

Growth of old field herbs on a nitrogen gradient

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Abstract. Eight species of herbs that reach peak abundance at different times during the first 50 years of secondary succession on a nitrogen impoverished sand plain were grown at both low and high density for one and two field seasons along an experimental nitrogen gradient. The data demonstrate that intraspecific competition is strong even on extremely nitrogen poor soils. The dependence of relative growth rates (RGR), biomass per plant, yield per pot, root:shoot ratios and seed:shoot ratios on soil total nitrogen were determined. These nitrogen-dependent characteristics were compared with the known successional status of the species. Species most abundant on early successional, nitrogen poor soils tend to have higher RGR_{max} , lower root:shoot ratio, higher yield per pot and higher seed:shoot ratio than late successional species of more nitrogen rich soils. This suggests that early successional species may be inferior nitrogen competitors but have faster growth rates and better colonization abilities than later successional species. This supports the hypothesis that the successional dynamics of these herbs are the transient dynamics of colonization and competitive displacement, but tends to refute the equilibrium version of the resource ratio hypothesis of succession (i.e. succession caused by changing nitrogen to light ratios).

Key-words: Successional herbs, nitrogen-limited growth, root:shoot, seed:shoot, succession on a sand plain, relative growth rates, transient dynamics, successional trade-offs

Introduction

The rate and pattern of secondary succession depends on many factors, including the original vegetation of a site, its soil and the type, intensity and duration of disturbance (e.g. papers in West, Shugart & Botkin, 1981). However, even within a restricted subset of successions, such as those on formerly forested sites that had been cultivated for many years, there is much variability in the rate

and pattern of succession, especially in the duration of the herbaceous stage. In the Piedmont of North Carolina, for instance, *Andropogon virginicus* L., an early dominant, is replaced by dense stands of 3–5 m tall pines (*Pinus echinata* Mill.) after 10–15 yr (Billings, 1938), whereas *Andropogon virginicus* persists and woody plants remain rare in fields three times this age on the coastal sandplain of this region (Odum, 1960; Golley, 1965; Monk & Gabrielson, 1985; Pinder & Kroh, 1987). Herbs also have a long period of dominance during succession on the sandplain of Cedar Creek Natural History Area (CCNHA), Minnesota, where the study reported here was performed. Although abandoned fields are surrounded by forest, woody plant cover, mainly from shrubs and vines, is less than 1% after 25 yr of succession, less than 5% after 40 yr and less than 15% after 60 yr (Inouye *et al.*, 1987). Nutrient addition experiments (Tilman, 1987, 1988) have suggested that the extreme nitrogen impoverishment of soils caused by cultivation and the 100+ yr required for total soil nitrogen to return to that of undisturbed forest (Inouye *et al.*, 1987; Tilman, 1988) may be major causes of the slow rate of woody plant dominance and thus the long duration of the herbaceous stage. Such patterns tend to support the resource ratio hypothesis (Tilman, 1985, 1988) as an explanation for the successional transition from herbaceous to woody species.

It has been hypothesized (Tilman, 1985, 1988) that the dynamics of primary successions (e.g. Cowles, 1899; Olson, 1958; Robertson & Vitousek, 1981) may be caused by the effect on plant competition of slow increases in soil nitrogen supply rates and concomitant decreases in light penetration. Might this same hypothesis, the resource ratio hypothesis, apply to the early, herbaceous stages of secondary successions on impoverished soils? Or, might the dynamics of herbs on impoverished soils be the transient dynamics of interspecific competition that result from trade-offs in maximal growth rates, colonization abilities, competitive abilities and life history characteristics (e.g. Horn, 1971; Connell & Slatyer, 1977; Tilman, 1985, 1988; Huston & Smith, 1987)?

The resource ratio hypothesis and the transient

dynamics hypothesis make quite different predictions (summarized in the discussion) about a variety of traits of early and late successional species, including their patterns of nitrogen-dependent growth. As a partial test of these alternative hypotheses, and to gain insight into the potential role of nitrogen in structuring the herbaceous portion of succession, we grew eight CCNHA old field herb species for one and two field seasons in both high and low density monocultures along an experimental soil nitrogen gradient. Upon harvesting, we determined the dependence on soil total nitrogen of the above- and below-ground mass per plant, yield per pot, plant height, root:shoot ratio, relative growth rate and reproductive output of each species. In this paper, we compare these results with other data on the successional status of these CCNHA species (Tilman, 1987, 1988) and their abundance along a successional soil nitrogen gradient (Tilman, 1987).

Materials and methods

We studied four grasses [*Agrostis scabra* Willd., *Poa pratensis* L., *Sorghastrum nutans* (L.) Nash, *Schizachyrium scoparium* (Michx.) Nash-Gould] and four forbs [*Solidago nemoralis* Ait., *Solidago rigida* L., *Aster azureus* Lindl.-Rydberg and *Berteroa incana* (L.) DC.]. These were grown from seed in pots (30 cm in diameter by 30 cm deep) containing 18 l of soil in a field at CCNHA, East Bethel, Minnesota, USA. Seeds were collected at CCNHA during 1984. *Agrostis*, *Poa* and *Berteroa* seed were stored at room temperature. The other species were stratified under cold, dry conditions at 4°C for the winter. Pots were seeded in mid-May, 1985. Some pots were harvested at the end of the first growing season (mid-September 1985) after 16 weeks of growth and other pots were harvested after two field seasons (late August to

early September 1986). Each species was grown both at high density (c 100 plants per pot) and at low density (seven plants per pot) on each of seven different soil mixtures. The seven mixtures formed an experimental nitrogen gradient. For brevity we will refer to these species by generic names except for *Solidago nemoralis* and *S. rigida*.

