

Initial size and the competitive responses of two grasses at two levels of soil nitrogen: a field experiment

SCOTT D. WILSON

Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada

Received February 1, 1994

WILSON, S.D. 1994. Initial size and the competitive responses of two grasses at two levels of soil nitrogen: a field experiment. *Can. J. Bot.* 72: 1349–1354.

I tested whether initial size influenced the ability of grasses to compete against established perennial vegetation in an old field, both in plots with little competition for light and in plots with intense light competition. Seedlings of *Schizachyrium scoparium* (a perennial) and *Setaria viridis* (an annual) were assigned to three classes of initial size; small seedlings had about half the initial mass of medium seedlings, which had about half the mass of large seedlings. Seedlings were transplanted into subplots with neighbours either present or absent, within 10 plots that received either NH_4NO_3 or no additional nitrogen. Transplant final mass (roots and shoots) was significantly lower in the presence of neighbours and increased significantly with initial size. There was no significant interaction between competition and initial size, however, indicating that competition suppressed seedlings of all sizes to about the same extent. Further, there was no significant three-way interaction, suggesting that size did not influence competitive response more in environments where light was limiting. These results differ from pot experiments and monocultures by suggesting that initial size does not influence the ability of a plant to compete against neighbours on either nutrient-rich or nutrient-poor soils.

Key words: competition, competitive response, competitive ability, size, removal experiments, nitrogen.

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- L'auteur a vérifié si la dimension initiale peut influencer la capacité de graminées à compétitionner avec la végétation pérenne pré-installée dans une vieille prairie, à la fois dans des parcelles où il y a peu de compétition et beaucoup de compétition pour la lumière. Des plantules de *Schizachyrium scoparium* (pérenne) et de *Setaria viridis* (annuelle) ont été regroupées en trois classes de dimensions initiales; la masse des petites plantes était environ la moitié de celle des plantes moyennes, dont la masse elle-même était la moitié des grandes plantes. Les jeunes plantes ont été transplantées dans des sous-parcelles, en présence ou en absence de voisins, situées dans 10 parcelles qui ont reçu du NH_4NO_3 ou encore aucun supplément azoté. La masse finale des plantes relocalisées (racines et tiges) est significativement plus faible en présence de voisins et augmente significativement en fonction de la dimension initiale. Il n'y a pas d'interaction significative entre la compétition et la dimension initiale, ce qui indique que la compétition supprime les plantules de toutes dimensions sans distinction. De plus, il n'y a pas d'interaction tri-dimensionnelle significative, ce qui suggère de plus que la dimension n'influence pas non plus la compétition dans un environnement où la lumière est un facteur limitant. Ces résultats divergent de ceux obtenus en pots et en monocultures en démontrant que la dimension initiale n'influence pas la capacité d'une plante à compétitionner avec les voisins, que ce soit dans des sols riches ou dans des sols pauvres en nutriments.

Mots clés : compétition, réaction compétitive, capacité à compétitionner, dimension, expérience d'exclusion, azote.

[Traduit par la rédaction]

Introduction

Competitive ability is thought to be an important trait in determining the species composition of plant communities (Grime 1979; Tilman 1988; Keddy 1989). Competitive ability is frequently influenced by individual size. Seed size is positively correlated with competitive ability in clover (Black 1958) and old-field perennials (Gross 1984). Biomass determines the competitive ability of wetland plants (Gaudet and Keddy 1988; Grace et al. 1992). Variation in emergence time in monocultures produces size inequalities that result in the competitive suppression of small individuals both in greenhouse flats (Ross and Harper 1972; Weiner and Thomas 1986) and in natural stands (Schmitt et al. 1987). All of these examples come from relatively even-aged mixtures in pots or monocultures. In contrast, initial size did not influence the competitive responses of seedlings of six species grown in a perennial grassland (Gerry and Wilson 1994).

Competitive ability can be classified as response, the extent to which an individual can grow in the presence of neighbours, and effect, the extent to which an individual can inhibit the growth of its neighbours (Goldberg 1990). The influence of initial size on competitive response is important for two reasons.

