RESEARCH ARTICLE

Tree Growth Patterns, Mortality, and Colonization in a Restored Maple-Basswood Forest

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ABSTRACT

With the increased interest in forest restoration, many projects include goals to increase biological diversity and enhance ecological services but provide little information about results of species composition over time, tests of ecological concepts, and resulting management guidelines. The aim of this project was to study maple-basswood forest restoration in former agricultural fields in what was part of the Big Woods landscape in southeastern Minnesota, USA. Tree seedlings were planted in two adjacent fields in 1990 at a density of 1024 trees/ha and measured every two–four years for twenty-three years. Colonizing trees were also measured in 2013. *Quercus rubra* (northern red oak), *Tilia americana* (basswood), *Quercus alba* (white oak), and *Fraxinus americana* (white ash) were the largest trees (mean DBH [diameter at breast height] of 9–12 cm) and *Acer saccharum* (sugar maple) and *Juglans nigra* (black walnut) were smaller with a mean DBH of 4.5–6 cm. The overall tree mortality of 35.8% since 1990 has been balanced by a nearly equal number of colonizing species from nearby forest fragments and internal seed production. Colonizing species, with *F. americana* and *Acer negundo* (boxelder) the most common, led to increases in species diversity. While *A. saccharum* and *T. americana* currently make up less than 10% of the individuals, they are expected to increase in frequency over time. The restored forest area can be characterized as an early successional maple-basswood forest in which priority effects and microhabitat variation support a diverse forest likely to survive future changes in climate and invasive species.

Keywords: Big Woods, deciduous forest restoration, forest succession, maple-basswood forest, tree seedling mortality

Restoration Recap

- Understanding early growth patterns of deciduous trees in open field habitats is needed to improve forest restoration success.
- Planting all tree species found in mature deciduous forests at the beginning of a restoration project led to canopy closure of a forest dominated by species that grow well in open environments. Although all the intended species were present after 23 years, their relative abundances were different from those of nearby mature forest dominated by more shade tolerant species.
- Differences in mortality rates among tree species suggest that shade tolerant species would survive at a higher rate if planted after faster growing species became established.
- Microclimate, soil differences, and priority effects from the initial planting lead to variation in tree dominants in different sections. Over time the restored forest will become more similar to nearby mature forests.

As an applied science, restoration is informed by and offers practical insights into ecological processes. With the development of restoration ecology as an academic field and the long time frame required for results, especially in forest restoration, many projects proceed by simultaneously setting up the project and testing methods or theories. Ecological succession models describe how communities develop over time and long-term field studies of restoration help determine time-lines for recovery and effects of critical points such as forest canopy closure. Depending on local population dynamics and the regional species pool, the process of community assembly may result in alternative stable or transient states (Suding and Gross 2006, Fukami 2015). According to the initial floristics composition model (Egler 1954), some species present early in succession will persist, and later stages reflect the

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initial species composition. In this project, the desired species were planted initially, and limited colonization has occurred over a 23-year period.

In the field of restoration ecology, there has been much discussion about setting appropriate goals for restoration projects (Kloor 2000, Hobbs and Harris 2001, Hobbs and Cramer 2008), but there is less information on the results of projects. The overall goal of ecological restoration is to produce a self-sustaining ecosystem that requires little to no human inputs (Hobbs et al. 2007). Restoration goals are more likely to be achieved if they are based on an ecological understanding of the site. When degradation is mainly biotic, planners may choose either the "moving target" or "museum approach" (Frelich and Puettmann 1999). The "museum approach" aims to restore species composition at a particular period in history, often pre-European settlement. The "moving target" approach acknowledges that changes have occurred since the designated time period, makes predictions about how the area would have changed naturally since that time period and incorporates these predictions into the restoration project goals. Because human activities such as urbanization, farming, mining, and logging have altered nearly half of the earth's ice-free terrestrial habitat (Vitousek et al. 1997), the emphasis on historical or "museum approach" views of restoration at a given location have shifted to optimizing ecological services while acknowledging human influence (Palmer et al. 2004). As global climate change and other drivers, such as invasive species, lead to the development of novel ecosystems, goals focus on restoration of natural capital with ecological integrity, not simply the numbers and types of species (Harris et al. 2006, Cramer et al. 2008, Nunez-Mir et al. 2015).

