



Patterns of woody plant abundance, recruitment, mortality, and growth in a 65 year chronosequence of old-fields

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Abstract

We surveyed vegetation along forest margins in a 65-year chronosequence of old-fields at the Cedar Creek Natural History Area in east-central Minnesota, USA, to identify successional patterns of woody plants and to determine if these were correlated with soil nitrogen. We predicted that shrub and tree abundance, size, and distance of occurrence from the forest edge would be correlated with field age or soil nitrogen. Instead we did not find successional trends in the abundance or composition of woody species. Even in the oldest field the abundance of trees and shrubs was low and concentrated in areas close to the forest. Though trees were larger and present further from the forest edges in older fields, average tree height was less than 126 cm in all fields.

Since we did not find successional trends we looked at various local factors (local seed sources, deer browsing, and forest edge aspect) and their relation to recruitment, mortality, or growth to explain variation among fields in abundance of trees or shrubs. The three most common tree species (*Quercus rubra*, *Q. macrocarpa*, and *Populus tremuloides*) all had a higher relative abundance of seedlings, and two (*Q. rubra* and *Q. macrocarpa*) had a higher relative abundance of large trees adjacent to forests with a high abundance of conspecific adults. Most trees taller than 20 cm were browsed by deer and were shorter in 1995 than they were in 1993. Mortality was higher for trees less than 30 cm indicating that mortality was size-dependent. Forest edge aspect did not significantly influence the abundance or demography of any species. Our results suggest that the patterns of seedling recruitment were largely determined by the proximity of seed sources and that these patterns may persist so that tree communities in old-fields resemble adjacent forests. Deer may be a significant factor in the suppression of tree populations in old-fields through repeated browsing which reduces tree growth and elevates tree mortality by prolonging the period of time trees remain susceptible to size-dependent mortality.

Introduction

Many mechanisms have been proposed to explain successional changes in species composition and abundance in old-fields following their abandonment from agriculture (Gleason 1927; Pickett et al. 1987; Myster 1993). Though rates of succession and patterns of species replacement vary among sites, abandoned agricultural fields in the eastern and mid-western United States typically develop a forest canopy despite the initial absence of woody species in the seed bank (Bard 1952; Bazzaz 1968; Myster 1993). The goal of our study was to evaluate the capacity of existing

models to explain patterns of successional changes in woody plants in a chronosequence of old-fields bordered by forests composed of multiple species of trees and shrubs.

The models of succession all predict shifts in species dominance during succession but each emphasizes a different set of life-history strategies. The 'initial floristic composition' model, predicts that all species establish soon after abandonment, but that each expresses dominance at different times during succession, with faster-growing, short-lived species sequentially replaced by slower-growing and longer-lived species (Drury & Nisbet 1973; Egler 1954; Pick-

ett 1982). A second model, the 'relay floristics' model, emphasizes differences among species in their rates of reproduction and dispersal (Egler 1954; Myster 1993). Based upon this second model, species that produce copious amounts of wind-dispersed seeds should dominate earlier in succession, but be replaced through time by slower growing species that produce fewer, heavier seeds. The third or 'resource-competition' model predicts that the pattern of temporal dominance is determined by the response of each species to the increasing availability of a limiting soil resource (Huston & Smith 1987; Peet & Christensen 1980; Tilman 1987).

The three successional models share a reliance upon the population parameters of recruitment and mortality of individuals to predict temporal shifts in species dominance. Growth of individuals also can be considered as an important parameter of these models if size-dependent mortality is demonstrated. Factors unique to forest edges that may impact recruitment, mortality, and growth of woody plants, and hence the successional patterns, include microclimatic conditions (Matlack 1993, 1994), high deer activity (Alverson et al. 1988), and the species composition (McQuilkin 1940; Wales 1972) and density of trees (McQuilkin 1940) in the adjacent forest. The influences of these unique factors of the forest edge can vary depending upon the compass orientation of the forest edge ('forest edge aspect') (Wales 1972) and typically decline with time since disturbance (Matlack 1994) and distance from the forest edge (McQuilkin 1940; Wales 1972).

This study was conducted at the Cedar Creek Natural History Area, MN. Here, the development of forest-canopies in old-fields is substantially slower (Inouye et al. 1987) than at many other sites (Bazzaz 1968; Beckwith 1954; Buell et al. 1971; Halpern 1989; Pickett 1982). A survey of vegetation in a 56 year chronosequence of 22 old-fields showed that woody plants were a minor component of plant cover (<15% cover) even in the oldest fields (Inouye et al. 1987). The availability of nitrogen, the primary limiting nutrient at Cedar Creek, plays an important role in the successional shifts in composition and abundance of herbaceous species (Tilman 1987) and is suspected to contribute to the slow rate of canopy development by controlling rates of establishment, mortality, and growth of woody plants. Alternatively, Inouye et al. (1994) have shown that canopy development in old-fields at Cedar Creek is slowed by the low dispersal of

woody plants, high mortality of small trees, and high occurrence of browsing of trees by deer.

Methods

Study area

To evaluate the efficacy of the three models in explaining patterns of woody plant succession as well as the possible roles of species composition of trees in bordering forests, deer, and forest edge aspect, we surveyed trees and shrub species along forest-field margins in a 65 year chronosequence of old fields. These fields are located at Cedar Creek Natural History Area (Cedar Creek), a 2300 ha Long Term Ecological Research (LTER) site located about 50 km north of Minneapolis in east-central Minnesota, USA (lat. 45 °25' N, long. 93 °10' W). Cedar Creek is seated on a 1200–1300 year-old sand moraine and has flat to gently rolling topography with poorly developed sandy soils. Prior to European settlement much of the area was a mixture of closed canopy forest, fire-maintained oak-savanna ('scrub oak'), cypress swamp, meadow, and prairie grassland (Pierce 1954; White 1981). Between the mid-1800s and the 1920s settlers farmed much of the upland area and suppressed fires in surrounding areas not used for farming or livestock (Pierce 1954). Since the 1920's, farmers have abandoned most agricultural fields. Presently, Cedar Creek is a mosaic of abandoned agricultural fields, forest-fragments dominated by *Quercus rubra* (red oak), fire-maintained oak [*Q. macrocarpa* (bur oak)] savanna, wetland, and low-elevation, occasionally flooded, forest.

Transect placement and data collection

We established transects in each of 23 forest-field margins in 18 old-fields abandoned from agriculture between 1927 and 1993. Field age was determined from historical records and aerial photographs. We chose margins with forest edge aspects representing each of the four cardinal compass directions in the widest possible range of field ages. All margins were bordered by a straight forest edge that was at least 140 m long. In each margin, five 4 m wide by 40 m long transects were established at randomly selected points along a 100 m length of forest edge with the long axis of each transect perpendicular to the forest; transects were placed at least 40 m from other nearby forest edges.

