

NITROGEN-LIMITED GROWTH IN PLANTS FROM DIFFERENT SUCCESSIONAL STAGES¹

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Abstract. The effect of nitrogen availability on plant growth was studied using nine plant species, some of which are commonly found in recently abandoned old fields while others are more characteristic of native prairie. Each species was grown by itself in nine different soil mixtures in which total soil nitrogen (as N) per unit soil mass ranged from 20 to 850 mg/kg, spanning the range of total soil nitrogen observed in a chronosequence of old fields at Cedar Creek Natural History Area, Minnesota. For each species there was a significant ($P < .05$), positive correlation between the biomass attained after 12 wk of growth and the total soil nitrogen. These data allowed the species to be ranked, from those that attained the greatest biomass as seedlings at low nitrogen levels to those that attained the least, as follows: *Ambrosia artemisiifolia*, *Achillea millefolium*, *Chenopodium album*, *Agropyron repens*, *Agrostis scabra*, *Poa pratensis*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Liatris aspera*. There was a highly significant tendency for early successional species to grow more rapidly at low nitrogen levels and to acquire more nitrogen per plant from nitrogen-poor soils than late successional species. However, late successional species did not grow more rapidly at high nitrogen levels than early successional species. These results are consistent with the hypothesis that early successional species are dominant following old field abandonment at Cedar Creek because of their ability to compete for soil nitrogen.

Key words: Cedar Creek Natural History Area; Minnesota; nitrogen-limited growth; old fields; plant heights; prairie; succession; terrestrial plants; tissue nitrogen.

INTRODUCTION

Many studies have suggested that the availability of such soil resources as nitrogen, water, and phosphorus may influence successional dynamics (Olson 1958, Rice et al. 1960, Lloyd and Pigott 1967, Walker et al. 1981). In addition, soil resources are known to influence community structure. For instance, fertilization can lead to dramatic shifts in the species composition and diversity of plant communities (Milton 1947, Willis and Yemm 1961, Specht 1963, Ginzo et al. 1982, Tilman 1982, 1984), and there are often strong correlations between soil chemistry and the local distributions of species (Snaydon 1962, Pigott and Taylor 1964, Whittaker and Niering 1975, Christensen and Peet 1984). Such results led me to suggest that it might be possible to predict the effects of resource availability on community structure and succession if the resource-dependence of plant growth were known (Tilman 1980, 1982, 1985).

In this paper I report the pattern of nitrogen-dependent seedling growth for nine species of plants that occur at different times during the secondary successional sequence on the sandy, nitrogen-poor (Tilman 1984) soils of Cedar Creek Natural History Area, Minnesota. Data from a chronosequence of 22 old fields at Cedar Creek have shown that total soil nitrogen increases significantly with the number of years since abandonment (R. Inouye et al., *personal observation*). The estimated total soil nitrogen as N in newly aban-

doned fields (intercept of the regression) was 369 mg/kg, and the slope of the regression against time was $6.8 \text{ mg} \cdot \text{kg}^{-1} \cdot \text{yr}^{-1}$ ($r = 0.67$; $n = 22$, $P < .01$). Thus, it takes ≈ 70 yr, on average, for newly abandoned fields to go from their initially low total soil nitrogen level to the highest level observed (852 mg/kg) in native, undisturbed prairie or savanna at Cedar Creek. Similar increases in soil nitrogen have been observed in other successions (Crocker and Major 1955; Olson 1958, Rice et al. 1960).

If interspecific competition for nitrogen is one of the important processes during secondary succession at Cedar Creek, then early successional species, which are dominant in the more nitrogen-poor soils, should grow more rapidly at low nitrogen levels than later successional species (Tilman 1982). Their greater growth rate, according to resource competition theory (Tilman 1982), should allow these species to acquire a larger proportion of available soil nitrogen, and thus to inhibit the growth of later successional species. The resource ratio hypothesis of succession (see Tilman 1985) predicts that succession could occur on such nitrogen-limited soils only if another resource, such as light, becomes more limiting as soil nitrogen levels increase, and if plants that are superior competitors for light (i.e., more shade tolerant) are poorer competitors for nitrogen. Thus, if nitrogen competition is important during early succession, and if another process, such as competition for light, becomes increasingly important in later succession, the ability of various plant species to grow at low nitrogen levels should correspond with their order of occurrence during secondary

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succession. The experiment reported in this paper was designed to determine if the nitrogen-limited growth of nine plant species was consistent or inconsistent with this theory.

METHODS

The five grass and four forb species used in these experiments are common at some time during the secondary succession in abandoned fields on dry, upland soils. The grasses were *Agropyron repens* (quack grass, an introduced perennial), *Agrostis scabra* (bent grass, a native perennial), *Poa pratensis* (blue grass, a native perennial), *Schizachyrium scoparium* (little bluestem, a native perennial formerly called *Andropogon scoparius*), and *Sorghastrum nutans* (Indian grass, a native perennial). The forbs were *Ambrosia artemisiifolia* (ragweed, a native annual), *Chenopodium album* (lamb's quarters, annual and probably native), *Achillea millefolium* (yarrow, a native perennial), and *Liatris aspera* (blazing star, a native perennial). The life form and designation as native or introduced are based on Gleason and Cronquist (1963).