Three soils were mixed to construct the nitrogen gradient. The three soils were: sub-surface sand from the study site (c 25 mg of N per kg of soil, pH = 6.0), top soil from the study site (N of c 350 mg kg⁻¹, pH = 5.4) and black loam (N of c 5000 mg kg⁻¹, pH = 7.2) obtained from the sandplain on which CCNHA is located, but offsite. The topsoil and loam were sieved through a wire mesh screen (6 mm × 6 mm) to remove plant parts. Soil pH was adjusted to the average pH of Cedar Creek old fields (Inouye *et al.*, 1987), pH = 5.5, by adding 300 g of aluminium sulphate (Al₂(SO₄)₃) per 45 kg of loam. The three soils were then thoroughly mixed, using a commercial cement mixer, in different proportions to make seven soil mixtures ranging from c 125 to c 1800 mg kg⁻¹ of total N (Table 1). A 3 cm layer of pea-sized stones was placed in the bottom of each pot to assure free drainage. To assure that other nutrients were not limiting, each pot received 7.3 g P₂O₅, 7.3 g K₂O, 7.3 g CaCO₃, 3.5 g MgSO₄, and a trace metal mixture at the time of planting and at the start of the second growing season. Three 15 cm long by 2.5 cm diameter soil cores were collected from each pot, mixed and then analysed, in duplicate, for soil total N using a presulphate digestion technique (D'Elia, Steudler & Corwin, 1977, as modified in Tilman, 1984). Because this was planned as a regression experiment rather than an ANOVA experiment, we use the average total N of each pot in analyses.

For each species, we planted six replicate low density pots and three replicate high density pots

Table 1. Percentages (by mass) of the three soils in each soil mixture. Because of soil heterogeneity and variation in weighing and mixing, actual total soil N in pots varied from the target levels. To allow for this variation, the actual measured level of total soil nitrogen in each pot was used in all analyses of results.

Target nitrogen level (mg kg ⁻¹)	% Black loam	% Top soil	% Sub-surface sand
100	1.5	4.5	94
200	3	9	88
375	6	19	75
575	9	30	61
800	13	40	47
1100	18	55	27
1500	25	75	0

at each of the seven soil mixtures in May, 1985. This gave a total of 567 pots. Low density pots were started with 20 plants per pot and were randomly thinned to seven plants per pot during the 4th week of growth. Although we wanted 100 plants per pot for the high density treatment, germination rates in the field varied from those in greenhouse trials, resulting in 30–300 plants per pot in the high density treatment. The number of plants per pot was fairly constant within each species, independent of soil type (Table 2). The actual number of plants in each pot was used in analyses. Pots were periodically weeded to remove seedlings of other species.

The pots were kept outdoors in full sun throughout the growing season. The study area was fenced to exclude vertebrate herbivores. Black plastic was placed on the soil to prevent plant growth around the pots. Almost no insect herbivory occurred. Soil moisture was regularly monitored and all plants were watered to soil saturation at least twice each week (unless there had been sufficient rain to do this). This was done to assure that nitrogen, not water, would be limiting. Such regular watering meant that differences among treatments in soil texture, and thus in water holding capacity, are unlikely to have influenced the results of these experiments because water was not allowed to become limiting in any treatments. All soil mixtures were sufficiently well drained that soils were not waterlogged.

Nitrogen mineralization rates were estimated by the *in situ* buried bag technique (Eno, 1960; Pastor *et al.*, 1984) in pots without plants. Two replicate pots of each soil mixture were sampled every 4 weeks during each growing season, with half of the sample from each pot analysed immediately for 2M KCl extractable ammonia and nitrate. The second half was placed in a gas-permeable polyethylene bag, buried in the pot about 8 cm below

the surface for 4 weeks, and then removed and analysed for extractable ammonia and nitrate. At that time, another soil sample was prepared for incubation. The *in situ* buried bag N mineralization rate of each pot was summed over each growing season to give average seasonal total mineralization. These 14 values were regressed on the soil total N of each pot to determine the dependence of N mineralization on soil total N.

A set of 224 pots (three of the low density and one of the high density replicates of each treatment for each species) was harvested in September 1985. The remaining 280 pots (three low density and two high density replicates) were harvested after two seasons of growth. Upon harvest, plant heights were measured and soil was carefully washed from roots. Plants were separated into roots (all below-ground structures) and shoots (all above-ground structures), dried for one week at 50°C and weighed. In the second year, shoots of all species except *Berteroa* were separated into vegetative and reproductive structures (flowers). Pots to be harvested the second year were stored in a shallow, straw-covered trench during the intervening winter to prevent death from exposure to extremely cold temperatures. After snow melt in the spring, but before plant growth, pots were removed from the trench and all straw was removed.

All data were analysed using Statgraphics software on an IBM-PC microcomputer. Relative growth rates (RGR, week⁻¹) were calculated using initial seed mass and plant mass after 16 weeks of growth as:

$$\text{RGR} = (\ln[B_{16}/B_0])/16$$

where B_0 and B_{16} are mass per plant at weeks 0 and 16. Dependence of biomass per plant, yield per pot, seed:shoot ratio, and relative growth rate on total soil nitrogen was fit with the Monod (1950) equation,

$$Y = M/(T/[K + T])$$

using non-linear regression, where Y is the independent variable, M = maximal response, K = total soil nitrogen level at which half of the maximal response is reached (i.e. half-saturation constant) and T is soil total N in mg kg⁻¹ for dry soil. The Monod equation was used because it includes a maximal, asymptotic value for the dependent variable. It is unlikely that any of these dependent variables would increase in a linear, unbounded manner with soil total nitrogen. (Moreover, the Monod model generally provided a

Table 2. Average number of plants per pot, as determined by a direct count, and standard deviation, for the high density treatment of each species, using all replicates at all seven nitrogen levels ($n = 21$ for each entry).

Species	Mean	SD
<i>Agrostis scabra</i>	209	42
<i>Berteroa incana</i>	104	24
<i>Poa pratensis</i>	147	18
<i>Solidago nemoralis</i>	80	12
<i>Solidago rigida</i>	112	32
<i>Aster azureus</i>	32	13
<i>Schizachyrium scoparium</i>	127	21
<i>Sorghastrum nutans</i>	304	95

better fit than a linear model. For instance, the dependence of RGR on total soil nitrogen was better fit by the Monod model for 11 of 16 cases.) Linear regression was used to fit the dependence of log (root:shoot ratio) on total soil nitrogen.

Spearman rank order correlations, r_s , and Pearson correlations, r , were used to compare the responses of the eight species. Because such correlations are based on eight data points (one data point per species), only strong trends are likely to be significant. Correlations for which $0.10 \geq P \geq 0.05$ will be called marginally significant and indicated by 'M', $0.05 \geq P > 0.01$ will be termed significant and $P \leq 0.01$ will be called highly significant. Only linear and rank-order correlation were considered because, with only eight species to compare, there would be little power for meaningful analyses of nonlinear relations among species.

