

SOIL NUTRIENT HETEROGENEITY ALTERS COMPETITION BETWEEN TWO PERENNIAL GRASS SPECIES

BART FRANSEN, HANS DE KROON,¹ AND FRANK BERENDSE

Nature Conservation and Plant Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, The Netherlands

Abstract. Differences in root foraging behavior between species have been well documented, but the effects of these differences on belowground competitive ability are only beginning to be studied. Here we report the results of a competition experiment in homogeneous and heterogeneous soils between two species that differ in their ability to acquire nutrients from patchy environments. The perennial grasses *Festuca rubra* and *Anthoxanthum odoratum* have comparable growth rates, but results of previous studies with isolated plants designated the latter species as the more effective forager, probably due to its higher physiological plasticity (stronger increase in nutrient uptake rates per unit root mass in enriched nutrient patches). We introduced nutrient soil heterogeneity at two spatial scales. In a fine-grained heterogeneous treatment, the nutrient-rich patches were smaller and more concentrated than in a coarse-grained heterogeneous (checkerboard) treatment. Overall, the level of nutrient availability in these heterogeneous treatments was similar to a third treatment with homogeneous soils. The species were grown in monocultures and mixtures in a standard replacement design during two growing seasons.

In the homogeneous treatment, the relative competitive ability of *F. rubra* was higher than of *A. odoratum*, but *F. rubra*'s advantage declined in the heterogeneous environments, and the relative competitive abilities became the same. Both species produced higher root densities in the richer patches of the fine-grained heterogeneous treatment, but not significantly so in the coarse-grained heterogeneous treatment, and these responses were the same for both species. The root activity of the species was assessed by determining the amount of strontium captured by a species at the end of the experiment, after injecting SrCl_2 in the nutrient-rich patches and in equivalent locations in the homogeneous treatment. *F. rubra* acquired significantly more Sr in the mixtures in the homogeneous treatments, but in the coarse- and fine-grained heterogeneous treatment the nutrient acquisition abilities of the species were equal. These results suggest that a more effective root foraging behavior confers a higher competitive ability in heterogeneous environments. Moreover, the results on root-proliferation and nutrient-acquisition ability suggest that a higher physiological (rather than morphological) plasticity is critical in obtaining a long-term competitive advantage. Analyses of shoot size inequalities suggest that competitive interactions were size-symmetric in homogeneous soil and size-asymmetric in the heterogeneous treatments. However, in the long term, competition becomes more size-symmetric in the heterogeneous soils, consistent with the increasing importance of physiological plasticity.

Key words: *Anthoxanthum odoratum*; competition; *Festuca rubra*; grasses, perennial; heterogeneity, soil nutrients; morphological and physiological plasticity; nutrients in soils; plant competition underground; replacement design; root foraging; soil nutrient heterogeneity changes competition.

INTRODUCTION

Nutrient heterogeneity is ubiquitous within natural habitats (Jackson and Caldwell 1993, Gross et al. 1995, Ryel et al. 1996, Cain et al. 1999). Plants are able to proliferate roots and to enhance root uptake kinetics in patches of high nutrient concentrations, enhancing the acquisition of nutrients in heterogeneous environments (Hutchings and de Kroon 1994, Robinson 1994, Robinson and Van Vuuren 1998). The degree of root pro-

liferation in response to nutrient heterogeneity is species specific (Crick and Grime 1987, Jackson and Caldwell 1989, Gross et al. 1993, Fransen et al. 1998), as well as nutrient specific (Drew 1975, Jackson and Caldwell 1989). Species also differ in root physiological plasticity, i.e., an increase in nutrient uptake capacity per unit root length in response to localized nutrient enrichment (e.g., Jackson et al. 1990).

In spite of its generality, the ecological significance of enhanced root proliferation especially in nitrogen-enriched patches is far from straightforward. Species display similar degrees of root proliferation in response to NO_3^- -enrichment and to PO_4^- -enrichment, but the high mobility of NO_3^- limits the contribution of root proliferation to N capture (Jackson and Caldwell 1996,

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¹ Corresponding author: Department of Ecology, University of Nijmegen, Toernooiveld, 6525 ED Nijmegen, The Netherlands. E-mail: Hans.deKroon@sci.kun.nl

Robinson 1996). Furthermore, the benefits of root proliferation in terms of N acquisition are limited if patch depletion occurs (Fransen et al. 1998). Remarkably, root proliferation in response to N enrichment may occur even after most of the N has been taken up (van Vuuren et al. 1996). Accordingly, modeling studies have suggested that physiological responses may be more important for the capture of patchy N than morphological responses (Jackson and Caldwell 1996, Robinson 1996, Ryel and Caldwell 1998).

As a solution to these paradoxical root morphological responses, it has recently been suggested that root proliferation in N-enriched patches may confer a distinct advantage during interspecific competition for finite, local N-enriched patches (Hodge et al. 1999, Robinson et al. 1999; but see Cahill and Casper 1999). These effects of root foraging behavior on plant competitive ability are only beginning to be studied. Given its dramatic consequences for the capture of nutrients by isolated plants, a higher root physiological plasticity may be expected to similarly enhance the competitive ability of a species in heterogeneous environments, but we are unaware of studies that have investigated these effects.

Results of competition experiments indicate that in homogeneous environments competition for nutrients is relatively size symmetric, i.e., plants acquire nutrients in proportion to their biomass (Weiner 1986, 1990, Casper and Jackson 1997, Weiner et al. 1997, Berntson and Wayne 2000). It has been suggested that this picture may change in heterogeneous habitats (Casper and Jackson 1997, Schwinning and Weiner 1998). Larger plants may reach nutrient-rich patches and deplete them of nutrients before smaller plants can gain access, providing them with a disproportionate advantage in terms of nutrient acquisition and resulting in asymmetric competition. Asymmetric, rather than symmetric, competition is known to aggravate size differences among competing plants and accelerate competitive exclusion. However, we know of no published studies testing this hypothesis of asymmetric belowground competition in heterogeneous soils.

When considering belowground competition between plants of different species this picture may further change if the root foraging abilities of the species are very different. We hypothesize that one out of two scenarios may occur. If the larger species is better able to capture nutrients from enriched patches than the smaller species, the foraging behavior of the larger species will exacerbate the size difference with the smaller species and increase its competitive ability. Alternatively, if the smaller species is the better forager, it may have access to nutrient patches that are unavailable for the larger species by which the size differences between the species will be reduced and competitive abilities become more equal (cf. Weiner et al. 1997). This latter scenario is reminiscent of the suggestion that small, subordinate plant species are capable of "high-prec-

sion" foraging by which they are better able to exploit small patches of high nutrient availability than the larger dominant species (Campbell et al. 1991). Hence, in patchy environments, both plant size and foraging behavior in interaction are expected to determine the competitive ability belowground.