To promote germination, *Agropyron repens*, *Agrostis scabra*, *Ambrosia artemisiifolia*, *Poa pratensis*, and *Sorghastrum nutans* were stratified under cold, moist conditions after the seeds were treated with dilute bleach to prevent fungal growth. *Schizachyrium scoparium* and *Liatris aspera* were stratified under cold, dry conditions. Immediately before planting, *Chenopodium album* was scarified with concentrated sulfuric acid for 5 min. *Achillea millefolium* was untreated.

The soils used in these experiments were mixtures of a fine, commercial silica sand with a Sartell fine sand soil (Grigal et al. 1974). The soil was collected to a depth of 25 cm from a grassy, open area adjacent to a fenced area used for single-nutrient fertilization experiments at Cedar Creek in native oak savannah that has undergone prescribed burning for two of every three years since 1966. The soil was air dried and sieved through two wire-mesh screens (hole sizes of 0.8 × 0.8 cm followed by 0.1 × 0.15 cm) to remove all but the finest plant parts. After sieving, the soil had a pH of 3.9 (determined by mixing equal volumes of soil and distilled water) and had total soil nitrogen (as N) of 852 mg/kg. The silica sand had undetectably low levels of total nitrogen (<5 mg/kg) and a pH of 7.1. Because the pH of most Cedar Creek old fields is ≈5.5, soil pH was adjusted to 5.5 by adding 6.8 g of fine-ground agricultural lime (CaCO₃) to every litre of dry, sieved soil. The pH of the sand was adjusted to 5.5 by adding 18 g of commercial Al₂SO₄ and 30.8 g of lime per litre of sand. The modified Cedar Creek soil and the modified silica sand were then mixed in nine different proportions to give the nine total soil nitrogen levels used in these experiments. To assure that nitrogen would be the only limiting soil resource in these experiments, each litre of the dry soil mixture also received 2.1 g of slow-release, microencapsulated P₂O₅ (Osmocote 0-40-

0), 2.1 g of slow-release, microencapsulated K₂O (Osmocote 0-0-46), 1.0 g of U. S. Pure MgSO₄, and 0.3 mL of a trace metal solution (Guillard 1973) containing EDTA-chelated Mn, Mo, Cu, Zn, Fe, B, and Co. Each soil type was made as a single large batch and was thoroughly mixed.

Each species was grown from seed in each of the nine soil mixtures, with five replicate pots (each 10 × 10 × 10 cm, holding 1 L of soil) for each species at each level of nitrogen. A layer of cotton gauze in the bottom of each pot prevented soil from being washed from the pots during watering. After pots were filled with a given soil mixture, 10 pots, chosen at random, were removed for analysis of soils. The mean value of the nitrogen in each set of 10 samples is reported as the nitrogen level for that treatment.

Each pot was thoroughly watered with deionized water two times before seeds were planted on 1 and 2 March 1983. Seeds were spread uniformly over the soil surface and then covered with 0.6 cm of dry, sterilized silica sand to give all pots the same surface color and to minimize fungal attack. After germination, forbs (except *Liatris*) were thinned to a density of two plants per pot, and grasses and *Liatris* were thinned to nine plants per pot. *Liatris* was treated differently than other forbs because its life-form resembles that of grasses more than that of the other forbs. Plants were thinned to give as uniform spacing as possible to the remaining plants. These densities were chosen to be sufficiently low to prevent intraspecific competition for nitrogen or light. Because of poor germination, *Agropyron repens* and *Chenopodium album* were replanted on 25 March 1983 and 7 April 1983, respectively.

After the planting, all pots were watered at least three times each week (more often if soils became dry) with deionized water that had passed through an activated charcoal filter (minimum purity of 1 MΩ; no detectable nitrogen). Each pot was placed on a 12.5 × 12.5 cm plastic tray to prevent any possible transfer of nutrients from nearby pots and to provide a reservoir of water for the pot. All plants were grown in an unshaded greenhouse, which received ≈350–400 μE·m⁻²·s⁻¹ of solar photosynthetically active radiation (PAR) at midday on cloudy days and ≈1300–1400 μE·m⁻²·s⁻¹ on clear days. An additional 150 μE·m⁻²·s⁻¹ PAR were provided for 12 h each day by 1000-W multi-vapor lights. Greenhouse temperature changed with ambient spring temperature, but was always kept at a minimum of 18°C by a thermostat-controlled heater. Nighttime low temperatures were ≈18°. Daytime high temperatures ranged from 18° to 35°.

