

## ALLOCATION AND THE TRANSIENT DYNAMICS OF SUCCESSION ON POOR SOILS<sup>1</sup>

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**Abstract.** Biomass and nitrogen allocation to leaf, root, stem, and reproduction was determined in a 35-field chronosequence that spans the first 60 yr of secondary succession on a Minnesota sand plain. Biomass (grams per square metre) in leaf and root increased during succession, but reproductive biomass declined, and that in stem remained constant. Because root biomass increased twice as rapidly as leaf biomass, the proportion of total biomass in root increased during succession, whereas that in leaf, reproduction, and stem declined. In an additional study, biomass allocation was determined on a species-by-species basis for 46 species common at different times during succession. This study showed a similar pattern of increasing proportional root allocation and declining proportional reproductive and stem allocation during succession. These changes were accompanied by an increase in total soil nitrogen and a decrease in light penetration to the soil surface during succession.

Increasing root allocation and decreasing reproductive allocation suggest that succession on these nutrient-poor soils is the transient dynamics of colonization and competitive displacement, with later successional species being superior nitrogen competitors because of higher root allocation. Allocation trade-offs between root, stem, leaf, and seed can lead to initial dominance by species with high seed and leaf allocation, presumably because of greater colonization and/or maximal growth rates. Thus, this succession differs markedly from successions on rich soils, for which stem allocation is increasingly important. These results contradict the resource ratio hypothesis as an explanation for the pattern of early succession on impoverished soils.

*Key words:* biomass allocation; leaf; light; old fields; plant competition; reproductive mass; root; sand plain; soil nitrogen; stem; succession; transient dynamics; vegetation dynamics.

### INTRODUCTION

The distinction commonly drawn between primary successions and secondary successions reflects the belief that different processes are responsible for controlling the pattern of succession in these two cases. Primary successions, such as the classical examples of succession at Glacier Bay (e.g., Cooper 1923, Lawrence 1958) and in the sand dunes of southern Lake Michigan (e.g., Cowles 1899, Robertson and Vitousek 1981), begin with a bare mineral soil that lacks nitrogen and plant propagules. The slow accumulation of nitrogen in these soils (e.g., Crocker and Major 1955) is thought to result in increased plant biomass, which, in turn, captures a larger proportion of the incident light. The morphology and physiology of plants dominant at different times during primary successions might then be explained as resulting from this change in the relative availability of nitrogen and light. This has been termed the resource ratio hypothesis of succession (Tilman

1985), and assumes that much of the dynamics of primary succession are driven by slow changes in soil quality, as measured by the supply rate of nitrogen. This explanation of succession as a soil-driven process assumes that vegetation composition at any instant approaches a quasi-equilibrium with current resource availabilities, and that succession occurs as resource availabilities change.

In contrast, secondary successions, because they occur on existing soils that contain nitrogen and plant propagules, are often thought not to be soil driven, but to have transient dynamics that are caused by the life histories of the species, their maximal growth rates, colonization abilities, and the dynamics of their interactions (e.g., Horn 1971, Werner and Platt 1976, Connell and Slatyer 1977, Bazzaz 1979, Tilman 1985, 1988, Huston and Smith 1987). For instance, one possible explanation for secondary successions is that there is a trade-off between competitive ability and maximal growth rate. On a nutrient-rich soil, where competition for light is important, the initial dominants would be short, leafy species with high maximal growth rates, but with low allocation to woody stems. These would be displaced by a sequence of ever taller, but more slowly growing, species. All species except the final dominants would be inferior competitors, but would

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have periods of transient dominance because of their greater maximal growth rates (Tilman 1988). Other trade-offs, such as a trade-off between colonization ability and competitive ability, could also cause succession (Werner and Platt 1976). Such a successional sequence would not be the quasi-equilibrium result of slow changes in site quality, but would be the transient dynamics of competitive displacement, with better colonists being replaced by species that are superior competitors but poorer colonists.

Secondary successions that begin on nutrient-impooverished soils, such as those that have lost most of their fertility because of agricultural disturbances (e.g., Odum 1960, Golley 1965, Monk and Gabrielson 1985, Inouye et al. 1987, Tilman 1987), may have more in common with primary successions than with secondary succession on rich soils. However, transient and soil-driven dynamics are not mutually exclusive processes. A given succession could be a series of transient states, each moving toward a continually shifting potential equilibrium, or transient dynamics could be more important during early succession and slowly grade into soil-driven dynamics.

Tilman (1988) has presented a theory of succession based on resource competition and plant allocation patterns. This theory explicitly distinguishes between transient and soil-driven dynamics. The model assumes that plants grow by allocating their net production to leaves, stems, roots, or reproduction (Mooney 1972). The allocation process creates morphological trade-offs because allocation of a given unit of photosynthate to one structure or process precludes allocation to another. The resulting morphology determines a plant's ability to compete for light (via leaves and stems) and a soil resource (via roots). As a result, each species, as defined by its allocation pattern, is more competitive in some sites and times than in others. Species that have relatively more root than leaf and stem are competitively favored on poor soils at equilibrium, whereas species with higher stem but lower root biomass are favored on richer soils at equilibrium. Thus, if the resource ratio hypothesis were applied to primary successions on nutrient-poor soils, the initial dominants would be predicted to have high root and low stem and leaf biomass, whereas the dominants of the richer soils of late succession would have low root, but high stem biomass.

Quite a different pattern is predicted if succession on an initially nutrient-poor soil results from the transient dynamics of competitive displacement. For theoretical cases in which all species were equally good colonists, the initial dominants were species with relatively high leaf biomass (and thus high maximal growth rates) and low root biomass (Tilman 1988). They were competitively displaced, through time, by a sequence of species that were progressively better competitors for the limiting soil nutrient because of proportionately higher root biomass, but which had lower maximal

growth rates because of proportionately lower leaf biomass. Transient dynamics could also be caused by a trade-off between colonization ability (i.e., seed allocation) vs. nutrient competitive ability (i.e., root allocation). Thus, for nutrient-poor soils, the two models predict opposite trends in root allocation, with soil-driven dynamics favoring decreasing root over time, and with transient dynamics favoring increasing root.

This paper documents the pattern of change in plant morphology for an old-field chronosequence on the unproductive, nitrogen-depleted sandy soils of Cedar Creek Natural History Area (CCNHA). Successional patterns in plant functional groups (Inouye et al. 1987) and species (Tilman 1988) have already been studied in detail at this site. These studies have shown that increases in field age are accompanied by a continuous series of species replacements and by increases in total soil nitrogen, total plant cover, perennial cover, woody plant cover, and native prairie plant cover, and by decreases in light penetration to the soil surface. These trends seem consistent with succession being a soil-driven process, as formalized in the resource ratio hypothesis (Tilman 1985). On the other hand, a study of three fields of different age shows a trend of increasing root allocation with successional age (R. McKane and M. Norland, *personal communication*), which is more consistent with succession being the transient dynamics of competitive displacement on poor soils. A study of the nitrogen-dependent growth of eight CCNHA species is also more consistent with the transient dynamics hypothesis (Tilman and Cowan 1989). The data presented here on biomass allocation and nitrogen content across a chronosequence of 35 old fields can help determine the importance of soil-driven processes vs. transient dynamics in this successional sequence, and thus add to our understanding of the mechanisms of successional change.