The study site examined here was located in part of the original Minnesota Big Woods landscape (elm-maple-basswood forest), a forested area of 784,766 ha (3,030 square miles) that extended from southeastern Minnesota to central Minnesota (Daubenmire 1936). Oak dominated the woodland vegetation until about 300–400 years ago when species such as *Ulmus americana* (American elm), *Acer saccharum* (sugar maple) and *Tilia americana* (basswood) expanded rapidly (Grimm 1984, Berland et al. 2011). Today maple-basswood forest occupies less than ten percent of its former area in scattered, isolated parcels (Minnesota Department of Natural Resources 2006). According to the bearing-tree data from the mid 1800's land surveys, *U. americana* and *Ulmus rubra* (slippery elm) were the most common tree species in the Big Woods, followed by *T. americana* and *A. saccharum* (Grimm, 1984). Other tree species included *Quercus macrocarpa* (bur oak), *Quercus rubra* (northern red oak), *Fraxinus americana* (white ash), *Fraxinus nigra* (black ash), *Ostrya virginiana* (ironwood), and *Carya cordiformis* (bitternut hickory). The frequency of each species varied according to moisture, soil type, and disturbance history, with oaks more common in drier areas. *Acer saccharum* and *T. americana* were the most common species in studies of the Big Woods by Daubenmire (1936). Being located along the forest-prairie border, Big Woods ecosystem boundaries have been affected by fire, moisture, topography, and human influence. Current disturbance factors within the remaining Big Woods fragments are mainly tree fall and invasive species (Berland et al. 2011). In setting goals for the restoration, we used a "moving target" approach, taking into account past studies and current local forest composition. Due to the devastation of Dutch elm disease, no elms were planted, but other trees from the previous list were included in the restoration.

We report on the results of a 23-year-old deciduous forest restoration project in southeastern Minnesota, USA. The overall goals of the project were to return land formerly used for conventional corn agriculture to maple-basswood deciduous forest and to better understand early successional patterns in these forests. We planted all the main species desired at one time so that succession would occur more rapidly than if left to natural colonization. We predicted that all tree species would have similar mortality rates and that tree density and composition would become similar to that found in studies by Daubenmire (1936) and Bray (1956), with fewer elms, as the forest matured. The specific objectives of this study were to: 1) compare growth and mortality patterns among tree species; 2) examine how colonization has changed tree species composition; and 3) make recommendations for future forest restoration projects.

Methods

Site Description

Study sites were established on former agricultural fields in Rice County in southeastern Minnesota (44°27′36″ N, 93°11′25″ W) on property west of the St. Olaf College campus (Figure 1) in Northfield, Minnesota. In 1989 the land was enrolled in the Federal Conservation Reserve Program, established to remove marginal agricultural land from production. The forest restoration project became part of a long-term plan to surround the campus with a green-belt to be used for education, research and recreation. The trees in this study were planted in 1990 at a density of approximately 1,024 tree seedlings per hectare. After the corn crop was harvested in 1989, the soil was prepared with a fall plowing followed by spring planting of perennial grasses (*Lolium perenne* [perennial rye] and *Phleum pratense* [timothy]). No mowing or herbicides were used during seedling establishment. Two-year-old bare root nursery stock of local origin was obtained from the Minnesota Department of Natural Resources and local private nurseries. Eleven species of trees were planted, with individuals at least two meters apart, in no set pattern