Successional status of species

We determined the successional status of these eight species in two different manners. The first way involved direct observation of plant abundances in fields of different ages. For this we combined two data sets: a survey of soils and vegetation in a chronosequence of 22 CCNHA old fields (Inouye *et al.*, 1987; Tilman, 1988) and repeated annual surveys of 11 strips of vegetation (20 m \times 100 m each) sequentially abandoned from agriculture (one strip per year) starting in 1974. The latter data were kindly provided by Barbara Delaney. The average abundance of each common species in each of these 33 fields or successional strips was graphed against successional age and a smooth curve was drawn to show its approximate successional dynamics (Tilman, 1988, p. 284). These curves were used to estimate the *successional rank* of these eight species (from early to late successional species) as: *Agrostis scabra*, first; *Berteroa incana*, second; *Poa pratensis*, third; *Solidago nemoralis*, *Solidago rigida* and *Aster azureus*, tied for fifth; *Schizachyrium scoparium*, seventh; and *Sorghastrum nutans*, eighth (latest successional species). The old field survey data also were used to determine the dependence of the per cent cover of each species on soil total N (Tilman, 1987). To do this, data from all quadrats of each field in which a species occurred were assigned to one of 40 soil total N classes and the average per cent cover of that species was calculated for each class. Histograms for all species except *Solidago rigida* and *Aster azureus* are in

Tilman (1987). Such histograms were used to rank these eight species from those that reach peak abundance on nitrogen poor (often early successional) soils to those that reach peak abundance on more nitrogen rich soils as: *Agrostis scabra*, first (peak abundance on poorest soil); *Berteroa incana*, second; *Solidago nemoralis*, *Solidago rigida*, and *Aster azureus*, tied for fourth; *Schizachyrium scoparium* and *Sorghastrum nutans*, tied for sixth and a half; and *Poa pratensis*, eighth (peak abundance on most nitrogen rich soils). Because soil total N increases with successional age (Tilman, 1987), this ranking is an index of both the successional status and the soil nitrogen status of these species, with species ranked from those of N poor, early successional fields to those of more N rich, later successional fields. Thus, we call this the *successional soil nitrogen rank*.

Results

Total mineralized N per gram of dry soil was significantly linearly correlated with soil total N in the pots ($R^2 = 0.70$, $0.05 > P > 0.01$, d.f. = 12). Therefore, the experimental soil total N gradient in the pots was also a gradient of nitrogen supply rate.

The maximal RGR of a species, RGR_{max} , is the asymptote of a Monod curve of RGR on soil total nitrogen (Fig. 1). The RGR_{max} of species growing at high population density was significantly positively correlated with RGR_{max} at low density using rank order correlations ($r_s = 0.78$, $P < 0.01$, $n = 8$). At both low and high density, *Agrostis* had the highest RGR_{max} and *Sorghastrum* had the lowest. RGR_{max} of each species was from 15% (for *Aster*) to 38% (for *Sorghastrum*) lower for the high density pots than for the low density pots (Fig. 1). We will use the RGR_{max} of the low density treatments as *the* RGR_{max} of each species throughout the remainder of this paper. In general, the greater the density that a given species had in the high density pots (Table 2), the greater was the per cent reduction in its RGR in the high density treatments compared to the low density treatments. Indeed, comparison of the eight species shows that the average per cent reduction in the RGR of a species was significantly positively correlated with its average density in the high density pots ($r = 0.89$, $P < 0.01$, $n = 8$) indicating that increased density led to lower growth rates for these species. ANOVA of the effects of soil nitrogen (divided into four classes), plant species (eight classes: one per species), and density (two classes: low and high plant density) on RGR revealed highly significant density effects