## METHODS

### *Community patterns*

This study was conducted at CCNHA, owned by the University of Minnesota, and located on a large glacial outwash sand plain 50 km north of Minneapolis in southeastern Minnesota. The major portion of this study consisted of samples of community-wide biomass and nitrogen distributions among leaves, roots, stems, and reproductive structures, and of soil chemistry in a chronosequence of 35 old fields. Of the 35 fields studied, 22 were formerly farmed fields that had been sampled in 1982 when permanent transects were established (Inouye et al. 1987). These 22 fields had successional ages of 5, 12, 15, 16, 19, 19, 26, 26, 28, 30, 30, 32, 35, 35, 40, 40, 44, 46, 46, 53, and 60 yr postagriculture in 1987, and thus mainly represent the later stages of succession. An additional 13 sampling sites cover the early stages of succession. These form a series of adjacent 20 × 100 m plots, abandoned

sequentially, one plot per year, for the last 13 yr, and will be called the 1–13 yr fields.

All fields were sampled during 13–30 July 1987. There were five sampling locations, spaced uniformly within a field, for each of the 35 fields. For the 22 old fields, the five sampling locations were evenly positioned with respect to the permanent transects (Inouye et al. 1987) in the fields. For the 1–13 yr fields, the five sampling locations were spaced at 15-m intervals along a 100-m line bisecting each field. At each of the five sampling locations in each field, light intensity above the vegetation and at the soil surface was measured in duplicate using a Lambda Instrument PAR cosine collector. In each of the five sampling locations in each field, a 0.1 × 1.0 m strip of vegetation was sampled by clipping at the soil surface. This aboveground sample was then sorted to litter, grass, and forb, measured for modal height, dried to constant mass at 40°C, and weighed. After drying, ramets were counted, living vegetation was separated to leaf, stem, and reproductive parts (inflorescences and infructescences), and the parts re-dried and weighed. Three 30 cm deep by 4.8 cm diameter soil cores, evenly spaced along the clipped strip, were collected from each of the five strips in each field. These were rinsed of soil and litter on a screen under a fine water spray to obtain roots, which were dried and weighed. Three additional 10 cm deep by 2.5 cm diameter soil cores per strip were pooled and mixed, with 20 g placed in 50 mL of 2 mol/L KCl to obtain extractable nitrate. The remainder of the soil was used for moisture determination and for total soil nitrogen analysis. Leaf, stem, and root tissue and litter from each field were ground and analyzed for total nitrogen content. Total nitrogen of tissue and soil were obtained by potassium persulfate digestion, with the resulting nitrate measured using a Technicon II autoanalyzer. Nitrate in the soil extracts was also determined on the autoanalyzer, and is reported as milligrams of NO<sub>3</sub>-N per gram of dry soil.

#### *Species patterns*

The other portion of this project took an alternative approach. The biomasses of roots, leaves, stems, and reproductive parts of 46 common plant species were determined, on a species-by-species basis, at the time during the growing season of 1987 when each was in reproductive growth form. The species were chosen on the basis of previous surveys of species abundance through successional time (Tilman 1988) so as to explain a large proportion of cover across the entire span of field ages. Individual plants were chosen as encountered in the old fields. We sampled 5–20 plants per species (generally 15, see Appendix), with a maximum of five plants per species per site to minimize confounding local habitat and genetic effects. Each species was represented by a range of sizes, but woody species (e.g., *Rhus*, *Quercus*) were limited to the low end of their size range. For each species, individuals were har-

vested by extracting a 30 cm deep by 20 cm diameter soil core centered around a plant. Much of the loose sand was then removed by gentle tapping. Next, the central plant was separated from other plants in the core, with care taken to remove both above- and belowground parts of all plants except the central plant. The central plant, and the attached roots, were then rinsed, dried, separated to leaf, stem, root, and reproductive parts, and weighed. These were analyzed by associating the allocation pattern of each species with the successional age at which it was most abundant (see Results). Successional age is the mean of the distribution of relative cover values of each species against field age for that species as measured in the 22-field survey (Inouye et al. 1987), with data broken into histograms with 8-yr time steps. Because early successional species persist for many years during succession at CCNHA (Tilman 1988), even an early successional species, such as *Crepis tectorum*, has a mean successional age of 8.8 yr (Appendix). The mean ages for early successional species are also increased because the 22-field survey had few extremely young fields. Unless otherwise noted, all data were analyzed using linear regression of a variable against successional age.

## RESULTS

### *Community patterns*

For the survey of root, leaf, stem, and reproductive biomass in the old fields, the five samples from each field were averaged and all analyses done on means per field. The data from the 35 old fields were analyzed as a unit, and were also analyzed separately in two samples: the set of 22 old fields and the set of 1–13 yr fields. This was done to determine if the pattern during the initial portion of succession as represented by the 1–13 yr fields differed from the longer term pattern as represented by the sequence of 22 old fields. Unless otherwise noted, discussions of significant trends refer to the full 35-field data set.

Total plant biomass per unit area (root + leaf + stem + reproductive) increased with successional age in the overall sample (Fig. 1A,  $r^2 = 0.51$ ,  $df = 33$ ,  $P < .001$ ), but had the opposite trend for the 1–13 yr fields considered alone, with total biomass declining for the first 13 yr ( $r^2 = 0.33$ ,  $df = 11$ ,  $P = .04$ ). Mean biomass per ramet (total biomass per unit area ÷ no. ramets per unit area) increased with age (Fig. 1B,  $r^2 = 0.22$ ,  $df = 33$ ,  $P = .005$ ). Ramet density (ramets per square metre) declined with age but not significantly (Fig. 1C,  $r^2 = 0.09$ ,  $df = 33$ ,  $P = .07$ ). The regression of  $\log_{10}$  of mean biomass per ramet ( $y$ ) vs.  $\log_{10}$  of ramet density ( $x$ ) is significant ( $r^2 = 0.55$ ,  $df = 33$ ,  $P < .001$ ). The equation of the reduced major axis of this relationship is  $y = -1.52x + 4.29$ . The correlation of  $\log_{10}$  of total biomass vs.  $\log_{10}$  of ramet density is not significant.

Total nitrogen in the soil increased with age (Fig.

2A,  $r^2 = 0.52$ ,  $df = 33$ ,  $P < .001$ ) as did total nitrogen in plant tissue (grams per square metre) (Fig. 2B,  $r^2 = 0.54$ ,  $df = 33$ ,  $P < .001$ ).

Light penetration to the soil surface (proportion of full sunlight) declined with age (Fig. 2C,  $r^2 = 0.26$ ,  $df = 33$ ,  $P = .002$ ) overall, but increased during the first 13 yr ( $r^2 = 0.60$ ,  $df = 11$ ,  $P = .002$ ). Light penetration to the soil surface was a decreasing function of living aboveground biomass ( $r^2 = 0.46$ ,  $df = 33$ ,  $P < .01$ ).

