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PLANT TRAITS AND RESOURCE REDUCTION FOR FIVE GRASSES GROWING ON A NITROGEN GRADIENT[1]

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Abstract. Five grass species (*Agrostis scabra, Agropyron repens, Poa pratensis, Schizachyrium scoparium* and *Andropogon gerardi*) were grown in monoculture for 3 yr on an experimental nitrogen gradient. The species differed significantly in the levels to which they reduced soil solution (0.01 mol/L KCl extractable) nitrate and ammonium concentrations and light penetration to the soil surface. Soil nitrate concentration was an inverse function of root mass, which explained 73% of the observed variance in nitrate. Other species differences explained an additional 9.2%, and total soil N an additional 5% of this variance. Extractable soil ammonium also depended on these variables, but total soil N explained the most variance. Light penetration to the soil surface in these monocultures was a negative exponential function of aboveground biomass ($R^2 = 0.79$).

Schizachyrium and *Andropogon*, the species that reduced soil solution N to the lowest levels on infertile soils, had lower vegetative growth rates, higher root allocation, lower reproductive allocation, and lower tissue N than the other species. Many of these traits are associated with plants of infertile habitats, suggesting a direct link between ecophysiology, resource reduction, and distributional patterns. Because all species survived on even our most nitrogen-poor soil (subsurface sand), differential nutrient reduction, not tolerance, may be the main mechanism favoring these traits in infertile habitats.

On infertile soils, the three earlier successional species (*Agrostis, Agropyron,* and *Poa*) allocated more to reproduction (rhizome or seed) than the later successional species, but did not reduce soil solution nitrate and ammonium to as low levels. This suggests that our early successional species may be superior colonists but inferior nitrogen competitors compared to the prairie bunchgrasses. Our results can be used to make explicit predictions as to the outcome of nitrogen competition among all possible combinations of these five species.

Key words: Agropyron repens; Agrostis scabra; *allocation;* Andropogon gerardi; *monoculture plots; nitrogen;* Poa pratensis; *productivity gradient; resource reduction; rhizomes; roots;* Schizachyrium scoparium; *seeds; shoots; successional grasses.*

INTRODUCTION

Numerous observational and experimental studies have shown that terrestrial plant distribution, abundance, dynamics, and diversity are affected by the availability of limiting resources (e.g., Milton 1947, Snaydon 1962, Pigott and Taylor 1964, Beadle 1966, Van den Bergh 1968, Thurston 1969, Grubb 1977, Vitousek and White 1981, Tilman 1982, 1988). Thus, there has been strong interest in determining the effects of resource availability on the growth, morphology, and life history of plant species (e.g., Ellenberg 1953, Bradshaw et al. 1958, 1960, 1964, Monk 1966*a, b,* Mooney 1972, Austin and Austin 1980, Chapin 1980, Field and Mooney 1986). Chapin (1980) reviewed such studies and found that species of undisturbed, infertile habitats have lower maximal growth and nutrient uptake rates, greater allocation to root, and are more likely to be evergreen than species of more fertile or disturbed habitats. These traits are favored, it is presumed, because they confer an advantage, perhaps a competitive advantage, in infertile habitats (Chapin 1980, Moore 1980, Berendse and Elberse 1990, Tilman 1990). However, there is not yet a clear link between these traits and the nutrient competitive ability that they might confer.

The most basic mechanism of competition for a limiting nutrient is nutrient reduction. As a plant consumes a soil nutrient and reduces its concentration in solution in the soil, its neighbors are denied some of that resource, and thus grow more slowly. Simple theories of plant competition for a single limiting nutrient predict, that, if competitive interactions go to steady state, the superior competitor will be the species that can reduce the concentration of the limiting nutrient to the lowest level in steady state monocultures (e.g., O'Brien 1974, Tilman 1976, 1982, 1988, Hsu et al. 1977). The identical prediction is made by a variety of more complex models that include many aspects of plant morphology and physiology (Tilman 1990). These models and their predictions, though, have never been explicitly tested using terrestrial plants. Do plant species differ in the levels to which they reduce the concentrations of limiting soil resources? If so, are such

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differences related to morphology, tissue chemistry, life history and successional status in a way that is consistent with both ecophysiological studies and the predictions of resource competition theory? Might species with high root allocation and low maximal growth rate, which often dominate infertile sites, also reduce the concentration of a limiting soil nutrient to a lower level, and thus be able to competitively exclude other species from infertile habitats?

This paper explores these questions by determining the relationships between plant traits and resource reduction for five perennial grass species that are dominant at different times during secondary succession at Cedar Creek Natural History Area (CCNHA), Minnesota, USA. These were grown for 3 yr in replicated field monocultures on soils prepared to have different total soil nitrogen, and thus different productivities. We measured light reduction in monocultures as the proportion of incident light that reached the soil surface. We estimated reduction in the concentration of nitrate and ammonium in soil solution by extracting soil cores with a dilute extractant that should remove little of the ammonium bound to cation exchange sites. Additional papers report the results of competition experiments among various combinations of these species, as well as the differing feedback effects of each species on soil nitrogen mineralization rates. All of this work was motivated by the desire to more fully understand the mechanisms of interactions among plants and their resources, in the belief that this may eventually allow prediction of the dynamics, diversity, and composition of plant communities (Mooney 1972, Tilman 1982, 1988, 1990).

Methods

Species

The five grasses are common prairie, grassland and old-field species that differ in their successional status and response to nutrient addition (Tilman 1987, 1988). They are the five most abundant grasses during old-field succession at CCNHA, where this work was performed. *Agrostis scabra* Willd. (a native C_3 bentgrass) and *Agropyron repens* (L.) Beauv. (quack grass, a C_3 grass introduced from Europe) are both early successional species at CCNHA (Fig. 1). *Poa pratensis* L. (Kentucky bluegrass; C_3; introduced) dominates mid-successional fields. *Schizachyrium scoparium* (Michx.) Nash-Gould (little bluestem, formerly *Andropogon scoparius* Michx.) and *Andropogon gerardi* Vitm. (big bluestem) are native C_4 prairie species that dominate later successional fields at CCNHA (Fig. 1). For brevity, we refer to each species by its genus name.

Experimental design and methods

This research was performed in an experimental garden at CCNHA, which is located on a large glacial outwash sandplain in Isanti and Anoka counties of Minnesota. Each species was grown both in monoculture and mixed-species plots in soils with a range of total soil N. In August 1985, we used a bulldozer to remove the upper 60–80 cm of soil from a 31 × 34 m area of a 25-yr old field, thus exposing subsurface sand. This substrate was 93% sand, 3% clay, and 4% silt, had a pH of 6.6, contained 0.3% organic matter, had total soil nitrogen, as N, of 90 mg/kg of dry soil, and a bulk density of 1.51 g/cm^3. This area was divided into 10 regions, 3 × 12 m each, with 1-m walkways between them. Each of the 10 regions was randomly assigned to be 1 of 10 soil mixtures. Nine soil mixtures were established by adding an amount of topsoil (a sandy loam of the Hubbard-Isanti-Duelm Association: 72% sand, 4% clay, 24% silt, 2.9% organic matter, total soil N of 1100 mg/kg, pH of 7.2, bulk density of 1.40 g/cm^3) such that, once topsoil and subsurface sand had been mixed to a depth of 22 cm, topsoil would comprise $\approx$0 (soil mixture 1), 10, 20, 40, 50, 55, 70, 90, or 100% (soil mixture 9) of the upper 23 cm of soil. To keep the surface of all soil mixtures level with their surroundings, the sand in each was excavated to a depth equal to the amount of top soil to be added. Soil mixture 10 was a duplicate of mixture 9, but also received 6.55 $g \cdot m^{-2} \cdot yr^{-1}$ of additional N as NH_4NO_3, added monthly in proportion to normal N mineralization at CCNHA (Pastor et al. 1987; April = 9%, May = 33%, June = 28%, July = 15%, August = 17%). After topsoil was added, each plot was thoroughly rototilled to give a uniform, 23 cm deep layer of soil underlain by unmixed sand. To assure that N would be the only limiting nutrient, we analyzed the soils, and based on these analyses, rototilled into each plot 12.2 g/m^2 of P_2O_5 (commercial 0-46-0 fertilizer), 14.6 g/m^2 of K_2O (commercial 0-0-61 fertilizer), 42 g/m^2 of $MgSO_4$ (commercial epsom salts), 42 g/m^2 of $CaSO_4$, 1.9 g/m^2 of $ZnSO_4$, 1.12 g/m^2 of $CuSO_4$, 0.28 g/m^2 of boric acid, and 0.56 g/m^2 of $MnSO_4$ in April 1986. These nutrients were also added to the soil surface in subsequent years. Soil pH was stable, at 7.2, in all plots except soil mixtures 1 and 2, which received fine-ground lime in 1987 and 1988 to adjust their pH to 7.2. In April 1986, galvanized sheet metal (26 gauge, 25 cm tall) was driven into the soil to a depth of 23 cm to divide each soil mixture into 64 experimental plots, each 0.75 × 0.75 m. The entire garden was then fenced to a height of 2 m and to 1.3 m belowground to exclude all mammalian herbivores. All plots were watered to receive at least 1.5 cm/wk in April, May, and October, and 2.5 cm/wk in June through September.

Seed of the five species were planted in the monoculture plots in late May 1986, at a density, based on germination trials, to yield 3000 seedlings/m^2. Seed were covered with 0.5 cm of sand. There were two replicate monocultures of *Andropogon,* three replicate monocultures of *Poa* and *Schizachyrium,* and four replicate monocultures of *Agrostis* and *Agropyron* in each soil mixture, giving a total of 160 monoculture plots.