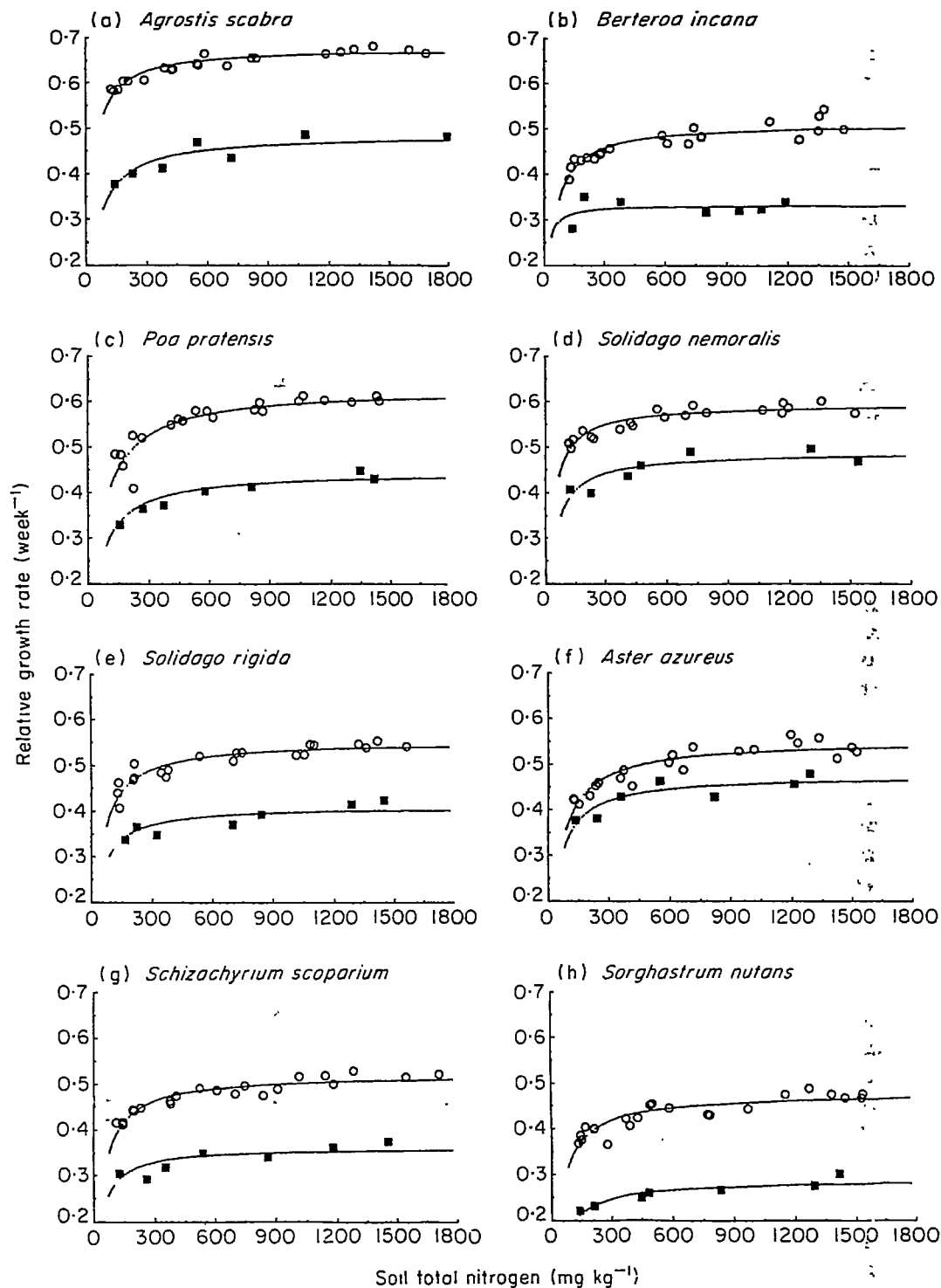


Fig. 1. Each portion of this figure shows the nitrogen-dependence of the relative growth rate (RGR) of a species during the first year of the experiment for plants growing at low plant density (open circles) and at high plant density (closed squares).

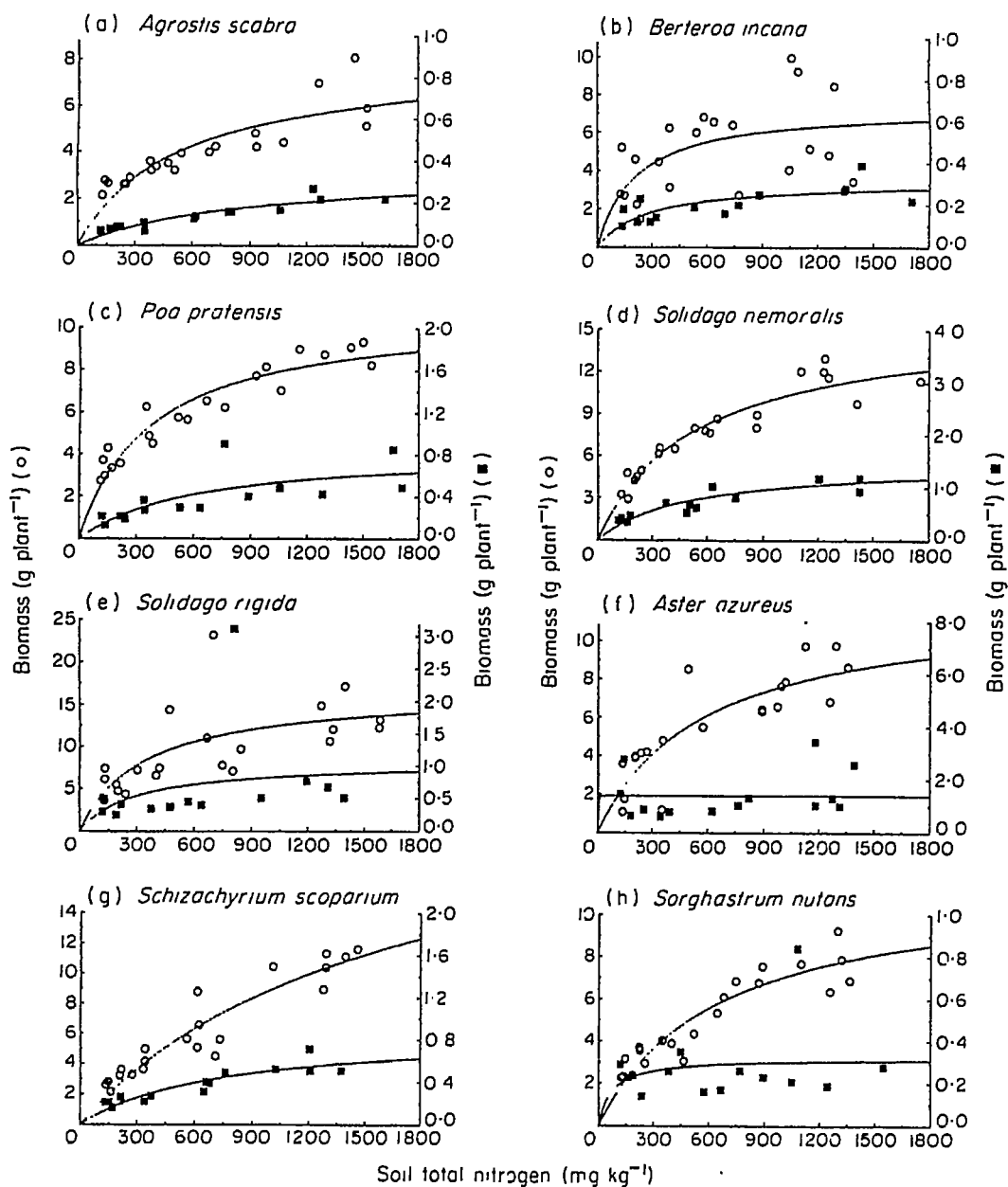


Fig. 2. The nitrogen-dependence of total biomass per plant (above-ground and below-ground) for each of the eight species in the second year of the experiment is shown for both the low plant density treatments (open circles) and for the high density treatments (closed squares).

($F = 2131$; d.f. = 1, 163, $P < 0.0001$), nitrogen effects ($F = 233$; d.f. = 3, 163; $P < 0.001$) and species effects ($F = 283$; d.f. = 7, 163; $F = 282$, $P < 0.0001$). There was a significant nitrogen \times density interaction ($F = 5.93$, d.f. = 3, 163, $P < 0.001$), with the greatest effect of density on RGR occurring at intermediate total soil N levels. However, there was no significant difference between the effect of density on RGR at high versus low total soil nitrogen (Duncan multiple range test, $P > 0.05$).

