Dynamics of Nitrogen Competition Between Successional Grasses

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DYNAMICS OF NITROGEN COMPETITION BETWEEN SUCCESSIONAL GRASSES[1]

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Abstract. Pairwise competition experiments were performed for 3 yr on an experimental nitrogen gradient at Cedar Creek Natural History Area, Minnesota, where N is the major limiting resource during early succession. *Agrostis scabra,* an early successional grass, competed against another early (*Agropyron repens*), a later (*Schizachyrium scoparium*), and an even later (*Andropogon gerardi*) successional species. On low N soils, *Agrostis* was competitively displaced by each of the later successional species, but persisted with *Agropyron.* On high N soils, *Agrostis* was displaced by all three of the other species. The inferior competitive ability for N of the early successional species refutes the resource ratio hypothesis of succession. Rather, the high allocation of *Agrostis* to seed and its rapid colonization of fields support a colonization–competition hypothesis of succession.

For two of three cases, the outcome of competition on low nitrogen soils was predicted by R^*, the nitrogen concentration to which monocultures of each species reduced extractable soil nitrate and ammonium on N-limited soils. In these cases, the species with the significantly lower R^* for nitrogen displaced the other species. In the third case, the species had more similar R^* values, and the species with the lower R^* had not displaced the other species within 3 yr (but it had done so after 5 yr; see *Note added in proof*).

Key words: Agropyron repens; Agrostis scabra; Andropogon gerardi; *colonization; grasses; nutrient reduction; plant competition;* R*; *resource competition theory;* Schizachyrium scoparium; *succession.*

INTRODUCTION

Interspecific competition influences the composition of plant communities (e.g., de Wit 1960, Van den Bergh 1968, Harper 1977, Berendse and Aerts 1984) and can be an important force in successional habitats (e.g., Pinder 1975, Abul-Fatih and Bazzaz 1979, Goldberg 1987, Gurevitch and Unnasch 1989). Several successional hypotheses assume that early successional species are poor competitors but are superior in another trait, such as colonization ability or maximal growth rate (e.g., Platt 1975, Connell and Slatyer 1977, Noble and Slatyer 1979, Huston and Smith 1987, Tilman 1988). An alternative hypothesis assumes that early successional species are superior competitors for a limiting nutrient but are poor competitors for a second resource (often light) that becomes increasingly limiting during succession (Tilman 1985). Observational and experimental studies performed at Cedar Creek Natural History Area (CCNHA) have provided contradictory results that seemed to support or refute each of these views. For instance, the ability of *Agrostis scabra, Ambrosia artemisiifolia,* and *Hedeoma hispida* to persist on low nitrogen soils for many years, and their rapid displacement from fertilized plots, was "suggestive of these early successional species being superior competitors for nitrogen compared to late successional species" (Tilman 1987*b*: 310). In contrast, Gleeson and Tilman (1990) used information on changes in plant allocation patterns during succession to conclude that the early successional species of CCNHA were likely to be inferior nitrogen competitors, but superior colonists, than later successional species. These conflicting conclusions can only be resolved through direct experimental determination of the competitive abilities of successional dominants. We report, here, the results of such experiments that were also designed to provide information on the mechanisms of nitrogen competition among these species and to test the predictive ability of resource competition theory (e.g., Tilman 1976, 1980, 1982, 1990).

We studied four grass species that are dominant at different times during secondary succession at CCNHA. *Agrostis scabra* Willd. and *Agropyron repens* (L.) Beauv. are early successional species at CCNHA and reach their peak abundance 5–10 yr after abandonment of fields from agriculture (Tilman 1988). *Schizachyrium scoparium* (Michx.) Nash-Gould is a later successional species that reaches its peak abundance in 35–45 yr old fields. *Andropogon gerardi* Vitm. is an even later successional species (Tilman 1988). Nitrogen is the major limiting soil resource in successional fields at CCNHA. Terrestrial plant biomass increases and community composition changes after N addition, but not after addition of P, K, Ca, Mg, S, and trace metals (Tilman 1987*a*, 1988). A chronosequence of old fields has suggested that total soil N accumulates during succession (Inouye et al. 1987), with ≈100 yr required for an old field to regain the total soil N lost during agri-

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culture (Tilman 1988). Thus, we performed our competition experiments along a gradient from low to high N soils. Species were grown for 3 yr in monoculture (Tilman and Wedin 1991) and in three different pairwise combinations on soils prepared so that N would be the only limiting soil resource. *Agrostis* was included in all pairs.

METHODS

Garden soil preparation.—CCNHA is located on a glacial outwash sandplain 50 km north of Minneapolis, Minnesota. Our methods, summarized here, are described in detail in Tilman and Wedin (1991). Plots that differed in total soil N were created in August 1985 by removing the upper 60–80 cm of soil from a 31 × 34 m region of a 25-yr old field, and then using a rototiller to mix the resulting subsurface sand (total soil N of 90 mg/kg of dry soil) with different amounts of a topsoil. The topsoil was a sandy loam of the Hubbard-Isanti-Duelm Association, obtained nearby but off-site. It contained 72% sand, 4% clay, 24% silt, 2.9% organic matter, and had total soil N of 1100 mg/kg and a pH of 7.2. Within the garden area, eight "macroplots" were prepared, each 3 m wide by 12 m long by 22 cm deep. Each macroplot was randomly assigned to receive a different soil mixture. The eight soil mixtures were to contain 0, 10, 20, 40, 50, 55, 70, or 90% topsoil, with the remaining soil coming from the subsurface sand with which it was mixed. Two additional macroplots with 100% topsoil mixtures were used in related experiments, but are not discussed here because *Agrostis* became inhibited by its own litter and failed to survive in monoculture (Tilman and Wedin 1991). There is little reason to discuss interspecific competition in a habitat in which a species cannot survive in monoculture. All nutrients except N (P, K, Ca, Mg, S, Mn, Mo, Co, Cu, B, Fe) were added each year to assure that only N was limiting. The soil in each macroplot was thoroughly mixed to a depth of 22 cm, and 25 cm tall galvanized sheet metal was driven to a depth of 23 cm to divide each macroplot into 64 smaller 0.75 × 0.75 m plots. The garden was fenced to exclude all mammalian herbivores. All plots were watered, generally twice a week, so as to receive at least 1.5 cm/wk in April, May, and October, and 2.5 cm/wk in June through September.

Experimental design.—Seed vs. seed competition experiments were performed for three different pairs of species: *Agrostis* vs. *Agropyron, Agrostis* vs. *Schizachyrium,* and *Agrostis* vs. *Andropogon.* Monoculture and competition treatments were randomly assigned to the 0.75 × 0.75 m plots within each macroplot, with each macroplot being independently randomized. The competition experiments were planted in May 1986 at an estimated total seedling density of 3000 seedlings/m^2, based on greenhouse germination trials. Seeds were covered with 0.5 cm of sand after planting. Plots were seeded to have initial seedling ratios of either 80% of *Agrostis* and 20% of the other species, 20% of *Agrostis* and 80% of the other species, or 50% of each. Because of interspecific differences in seed mass, these do not correspond with initial biomass ratios (see Figs. 1 and 3). Monocultures of each species were also planted to have 3000 seedlings/m^2. For *Agrostis* vs. *Agropyron* there were three replicates of each competition seeding ratio and four replicate monocultures per species in each macroplot. For *Agrostis* vs. *Schizachyrium* and for *Agrostis* vs. *Andropogon,* there was one of each of the three ratios in each macroplot and two (*Andropogon*) or three (*Schizachyrium*) monoculture replicates per macroplot. A low seed density competition experiment was performed for *Agrostis* vs. *Agropyron,* with methods identical to those described above in this section, except that total seedling density was 600 seedlings/m^2, and there was one plot for each seed ratio and two monocultures per species (with 600 seedlings/m^2) per macroplot. All plots were inspected on an approximately weekly basis throughout the growing season, with weed seedlings removed as they appeared.