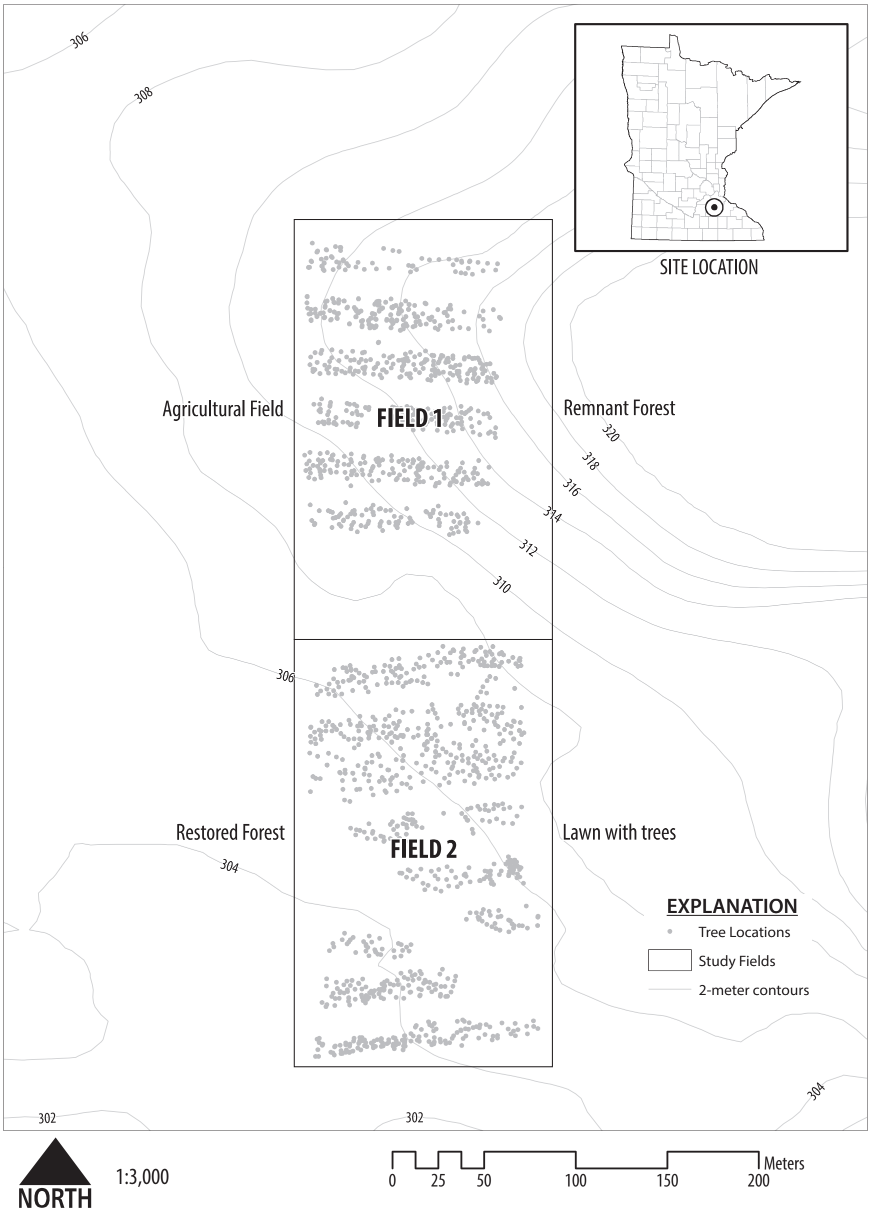


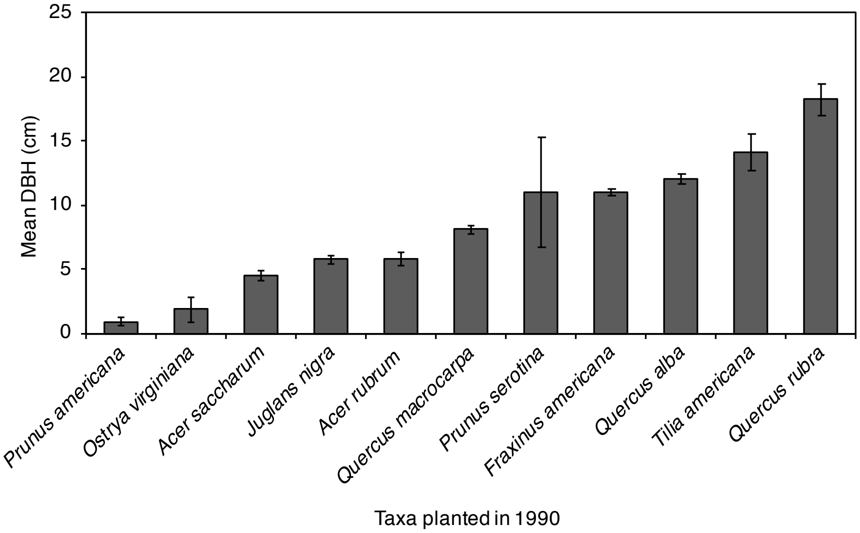
Figure 1. Map showing maple-basswood forest restoration site location in Rice County, southeastern Minnesota, USA, and the location of trees in study sites, Field 1 and Field 2.