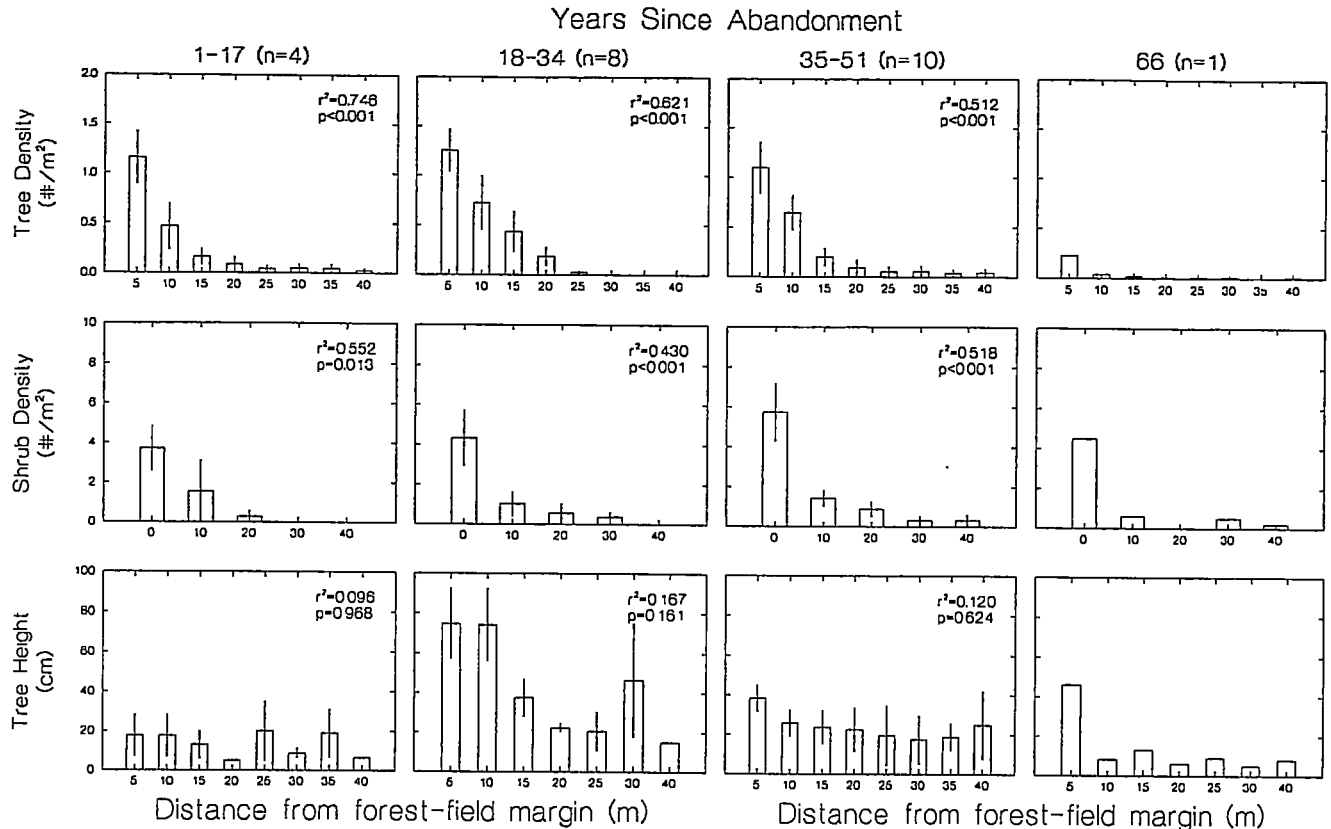


Figure 1. Average tree density ($\#/m^2$), tree height (cm), and shrub density ($\#/m^2$) at different distances in fields of different ages. Means were calculated using values for each field thus each bar represents variation among fields not within fields. Only one field was in the oldest age class.

We surveyed trees and shrubs in transects during the summers of 1993 and 1995. We recorded the species and location of every tree and seedling, and for trees we also measured diameter (7 cm from the ground) and height. For trees with multiple trunks, the tallest trunk was measured. Though some tree species were clonal only stems spaced two centimeters or closer were counted as ramets of a single individual. We also recorded whether browsing was present on the lateral or terminal branches of trees. In the 1995 survey we relocated and measured trees that were previously mapped and mapped and measured trees and seedlings that had established since 1993. Trees were recorded as having died between censuses if a dead stem was found at the map coordinates. Trees absent from their 1993 coordinates were recorded as missing and presumed to be dead. We surveyed woody vines and shrubs in $2\ m^2$ circular sub-plots at 10 m intervals along one side of each transect (5 sub-plots per transect) by counting the number of stems of each species present.

To evaluate the role of local seed source in tree recruitment, we characterized the forests adjacent to the

transects. Using the point-quarter method (Cox 1990), we surveyed adult trees at 10 m intervals, 10 m inside the forest, along a 100 m transect-line. The closest tree [>10 cm diameter at breast height (dbh)] in each quarter was identified to species and measured for (dbh) and distance from the center of the grid. We calculated two indices for each tree species found inside each forest edge. The dominance index value ($DIV = \text{density} * \text{average bole diameter}$) measures the absolute abundance of a species whereas the importance index value ($IIV = \text{relative density} + \text{relative frequency} + \text{relative dominance}$) measures the relative abundance of a species.

We measured soil nitrogen content from 10 cm deep soil cores collected in 1993 along each transect at 10 m intervals starting at the forest-field margin. We also collected 10 cm deep soil cores at 5 randomly chosen points along the 100 m transect-line used to characterize the forest. Each soil sample was dried, homogenized with a 1 mm soil sieve, and ground to a fine powder with a mortar and pestle or coffee grinder. We randomly chose soils from three transects in each field for analysis, in triplicate, of total nitrogen and

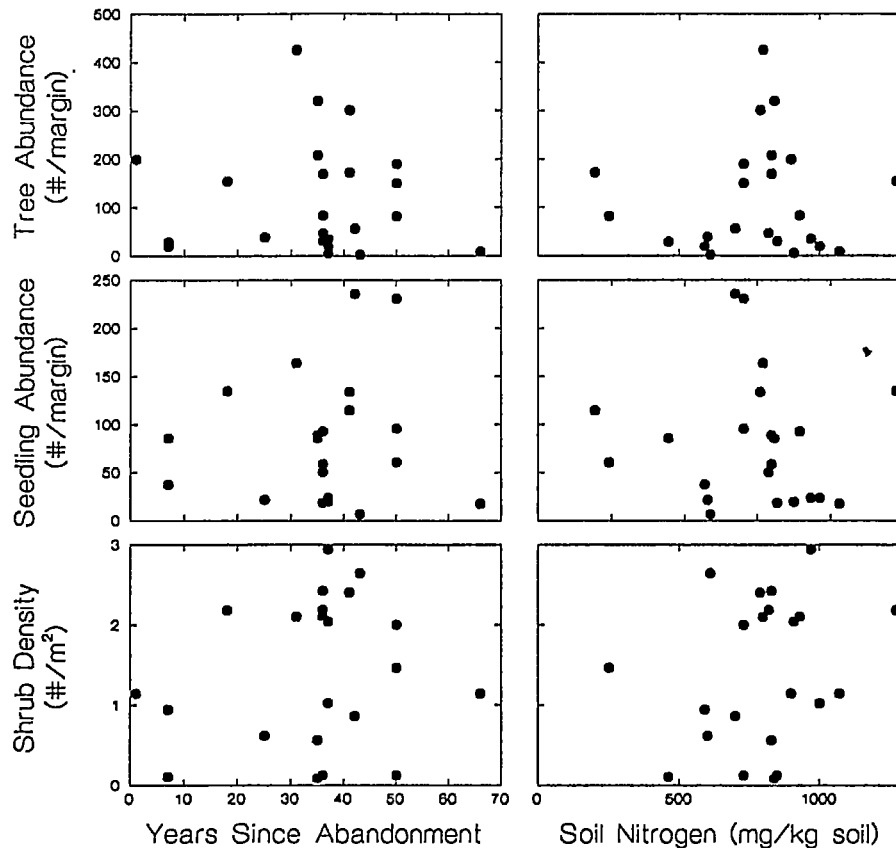


Figure 2. Tree abundance (#/margin), seedling abundance (#/margin), and shrub density ($\#/m^2$) in margins of fields of different age and soil nitrogen.