Plant sampling.—Initial biomass per square metre in each plot was estimated as density of germinated seedlings (number per square metre) of each species observed in early June of 1986 multiplied by average seed embryo mass (Tilman and Wedin 1991). Subsequently, aboveground biomass was harvested by clipping each plot at the soil surface. This was sorted to living biomass (by species) and litter, dried at 40°C for a week, and weighed. A 7.8 × 55 cm strip was clipped in each plot during 28 August–12 September 1986 and during 25 July to 5 August 1987. A 10 × 40 cm strip was clipped during 13–27 July 1988. Even though no edge effects were noticed, each clipped strip was at least 10 cm from a plot edge, in an area not previously clipped. Sampling dates were chosen based on phenology, being near the time of peak *Agrostis* flowering. This is near the time of peak aboveground living biomass of *Schizachyrium, Andropogon,* and *Agropyron,* but 2 wk after the peak for *Agrostis* and 2 mo before the slight autumnal peak of *Poa* (Wedin 1990).

Soil sampling.—Prior to planting in 1986, four 2.5 cm diameter by 20 cm deep soil cores were collected per plot, pooled, dried, and analyzed in duplicate for total soil N using alkaline persulfate digestion followed by NO_3 measurement on a Technicon II Autoanalyzer. Total soil N is expressed as milligrams of N per kilogram of dry soil because soil bulk densities only varied slightly among soil mixtures. Soils of the competition and monoculture plots were also sampled for 0.01 mol/L KCl extractable ammonium and nitrate on 28 July and again on 3 August 1988. Monocultures, but not competition plots, were sampled on an additional date (Tilman and Wedin 1991), which is not included in comparisons of competition and monoculture plots to avoid any possible sampling date effects. A 2 cm diameter × 16 cm deep soil core was collected from each plot, homogenized, and two-thirds of the core was added to

50 mL of 0.01 mol/L KCl in a preweighed vial. This was then weighed, shaken for 0.5 h, settled overnight at 4°, and the supernatant analyzed for ammonium and nitrate using a Technicon II Autoanalyzer. The other one-third was used to determine soil moisture. Concentrations of ammonium and nitrate are expressed as milligrams of N per kilogram of dry soil.

Data analysis.—To avoid the possibility of pseudoreplication (sensu Hurlbert 1984), all of our analyses used the means of the replicate plots within a given macroplot. We performed five different types of statistical analyses, all using SAS (1988: Release 6.03) on a Sun Sparc workstation. (1) General Linear Models (GLM) regressions were used to determine if initial seed ratio had a significant effect on the 1986, 1987, or 1988 biomass of each species in each case of interspecific competition. Initial seed ratio was included as a categorical variable in regressions of aboveground biomass against total soil N. A significant F value for seed ratio indicates that at least one of these three regressions per species (one regression for each seed ratio) differed and thus that initial seed ratio influenced aboveground biomass of that species in that pairwise interaction. (2) For each species pair, ANOVA was used to compare the 1988 aboveground biomass responses of the two competitors among nitrogen treatments. To do this, the eight soil mixtures were grouped into three different nitrogen levels. Although such grouping decreased the power of the experimental design, it allowed contrasts between group means and provided a convenient way to summarize results and to analyze for the nitrogen dependence of species responses in pairwise competition. N-level 1 consisted of the three soil mixtures that had the lowest total N, N-level 2 contained the next three soil mixtures, and N-level 3 included the two soil mixtures with the highest total soil N. ANOVA tested for the effects of species, total soil N, and a species × total N interaction on 1988 aboveground biomass of each species in a given pair. For these analyses, each species pair was analyzed separately, monoculture data were not included in the ANOVA, and the mean value for the three seed ratios was used as a single datum. We analyzed each pair separately because each species pair provides a separate test of the predictive ability of resource competition theory. (3) To determine if the species identity of its competitor had a significant effect on the 1988 aboveground biomass response of *Agrostis,* an ANOVA was performed in which the factors were competitor identity (*Schizachyrium, Agropyron,* or *Andropogon*), N level, and the species identity by N-level interaction. (4) For each species pair, we determined if the presence of another species depressed the biomass of a species compared to its monocultures within each N level, by comparing the aboveground biomass of each species in two-species plots with that in monoculture via t tests. We also used t tests to determine if the aboveground biomass of *Agrostis* or of *Agropyron* differed between monocultures planted at 3000 vs. 600 seedlings/m^2. (5) For each of the species pairs, at each N level, Duncan's multiple-range test was used to determine if extractable soil ammonium or nitrate concentrations in competition plots were significantly ($P < .05$) different than in the monocultures of those two species, and if the monocultures of those two species differed in ammonium and nitrate.

RESULTS

Soil characteristics.—The three soil N levels differed in their total soil N content. For the competition plots and related monocultures, N-level 1 soils had a total soil N of 178 ± 2.72 mg/kg ($\bar{X}$ ± SE, $n = 96$) and a bulk density of 1.49 g/cm^3; N-level 2 had a total N of 452 ± 3.1 mg/kg ($n = 96$) and a bulk density of 1.46 g/cm^3; and N-level 3 had a total N of 700 ± 8.24 mg/kg ($n = 64$) and a bulk density of 1.44 g/cm^3. All three pairwise comparisons among these total soil N means differed significantly at $P < .01$ (Duncan's new multiple range test).

