Zeitschrift:	Bulletin of the Geobotanical Institute ETH
Herausgeber:	Geobotanisches Institut, ETH Zürich, Stiftung Rübel
Band:	62 (1996)
Artikel:	Competitive ability of three ecologically contrasting grass species at low nutrient supply in relation to theri maximal relative growth rate and tissue density
Autor:	Notz, Regina / Ryser, Peter
DOI:	https://doi.org/10.5169/seals-377792

#### Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. <u>Mehr erfahren</u>

#### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. <u>En savoir plus</u>

#### Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. <u>Find out more</u>

# Download PDF: 08.07.2025

ETH-Bibliothek Zürich, E-Periodica, https://www.e-periodica.ch

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

# PETER RYSER\* & REGINA NOTZ

Geobotanisches Institut ETH, Gladbachstrasse 114, 8044 Zürich, Switzerland, \*corresponding author: ryser@geobot.umnw.ethz.ch

### 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 *RGRs* 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

Bulletin of the Geobotanical Institute ETH (1996), 62, 3-12

# Introduction

Under productive conditions species with a high maximal relative growth rate (RGR<sub>max</sub>) are competitively superior to more slowly growing species (Grime & Hunt 1975). High RGR<sub>max</sub> 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  $484 \pm 20$  g m<sup>-1</sup> (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 relationship 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 nutrient-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 supplemented by artificial illumination of 70–100  $\mu$ mol m<sup>-2</sup>s<sup>-1</sup> 12 h a day. Day and night temperatures were 20–30 °C and 15 °C, respectively. 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 (subsequently referred to as stem) and roots, and fresh weight and dry weight (after 24 hours at 75  $^{\circ}$ C) were measured.

#### COMPETITION EXPERIMENT

In this experiment plants were grown in 1.3 1 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 competition 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 neighbouring plants were left intact, in the control treatment (without competition) above-ground parts of the neighbouring *D. glomerata*plants were removed by cutting them at the soil-surface. Resprouting leaves were also removed. 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 separated from those of the neighbouring plants. Fresh weight of leaf blades and stems was measured at harvest, the dry weight after drying for 24 hours at 75 °C.

#### DATA ANALYSIS

Relative growth rates were calculated using a linear regression after logarithmic transformation of the dry weight data. In the first experiment 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 differences were lowest at that time. In the second 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 transformation was conducted on all biomass data and arcsine-square root transformation on proportional data, i.e. allocation data and dry/ fresh weight ratios.

# 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  $\pm 1SE$ ), seedling dry weight (DW) at planting (day<sub>0</sub>) and the range of mean plant dry weight used for the determination of RGR (days<sub>21-31</sub>) on nutrient-rich substrate

	RGR (day-1)	DW at day <sub>0</sub> (mg)	DW range (mg)
A. elatius	$0.119 \pm 0.011$	8.1	83–283
B. erectus	$0.082 \pm 0.012$	11.2	44–103
D. glomerata	$0.146 \pm 0.013$	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	Р	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<sub>21</sub> after planting (mean  $\pm 1SE$ ); results of one-way ANOVA included (\*, P < 0.01; \*\*, P < 0.01; \*\*\*, P < 0.001)

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

Table 4. Dry/fresh weight ratio of leaf blades, leaf sheaths and roots on nutrient-rich substrate at  $day_{2l}$  after planting (mean ± 1SE); results of one-way ANOVA included

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

#### 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 nutrientpoor substrate. (A, A. elatius; B, B. erectus; D, D. glomerata; regression coefficient  $\pm 1SE$ ).

	df	Dry weight		DW/FW leaves		DW/FW stems	
		Р	SS	Р	SS	Р	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

**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

*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-

Table 6. Above-ground dry weight in mg (mean  $\pm 1SE$ ) 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		
	<i>day</i> <sub>27</sub>	day <sub>57</sub>	<i>day</i> <sub>27</sub>	<i>day</i> <sub>57</sub>	
Target plants					
A. elatius	$26.85 \pm 2.43$	$226.14 \pm 21.73$	$6.21 \pm 0.67$	$11.77 \pm 1.00$	
B. erectus	$26.92 \pm 4.11$	177.87 ± 12.76	$9.09 \pm 0.85$	$12.73 \pm 1.17$	
D. glomerata	$19.10 \pm 3.39$	$174.50 \pm 12.05$	$3.37\pm0.45$	$7.01 \pm 1.00$	
Neighbouring pla	nts (5)				
D. glomerata	- • —	_	$609 \pm 50$	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  $\pm 1SE$ ).