First, it may affect tests of proposed relationships between competitive hierarchies and community structure (Grime 1979; Tilman 1988). If competitive ability is influenced by size, then differences among species in competitive abilities measured in removal experiments (e.g., Taylor and Aarssen 1990; Wilson 1993a, 1993b) might be a simple reflection of differences in size among species. Second, variation in germination time produces variation in initial size (Ross and Harper 1972; Weiner and Thomas 1986), which could increase variability in competitive ability within a species and decrease relative differences among species, potentially allowing the coexistence of many species in the presence of competition (Aarssen 1989). This mechanism requires size-linked competitive abilities to work.

Competitive response might be influenced by size most strongly in habitats where there is competition for light (Zobel 1992). In contrast, size did not influence competitive ability in experiments in which competition was restricted to roots, either in the greenhouse (Newbery and Newman 1978; Wilson 1988a) or in the field (Gerry and Wilson 1994). Thus, the influence of size on competitive response might be small in nutrient-poor habitats where root competition is intense (Swank

TABLE 1. Initial mass and root to shoot ratios (R:S) of three classes of initial size for the two species (*Schizachyrium scoparium* and *Setaria viridis*) used in the experiment

Species and size	Mass (mg)		R:S	
	Mean	SD	Mean	SD
<i>Schizachyrium</i>				
Small	5.0	2.5	0.75	0.02
Medium	13.8	5.2	0.80	0.02
Large	31.8	12.3	0.82	0.01
<i>Setaria</i>				
Small	5.0	3.0	0.75	0.02
Medium	11.1	3.9	0.79	0.01
Large	24.2	5.0	0.81	0.01

and Oechel 1991; Wilson 1993a, 1993b), and greater in nutrient-rich, shady habitats where light competition is more important (Wilson and Tilman 1993).

I tested whether initial size influenced the ability of transplants of two species to compete against established perennial neighbours in both fertilized and unfertilized vegetation. Transplant mass and allocation patterns were examined. Biomass, resource availability, and species composition in the neighbouring vegetation were also measured.

Methods

Vegetation

The experiment was conducted in 1991 in an old field (field B) at Cedar Creek Natural History Area, 45°24'N, 93°12'W, 50 km N of Minneapolis, Minn. Nitrogen is the limiting nutrient in the fine sand soil of the field (Tilman 1988). Fourteen plots (each 5 × 5 m) received commercial NH₄NO₃ at 17 g N/(m² · year) in early May and late June each year during 1988–1991. Fourteen other plots received no additional nitrogen. Treatments were assigned in a completely randomized design. Plots were separated by 2-m wide corridors. The following nutrients and trace elements were also added to plots in both treatments to ensure that only nitrogen was limiting: P₂O₅, 20 g/(m² · year) as commercial 0–46–0 fertilizer; K₂O, 20 g/(m² · year) as commercial 0–0–61; CaCO₃, 40 g/(m² · year) as fine-ground commercial lime; MgSO₄, 30 g/(m² · year) as U.S. pure Epsom salts; CuSO₄, 18 μg/(m² · year); CoCO₂, 15.3 μg/(m² · year); MnCl₂, 322 μg/(m² · year); NaMoO₄, 15.1 μg/(m² · year). The experiment was surrounded by a 2-m tall fence and hardware cloth buried to a depth of 0.5 m to exclude large mammals and pocket gophers. The plots are part of a larger experiment (Wilson and Tilman 1991b).

Standing crop and litter were measured in each plot by clipping all aboveground plant material within a 10 × 100 cm quadrat in August 1991. Standing crop and litter were separated, dried, and weighed. Root biomass was measured by taking four soil cores (each 2 cm in diameter, 10 cm deep) evenly spaced along a transect 1 m inside the west edge of each plot, pooling them, and freezing them. This depth contains most of the root biomass in the field. Samples were thawed in September, washed to remove soil, and then dried and weighed.

Light penetration to the soil surface was measured on 20 August using a 40-cm long integrating light probe (Decagon Devices, Pullman, Wash.). Measurements were taken within 2 h of solar noon on a clear day 1 m inside the center of the south edge of each plot. Four measurements were made on the soil surface and averaged. One measurement was made 10 cm above the vegetation. Light penetration to the soil surface was calculated as a proportion of light above the vegetation.