Because plants received full sunlight and auxiliary light, and were planted sufficiently far apart to minimize shading, light should not have been limiting in these experiments. Nitrogen should have been the only limiting soil resource in all nine of the soil mixtures used in these experiments, because all pots received auxiliary P, K, Ca, Mg, and trace metals, and because

the soil was collected in an area in which field fertilization experiments had shown N was the only limiting soil resource (of N, P, K, Ca, Mg, S, trace metals, and water). Because the homogenized natural soil was the source of all the nitrogen in these experiments, all of the soil mixtures should have had the same carbon:nitrogen ratio and the same proportions of different types of organic compounds. The adjustment of pH, the frequent watering, and the uniform soil surface color should have kept soil pH, moisture, and temperature the same for the different soil mixtures. It is thus likely that the mineralization rate of nitrogen in these soil mixtures was proportional to the total soil nitrogen in these mixtures (Chichester et al. 1975, Melillo et al. 1982, Vitousek et al. 1982).

Plants were harvested starting 5 May and ending 8 June 1983. Comparison of the number of plants alive at the time of harvest with the number alive at the time of thinning revealed that there had been almost no mortality during that period. All pots of each species were harvested within a 3–4 d period. At the time of harvest, the height (soil surface to tip of highest part of plant) of each plant was measured to the nearest 0.1 cm. For *Achillea millefolium*, which is a rosette as a seedling, the length of the longest leaf was measured as its "height." All the plants in a pot were then clipped at the soil surface, dried and weighed. Belowground biomass was obtained by sieving and washing the soil away from the roots. All biomass and heights are average values per individual. Because different species grew for different lengths of time (from 9 to 14 wk), the results obtained have been standardized into units of biomass and height per 12-wk period by dividing the measured biomass or height by the number of weeks of growth and multiplying this by 12. The species, ordered by the number of weeks of growth, are *Chenopodium album* (9 wk), *Agropyron repens* (10.3 wk), *Sorghastrum nutans* (10.9 wk), *Agrostis scabra* (12 wk), *Ambrosia artemisiifolia* (12.5 wk), *Poa pratensis* (13 wk), *Schizachyrium scoparium* (13.1 wk), *Liatris aspera* (13.3 wk), and *Achillea millefolium* (14 wk).

After plant tissue samples were dried and weighed, all aboveground portions of a given species in a given treatment were combined and ground in a Wiley mill. Belowground portions were similarly combined and ground. Tissue nitrogen concentrations were then measured using the persulfate digestion technique on an AutoAnalyzer equipped with an Apple computer as a data logger (Tilman 1984).

I used an unpublished data base (R. Inouye et al., *personal observation*) to rank the approximate order of appearance, dominance, and disappearance of these species during secondary succession at Cedar Creek. In 1983 we surveyed 22 Cedar Creek fields ranging in time since abandonment from 1 to 56 yr. Because all fields were flat, upland, well drained, and contained well-sorted fine sand to a depth of 20–40 m (Grigal et al. 1974), we consider them to form a chronosequence.

For 100 0.5-m² quadrats in each field, we recorded the percent cover of all species. In addition, we created a newly disturbed field (0 yr old) by thorough disking of a 14-yr-old field in 1982, and recorded the aboveground biomass of all species in six otherwise unmanipulated plots. I used both data sets to rank each of the nine species according to the age of the field in which it was first observed during succession. In addition, I used the old-field survey data to rank each species by the age of the field in which it reached its greatest percent cover. Finally, I ranked each species by the age of the field in which it was last observed during succession. In all these rankings, 1 = youngest, 9 = oldest. To obtain an estimate of the rank order of occurrence of these species during secondary succession at Cedar Creek, I summed the three separate ranks for each species and ranked the species by these sums.

RESULTS

For each of the nine species, the regressions between their biomass or height at 12 wk and total soil nitrogen were significant (Figs. 1 and 2). The slope of each regression indicates how rapidly the biomass or height of each species increased with increases in total soil nitrogen. The growth of most species did not show any tendency to reach an asymptotic level within the range of total soil nitrogen levels used. However, *Agrostis scabra*, *Agropyron repens*, and *Ambrosia artemisiifolia* may have been close to their maximal growth rates at the highest soil nitrogen levels (Fig. 1).