Based on the fitted Monod curves (1986 results in Fig. 2), in 1985 and 1986, for each species at each soil total N level, low density pots had higher mass per plant than did high density pots. Mass per plant was greater after 2 years of growth than after one for each species in both low and high density treatments. The increase in mass per plant from 1985 to 1986 ranged from a 1.5-fold increase for *Agrostis* at high density to a 2.9-fold increase for *Poa* at high density. Log of root:shoot ratio was significantly negatively correlated with soil total N (1986 data in Fig. 3), except for *Berteroa* at high density in 1985. In 1985, there were large species-to-species differences in the intercepts of these regressions but not in slopes. In 1986, most species differed both in slopes and intercepts (Fig. 3).

Successional and soil nitrogen ranks

Spearman rank order correlations were used to compare the successional rank and the success-

ional soil nitrogen rank of these eight species with various aspects of their nitrogen dependent growth (Table 3). Successional rank and soil nitrogen rank were marginally positively correlated with each other, indicating that early successional species often attain peak abundance on nitrogen-poor soils. RGR_{max} was marginally negatively correlated with successional rank, indicating that early successional species often have higher maximal growth rates than later successional species. Root:shoot intercepts from the low density treatment were marginally positively correlated with successional rank, indicating that early successional species tend to have lower root:shoot ratios. Successional soil nitrogen rank was correlated with root:shoot intercept. Thus, species dominant in nitrogen poor, early successional habitats have lower root:shoot ratios than those dominant in nitrogen rich, late successional habitats (Table 3). The proportion of above-ground biomass dedicated to reproductive tissues on poor soils (soil total N of 300 mg kg^{-1}), termed the seed:shoot ratio, was significantly negatively correlated with the soil nitrogen rank, indicating that species dominant on the nitrogen poor soils of early succession allocate a higher proportion of their biomass to reproduction.

Correlations among descriptors of nitrogen-limited growth

The N-limited growth experiments can determine if these eight species have suites of correlated

Table 3. Spearman rank order correlations between the successional rank of the eight species, the successional soil nitrogen rank, and various aspects of their nitrogen dependent growth. Based on two-tailed comparisons, M, which stands for 'marginal', means that $0.10 > P > 0.05$; * means $0.05 \geq P > 0.01$; ** means $P \leq 0.01$.

	Successional rank		Soil N rank	
	r_s	N	r_s	N
Soil N rank	0.62M	8		
RGR_{max} (low density, 1985)	-0.61M	8	-0.20	8
Root:shoot slope (low density, 1986)	-0.49	8	-0.65M	8
Root:shoot slope (high density, 1986)	-0.10	8	0.11	8
Root:shoot intercept (low density, 1986)	0.61M	8	0.97**	8
Root:shoot intercept (high density, 1986)	0.22	8	0.61M	8
Seed:shoot @ $n = 300$ (low density, 1986)	-0.41	7	-0.95*	7
Seed:shoot @ $n = 300$ (high density, 1986)	-0.51	7	-0.93*	7