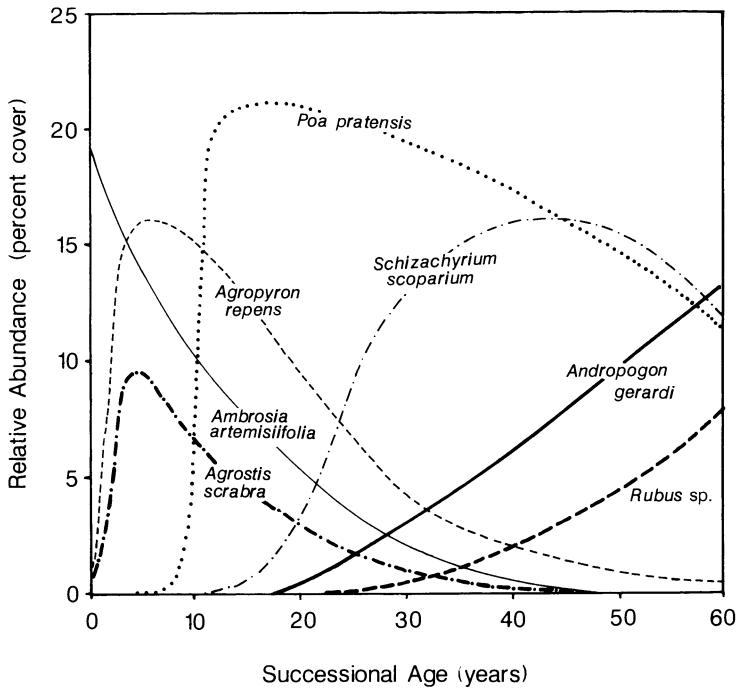

FIG. 1. Successional dynamics at Cedar Creek Natural History Area. The relative abundances of seven of the most abundant species during secondary succession were calculated using data from a chronosequence of 22 old fields (Inouye et al. 1987) and other observations (B. Delaney, *personal communication*). See Tilman (1988) for further details. Figure modified from Tilman (1988).

This design was imposed by limited space and the need for a balance between monoculture and competition plots in the various competition experiments that were performed simultaneously in these gardens. Monoculture and competition treatments were randomly assigned to the 64 plots within a soil mixture, with each soil mixture independently randomized.

Vegetation sampling

Aboveground biomass was sampled in each plot each year. A 7.8 × 55 cm strip was clipped at the soil surface during 28 August–12 September 1986. The same size strip was harvested during July 25–August 5 1987. A 10 × 40 cm strip was clipped during 13–27 July 1988. These three strips were located at least 10 cm from a plot edge in an area that had not been previously clipped. Sampling dates were chosen based on phenology, to be near the time of peak *Agrostis* flowering. Clipped material was sorted to living biomass and litter, dried at 40°C for a week, and weighed. The aboveground living biomass (grams per square metre), called plant shoot, contains leaves, stems, and reproductive plant parts. One *Schizachyrium* plot in soil mixture 10 is excluded because of heavy damage by a nesting small mammal. Two *Poa* plots in soil mixture 1 are excluded because of low germination caused by poor initial arrangement of water sprinklers.

Root mass in each plot (grams per square metre) was determined by collecting two 4.5 cm diameter by 25 cm deep soil cores from each plot, and carefully rinsing these to obtain belowground living biomass. For the two rhizomatous species, *Poa* and *Agropyron,* these were further sorted to root and rhizome. Although *Schizachyrium* and *Andropogon* can be rhizomatous on rich soils (Weaver 1958), they were not rhizomatous in our soils. Their crowns were included with root biomass. Total belowground biomass is the sum of root and rhizome biomass, whereas root mass does not include rhizome. Root:shoot ratio was calculated as the ratio of the soil-mixture-average root (but not rhizome) mass to the soil-mixture-average nonreproductive aboveground mass of a species. We used this ratio, rather than that of total belowground to total aboveground mass, because it should better indicate allocation for the acquisition of nutrients vs. light.

Reproductive biomass (seeds and flowering stems) was determined by counting the number of flowering stems within each plot at the time of peak reproductive biomass and subsampling flowering stems to determine mass per stem and seeds per stem. This was used to calculate the total reproductive mass per square metre, seed mass per square metre and seeds per square metre. These data were combined with germination rates to estimate the number of viable seeds produced per square metre. Plant height was determined by placing a 25 cm diameter, 5.2 g paper disk on top of the plants in a monoculture, and measuring the height that the center of the disk was held above the soil surface.

The average embryo mass per seed was determined for each species by removing seed cases and dispersal structures from a sample of 50 seeds per species, which was weighed to ±0.0001 g. These data were combined with data on the number of germinated seedlings per square metre in mid-June to calculate initial plant mass, B_i (in grams per square metre), in each plot. The vegetative growth rate (VGR, dB/Bdt, per week) during the first season of growth was then calculated for each monoculture using B_i and total (aboveground + belowground) plant mass per square metre at harvest in 1986 (B_f), as VGR = $[\ln(B_f/B_i)]/t$, where t is weeks from germination to harvest.

Chemical analyses

Prior to planting in May 1986, four 2.5 cm diameter by 20 cm deep soil cores were collected from each plot. These were pooled, homogenized, dried, and analyzed in duplicate for total soil N via alkaline persulfate digestion, as modified in Tilman (1984), followed by nitrate determination on a Technicon II Autoanalyzer, using the cadmium reduction method. We used the average of the duplicates for each plot.

After being dried and weighed, 1988 aboveground biomass and root biomass from each monoculture were ground (UDY Cyclone mill with 0.25-mm mesh screen) and analyzed for total tissue N in a Carlo-Erba Carbon-Nitrogen Analyzer. This instrument combusts organic matter in an atmosphere of pure O_2, puts the combustion products through a gas chromatograph, and determines N concentrations by comparison with reagent-grade organic chemicals with appropriate C:N ratios.

Monoculture soils were sampled for concentrations of extractable ammonium and nitrate using KCl at 0.01 mol/L. This weak extractant removes ammonium and nitrate from soil solution but not ammonium tightly bound to exchange sites on clays or organic matter. Such an extraction should average over numerous diffusion-limited depletion zones around individual roots, and thus provide an estimate of average ammonium and nitrate levels in soil solution experienced by a root at any given instant. These extracts were taken only on 12 July, 28 July, and 3 August 1988. A 2 cm diameter × 16 cm deep core was taken from a plot, homogenized, and divided into two parts. About two-thirds was added immediately to a vial containing 50 mL of the extractant. This was reweighed, shaken for 0.5 h, settled overnight at 4°C, and the supernatant analyzed for ammonium and nitrate using a Technicon II Autoanalyzer. The remaining one-third was used to determine soil moisture. Concentrations of ammonium and nitrate are expressed as milligrams of N per kilogram of dry soil. The bulk density difference between our poorest soils (N level 1, bulk density of 1.49 g/cm^3) and our richest soils (N level 4, 1.40 g/cm^3) was only 6%, but our nitrogen results could be converted from milligrams per kilogram soil to kilograms per hectare using the observed dependence of bulk density (B) on total soil N (TN) treatment in our plots ($B = 1.509 - 0.000103$ TN, $r^2 = 0.98$) and the 23 cm average depth of the mixed-soil layer. These soils were also sampled with KCl at 2 mol/L in a separate study of N mineralization rates (Wedin and Tilman 1990). Because KCl at 2 mol/L removes all ammonium, including that bound to cation exchange sites, this extractant does not provide a measure of soil solution ammonium, and will not be reported here. However, because nitrate is equally effectively extracted by either method, we report some of the nitrate data here.

Light penetration through the vegetation was measured as photon flux at the soil surface divided by photon flux above the vegetation, using a LI-COR photosynthetically active radiation cosine collector and integrating meter. Light at the soil surface (actually 2.5 cm above because of the thickness of the probe) was integrated over a 10-s period, during which the probe was moved along a 30-cm path. This was done monthly, but we report only data collected at the time of harvest.

Data analysis

Data were analyzed using the General Linear Models (GLM) routine of SAS, running on a Sun Sparc workstation. For some analyses, GLM was used, on a species by species basis, in regressions of a plant trait against total soil N. In designing the experiment, we had hoped that the replicates within a given soil mixture would be statistically independent, and thus could be treated as distinct replicates. We tested this hypothesis by performing regressions using data on a plot by plot basis, with the independent variable being the total soil N (TN) of each plot, or TN and (TN)^2. The quadratic term was included only if its addition explained significantly ($P < .05$ for inclusion) more of the variance in a plant trait than the linear model. We then determined if the addition of soil mixture as a categorical variable (a block) explained significantly more variance than the linear or quadratic model based solely on TN. Because there was a significant soil mixture effect in ≈20% of the analyses, we concluded that the replicates within a given soil mixture were not always statistically independent. Thus, to avoid any chance of pseudoreplication in our analyses (Hurlbert 1984), we have followed a conservative approach throughout this paper. For comparisons involving different soil mixtures, including regressions, we have used the average response of each species within a given soil mixture, and the average total soil N of the plots in which it occurred. We illustrate the extent of within-soil-mixture variance by graphing means with their standard errors.