Linear regression showed that the concentration of tissue (roots + shoots) nitrogen increased significantly with total soil nitrogen in *Ambrosia artemisiifolia* ($r = 0.96$, $n = 9$ nitrogen levels, $T = 4600 + 6.6N$, where T is the tissue nitrogen concentration and N is the concentration of total soil nitrogen [both in milligrams per kilogram] in a treatment), *Liatris aspera* ($r = 0.83$, $n = 9$, $T = 4200 + 5.1N$), *Poa pratensis* ($r = 0.83$, $n = 9$, $T = 4400 + 3.1N$), and *Sorghastrum nutans* ($r = 0.89$, $n = 9$, $T = 7800 + 3.7N$). There were positive but nonsignificant correlations for *Agropyron repens*, ($r = 0.31$, $n = 8$ because an extreme outlier was omitted, $T = 6200 + 1.0N$), *Schizachyrium scoparium* ($r = 0.25$, $n = 9$, $T = 8000 + 0.6N$), and *Agrostis scabra* ($r = 0.46$, $n = 9$, $T = 3400 + 1.7N$). *Chenopodium album* had a significantly negative regression ($r = -0.72$, $n = 9$, $T = 8200 - 6.7N$) and *Achillea millefolium* had a negative but nonsignificant relationship ($r = -0.27$, $n = 9$, $T = 5800 - 0.4N$).

The total amount of nitrogen extracted from the soil by each individual of a species was calculated by multiplying its belowground biomass by its belowground tissue nitrogen concentration, multiplying its aboveground biomass by its aboveground tissue concentration, and then summing these two numbers. For all nine species, nitrogen extraction per plant increased linearly with total soil nitrogen (Table 1). The slope of the regression line for each species indicates the amount