Soil nitrate levels were low throughout the chronosequence. There was no significant trend in nitrate levels with age (Fig. 2D,  $r^2 = 0.02$ ,  $df = 33$ ,  $P = .37$ ). The high nitrate values for three of the fields are due to one (in the case of the two 30-yr fields) or two (for the 60-yr field) of the five samples being exceptionally high.

Allocation to roots, leaves, stems, and reproductive structures was calculated as absolute values (grams per square metre), on a mass per ramet basis (grams per ramet), and as proportions (Fig. 3). Proportion leaf, stem, and root was calculated as proportion of total vegetative biomass (leaf + stem + root) to avoid confounding interpretations of resource competition, and proportion reproduction as the proportion of total biomass (vegetative + reproductive). Leaf biomass per unit area (Fig. 3A,  $r^2 = 0.59$ ,  $df = 33$ ,  $P < .001$ ) and per ramet (Fig. 3D,  $r^2 = 0.15$ ,  $df = 33$ ,  $P = .02$ ) increased with field age. Proportion leaf decreased with age (Fig. 3G,  $r^2 = 0.20$ ,  $df = 33$ ,  $P = .007$ ). Neither stem biomass per unit area nor per ramet was significantly correlated with age. For the first 13 yr, there was a negative correlation of stem per ramet with age ( $r^2 = 0.31$ ,  $df = 11$ ,  $P = .046$ ) caused by the high stem biomass per ramet during the first 2 yr when ramet density was unusually low (Fig. 1C). Proportion stem declined with age (linear:  $r^2 = 0.50$ ,  $df = 33$ ,  $P < .001$ , for  $y = ax^b$ ,  $r^2 = 0.62$ ,  $df = 33$ ,  $P < .0001$ , shown in Fig. 3H). Root biomass per unit area (Fig. 3C,  $r^2 = 0.52$ ,  $df = 33$ ,  $P < .001$ ), per ramet, (Fig. 3F,  $r^2 = 0.37$ ,  $df = 33$ ,  $P < .001$ ) and proportion root (linear:  $r^2 = 0.46$ ,  $df = 33$ ,  $P < .001$ ; for  $y = a + bx^{0.5}$ ,  $r^2 = 0.52$ ,  $df = 33$ ,  $P < .0001$ , Fig. 3I) all increased with age. In the first 13 yr, root, leaf, and stem biomass all declined with age, but none of these trends was significant ( $P > .05$ ).

Reproductive allocation decreased with field age both on a gram per square metre basis ( $r^2 = 0.46$ ,  $df = 33$ ,  $P < .001$ ) and as a proportion of total biomass (linear:  $r^2 = 0.40$ ,  $df = 33$ ,  $P < .001$ ; for  $y = ax^{-b}$ , shown in Fig. 4A,  $r^2 = 0.47$ ,  $df = 33$ ,  $P < .001$ ).

There were no significant overall linear correlations between age and tissue nitrogen concentrations, but when the early fields (1–13) and 22-field group were analyzed separately, there were significant but opposite trends. For the 22 fields, tissue nitrogen concentration declined with age for leaf (Fig. 3J,  $r^2 = 0.40$ ,  $df = 33$ ,  $P = .002$ ), stem (Fig. 3K,  $r^2 = 0.18$ ,  $df = 33$ ,  $P = .05$ ), and root (Fig. 3L,  $r^2 = 0.23$ ,  $df = 33$ ,  $P = .02$ ). In the 1–13 yr fields, tissue nitrogen increased in stem ( $r^2 =$

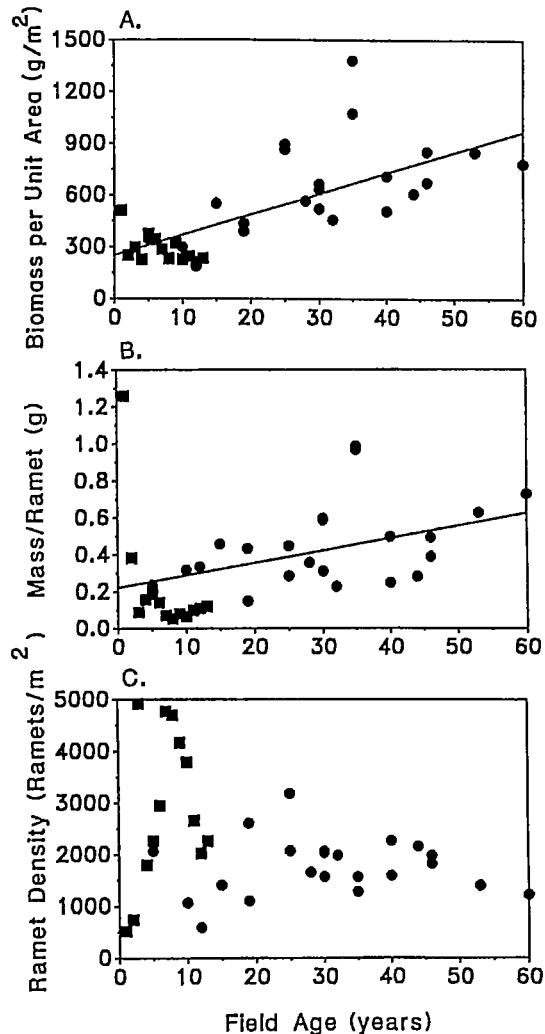


FIG. 1. (A) Total (aboveground + belowground) plant biomass per square metre, (B) plant size, calculated as biomass per ramet, and (C) plant density, calculated as ramets per square metre, are graphed against field age (time since abandonment) using data from all 35 old fields. Each point is the average value of a variable in a particular field. ■ the set of 1–13 yr old fields; ● the other 22 fields. Lines are based on linear regressions that used all 35 points.

0.45,  $df = 11$ ,  $P = .02$ ) and root ( $r^2 = 0.64$ ,  $df = 11$ ,  $P = .001$ ) but not in leaf. Using the entire 35-field data set, there were significant nonlinear relationships between root nitrogen and field age ( $r^2 = 0.18$ ,  $df = 32$ ,  $P < .05$ , fitted curve shown in Fig. 3L), between stem nitrogen and age ( $r^2 = 0.15$ ;  $df = 32$ ;  $P < .05$ ; Fig. 3K), but not between leaf nitrogen and age.