To allow easier comparisons among species responses than is provided by regression, the 10 soil mixtures were lumped into four different N levels and analyzed using ANOVA and contrasts. N level 1 con-

sisted of the three soil mixtures with the lowest total soil N. N level 2 contained the three soil mixtures with the next three higher total soil N. N level 3 had the soil mixtures with the next three higher total soil N concentrations. N level 4 consisted of the 100% top soil mixture that received additional NH_4NO_3. As before, results for the replicate monocultures of a species within a given soil mixture were averaged before analysis. Contrasts were based on Duncan's multiple-range test. The resulting contrasts are conservative estimates of species differences because of the increased within-level variance that results from combining different soil mixtures and the decreased degrees of freedom resulting from averaging within-soil-mixture replicates. The general linear models technique of SAS was used to allow for the unbalanced design necessitated by the lack of *Agrostis* data on N level 4 (see *Results: Survival*). Because N level 4 consisted of a single soil mixture, replicate plots within it are true replicates. These were used for contrasts within N level 4, but averages were used in all comparisons among N levels, including ANOVAs. Unless otherwise noted, a statistical test will be called significant if a two-tailed test has $.05 \geq P > .01$ and will be called highly significant if a two-tailed test has $P \leq .01$.

Results

Total soil N

The four N levels differed significantly in total soil N. The plots in N level 1 had an average total soil N of 181 ± 10.2 mg/kg ($\bar{X}$ ± SE, $n = 48$); the means for N levels 2–4, respectively, were 464 ± 11.1 mg/kg ($n = 48$), 839 ± 35.2 mg/kg ($n = 48$), and 1060 ± 48.9 mg/kg ($n = 16$; measured before addition of 6.55 $g \cdot m^{-2} \cdot yr^{-1}$ of N as NH_4NO_3). All pairwise comparisons of these means differed significantly ($P < .05$; Duncan's). Based on a regression of 1988 in situ annual N mineralization rates on total soil N in these plots (Wedin 1990), the addition of NH_4NO_3 to N level 4 soils makes them roughly equivalent to a soil with total soil N of 1600 mg/kg.

Survival

All species survived on the most N-poor soil, pure subsurface sand. However, two of the three *Poa* replicates on this soil mixture had poor initial establishment because of poor water sprinkler placement early in the 1st yr, and individual plants were widely spaced and thus difficult to sample with our methods. Data from these two plots are excluded from our analyses. Total plant biomass (aboveground + belowground) was increasingly greater on the more N rich soil mixtures for each species each year (1988 data in Fig. 2A–E). The only exception was *Agrostis,* which had much lower biomass in soil mixtures 9 and 10 in 1988 than in previous years (Fig. 3A). This corresponded with the presence in these plots of a deep layer of *Agrostis* litter in the spring of 1988 and a low density of living *Agrostis* plants, which mainly were in the areas that were harvested in 1986 or 1987 and had less litter. Although this litter feedback effect is interesting and important, the *Agrostis* data from these two soil mixtures are excluded from many of the results presented here (Tables 1–4 and Figs. 4 and 5) because it is impossible to determine morphology when a sample contains no plants. Aboveground biomass of two other species decreased, somewhat, from the 2nd to the 3rd yr of the experiment on N level 4 (Fig. 3A–E), but all species except *Agrostis* were able to grow in the dense litter each produced (Table 1). In the lower N levels, aboveground biomass seemed to have stabilized by the 3rd yr of the experiment (Fig. 3A–E).

Plant traits

These species often differed in their vegetative growth rate, morphology, seed production, accumulated litter mass, and root and shoot N content when compared within an N level (Table 1), and these traits changed in response to total soil N (Fig. 2, Table 1). For all traits except vegetative growth rate, only 1988 data are presented both for brevity and because data collected after 3 yr of growth should better describe species than earlier data.

Morphology changed in response to total soil N, with plants having lower root:shoot ratios (Fig. 2F–J) and a higher proportion of reproductive tissue (Table 1) on more N-rich soils. There were marked differences among species at each N level (Table 1). Two-way ANOVA of each plant trait (such as proportion of root) with species and N level as the factors, revealed significant species and N level effects for all traits except proportion of rhizome (Table 2). Most species × N level interactions were also significant (Table 2). Because of these interactions, contrasts among species means (Table 1) were made within an N level.

Roots.—*Schizachyrium* and *Andropogon* had significantly higher proportions of their biomass in roots than did the other species on N levels 1–3 (Table 1; Fig. 2F–J). *Agrostis, Agropyron,* and *Poa* were similar in their proportion of root, and did not differ significantly at N level 1. For N level 2, *Poa* had a significantly higher proportion of root than *Agrostis* or *Agropyron.* On N level 3, *Agrostis* had a significantly lower proportion of root than either *Agropyron* or *Poa* (Table 1). Proportion root corresponded closely with total root biomass (in grams per square metre). *Schizachyrium* and *Andropogon* had the greatest root biomass on all N levels, *Poa* was intermediate, and *Agrostis* and *Agropyron* had the lowest root mass (also see Fig. 4). Although we sampled these plots only once per year, in a related study, other monocultures on 100% black soil were sampled every 3 wk throughout the growing season to determine patterns of above- and belowground productivity and N use efficiency (Wedin 1990). Comparisons of these two studies indicate that the results

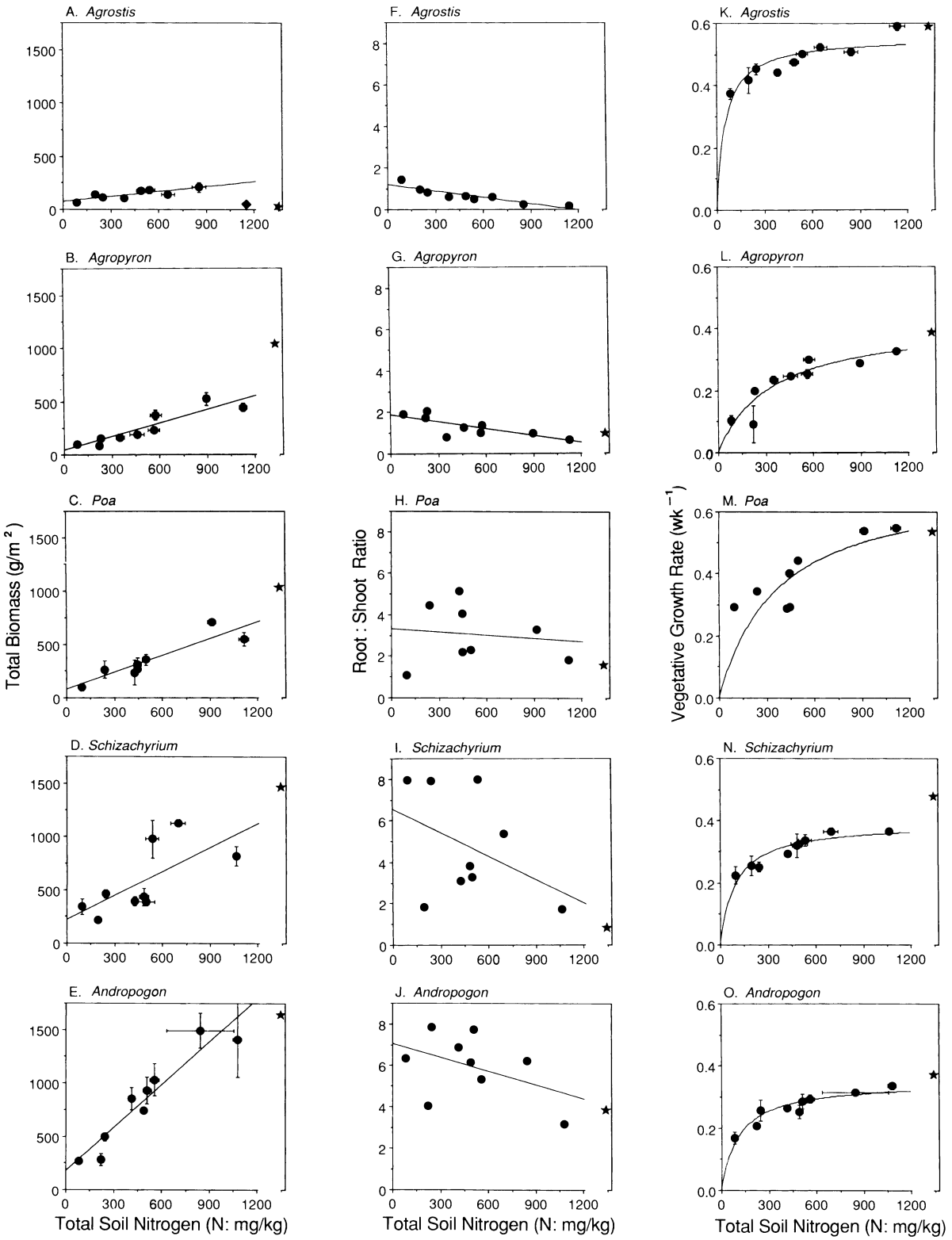

FIG. 2. The dependence on total soil nitrogen of (A–E) 1988 total biomass (aboveground+belowground), (F–J) 1988 root: shoot ratio (nonrhizome root mass to nonreproductive aboveground mass), and (K–O) 1986 vegetative growth rate (wk^{-1}; *dB/Bdt*; for seed to harvest in 1986) for five grass species. Each point represents the mean response for a species in a given soil mixture. (See *Methods: Experimental design and methods.*) Standard errors for the replicate monocultures within each soil mixture are shown for total biomass and for vegetative growth rate, but are not shown for root : shoot ratio because root :

reported here are proportional to species differences in above- and belowground production and allocation patterns. Roots of *Agrostis* had significantly higher tissue N content than those of *Agropyron,* and *Agropyron* roots had more N than *Poa* (Table 1). The roots of these species had significantly higher tissue N than roots of *Schizachyrium* and *Andropogon.*

Rhizomes.—*Agropyron* and *Poa* were the only two species that were rhizomatous in our plots. On average, 47% of the belowground biomass of *Agropyron* and 36% of that of *Poa* was in rhizome (Table 1). *Poa* and *Agropyron* did not differ in their proportion of rhizome on the lowest and highest N levels, but *Agropyron* had a greater proportion of rhizome on the intermediate N levels (Table 1).