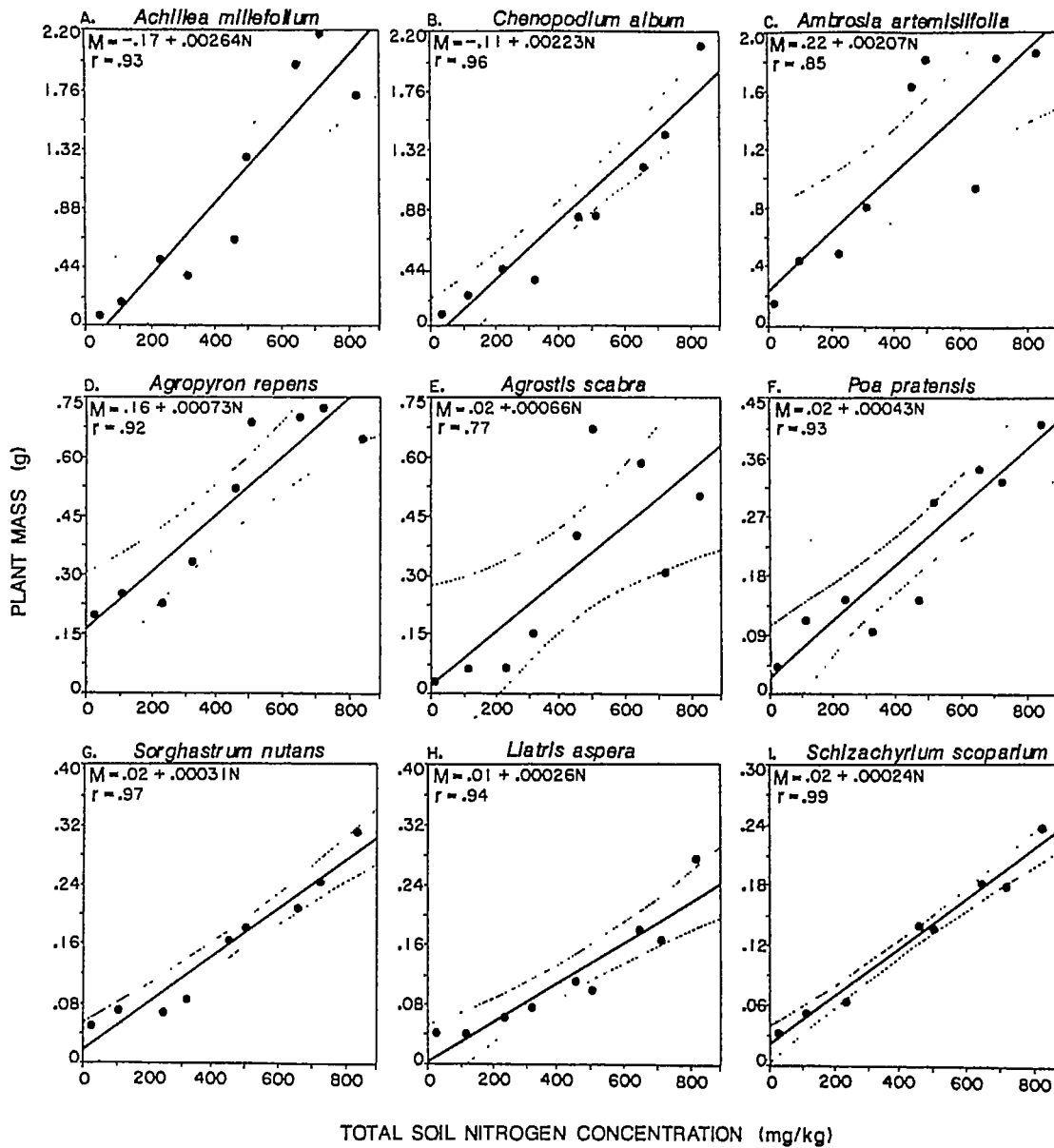


FIG. 1. Plant mass at 12 wk graphed against total soil nitrogen for all nine species. Because the maximal mass per plant differed by an order of magnitude among these species, the vertical axis of each graph has a different scale. Each data point (●) is the observed average mass per plant for a given treatment (soil mixture). The solid line through the points is a least squares linear regression, and the dotted curves show its 95% confidence intervals. In the regression equations, M is the mass (g) per plant, N the concentration of total soil nitrogen as N (mg/kg), and r the correlation coefficient. The order of appearance of species is from those that grow most rapidly at low soil nitrogen to those that grow most slowly at low soil nitrogen.

of nitrogen (in milligrams) that each individual extracted in 12 wk from each unit of nitrogen concentration (milligrams per kilogram) in the soil. I call this slope the nitrogen extraction efficiency of the species. The high degree of linearity observed suggests that the efficiency with which a species extracted nitrogen was not dependent on the concentration of total soil nitrogen.

The survey of 22 old fields and a newly disturbed

field allowed the species to be ranked (see Methods) as follows, from those occurring early to those occurring late in secondary succession at Cedar Creek: *Ambrosia artemisiifolia* (0-yr-old, 22-yr-old, and 43-yr-old fields; ages of fields of first appearance, peak abundance, and last presence, respectively), *Agropyron repens* (0, 15, and 48 yr, respectively), *Achillea millefolium* (8, 11, and 48 yr), *Chenopodium album* (0, 36, 48 yr), *Agrostis scabra* (tied with *Chenopodium*: 1, 11, 56+ yr, where