Aboveground litter biomass increased with field age ( $r^2 = 0.54$ ,  $df = 33$ ,  $P < .001$ ) as did litter nitrogen concentration ( $r^2 = 0.32$ ,  $df = 33$ ,  $P < .001$ ). Grasses, as a percentage of total aboveground biomass, increased with age ( $r^2 = 0.13$ ,  $df = 33$ ,  $P = .04$ ), with most of this increase being in the early years. Grass height increased with age ( $r^2 = 0.15$ ,  $df = 33$ ,  $P = .02$ ),

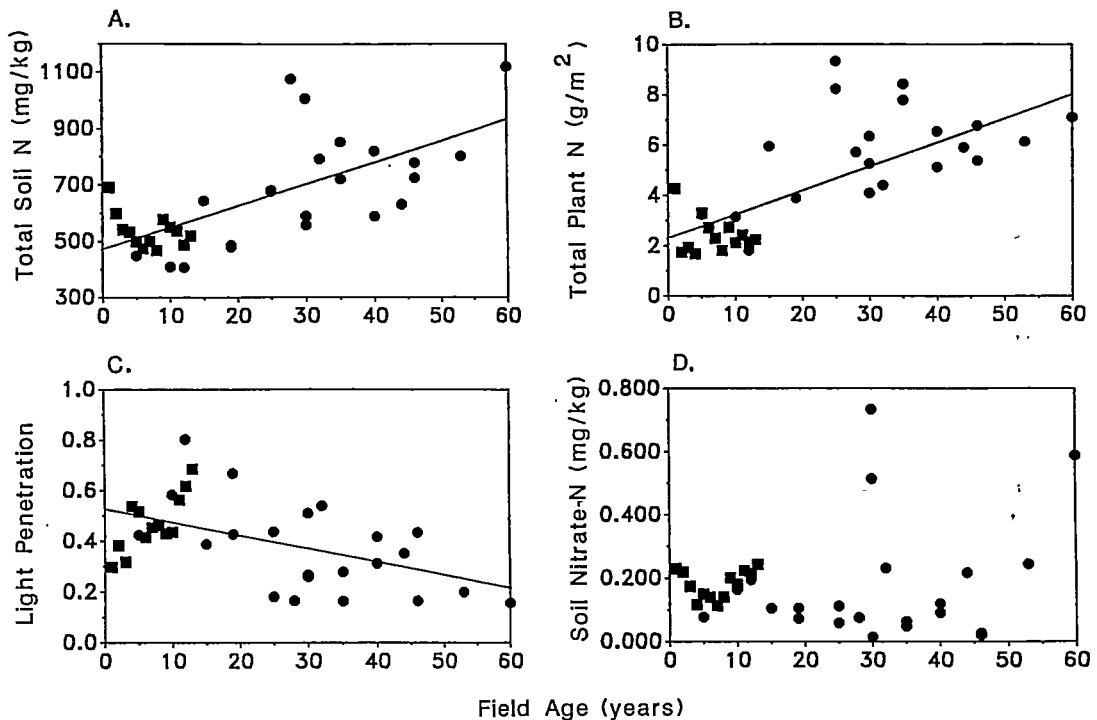


FIG. 2. Trends in nitrogen and light with field age (time since abandonment) for the 35 old fields. (A) Total soil nitrogen mass per unit soil mass, (B) total nitrogen content of aboveground + belowground living plant biomass per unit area, (C) proportion of full sunlight reaching the soil surface, and (D) 2 mol/L KCl-extractable nitrate. Each point is the average value in a field. ■ the set of 1–13 yr old fields; ● the other 22 fields. Lines are based on linear regressions that used all 35 points.

but the overall increase averaged only 5 cm for the 60-yr period.

#### Species patterns

The allocation pattern of each of the 46 species sampled is graphed against its successional status (mean field age) in Fig. 5. Species and sample sizes are given in the Appendix. Successional status ("field age") is an index of the successional time when each species is abundant (truncated at 60 yr, the age of the oldest field in the 22-field survey). Mean proportion of mass as leaves is unrelated to successional status (Fig. 5A,  $r^2 = 0.02$ ,  $df = 44$ ,  $P = .4$ ), while mean proportion stem declined (Fig. 5B,  $r^2 = 0.22$ ,  $df = 44$ ,  $P = .001$ ) and mean proportion root increased (Fig. 4C,  $r^2 = 0.13$ ,  $df = 44$ ,  $P = .02$ ) with field age. Proportion reproduction also decreased with field age (Fig. 4B, based on a non-linear regression,  $1/y = a + bx$ ,  $r^2 = 0.27$ ,  $df = 38$ ,  $P < .001$ ). Species that were not reproductive at harvest (see Appendix) were not included in the analysis.

#### DISCUSSION

The most pronounced pattern in these data is the increase in proportional root biomass with successional age. This occurred both in the community-wide study and the study of the morphology of 46 different successional species. Although absolute leaf biomass increased with successional age, proportion leaf decreased almost twofold. This is because absolute root

biomass increased almost twice as rapidly during succession as absolute leaf biomass. Coupled with the lack of increase in stem biomass, the decrease in proportion stem, and the minor increase in plant height, this demonstrates that this successional community was increasingly dominated by species with morphologies associated with superior competitive ability for limiting soil resources (Mooney 1972, Chapin 1980, Tilman 1988, 1989). It does not support the hypothesis that light competition is increasingly important during the first 40–60 yr of this succession.

Numerous nutrient-addition experiments at CCNHA have shown that nitrogen is the most important limiting soil resource throughout succession (Tilman 1983, 1984, 1987, 1988). These experiments have been underway since 1982, and water has had a significant effect, with reduced nitrogen effect, only in the driest year, 1988 (D. Tilman, *personal observation*). Total soil nitrogen doubled during the 60 yr of this chronosequence, but total nitrogen in plant tissues more than tripled. Thus, an increasingly larger proportion of the nitrogen was contained in plants. Despite the increase in total soil nitrogen, which is associated with an increase in nitrogen mineralization rates (Pastor et al. 1987), there was no significant increase in extractable soil nitrate. In total, these observations suggest that nitrogen remained limiting throughout this successional sequence. Further, after an initial rise, tissue nitrogen concentrations fell during succession, with late

successional leaves averaging  $\approx 1\%$  N and roots and stems averaging  $\approx 0.7\%$  N. Thus, the species dominant after 40–60 yr of secondary succession at CCNHA had lower tissue nitrogen concentrations than many earlier successional species. These low tissue N levels are consistent with limitation by and competition for N because they imply higher nitrogen-use efficiency (Chapin 1980).

The decline in light at the soil surface and the increase in total soil nitrogen are consistent with the resource ratio hypothesis. However, the changes in plant morphology associated with these resource changes contradict the equilibrium predictions of this theory and thus, also, the equilibrium predictions of optimal foraging theory (Bloom et al. 1985, Tilman 1988). That theory predicts that, as the availabilities of shoot resources decrease relative to root resources, plants which allocate more to shoot than root would have higher growth rates and would be favored. In these old fields, a trend of decreased light relative to nitrogen is paralleled by increased root relative to shoot. Considering the strength of other evidence supporting the predictions of optimal foraging theory (Bloom et al. 1985), this suggests that there are few species for which light is becoming an increasingly important resource during the first 40–60 yr of succession at CCNHA.