Shoot.—Of the five species, *Agrostis* allocated the greatest proportion of its total biomass to shoot (aboveground biomass) on N levels 1–3, and had the highest proportion of leaf and stem (percent shoot minus percent reproductive). In general on N levels 1–3, *Agropyron* had the next greatest shoot allocation, followed by *Poa, Schizachyrium,* and then *Andropogon,* but few of these differences were significant (Table 1). On N level 4, *Schizachyrium* had a significantly greater proportion in shoot than the other species, with *Andropogon* having the least. Shoot mass (in grams per square metre) was less variable among these species than was percent shoot, especially on the low N levels (Fig. 3). *Andropogon* had the lowest proportion shoot on all N levels (Table 1). Comparable patterns were observed in the monocultures sampled every 3rd wk all growing season (Wedin 1990). These species also differed in their aboveground tissue N (Table 1). *Agropyron, Agrostis,* and *Poa* had greater aboveground tissue N than *Schizachyrium* or *Andropogon* on all N levels, but did not differ significantly from each other (Table 1). Likewise, *Schizachyrium* and *Andropogon* did not differ from each other. These midseason tissue concentrations were higher than those observed near the time of senescence (Wedin 1990), but, for the most part, the rankings of the species did not change.

Reproduction.—For N levels 1–3, *Agrostis* allocated the highest proportion of its total biomass to reproduction of these five species, with 40% in reproductive structures (seeds and flowering stems) on N level 3 (Table 1). *Poa* had the next greater reproductive allocation. On N level 4, *Schizachyrium* had a significantly greater reproductive allocation than the other species. In general, reproductive allocation was greater on more N rich soils, but the peak for *Poa* was on N level 2.

Seeds.—The average mass of a seed embryo was 0.082 mg for *Agrostis,* 2.3 mg for *Agropyron,* 0.25 mg for *Poa,* 1.2 mg for *Schizachyrium,* and 1.9 mg for *Andropogon.* On N levels 1–3, *Agrostis* produced a significantly greater number of viable seeds than the other species. This resulted from both its greater allocation to reproduction and its smaller seed size. *Poa,* which produced the next smallest seed, tended to have the next greatest allocation to reproduction, but did not often differ significantly from the other species (Table 1). *Poa* produced the second largest number of seed on N levels 1–3, with most comparisons with other species being significant (Table 1). On N levels 1–3, *Schizachyrium, Andropogon,* and *Agropyron* had low allocation to reproduction, produced few viable seeds, and rarely differed significantly in these traits (Table 1). *Schizachyrium,* though, had a high reproductive allocation and had as high a rate of seed production as *Poa* on N level 4 (Table 1).

Height.—As measured, plant height included the height of flowering stems. *Agrostis* was taller than the other species on N levels 1 and 2, but did not differ from the others on N level 3 (Table 1). *Schizachyrium* was the tallest and *Poa* the shortest on N level 4. This pattern would have been different if leaf heights, but not flowering stem heights, had been measured. Almost all of the leaf mass of *Agrostis* and *Poa* emerges directly from the soil, whereas much of the leaf mass of *Agropyron* and *Andropogon* is held a distance above the soil by stems or pseudostems. *Schizachyrium* is intermediate in this trait.

Accumulated litter.—There were significant species and N level effects on the litter that had accumulated in monocultures by 1988 (Table 2). There were much greater species differences in litter mass than in aboveground biomass on all N levels (Table 1), which is suggestive of species differences in rates of litter decomposition. *Agrostis* litter disappeared rapidly during the growing season, but *Schizachyrium* and *Andropogon* litter seemed to decompose more slowly.

Vegetative growth rates.—During the first growing season, the VGR of each species increased significantly with total soil N (Fig. 2F–J). The maximal observed vegetative growth rate of each species, VGR_{max}, occurred on N level 4 (Table 1). The VGR_{max} of *Agrostis* (0.60 wk^{-1}) and *Poa* did not differ significantly, but both were significantly greater than *Agropyron, Schizachyrium,* and *Andropogon. Schizachyrium* was significantly greater than *Andropogon* and *Agropyron,* which did not differ. *Agrostis* had the highest vegetative growth rate at all N levels, and was generally followed by *Poa, Schizachyrium, Andropogon,* and then *Agropyron.* There was a perfect inverse correlation between the VGR_{max} of these species and the embryo mass of

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shoot ratio was calculated using soil mixture means. (This minimizes bias introduced into ratios by experimental errors.) For comparison, results for soil mixture 10, which received added ammonium nitrate, are shown, off-scale, with a star. Soil mixture 10 results were omitted from regressions, as were results for total biomass in soil mixture 9 for 1988 *Agrostis,* which are shown with a diamond.

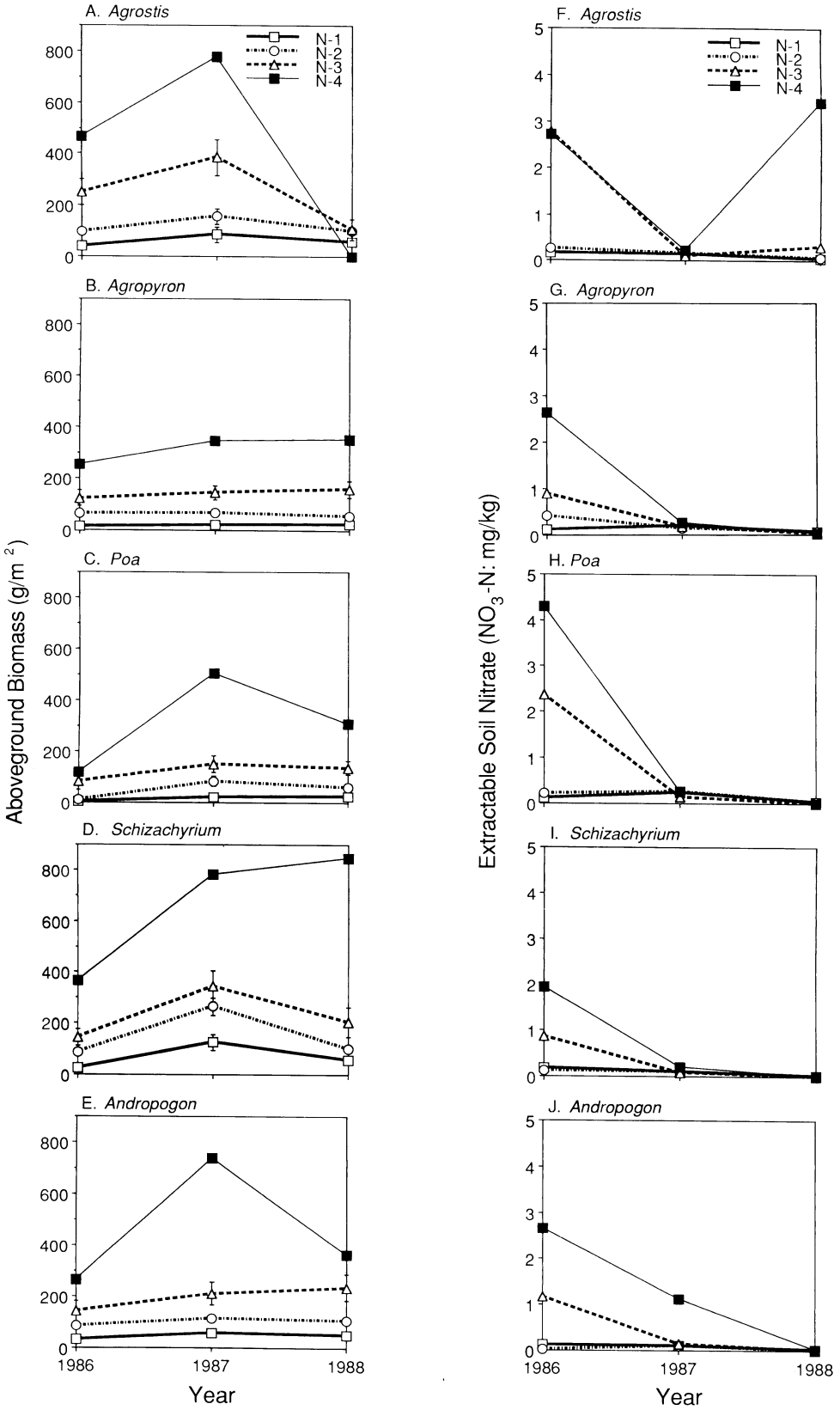

FIG. 3. The dynamics of (A–E) aboveground biomass and (F–J) soil nitrate (as extracted with 2 mol/L KCl during July) for monocultures of each species during the 3 yr of the experiment. Data shown are means for each N level. N level 1, which is the lowest line in all parts of this figure, has an □——□. N level 2: ○-·-·-○. N level 3: △– – –△. N level 4: ■——■.

their seed, with the smallest seeded species, *Agrostis,* having the greatest VGR_{max}.