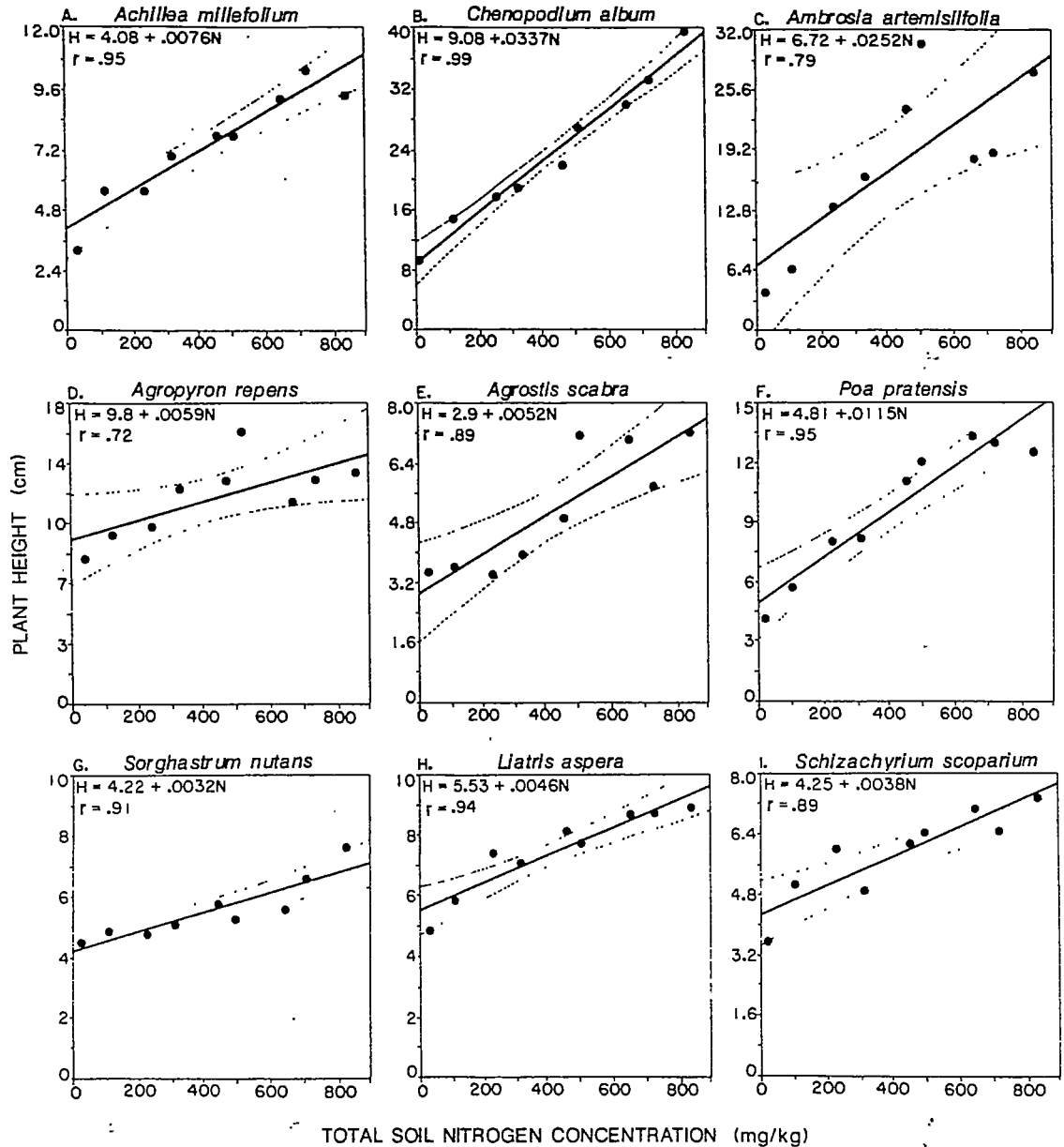


FIG. 2. Plant height at 12 wk graphed against total soil nitrogen. Note that each portion of this figure has a different scale for the vertical axis. Solid lines are least squares regressions and dotted curves are 95% confidence intervals. In the regression equations H is plant height (cm). N is the concentration of total soil nitrogen as N (mg/kg), and r is the correlation coefficient. For *Achillea*, "height" is actually leaf length. Species order is that of Fig. 1.

56+ means that it was still present in the 56-yr-old field), *Schizachyrium scoparium* (12, 36, 48 yr), *Poa pratensis* (11, 30, 56+ yr), *Liatris aspera* (26, 26, 56+ yr), and *Sorghastrum nutans* (48, 48, 56+ yr).

Except for *Chenopodium album*, the order of occurrence of these species during secondary succession estimated by the old field surveys agrees with that of Parrish and Bazzaz (1982). Their report that *Chenopodium album* was codominant with *Ambrosia artemisiifolia* during early secondary succession in Illinois agrees well with observations I have made in other

fields at Cedar Creek. The apparent dominance by *Chenopodium* later in succession than *Ambrosia* at Cedar Creek may result from the absence of fields aged 2 to 7 yr in the survey.

DISCUSSION

These experiments revealed a strong dependence of seedling biomass and height on soil nitrogen, but a less clear dependence of tissue nitrogen concentration on soil nitrogen. Tissue nitrogen concentrations increased with soil nitrogen levels for all species except *Cheno-*

TABLE 1. Total nitrogen accumulation per plant (extraction from the soil) for each of nine species at Cedar Creek, Minnesota. For each species, the dependence of the total amount of nitrogen per plant on the concentration of total soil nitrogen was determined by linear regression.

Species†	Correlation coefficient (r)	Slope‡ (plant N/soil N) (mg/[mg/kg])	Intercept (mg N)
<i>Ambrosia artemisiifolia</i>	0.92	0.0228§	-0.61 NS
<i>Achillea millefolium</i>	0.91	0.0138§	-0.61 NS
<i>Chenopodium album</i>	0.80	0.0053**	0.78 NS
<i>Agropyron repens</i>	0.91	0.0038§	0.76 NS
<i>Agrostis scabra</i>	0.93	0.0033§	-0.16 NS
<i>Poa pratensis</i>	0.95	0.0032§	-0.09 NS
<i>Sorghastrum nutans</i>	0.98	0.0035§	0.02 NS
<i>Schizachyrium scoparium</i>	0.99	0.0020§	0.15*
<i>Liatris aspera</i>	0.97	0.0021§	-0.09 NS

† There were nine data points (soil nitrogen concentrations) for each species except *Agropyron repens*, for which there were eight because an extreme outlier of tissue nitrogen concentration was deleted. Species are listed in the same order as in Figs. 1 and 2.

‡ Each slope has units of N mass accumulated per plant divided by the concentration of N in the soil: mg/(mg/kg) = kg.

* .05 ≥ P > .01; ** .01 ≥ P > .005; § P ≤ .005; NS P > .05; tests of the null hypotheses that slopes and intercepts are equal to 0.0.

podium album and *Achillea millefolium*. The trends for these two species contrast with the generally reported tendency for tissue nitrogen to increase with soil nitrogen availability, at least in photosynthetic tissues (Chapin 1980), but the values reported here include nitrogen in photosynthetic tissues, structural tissues, and roots. Because structural tissues often have lower nitrogen concentrations than photosynthetic tissues, the decreases in tissue nitrogen concentrations at higher soil nitrogen levels may have been caused by a disproportionate increase in structural tissues. *Chenopodium album* and *Achillea millefolium* were the two fastest growing species in these experiments, and thus they may have had the greatest proportion of structural tissues in the high-nitrogen treatments.

Because tissue nitrogen levels changed with soil nitrogen, it is difficult to make a single comparison of tissue nitrogen levels among these species. There is, though, no significant Spearman rank correlation ($r_s = 0.02$, $n = 9$) between the order of occurrence of these species in succession and their ranking by the tissue nitrogen concentrations in plants on very poor soils (the y-intercepts of the regressions of tissue nitrogen against soil nitrogen).