Nitrogen availability was measured using four soil cores (2 cm in diameter, 10 cm deep) taken from each plot on 19 August. Cores

were taken from evenly spaced locations along a transect 1 m inside each plot. The four cores were pooled and mixed. A 10-g subsample of soil was extracted for 2 h with 0.02 M KCl, shaken for 1 h, and allowed to settle. Supernatant fluid was decanted and frozen until analysis for available nitrogen, in the form of ammonium and nitrate, using an Alchem Rapid Flow analyzer. Mean available nitrogen (sum of ammonium and nitrate) was determined for each plot.

Species composition was determined in August 1991 along a transect that ran diagonally across each plot. Two quadrats (100 × 50 cm) were placed along the transect, each 1.5 m towards the center of the plot from the ends of the transect. The percent cover of each species was recorded using Daubenmire's scale (Mueller-Dombois and Ellenberg 1974). The mean cover of each species in each plot was determined as its average in the two quadrats. The covers of mosses and lichens in each plot were summed to examine the effect of nitrogen on cryptogams as a whole.

Nonproportional data were log₁₀ transformed to improve normality and reduce heteroscedasticity. Proportional data were arcsine square root transformed. The hypothesis that variables differed significantly between nitrogen treatments was examined using unpaired *t*-tests.

Initial size and competitive response

The influence of initial size on competitive response was measured in 10 plots of each nitrogen treatment. The remaining four plots were used for annual measurements of vegetation. Seedlings were grown singly in subplots with neighbours either present or absent. Subplots were arrayed in a grid within main plots and spaced by 50 cm. Neighbours were removed from subplots by driving a plastic tube (10 cm deep, 11 cm in diameter) into the soil in the center and spraying neighbours inside the tube with glyphosate ("Roundup"), a systemic, rapidly decomposing herbicide (Grossbard and Atkinson 1985). The vegetation surrounding each tube was tied back with garden net (50 × 50 cm). The center of the net was fastened to the ground at the edge of the tube using four steel pins, each 15 cm long. The outer edges of the net were held 20 cm above the ground. This ensured that the center of the subplot was not shaded by neighbours outside the subplot. Subplots with neighbours present had tubes installed in vegetation that was not sprayed or tied back. Experiments nearby showed that subplots with no neighbours have significantly lower root and shoot mass, and significantly higher soil nitrogen and light penetration, than subplots with all neighbours (Wilson and Tilman 1991a; Wilson 1993b).

I used two species, *Schizachyrium scoparium*, a native tussock grass that dominates unfertilized plots in the experiment, and *Setaria viridis*, an introduced annual grass that is absent from unfertilized plots but establishes at low density in fertilized plots. The species are referred to by their genus names. Seedlings were grown singly in pots (7.6 cm deep, 2.5 cm in diameter) filled with a 3:1 mixture of peat moss and Cedar Creek sand. Several cohorts were started between 1 March and 6 May 1991 to obtain seedlings of a range of sizes. Immediately before transplanting, the length of each leaf was recorded for 30 seedlings of each species. The roots and shoots of the same seedlings were washed, dried, and weighed. Regression analysis described the relationship between individual total leaf length (TLL; mm) and root (R) and shoot mass (S; g) for each species (*Schizachyrium*: R = (0.00311 × TLL + 0.0170)², *r*² = 0.89; S = (0.00345 × TLL + 0.0257)², *r*² = 0.94; *Setaria*: R = (0.00351 × TLL + 0.0370)², *r*² = 0.94; S = (0.00355 × TLL + 0.0329)², *r*² = 0.92). The total leaf length of every seedling was measured on May 26 and the initial root and shoot mass of each seedling was determined. Each seedling was assigned to one of three size classes according to its initial total mass. Plants in the large size class had about twice the mass of plants in the medium size class, which had about twice the mass of plants in the small size class (Table 1). Root to shoot ratios were similar between species and increased slightly with initial size.