Interspecific competition

Agrostis *vs.* Schizachyrium.—The general linear models regressions revealed that initial seed ratios had a significant effect on the 1986 and 1987 aboveground biomass of *Agrostis* in two-species plots, but not on that of *Schizachyrium* (Table 1). However, after growing together for 3 yr, the aboveground biomasses of both *Agrostis* and *Schizachyrium* were independent of initial seed ratio (Table 1, Fig. 1A). Thus, initial seed ratio was not included as a factor in ANOVA of 1988 aboveground biomass (in interspecific competition plots) by N level and species (Fig. 2A–C). This ANOVA revealed significant species effects ($F_{1,30} = 155$) and N-level effects ($F_{2,30} = 15.5$), and a significant species × N-level interaction ($F_{2,30} = 15.3$). The interaction was caused by the biomass of *Agrostis* being unaffected by N level, whereas the biomass of *Schizachyrium* increased with N level. To compare interspecific competition plots with monocultures, we combined the three initial seed ratios. The aboveground biomass of *Schizachyrium* in two-species plots differed significantly from its biomass in monoculture only for N-level 2 in 1986 and for N-levels 1 and 2 in 1987 (t test, $P < .01$), but did not differ significantly for any N level in 1988 (t test, $P > .05$ for all three 1988 comparisons; Fig. 2A–C). However, *Agrostis* had significantly lower aboveground biomass in competition plots than in monoculture for all N levels in each of the 3 yr (t test, $P < .01$ for all nine comparisons; Fig. 2A–C). By 1988, *Agrostis* was almost extinct in all the competition plots. Thus, independent of their initial seed ratios, *Schizachyrium* displaced *Agrostis* along the full N gradient by 1988. The dynamics of competitive displacement (Fig. 2A–C) differed with N level. On N-level 1, both species grew at approximately equal rates from seed until harvest in 1986, and then *Agrostis* was displaced

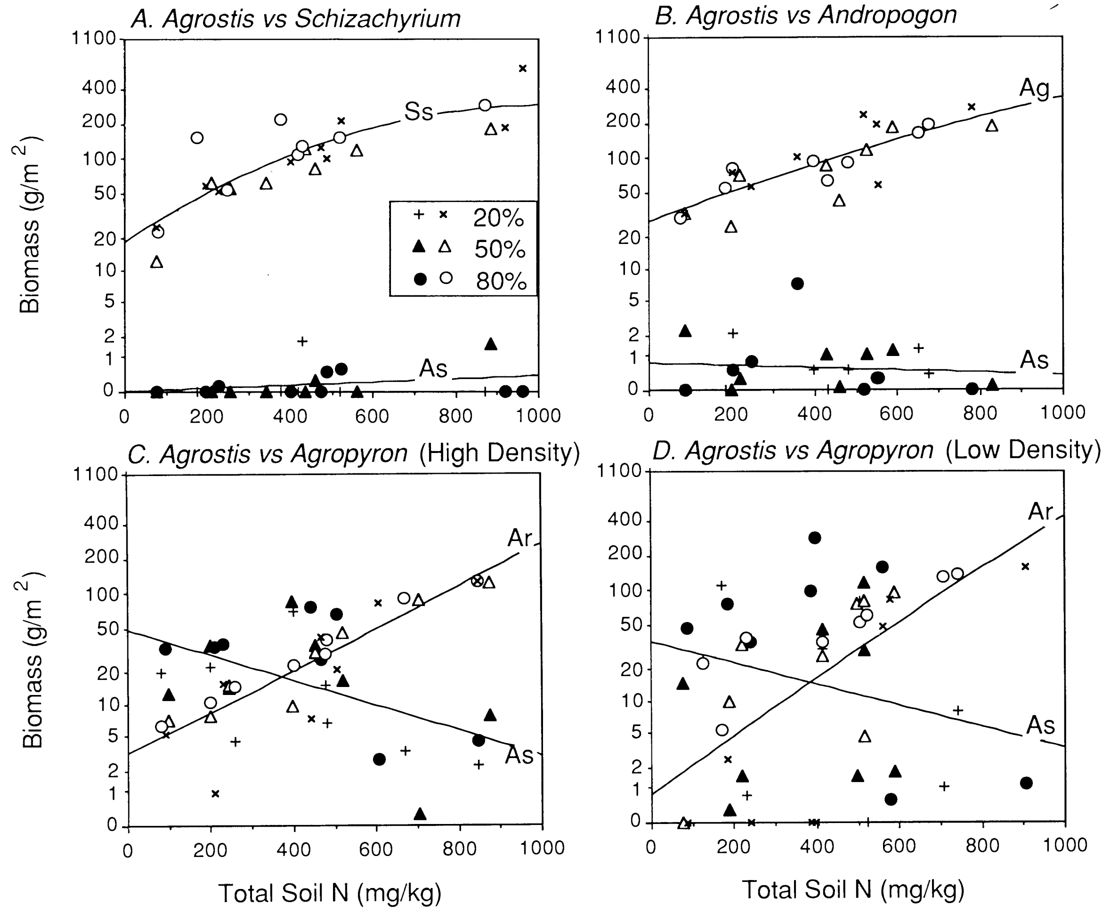

FIG. 1. (A) Aboveground 1988 biomass in *Agrostis* (solid symbols, curve labeled As) vs. *Schizachyrium* (open symbols, curve labeled Ss) competition plots is graphed against total soil nitrogen. Curves are from linear or quadratic least squares regressions. The three different initial seed ratios are indicated by diamonds for plots with 20% initial seed abundance of a species, by triangles for plots with 50% initial seed abundance, and by circles for plots with 80% initial seed abundance. See, also, Table 1. (B) The 1988 results, similarly displayed, for *Agrostis* (open symbols, curve labeled As) vs. *Andropogon* (solid symbols, curve labeled Ag). (C) The 1988 results for *Agrostis* (open symbols, curve labeled As) vs. *Agropyron* (solid symbols, curve labeled Ar) at high initial seed density. (D) The 1988 results for *Agrostis* vs. *Agropyron* at low initial seed density.

at a constant rate during the next 2 yr as *Schizachyrium* increased in biomass. On N-levels 2 and 3, both species increased in parallel the 1st yr, both tended to level off the 2nd yr, and *Agrostis* was displaced during the 3rd yr. In midseason 1988, the concentrations of extractable (0.01 mol/L KCl) nitrate and ammonium in all N levels for all initial seed ratios were significantly ($P <$ .05, Duncan's test) lower than in the appropriate *Agrostis* monocultures, but did not differ significantly ($P >$ .1, Duncan's test) from the *Schizachyrium* monocultures (Fig. 3A–B).

Agrostis vs. Andropogon.—When growing with *Andropogon*, the aboveground biomass of *Agrostis* in 1986 and 1987 depended on initial seed ratios, but this effect disappeared in 1988 (Table 1, Fig. 1B). The aboveground biomass of *Andropogon* was never significantly dependent on initial seed ratio (Table 1). ANOVA of aboveground biomass in competition plots, when classified by N level, revealed significant species ($F_{1,30}$ = 167) and N-level effects ($F_{2,30}$ = 21.6), and a significant species × N-level interaction ($F_{2,30}$ = 21.7). The interaction resulted from *Andropogon* but not *Agrostis* having greater biomass at higher N levels. Comparisons within each N level for each year showed that *Andropogon* attained a significantly lower aboveground biomass in N-level 1 than in monoculture in 1987 (*t* test, $P <$ .01), but that its monoculture and two-species plots did not differ significantly for any other years or N levels (*t* test, $P >$ .05 for all eight comparisons; Fig. 2D–F). For all three N levels, in all 3 yr, *Agrostis* had significantly lower biomass in competition plots than in monoculture (*t* test, $P <$ .01 for all nine comparisons; Fig. 2D–F). The dynamics of competition changed with N level and depended on initial seed ratios (Fig. 2D–F), with a pattern similar to that for *Agrostis* vs. *Schizachyrium*. The final outcome was always the displacement of *Agrostis* by *Andropogon*. For each N level, Duncan's test showed that midseason 1988 concentrations of ammonium and nitrate in two-species plots were significantly ($P <$ .05) lower than in *Agrostis*