There were marked differences in the nitrogen dependence of the growth of seedlings of these species. Because for most species biomass at 12 wk showed a fairly linear dependence on soil nitrogen, the fitted curves of Fig. 1 can be used to rank these species by their ability to grow at low nitrogen levels. (Fig. 3A shows the fitted curves of Fig. 1 all at the same scale.)

Using the biomass attained by individuals of each species at a total soil nitrogen level of 300 mg/kg, these species may be ranked from those that attained the greatest biomass as seedlings under nitrogen limitation to those that attained the least: *Ambrosia artemisiifolia*, *Achillea millefolium*, *Chenopodium album*, *Agropyron repens*, *Agrostis scabra*, *Poa pratensis*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Liatris aspera*. Similarly, the fitted curves for the dependence of plant height on soil nitrogen (Fig. 3B) may be used to rank the species from tallest to shortest on low-nitrogen soils (total N: 300 mg/kg): *Chenopodium album*, *Ambrosia artemisiifolia*, *Agropyron repens*, *Poa pratensis*, *Liatris aspera*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Agrostis scabra*. *Achillea millefolium* is not included because leaf length, not height, was measured.

These rankings of species by the biomass and height attained at low nitrogen levels may be compared with several other measured variables using nonparametric Spearman rank-order correlations (Table 2). Excluding *Achillea millefolium* (for which height was not measured), there was no significant dependence of seedling height at low nitrogen on time of occurrence during succession, biomass at low nitrogen, or nitrogen extraction efficiency (Table 2). In contrast, the ranking of the species by the biomass per plant attained at low soil nitrogen was highly significantly correlated with the earliness of occurrence of these species during secondary succession at Cedar Creek (Table 2). Plant biomass at low soil nitrogen was also highly significantly correlated with nitrogen extraction efficiency, but was independent of plant height at low soil nitrogen levels (Table 2). Thus, species that are dominant during the early stages of secondary succession at Cedar Creek attain greater biomass in low nitrogen soils and extract more nitrogen per unit of soil nitrogen (Table 1) than do plants that are dominant late in succession. Because fertilization experiments performed in four different old fields (7, 14, 25, and 48 yr since agriculture) have shown that nitrogen is the most important limiting soil resource at Cedar Creek (Tilman 1984, and *personal observation*), and because nitrogen concentration of soils increases with successional age, these results suggest that dominance in early successional fields may be influenced by the abilities of species to acquire nitrogen and grow at low nitrogen levels.

These results are similar to those of Rice et al. (1960) who found that the annual grass *Aristida oligantha* grew more rapidly at low nitrogen levels than the later successional grass *Schizachyrium scoparium* which, in turn, grew more rapidly at low nitrogen levels than the even later successional grass *Panicum virgatum*. Parrish and Bazzaz (1982) grew 17 species of old field and prairie plants along a soil gradient created by enriching a soil mixture with different amounts of a fertilizer containing ammonia, urea, P, and K. Because their experimental gradient included sufficiently high nu-

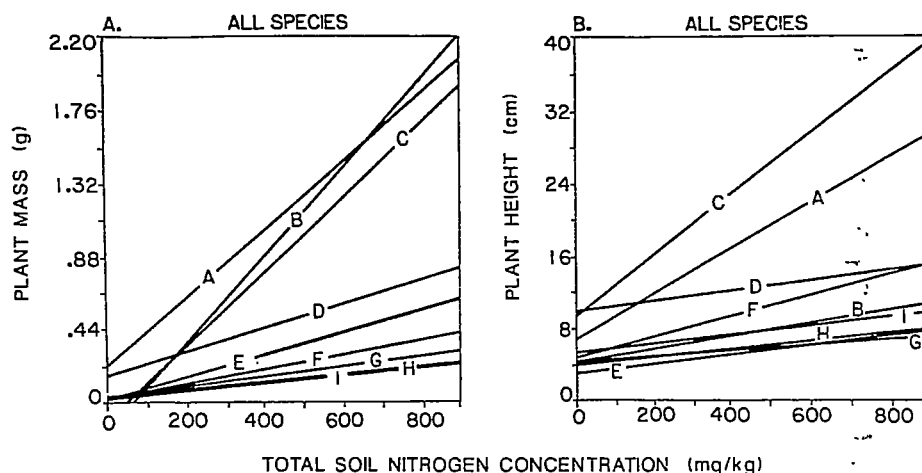


FIG. 3. To allow comparison of the fitted curves of Figs. 1 and 2, these curves are graphed on the same scale. The regression lines, labeled A to H, correspond with the species of parts A to H of Figs. 1 and 2, with A = *Ambrosia*, B = *Achillea*, C = *Chenopodium*, D = *Agropyron*, E = *Agrostis*, F = *Poa*, G = *Sorghastrum*, H = *Schizachyrium*, and I = *Liatris*.