Seedlings were transplanted into the field from 3 to 6 June by removing the seedling and its associated soil from the pot and planting it in a hole the same size as the pot in the center of each subplot. Holes for transplanting were formed by pressing a round metal bar into the soil. Examination upon harvest showed prolific growth of

TABLE 2. Biomass, resource availability, and species composition in plots receiving either no added nitrogen or added nitrogen ($N = 14$) for 4 years in a Minnesota old field

Variable	No added nitrogen	Added nitrogen	<i>t</i>
Standing crop (g/m ²)	137	403	6.4***
Litter (g/m ²)	253	1041	7.7***
Roots (g/m ²)	284	361	1.8
Soil ammonium and nitrate (g N / kg soil)	0.68	5.93	8.76***
Light penetration (%)	23.7	0.4	10.22***
Species covers (%)			
<i>Schizachyrium scoparium</i>	46.5	43.4	
Mosses and lichens	9.6	0.0	
<i>Poa pratensis</i>	3.1	16.9	
<i>Setaria viridis</i>	0.0	1.1	
<i>Polygonum convolvulus</i>	0.4	9.2	
<i>Elytrigia repens</i>	0.0	28.4	

*** $P < 0.001$.

transplant roots into the surrounding soil and growth of neighbour roots into the transplanted soil. Soil structure and roots were not otherwise disrupted by planting. Seedlings were covered with 70% shade cloth and watered on days without rain for 2 weeks to promote establishment. The few seedlings that died soon after planting were replaced until 1 July.

Each of the 20 plots contained at least one subplot for each of two species, each of two competition treatments, and each of three size classes. Treatments were assigned to subplots randomly. Additional subplots, which had originally been assigned to a third species that failed to germinate, were used for extra replicates of some treatment combinations. For *Schizachyrium*, there were two additional subplots for the smallest size class with neighbours present and one extra subplot with neighbours absent. For *Setaria*, there were two extra subplots for the smallest size class, one extra for the medium class, and one extra for the largest size class grown without neighbours. Treatments with more than one subplot per plot had subplot results pooled for each plot prior to analysis.

Transplants were harvested near the end of the growing season, from 9 to 12 September. The tubes containing transplants, neighbouring vegetation, and soil were removed and frozen for up to 3 months. Frozen tubes were thawed, and roots and shoots were washed, dried, and weighed. Transplants and neighbours were separated by hand.

The influence of initial size, competition, and nitrogen on the final mass and root to shoot ratio of each species was examined using split-plot analysis of variance (ANOVA) with nitrogen as the main plot effect, and size and competition as subplot effects. A significant interaction between initial size and competition would suggest that initial size influenced competitive response. Growth rate was not used as a dependent variable because initial mass would be used for both the independent variable (the size treatment) and dependent variable (growth rate) and would confound the analysis. Dependent variables were not transformed because transformations that reduce correlations between means and variances also remove factor interactions (Snedecor and Cochran 1980; Day and Quinn 1989).

Results

Vegetation

Standing crop and litter were significantly ($P < 0.05$) higher in plots that received additional nitrogen (Table 2), but root biomass did not vary significantly with nitrogen. Light penetration was significantly lower in fertilized plots, and available soil nitrogen was significantly higher.

Species composition varied markedly between fertilized and unfertilized plots, as shown by the covers of the five most

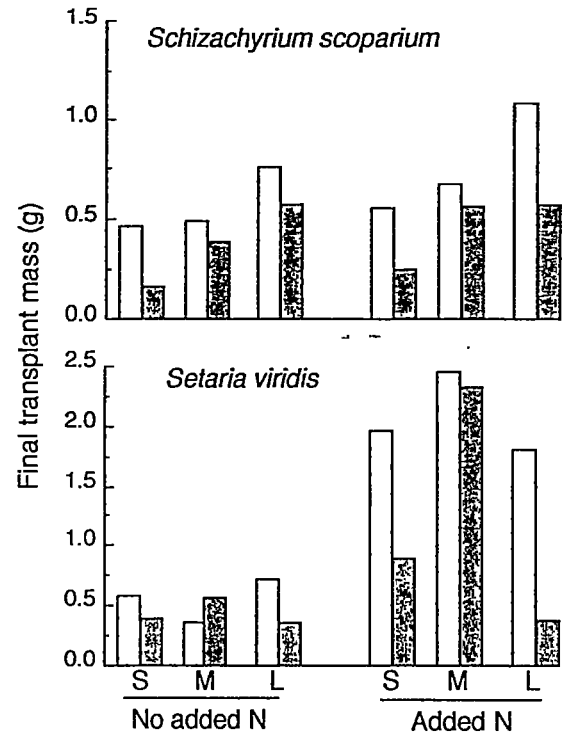


FIG. 1. Final mass (roots and shoots) of transplants of *Schizachyrium* and *Setaria* in three classes of initial size (S, small; M, medium; L, large) grown either with neighbours absent (open bars) or with neighbours present (shaded bars), in plots with no added nitrogen or with added nitrogen.