Published allocation data also fail to support the role of increasing light competition during other old-field successions. However, we must note that many of these data are for successions on nutrient-impooverished soils, and none of them distinguished between leaves and stems. In a comparison of nine herbs and six woody seedlings common at different times during secondary succession on the coastal sand plains of South Carolina, Monk (1966) reported increases in root:shoot ratios with successional status. This led him to suggest that root competition was the major driving force during that succession. Golley and Gentry (1966) found that a 12-yr field had threefold greater root biomass than a 1-yr field, but that aboveground biomass did not have a comparable increase. Mellinger and McNaughton (1975) reported a seasonal average root:shoot ratio that was 41% higher in a 17-yr field than in a 6-yr field. Newell and Tramer (1978) found an increase in root from 15 to 25% of total biomass when comparing a 1-yr with a 10-yr field. Although these studies were based on a much smaller sample of field ages than we used, and a shorter successional period, they all reported a pattern consistent with our findings.

The trends in allocation during succession at CCNHA, and the strong limitation by nitrogen throughout succession, suggest that the species dominant after 40–60 yr of succession may be superior competitors for nitrogen. Studies of some CCNHA species (Tilman and Cowan 1989) and a general review of successions (Bazzaz 1979) have shown that early successional species often have greater maximal rates of vegetative growth than later successional species.

This supports the growth rate–competition hypothesis of succession and is consistent with a trade-off between high maximal growth rate (which should result from high allocation to leaf; Monsi 1968), and high competitive ability for nitrogen (which should result from high allocation to roots).

Our trend of declining reproductive allocation during succession is consistent with other studies of successional species (Werner and Platt 1976, Newell and Tramer 1978, Abrahamson 1979, Evenson 1983), including CCNHA species (Tilman and Cowan 1989). This supports the colonization–competition hypothesis of succession (Werner and Platt 1976, Werner 1979). Early successional species often have smaller and thus more readily dispersed seed than late successional species (Salisbury 1942, Werner and Platt 1976, Tilman 1988). The early successional species of CCNHA, with their higher allocation to seed production, are likely to be better colonists than later successional species that allocate little to seeds. The later successional species, however, with their higher proportion root, are likely to be better competitors for nitrogen. This trade-off between seed production (colonization ability) and root production (competitive ability) could also be a cause of this succession. However, our data do not let us distinguish between the maximal growth rate–competition hypothesis and the colonization–competition hypothesis. This will require further studies of growth rate and dispersal rate differences among CCNHA species.

The pattern of secondary succession on nutrient-poor soils, such as those of CCNHA or of the coastal sand plains of the Carolinas, is quite different from the pattern of secondary succession on more fertile soils (e.g., Clebsch and Busing 1989). Billings (1938), for instance, reported that broomsedge, an early dominant, was replaced by dense stands of 3–5 m tall pines after 10 or 15 yr of succession on the relatively rich soils of the Piedmont of North Carolina. These pines were then replaced by a sequence of other tree species (e.g., Christensen and Peet 1985). In contrast, Odum (1960), Golley (1965), and Pinder and Kroh (1987) indicated that woody plants were rare and broomsedge and other herbs remained dominant for  $\geq 30$  yr during succession on the nutrient-poor coastal sand plains of this region. This suggests that there is a major contrast between the successional dynamics on nutrient-poor vs. nutrient-rich soils.

During successions that lead to rapid development of forest, the proportion of stem increases at the expense of the proportion of leaf and root. As an illustration (Fig. 6A), we have plotted proportion leaf, stem, and root for three forest chronosequences using data compiled by Cannell (1982). To do this, we use a triangle graph of vegetative allocation (see Tilman 1988), where proportion stem is plotted against proportion leaf, with the diagonals giving proportion root (assuming that leaf + stem + root = 1.0). The data are from

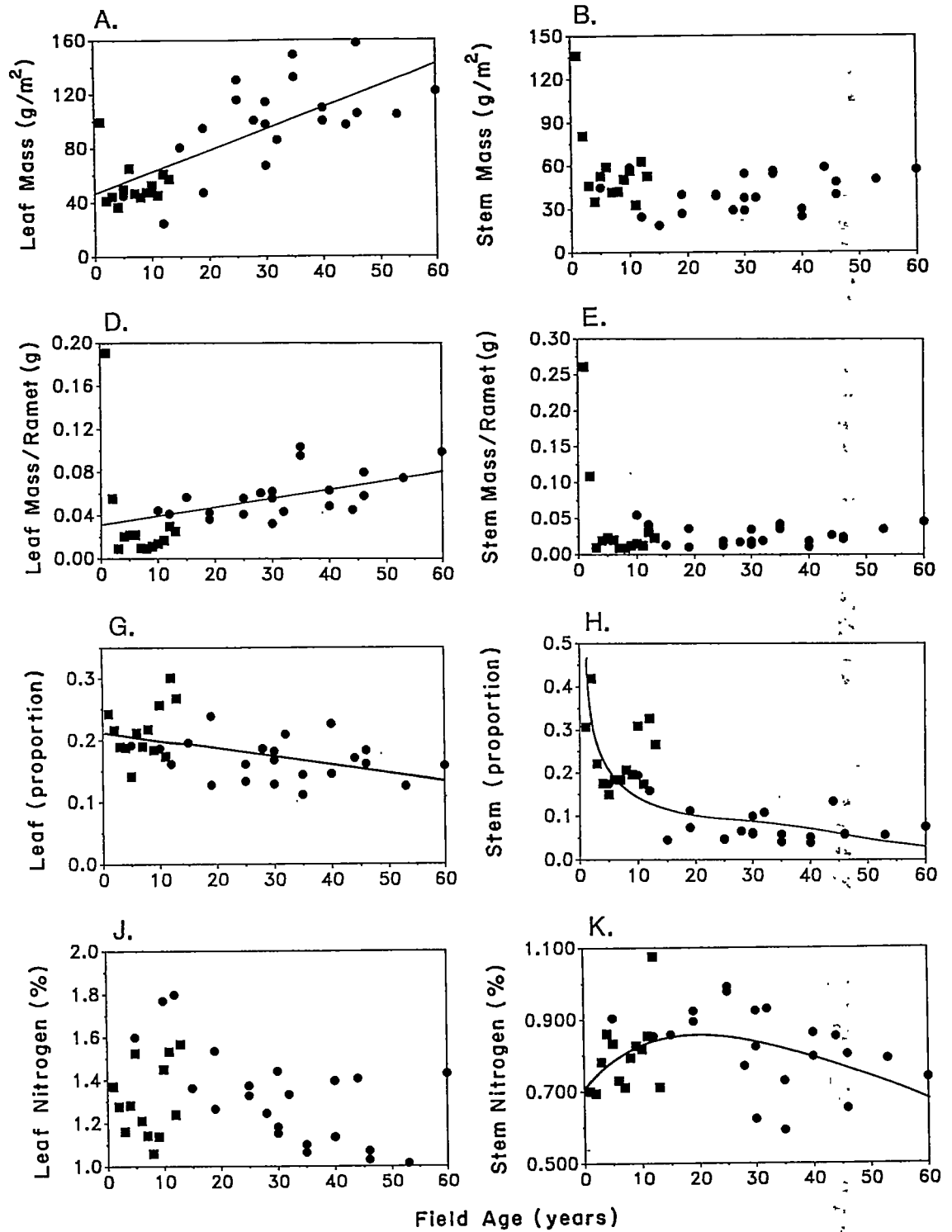


FIG. 3. Biomass and nitrogen allocation vs. field age (time since abandonment) for the 35 old fields: Absolute leaf dry mass (A), stem dry mass (B), and root dry mass (C) per unit area; dry mass per ramet for leaf (D), stem (E), and root (F); proportion of total plant dry biomass that is in leaf (G), stem (H), and root (I); and nitrogen content, as percent N in dry plant material, for leaf (J), stem (K), and root (L). Each point is the average of a variable in a field. ■ the set of 1–13 yr old fields; ● the other 22 fields. Straight lines are based on linear regressions and curves on nonlinear regressions (see Results: Community Patterns) that used all 35 points.