carbon using a Carlo Erba EA1106 or NA1500 CN analyzer

Statistical analyses

Our goals were to (1) evaluate the ability of three alternative models of succession to predict the among and within old-field patterns of abundance, distribution, and size of different species of trees and shrubs, and (2) determine how recruitment, mortality, and growth are influenced by the species composition and density of trees inside adjacent forests, by browsing, and by aspect of the forest edge. To satisfy our first goal, models were evaluated by using simple and partial correlations. We tested field age and soil nitrogen as predictors of woody plant abundance, tree size, and distance of occurrence of trees from the forest edge. Relative abundance was calculated for trees and shrubs separately. Dependent data were either log or arcsine transformed as needed to satisfy the assumption of homoscedasticity (Zar 1984). Seedlings were omitted from calculations of average density or abundance and size of trees. To examine whether tree and shrub den-

sity varied significantly with soil nitrogen at a scale smaller than the field, we calculated tree density at 0–2.5 m, 7.5–12.5 m, 17.5–22.5 m, 27.5–32.5 m, 37.5–40 m (i.e. centered ± 2.5 m from soil cores) and used shrub density data from all transects in which soil samples had been analyzed.

Tree mortality was calculated as the percentage of trees measured in 1993 that was missing or found dead in 1995. Growth in height and diameter of each tree was calculated as the percent relative increase [(1995–1993 size)/1993 size]. Incidence of browsing by deer was calculated as the percentage of trees that were browsed. To examine size-related patterns we divided trees into 11 categories based upon their height in 1993: for each category, mortality, average growth, and browsing were calculated. Seedlings were excluded from calculations of tree growth. Using simple correlation or ANOVA, forest edge DIV and IIV, incidence of browsing, and forest edge aspect were tested as predictors of recruitment, mortality, and/or growth.

Patterns of absolute and relative abundance of species are presented for the five and three most com-

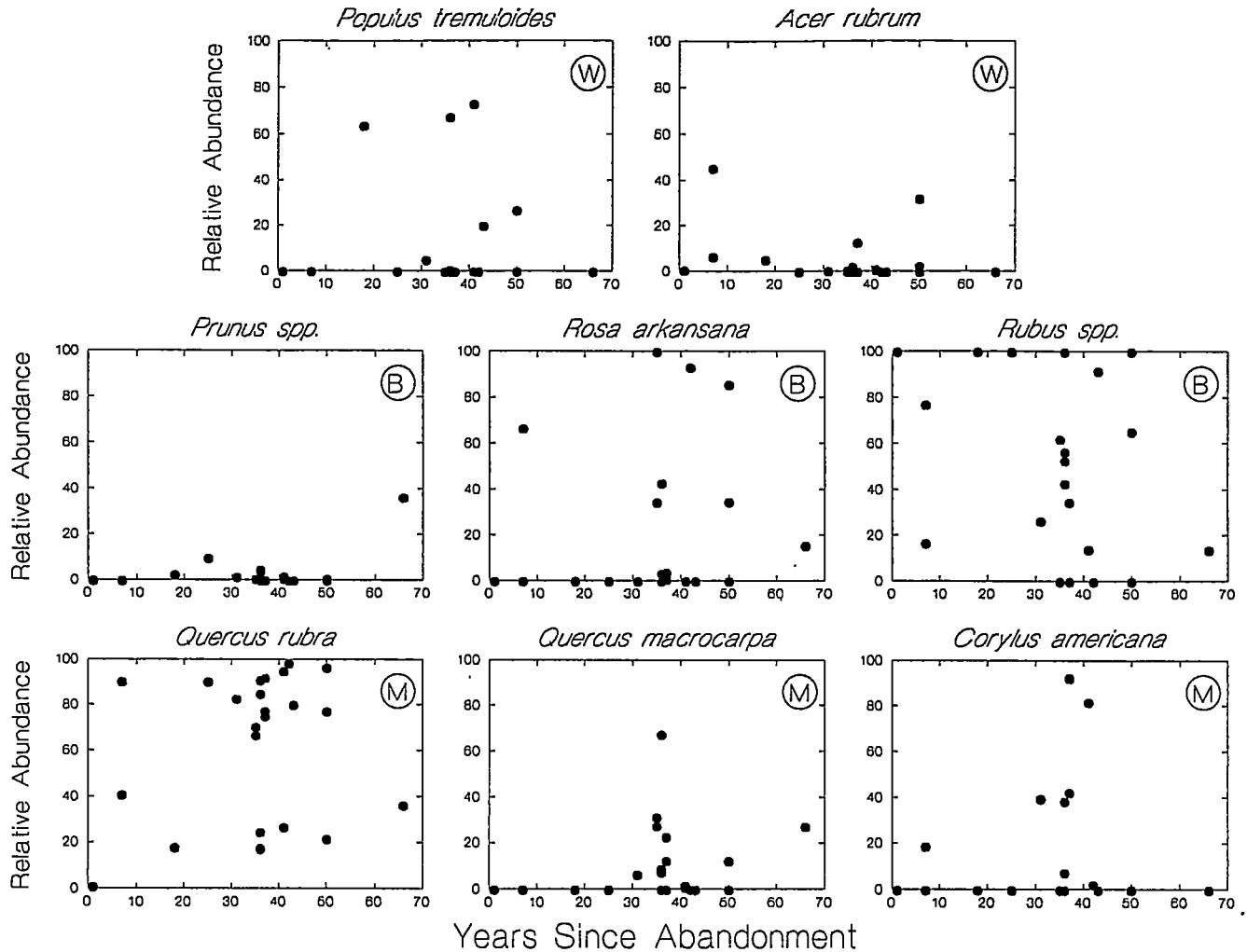


Figure 3. The relative abundance of the most commonly occurring species of trees and shrubs dispersed by wind (W), birds (B) and mammals (M) plotted against field age. Relative abundance was calculated separately for tree and shrub species (see Table 1).

mon species of trees and shrubs, respectively, which account for 80% or more of all stems. All statistical analyses were performed using Systat for Windows (version 5.02, Systat Inc., Evanston, IL).