throughout the area: *A. saccharum*, *Acer rubrum* (red maple), *F. americana*, *Juglans nigra* (black walnut), *Q. macrocarpa*, *Q. rubra*, *Quercus alba* (white oak), *T. americana*, *O. virginiana*, *Prunus americana* (wild plum), and *Prunus serotina* (black cherry). All trees were tagged in every other 0.1 ha transect (14 × 75 m) in two adjacent fields with north and south sections for a total of 1,506 trees in fourteen transects. The north end of Field 1 was slightly higher in elevation with a slight south-facing slope, while Field 2 was approximately 60 m south of Field 1 and more level (Figure 1). Six transects in Field 1 and eight transects in Field 2 had tagged trees. No trees were planted over a gas pipeline in the southern half of Field 2. Soil type in Field 1 was mainly Blooming silt loam, considered a well-drained soil and Field 2 was mostly Cordova clay loam, considered a poorly drained soil with higher organic matter and soil moisture content than Blooming silt loam (Web Soil Survey 2016). Measurements of soil organic matter in 2017 ranged from 3.45–4.84% in Field 1 and 6.92–7.09% in Field 2 (R. Holmes, St. Olaf College, unpublished data).

Understory vegetation covered more than 50% of the ground surface throughout the restoration, with grasses and mosses making up much of the ground cover. Other common plants identified in six 1-m² plots in each field were *Parthenocissus quinquefolia* (woodbine), *Vitis riparia* (riverbank grape), *Taraxacum officinale* (common dandelion), and in Field 2, *Solidago canadensis* (Canada goldenrod). Although woody plants were not included in this study until they had a DBH of 2.5 cm, smaller woody plants observed in the transects included *C. cordiformis*, *F. americana, T. Americana, Acer negundo* (boxelder), *Rhamnus cathartica* (common buckthorn), and *Lonicera tatarica* (Tatarian honeysuckle).

Weather during the study period was typical for southeastern Minnesota. Local weather data (Midwest Regional Climate Center 2018) showed average precipitation for the

Figure 2. Comparison of mean DBH (cm) for 11 species of trees planted in 1990 using one-way ANOVA. Means were significantly different ($F_{10,864} = 34.3$, $p < 0.001$), error bars are ± SE.



period of the restoration (1990–2013) was 87.8 cm per year and the mean annual temperature was 7.1°C. No unusual climatic events occurred during this time period. During 1990–1992 it was warmer and dryer than average, and seedlings were watered during very dry periods. Especially dry years occurred in 2003 and 2008 (when precipitation was 57.9 and 67.8 cm, respectively). Mean annual temperatures were warmer than usual in 1998 (8.8°C) and 2012 (10.2°C).

Data Collection and Statistical Analyses

Trees were individually tagged and numbered with a metal tag nailed into the ground on the south side of each seedling. When individuals were greater than 2.5 cm DBH (diameter at breast height, 1.37 m), a tree tag was attached to the stem at a height of 1.47 m. The height of the tallest stem for each tree was measured every two to four years over the period from 1990 to 2013. In 2013, new colonizing trees with a DBH > 2.5 cm were measured and recorded for the first time. A total of 502 colonizing trees were measured and the following new species were found: *A. negundo*, *Acer ginnala* (amur maple), *Populus tremuloides* (quaking aspen), and *U. americana*. A clinometer was used to measure the height of trees taller than 3 m. Trees taller than 5 m were considered canopy trees. Beginning in 1997, DBH was measured on trees at 1.37 m above the ground when possible. A tree was considered dead if no leaves were growing or if the tree was missing. Annual mortality was calculated using a negative exponential formula as described in Lorimer et al. (2001). Estimates of canopy cover were made with a densiometer in six 25-m^2 plots in each field section in 2015 according to methods of Kilgore and Dolan (2016). GPS coordinates, accurate to within decimeters, were determined for each tree and transect corners using the Trimble Geo 7X handheld GPS (Sunnyvale, California).