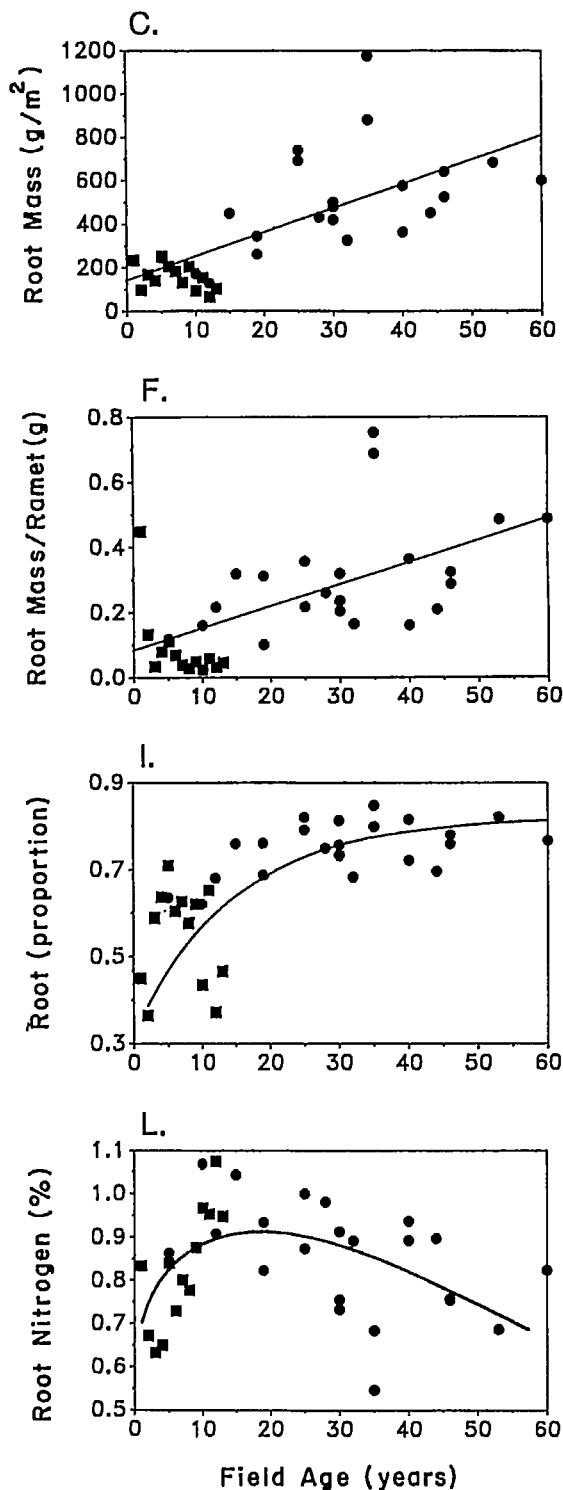


FIG. 3. Continued.

a spruce forest (age 22–138 yr), a pine forest (9–100 yr), and an oak forest (12–220 yr). Over time, proportion stem increased at the expense of proportion leaf and/or root. This suggests that light competition may become increasingly important in these chronose-

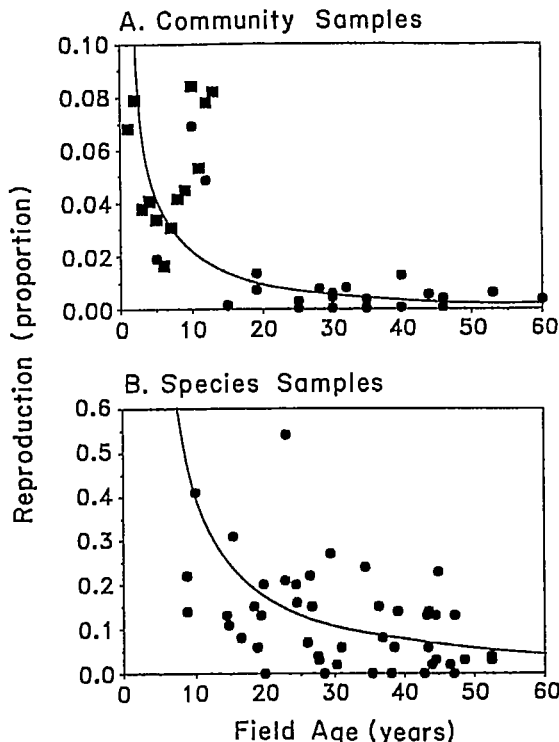


FIG. 4. Proportion of total plant biomass in reproductive structures for (A) the 35 old fields and (B) for the species-by-species analyses. For the 35 old fields, ■ the 1–13 yr old fields and ● the other 22 fields. Nonreproductive plants were excluded from the species-by-species analyses, giving a total of 40 species (see Appendix).

quences. The data from our old field chronosequence, plotted for comparison with the forest data (Fig. 6B), illustrate the contrast between succession in our nutrient-impooverished old fields and in more nutrient-rich forests. Interestingly, these trajectories do not correspond to the trajectories associated with the transient dynamics predicted by ALLOCATE (Tilman 1988), because ALLOCATE did not predict a decline in proportion stem. ALLOCATE, though, did not include differential seed allocation. For our old fields to become forests, there must be some point during the process when there is a major change in allocation trends. This has not occurred during the first 60 yr of succession at CCNHA.