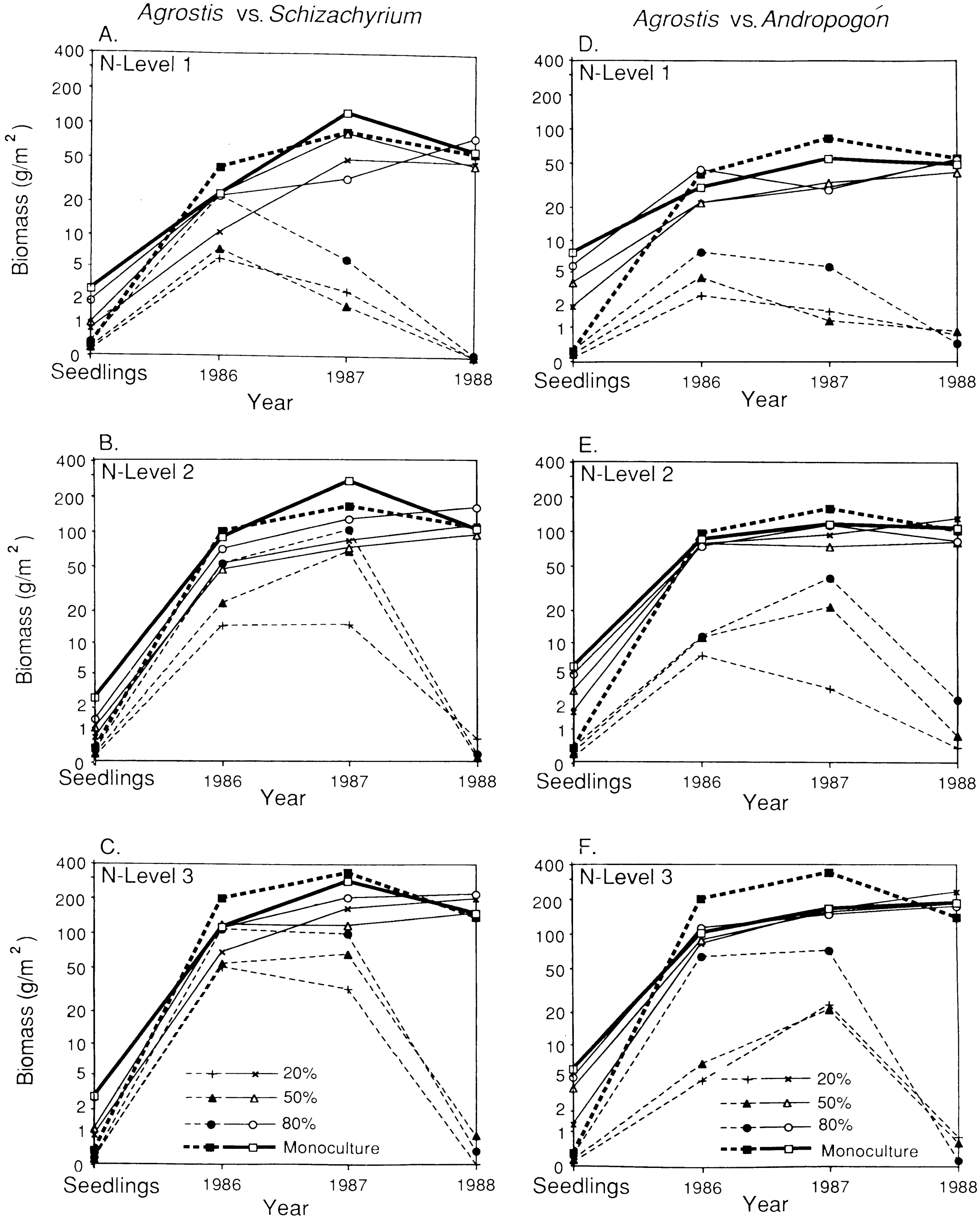

FIG. 2. (A–C) Dynamics of monocultures and of seed vs. seed competition between *Agrostis scabra* (broken lines and solid symbols or +) and *Schizachyrium scoparium* (solid lines and open symbols or ×) at three different soil nitrogen levels. Seedling biomass is the seed embryo mass per unit area for May 1986, based on the observed germination rate in each plot. All other values are aboveground biomass at the time of harvest. All values shown are averages over all soil mixtures within an N level. The four curves shown for each species are results for monocultures (squares and thicker lines), for plots with initial seed abundance (by number of seed) of 20% for a species (+, ×), for plots with initial seed densities of 50% for both species (triangles), and for plots with initial seed density of a species of 80% (circles). Note that a plot that had 20% of one species had 80% of the other, meaning that the 20% line for one species is associated with the 80% line for the other species. Independent of initial seedling ratio, *Agrostis* was displaced by *Schizachyrium.* (D–F) Competition between *Agrostis* (broken lines and solid symbols) and *Andropogon* (solid lines and open symbols), with results presented as described above.