Results

Species composition in the field and the forest

In 1995 we counted 5312 trees of 14 species and 1541 stems of 16 shrub species. Five tree species [*Q. rubra*, *Populus tremuloides* (trembling aspen), *Q. macrocarpa*, *Acer rubrum* (red maple), and *Prunus serotina* (black cherry)] comprised approximately 80% of the trees, and five shrub species [*Corylus americana* (hazelnut), *Rubus flagellaris* (dewberry), *R. idaeus* (raspberry), *R. allegheniensis* (black-

berry), and *Rosa arkansana* (rose)] comprised 89% of the shrubs (Table 1).

Twelve species were identified in the forest edges (Table 1) with species richness per forest edge ranging from two to eight (Table 2). *Q. rubra* was the most abundant (61% of trees) and was the only species found inside all forest edges. Density of adult trees inside the forest edges bordering our fields ranged from 255 ha⁻¹ to 1180 ha⁻¹ (average density of 541 ha⁻¹).

Community patterns

Tree and shrub density declined dramatically with distance from the forest edge particularly within the first 20 m (Figure 1). The average height of trees was similar at all distances in fields that were 17 years or younger, but in older fields, tended to decline with distance (Figure 1).

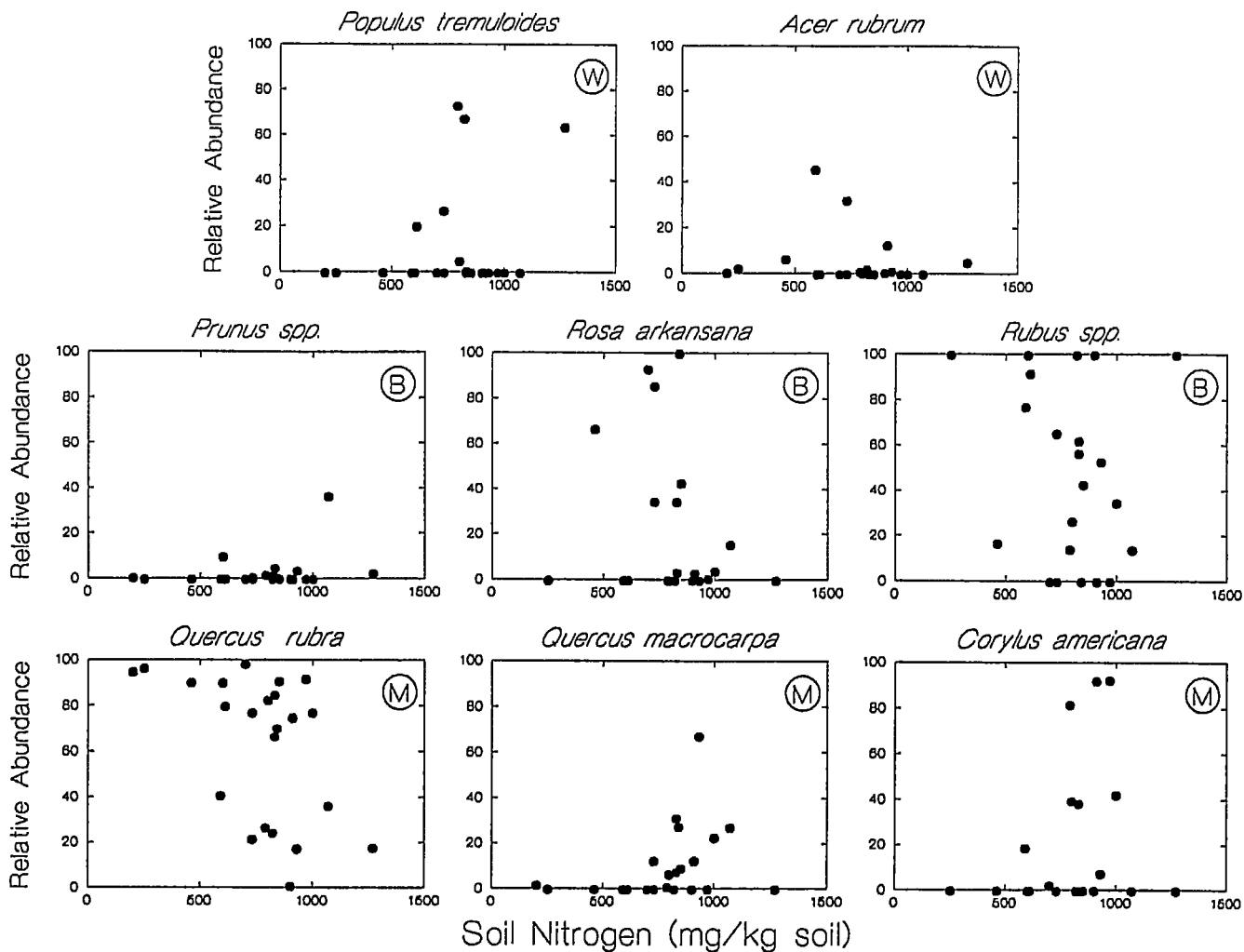


Figure 4. The relative abundance of the most commonly occurring species of trees and shrubs dispersed by wind (W), birds (B) and mammals (M) plotted against soil nitrogen. Relative abundance was calculated separately for tree and shrub species (see Table 1).

Surprisingly, tree abundance and shrub density did not increase with either field age, soil nitrogen, or field age when soil nitrogen was controlled (Figure 2), nor did we find a pattern of species abundance suggesting that species replacement is occurring (Figures 3 and 4). Though trees and shrubs were more abundant in many older fields than in younger fields, the abundance of trees and shrubs was highly variable among intermediate-aged fields. *Q. rubra* was the only species found in all margins. Abundance and relative abundance of all tree and shrub species were highest in fields between the ages of 25 to 50 years old but did not change significantly with field age, soil nitrogen, or field age when soil nitrogen was controlled (Figures 3 and 4). The absolute and relative abundance of *Q. rubra* was independent of field age, soil nitrogen, or field age when soil nitrogen was controlled (Figures 3 and 4). Rather, fields divided into two groups:

those dominated by *Q. rubra* and those where *Q. rubra* comprised less than 30–40% (Figure 4).

Though we found a number of wind- or bird-dispersed species these were a minor component of cover in most margins of our survey and were not restricted to the younger fields (Figures 3 and 4). *P. tremuloides*, the second most abundant species in our survey, was found in 9 of 23 margins in fields between the ages of 15 and 50 years old, but not in the youngest fields. The bird-dispersed tree, *Prunus spp.*, also absent from the youngest fields, was most abundant in 30–40 year-old fields but density was less than 0.01 stems/m². *R. arkansana*, a bird-dispersed shrub, was found in a 7 year-old field but was most abundant in the oldest fields.