This study examines the question whether a better root foraging ability of a species confers a competitive advantage in heterogeneous soils. To answer this question we investigated the effects of nutrient heterogeneity on the competition between the perennial grass species *Anthoxanthum odoratum* L. and *Festuca rubra* L. The two species co-occur in natural grasslands and have comparable growth rates and plant sizes, but differ in root foraging ability in heterogeneous environments (Fransen et al. 1998, 1999). Both tend to proliferate their roots in response to localized nutrient enrichment, but the increment in root-length density was significant only for *F. rubra* (Fransen et al. 1998). However, the root morphological response of *F. rubra* resulted only in a small, nonsignificant increase in N acquisition in a heterogeneous treatment compared to a homogeneous treatment (Fransen et al. 1998). In contrast, *A. odoratum* acquired significantly more N in the heterogeneous environment than in the homogeneous environment, probably due to its high root physiological plasticity (Fransen et al. 1999).

In the experiment described below, the two species were grown in monocultures and mixtures, both in homogeneous and heterogeneous soils. Nutrient heterogeneity was introduced at two spatial scales, keeping the overall nutrient availability the same as in the homogeneous treatment. The experiment ran for two years. Such a relatively long duration may be critical for a reliable outcome of such an experiment with perennial plants because the benefits of root foraging behavior may dramatically change on the longer term due to patch depletion and nutrient losses associated with the turnover of plant parts (Fransen and de Kroon 2001). The two experiments so far that had looked at competitive ability in relation to root proliferation have both been carried out over a very short term (8–9 wk) (Hodge et al. 1999, Cahill and Casper 1999).

Our central hypothesis is that the competitive ability of *Anthoxanthum odoratum* relative to *Festuca rubra* will increase in the heterogeneous compared to the homogeneous environments, due to the better ability of the former species to acquire nutrients in heterogeneous environments. To test this hypothesis we measured mean shoot biomass and plant size inequality of the species in the different treatments. Competitive ability was assessed using the replacement-design methodology (de Wit 1960). To check whether the root foraging abilities of the species were indeed different and were consistent with the behavior of the species in our previous experiments, the root biomass production was measured in the nutrient-rich and nutrient-poor patches. In addition, a strontium solution was added to the nu-

trient-rich patches and the uptake of this tracer was used to estimate the root activity of the species in these patches in both the monocultures and the mixtures at the end of the experiment.

MATERIALS AND METHODS

The species

Festuca rubra L. and *Anthoxanthum odoratum* L. are perennial grass species, characteristic of moderately nutrient-poor habitats. Both are bunchgrasses that do not produce rhizomes or stolons. Estimates of potential relative growth rates range from 168–176 mg·g⁻¹·d⁻¹ for *F. rubra* and 134–208 mg·g⁻¹·d⁻¹ for *A. odoratum* (Grime and Hunt 1975, van der Werf et al. 1998). To standardize the experimental plant material, the experiment was carried out with cloned individuals. The original plants of the two species were collected at various hay meadows within a former agricultural grassland area along the Anloeër Diepje, a brook in the 'Drentse Aa' Nature Reserve (53° N, 6°40' E) (see Bakker 1989). The plants used in this study were propagated from the field material in a heated greenhouse. At the start of the experiment, young tillers, isolated from four original plants of each species, were randomly assigned to an initial harvest or to the experiment.

Experimental design

The experiment was carried out in an open greenhouse. In May 1997 large containers (90 × 70 × 40 cm) were filled either with a homogeneous soil, or a coarse-grained heterogeneous soil, or a fine-grained heterogeneous soil and planted to contain 30 individuals (i.e., 48 individuals/m², Fig. 1). Individual tillers of each species were planted in a regular pattern in a standard replacement design, i.e., containers consisted either of the monocultures of the two species or their 0.5:0.5 mixture. Each Treatment × Planting combination was replicated 6 times.

Polyvinyl-chloride (PVC) frames consisting of 20 cells of 15 × 15 cm were placed in each container before filling to maintain the same soil compaction in each treatment. At the bottom of each container a 5 cm layer of gravel was placed and covered with root cloth, to ensure drainage. The different soils were constructed by using different mixtures of humus-rich black soil and coarse sand. The total amount of the humus-rich black soil and sand used in each of the treatments was identical. Hence, the overall nutrient availability was the same in all treatments. The soil moisture content in each container was kept at ±10% (mass %) by weighing the containers once a week and watering them three times a week during the experiment. In all containers the PVC frames were removed after filling.

In the homogeneous treatment, the cells of the PVC frame were filled with a homogeneous soil mixture consisting of 12.5% black soil and 87.5% sand (mineral

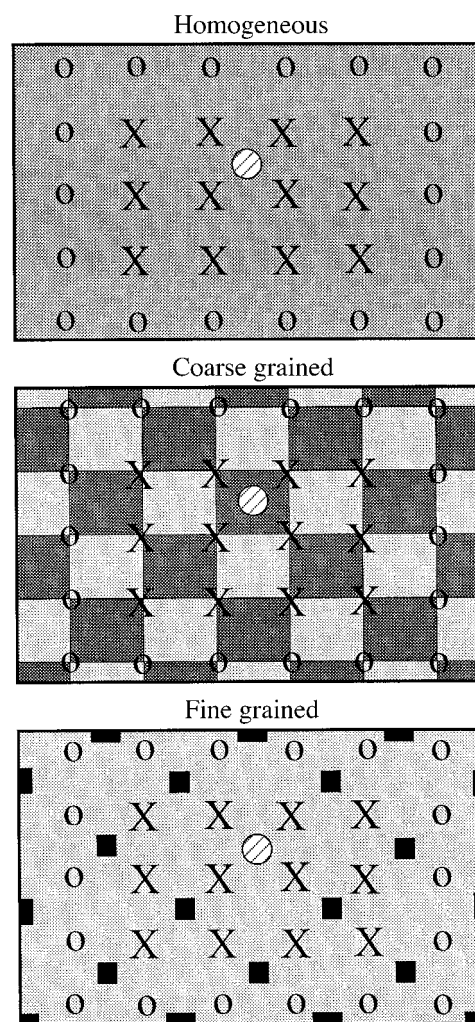


FIG. 1. The planting pattern and the three soil treatments used in the perennial-grass competition experiments. The nutrient-rich patches in the heterogeneous treatments, indicated by dark shading, differed in size and nutrient concentration. The planting locations are indicated by O and X. The plants consisted either of 100% *Festuca rubra* or 100% *Anthoxanthum odoratum* in the monocultures, or 50% of each of the species in the mixtures. In the mixtures, the planting positions of the two species were alternated. The 12 center plants (indicated with X) are included in all analyses, while the remainder of the plants (indicated with O) was used as a buffer to reduce edge effects. The hatched circle gives the position of the SrCl₂ injection in each of the treatments.

N = 2.72 mg N/kg, 1 mol/L KCl extraction). In the coarse-grained heterogeneous treatment the same frame was used, but the cells were filled with either a mixture of 20% black soil–80% sand or with a mixture of 5% humus-rich black soil–95% sand, in a checkerboard arrangement (Fig. 1). In this treatment, the nutrient-rich patches contained 4.02 mg N/kg vs. 1.65 mg N/kg for the nutrient-poor patches (mineral N, 1 mol/L KCl extraction). Plants were placed at the corners of the cells and their roots had immediate access to two rich and two poor patches.