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 relationship 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



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.

B3

4

5

Fresh weight / dry weight of leaves

6

3

0.008

2

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

term response of a species to competition can be different than could be deduced from the 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 RGRs 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.

# Acknowledgement

We thank Tino Fotsch for taking care of the plants during the experiment.

### References

- Aerts, R. & de Caluwe, H. (1995) Interspecific and intraspecific differences in shoot and leaf lifespan of four *Carex* species which differ in maximum dry matter production. *Oecologia*, **102**, 467–477.
- Aerts, R. & van der Peijl, M.J. (1993) A simple model to explain the dominance of low-productive perennials in nutrient poor habitats. *Oikos*, **66**, 144–147.
- Berendse, F. (1994) Competition between plant populations at low and high nutrient supplies. *Oikos*, **71**, 253–260.
- Campbell, B.D. & Grime, J.P. (1989) A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytologist*, **112**, 261–267.
- Escudero, A., del Arco, J. M., Sanz, I.C. & Ayala, J. (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia*, **90**, 80–87.
- Garnier, E. (1992) Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology*, **80**, 665–675.
- Garnier, E. & Laurent, G. (1994) Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytol*ogist, **128**, 725–736.
- Gaudet, C. L. & Keddy, P. A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.
- Gerry, A. K. & Wilson, S. D. (1995) The influence of initial size on the competitive responses of six plant species. *Ecology*, **76**, 272–279.
- Goldberg, D. E. (1987) Neighborhood competition in an old-field plant community. *Ecology*, **68**, 1211–1223.
- Grace, J. B. (1990) On the relationship between plant traits and competitive ability. *Perspectives* in *Plant Competition* (eds. J.B. Grace & D. Tilman), pp. 51–65. Academic Press, San Diego.
- Grime, J. P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester.

- Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) Comparative Plant Ecology. A Functional Approach to Common British Species. Unwin Hyman, London.
- Grime, J. P. & Hunt, R. (1975) Relative growthrate: its range and adaptive significance in a local flora. *Journal of Ecology*, **63**, 393–422.
- Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research, 23, 187–261.
- Mahmoud, A. & Grime, J. P. (1976) An analysis of competitive ability in three perennial grasses. *New Phytologist*, **77**, 431–435.
- Marti, R. (1994) Einfluss von Wurzelkonkurrenz auf die Koexistenz von seltenen mit häufigen Pflanzenarten in Trespen-Halbtrockenrasen. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich, 123, 1–147.
- Poorter, H., van de Vijver, C.A.D.M., Boot, R.G.A. & Lambers, H. (1995) Growth and carbon economy of a fast-growing and a slow-growing grass species as dependent on nitrate supply. *Plant* and Soil, **171**, 217–227.
- Ryser, P. (in press) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology*.
- Ryser, P. & Lambers H. (1995) Root and leaf attributes accounting for the performance of fastand slow-growing grasses at different nutrient supply. *Plant and Soil*, **170**, 251–265.
- Schläpfer, B. & Ryser, P. (1996) Leaf and root turnover of three ecologically contrasting grass species in relation to their performance along a productivity gradient. *Oikos*, **75**, 398–406.
- Shipley, B. (1995) Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. *Functional Ecology*, 9, 312–319.
- SyStat (1992) *Statistics*, Version 5.2 Edition. SyStat, Inc., Evanston.
- Tilman, D. & Wedin, D. (1991) Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, 72, 685–700.
- Tremmel, D.C. & Bazzaz, F.A. (1993) How neighbor canopy architecture affects target plant performance. *Ecology*, **74**, 2114–2124.

- Wedin, D. A. & Pastor, J. (1993) Nitrogen mineralization dynamics in grass monocultures. *Oecologia*, **96**, 186–192.
- Wilson, S. D. & Tilman, D. (1991) Components of plant competition along an experimental gradient of nitrogen availability. *Ecology*, **72**, 1050–1065.

Received 14 March 1996 revised version accepted 7 May 1996