The outcome of succession at CCNHA is generally assumed to be oak savannah or oak forest, depending on fire frequency (White 1983). This is based on the pre-agricultural vegetation of the site, and the slow, but significant, increase in woody plant biomass during succession (Inouye et al. 1987). Ovington et al. (1963) determined above- and belowground biomass in three upland vegetation types at CCNHA: prairie, oak savannah, and oak forest. The total biomass in our older fields is well within the range Ovington et al. (1963) reported for their prairie site (528 g/m<sup>2</sup>), but well below that of their oak savannah (4400 g/m<sup>2</sup>) and oak forest



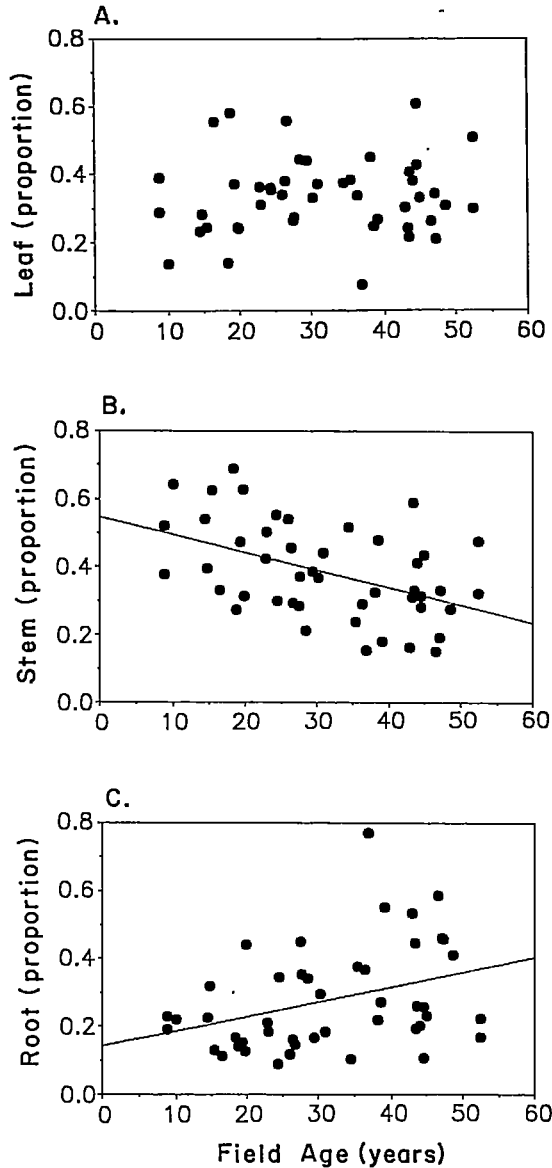


FIG. 5. Proportion of total plant biomass that is in (A) leaf, (B) stem, and (C) root for all species of the species-by-species sampling of morphology of successional plants. Lines are linear regressions.

(17 900 g/m<sup>2</sup>). Moreover,  $\approx 90\%$  of the biomass in their prairie site was in roots, whereas only  $\approx 30\%$  was in roots for savannah and only  $\approx 10\%$  for oak forest. Thus, based on our allocation trends alone (Fig. 3C and 3I), one might assume that the result of old-field succession at CCNHA would be prairie. Alternatively, if prairie-like old fields do become savannah and oak woods as soil mineralization rates slowly increase, there must be a reversal in allocation trends at some point. Nitrogen addition experiments, now in their 8th yr, have shown such a reversal, with woody plants increasing highly significantly in abundance in old field and savannah plots receiving high rates of N addition (Tilman 1987, 1988). Comparison of the total soil nitrogen levels in

the chronosequence with levels in undisturbed forests surrounding the old fields suggests that  $>100$  yr are required for an old field to regain its pre-agriculture nitrogen level (Tilman 1988). Once this occurred, it might take a comparable period for trees to grow to maturity. Thus, it may be many years before woody plants dominate these old fields. If this does occur, their dominance would be consistent with the resource ratio hypothesis. This would suggest that the initial period of succession (the first 40-60 yr) is caused by

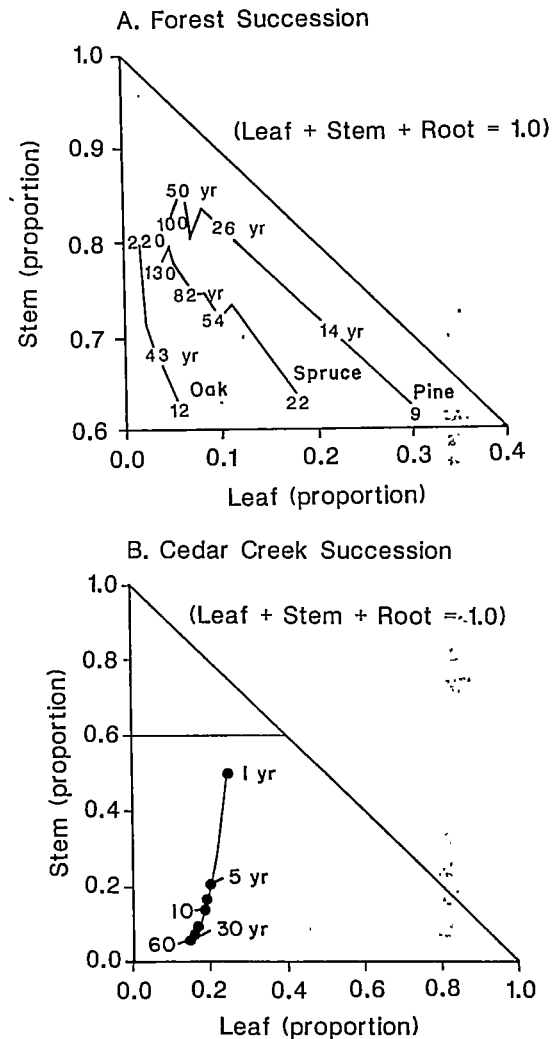


FIG. 6. (A) Successional trajectories in proportion leaf, proportion stem, and proportion root (root shown as root = 1 - leaf - stem) for three forest successions described in Cannell (1982). Numbers shown within the figure are representative successional years. Thus the pine succession is illustrated for years 9, 14, 26, 50, and 100. These forest successions can be compared with the pattern observed at Cedar Creek. (B) Cedar Creek old-field succession, with trends shown based on curves fit to the data of Fig. 3. Note the contrast between the direction of the successional trajectories of parts A and B. The two parts of this figure are drawn to different scales. The forest succession dynamics fit into the upper triangle of part B.

the transient dynamics of plant colonization, growth, and competition, whereas the longer term replacement of herbs by woody plants is caused by the slow accumulation of nitrogen, the associated decrease in light penetration, and the superior competitive ability for light of tall woody perennials (i.e., by the resource ratio hypothesis).

As for all observational studies, there are alternative ways to interpret the data presented here. Structure may not correlate perfectly with function. For example, reproductive allocation is only a crude estimate of dispersal potential, and more detailed study of seed size, number, and mobility would be desirable. Indeed, much of the stem mass measured for early successional species in our survey may play as great a role in seed dispersal as in supporting leaves above the leaves of potential competitors. An alternative explanation for the increase in root biomass during succession is that the root mass may be photosynthate stored as a hedge against herbivory or fire. However, herbivory rates are low in these fields, and fire has never occurred in any of the old fields. If increased root allocation were storage for the purpose of rapid aboveground development in the spring to shade out competitors (thus roots are really underground stems), then light competition must be invoked as the driving process of succession. However, it then must be explained why there is no significant increase in stem biomass, and why it is that cool-season species, which initiate growth early in the growing season, are displaced during succession by warm-season prairie grasses (Tilman 1988), which do not initiate growth until many weeks later. We think it much more likely that the high root biomass of warm-season grasses corresponds with superior competitive ability for nitrogen. A portion of the belowground biomass may be structural, used for building a more permanent (perennial) root system from which more active uptake surfaces could develop seasonally. If true, this would underscore the importance of belowground competition.