Soil nitrogen varied considerably among transects and distances from the forest-field margin, so we examined whether tree or shrub density varied with av-

Table 1. List of tree and shrub species found. The number of trees in the field and in the forest, seedling abundance, and the number of fields and forest edges in which each species was found are reported for tree species. The number of stems and the number of fields in which each species was found are reported for shrub species. Stems of vine species were not counted (indicated by the symbol \emptyset)

| Trees | | | | | | Shrubs | | |
|-------------------------------|---------|----------|-------------|----------------|----------------------|-----------------------------------|-------------|----------|
| Species | # trees | # fields | # seedlings | # forest edges | # inside forest edge | Species | # stems | # fields |
| <i>Quercus rubra</i> | 2706 | 23 | 905 | 23 | 553 | <i>Corylus americana</i> | 460 | 10 |
| <i>Populus tremuloides</i> | 736 | 9 | 313 | 6 | 46 | <i>Rubus flagellaris</i> | 386 | 8 |
| <i>Fraxinus pennsylvanica</i> | 432 | 2 | 358 | 1 | 2 | <i>Rubus idaeus</i> | 142 | 6 |
| <i>Acer negundo</i> | 421 | 2 | 368 | 1 | 32 | <i>Rosa arkansana</i> | 123 | 12 |
| <i>Quercus macrocarpa</i> | 406 | 14 | 106 | 18 | 109 | <i>Rubus allegheniensis</i> | 258 | 12 |
| <i>Acer rubrum</i> | 305 | 13 | 220 | 6 | 21 | <i>Amorpha canescens</i> | 41 | 1 |
| <i>Prunus spp.</i> | 164 | 20 | 121 | 17 | 45 | <i>Cornus spp.</i> | 41 | 5 |
| <i>Robinia pseudo-acacia</i> | 19 | 2 | 4 | 0 | 0 | <i>Amelanchier spp.</i> | 31 | 4 |
| <i>Beula papyrifera</i> | 22 | 3 | 6 | 7 | 49 | <i>Rhus glabra</i> | 7 | 2 |
| <i>Juniperus communis</i> | 32 | 5 | 17 | 0 | 0 | <i>Vitis ripara</i> (vine) | \emptyset | 1 |
| <i>Pinus strobus</i> | 42 | 6 | 30 | 2 | 12 | <i>Parthenocissus spp.</i> (vine) | \emptyset | 14 |
| <i>Populus grandidentata</i> | 22 | 2 | 16 | 2 | 16 | <i>Diervilla lonicera</i> | 0 | 1 |
| <i>Salix spp.</i> | 4 | 1 | 4 | 0 | 0 | <i>Rhus toxicodendron</i> | \emptyset | 7 |
| <i>Ulmus rubra</i> | 1 | 1 | 1 | 4 | 10 | <i>Ceanothus americanus</i> | 0 | 0 |
| <i>Cornus spp.</i> | 0 | 0 | 37 | 1 | 1 | <i>Vaccinium myrtilloides</i> | 0 | 0 |
| Unknown | 0 | 0 | 11 | 0 | 0 | <i>Ribes cynosbati</i> | 9 | 1 |
| Total: | 5312 | | | | | Total | 1541 | |

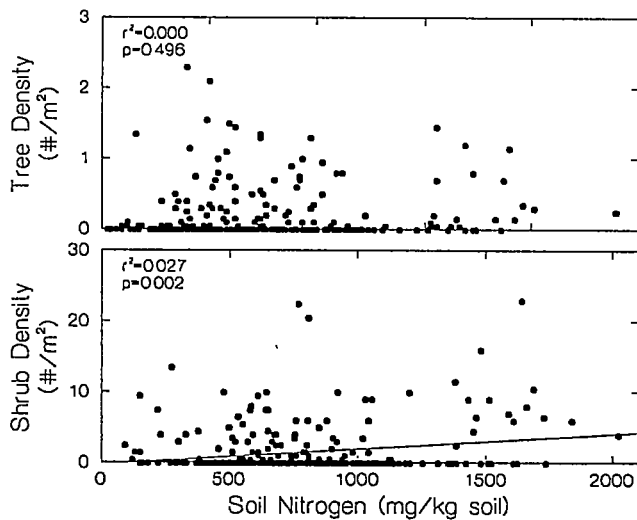


Figure 5. Density ($\#/m^2$) of trees and shrubs plotted against soil nitrogen. Tree density was calculated for areas 0–5 m, 7.5–12.5 m, 17.5–22.5 m, 27.5–32.5 m, 37.5–40 m along each transect.

erage soil nitrogen at a smaller spatial scale. Whereas tree abundance was independent of soil nitrogen, shrub density increased with soil nitrogen; however, soil nitrogen explained less than 3% of the variance in shrub density (Figure 5).

Recruitment of tree seedlings over the two-year period occurred in all margins (Table 2) and primarily in areas close to the forest. In many margins, the abundance of seedlings in 1995 exceeded the number of trees present in 1993 (Table 2). *Q. rubra* contributed the most to recruitment during the two year period (905 stems, 36% of all seedlings) and was the only species with seedlings in all margins. Other species were abundant only in small subsets of the margins. For example, in one margin (field #9) we found 358 green ash and 383 box elder seedlings (Table 2). Excluding field #9, seedling abundance in margins ranged from 8 to 238 (Table 2). Abundance of seedlings was not correlated with field age, soil nitrogen, or field age when soil nitrogen was controlled (Figure 2, outlier field #9 excluded from analysis).

Seedling recruitment and species composition of trees in old-fields were associated with the species composition of adjacent forests. For example, the relative abundance of seedlings and large trees (taller than 50 cm) of *Q. rubra* and *Q. macrocarpa* increased with the relative abundance of conspecifics in the forest (increasing importance index value, Figure 6). There were also more *P. tremuloides* and *Q. rubra* seedlings in fields that were adjacent to forests where these

Table 2. Year of abandonment, forest edge aspect, average field-soil nitrogen, standard deviation of average field-soil nitrogen, average forest edge soil nitrogen, number of trees, shrub density, and number of seedlings in each field.

| Field | | | | | | | | Forest edge | |
|---------|---------------------|--------|------------------------------------|-----------------------------------|---------|------------------------------------|-------------|-----------------------------------|--------------|
| Field # | Year of abandonment | Aspect | Soil N mean (mg kg ⁻¹) | Soil N SD* (mg kg ⁻¹) | # Trees | Shrub density (# m ⁻²) | # Seedlings | Soil N mean (# ha ⁻¹) | Tree density |
| 72 | 1927 | west | 1067 | 380 | 11 | 1.16 | 19 | 1026 | 312 |
| 35 | 1943 | north | 731 | 160 | 153 | 2.02 | 232 | 639 | 536 |
| 45 | 1943 | east | 251 | 130 | 85 | 1.48 | 62 | 1130 | 500 |
| 45 | 1943 | west | 726 | 340 | 193 | 0.14 | 97 | 1401 | 697 |
| 27 | 1950 | east | 614 | 250 | 5 | 2.66 | 8 | 1158 | 1180 |
| 70 | 1951 | south | 701 | 140 | 59 | 0.88 | 237 | 820 | 532 |
| 76 | 1952 | west | 795 | 400 | 304 | 2.42 | 135 | 1896 | 539 |
| 77 | 1952 | south | 200 | 90 | 175 | no data | 116 | 1586 | 557 |
| 74 | 1956 | north | 911 | 240 | 8 | 2.06 | 21 | 1425 | 473 |
| 74 | 1956 | east | 999 | 220 | 22 | 1.04 | 25 | 1383 | 377 |
| 74 | 1956 | west | 974 | 330 | 37 | 2.96 | 25 | 1294 | 636 |
| 47 | 1957 | north | 835 | 250 | 172 | 2.40 | 60 | 1367 | 465 |
| 47 | 1957 | west | 847 | 130 | 33 | 0.14 | 20 | 2099 | 496 |
| 68 | 1957 | south | 926 | 350 | 86 | 2.12 | 94 | 1871 | 392 |
| 38 | 1957 | east | 815 | 1330 | 49 | 2.20 | 52 | 1599 | 255 |
| 56 | 1958 | north | 829 | 400 | 211 | 0.58 | 90 | 946 | 405 |
| 56 | 1958 | south | 840 | 260 | 323 | 0.10 | 87 | 1635 | 272 |
| 53 | 1961 | north | 795 | 370 | 428 | 2.12 | 165 | 1179 | 430 |
| 29 | 1968 | south | 602 | 210 | 41 | 0.63 | 23 | 1122 | 636 |
| 24 | 1975 | east | 1266 | 1730 | 157 | 2.20 | 136 | 1428 | 769 |
| 28 | 1988 | north | 593 | 380 | 22 | 0.96 | 39 | 1076 | 672 |
| 28 | 1988 | west | 456 | 100 | 31 | 0.12 | 87 | 1294 | 426 |
| 9 | 1992 | north | 900 | 400 | 203 | 1.16 | 742 | 1354 | 884 |