Tree sizes (diameter and height) in 2013 were compared among species and field sections with analysis of variance (R version 3.4.3, the R Foundation for Statistical Computing, Vienna, Austria). We used multiple linear regression to examine the effects of transect tree density and species on current growth rates, from 2010 to 2013. The response variable, growth rate, was created by dividing change in diameter at breast height between 2010 and 2013 by change in time (three years). Variables in the regression model were growth rate at centered (average) density, species, and density × species interaction. This model used *F. americana,* species 8, as the reference group.

To quantify the change in species composition from 1990 to 2013, dissimilarity indices were calculated for each field using the R package "vegan." (Oksanen 2018). Values of zero indicated identical species composition and values of one indicated complete change in composition. The Jaccard and Bray-Curtis dissimilarity indices, each with a binary and regular method, were used for comparisons (Zhang et al. 2014). Binary methods only account for presence/absence of species, while the regular method is based on the relative abundance of species. Species diversity was calculated using the Shannon and Simpson diversity indices (Brower et al. 1998), $H = -p_i (\ln p_i)$ and $D=1-p_i^2$, where p_i = proportion of individuals of a given species.

Results

Growth and Mortality

A comparison of mean height after 23 years showed that *Q. rubra, T. americana, Q. alba,* and *F. americana* were the tallest species with the largest DBH, while *P. americana, O. virginiana, A. saccharum,* and *J. nigra* were shorter with a smaller DBH (Figure 2). Mean heights of the taller species ranged from 9–12 m and they had a mean DBH of 11–18 cm. *Acer saccharum* and *J. nigra,* both expected to be future canopy trees, had smaller mean heights of 5 m and 6 m and a mean DBH of 4.5cm and 6 cm, respectively. The more common tree species grew slowly for the first 10

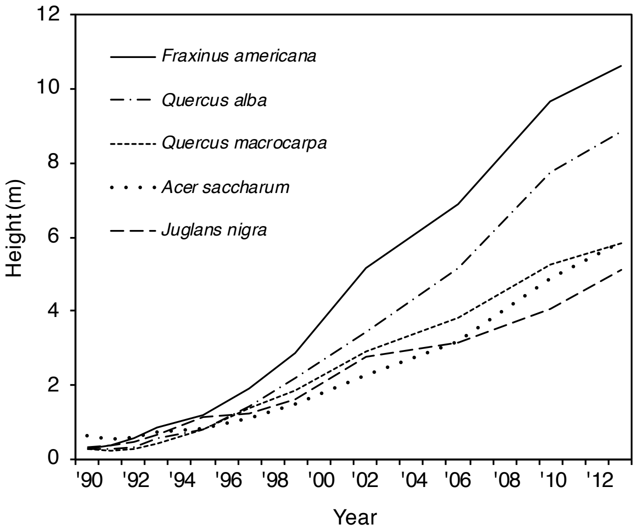


Figure 3. Height growth curves of five common originally planted tree species: *Fraxinus americana, Quercus alba, Quercus macrocarpa, Acer saccharum,* and *Juglans nigra*, measured between 1990 and 2013.

years and then more rapidly over time (Figure 3). Growth patterns differed among species, with faster growth rates measured in *F. americana* and *Q. alba* and slower growth rates found in *A. saccharum, Q. macrocarpa,* and *J. nigra.*

Six species (*T. americana*, *J. nigra*, *Q. rubra*, *A. saccharum*, *F. americana,* and *Q. alba* dominated the canopy, making up nearly 80% of all canopy trees (Table 1). The mean canopy heights varied significantly by field section ($F_{3,764} = 25.32$, $p < 0.001$) when all trees taller than 5 m were compared, with the tallest mean height in Field 1 South. When mean heights of each of the six common canopy tree species were compared individually across field sections, *T. americana* ($F_{1,15} = 9.96$), *J. nigra* ($F_{3,96} = 14.86$), *Q. rubra* ($F_{1,57} = 7.18$), and *F. americana* ($F_{3,254} = 23.71$) were all significantly taller (*p < 0.01*) in Field 1 South. *Acer saccharum* and *Q. alba* canopy trees did not vary significantly in height across sections. Canopy cover estimates made with a densiometer were 96.4–96.7% coverage in Field 1 and 72.8–96.5% coverage in Field 2.