Another difficulty with our study is the distinction between the functions of stem and leaf. As with roots, structures may have multiple functions. Many stems are photosynthetic and the midveins of many grass leaves function as stem. However, Reekie and Bazzaz (1987) have shown for *Agropyron repens* (quack grass) that, while stems are photosynthetically active, their maximal rate is 20% that of leaves. Although there are some ambiguities in the functions of roots, leaves, and stems, we feel that these ambiguities are not sufficient to outweigh the major successional trends in plant morphology and function that we have found.

The occurrence of successional changes in allocation pattern in conjunction with changes in life history, probably including mean plant age, and in life form (Inouye et al. 1987, Tilman 1988), raises the possibility that some other factor is determining successional replacement, and that allocation pattern changes as a

correlated character. We doubt this possibility for two reasons. First, we view allocation pattern as a cause rather than consequence of life form and life history. Second, there is a growing body of experimental data at CCNHA that partially controls for this possibility. Several of the most important successional species (both forbs and grasses) were grown from seed along prepared soil quality gradients (Tilman and Cowan 1989, D. Tilman and D. Wedin, *unpublished manuscript*). These experiments control for life form, age, and, to a somewhat lesser extent, life history. All species showed reduced root allocation with increased soil quality, but variation within species was less than variation between species, with later successional species showing higher root allocation than early species across the gradient (Tilman and Cowan 1989). Similarly, Parrish and Bazzaz (1982) found, for a different set of successional species, that root allocation decreased with increasing nutrients for some species, but that on average later successional species had higher root allocation than early species. When various pairs of CCNHA grasses were grown in competition on a nitrogen-poor soil, late successional species, which had higher proportion root and lower percent N in their tissues, were superior nitrogen competitors compared to early species (D. Wedin and D. Tilman, *unpublished manuscript*). These data are consistent with allocation pattern being a causal, rather than correlated, factor determining the dynamics of succession in these old fields.

In conclusion, the trend of decreased light and increased nitrogen with successional age is consistent with the hypothesis of this succession having a soil-driven component. However, the observed patterns of successional changes in proportion root, leaf, stem, and reproductive biomass and in tissue nutrient concentrations suggest that the changes in nutrient and light levels during the first 40–60 yr of succession are not great enough to cause increased competition for light. Rather, these data, together with other studies (Inouye et al. 1987, Tilman 1987, 1988, Tilman and Cowan 1989) suggest that the first 40–60 yr of succession are a period of strong competition for soil nitrogen. The initial dominants have higher allocation to seed (Fig. 4) and may have higher maximal relative growth rates than later successional species (Bazzaz 1979, Tilman and Cowan 1989). They seem to achieve rapid relative growth rates by having high allocation to leaves (Monsi 1968, Tilman 1988), and thus necessarily having low allocation to roots and/or stems. These species are displaced, during the initial 40–60 yr of succession, by species that have higher proportional root biomass but lower proportional seed and leaf biomass, and tend to have lower maximal growth rates (Tilman and Cowan 1989). This pattern is consistent with the hypothesis that the first 40–60 yr of this succession is mainly the transient dynamics of competitive displacement, with the pattern caused, in part, by a trade-off between maximal growth rate and competitive ability for nitrogen

and, in part, by a trade-off between colonization ability (seed production) and competitive ability for nitrogen.

These trends are generally consistent with the predictions of an allocation-based model of plant competition and succession on nutrient-poor soils (Tilman 1988), although the decrease in proportional stem biomass observed at CCNHA (Fig. 6B) was *not* predicted by that model. A comparable trade-off, but between maximal growth rate and competitive ability for light, may explain the dynamics of succession on rich soils (e.g., Tilman 1985, 1988, Huston and Smith 1987). On rich soils, fast-growing, leafy plants with low allocation to stem would attain an initial, but transient, period of dominance, and then be displaced by progressively taller, but more slowly growing plants that allocated progressively more to stem but less to leaf and/or root (see Fig. 6A). Studies of plant morphology may thus provide insights into the causes of successional patterns in different communities. Clearly, though, this will require detailed comparisons of successions that begin on soils of different fertilities.

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## APPENDIX

This appendix lists the species, sample sizes, and mean field age of appearance (based on relative cover, see Results: Species Patterns) of the species used in the species-by-species analysis. Mean field ages were calculated using data from a survey of 22 old fields at Cedar Creek (Inouye et al. 1987).

Species	.N	Field age
Grasses and sedges		
<i>Agropyron repens</i> *	11	24.6
<i>Agrostis scabra</i>	14	14.4
<i>Andropogon gerardi</i>	16	38.6
<i>Cenchrus longispinus</i>	12	24.4
<i>Panicum oligosanthos</i>	15	30.2
<i>Poa pratensis</i>	15	27.5
<i>Schizachyrium scoparium</i>	15	43.4
<i>Setaria glauca</i>	16	19.3
<i>Sorghastrum nutans</i>	15	52.5
<i>Carex</i> sp.*	16	42.9
<i>Cyperus filiculmis</i>	15	39.1
Forbs		
<i>Achillea millefolium</i>	7	22.2
<i>Ambrosia artemisiifolia</i>	20	16.4
<i>Ambrosia coronopifolia</i>	16	44.6
<i>Anemone cylindrica</i>	15	43.6
<i>Artemisia caudata</i>	15	29.4
<i>Artemisia ludoviciana</i>	15	52.5
<i>Asclepias syriaca</i> *	16	35.4
<i>Asclepias tuberosa</i>	9	46.6
<i>Berteroa incana</i>	15	18.4
<i>Chenopodium album</i>	15	30.9
<i>Crepis tectorum</i>	16	8.8
<i>Erigeron canadensis</i>	16	15.3
<i>Erigeron strigosus</i>	15	19.7
<i>Hedcoma hispida</i>	15	23.0
<i>Helianthemum bicknellii</i>	11	36.9
<i>Hieracium longipilum</i>	8	27.6
<i>Lathyrus venosus</i> *	17	38.1
<i>Lepidium densiflorum</i>	19	10.0
<i>Lеспедеза capitata</i>	15	36.3
<i>Liatris aspera</i>	5	47.2
<i>Lychnis alba</i>	15	14.7
<i>Polygonum convolvulus</i>	16	18.7
<i>Rudbeckia serotina</i>	15	34.4
<i>Rumex acetosella</i>	15	24.5
<i>Solidago graminifolia</i>	15	44.0
<i>Solidago nemoralis</i>	16	45.0
<i>Solidago rigida</i>	17	44.6
<i>Tradescantia occidentalis</i>	15	43.4
<i>Tragopogon dubius</i>	12	26.4
<i>Trifolium</i> sp.	5	8.8
<i>Verbascum thapsus</i>	10	26.7
<i>Vicia villosa</i>	18	26.0
Woody		
<i>Rhus glabra</i> *	15	28.5
<i>Rosa arkansana</i>	15	48.6
<i>Rubus</i> sp.*	15	47.1

\* Nonreproductive status at harvest.