species were more abundant (i.e., higher dominance index values).

The expansion of a forest canopy depends upon the establishment and subsequent growth of plants at greater distances from forests. The average distance of trees from the forest-field margin did not vary systematically with field age, soil nitrogen, or with field age when soil nitrogen was controlled (Figure 7). Only for *Q. rubra* did we find a significant relationship (positive) between the average distance of occurrence of trees and field age, but age only explained 13% of the variance (Figure 7). Though average tree height and diameter were below 126 cm and 2.5 cm, respectively, in all forest-field margins, both increased significantly with field age, but neither was correlated with soil nitrogen (Figure 7). For individual species, average tree size (height and diameter) was independent of field age, soil nitrogen, and field age when soil nitrogen was controlled.

Aspect of the forest edge had no effect on the successional patterns of woody plants. Abundance of trees and seedlings, shrub density, shrub cover, growth, mortality, and average distance of occurrence of trees were independent of aspect. Furthermore, individual species were not segregated among the aspects.

Mortality, growth and incidence of browsing

Of the 4360 trees counted in 1993, 24% were either dead (128 stems) or missing (924 stems) in 1995. Most tree stems recorded as missing in 1995 were less than 10 cm tall in 1993 (Figure 8), and many of these probably broke off or decomposed during the two-year period between surveys. As an example, in the youngest field (field #9) 742 seedlings were found in 1993, but were missing in 1995. Mortality was highest for trees less than 10 cm tall in 1993 (52%) and

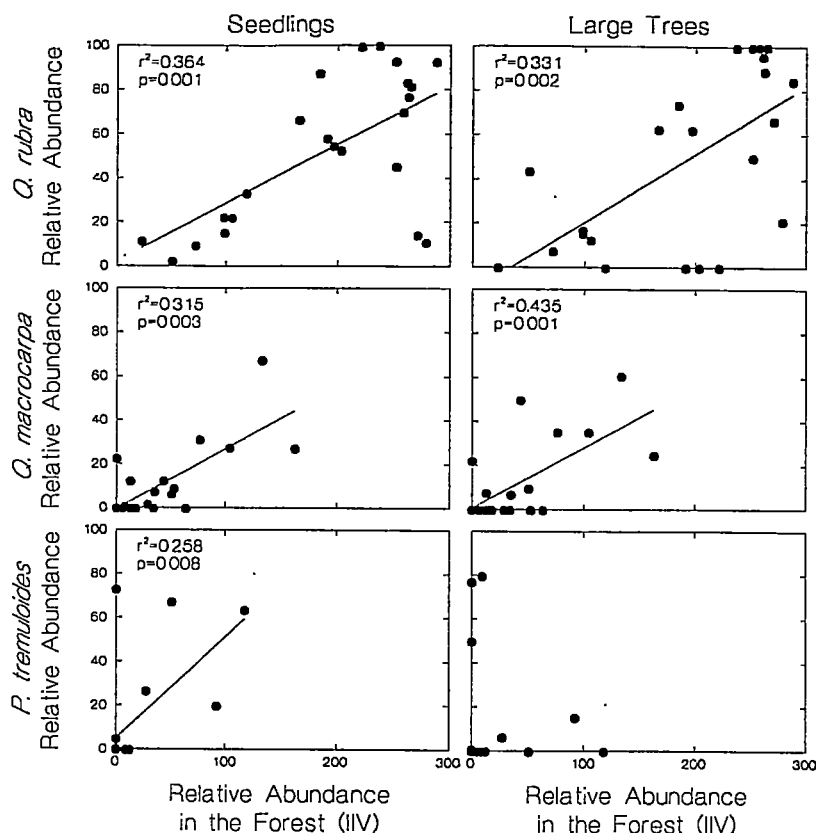


Figure 6. The relative abundance of seedlings and large trees (>50 cm in 1993) of *Q. rubra*, *Q. macrocarpa* and *P. tremuloides* as a function of their relative abundance in the forest (importance index value).

declined with tree size; for trees taller than 50 cm, the mortality rate was on average less than 14% (Figure 8).

Mortality of small trees (those that were less than 50 cm tall in 1993) was significantly higher in younger fields and declined rapidly during the first thirty years of succession (Figure 8). In fields older than 30 years, mortality was independent of field age. Mortality of large trees (taller than 50 cm in 1993) tended to decline with field age, but this relationship was only marginally statistically significant ($r^2 = 0.170$, $p = 0.080$).

Growth in tree height and diameter from 1993 to 1995 averaged 6.66% and 30.79%, respectively, and varied with tree size and species. *Q. rubra*, *Q. macrocarpa*, and *P. tremuloides* showed similar patterns of decreasing growth with increasing size (Figure 9). Many trees 30 cm or taller decreased in height or did not grow. *P. tremuloides* had a higher average rate of growth for the three year period (25.8% in height, 63.7% in diameter) than *Q. rubra* (4.7% in height, 26.6% in diameter) and *Q. macrocarpa* (0.4% in height, 16.9% in diameter). No species had a growth rate that was significantly correlated with soil nitrogen.

The incidence of browsing increased with tree height, potentially reducing growth rates for many trees. We found signs of terminal or lateral browsing on 76% of trees 30 cm or taller but on only 3% of trees 10 cm or less tall (Figure 9). Trees that were browsed by deer grew less in height than those that were not browsed.