abundant taxa and *Setaria* (Table 2). Unfertilized plots were dominated by *Schizachyrium scoparium*, mosses, and lichens. Fertilized plots were also dominated by *Schizachyrium scoparium*, but mosses and lichens were absent, and the grasses *Elytrigia repens* (formerly *Agropyron repens*; Gleason and Cronquist 1991) and *Poa pratensis* were abundant. Annuals, such as *Polygonum convolvulus* and *Setaria viridis*, appeared mostly in fertilized plots.

Initial size and competitive response

Transplants of *Schizachyrium* accumulated significantly less mass in the presence of neighbours (Fig. 1; Table 3). Mass varied significantly among size classes because initial size differences were reflected by final mass. Final mass did not vary significantly with added nitrogen. There was no significant interaction between size and competition, suggesting that initial transplant mass did not influence the degree to which plants were suppressed by neighbours. Further, there was no three-way interaction among size, competition, and nitrogen, suggesting that size did not affect competitive response at either level of nitrogen.

Transplants of *Setaria* likewise accumulated significantly less mass in the presence of neighbours (Fig. 1; Table 3), and final mass varied significantly among size classes. Mass increased significantly with nitrogen addition. Mass did not vary significantly with the interaction between size class and competition or with the three-way interaction among competition, size, and nitrogen. A significant interaction between size class and nitrogen treatments may have been produced by the relatively large final mass of individuals in the middle size class in plots receiving additional nitrogen (Fig. 1).

The root to shoot ratios of both species did not vary with any

TABLE 3. ANOVA results for the influence of size, competition, and nitrogen on the mass and root to shoot ratios (R:S) of *Schizachyrium scoparium* and *Setaria viridis*

Source	df	Mass		R:S	
		MS	F	MS	F
<i>Schizachyrium</i>					
Size	2	1.0910	5.74**	0.0290	0.12
Competition	1	2.1834	11.49**	0.0627	0.27
Nitrogen	1	0.6108	1.74	0.8166	2.57
Plot	18	0.3594	1.89*	0.3222	1.38
Size × competition	2	0.1408	0.74	0.0914	0.39
Size × nitrogen	2	0.0106	0.06	0.0408	0.17
Competition × nitrogen	1	0.2678	1.41	0.2938	1.26
Size × competition × nitrogen	2	0.1045	0.55	0.0065	0.03
<i>Setaria</i>					
Size	2	4.634	4.34*	0.0014	0.09
Competition	1	6.676	6.26*	0.0001	0.01
Nitrogen	1	33.148	15.51**	0.0331	1.87
Plot	18	2.167	2.03*	0.0178	1.14
Size × competition	2	2.899	2.72	0.0118	0.76
Size × nitrogen	2	5.399	5.06**	0.0168	1.08
Competition × nitrogen	1	4.078	3.82	0.0031	0.20
Size × competition × nitrogen	2	0.823	0.77	0.1042	6.66**

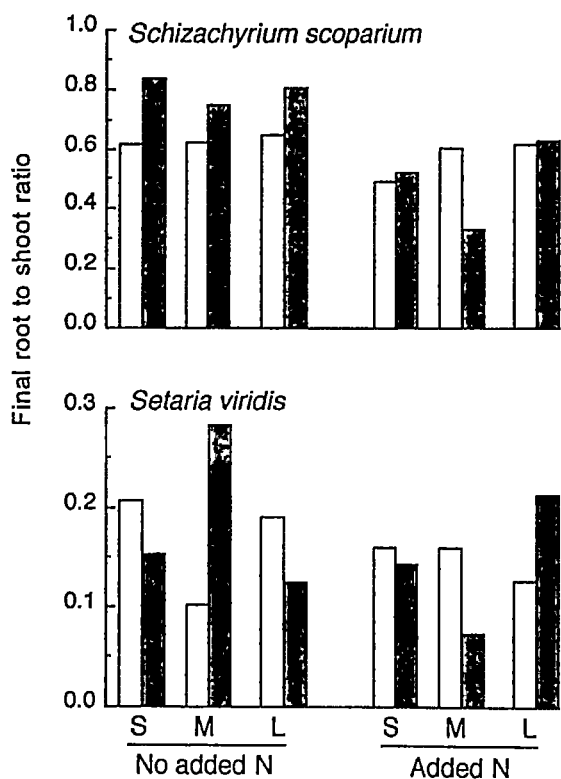
* $P < 0.05$.** $P < 0.01$.