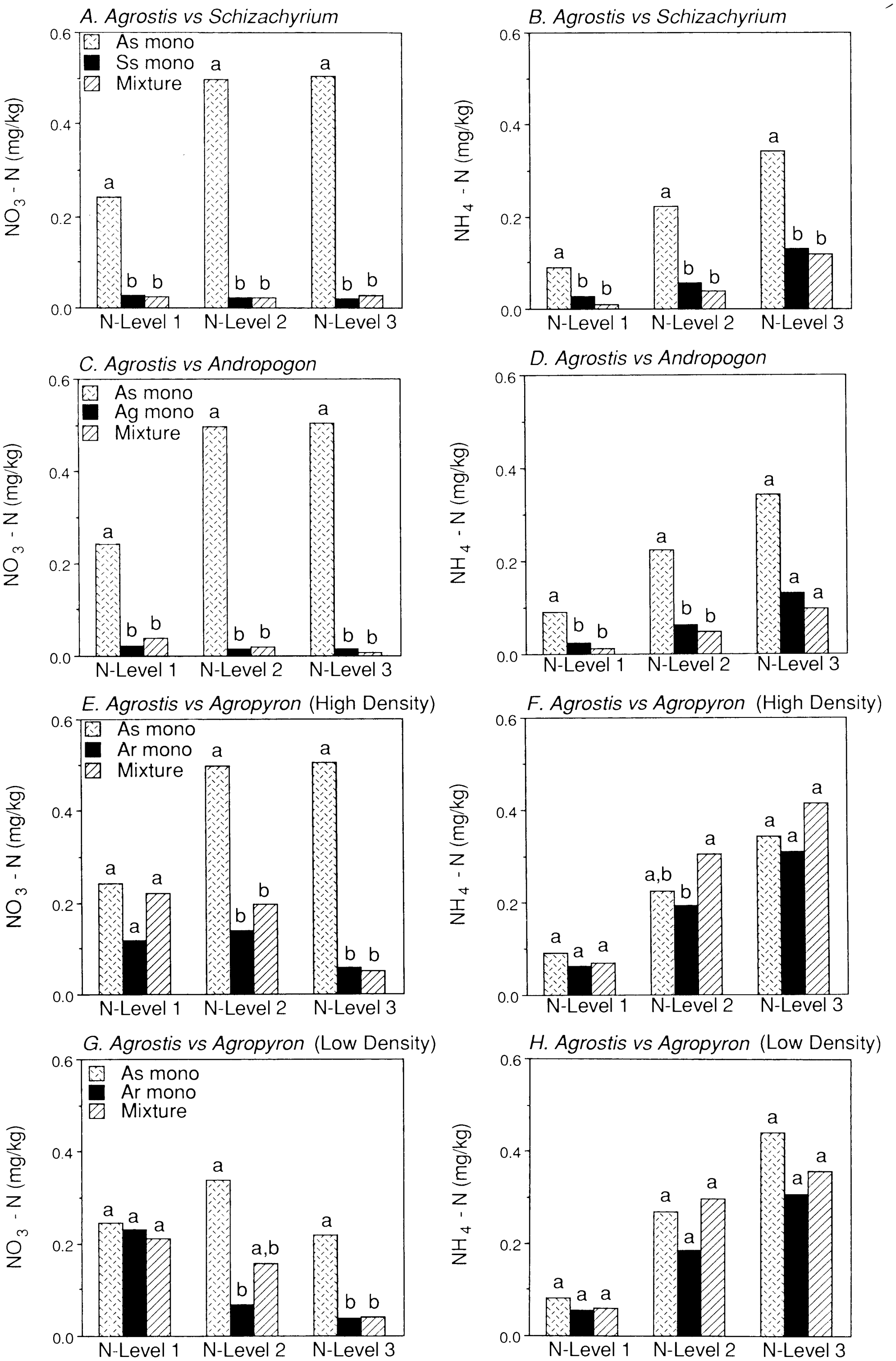

FIG. 3. Extractable (0.01 mol/L KCl) soil nitrate and ammonium in 1988 in monoculture plots (called "mono") and in the two-species plots (called "mixture") for *Agrostis* (As) vs. *Schizachyrium* (Ss), for *Agrostis* vs. *Andropogon* (Ag), for *Agrostis* vs. *Agropyron* (Ar) at high seed density, and for *Agrostis* vs. *Agropyron* at low seed density. In all cases, ☐ are results for *Agrostis* monocultures, ■ are results for monocultures of its competitor, and ▨ are results for competition plots (all seed ratios combined; there was no significant seed ratio effect in 1988). Within an experiment type and N level, bars that share the same letter do not differ significantly ($P > .05$) based on Duncan's test. Note that monoculture means reported here differs somewhat (but not significantly) from those in Tilman and Wedin (1991) because of one different sampling date.

TABLE 1. F values for general linear model regressions of 1986, 1987, or 1988 aboveground biomass of each competitor against soil total N, with initial seed ratio as a categorical variable.† All regressions based on results of pairwise competition experiments.

	1986		1987		1988	
Case	Total N	Seed ratio	Total N	Seed ratio	Total N	Seed ratio
Agrostis vs. *Schizachyrium*:						
Agrostis	36.2**	5.66*	19.8**	4.09*	3.17 NS	1.21 NS
Schizachyrium	20.1**	1.45 NS	12.6**	0.56 NS	44.3**	0.19 NS
Agrostis vs. *Andropogon*:						
Agrostis	6.44*	3.53*	20.7**	4.79*	0.23 NS	0.25 NS
Andropogon	47.0**	2.00 NS	104.8**	1.05 NS	41.3**	0.07 NS
Agrostis vs. *Agropyron* (high seed density):						
Agrostis	18.3**	11.50**	18.90**	3.26 NS	1.85 NS	0.30 NS
Agropyron	87.2**	12.4**	53.2**	3.19 NS	96.8**	0.04 NS
Agrostis vs. *Agropyron* (low seed density):						
Agrostis	17.9**	3.50*	7.63*	1.49 NS	0.06 NS	1.11 NS
Agropyron	14.3**	2.48 NS	6.71*	5.48*	49.7**	0.98 NS

* = $.05 \geq P > .01$, ** = $P < .01$, and NS = $P > .05$.

† F values for total N indicate whether aboveground biomass increases significantly with total soil N. F values for seed ratio indicate whether initial seed ratio was a significant categorical variable in these regressions, i.e., if there were distinct regression lines for one or more of the three initial seed ratios. For all cases, the F values for total N have df = 1, 18, and those for seed ratio have df = 2, 18.

monocultures, but did not differ significantly from *Andropogon* monocultures (Fig. 3C–D).

Agrostis *vs.* Agropyron *(high seed density).* —The GLM regressions revealed significant effects of initial seed ratio on the 1986 aboveground biomass of both *Agrostis* and *Agropyron* when growing together, but no significant effects in 1987 or 1988 (Table 1, Fig. 1C). ANOVA of 1988 biomass in competition plots revealed highly significant species ($F_{1,30} = 18.8$), N level ($F_{2,30} = 15.2$), and interaction ($F_{2,30} = 44.6$) effects. The interaction was caused by *Agrostis* doing relatively better than *Agropyron* on low N soils and *Agropyron* doing much better than *Agrostis* on high N soils (Figs. 1C and 4A–C). The above ground biomass of *Agrostis* was significantly lower in the two-species plots than in monocultures for all three N levels in both 1986 and 1988 (t test, $P < .01$ for all six comparisons; Fig. 4A–C), but did not differ significantly in 1987 (t test, $P > .05$). The aboveground biomass of *Agropyron* was significantly lower in competition plots than in monocultures for N-level 2 in 1986, for all three N levels in 1987, and for N-levels 1 and 2 in 1988 (t test, $P < .01$ for all), but did not differ significantly for the other comparisons (t test, $P > .05$; Fig. 4A–C). For each of the seed ratios, *Agrostis* attained higher abundance in 1987 than in either 1986 or 1988 for all three N levels. There were no consistent differences between the 1988 ammonium and nitrate concentrations in *Agrostis* and *Agropyron* monocultures and in the various competition plots for N-level 1 (Fig. 3E–F). On N-levels 2 and 3, all plots containing *Agropyron* had significantly (Duncan's test: $P \leq .05$) lower nitrate (but not ammonium) concentrations than *Agrostis* monocultures (Fig. 3E–F).

Agrostis *vs.* Agropyron *(low seed density).*—When the total density of *Agrostis* and *Agropyron* was 600 seeds/m^2, the qualitative dynamics of interspecific interactions were similar to, but more stochastic than, those of the high seed density plots (compare Fig. 4A–C with Fig. 4D–F). Initial seed ratio had a significant effect on *Agrostis* but not *Agropyron* in 1986, on *Agropyron* but not *Agrostis* in 1987, and no significant effects in 1988 (Table 1, Fig. 1D). ANOVA showed no significant species effect ($F_{1,30} = 0.74$), but the N-level effect ($F_{2,30} = 5.80$) and the species × N-level interaction ($F_{2,30} = 19.1$) were significant. The aboveground biomass of *Agropyron* was significantly lower than in monoculture in N-levels 2 and 3 in 1987 (t-test, $P < .01$), but was never significantly lower than in monoculture in 1986 or 1988 (t test, $P > .05$; Fig. 4D–F). Compared to its monocultures, aboveground biomass of *Agrostis* was significantly inhibited by *Agropyron* only for N-level 3 in 1986 and 1988 (t test, $P < .01$; Fig. 4D–F). *Agrostis* did relatively better than *Agropyron* at low total soil N, and the opposite occurred at high soil N. In most treatments *Agrostis* attained a greater abundance in 1987 than in 1986 or 1988. The response of soil nitrate and ammonium in the low density monocultures and competition plots was quite similar to that in the high density plots (compare Fig. 3E–F with 3G–H). Comparisons of aboveground biomass between the low and high density monoculture of *Agrostis* revealed no significant differences in 1986, 1987, or 1988 for any of the N levels (t test, $P > .05$ for all nine cases). Similarly, there were no significant differences in *Agropyron* monoculture biomass between the low and high density plots (t test, $P > .05$ for all nine cases). Thus, the biomass each species attained in monoculture was independent of its initial seed density.