Discussion

The development of a forest canopy in old-fields at Cedar Creek has been very slow when compared to other post-agricultural systems in the eastern United States (Bazzaz 1968; Beckwith 1954; Myster 1993; Pickett 1982; Quarterman 1957). The low abundance of trees and shrubs and their close proximity to forests reflects both low establishment and high mortality. Abundance of large trees (> 50 cm tall) ranged from 0–2950 ha⁻¹ and shrub cover was less than 18% (density ranged from 0.10 stems/m² to 29.6 stems/m²) in all margins surveyed. Though trees were larger in older fields, tree growth has been slow; even in the

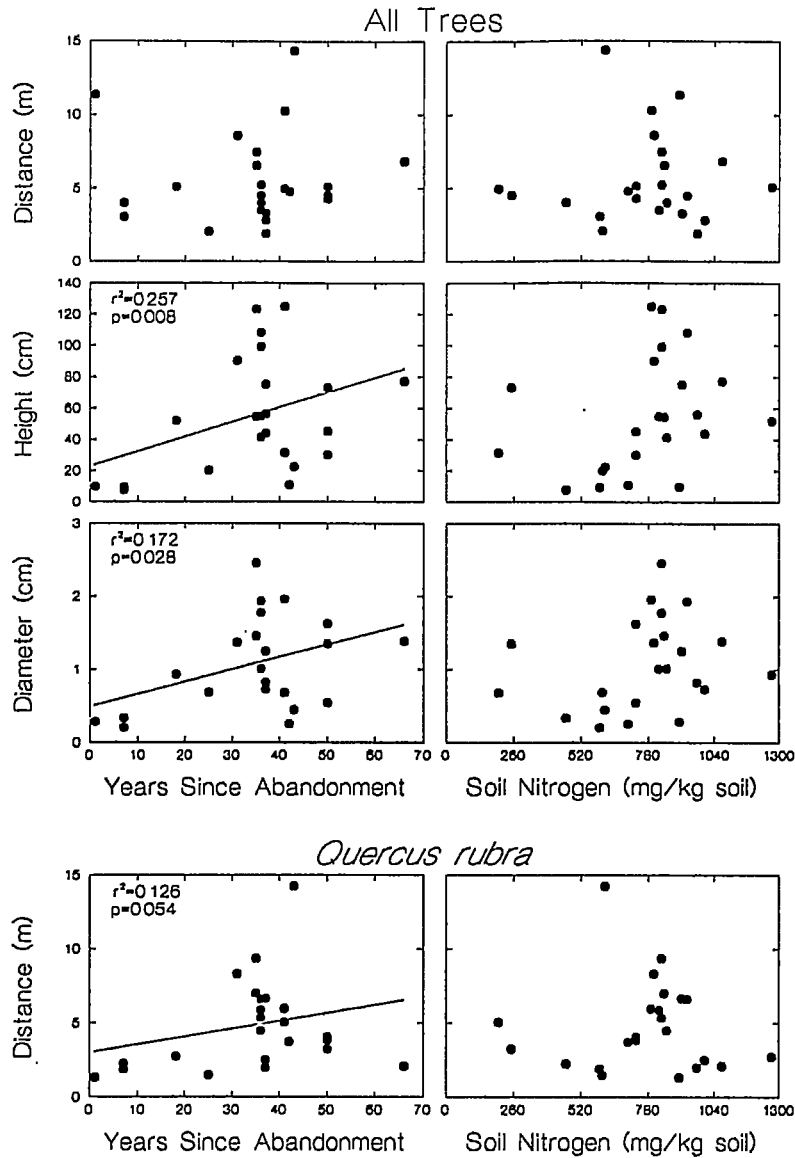


Figure 7. Average distance (m) from the forest, height (cm) and diameter (cm) of all trees, and average distance (m) of *Quercus rubra* in fields of different age and soil nitrogen.

oldest field, the average tree size was less than 126 cm tall and 2.5 cm in diameter (Figure 7).

Evaluation of models

The 'initial floristic composition' model, predicting a successional shift in community dominance from fast to slow growing species (Egler 1954; Pickett 1982), and the 'relay floristics' model, predicting a shift in dominance due to differences in dispersal rates (Egler 1954; Myster 1993), were not supported by our data. We did not find patterns of species replacement in trees or seedlings along the chronosequence that would indicate that differences in seed dispersal mode or growth rates contributed significantly to

the pattern of woody plant succession over the first 65 years (Figures 3 and 4). The patterns in relative species abundances that we found were unlike those at other sites in the eastern and mid-western United States, where wind- and bird-dispersed species typically reach peak abundance within 20–30 years after abandonment (Bazzaz 1968; Pickett 1982). Rather, in most fields densities of the bird-dispersed species, *A. rubrum*, *Prunus spp.*, *R. arkansana*, and *Rubus spp.* were lower than that of mammal-dispersed species such as *Q. rubrum* and *C. americana* (Figures 3 and 4). Though these bird-dispersed species were more abundant in 30–50 year-old fields, they varied in density among fields of similar ages and were absent from

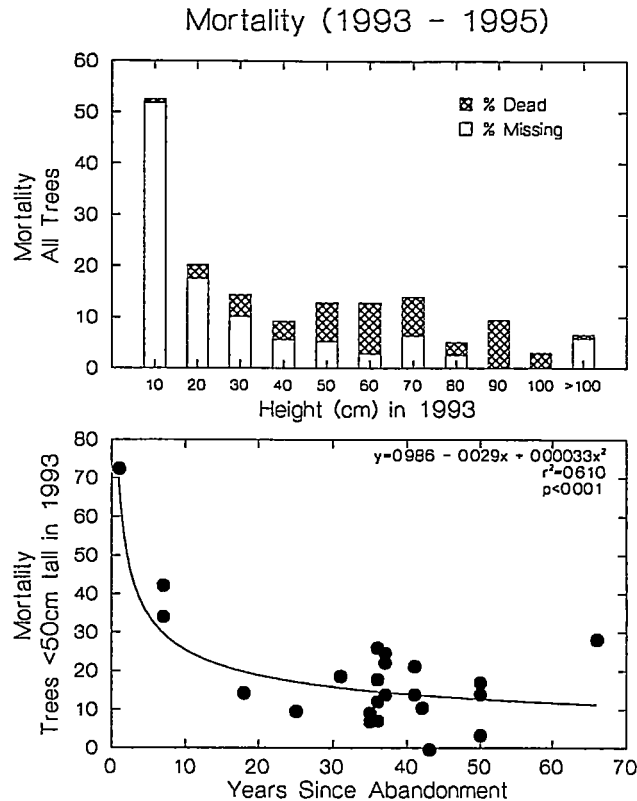


Figure 8. Mortality (the percentage of trees measured in 1993 that was missing or found dead in 1995) as a function of tree height in 1993 and field age.

many fields throughout the chronosequence. *P. tremuloides*, whose seeds are dispersed by wind, was the second most abundant species in our survey, but was found primarily in 30–50 year-old fields. Also, in many fields seedlings of species whose seeds are dispersed by mammals were more abundant than species dispersed by wind or birds. For example, *Q. rubra* comprised 40 percent or more of the seedlings in a number of young to middle-aged fields, exceeding that of any wind- or bird-dispersed species.