In a third fine-grained heterogeneous treatment, a different frame was used to fill the containers, consisting of 10 cells of 6×6 cm. These small cells were filled with 100% humus-rich black soil (the nutrient-rich patches, mineral N = 8.67 mg N/kg, 1 mol/L KCl extraction), and were in exactly the same positions as the nutrient-rich patches in the coarse-grained heterogeneous treatment. The rest of the container was filled with nutrient-poor soil, consisting of 5% humus-rich black soil and 95% sand (mineral N = 1.65 mg N/kg, 1 mol/L KCl extraction). The nutrient-rich patches in the fine-grained heterogeneous treatment were thus smaller and more concentrated than the nutrient-rich patches in the coarse-grained heterogeneous treatment, while the nutrient-poor soil surrounding the patches was similar to the soil of the poor patches in the other heterogeneous treatment. One other difference with the coarse-grained heterogeneous treatment is that, in the fine-grained heterogeneous treatment, all plants started growing in poor soil and had to extend their root systems before they could reach the nutrient-rich patches. Note that containers of both patchy soil treatments contained all together the same mixture of black soil and sand.

At the end of both the first (i.e., October 1997) and the second (i.e., September 1998) growing seasons, plants were clipped at a height of 2 cm and divided into living and dead leaves and flowering stalks if present. Plants were harvested individually within each of the containers. Both species are well adapted to the removal of aboveground biomass because they grow in frequently mown grasslands. The species did not flower during the first growing season, but both flowered abundantly during the second growing season. The harvested biomass was dried at 70°C for at least 48 h prior to weighing. All results (biomass production, competitive ability, and size inequality) were based on only the 12 center plants (Fig. 1) in each container to reduce possible edge effects, i.e., 12 plants per species per container in the monocultures and 6 plants of each of the two species per container in the mixtures.

To determine the degree of selective root placement of the species, six soil cores (diameter, 5 cm; depth, 0–20 cm), equally divided among the nutrient-rich and nutrient-poor patches, were taken in the monocultures in each treatment at the end of the experiment. Roots in these soil cores were washed clean of soil particles, and root biomass in the soil cores was determined after drying at 70°C for at least 48 h. Soil cores were also taken in the mixtures in each treatment, but the roots of the two species could not be distinguished with certainty.

Analysis of competitive ability

In a standard replacement design (de Wit 1960), total plant density in the mixture is equal to the plant density used in the monoculture of each component species. The competitive ability of a species is given by the

relative crowding coefficient ($k_{1,2}$; de Wit 1960) quantifying the growth of an individual during interspecific competition, relative to the growth during intraspecific competition. The relative crowding coefficient is defined as

$$O_1 = k_{1,2}z_1(k_{1,2}z_1 + z_2)^{-1} M_1$$

$$O_2 = k_{2,1}z_2(k_{2,1}z_2 + z_1)^{-1} M_2$$

with O_1 and O_2 as the yield (total species biomass) in the mixture, z_1 and z_2 the initial plant frequencies in the mixture (with $z_1 + z_2 = 1$) and M_1 and M_2 as the yield of the monocultures, of species 1 and 2, respectively. Note that O_1 and O_2 are the summed biomass of 6 plants per container, and M_1 and M_2 are the summed biomass of 12 plants. $k_{1,2} = 1$ indicates that the interspecific competition that species 1 experiences from species 2 is equally severe as the intraspecific competition from individuals of its own species. If $k_{1,2} > 1$ the growth of species-1 individuals is less suppressed by individuals of species 2 than by individuals of its own species, and projects species 1 as the better competitor.

It should be noted that the relative crowding coefficient is not an inherent species characteristic, but depends on the plant material, the experimental conditions, and the harvest time. As in any competitive design, the initial material and the initial growth rates influence the outcome of competition and these initial conditions are not necessarily the same for both species investigated. One implication is that the results are size biased, favoring the initially larger species (Connolly 1986, 1997, Grace et al. 1992, Gibson et al. 1999). Notwithstanding this effect, replacement-design experiments have proven to be most appropriate for comparing the relative competitive abilities of plant species under different conditions (Firbank and Watkinson 1990, Berendse et al. 1992, van der Putten and Peters 1997). In this study we are using the design for exactly such comparative purpose. Nevertheless, we made sure that the plants of *F. rubra* and *A. odoratum* used in the experiment did not differ significantly ($P = 0.21$) in their initial size. Individuals of *F. rubra* had an average initial dry mass of 47.9 ± 5.5 mg (mean \pm 1 SE, $n = 22$), individuals of *A. odoratum* an initial dry mass of 40.3 ± 3.3 mg ($n = 38$).

One other point of critique on the replacement-design methodology is that the results may be density dependent (Connolly 1986, Taylor and Aarssen 1989, Snaydon 1991, Cousens and O'Neill 1993). de Wit (1960) already pointed out that the competitive ability of species, as indicated by the relative crowding coefficient, could only be properly analyzed at densities at which all resources are absorbed, i.e., at a constant final yield. To check whether constant final yield was reached under the conditions of our competition experiment, we determined the yield-density curves for both species in an additional experiment. For this purpose, plants were grown in homogeneous soils of the

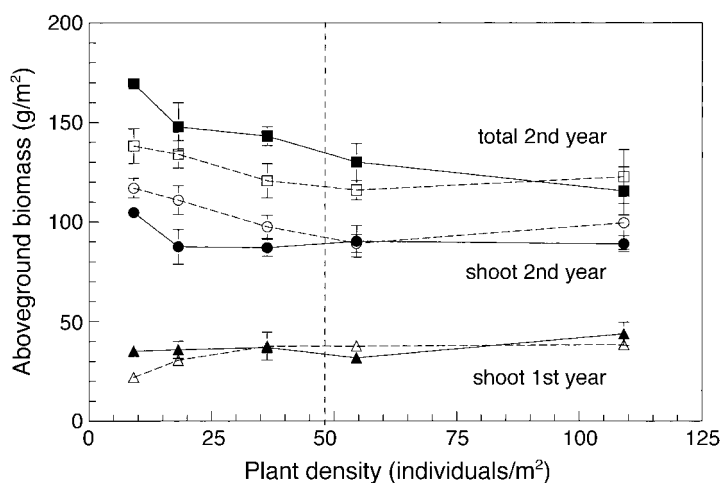


FIG. 2. Yield-density curves of *Festuca rubra* (solid symbols) and *Anthoxanthum odoratum* (open symbols) monocultures under a homogeneous nutrient distribution, as determined in an additional experiment. For the first year of the experiment (1998) live shoot biomass is given, and for the second year (1999) the figure presents live as well as total (live + dead) aboveground biomass. Data are means \pm 1 SE ($n = 4$ replicates). The vertical dashed line indicates the plant density used in the competition experiment (i.e., 48 plants/m²). The higher total aboveground biomass by the larger plants at lower densities in the second year was due to more profuse flowering compared to the smaller plants at higher densities.

same mixture as in the competition experiment. The containers used were smaller (0.22 m²) but of equal depth as the containers used in the main experiment. Plants were grown in densities of 2, 4, 8, 12, and 24 individuals per container, corresponding with densities of 9, 18, 36, 54, and 108 individuals/m², respectively. The plant density used in the competition experiment was 48 individuals/m². The density trial was carried out in the same open greenhouse as the main competition experiment, and also run for two years but was started one year later than the competition experiment (1998).