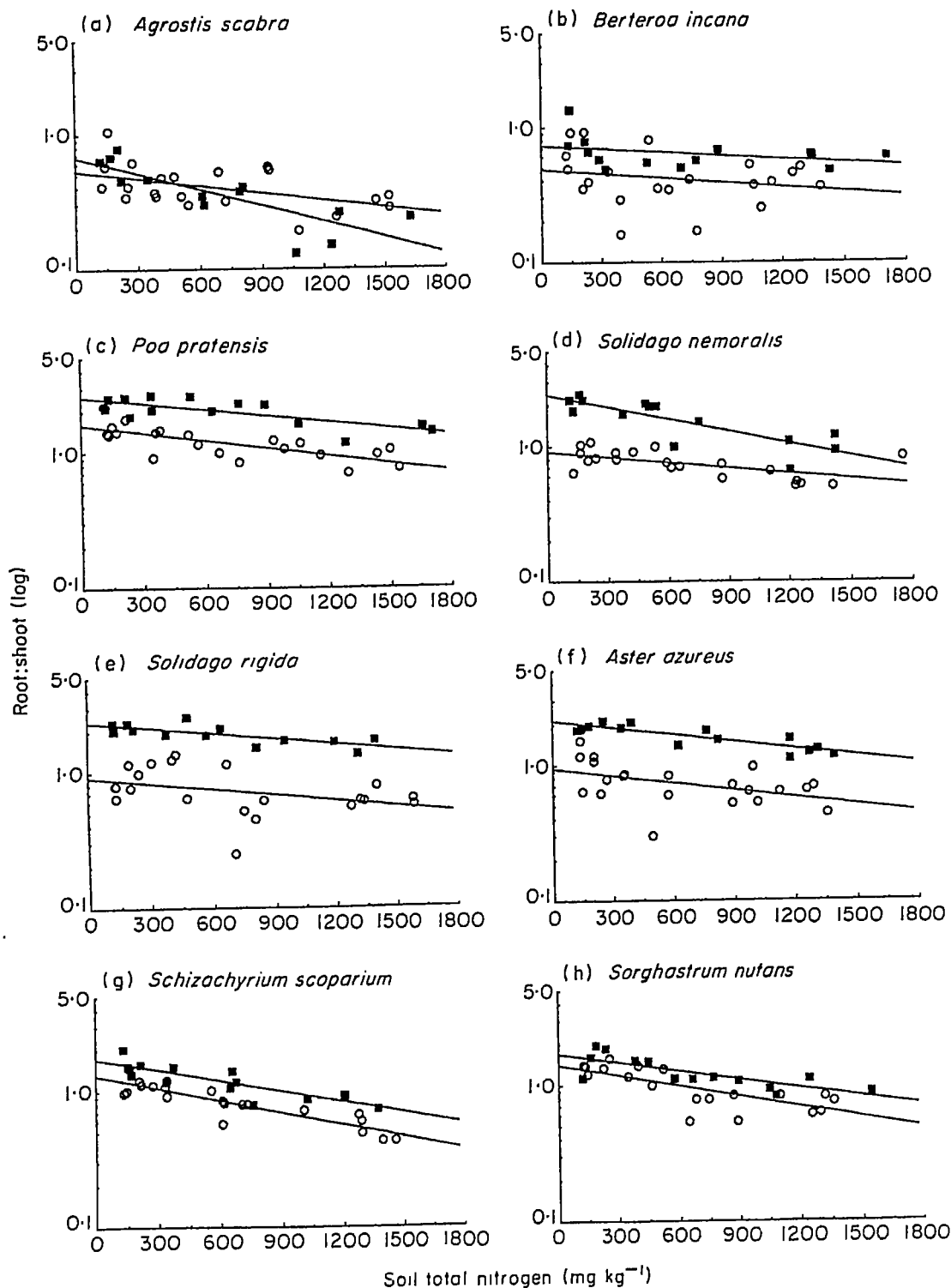


Fig. 3. The nitrogen-dependence of the root:shoot ratio of each species in the second year of the experiment is shown (on a log scale) for both the low plant density treatments (open circles) and for the high density treatments (closed squares). Lines are linear regressions of $\log(\text{root:shoot})$ on total soil nitrogen, based on 21 data points for the low plant density treatment and 14 for the high plant density treatment. All data points are shown. The Pearson correlation coefficients associated with each of these regression lines, listed for low and then high density, respectively, are (a) *Agrostis*: $r = -0.52$, $r = -0.82$; (b) *Berteroa*: $r = -0.24$, $r = -0.39$; (c) *Poa*: $r = -0.76$, $r = -0.76$; (d) *Solidago nemoralis*: $r = -0.64$, $r = -0.83$; (e) *Solidago rigida*: $r = -0.42$, $r = -0.84$; (f) *Aster*: $r = -0.48$, $r = -0.87$; (g) *Schizachyrium*: $r = -0.90$, $r = -0.86$; (h) *Sorghastrum*: $r = -0.81$, $r = -0.79$.

To keep comparisons to a reasonable level, we use only the 1986 data for summary variables such as slopes and intercepts of fitted curves or values of a variable on poor (soil total N = 300 mg kg⁻¹) and rich (soil total N = 1500 mg kg⁻¹) soils as estimated by fitted curves (e.g. Figs 1–3). Highly correlated variables, such as seed:shoot ratios on poor soils and those on rich soils, are shown only for their response on poor soils.

The slopes of the regressions of log (root:shoot) on soil total nitrogen were significantly negatively correlated with their intercepts for both high and low density (Table 4). In many cases, root:shoot slopes in high density pots were negatively correlated with mass per plant on both poor and rich soils and with yield per pot on both rich and poor soils, but were positively correlated with the seed:shoot ratio (Table 4). Intercepts of the log (root:shoot) vs soil total N regressions, especially for high density pots, were significantly positively correlated with yield per pot on both rich and poor soils and negatively correlated with the seed:shoot ratios (Table 4). Yield per pot on both poor and rich soil was often significantly negatively correlated with the seed:shoot ratio.

Discussion

Many of the patterns of N-dependent growth we found are consistent with long-standing generalizations. For instance, reviews by Mooney (1972) and Chapin (1980) showed that, within a plant species, root:shoot ratios decrease with an increase in soil nutrient richness. Our results show just this pattern (Fig. 3). Mass per plant, yield per pot, and seed:shoot increased with increased nutrient supply, as frequently reported (e.g. Bradshaw *et al.*, 1964; Austin & Austin, 1980; Austin *et al.*, 1985; Tilman, 1986). That mass per plant and RGR decreased with increased population density is consistent with Harper (1977).

The eight herbaceous successional species studied here have correlated suites of traits. Early successional species, which tend to occur on nitrogen poor soils, tend to have higher RGR_{max}, higher seed:shoot ratios and lower root:shoot ratios than later successional species (Tables 3 and 4). Higher growth rates for early successional species have also been reported by Rice, Penfound & Rohrbaugh (1960), Parrish & Bazzaz (1982) and Tilman (1986). Species with lower root:shoot ratio intercepts (and thus with lower root:shoot ratios; see Fig. 3) tend to produce less mass per plant and yield per pot but to have a higher proportion of

above-ground production as seed, than species with higher root:shoot intercepts (Table 4). Root:shoot slopes are a measure of plasticity of allocation. The steeper the slope, the more the morphology of a plant changes in response to soil total N. Root:shoot intercepts are negatively correlated with root:shoot slopes, indicating that plants with low root:shoot intercepts, which tend to be early successional species and/or species of nitrogen-poor soils, have greater plasticity than those with higher intercepts. Thus, as frequently reported (e.g. Hickman, 1975; Bazzaz, 1979), early successional species are more plastic than later successional species.

The correlations among these traits suggest that plants face allocation-based trade-offs (Mooney, 1972). Plants that allocate a higher proportion of their above-ground biomass to seed produce less total biomass (mass per plant and yield per pot) than species with lower allocation to seed. This agrees with within-species but between-population variation in *Polygonum cascadense* Baker (Hickman, 1975), in *Poa annua* L. (Law, 1979), in *Fragaria* sp. (Hancock & Bringhurst, 1980) and in other species (reviewed in Evenson, 1983). For the eight CCNHA species, species with a higher proportion of their biomass in roots tend to have lower maximal growth rates but greater mass per plant and yield per pot than species with proportionately less root biomass. This decrease in RGR_{max} is consistent with the theoretical prediction that RGR_{max} should be proportional to percent leaf biomass (Monsi, 1968; Tilman, 1988) and with a review of the effects of different allocation patterns on RGR_{max} (Tilman, 1988). Another allocation-based trade-off is suggested by the inverse correlation between root biomass and seed biomass.

Grime (1979) suggested that plants do not compete on low nutrient soils but rather that low nutrient levels act as a 'stress' that prohibits plants from attaining a sufficient biomass to compete. In contrast, Newman (1973), Tilman (1982, 1988) and Grubb (1985) have suggested that there should be strong competition on nutrient-poor soils. Our experiments did not include interspecific competition, but the two density levels allow a measure of intraspecific competition. If there were no intraspecific competition on nutrient-poor soils, plant density would have no effect on RGR or mass per plant. However, mass per plant and RGR were higher in the low density treatments than in the high density treatments for each of the eight species across the full range of soil N (Figs 1 and 2). ANOVA and contrasts showed a highly significant

Table 4. Correlations among parameters describing aspects of the nitrogen-limited growth of the eight plant species, based on parameters for the fitted curves shown in Figs 1-3 and similar fitted curves not illustrated. Each element in this table is a Pearson correlation coefficient, r . The correlations compare a pair of traits to determine if there is a simple pattern of variation in these traits among the eight species. Note that $n = 8$ for all comparisons except those involving seed:shoot ratios, for which $n = 7$. M means $0.10 \geq P > 0.05$; * means $0.05 \geq P > 0.01$; and ** means $P \leq 0.01$.