Species identity.—ANOVA of the 1988 biomass of *Agrostis* by N level, initial seed ratio, and species iden-

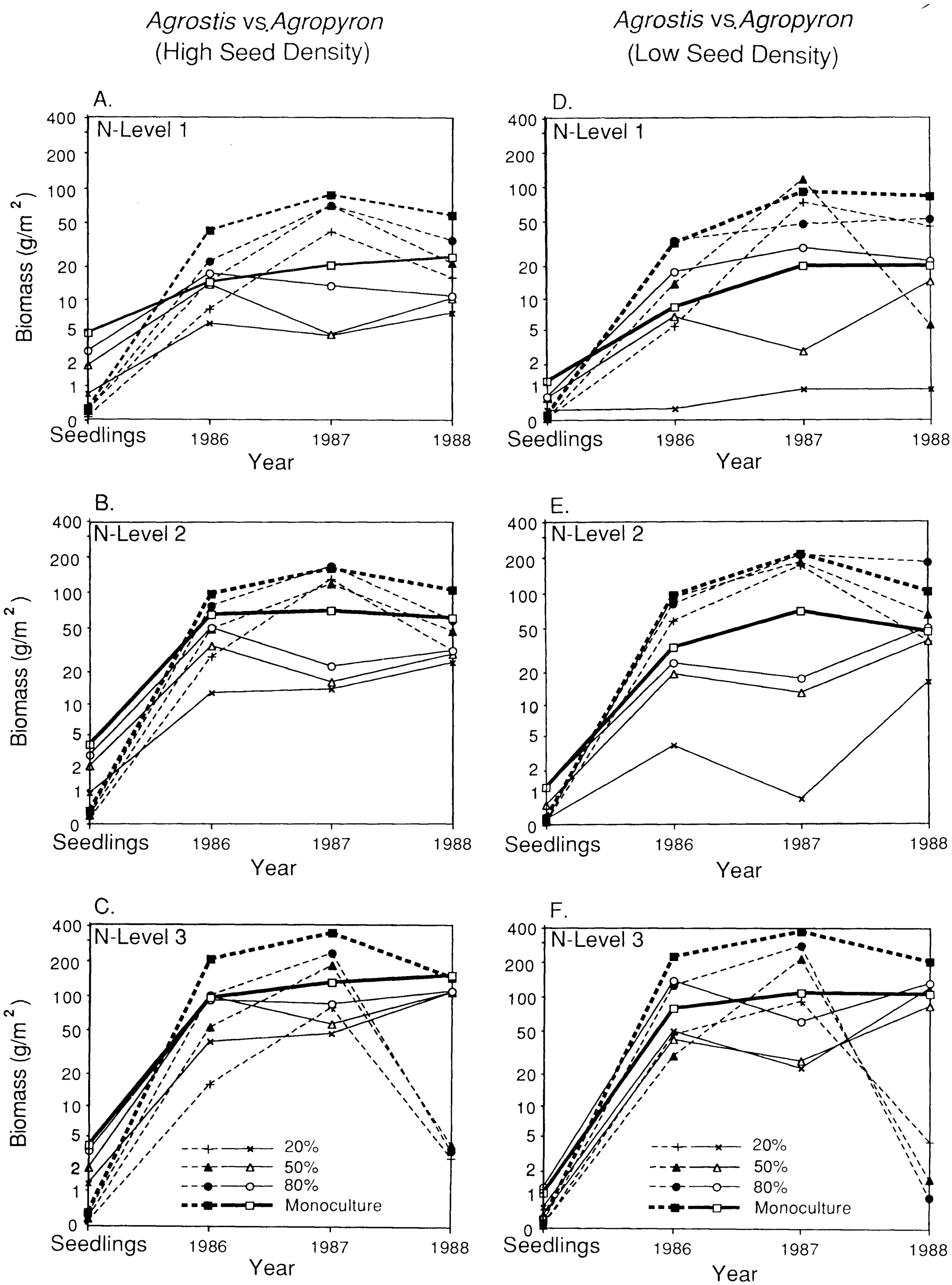

FIG. 4. (A–C). Seed vs. seed competition between *Agrostis* (broken lines and solid symbols) and *Agropyron* (solid lines and open symbols) when planted at high seed density (3000 seeds/m²). See legend to Fig. 2 for details of data presentation. (D–F). Seed vs. seed competition between *Agrostis* (broken lines and solid symbols) and *Agropyron* (solid lines and open symbols) when planted at low seed density (600 seeds/m²).

tity (for the case in which *Agrostis* data were combined from all three species pairs) revealed highly significant N-level ($F_{2,108} = 5.01$, $P < .01$) and species identity ($F_{2,105} = 24.5$, $P < .001$) effects, but no initial seed ratio effect ($F_{2,105} = 0.62$, $P = .54$). This indicates that *Schizachyrium, Andropogon,* and *Agropyron* differ in their ability to suppress *Agrostis.* Similarly significant species identity and N-level effects occurred in 1986 and

1987 ($P < .01$ for all), as did initial seed ratio effects ($P < .01$ for both years).

DISCUSSION

Competitive dynamics and outcomes

All species survived in monoculture, and monocultures showed no signs of nitrogen or litter inhibition on soils with total soil N <1000 mg/kg (Figs. 2 and 4). The various species pairs did compete when growing together. For at least one of the N levels, each species attained lower aboveground biomass when growing with another species than in monoculture in at least 1 of the 3 yr. Although both *Schizachyrium* and *Andropogon* had competitively displaced *Agrostis* from the entire soil N gradient by 1988, *Agrostis* inhibited each of these in 1986 or 1987. *Agrostis* and *Agropyron* persisted together on N-levels 1 and 2 for the 3 yr, suggesting that they were more similar in their competitive abilities than the other two species pairs. By 1988, *Agropyron* had virtually displaced *Agrostis* on N-level 3. Thus, the relative competitive abilities of these two species changed along the N gradient, but did not depend on initial total seed densities or initial seed ratios. Although the experimental design we used differs greatly from that of Goldberg (1987), the differing effects of *Schizachyrium, Andropogon,* and *Agropyron* on the biomass of *Agrostis* demonstrate that these three species are not competitively equivalent in their interactions with *Agrostis.*

As frequently observed (Harper 1977), seed ratios affected the initial dynamics of pairwise interactions (Table 1). However, these effects disappeared after 3 yr. The long-term outcomes were independent of initial densities as predicted by theory (Tilman 1982). Additional experiments with *Agrostis* and *Agropyron,* and with three other species pairs, have shown that other differences in initial conditions also had little effect on the long-term outcome of nitrogen competition (D. Wedin and D. Tilman, *unpublished manuscript*). Similarly, Inouye and Tilman (1988) found that the long-term outcome of interactions among these and other species in old fields were largely independent of initial abundances. *Agrostis,* which has smaller seed and a higher maximal rate of vegetative growth than the other species, did have an initial advantage in competition. It often attained its greatest biomass and had its greatest effect on competitors in the 2nd yr of the experiment, and then declined. However, its competitive dynamics changed with N level (Figs. 2 and 4).