Strontium injection and analysis

Three weeks prior to the end of the experiment, a 15-mL solution of 0.2 mol/L SrCl₂·(6H₂O) was injected in a nutrient-rich patch in the heterogeneous treatments at a depth ranging from 5 to 20 cm (see Fig. 1). In the homogeneous treatment the same solution was injected in an equivalent position within the container. Strontium (Sr⁺⁺) is physiologically analogous to Ca⁺⁺ and can be used as a tracer to assess the root activity of different coexisting plant species at one location (Veresoglou and Fitter 1984, Mamolos et al. 1995).

In this experiment the strontium uptake was measured and used to estimate the root activity of the species in the nutrient-rich patches in the heterogeneous treatments. All 12 center plants were used to determine the Sr acquisition of the species. Individually harvested shoots were dried at 70°C for at least 48 h and ground prior to the analyses. To determine the amount of Sr taken up by the individual plants, 0.5 g of the ground material was dry-ashed in an oven at 500°C for at least 4 h and the ash was dissolved in a 10-mL solution of 2 mol/L HCl (Mamolos et al. 1995). The Sr concentration in this solution was measured by atomic absorption spectrometry (SpectrAA 600, Varian, Bergen op Zoom, The Netherlands).

Statistical analysis

Analysis of variance (SPSS 1995: GLM procedure) was used to test for significant differences in shoot biomass and strontium uptake among the two species, the three soil heterogeneity treatments, and the two levels of competition (monocultures vs. mixtures). Mean values per replicate container were used in the test, based either on 12 (monocultures) or 6 (mixtures) individual plant measurements per container. Root densities were tested similarly, but based on the means of three soil cores in the rich patches and three in the poor patches per container. Data were ln-transformed where necessary to ensure normality and homogeneity of variance. A posteriori comparisons within treatments were carried out using Tukey's HSD test where appropriate.

The CV of (live) shoot biomass was calculated from a pooled sample of all individual plants of a given species-treatment-competition combination, yielding a sample size of 72 plants for the monocultures and 36 plants for the mixtures. Differences in CV were tested by bootstrapping, as routinely used for CVs (Weiner 1986) and other measures of size inequality (Dixon et al. 1987). For this purpose the CV was recalculated for each of 1000 artificial samples of the same size (72 or 36 plants), which were taken from the original sample with replacement. We determined 95% confidence intervals for the CV from the distribution of the bootstrapped estimates of the CV (cf. Dixon et al. 1987).

RESULTS

Analysis of competitive ability

The *Festuca rubra* and *Anthoxanthum odoratum* monocultures, growing in the same soils as in the competition experiment and with the same rooting volume per plant, reached their constant final yield well below the plant density used in the competition experiment (Fig. 2). This constant biomass per unit area was already achieved in the first growing season. Yield was

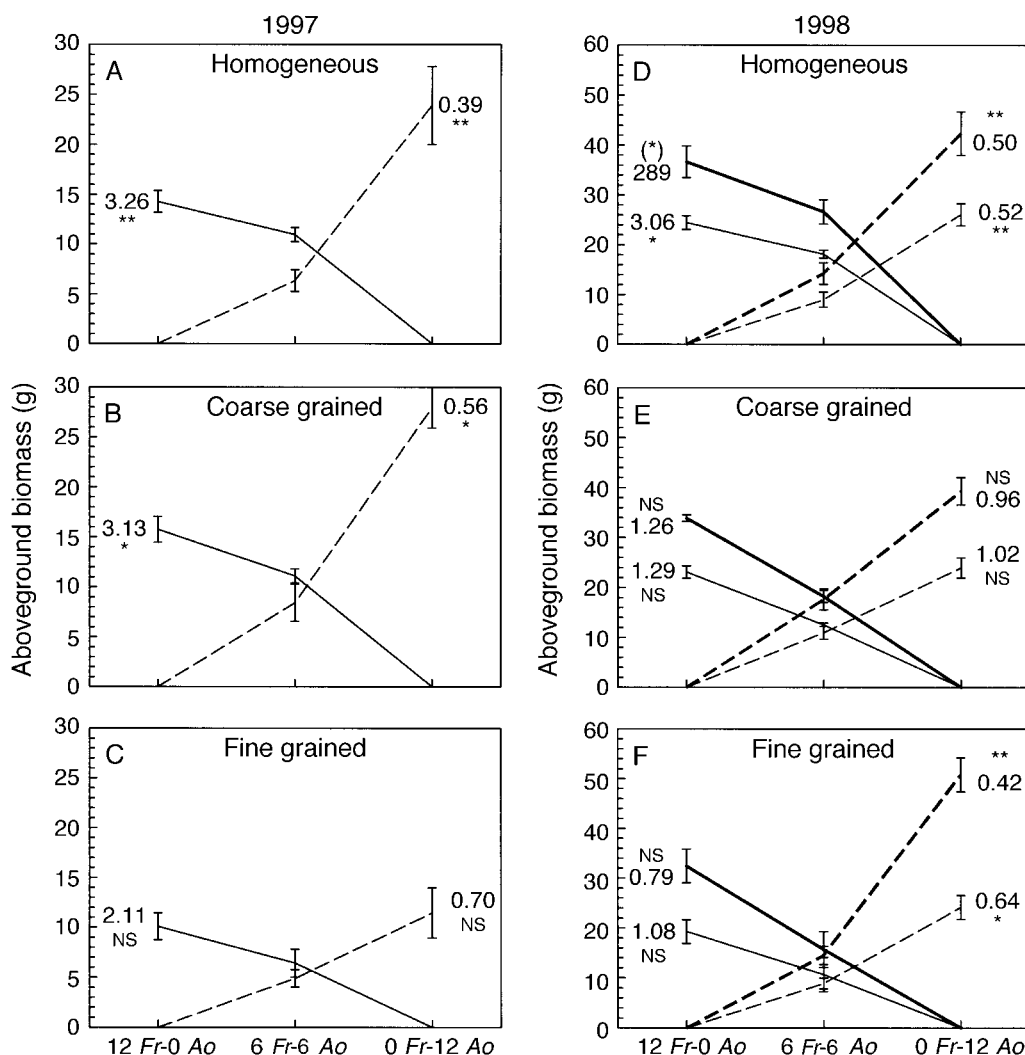


FIG. 3. Replacement diagrams (de Wit 1960) based on shoot biomass per container (yield) of *Festuca rubra* (Fr, thin solid lines) and *Anthoxanthum odoratum* (Ao, thin dashed lines) in the homogeneous treatments, the coarse-grained heterogeneous treatments, and the fine-grained heterogeneous treatments in the first (1997) and second (1998) growing seasons. The x-axis indicates the number of plants per species on which the yields are based, either 12 in the monocultures or 6 in the mixtures. The thick lines in the second growing season (1998) indicate the results based on the total aboveground biomass (including senesced shoots and culms). Data are means \pm 1 SE ($n = 6$ replicates). The numbers adjacent to each of the curves are the average relative crowding coefficients (k_{ij}) of each of the species. An asterisk indicates that k_{ij} deviates significantly from 1 (one-sample T test): * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$, NS = not significant; the (*) indicates a marginally significant difference ($P = 0.057$).

larger in the second year, in which the larger plants at the lower densities tended to produce a higher biomass per unit area as a result of their profuse flowering, in contrast to the smaller plants at the higher densities that hardly flowered. At the densities in the competition experiment (48 individuals/m²), the canopies of the bunchgrass individuals hardly touched each other at the end of the second growing season. Together with the results of the yield-density curves (Fig. 2) this indicates that the competition in the experiment was severe and predominantly belowground.