2 mol/L KCl extractable soil nitrate.—The concentration of 2 mol/L KCl extractable nitrate was greatest immediately after planting and declined throughout the first growing season for all species on all N levels. The July average nitrate concentration in 1986 was significantly higher than that in 1988 for all species on all N levels except for *Agrostis* on N levels 3 and 4 (Fig. 3F–J; ANOVA with Duncan contrasts, $P < .05$). Nitrate increased dramatically following plant death in the *Agrostis* monocultures. Comparable analyses were not performed for ammonium because 2 mol/L KCl removes the ammonium bound to exchange sites, and is thus more a measure of cation exchange capacity than of soil solution concentration.

Differential soil nutrient reduction.—The soil concentrations of 0.01 mol/L KCl extractable nitrate and ammonium were determined on three different dates during the middle of the third growing season. ANOVA of soil nitrate by species, by date, and by N level showed a highly significant species effect, but no significant N level effect or date effect (Table 3). The species × date and species × N level interactions were significant. ANOVA of extractable soil ammonium by species, date, and N level revealed significant species, N level, date, and species × N level effects, but no significant species × date interaction (Table 3). Contrasts using Duncan's multiple-range test revealed that the date effect for ammonium was caused by *Agropyron* and *Agrostis,* which had significantly higher ammonium concentrations on the second and third sampling dates than on the first. We summarize differences among species by averaging over sampling dates because species' rankings are the same on the three dates.

For N level 1, contrasts using Duncan's multiple-range test show that *Agrostis* monocultures had significantly ($P \leq .05$) higher 0.01 mol/L KCl extractable soil nitrate concentrations than monocultures of all other species except *Poa* (Table 4). Monocultures of *Agropyron* and *Poa* did not differ in soil nitrate, but both were significantly higher than *Schizachyrium* and *Andropogon,* which did not differ on N level 1 (Table 4). The same pattern occurred when sampling dates were analyzed separately. Similar contrasts, performed using 0.01 mol/L KCl extractable soil ammonium, showed no significant differences between *Agrostis* and *Agropyron* monocultures on N level 1, but *Agrostis* monoculture soils had significantly more ammonium than *Poa, Schizachyrium,* or *Andropogon* monocultures. *Agropyron* monocultures had significantly greater ammonium concentrations than *Andropogon,* but *Poa, Schizachyrium,* and *Andropogon* monocultures did not differ significantly in soil ammonium (Table 4). A similar pattern occurred when each sampling date was analyzed separately. Monocultures of these species had similar differences in 0.01 mol/L KCl extractable ammonium and nitrate on N levels 2 and 3 (Table 4). *Agrostis* and *Agropyron* monocultures had significantly higher soil nitrate and ammonium than all species except for *Poa* on N level 3. On N level 2, *Poa* had significantly lower average soil nitrate and ammonium than *Agropyron.* However, this difference was not detectable on any individual sampling date. *Schizachyrium* and *Andropogon* had significantly lower nitrate and ammonium levels than either *Agrostis* or *Agropyron* on N levels 2 and 3. There were no significant differences among species on N level 4.

Thus, there were statistically significant, repeatable differences in the levels to which monocultures of these five species reduced the soil concentrations of ammonium and nitrate on nitrogen-poor soils. The 2 mol/L KCl extracts that were taken monthly (eight times) during the 1988 growing season provide another test of differences in the pattern of nutrient reduction by these species. On N levels 1 and 2, the ranking of the species by their seasonal average 2 mol/L KCl extractable nitrate concentration was identical to the ranking by their 0.01 mol/L KCl extractable nitrate concentrations. The patterns on N level 3 were also identical except that *Schizachyrium* (seasonal average 2 mol/L KCl extractable soil NO_3-N of 0.02 mg/kg) and *Andropogon* (seasonal average 2 mol/L KCl NO_3-N of 0.03 mg/kg) were reversed. Thus, the available evidence demonstrates that these species differed in their abilities to reduce soil solution concentrations of the limiting nutrient on low nitrogen soils.

Root biomass and nitrate reduction.—When data for all five species, across all 10 soil mixtures, were considered together, soil nitrate (0.01 mol/L KCl extractable, averaged over all dates for all replicates of a species in a given soil mixture) was inversely correlated with root biomass (also the species average for each soil mixture), with 72% of the total variance in soil nitrate-N being explained by root biomass (Fig. 4A; $r^2 = 0.72$, $df = 45$, $P < .01$ for correlation between NO_3-N and 1/[root mass]). A log-log plot of nitrate against root mass linearized the relationship and explained 73% of the variance (Fig. 4B; $r^2 = 0.73$, $df = 45$, $P < .01$). In a multiple regression that included root mass, species identity and total soil N as variables, species density explained only an additional 9.2% of the variance after root mass ($F = 7.11$, $P < .05$ for the addition of species to the regression) and total soil N explained 5% ($F = 9.98$, $P < .05$ for inclusion after root mass and species). Nitrate was higher in plots with higher total soil N. These three variables explained, in total, 87% of the variance observed in soil nitrate concentrations across all species and all soil mixtures, with most of the variance explained by root mass.

Ammonium reduction.—The relationships between the soil-mixture-average extractable ammonium of each species and root mass, species identity, and total soil N were different than for nitrate. Using log-log plots to linearize data, a multiple regression of extractable ammonium on root mass, species, and total soil N had

TABLE 1. Plant traits in the monoculture plots of the four N levels. All data are for the 1988 harvest (3rd yr of growth) except that vegetative growth rate (VGR) is based on growth during the 1st yr. Within an N level, species that share a superscript letter do not differ significantly ($P > .05$; Duncan multiple-range test) for that particular trait.

	Proportion of plant total dry mass						
	Root	Rhizome	Reproduction	Shoot	VGR (wk^{-1})	Seed/m^2* (viable)	Height (cm)
N level 1:							
Agrostis	0.48[b]	0.0†	0.10[a]	0.52[a]	0.41[a]	12 533[a]	21.3[a]
Agropyron	0.45[b]	0.27[a]	0.00[b]	0.28[a,b]	0.13[d]	11[b]	13.6[b]
Poa	0.34[b]	0.21[a]	0.02[b]	0.44[a,b]	0.32[b]	1030[b]	10.2[b,c]
Schizachyrium	0.79[a]	0.0†	0.01[b]	0.21[a,b]	0.24[b,c]	143[b]	8.00[c]
Andropogon	0.85[a]	0.0†	0.00[b]	0.15[b]	0.21[c,d]	6[b]	10.00[b,c]
N level 2:							
Agrostis	0.35[d]	0.00†	0.14[a]	0.65[a]	0.47[a]	21 252[a]	19.6[a]
Agropyron	0.30[d]	0.39[a]	0.00[b]	0.31[b]	0.25[b]	24[c]	17.3[b]
Poa	0.50[c]	0.27[b]	0.07[a]	0.23[c]	0.29[b]	3490[a,b]	13.6[c]
Schizachyrium	0.75[b]	0.00†	0.02[b]	0.25[c]	0.31[b]	309[b]	14.0[c]
Andropogon	0.87[a]	0.00†	0.00[b]	0.13[d]	0.27[b]	32[c]	14.0[c]
N level 3:							
Agrostis	0.22[c]	0.00†	0.40[a]	0.78[a]	0.52[a]	56 034[a]	23.6[a]
Agropyron	0.34[b,c]	0.30[a]	0.00[b]	0.36[b]	0.30[b]	31[d]	25.8[a]
Poa	0.51[b]	0.22[b]	0.05[b]	0.27[b]	0.50[a]	5507[b]	20.5[a]
Schizachyrium	0.77[a]	0.00†	0.02[b]	0.23[b]	0.35[b]	338[c]	20.0[a]
Andropogon	0.82[a]	0.00†	0.00[b]	0.18[b]	0.31[b]	30[d]	22.7[a]
N level 4:‡							
Agropyron	0.34[b]	0.32[a]	0.00[b]	0.34[b]	0.37[c]	63[c]	35.8[b,c]
Poa	0.44[b]	0.28[a]	0.02[b]	0.28[b,c]	0.53[a]	3921[a]	29.3[c]
Schizachyrium	0.42[b]	0.00†	0.14[a]	0.58[a]	0.46[b]	3190[a]	53.5[a]
Andropogon	0.78[a]	0.00†	0.03[b]	0.22[c]	0.37[c]	457[b]	39.0[b]

* Contrasts for viable seed were based on log (seed density + 1), but actual seed densities are shown below.
† Not measured.
‡ Note that *Agrostis* is omitted from N level 4 (see *Results: Survival*).
§ All aboveground biomass.

$r^2 = 0.80$. Most of the variance in ammonium was explained by total N ($r^2 = 0.54$, $F = 53.3$, $P < .05$). After inclusion of total N, root biomass explained an additional 12.6% ($F = 16.8$, $P < .05$), and species an additional 13.4% of the variance in ammonium ($F = 6.83$, $P < .05$). Ammonium concentrations were higher in plots with higher total soil N, and lower in plots with higher root biomass.

Light reduction.—The proportion of incident light that reached the soil surface differed among species and N levels (Table 4). Higher N levels, which had greater aboveground biomass, also had lower penetration of light to the soil surface. Less light reached the soil surface in *Agrostis* monocultures than in monocultures of the other four species for N levels 1 and 2. For N level 3, *Andropogon* had significantly lower light penetration than *Agropyron, Agrostis,* or *Poa,* but did not differ from *Schizachyrium* (Table 4). On N level 4, *Andropogon, Poa* and *Schizachyrium* had significantly lower light penetration than *Agropyron,* but did not differ from each other. When the replicates of a species within each soil mixture were averaged, and data for all five species were pooled (as for Fig. 4), the proportion of incident light that penetrated to the soil surface was a significantly negative function of total aboveground biomass of the monocultures. The relationship was improved by using the natural logarithm of light penetration ($r^2 = 0.79$, $P < .05$, $n = 48$; Fig. 5). By itself, species identity had no significant effect on light penetration (ANOVA: $F = 0.63$, $P = .64$), and only explained 2% of the variance ($F = 1.12$, $P > .1$) in a multiple regression that included aboveground biomass.