Competition and resource reduction

According to resource competition theory, the species that can reduce monoculture resource concentration (called R^*) to the lowest level should, when growing in mixed-species plots, eventually competitively displace all other species limited by that resource (e.g., O'Brien 1974, Tilman 1976, 1982, 1990, Hsu et al. 1977). The rate of competitive displacement should be slower the more similar the R^* values of two species. Although our monocultures probably had not reached population equilibria after 3 yr of growth, monoculture biomass seemed to have stabilized (Figs. 2 and 4). Thus, the levels of extractable soil NO_3 and NH_4 in low-N monocultures of each species in the 3rd yr may provide estimates of R^* (Fig. 3; Tilman and Wedin 1991). N-levels 1 and 2 provide tests of the predictive abilities of these nitrogen R^* values because these plots had low soil total N, low biomass, and probably little light limitation even of seedlings (Tilman and Wedin 1991). Because theory predicts that such soil ammonium and nitrate concentrations should be higher on more N-rich soils, on which plants would be increasingly more limited by light (i.e., resource-dependent growth isoclines are curved; Tilman 1988), the best estimate of R^* for N may be provided by N-level 1.

Using the values observed on N-levels 1 and 2, *Schizachyrium* and *Andropogon,* which have much greater allocation to root than *Agrostis* (Tilman and Wedin 1991), had significantly lower R^* values for soil nitrate and ammonium on both N levels than *Agrostis* (Fig. 3), and are thus predicted to be superior N competitors compared to *Agrostis.* On both N-level 1 and 2, *Agrostis* was competitively displaced by both *Schizachyrium* and *Andropogon,* as predicted by the differential abilities of these species to reduce soil ammonium and nitrate concentrations in monoculture. This competitive displacement was accompanied by the predicted reductions in soil ammonium and nitrate concentrations (Fig. 3). Soil ammonium and nitrate concentrations in the competition plots were significantly lower than in *Agrostis* monocultures, but did not differ from those in *Schizachyrium* or *Andropogon* monocultures.

Agrostis and *Agropyron* did not differ significantly in their estimated R^* values for soil ammonium on either N-level 1 or 2. *Agropyron* had a significantly lower R^* value for soil nitrate on N-level 2 but not on N-level 1 (Fig. 3). If data from a third sampling date are included, *Agropyron* has a significantly lower R^* for nitrate than *Agrostis* on N-level 1 (Tilman and Wedin 1991). Thus, in total, these data suggest that *Agropyron* should be a superior N competitor compared to *Agrostis,* but the similarity of their R^* values means that competitive displacement is predicted to be slower for this pair than for the other pairs. However, *Agrostis* had not been displaced by *Agropyron* on N-level 2 within 3 yr despite the significantly lower soil nitrate concentration in the competition plots than in *Agrostis* monocultures. Rather the species persisted, with *Agrostis* having an initial advantage over *Agropyron* on lower N soils (Fig. 4; but see *Note added in proof*).

These results suggest that R^* may be best at predicting the outcome of competition among species with large differences in R^* values. Factors not included in R^*, such as the seasonality of nutrient supply and uptake, the vertical distributions of nutrients and roots, and the mode and timing of reproduction, may be increasingly important determinants of competition when species have similar R^* values.

On N-level 3, there is a greater potential of light limitation. The displacement of *Agrostis* by *Agropyron* on N-level 3 is consistent with *Agropyron*'s lower monoculture soil nitrate concentrations, but displacement may have resulted from light limitation. In another experiment in which N-level 2 plots were shaded, *Agropyron* displaced *Agrostis* from shaded plots, but both species survived in monoculture (Wedin 1990), suggesting that *Agropyron* may be a superior light competitor. However, *Agrostis* and *Agropyron* did not differ significantly in the level to which each reduced light at the soil surface in N-level 3 monocultures (Tilman and Wedin 1991). Rather, traits other than light intensity at the soil surface, such as phenology, seed size, height, and leaf placement may be more important determinants of competitive ability for light (e.g., Harper 1977, Givnish 1982, 1986, Schulze et al. 1986, Tilman 1988). Compared to *Agropyron, Agrostis* had smaller seeds and had more of its leaf mass near the ground. Moreover, *Agropyron* produced rhizomes that penetrated deep litter, which *Agrostis* seed cannot do.

On N-level 3, monocultures of *Schizachyrium* and *Andropogon* reduced both soil ammonium and nitrate concentrations (Fig. 3) and light at the soil surface (Tilman and Wedin 1991) to significantly lower levels than did *Agrostis.* Thus, the displacement of *Agrostis* by *Schizachyrium* and by *Andropogon* is consistent with both N and light competition on N-level 3.

Agrostis was an inferior competitor on both poor and rich soils compared to *Schizachyrium* and *Andropogon,* but *Agrostis* and *Agropyron* were differentiated in their competitive abilities along the N gradient. Some other studies have shown interspecific trade-offs in competitive ability along productivity gradients (e.g., Stern and Donald 1962, Eagles 1972, Harper 1977, McGraw and Chapin 1989) and some have not (e.g., Mahmoud and Grime 1976, Grime 1979, Wilson and Keddy 1986, Keddy and Shipley 1989). *Agrostis,* an early successional species, differs from *Schizachyrium* and *Andropogon* in having greater allocation to seed, which may give it an advantage in disturbed sites but reduce competitive ability in undisturbed habitats. If plants are compared that have major differences in allocation to reproduction (seed and rhizome), such as occurs for plants of disturbed habitats, species with high reproductive allocation are likely to be inferior competitors for both nutrients and light in undisturbed habitats. However, if species with similar patterns of allocation to reproduction are compared, interspecific differences in allocation to root vs. shoot could cause trade-offs in competitive abilities along a productivity gradient (Tilman 1988). Interestingly, most studies that have not found competitive trade-offs have used plants from pastures and lakeshores, which have high disturbance rates from grazers (Tilman 1988) or waves (Wilson and Keddy 1986), respectively. These species may be mainly differentiated in their patterns of allocation to reproduction.