FIG. 2. Root to shoot ratios of transplants of *Schizachyrium* and *Setaria* in three classes of initial size (S, small; M, medium; L, large) grown either with neighbours absent (open bars) or with neighbours present (shaded bars), in plots with no added nitrogen or with added nitrogen.

treatment or two-way interaction (Table 3), although root to shoot ratios tended to be higher in unfertilized plots (Fig. 2). The root to shoot ratio of *Setaria* varied significantly with the

three-way interaction; pairwise comparisons showed that ratios for middle-sized transplants grown with neighbours were significantly greater than those for large transplants in unfertilized plots and significantly smaller in fertilized plots (Fig. 2).

Biomass and root to shoot data were also analyzed using transformed values (log and arcsine square root) to determine whether transformation affected the outcome. Results for transformed data were not substantially different.

Discussion

Nitrogen produced a threefold increase in standing crop and a fourfold increase in litter (Table 2). Litter probably increased more than standing crop because of accumulation during the previous 3 years of the experiment. Root mass did not vary significantly between fertilized and unfertilized vegetation in 1991, nor in the previous 2 years (Wilson and Tilman 1991b, 1993), probably due to decreased root allocation at high nitrogen availability. The greatest difference in species composition associated with increased nitrogen was the replacement of mosses and lichens by the perennial grasses *Poa pratensis* and *Elytrigia repens* (Table 2).

Both competition and initial size had large and significant effects on the final mass of both species (Fig. 1; Table 3), so the experiment should have been able to detect any important interaction that might have existed between these factors. The lack of a significant interaction between competition and initial size indicated that competition suppressed both small and large transplants to the same extent. In the case of *Setaria*, the interaction between competition and initial size was almost significant ($P = 0.07$). This probably resulted because medium-sized transplants were less suppressed by neighbours than were small or large transplants (Fig. 1). Thus, neither species provided evidence that the smallest transplants were at a disadvantage in competition with neighbours.

Large initial size has been shown to confer competitive advantage in many pot experiments (Black 1958; Ross and

Harper 1972; Gross 1984; Gaudet and Keddy 1988) and in natural monocultures (Weiner and Thomas 1986; Schmitt et al. 1987). One explanation for the lack of an interaction between size and competition in my experiment is that large initial seedling size might provide no advantage to transplants competing against established neighbours that have a relatively much greater mass. This explanation seems unlikely, however, because each 11-cm diameter tube in this experiment contained approximately 4.0–7.2 g of neighbour mass (standing crop and roots, Table 2), while average transplant mass in the presence of neighbours was as high as 2.5 g (Fig. 1). Thus, the disparity between neighbours and transplants, which was very large at the start of the experiment (Table 1), was greatly diminished over the growing season by the ability of transplants to grow, even in the presence of neighbours (Fig. 1). A second possible explanation is that large initial size confers advantage only in situations where plants grow into previously empty environmental space, as in pots or in natural populations of annuals. In the perennial vegetation studied here, all space is physically filled at the start of the experiment, either by litter, shoots, or roots. Large size may confer no advantage to a seedling growing in an already filled environment. A third possible explanation is that size influences competitive effect but not response. Competitive effect varies with neighbour mass in transplant experiments (Goldberg 1987; Wilson and Tilman 1993), and competitive response might also be expected to vary with mass (Goldberg 1990) but did not in this experiment (Table 3) or in the six species examined by Gerry and Wilson (1994). Lastly, it is possible that a much greater range in size classes than that used here might provide evidence for differences in competitive response, but my aim was to examine sizes relevant to the establishment phase.