Nitrogen and light isoclines.—The data in Table 4 can be used to construct resource-dependent zero net growth isoclines for each species (Tilman 1982, 1988) by graphing the sum of soil ammonium and nitrate against light at the soil surface. Inspection of these data (Table 4) shows that the isocline for each species is curved, indicating that a decline in light at the soil surface is associated with an increase in soil nitrate plus ammonium, and vice versa.

DISCUSSION

Plant traits, total plant biomass, and soil nutrient levels seemed to have stabilized by the 3rd yr of growth. At that time, the monocultures of our five species differed in their abilities to reduce the concentrations of extractable soil ammonium and nitrate and light penetration to the soil surface (Table 4). Curved resource-dependent isoclines and the changes in each species' root and shoot allocation patterns along the nitrogen

TABLE 1. Continued.

Shoot nitrogen (%)	Root nitrogen (%)	Litter mass (g/m^2)	Shoot mass§ (g/m^2)	Root mass (g/m^2)
1.17[a]	1.24[a]	3.99[a]	56.0[a]	47.7[b]
1.43[a]	1.11[a]	8.89[a]	26.4[a]	50.1[b]
1.20[b]	0.78[b]	27.8[a]	37.8[a]	90.4[b]
0.68[c]	0.45[c]	19.2[a]	58.3[a]	280[a]
0.59[b]	0.49[c]	28.4[a]	49.7[a]	299[a]
1.30[a]	1.28[a]	47.9[c]	102[a]	51.1[d]
1.36[a,b]	0.97[a]	40.1[c]	58.4[b]	59.2[d]
1.19[b]	0.73[b]	60[bc]	59.3[b]	149[c]
0.61[c]	0.34[d]	87[b]	99.2[a]	303[b]
0.61[c]	0.44[c]	143[a]	107[a]	735[a]
1.16[a]	1.13[a]	78.4[b]	140[a]	34.3[b]
1.21[a]	0.96[b]	130[b]	161[a]	148[b]
1.11[a]	0.75[c]	170[b]	136[a]	275[b]
0.63[b]	0.39[d]	154[b]	205[a]	770[a]
0.63[b]	0.45[d]	443[a]	237[a]	1074[a]
1.34[ab]	1.16[a]	346[c]	353[a]	348.3[b]
1.61[a]	0.91[b]	527[c]	308[a]	466[b]
1.11[bc]	0.65[c]	1208[a]	844[b]	617[b]
1.02[c]	0.66[c]	871[b]	364[a]	1282[a]

gradient (Fig. 2, Table 1) are consistent with the hypothesis that each species is modifying its morphology so as to forage "optimally" for nutrients and light (Bloom et al. 1985, Tilman 1988).

Schizachyrium and *Andropogon* monocultures, which had the lowest soil concentrations of ammonium and nitrate on the three lowest N levels (Table 4), had the greatest root biomass, the greatest proportion of their biomass in roots, and the lowest root and shoot N concentrations. They also had the lowest proportion of their biomass in both seed and vegetative (rhizome) reproduction, and low vegetative growth rates. On these low N soils, *Agrostis* monocultures had the highest soil nitrate and ammonium concentrations, the lowest root mass per square metre, low proportions of biomass in roots, and the highest in seed. *Agropyron* and *Poa,* which generally had the next highest soil nitrate and ammonium concentrations, had the highest proportion of their biomass in rhizome, but a low proportion in seed on low N soils. Thus, for this group of five successional grasses, the concentration to which each species reduced soil ammonium and nitrate was related to its tissue N and its pattern of allocation to root, rhizome, seed, and shoot. Moreover, there was an inverse relation between root biomass and monoculture nitrate concentrations (Fig. 4). This is analogous to the well known relationship between aboveground biomass and light reduction (Beer's Law; Fig. 5) that is frequently invoked as a mechanism of plant competition. This suggests that interspecific differences in root mass may be just as important an aspect of nutrient competition as differences in leaf mass are for light competition. Clearly, though, nutrient use efficiency, litter quality, the physiology, morphology, and spatial patterning of roots, and other plant traits also contribute to monoculture nutrient reduction (Tilman 1990) and may be correlated with root mass for our species.

Chapin (1980) found that species of infertile habitats have a high proportion of their biomass in roots, low maximal growth rates, long-lived leaves, and low rates of reproduction. The association between such traits and soil infertility led Grime (1979), Chapin (1980), and others to suggest that these traits allow such species to tolerate the stress of low nutrient availability. In contrast, Tilman (1976, 1982) suggested that the most

TABLE 2. *F* values and significance levels for two-way ANOVA of data presented in Table 1 and Fig. 2. ANOVA based on the General Linear Models approach of SAS, which adjusts for the missing *Agrostis* data on N level 4.

Plant traits	Source of variation†		
	Species	N level	Species × N level
Root (proportion‡)	51.6***	2.86[ns]	2.80[ns]
Rhizome (proportion‡)	54.15***	0.95[ns]	0.47[ns]
Reproductive (proportion‡)	26.99***	5.24**	4.42***
Shoot (proportion‡)	21.55***	1.48**	1.60[ns]
Vegetative growth rate	25.50***	22.2***	1.17[ns]
Viable seeds	37.55***	8.33***	0.9[ns]
Plant height	8.92***	94.7***	4.35***
Shoot nitrogen (%)	115.2***	21.14***	2.94**
Root nitrogen (%)	81.75***	8.47**	0.33[ns]
Total biomass	47.35***	95.37***	4.97***
Aboveground biomass	17.31***	101.9***	7.77***
Reproductive biomass	152.1***	162.4***	77.86***
Root biomass	61.68***	29.09***	5.77***
Litter biomass	33.31***	190.4***	15.07***

[ns] = $P > .05$; * $.05 \geq P > .01$; ** $.01 \geq P > .001$; *** $P \leq .001$ (ANOVA *F* values).

† There are five species and four N levels. For species effects, df = 4, 29; for N level effects, df = 3, 29; for the species × N level interaction, df= 11, 29.

‡ Plant part as proportion of plant total dry mass.

TABLE 3. F values for three-way ANOVA of soil solution nitrate and ammonium on species, N level, and date. ANOVA performed using General Linear Models approach of SAS, which adjusted for missing *Agrostis* data on N level 4. The data used were from the 0.01 mol/L KCl extracts taken on three different dates during mid-growing season of 1988.

	Source of variation				
Nutrient	Species F value	N level F value	Date F value	Species × date F value	Species × N level F value
NO_3	59.2***	0.38 ns	2.55 ns	3.34**	3.27***
NH_4	35.9***	229***	27.6***	1.98 ns	4.44***

ns = $P > .05$; * $.05 \geq P > .01$; ** $.01 \geq P > .001$; *** $P \leq .0001$.
† For species effects, df = 4, 69; for N level effects, df = 3, 69; and for date effects, df = 2, 69. For species × date interactions, df = 8, 69; and for species × N level interactions, df = 11, 69.

important determinant of the nutrient competitive ability of a species is the concentration (called R^*) to which the limiting nutrient is reduced in a steady-state, nutrient-limited monoculture. This theory predicted that infertile habitats should be dominated by species with the lowest R^*.

Tilman (1990) tried to reconcile these different perspectives by determining the theoretical relationship between plant traits, resource reduction, and competitive ability. For a model in which plant species differed in allocation to roots and shoots, in tissue nutrient concentrations, in maximal growth rates and maximal rates of nutrient uptake, in longevity of roots and leaves, and in rates of herbivory, the best nutrient competitor was the species with the lowest R^*. This species had high root allocation, low allocation to reproduction, low tissue nutrient concentration, long-lived leaves and roots, efficient nutrient conservation mechanisms, a low maximal growth rate, and low susceptibility to herbivory. Thus, the traits associated with plants of infertile habitats (e.g., Chapin 1980, Vitousek 1982, Coley et al. 1985, Berendse and Elberse 1990) are the same traits predicted, in theory, to lead to the greatest reduction of a limiting soil nutrient by a species when growing in monoculture.