Successional dynamics

Succession at CCNHA begins on N-impoverished soil, which is intermediate between N-level 1 and 2 (Inouye et al. 1987, Tilman 1987*a*). *Agrostis* and *Agropyron,* the two early successional species, had relatively similar competitive abilities on low N soils, but *Agrostis* was a markedly inferior competitor on low N soils compared to both later successional species, *Schizachyrium* and *Andropogon.* In other experiments (D. Wedin and D. Tilman, *unpublished manuscript*), *Agropyron* was displaced from low-N soils by *Schizachyrium.* This contradicts the resource ratio hypothesis of succession (Tilman 1985), which, as applied to CCNHA, states that succession is caused by a trade-off between the N and light competitive abilities of species. Early successional species, the presumed superior N competitors, are hypothesized to be displaced by superior light competitors as total soil N accumulates at CCNHA. However, our results demonstrate that our early successional dominants were inferior N competitors compared to later successional species.

Monk (1966) found that proportional root biomass increased during old-field succession on sandy soils in South Carolina. Gleeson and Tilman (1990) found a similar pattern at CCNHA, and reported that allocation to seed was maximal in young fields. When growing in monoculture, our early successional species had a lower proportion of their biomass in root, and had higher tissue N than the later successional species (Tilman and Wedin 1991). If, as our competition results suggest, high root biomass is indicative of nutrient competitive ability, these allocation patterns also contradict the resource ratio hypothesis as an explanation for herbaceous succession on N-poor soils.

Our results support an alternative hypothesis of succession, that there is a trade-off between the colonization ability of a species vs. its competitive ability (e.g., Platt 1975). Our early successional grasses, *Agrostis* and *Agropyron,* are poor N competitors but have high allocation to either seed or rhizome on low N soils (Tilman and Wedin 1991). *Agrostis* is a rapid colonist of abandoned fields, invading most fields during the 1st or 2nd yr (Tilman 1988). *Agropyron,* an agricultural weed, is present at the time of abandonment, and spreads rapidly via rhizomes (Hakansson 1967, Werner and Rioux 1977). In contrast, *Schizachyrium* and *Andropogon* are superior N competitors but produce few seed on low N soils (Tilman and Wedin 1991) and are poor at spreading vegetatively. *Schizachyrium* requires ≈11 yr and *Andropogon* ≈17 yr to colonize an abandoned field (Tilman 1988: Fig. 8.22). When the colonization advantage of early successional species was eliminated by planting them simultaneously with late successional species, displacement occurred in 2 or 3 yr (Fig. 2), rather than the 15–30 yr required during succession.

The slower colonization rates of the superior N competitors may explain why the abundance of *Agrostis,* a poor N competitor, was significantly negatively correlated with total soil N in our old fields, whereas *Schizachyrium,* a better N competitor, reached peak abundance in successional fields with higher total soil N (Tilman 1988: 274–275). Although total soil N does accumulate at CCNHA, extractable soil nitrate does not increase during the first 40 yr (Gleeson and Tilman 1990), and most species are N limited in a 50-yr old field (Tilman 1988). Thus, the successional replacement of *Agrostis* and *Agropyron* by *Schizachyrium* is consistent with the N competitive ability of *Schizachyrium.* The correlations between total soil N and plant abundances are likely spurious, caused by the greater total soil N of older fields and the absence of *Schizachyrium* in younger fields.

A trade-off between maximal vegetative growth rate vs. competitive ability could also, in theory, cause succession (e.g., Horn 1971). *Agrostis,* which had a significantly greater vegetative growth rate than *Agropyron, Schizachyrium,* and *Andropogon* (Tilman and Wedin 1991), generally increased in biomass more rapidly than *Agropyron* during competition in 1986 and 1987 on N-levels 1 and 2 (Fig. 4A–B). However, in only 2 of the 12 cases of competition between *Agrostis* and either *Schizachyrium* or *Andropogon* on N-levels 1 and 2 (Fig. 2), did *Agrostis* increase more rapidly than its competitor during 1986. Thus, for the seed densities we used, the greater vegetative growth rate of *Agrostis* did not give it a significant period of dominance over species that were superior N competitors. However, transient dominance could be more prevalent at lower seed densities, which would provide a longer period during which species grew at maximal rates.

In total, our experiments suggest that the ability of species to reduce resource levels in monoculture is related to their ability to compete for those resources. Our competition experiments refute the resource ratio hypothesis of succession but support the hypothesis that a trade-off between nitrogen competitive ability and colonization ability may be a cause of the first 30–40 yr of herbaceous secondary succession on the nitrogen-poor soils of CCNHA. However, the eventual replacement of prairie grasses by trees and shrubs, and the increased rate at which this occurs in fertilized plots (Tilman 1988), suggest that additional processes, such as those included in the resource ratio hypothesis, may be required to explain the transition from prairie grasses to oak savanna or oak forest.

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NOTE ADDED IN PROOF

When this experiment was resampled in 1990, its 5th yr, the only qualitative change was in the outcome of competition between *Agrostis* and *Agropyron* on N-levels 1 and 2. Although *Agrostis* had been more abundant than *Agropyron* in competition on N-levels 1 and 2 in 1988, *Agropyron* had become more abundant by 1990 (Fig. 5). This suggests that *Agropyron* is displacing *Agrostis,* and that *Agropyron* is the superior competitor on low nitrogen soils. The transient dominance by *Agrostis* (Fig. 5) shows that even 3-yr competition experiments may not reveal the long-term outcome of competition.

For *Agrostis* vs. *Schizachyrium* and *Agrostis* vs. *Andropogon* on all 3 N levels, and for *Agrostis* vs. *Agropyron* on N-level 3, *Agrostis* had been competitively displaced by 1988 and remained rare in 1990.

The competitive dominance of *Agropyron* over *Agrostis* on low nitrogen soils is consistent with *Agropyron*'s lower R^* for soil nitrogen (Fig. 3E–F). R^* also predicted the long-term outcomes of nitrogen competition for the other two pairs of species. As predicted by theory, competitive displacement was slower for the species pair with the most similar R^* values, and the eventual outcome of competition was independent of initial densities and seed ratios. The 1990 results thus further support the ability of resource competition theory (Tilman 1976, 1982, 1990) to predict the outcome and qualitative dynamics of nutrient competition among terrestrial plants.

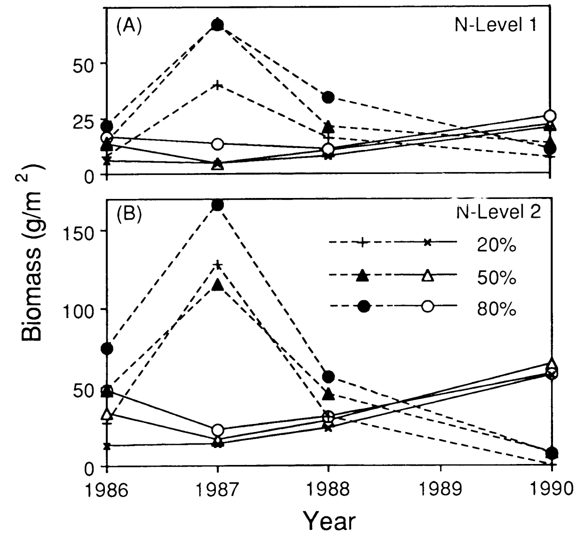

FIG. 5. Dynamics of competition between *Agrostis* (broken lines) and *Agropyron* (solid lines) for high seed density plots on N-levels 1 and 2, using symbols as in Fig. 4. Similar results occurred on low seed density plots.