	A	B	C	D	E	F	G	H	I	J	K	L	M
Root:shoot parameters													
A. Slope, low density	1.00												
B. Slope, high density	0.39	1.00											
C. Intercept, low density	-0.92**	-0.54	1.00										
D. Intercept, high density	-0.42	-0.77*	0.70M	1.00									
Mass per plant at:													
E. Low density, poor soil	0.21	-0.31	0.05	0.60	1.00								
F. Low density, rich soil	-0.12	-0.66M	0.29	0.74*	0.82*	1.00							
G. High density, poor soil	0.06	-0.81*	0.03	0.48	0.27	0.61	1.00						
H. High density, rich soil	0.05	-0.78*	0.02	0.35	0.21	0.53	0.94**	1.00					
Yield per pot at:													
I. Low density, poor soil	0.21	-0.32	0.06	0.60	1.00**	0.83**	0.27	0.21	1.00				
J. Low density, rich soil	-0.12	-0.66M	0.29	0.74*	0.82*	1.00**	0.61	0.54	0.83**	1.00			
K. High density, poor soil	-0.44	-0.82*	0.67M	0.89**	0.66	0.80*	0.44	0.43	0.66M	0.80*	1.00		
L. High density, rich soil	-0.62M	-0.89**	0.77*	0.83**	0.42	0.71*	0.50	0.53	0.42	0.71*	0.95**	1.00	
Seed:shoot at:													
M. Low density, poor soil	0.89**	0.15	-0.90**	-0.36	-0.06	-0.15	0.30	0.17	-0.07	-0.15	-0.51	-0.67M	1.00
($n = 7$)													
N. High density, poor soil	0.60	0.65	-0.77*	-0.83*	-0.50	-0.67M	-0.31	-0.27	-0.51	-0.68M	-0.85*	-0.91**	-0.71M

and equally strong effect of density on RGR in both nutrient poor and nutrient rich soils. Thus, every one of these species experienced intraspecific competition, even on the most nitrogen poor soils. These soils, with total soil N of c 125 mg-N kg⁻¹-soil are poorer than the poorest soils we observed in sampling 2300 old field quadrats at CCNHA (Inouye *et al.*, 1987), and would normally be denominated by lichens, mosses and soil algae. Our results suggest that, contrary to Grime (1979), intraspecific competition is not weaker on nutrient poor soils.

The data presented here can test between two qualitatively different theories of succession: One, the resource ratio hypothesis, views succession as a slowly moving equilibrium. The other views succession as a transient, non-equilibrium process. The resource ratio hypothesis (Tilman, 1985), which has been applied to primary successions and to secondary successions on impoverished soils, states that plants face an allocation-based trade-off (Tilman, 1988) between their competitive ability for a limiting nutrient versus their competitive ability for light. Succession is hypothesized to occur as nutrient accumulation causes changes in the ratio of nutrients to light. The successional sequence is viewed as a moving equilibrium, with species composition being almost in competitive equilibrium with current nutrient:light ratios. Early successional species are hypothesized to be superior competitors at low nutrient:light ratios because of higher allocation to roots (Chapin, 1980; Tilman, 1988) lower tissue nutrient concentrations, leaf longevity (Chapin, 1980), and more efficient internal recycling of nutrient (Berendse & Aerts, 1984, 1987; Berendse & Elberse, 1989). Late successional species are hypothesized to be superior competitors for light because of greater allocation to stem and thus greater height (Horn, 1971; Givnish, 1982; Tilman, 1985, 1988), lower light compensation points (Bazzaz, 1979), and leaf location, size and shape (Horn, 1971).

The other approach, which has been embodied in many different formulations (e.g. Horn, 1971; Werner & Platt, 1976; Connell & Slatyer, 1977; Tilman, 1985, 1988; Huston & Smith, 1987) views secondary succession as a transient process caused by trade-offs between competitive ability versus colonization ability and/or maximal growth rate. The eventual successional dominants are hypothesized to be superior competitors. The initial dominants are inferior competitors but either are superior colonizers or have greater maximal growth rates. These traits would allow

them to attain a period of transient dominance during the time required, on average, for superior competitors to colonize the habitat and/or to grow to a biomass sufficient to displace them. The trade-offs required by this model could be allocation based. Colonization ability depends on seed size, but so does competitive ability for light (Werner & Platt, 1976; Tilman, 1988). Plants that produce many small seeds are more likely to colonize a disturbance, but would have seedlings that are inferior competitors for light. On nutrient rich soils, high allocation to leaves would give high RGR_{max}, but would result in poor competitive ability for light compared to lower leaf allocation accompanied by greater stem allocation and thus greater height (Tilman, 1988). Similarly, high allocation to roots would lead to superior competitive ability on poor soils, but would cause lower RGR_{max} because of low allocation to leaves (Tilman, 1988) and poor colonization because of low allocation to seed.

The data reported here for eight herbaceous species support the hypothesis that the herbaceous portion of secondary succession at CCNHA results from the transient dynamics of colonization and competitive displacement, and tend to refute the equilibrium version of the resource ratio hypothesis. Contrary to the predictions of the resource ratio hypothesis, early successional species tend to have lower root:shoot ratios than late successional species (Table 3, Fig. 3). The results are more clearly contradictory if successional soil nitrogen rank is used. The species that reach peak abundance on the most nitrogen poor soils have the lowest root:shoot ratios whereas those that reach peak abundance on the most nitrogen rich soils have the highest root:shoot ratios. Similarly, a survey of root, stem and leaf biomass distribution in a chronosequence of 37 CCNHA old fields has shown that root:shoot ratios increase significantly through time (Gleeson & Tilman, in preparation). On average, root:shoot ratios increased from 0.8 in one year old fields, to 4.3 in 55 year old fields, to almost 9 in native prairie.