Fig. 3 shows the replacement diagrams of *F. rubra*

and *A. odoratum* for the different treatments in the two growing seasons. In the homogeneous treatment, *F. rubra* shows a convex curve in both years, indicating that total shoot biomass production of *F. rubra* in the mixtures was higher than expected based on the yield in the monocultures. With a concave curve in both years, the yield of *A. odoratum* in the mixtures was lower than expected. Based on these shoot biomass productions in the mixtures compared to the monocultures, the relative competitive abilities of *F. rubra* and *A. odoratum* were assessed in terms of their relative crowding coefficients (de Wit 1960). In the homoge-

neous soils, the relative crowding coefficients of both species deviated significantly from 1 in both the 1st and the 2nd year of the experiment (Fig. 3), projecting *F. rubra* as the better competitor in the homogeneous soils. The relative crowding coefficients indicate that the growth of an *F. rubra* individual was less suppressed by an *A. odoratum* individual than by an individual of its own species at the density applied; conversely, *A. odoratum* individuals were more suppressed by interspecific competition from *F. rubra* than by intraspecific competition.

These relative competitive abilities were different in the heterogeneous treatments. In the coarse-grained heterogeneous (checkerboard) treatment, the relative crowding coefficients deviated significantly from 1 as in the homogeneous treatment, but only in the 1st year (Fig. 3). At the end of the second growing season, the different strengths of inter- vs. intraspecific competition had evened out and the relative competitive abilities of *F. rubra* and *A. odoratum* became similar. In the fine-grained heterogeneous treatment, the plants remained small in the 1st year of the experiment compared to the other treatments, and the relative crowding coefficients of the species did not differ significantly from 1 (Fig. 3). Yield increased considerably during the second growing season. In the mixtures, the *A. odoratum* plants grew less than expected based upon their yield in monoculture (relative crowding coefficients <1), irrespective of whether only live biomass or live and dead biomass at the end of the growing season was taken as a measure (Fig. 3). The relative crowding coefficients of *F. rubra*, however, also did not significantly differ from 1 in the 2nd year. These results indicate that, in the fine-grained heterogeneous treatment, *F. rubra* plants were equally suppressed by intra- and interspecific competition, while *A. odoratum* plants grew less together with *F. rubra* plants than with plants of its own species.

Individual shoot biomass

The trends in individual shoot biomass are obviously the same as those reported for the yields in the previous section. A significant Species \times Competition interaction (Table 1) implies that the species responded differently to the form of competition (i.e., intra- vs. interspecific). On average, the mean shoot biomass of *A. odoratum* was lower in the mixtures than in the monocultures while *F. rubra* showed the reverse trend (Fig. 4). This response was treatment dependent, as indicated by the marginally significant Species \times Competition \times Treatment interaction ($P = 0.059$). As a result, mean shoot biomasses of *A. odoratum* and *F. rubra* in the mixtures were significantly different in the homogeneous treatment, but essentially identical in the heterogeneous treatments, especially in the 2nd year of the experiment (Fig. 4). An analysis of total (live and dead) biomass rather than live biomass at the end of the second growing season revealed basically the same

TABLE 1. Analysis of variance of mean shoot biomass, in the first and the second years of the experiment, and Sr uptake by the plants at the end of the second growing season.

Effects	Shoot biomass		Sr uptake	
	df	F	df	F
Species, S	1	1.19 NS	1	0.05 NS
Treatment, T	2	23.78***	2	2.00 NS
Competition, C	1	1.45 NS	1	2.47 NS
Year	1	48.87***
S \times T	2	1.87 NS	2	1.49 NS
S \times C	1	27.82***	1	3.03†
S \times Y	1	0.59 NS
T \times C	2	0.02 NS	2	2.42†
T \times Y	2	5.43**
C \times Y	1	0.01 NS
S \times T \times C	2	2.90†	2	2.91†
S \times T \times Y	2	1.75 NS
S \times C \times Y	1	2.35 NS
T \times C \times Y	2	0.91 NS
S \times T \times C \times Y	2	0.85 NS
Error	120		60	

Notes: The species are *Festuca rubra* and *Anthoxanthum odoratum*. The treatments are homogeneous, heterogeneous coarse-grained, and heterogeneous fine-grained soils. The competition effect refers to monocultures vs. mixtures. Mean values per replicate container are tested as explained in Methods. Biomass data were ln-transformed prior to analysis.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; † $0.05 \leq P < 0.10$; NS = not significant; ($P > 0.10$).

patterns. The only difference was the markedly higher total shoot biomass than live biomass of *A. odoratum* in the fine-grained heterogeneous monocultures (Fig. 4F). This was due to the massive flowering of this species early in the season, particularly in these monocultures, with the dead flowering stalks adding to their total mass.

Selective root placement

Overall, rooting densities (root biomass per unit soil volume) in the monocultures of *F. rubra* tended to be higher than those in the monocultures of *A. odoratum* at the end of the 2-yr experiment (Fig. 5). In the coarse-grained heterogeneous treatment neither species was able to produce significantly more root biomass in the nutrient-rich patches than in the nutrient-poor patches (Fig. 5B). By contrast, in the fine-grained heterogeneous treatment, the richer patches contained significantly higher root densities than the nutrient-poor soil in between the patches, in the monocultures of both species (Fig. 5C). The root proliferation of the species responded the same to soil patchiness, as is also apparent from the nonsignificant Group \times Patch type interaction in Table 2.