trient concentrations that all species were inhibited at their highest nutrient level, it is difficult to compare their results with those reported here. However, a qualitative comparison is possible by looking at the nutrient dependence of growth of the 14 species that were not inhibited at their three lowest nutrient levels (*Solidago canadensis*, *Oenothera biennis*, and *Aster pilosus* were inhibited at their third level). I estimated the responses of these 14 species by taking the slope of a line from the origin through the biomass per plant at the third nutrient level (their "M"). I then adjusted this slope to allow for the different time periods for which the plants had grown (from 90 to 150 d). The three fastest growing plants were all early successional species (*Setaria faberii*, *Amaranthus retroflexus*, and *Polygonum pensylvanicum*). The four most slowly growing species were mid- and late successional species (*Petalostemum purpureum*, *Ratibida pinnata*, *Veronia altissima*, and *Sorghastrum nutans*). The remaining seven species were intermediate in their growth rates, with no obvious pattern. Thus, for the portion of their nutrient gradient for which nutrients were not inhibiting, the results of Parrish and Bazzaz (1982) seem generally consistent with the results reported here.

The consistency between the pattern reported in this paper for nine species, that reported by Rice et al. (1960) for three species, and the experiments performed by Parrish and Bazzaz (1982) suggests that the availability of soil nitrogen and the dependence of plant growth on nitrogen may be an important determinant of the order of occurrence of these species during secondary succession on nitrogen-poor soils. These experiments have demonstrated that early successional plants can extract more nitrogen from, and can grow more rapidly in, a nitrogen-poor soil than late successional species. The greater ability of early successional species to acquire nitrogen and grow in nitrogen-poor

soils suggests that they may be superior competitors for soil nitrogen compared to later successional species (Tilman 1982), and is consistent with the resource ratio hypothesis of succession (Tilman 1985).

However, these differences, by themselves, cannot explain the successional sequence. At least one other process or factor must also change during succession to explain the ability of later successional species to displace earlier species that have lower nitrogen requirements. The resource ratio hypothesis of succession predicts that plants that are superior competitors for nitrogen must be inferior competitors for another resource that becomes limiting in nitrogen-rich soils, such as light (Tilman 1982, 1985). Because no data are available on the light-limited growth of these species, this aspect of the theory cannot be evaluated.

There are at least two alternative explanations for the ability of later successional species to displace early successional species from nitrogen-rich soils. First, it may be that these plant species have "included niches," i.e., that later successional species cannot survive at low levels of soil nitrogen but are superior competitors at higher levels. The data for seedling growth in Fig. 3 do not support that hypothesis. Second, species that are superior competitors for nitrogen may be more susceptible to herbivory, and the intensity of herbivory may increase through succession as total plant biomass increases.

There are several reasons why the results presented here should be considered only an initial step in trying to understand the role of soil resources in succession. First these nutrient-dependent growth experiments have focused on a short period of the life of long-lived vascular plants. They only provide a partial indication of the dependence of growth on resource availability. Second, although nitrogen may be the most important limiting soil resource at Cedar Creek (Tilman 1984).

TABLE 2. Spearman rank-order correlation coefficients for four variables of nine plant species at Cedar Creek, Minnesota.†

	Biomass at low soil N	Height at low soil N	Nitrogen extraction efficiency‡
	Spearman rank correlation coefficients		
Time of occurrence during succession§	0.85**	0.54 NS	0.71*
Biomass at low soil N		0.64 NS	0.93**
Height at low soil N			0.64 NS

† All nine species were used in each correlation except those involving plant height, for which *Achillea millefolium* was excluded.

‡ Slope of linear regression of N accumulation vs. soil N concentration.

§ The old-field survey was used to rank each species by the age of the field in which it was first observed during succession. Each species was also ranked by the age of the field in which it reached peak abundance (as cover). Finally, each species was ranked by the age of the field in which it was last observed during succession. In all cases, a rank of 1 was assigned to the species in the youngest field, a rank of 2 for the species in the next oldest field, etc. For each species, these three ranks were then summed. The sums were then used to rank the species from those that occur early (low sums) to those that occur late (high sums) during succession at Cedar Creek.

* $.05 \geq P > .01$; ** $P \leq .01$; NS $P > .05$; significance of deviation from independence for the Spearman correlations. All tests of significance were performed using the formulae of Steel and Torrie (1980).

other resources, including water, light, and phosphorus, may limit some species. Third, plants may be limited by a different resource as adults than as seedlings. Fourth, plant growth is temperature dependent, and seasonal temperature changes may be an important determinant of plant competitive abilities. Other processes, including herbivory, disturbance, dispersal, time of germination, mutualism, and variability in the physical environment can greatly influence the composition and dynamics of plant communities. However, whatever other processes may be involved, the results reported here suggest that the abilities of plants to grow at low nitrogen levels may be an important determinant of the successional sequence on nitrogen-poor soils.

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