competition, *D. glomerata* achieved the highest *RGR* and *B. erectus* the lowest. This supports the idea, that competitive superiority is not dependent on resource supply level (Grime 1979). The same order of competitive ability for three grass species at high and low nutrient supply has also been found by Mahmoud & Grime (1976). However, their results do not show clearly that the competitive ability is a result of a high *RGR*. *A. elatius,* the species with the highest competitive ability, had the largest seeds of the species used (Grime *et al.* 1988). The possibility cannot be excluded that this might have been the reason for its high competitive ability in the pairwise comparison of species, since ability to suppress growth of other plants is directly related to plant biomass (Goldberg 1987; Gaudet & Keddy 1995; Gerry & Wilson 1995). In our experiment we avoided this problem by achieving the same competitive neighbourhood for all species. Different neighbouring species might have had a different effect on growth of the target, but the ranking of growth rates among the species would most likely have remained unchanged (Goldberg 1987).

In our experiment high growth rates were associated with low tissue density under all circumstances. Besides the interspecific differences, tissue density showed also a high phenotypic plasticity. Low tissue density is usually associated with a high leaf area ratio (Garnier 1992; Ryser & Lambers 1995) or a high specific leaf area (Shipley 1995). A strong correlation between the biomass of a target species and its light-interception ability with different neighbouring species was found by Tremmel & Bazzaz (1993). The low tissue density also allows a plant simultaneously to have a long root system (Ryser & Lambers 1995) which explains the interdependence of plants abilities to compete both above- and below-ground resources (Campbell & Grime 1989).

In the long term the low tissue density is a disadvantage at low nutrient availability. The watery leaves and roots of *D. glomerata* and *A. elatius* have a shorter life-span than those of *B. erectus* (Schlaepfer & Ryser 1996). Short life-span leads to high nutrient losses (Escudero *et al.* 1992; Aerts & de Caluwe 1995) which the plant cannot sustain in low-nutrient environments (Aerts & van der Peijl 1993; Berendse 1994). In a nutrient-poor limestone grassland over several years, growth of *D. glomerata* with low tissue density is more suppressed by competition than that of *B. erectus* with a higher tissue density (Marti 1994).

Biomass allocation either to leaves or roots did not explain the observed behaviour of the plants: *B. erectus* had even at high nutrient supply the largest allocation to leaf blades, and simultaneously to the roots. The resulting low investment in the stem keeps it stature low and is a disadvantage under productive conditions.

The five *D. glomerata* seedlings planted as neighbouring plants strongly suppressed the growth of the target plant, which was planted into the pot three weeks after them. This indicates the importance of timing of germination for the outcome of competition among seedlings.

We conclude that tissue density is a constraint which influences the time scale of the competitive ability of a species. In the short term low tissue density enables a competitive superiority due to fast resource acquisition, but leads in the long term to nutrient losses because a short organ-life span. This is a competitive disadvantage if the nutrient supply is not high enough to compensate for these losses.

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Acknowledgement

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