In the mixtures, no distinction could be made between roots produced by *F. rubra* and by *A. odoratum*. Root biomass production in the mixtures followed exactly the same pattern in response to the different soil treatments as in the monocultures; only in the fine-grained heterogeneous treatment, significantly more

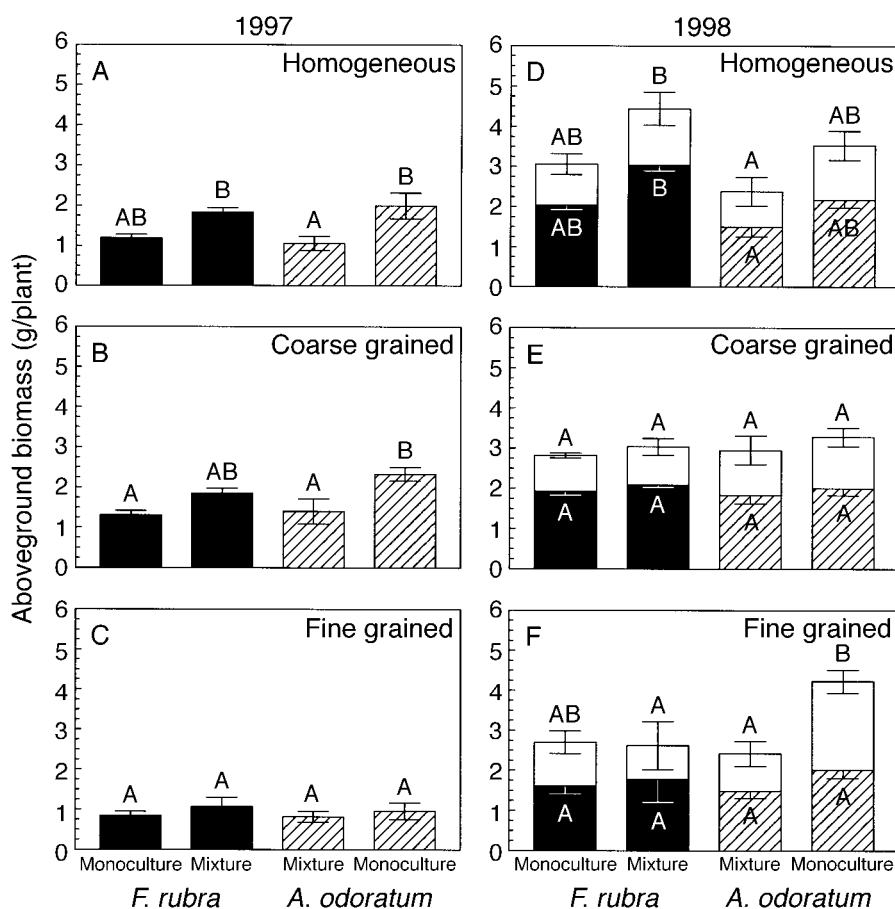


FIG. 4. Average shoot biomass per plant of *Festuca rubra* (solid bars) and *Anthoxanthum odoratum* (hatched bars) in the homogeneous, the coarse-grained heterogeneous, and the fine-grained heterogeneous treatments in the first (1997) and the second (1998) growing seasons. The stacked bars in the second growing season (1998) indicate the mean total aboveground biomass (including senesced shoots and culms). In the monocultures, mean shoot biomass per container was calculated from all 12 center plants, while in the mixtures it was based on six plants per species. Data are means \pm 1 SE ($n = 6$ containers). For each treatment-year combination, bars with the same uppercase letter are not significantly different (Tukey hsd, $P > 0.05$).

root biomass was produced in the nutrient-rich patches than in the nutrient-poor patches (Fig. 5).

Root activity

On average, the amount of Sr taken up per individual plant did not differ significantly between the species, or between the different treatments (Fig. 6, Table 1). For both species, and in all treatments, Sr uptake was highly significantly linearly related to plant size (aboveground biomass). The R^2 values of linear regressions for Sr uptake with plant size ranged from 0.24 (*F. rubra* monocultures) to 0.38 (*A. odoratum* mixtures) (results not shown).

Overall, the amount of Sr acquired did not differ significantly between the monocultures and the mixtures (Table 1). The marginally significant Species \times Competition interaction ($P = 0.087$) indicates that *F. rubra* tended to capture larger amounts of Sr in the mixtures than in the monocultures, while the reverse

was true for *A. odoratum*. However, this effect was only apparent in the homogeneous treatment where *F. rubra* plants acquired significantly more Sr than the *A. odoratum* plants they competed with (Fig. 6). In the heterogeneous treatments this difference evened out, as is also reflected in the marginally significant Species \times Competition \times Treatment interaction ($P = 0.062$).

Shoot size inequality

In all treatments and for both species, shoot size inequalities, measured as the coefficient of variation (CV) of individual shoot biomass, increased in the course of the 1st year compared to the initial size differences at the start of the experiment (CV 51% and 50% for *F. rubra* and *A. odoratum*, respectively). In both years, shoot size inequalities of the species' monocultures were higher in the fine-grained heterogeneous treatment than in the homogeneous and coarse-grained heterogeneous treatments (significant in three out of

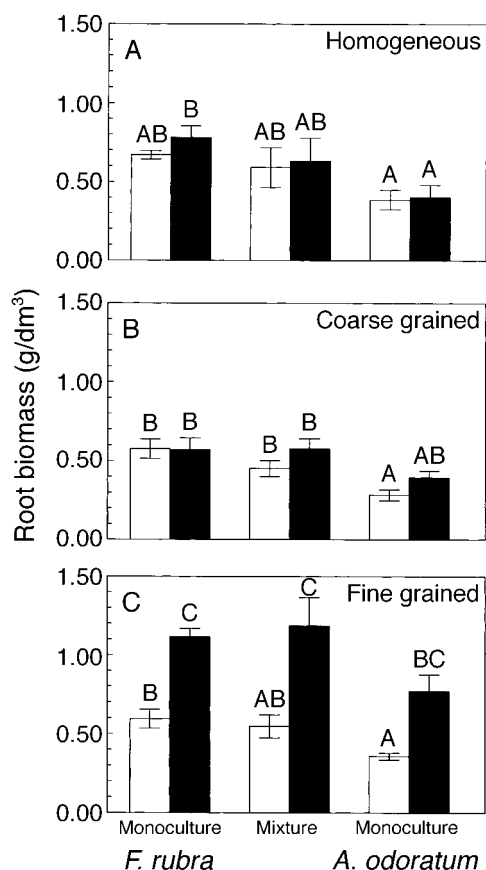


FIG. 5. Root biomass production in the nutrient-rich (solid bars) and nutrient-poor (open bars) patches of *Festuca rubra* and *Anthoxanthum odoratum* in monocultures and mixtures in the homogeneous, the coarse-grained heterogeneous, and the fine-grained heterogeneous treatments, based on three soil cores taken in each patch type per container at the end of the experiment. Note that the "nutrient-poor" and "nutrient-rich" patches in the homogeneous treatment refer to their equivalent positions in the heterogeneous treatments. Data are means \pm 1 SE ($n = 6$ containers). For each treatment, bars with the same uppercase letter are not significantly different (Tukey hsd, $P > 0.05$).

four cases; Fig. 7). Size inequalities were also influenced by the mode of competition (intra- vs. interspecific). In homogeneous soil the monocultures of the species exhibited similar cvs. In this soil treatment the cv of *F. rubra* tended to be lower in the mixture than in the monoculture, resulting in a significantly lower cv of this species than of *A. odoratum* in the mixtures in the 1st year of the experiment.

In the heterogeneous soil treatments the cvs in the monocultures tended to be higher for *A. odoratum* than for *F. rubra* (significant in the fine-grained heterogeneous treatment). Unlike the trend in homogeneous soil, in the heterogeneous treatments the cvs of *A. odoratum* tended to be lower, and those of *F. rubra* higher, in the mixtures than in the monocultures. Note that most of these differences in shoot size inequality were already established in the 1st year of the exper-

iment. Overall, shoot size inequalities decreased in the 2nd compared to the 1st year (in seven out of eight cases).