When plants compete for nutrients, resource reduction is the immediate mechanism whereby one plant inhibits another. Plant morphological and physiological traits that allow one species to have a lower R^* than another represent the next level of mechanistic detail. Although the former level of mechanistic detail has been emphasized by models of resource competition, and the latter by ecophysiological studies, our results suggest that they may be wholly compatible. Specifically, the traits that Chapin found to be associated with infertile habitats are the same traits associated with low concentrations of soil ammonium and nitrate in our monocultures (Tables 1 and 4). This lends further support to Chapin (1980). Moreover, it suggests that R^* may be a summary variable that integrates the effects of numerous traits on a plant's ability to survive and compete in nutrient-poor habitats. Although our monocultures may not have reached a true population steady state after just 3 yr of growth, the differential nutrient reduction we observed should be indicative of interspecific differences in R^* values. Competition experiments, performed using various pairs of the five species discussed in this paper (Wedin 1990, Tilman and Wedin 1990), show that the superior competitors on nitrogen-poor soils are, in general, the species that

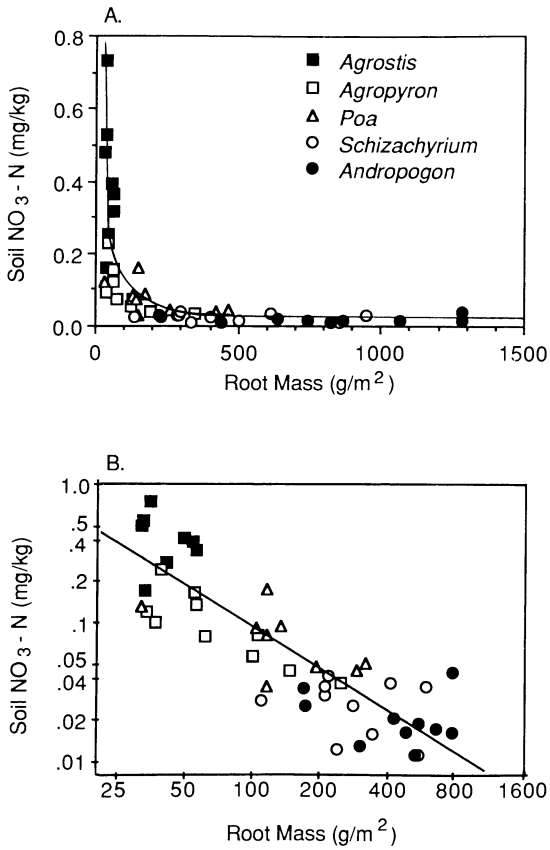

FIG. 4. The dependence of extractable soil nitrate (0.01 mol/L KCl extractant) on root mass. (A) Data graphed on linear scales. Note that each species has its own symbol. The curve shown is a nonlinear least squares fit of nitrate-N vs. 1/(root mass). Each point is the mean over all three 1988 sampling dates of nitrate for a given species averaged over all replicate monocultures of that species in a given soil mixture. Root mass was similarly averaged, but was determined only once per plot in 1988. (B) These same data are graphed on a log–log plot, using natural logarithms. The curve is a least squares regression.

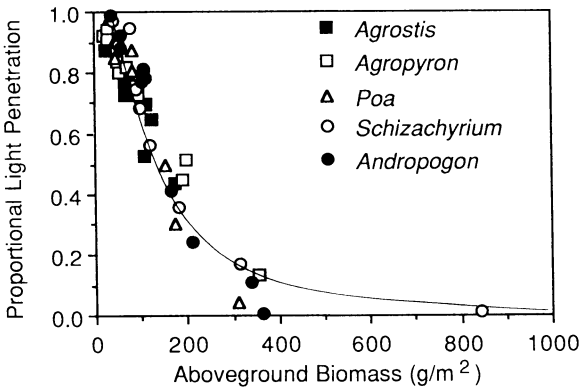

FIG. 5. The proportion of incident light that reached the soil surface is graphed against aboveground biomass. Each point represents average light penetration through the replicate monocultures of a species on a soil mixture and the average aboveground biomass of that species on that soil mixture, using 1988 data. The fitted curve shown is based on nonlinear regression of light penetration (y) on aboveground biomass (x), fitted to $y = a(e^{-bx})$. $R^2 = 0.79$.

reduce nitrate to significantly lower levels in monoculture. Thus, there may be a direct link between morphology, physiology, nutrient reduction, and competitive ability. Additional work, however, will be needed to determine if similar patterns occur when other groups of plant species are compared, the extent to which our results may depend on physiological differences between our C_3 and C_4 species, and the relative importance of root mass, root physiology, nutrient use efficiency, and other traits in determining R^* values.

All five of our species were tolerant of "nutrient stress," i.e., all survived, in monoculture, on even our most N poor soils, which had total soil N of about 100 mg/kg. This is lower than any of the 2200 soil samples analyzed in a survey of CCNHA fields (Inouye et al. 1987), and lower than any reported in a review of soils of Russia (Bowen 1979). Although all species tolerated low N conditions, their different abilities to reduce the concentrations of ammonium and nitrate on low N soils (Table 4) may influence which species dominate low N soils in nature. Thus, competitive ability, as measured by R^*, may be more important than tolerance. Grubb (1985) also questioned the utility of the tolerance concept, citing the lack of a correspondence between the tolerance of species and their natural distributions, and plants' absolute requirements for some conditions rather than mere tolerance of them.

The two species with the lowest R^* values for soil nitrogen, *Schizachyrium* and *Andropogon*, are both C_4 bunchgrasses with low tissue N concentrations, even for C_4 grasses (Andrew and Johansen 1978, Brown 1978, Field and Mooney 1986). Both have extensive root systems, with ≈80% of their total biomass in roots on low N soils. Although roots of a *Schizachyrium* bunch extend 50 cm or more from its center, the aboveground vegetative parts extend out only 5 to 10 cm at its base (Tilman 1989). Allocation to rhizome is minimal because aboveground parts are tightly packed. Because rhizomes do not function as root, and are not photosynthetic, the bunchgrass morphology allows a plant to allocate a higher proportion of its biomass to both root and leaf than is possible for a rhizomatous plant. Root and leaf allocation is also increased in *Schizachyrium* and *Andropogon* by their low allocation to seed on low nitrogen soils. Thus, the two species that are most effective in reducing 0.01 mol/L KCl extractable soil ammonium and nitrate concentrations achieve this, in part, by having low allocation to vegetative spread and sexual reproduction, and high allocation to root. Bunchgrasses with high root allocation and low tissue N (both C_3 and C_4 species) are common in infertile grasslands around the world. The roots produced by our bunchgrasses are low in nitrogen (Table 1), and thus may have low maximal rates of nutrient uptake, much as low nitrogen leaves have low maximal photosynthetic rates (Field and Mooney 1986). These species produce an extensive, but nitrogen-cheap, root system, which may increase a plant's ability to capture

TABLE 4. Concentrations of nitrate and ammonium in 0.01 mol/L KCl extracts of monoculture soils using averages over three mid-growing-season dates, and proportional penetration of incident light to the soil surface. All concentrations are expressed per unit mass of dry soil.*

Species	Soil nitrate-N (mg/kg)	Soil ammonium-N (mg/kg)	Light penetration (proportion)
N level 1:			
Agrostis	0.24[a]	0.09[a]	0.81[b]
Agropyron	0.12[b]	0.06[b]	0.92[a]
Poa	0.14[ab]	0.03[b,c]	0.96[a]
Schizachyrium	0.03[c]	0.03[b,c]	0.94[a]
Andropogon	0.02[c]	0.02[c]	0.93[a]
N level 2:			
Agrostis	0.50[a]	0.22[a]	0.69[d]
Agropyron	0.14[b]	0.19[a]	0.82[ab]
Poa	0.07[b]	0.05[b]	0.88[a]
Schizachyrium	0.02[c]	0.05[b]	0.75[cd]
Andropogon	0.01[c]	0.06[b]	0.79[bc]
N level 3:			
Agrostis	0.50[a]	0.34[a]	0.48[ab]
Agropyron	0.05[b]	0.33[a]	0.57[a]
Poa	0.05[b]	0.16[a,b]	0.53[ab]
Schizachyrium	0.02[c]	0.12[b]	0.37[bc]
Andropogon	0.02[c]	0.14[b]	0.25[c]
N level 4:			
Agropyron	0.03[a]	0.81[a]	0.14[a]
Poa	0.05[a]	0.45[a]	0.05[b]
Schizachyrium	0.03[a]	0.53[a]	0.01[b]
Andropogon	0.04[a]	0.55[a]	0.007[b]

* Duncan multiple-range tests were used to determine if the five species differed significantly within each of the four N levels. All data were transformed (natural logarithm) before analysis to attain homogeneous variance. Means are based on untransformed data. Species that did not differ significantly ($P > .05$) share a common superscript letter.

nitrogen at low concentrations (Nye and Tinker 1977, Barber 1984, Caldwell and Richards 1986). They also have extensive mycorrhizal symbionts.

Many of the roots of *Schizachyrium* and *Andropogon* are more lignified and apparently more long lived than those of *Agrostis* (Wedin 1990). The production of evergreen leaves is an important mechanism for nutrient conservation by plants of infertile habitats (e.g., Berendse et al. 1987). Similarly, the production of a permanent, long-lived root system would conserve nutrients by minimizing nutrient loss from the shedding of roots, and should thus lead to a lower R^* for nitrogen.

Our five grasses are among the most abundant species during succession on the nitrogen-poor, sandy soils of CCNHA (Fig. 1), and are differentiated in the time during succession when each attains peak abundance. The soils of newly abandoned fields at CCNHA have, on average, a total soil N of ≈330 mg/kg (Inouye et al. 1987), which is between that of N level 1 and N level 2. On N level 2 soils, *Agrostis,* an early successional species, has the greatest allocation to seed of the five species (Table 1). *Agropyron,* the other early successional species, has the greatest allocation to rhizome. High allocation to seed or rhizome should allow these species to rapidly colonize and spread across newly abandoned fields. *Agrostis* and *Agropyron* are good colonists, being present in most 1-yr-old fields (Fig. 1). However, *Agrostis* and *Agropyron* also have the highest R^* values for N of these five species, and thus are predicted to be poor competitors for N. Conversely, *Schizachyrium* and *Andropogon* have the lowest R^* values for N and are predicted to be the best N competitors, but should be poor colonists because of low allocation to seed and rhizome. Indeed, they rarely colonize fields before 10–18 yr postabandonment (Fig. 1). Once in a field, both spread slowly through it. This trade-off between predicted competitive ability vs. expected colonization ability could explain the successional sequence at CCNHA, with succession proceeding from dominance by good colonists that are poor N competitors to dominance by good N competitors that are poor colonists (Platt 1975).