Although the higher root:shoot ratios of later successional species are consistent with them being superior competitors for nitrogen, this is indirect evidence of competitive ability. Some direct evidence is provided by competition experiments that have been performed among various pairs of CCNHA grasses grown for 3 years in gardens with different soil mixtures (Tilman & Wedin, in preparation). Those experiments have shown that *Schizachyrium scoparium* almost

completely displaces *Agrostis scabra* from nitrogen poor soils, even though both species survive in the absence of interspecific competition. *Schizachyrium* similarly displaces *Poa pratensis* from low nitrogen soils. The superior competitive ability of *Schizachyrium* for nitrogen is consistent with its higher root:shoot ratio (Fig. 3).

Although higher root:shoot ratios of later successional species contradict the resource ratio hypothesis, they support the transient dynamics hypothesis, but only if early successional species have greater RGR_{max} and/or greater colonization abilities. Early successional species do tend to have higher RGR_{max} (Table 3; Tilman, 1986). Early successional species, especially those of nitrogen-poor soils, tend to have a much higher proportion of their biomass in seed (Table 3), which may make them better colonists. Our survey of 22 old fields and of 11 successional strips has shown that early successional species (*Agrostis scabra* and *Berteroa incana*) are present in most first year fields, that mid-successional species are not present until later (*Poa pratensis* at year 2, *Solidago nemoralis* and *S. rigida* at year 9), and that later successional species first occur ever later (e.g. *Schizachyrium scoparium* at year 12). Thus, early successional species are better colonists of old fields, perhaps partially because of their greater allocation to early, copious seed production. If further work supports the view that later successional species are superior nitrogen competitors, then the pattern of secondary succession at CCNHA would suggest that the first 30–40 years of herbaceous succession on this nitrogen poor soil may be just the transient dynamics of competitive displacement, with 10 or more years required for late successional species to colonize a given field and an additional 10–30 years required for these superior nitrogen competitors to spread across a field and competitively displace inferior nitrogen competitors.

Several other lines of evidence lend more support to the transient dynamics hypothesis than to the equilibrium resource ratio hypothesis. First, nutrient addition experiments at CCNHA have shown that nitrogen is limiting in fields of all successional ages, ranging from newly abandoned, to 50 years post-agriculture, to native, never-farmed prairie openings (Tilman, 1983, 1984, 1987, 1988). Thus, despite the increased levels of total nitrogen during succession, nitrogen remains an important limiting resource. Second, *Schizachyrium scoparium*, a late succession species, has decreased dramatically and highly significantly in abundance during 6 years of N addition at CCNHA,

whereas *Agropyron repens* Beauv., an early successional species, has dramatically and consistently increased (Tilman, 1987, 1988). This is inconsistent with the prediction of the resource ratio hypothesis that the successional replacement of *Agropyron* by *Schizachyrium* is caused by the increase in soil N during succession.

Tilman (1986), in analysing a short-term greenhouse study of the nitrogen-limited growth of nine CCNHA herbs, assumed that species attaining the greatest mass per plant on N poor soils would be superior competitors for N. Based on that assumption, he suggested that early successional species of CCNHA might be superior competitors for N, and thus considered those results as support for the resource ratio hypothesis. We reach the opposite conclusion in this paper based on the assumption that high root:shoot ratios are indicative of competitive ability for N. The issue of which plant traits are indicative of competitive ability for a given resource will be resolved only through additional experimental studies. However, if we analyse our data as did Tilman (1986), we find no significant rank order correlation between mass per plant on a poor soil (soil total N = 300, using fitted curve of Fig. 2 for low density treatment) and successional rank ($r_s = 0.0$, $P > 0.1$, $n = 8$). The difference between the results in Tilman (1986) and those reported here may be caused by the different durations of these experiments. The short-term (12 week) greenhouse experiments of Tilman (1986) were probably greatly influenced by the maximal, density-independent growth rates of those species, whereas our 2-year experiments were long enough for density-dependent, intraspecific competition to occur. Thus, the short-term experiments of Tilman (1986) probably measured the nitrogen-dependence of maximal growth rates in the absence of intraspecific competition, whereas the present experiments measured the effects of intraspecific competition on plant traits. As such, the higher mass per plant reported for early successional species in Tilman (1986) may mean that they have higher maximal growth rates, just as reported here. If this is so, the results of Tilman (1986) would support the transient dynamics hypothesis of succession.

Succession at CCNHA differs from many other secondary successions because at CCNHA plants may be competing more for N than light. The results presented here suggest that there is a trade-off between competitive ability for N and colonization rate. Species with low root:shoot ratios (intercepts) have a significantly higher proportional allocation to seed (Table 4). Thus, if

competitive ability for N is gained by high allocation to roots, this may result in lower allocation to seed, and thus lower colonization ability. High allocation to root, as already discussed, should also have a cost in terms of RGR_{max} (Tilman, 1988). Such trade-offs can cause successional transient dynamics on nutrient poor soils, just as other trade-offs can cause successional transient dynamics when plants compete for light on nutrient rich soils (Horn, 1971; Huston & Smith, 1987; Tilman, 1985, 1988).

Although the pattern of nitrogen-limited growth of these eight herbaceous species does not support the equilibrium version of the resource ratio hypothesis, other aspects of the successional sequence at Cedar Creek do. Silver maple, red oak and other woody seedlings are present, though not abundant, in many first-year fields, but barely grow. Experimental additions of nitrogen lead to highly significant, almost exponential, increases in woody plant biomass in successional fields and these woody plants shade out shorter herbaceous species on these high nitrogen treatments (Tilman, 1987, 1988). Similarly, woody plant cover increases significantly during years 20–60 of succession as nitrogen accumulates in the soils of Cedar Creek Natural History Area (Inouye *et al.*, 1987). Over a 100–200 year period, N accumulation may cause a gradual increase in plant biomass and decrease in light penetration, and thus favour taller, woody species, much as hypothesized by the resource ratio hypothesis. However, the N-dependent growth experiments reported here suggest that N accumulation may not be having a similar effect on the herbs that dominate succession during the first 50 years. Rather, their successional dynamics may reflect the transient dynamics of interactions among species that have trade-offs between their competitive ability for N versus their maximal growth rate and/or colonization ability.

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