DISCUSSION

The purpose of this 2-yr study was to examine whether differences in root foraging ability between species would invoke differences in competitive ability in heterogeneous compared to homogeneous environments. The two perennial grass species used, *Festuca rubra* and *Anthoxanthum odoratum*, have comparable growth rates—but previous experiments with isolated plants designated *A. odoratum* as the species with the better ability to acquire nutrients from heterogeneous soils (Fransen et al. 1998, 1999). Consistent with these earlier findings, our results show that, compared to homogeneous conditions, nutrient heterogeneity enhanced the competitive ability of *A. odoratum* relative to *F. rubra*.

Belowground competition in homogeneous environments

The notion that nutrient uptake is relatively size symmetric in homogeneous environments, i.e., plants acquire nutrients in proportion to their biomass (Weiner 1990, Casper and Jackson 1997, Schwinning and Weiner 1998), was confirmed by the results of our experiment. The strontium uptake per plant increased linearly with plant size in both species. When competition is symmetric it will not exacerbate initial size differences (Weiner 1990, Weiner et al. 1997). The cvs of individual shoot biomass of both species in the homogeneous monocultures and mixtures showed indeed a similar and modest increment compared to the cvs at the start of the experiment, and decreased rather than increased further in the 2nd year compared to the 1st year of the experiment (Fig. 7). This result suggests indeed that competition for nutrients, both intra- and

TABLE 2. Analysis of variance of the mean root biomass produced within the nutrient-poor and nutrient-rich patches in the different treatments.

Effects	Root biomass	
	df	F
Group, G	2, 3	1.79 NS
Treatment, T	2, 3	0.96 NS
G \times T	4, 6	0.45 NS
Patch type(Treatment)	3, 90	17.09***
G \times P(T)	6, 90	0.42 NS

Notes: Groups rather than species were used in the analysis, because in the mixtures no distinction could be made between roots produced by *Festuca rubra* and by *Anthoxanthum odoratum*. The three groups distinguished are *F. rubra* monocultures, *A. odoratum* monocultures, and the species mixtures. The treatments are homogeneous, heterogeneous coarse-grained, and heterogeneous fine-grained soils. Patch type (nutrient-poor or nutrient-rich) was nested within treatment. Data were ln-transformed prior to analysis.

*** $P < 0.001$; NS = not significant.

interspecifically, was relatively size symmetric in the homogeneous soils.

On average, *F. rubra* produced about twice the amount of root biomass within the soil cores than did *A. odoratum* (Fig. 5A), indicating that *F. rubra* has a denser and more extended root system. In the mixtures in homogeneous soils, these denser *F. rubra* root systems acquired on average a significantly larger proportion of the strontium than the sparser *A. odoratum* roots (Fig. 6A). In competition belowground, higher nutrient uptake is likely to enhance subsequent growth (see Berntson and Wayne 2000) and this may explain the higher competitive ability of *F. rubra* relative to *A. odoratum* in homogeneous soils.

Belowground competition in heterogeneous environments

Compared to the homogeneous treatment, the competitive ability of *F. rubra* in heterogeneous environments declined relative to *A. odoratum*, especially in the coarse-grained (checkerboard) arrangement of rich and poor patches (Figs. 3 and 4). The results on strontium uptake paralleled this shift in competitive ability (Fig. 6), suggesting that this shift was the result of the better ability of *A. odoratum*, relative to *F. rubra*, to acquire nutrients in the heterogeneous than in the homogeneous environments.

How is *A. odoratum*—with its less dense root systems—able to acquire an equally large proportion of the soil nutrients from heterogeneous soils as *F. rubra*, while it is unable to do this in homogeneous soils? In monoculture, the ability to produce more root biomass selectively in the nutrient-rich patches did not differ between the species, and hence cannot explain these differences (Fig. 5). However, care must be taken with this conclusion because we have been unable to separate the roots of both species when grown in mixtures. Root proliferation behavior may have been different in the mixtures than in the monocultures because the root morphological plasticity of plants may be altered when grown in competition (Mahall and Callaway 1992, Jastrow and Miller 1993, Caldwell 1994, Krannitz and Caldwell 1995). Yet, the most straightforward explanation for the relatively high nutrient uptake from the enriched patches by the sparser root systems of *A. odoratum* is its higher root physiological plasticity compared to *F. rubra*. These differences in root physiological plasticity between the species were already apparent from the results of previous experiments with isolated plants (Fransen et al. 1998, 1999).

It has been suggested that, in heterogeneous environments, larger plants may occupy nutrient-rich patches and deplete nutrients before smaller plants gain access, resulting in a disproportionate acquisition of nutrients by the larger plants and, thus, in asymmetric competition (Weiner et al. 1997, Casper and Jackson 1997, Schwinning and Weiner 1998). Consistent with this hypothesis, shoot size inequalities in the mono-

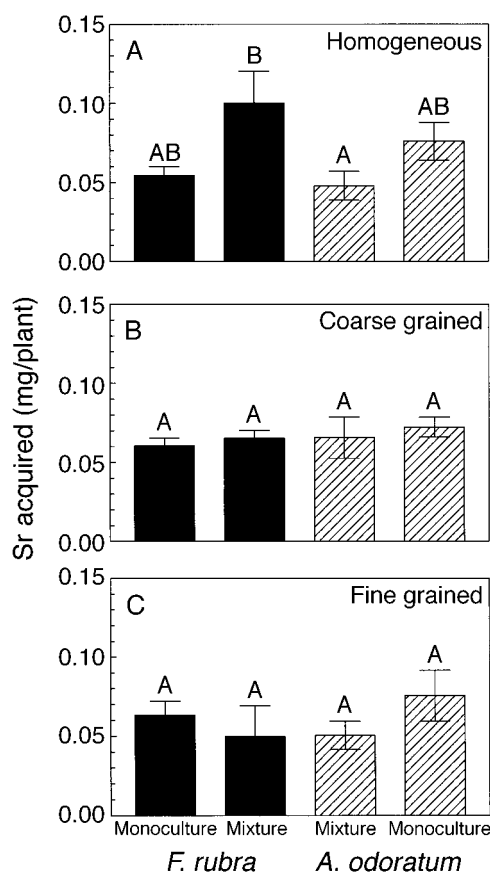


FIG. 6. The average amount of strontium acquired per plant by *Festuca rubra* (solid bars) and *Anthoxanthum odoratum* (hatched bars) grown in monocultures and mixtures in the homogeneous, the coarse-grained heterogeneous, and the fine-grained heterogeneous treatments. In the monocultures, the mean amount of Sr acquired per plant was based on all 12 center plants, while in the mixtures it was based on the acquisition by six plants per species. Data are means \pm 1 SE ($n = 6$ replicates). For each treatment, bars with the same uppercase letter are not significantly different (Tukey hsd, $P > 0.05$).

cultures were significantly higher in the fine-grained heterogeneous treatments compared to the homogeneous treatment, in three out of four cases (Fig. 7). This was especially apparent for *A. odoratum*. Plants of this species have been shown to very effectively acquire patchily distributed nutrients (Fransen et al. 1998), and in competition this behavior may have advanced some individuals at the expense of others and have aggravated the size differences within the population. However, in contrast to the hypothesis of asymmetric competition, shoot size inequalities did not further increase in the 2nd compared to the 1st year of the experiment, although mean shoot sizes were significantly higher in the 2nd year. Apparently, once patches have been occupied, size differences are consolidated or even reduced and competition between plants of different sizes becomes more symmetrical.