It has also been suggested that large size might confer competitive ability only in shaded habitats and that this advantage is lost where light competition is reduced, through repeated clipping (Newbery and Newman 1978), by the use of partitions (Wilson 1988a), or on nutrient-poor soil (Zobel 1992). Competition is among both roots and shoots in plots receiving additional nitrogen but almost exclusively among roots in unfertilized plots (Wilson and Tilman 1993), so a size-dependent ability to compete for light might be expected to occur only in fertilized plots. The lack of an interaction between nitrogen, size, and competition indicated that large size did not confer competitive advantage in nutrient-rich vegetation.

These results should be interpreted in light of the fact that classes of initial size differed in age as well as initial mass, allowing the possibility that phenology or developmental stage also influenced the results. None of the seedlings used here, however, differed in age by more than 10 weeks, and older plants did not appear to be any closer to flowering than younger plants. Differences in seedling sizes arising from differences in germination times have been proposed as a mechanism that increases variability in competitive ability within a species and diminishes differences among species, resulting in the coexistence of many species in the presence of intense competition (Aarssen 1989), but my results did not support this idea.

Nitrogen had no effect on the final mass of *Schizachyrium*, a result consistent with earlier experiments with this species (Wilson and Tilman 1991a, 1993). In contrast, *Setaria* accumulated significantly more mass in fertilized plots than in plots receiving no added nitrogen (Fig. 1). In a similar experiment, the growth rate of *Schizachyrium* in the absence of neighbours did not vary with nitrogen availability, but the growth rates of

two other species, *Poa pratensis* and *Elytrigia repens*, increased significantly with nitrogen (Wilson and Tilman 1991a). The lack of response of *Schizachyrium* to nitrogen may be due to its relatively high efficiency of nitrogen use, which might allow high growth rates at relatively low nitrogen availability (Tilman and Wedin 1991).

Root to shoot ratios did not vary significantly with any main effect for either species but were generally higher in unfertilized plots. Further, root to shoot ratios of *Schizachyrium* in unfertilized plots were higher in the presence of neighbours than in the absence of neighbours. Thus, the direction of changes in root to shoot ratios with regards to nutrient availability and competition conforms to results from other studies (Wilson 1988b). The lack of significant differences in this study may have arisen from the relatively high amount of environmental variation inherent in a field experiment.

The lack of a significant interaction between nitrogen and competition for both species (Table 3) suggests that transplants were suppressed by neighbours to the same extent in both fertilized and unfertilized vegetation, in accordance with other grassland experiments (Wilson and Tilman 1991a, 1993; DiTommaso and Aarssen 1991).

Initial size did not affect competitive response, so it may be possible to compare the competitive responses of different species with different initial sizes (e.g., Taylor and Aarssen 1990; Wilson 1993a, 1993b), at least for the two doublings of initial mass used here. Problems might arise, however, when attempting to compare species with different growth rates using a single-season experiment. Consider two species with similar sizes but different growth rates growing in limited environments for one growing season. The fast-growing species might achieve its maximum possible mass in the absence of neighbours, accumulate less mass in the presence of neighbours, and appear to be restricted by competition. The slow-growing species might not achieve its maximum mass in the absence of neighbours in one growing season, the difference in its mass grown with and without neighbours would be smaller than that for the fast-growing species, and the slow-growing species would appear to be less suppressed than the fast-growing species. Thus, even where care is taken to use plants with the same initial mass, differences in growth rates among species may produce apparent differences in competitive responses. This could be overcome by allowing all species to achieve their maximum possible sizes in the absence of neighbours, either by continuing the experiment for several years (e.g., Tilman and Wedin 1991), or by using sufficiently small environments such that all species achieve their maximum possible size during the course of the experiment.

In summary, the link between competitive ability and initial size found in pot experiments and in annual monocultures was not found in either the low-nitrogen or the high-nitrogen plots of this field removal experiment. This result suggests that differences in competitive abilities found among different species used as targets (e.g., DiTommaso and Aarssen 1991; Wilson and Tilman 1991a) may be due to their different physiologies or patterns of mass allocation and not simply to their different sizes at transplanting.