These grasses also differed in their responses when N was added to old-field vegetation (Tilman 1987, 1988). *Schizachyrium,* which dominated unfertilized regions of a 25- and a 48-yr-old field at CCNHA, was displaced (mainly by *Poa* and *Agropyron*) from plots that received high rates of N addition. This is consistent with *Schizachyrium* being a superior N competitor, but an inferior competitor for another resource (such as light) that became limiting on N-rich soils. Just such a reversal in competitive ability along a N gradient was reported by McGraw and Chapin (1989) for a circumpolar tussock-forming sedge (the superior N competitor) and a stoloniferous sedge (the superior competitor on fertile sites). *Poa,* which is intermediate in its R^* for nitrogen, reached peak abundance at intermediate rates of N addition at CCNHA (Tilman 1988). *Agropyron* was rare in low N control plots, dominated high N plots, but may be inhibited in some high N plots by invading woody plants.

The decline in the abundance of *Schizachyrium* and *Andropogon* following experimental N addition raises the possibility that increased rates of atmospheric N addition (e.g., acid rain) may cause a decline in those native bunchgrass species with high root mass and low tissue N and an increase in introduced pasture species in native grasslands. In the heathlands of northern Europe, N-conserving evergreen heath plants (*Calluna vulgaris* and *Erica tetralix*) are already being replaced by grasses and trees, in part because of high rates of deposition of N of anthropogenic origin (Berendse et al. 1987, 1988, Aerts and Berendse 1988).

Conclusions

These five grasses have significant differences in their abilities to reduce the soil solution concentration of ammonium and nitrate, to intercept light, and to reproduce via seeds and rhizomes. These differences are related to their morphologies (and, presumably, physiologies). The species with the greatest root biomass and the lowest root and shoot N concentrations reduced soil ammonium and nitrate to a lower level than other species. Comparably, species with the greatest aboveground biomass intercepted the most light. In contrast, early successional species had high allocation to seeds or rhizomes, did not reduce soil solution N concentrations to low levels, but had greater colonization abilities. These relationships are consistent with both the plant ecophysiological perspective (e.g., Mooney 1972, Chapin 1980, Field and Mooney 1986, McGraw and Chapin 1989) and resource competition theory (Tilman 1982, 1988, 1989). This suggests that the main difference between these approaches is not conceptual, but the level of mechanistic detail being sought.

For species with low allocation to sexual and vegetative reproduction, the pattern of allocation to root versus leaf or stem should, in theory, determine where on a soil fertility gradient the species attains its greatest competitive ability. The allocation pattern of each such species could allow it to have a point on a nitrogen : light gradient at which it is a superior competitor for both N and light. At this point, it would produce both more belowground and more aboveground biomass than its competitors (Tilman 1988), but would be displaced from other points along the gradient by species with different allocation patterns.

Differential resource reduction is a critical assumption of resource competition theory (e.g., O'Brien 1974, Tilman 1976, 1982, 1990, Hsu et al. 1977). Local resource reduction is an important mechanism whereby one plant may influence the growth of a neighboring plant (e.g., Goldberg 1987, Pacala 1987). The results presented here thus allow prediction of the outcome of N competition among these five species. We report tests of these predictions in additional papers.

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LITERATURE CITED

Aerts, R., and F. Berendse. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. Vegetatio **76**:63–69.

Andrew, C. S., and C. Johansen. 1978. Differences between pasture species in their requirements for nitrogen and phosphorous. Pages 111–127 *in* J. R. Wilson, editor. Plant relations in pastures. Commonwealth Scientific and Industrial Research Organization. East Melbourne, Australia.

Austin, M. P., and B. O. Austin. 1980. Behaviour of experimental plant communities along a nutrient gradient. Journal of Ecology **68**:891–918.

Barber, S. 1984. Soil nutrient bioavailability: a mechanistic approach. John Wiley & Sons, New York, New York, USA.

Beadle, N. C. W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology **47**:992–1007.

Berendse, F., and W. Th. Elberse. 1990. Competition and nutrient availability in heathland and grassland ecosystems. Pages 93–116 *in* J. Grace and D. Tilman, editors. Perspectives on plant competition, Academic Press, New York, New York, USA.

Berendse, F., C. Laurijsen, and P. Okkerman. 1988. The acidifying effect of ammonia volatilized from farm-manure on forest soils. Ecological Bulletins-NFR **39**:136–138.

Berendse, F., H. Oudhof, and J. Bol. 1987. A comparative study on nutrient cycling in wet heathland ecosystems. Oecologia (Berlin) **74**:174–184.

Bloom, A. J., F. S. Chapin, III, and H. A. Mooney. 1985. Resource limitation in plants: an economic analogy. Annual Review of Ecology and Systematics **16**:363–392.

Bowen, H. 1979. Environmental chemistry of the elements. Academic Press, London, England.

Bradshaw, A., R. Lodge, D. Jowett, and M. Chadwick. 1958. Experimental investigations into the mineral nutrition of several grass species. I. Calcium level. Journal of Ecology **46**:749–757.

Bradshaw, A., M. Chadwick, D. Jowett, R. Lodge, and R. Snaydon. 1960. Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. Journal of Ecology **48**:631–637.

Bradshaw, A., M. Chadwick, D. Jowett, and R. Snaydon. 1964. Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. Journal of Ecology **52**:665–676.

Brown, R. H. 1978. A difference in nitrogen-use-efficiency in C_3 and C_4 plants and its implication in adaptation and evolution. Crop Science **18**:93–98.

Caldwell, M., and J. Richards. 1986. Competing root systems: morphology and models of absorption. Pages 251–273 *in* T. J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, England.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233–260.

Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. Science **230**:895–899.

Ellenberg, H. 1953. Physiologisches und okologisches Verhalten derselben Pflanzenarten. Berichte der Deutschen Botanischen Gesellntaft **65**:351–362.

Field, C., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25–55 *in* T. J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, England.

Goldberg, D. 1987. Neighborhood competition in an old-field plant community. Ecology **68**:1211–1223.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester, England.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**:107–145.

———. 1985. Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. Pages 595–621 *in* J. White, editor. The population structure of vegetation. Dr. W. Junk, Dordrecht, The Netherlands.

Hsu, S. B., S. P. Hubbell, and P. Waltman. 1977. A mathematical theory for single-nutrient competition in continuous cultures of microorganisms. SIAM Journal of Applied Mathematics **32**:366–383.

Hurlbert, Stuart H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187–211.

Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. Ecology **68**:12–26.

McGraw, J., and F. S. Chapin, III. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. Ecology **70**:736–749.

Milton, W. 1947. The yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. I. Yield and botanical section. Journal of Ecology **56**:65–89.

Monk, C. D. 1966*a*. Ecological significance of evergreenness. Ecology **47**:504–505.

———. 1966*b*. Ecological importance of root/shoot ratios. Bulletin of the Torrey Botanical Club **93**:402–406.

Mooney, H. A. 1972. The carbon balance of plants. Annual Review of Ecology and Systematics **3**:315–346.

Moore, P. 1980. The advantages of being evergreen. Nature **285**:1168.

Nye, P. H., and P. B. Tinker. 1977. Solute movement in the soil–root system. University of California Press, Berkeley, California, USA.

O'Brien, W. J. 1974. The dynamics of nutrient limitation of phytoplankton algae: a model reconsidered. Ecology **55**: 135–141.

Pacala, S. W. 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. Theoretical Population Biology **31**.

Pastor, J., M. A. Stillwell, and D. Tilman. 1987. Nitrogen mineralization and nitrification in four Minnesota old fields. Oecologia (Berlin) **71**:481–485.

Pigott, C. D., and K. Taylor. 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. Journal of Ecology **52**:175–185.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger mounds in a tall-grass prairie. Ecological Monographs **45**:285–305.

Snaydon, R. W. 1962. Micro-distribution of *Trifolium repens* L. and its relation to soils factors. Journal of Ecology **50**:133–143.

Thurston, J. 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the

yield of hay. Pages 3–10 *in* I. Rorison, editor. Ecological aspects of the mineral nutrition of plants. Blackwell, Oxford, England.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen experimental confirmation of resource-based competition theory. Science **192**:463–465.

———. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

———. 1984. Plant dominance along an experimental nutrient gradient. Ecology **65**:1445–1453.

———. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**:189–214.

———. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

———. 1989. Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass. Functional Ecology **3**:215–219.

———. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117–141 *in* J. Grace and D. Tilman, editors. Perspectives on plant competition, Academic Press, New York, New York, USA.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. Ecology, *in press.*

Van den Bergh, J. P. 1968. An analysis of yields of grasses in mixed and pure stands. Verslagen van Landbouwkundigen Onderzoekingen **714**:1–71.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist **119**:553–572.

Vitousek, P. M., and P. S. White. 1981. Process studies in succession. Pp. 267–276 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession—concepts and application. Springer-Verlag, New York, New York, USA.

Weaver, J. E. 1958. Summary and interpretation of underground development in natural grassland communities. Ecological Monographs **28**:55–78.

Wedin, D. 1990. Nitrogen cycling and competition among grass species. Dissertation. University of Minnesota, Minneapolis, Minnesota, USA.

Wedin, D., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia (Berlin) **84**: 433–441.