The 'resource-competition' model, which predicted that vegetation composition would change in response to soil fertility, also was not supported by our data. Though nitrogen has been shown to limit old-field productivity at Cedar Creek (Tilman 1987), our data did not reveal any correlations between soil nitrogen and abundance, size, or growth of woody plants (Figures 2, 4, 5 and 7). Soil nitrogen was very low (200 to 1250 mg kg⁻¹ dry soil, Table 1) and did not explain variation in total tree abundance or in absolute or relative abundance of any tree species at either spatial scale we examined (Figures 4 and 5). The relative growth rates of species were not correlated with soil nitrogen, suggesting that soil fertility did not impact

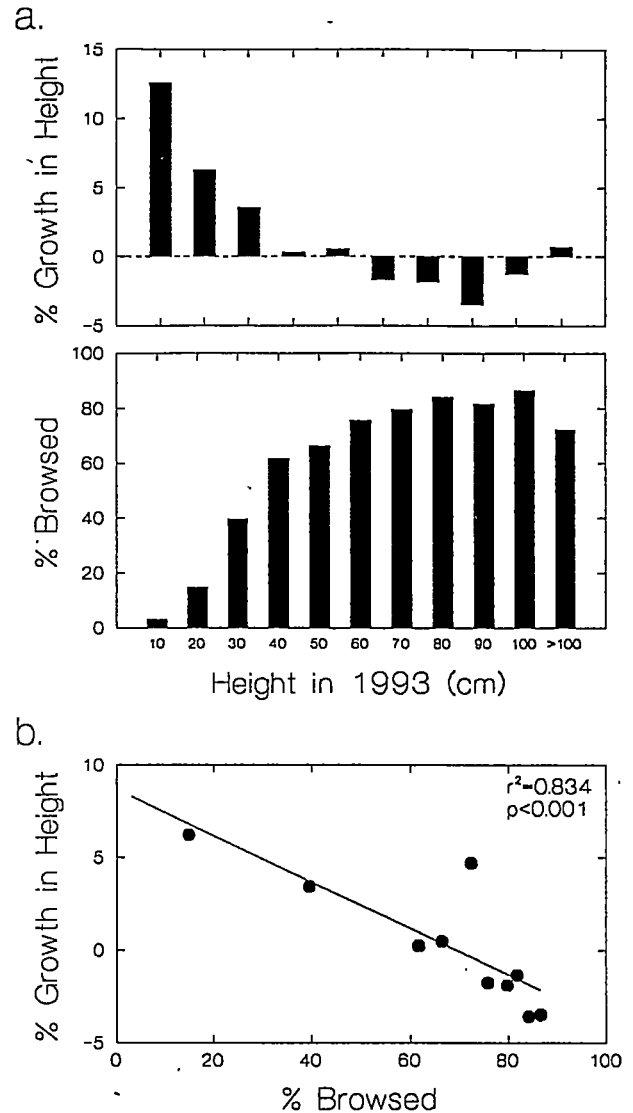


Figure 9. (a) Growth rate and the incidence of browsing as a function of tree size and (b) growth rate plotted against the incidence of browsing.

the growth or competitive ability of any species. However, the slow growth of trees at Cedar Creek does suggest that low soil nitrogen is at least in part responsible for the slow growth of all trees and the slow expansion of forest canopies.

Successional shifts in species abundance may be delayed by the slow rates of tree growth. Though growth rates differed among the three most common species of trees, slow growth may slow competitive sorting. For example, competitive sorting may have occurred in the middle-aged fields where *P. tremuloides*, a fast-growing, early-successional, clonal species, was dominant despite this species' low representation in the forest. Many trees between 20 cm and 100 cm in 1993 did not grow in height or were shorter

by 1995, probably due to browsing by deer (Figure 9). Inouye et al. (1994) reported a significant impact of deer browsing on *Q. rubra* and *P. tremuloides* growth (a reduction in height between 6.8 cm to 11.5 cm and 7.3 cm to 20.3 cm, respectively, between the fall and spring censuses for each year between 1983 and 1987). Our results suggest that slow growth rates, likely due to low soil fertility and deer browsing, contribute to the high mortality of trees and may delay the development of successional patterns in old-fields at Cedar Creek.

Q. rubra is the dominant tree species in forests at Cedar Creek; therefore, we expected this species to increase with field age and soil fertility. Yet abundance of *Q. rubra* was not correlated with field age. Instead, *Q. rubra* was dominant (more than 60%) in 15 margins but comprised less than 40% of trees in the remaining 8 margins independent of field age (Figures 3 and 4). These results suggest that some of these old-fields are not shifting towards *Q. rubra* dominance.

Mortality was highest for small trees (trees less than 50 cm tall in 1993), particularly in fields less than 30 years old, indicating that mortality was not primarily the result of 'self-thinning', an important process that often occurs in developing or mature forests (Peet & Christensen 1980). For example, in the youngest field (LTER #9), over 70% of the box elder and green ash seedlings and 100% of the *Q. rubra* seedlings recorded in 1993 were dead or missing in 1995. We suspect that pocket gophers (*Geomys bur-sarius*), which are more abundant in younger fields (Huntly & Inouye 1987) and have been identified as a significant source of mortality of seedlings and small trees at Cedar Creek (Inouye et al. 1994), contributed to mortality in the younger fields. Repeated browsing by deer also may have contributed to mortality, as well as increasing expected future mortality by extending the period of time that trees remain small and vulnerable.

Significance of local seed sources

Sharp declines in tree and shrub densities with distance from the forest (Figure 1) suggest that recruitment remains highly dependent upon seeds dispersed from adjacent forest. Similarly sharp declines in woody abundance with distance from forest edges have been shown in studies of other eastern deciduous forests (Hardt & Forman 1989; McQuilkin 1940; Myster & Pickett 1992). Typically, this pattern disappears within a few years after abandonment from agriculture as more seeds of wind- and bird-dispersed plants are

deposited at greater distances from the forest. Surprisingly, though species whose seeds are dispersed by wind or birds were present in many margins and fields (Table 1, Figures 3 and 4), we found that the density of trees and shrubs declined sharply within the first 20 m of the forest, even in the oldest fields (Figure 1).

Since adjacent forest edges are probably the primary contributors to seed rain into adjacent old-fields, we speculated that species composition of trees in forests would influence patterns of seedling recruitment and species composition of trees in adjacent old-fields. The species composition of seedling populations was correlated with the species composition of trees inside forests (Figure 6). For example, both the absolute and relative abundance of *Q. rubra* and *P. tremuloides* seedlings increased with the absolute (DIV) and relative abundance (IIV) (Figure 6) of adult trees in the forest edges. The relative abundance of large trees of *Q. rubra* and *Q. macrocarpa* were also significantly associated with their importance index values (Figure 6), indicating that differences in relative abundance of seedlings persist into the older age classes. These results suggest that the species composition of trees in the forest can have long-lasting effects on old-field tree communities by determining the rates of seedling recruitment for different species.

Conclusion

We evaluated three models that emphasize differences between species in their growth rates, dispersal rates, or responses to changes in soil fertility, in predicting patterns of woody plant succession in a 65-year chronosequence of old-fields. Neither time since abandonment nor nitrogen availability explained variation in tree or shrub abundance or relative abundance, indicating that none of the models were supported by our data. Instead, species composition of the forest edge was an important factor determining not only the rate of recruitment of seedlings, but also, more importantly, the subsequent abundance and relative abundance of trees over a 65 year chronosequence of fields. Once established, trees grow very slowly, probably due to the low soil fertility and high deer browsing, and experience high rates of mortality. Older fields did have larger trees that were established further into the field from the forest. Despite this successional trend in tree size and distance of occurrence, trees were small and concentrated near the field edges; hence trees remained a minor component of old-field veg-

etation, even after 65 years. Development of forest canopies in many of these fields may occur but only over a time scale of hundreds of years. Proximity of seed sources may play a significant role in other forest successions, but be particularly important where rates of establishment and maturation are low.

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