Acknowledgements

I thank T. Mielke for extensive field assistance, A. Gerry for help with the analysis, and M. Forbes, A. Gerry, and P. Klinkhamer for helpful comments on the manuscript. This

work was supported by National Science Foundation grant BSR 8612104 and the Natural Sciences and Engineering Research Council of Canada.

- Aarssen, L.W. 1989. Competitive ability and species coexistence: a 'plant's-eye view'. *Oikos*, 56: 386–401.
- Black, J.N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light microclimate. *Aust. J. Agric. Res.* 9: 299–318.
- Day, R.W., and Quinn, G.P. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59: 433–463.
- DiTommaso, A., and Aarssen, L.W. 1991. Effect of nutrient level on competition intensity in the field for three coexisting grass species. *J. Veg. Sci.* 2: 513–522.
- Gaudet, C.L., and Keddy, P.A. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature (London)*, 334: 242–243.
- Gerry, A.K., and Wilson, S.D. 1994. The influence of initial size on the competitive responses of six plant species. *Ecology*. In press.
- Gleason, H.A., and Cronquist, A. 1991. *Manual of vascular plants of Northeastern United States and adjacent Canada*. 2nd ed. New York Botanical Garden, New York.
- Goldberg, D.E. 1987. Neighborhood competition in an old-field plant community. *Ecology*, 68: 1211–1223.
- Goldberg, D.E. 1990. Components of resource competition in plant communities. In *Perspectives on plant competition*. Edited by J.B. Grace and D. Tilman. Academic Press, San Diego, Calif. pp. 27–49.
- Grace, J.B., Keough, J., and Guntenspergen, G.R. 1992. Size bias in traditional analyses of substitutive competition experiments. *Oecologia*, 90: 429–434.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Chichester, England.
- Gross, K.L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J. Ecol.* 72: 369–387.
- Grossbard, E., and Atkinson, D. 1985. *The herbicide glyphosate*. Butterworths, London.
- Keddy, P.A. 1989. *Competition*. Chapman & Hall, London.
- Mueller-Dombois, D., and Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, New York.
- Newbery, D.M., and Newman, E.I. 1978. Competition between grassland plants of different initial sizes. *Oecologia*, 33: 361–380.
- Ross, M.A., and Harper, J.L. 1972. Occupation of biological space during seedling establishment. *J. Ecol.* 60: 77–88.
- Schmitt, J., Eccleston, J., and Ehrhardt, D.W. 1987. Dominance and suppression, size-dependent growth and self-thinning in a natural *Impatiens capensis* population. *J. Ecol.* 75: 651–665.
- Snedecor, G.W., and Cochran, W.G. 1980. *Statistical methods*. 7th ed. Iowa State University Press, Ames, Iowa.
- Swank, S.E., and Oechel, W.C. 1991. Interactions among the effects of herbivory, competition, and resource limitation on chaparral herbs. *Ecology*, 72: 104–115.
- Taylor, D.R., and Aarssen, L.W. 1990. Complex competitive relationships among genotypes of three perennial grasses: implications for species coexistence. *Am. Nat.* 136: 305–327.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, N.J.
- Tilman, D., and Wedin, D. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, 72: 685–700.
- Weiner, J., and Thomas, S.C. 1986. Size variability and competition in plant monocultures. *Oikos*, 47: 211–222.
- Wilson, J.B. 1988a. The effect of initial advantage on the course of plant competition. *Oikos*, 51: 19–24.
- Wilson, J.B. 1988b. A review of evidence on the control of root:shoot ratio, in relation to models. *Ann. Bot. (London)*, 61: 433–449.
- Wilson, S.D. 1993a. Belowground competition in forest and prairie. *Oikos*, 68: 146–150.
- Wilson, S.D. 1993b. Competition and resource availability in heath and grassland in the Snowy Mountains of Australia. *J. Ecol.* 81: 445–451.
- Wilson, S.D., and Tilman, D. 1991a. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology*, 72: 1050–1065.
- Wilson, S.D., and Tilman, D. 1991b. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia*, 88: 61–71.
- Wilson, S.D., and Tilman, D. 1993. Plant competition in relation to disturbance, fertility, and resource availability. *Ecology*, 74: 599–611.
- Zobel, M. 1992. Plant species coexistence: the role of historical, evolutionary, and ecological factors. *Oikos*, 65: 314–320.