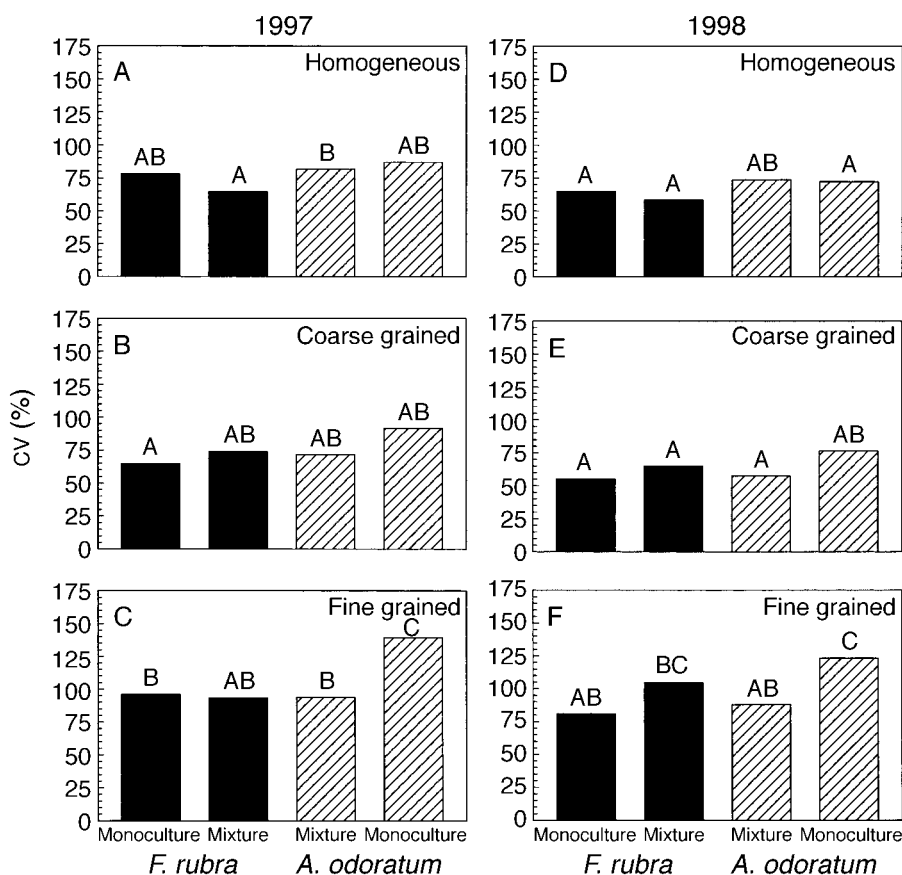


FIG. 7. The coefficient of variation (cv) of (live) shoot biomass of *Festuca rubra* (solid bars) and *Anthoxanthum odoratum* (hatched bars) in the homogeneous, the coarse-grained heterogeneous, and the fine-grained heterogeneous treatments, in the first (1997) and the second (1998) growing seasons. The way in which the coefficients of variation per Species \times Treatment \times Competition combination were computed are described in *Methods*. Significance tests were based on bootstrapping. Bars with the same uppercase letter within a given year are not significantly different at the $P = 0.05$ level.

This course of events is very different from asymmetric competition for light in which size differences are exaggerated as plants grow out.

In the mixtures, the mean shoot biomasses of the species were the same at the end of the experiment under the heterogeneous conditions supplied (Fig. 4). The shoot size inequalities however showed some distinct trends, suggesting that this similar competitive ability was achieved in different ways. The high cv of *A. odoratum* in the monocultures was lower in the mixtures, while the cv of *F. rubra* showed a reverse pattern and tended to be higher in the mixtures (Fig. 7). The more uniform shoot sizes of *A. odoratum* in the mixtures suggest that even the initially smaller plants of this species were able to capture their share of resources when competing with *F. rubra*, perhaps because of their more effective means of foraging by physiological plasticity. The somewhat more variable *F. rubra* plant sizes suggest that some larger individuals were able to monopolize the resources, by virtue of their size, while the growth of others has been suppressed by the more effectively competing *A. odoratum* plants. Note that

these trends for *F. rubra* were opposite in homogeneous soil (Fig. 7A and D) where this species was competitively superior. These results match those of Weiner (1985) and point perhaps to a more general trend for species mixtures in which the competitively superior species has lower size inequalities and the competitively inferior species has higher size inequalities. This trend suggests that a competitive advantage is relatively equally shared among individuals of a population, while suppression is less equally shared with some individuals that are able to escape suppression (Weiner 1985).

If a higher physiological plasticity was responsible for the higher relative competitive ability of *A. odoratum* in the heterogeneous compared to the homogeneous treatment, this advantage should have been already apparent in the beginning of the experiment because of nutrient depletion in the patches (van Vuuren et al. 1996, Fransen et al. 1999). Especially in the coarse-grained (checkerboard) treatment where the roots had immediate access to the richer patches, a high physiological plasticity should have conferred imme-

diate benefits in terms of nutrients. Surprisingly, this expectation is not borne out by the results. In the coarse-grained treatment *F. rubra* rather than *A. odoratum* had a higher competitive ability in the 1st year and this difference was not leveled off until the 2nd year (Fig. 3). It thus seems that the denser root systems of *F. rubra* did confer a competitive advantage in the short term, as suggested by Robinson et al. (1999). This advantage was not sustained, however, perhaps because in the long term the benefits of high root densities in enriched patches faded and may even have resulted in a growth disadvantage due to patch depletion and nutrient losses associated with the turnover of roots (Fransen and de Kroon 2001). The overall reduction in shoot size inequality from the 1st to the 2nd year is consistent with this hypothesis: differences in plant sizes were in place in the 1st year but the larger plants with presumably the denser root systems gradually lost their advantage compared to the smaller plants. In soils with patches of organic material in which a relatively low supply of nutrients persists due to mineralization, physiological plasticity may thus confer a competitive advantage belowground over the longer term.

Conclusions

Our results indicate that heterogeneity alone, without a change in the overall nutrient availability of the soil, can change the relative competitive ability of two perennial plant species. This shift is consistent with expectations based on differences in root foraging ability between the species observed in experiments with isolated plants, suggesting that root foraging ability is pivotal for belowground competition in heterogeneous environments. Most of the competition experiments have been and are being carried out under homogeneous conditions. Our findings suggest that, given the ubiquitous belowground heterogeneity in nature, the results of such competition experiments must be interpreted with caution. It will be a challenge for the future to design competition experiments in soils that simulate heterogeneity at the temporal and spatial scales appropriate for the field situation.

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