The long-term mortality of all species of planted trees since 1990 was 35.79%, with an annual mortality rate of 1.91% per year (Table 2). *Acer saccharum* and *P. americana* had the highest total mortality of 55.0% and 72.5%, respectively. *Acer rubrum* and *T. americana* had the lowest overall mortality rates at 16.7% and 17.7% respectively, while *F. americana* and the *Quercus* spp. had intermediate mortality rates, from 28–48%.

Multiple regression showed overall tree growth rate was significantly ($F_{20,668} = 9.68$, $p < 0.001$) reduced with increasing density and varied with tree species (Figure 4). According to the R^2 value, density and species explained 20.14% of the variation in growth rate. Compared with *F. americana,* growth rates decreased more than other species with increasing tree density for *J. nigra* ($t = -4.25$, $p < 0.001$) and *Q. alba* ($t = -2.41$, $p < 0.05$). DBH growth rates per year at average density varied from 0.38 cm in *Q. macrocarpa*, 0.47 cm in *A. saccharum*, 0.72 cm in *F. americana* to 1.72 cm in *Q. rubra*.

Colonization Effects on Forest Composition

Original density of trees planted in 1990 was 1,024 trees/ha. Mortality decreased the density of original trees to 658 trees/ha. With the addition of colonizing trees (399/ha), the current tree density was 998 trees/ha. The most prevalent colonizing tree species (DBH > 2.5 cm) were *F. americana* (39%), *A. negundo* (14%), *Q. rubra* (9%), and *U. americana* (6% [Table 3]). When new and original numbers are combined, the total 2013 forest composition was *F. americana* (32%), *J. nigra* (17%), *Q. macrocarpa* (11%), *Q. alba* (9%), *A. saccharum* (5%), and *A. negundo* (5%). When compared to the original tree species composition, the proportion of *J. nigra, Q. macrocarpa, Q. alba,* and *A. saccharum* decreased as *F. americana*, *A. negundo, Q. rubra,* and *U. americana* increased (Table 3). *Acer negundo* became established across the study site and Field 2 had the twice the number of colonizing trees as Field 1, mainly due to large numbers of new *F. americana* trees.

The colonizing tree species with the largest mean DBH were *Q. alba*, *T. americana*, *Q. rubra*, and *J. nigra*, with

Table 1. Mean canopy height (m [± SE]) and sample size, *n*, of all trees > 5 m in each field section. Mean canopy height was significantly different ($F_{3,764} = 25.32$, $p < 0.001$) among the four field sections. Mean heights of four of the six common species, *Tilia americana* ($F_{1,15} = 9.96$), *Juglans nigra* ($F_{3,96} = 14.86$), *Quercus rubra* ($F_{1,57} = 7.18$) and *Fraxinus americana* ($F_{3,254} = 23.71$) were significantly ($p < 0.01$) different among sections.

Species	One North	One South	Two North	Two South	% of Canopy Stems
Mean Height	8.33 (0.14)	10.65 (0.26)	9.03 (0.18)	9.28 (0.24)	–
n	238	196	196	138	100
Tilia americana	8.96 (0.74)	12.00 (0.62)	–	–	2.2
Juglans nigra	5.40	12.26 (0.91)	7.29 (0.29)	8.32 (0.39)	13.0
Quercus rubra	8.56 (0.35)	10.97 (0.84)	–	–	7.7
Acer saccharum	7.22 (0.37)	7.73 (0.47)	8.30 (0.65)	6.42 (0.28)	6.3
Fraxinus americana	10.58 (0.35)	13.41 (0.33)	10.28 (0.24)	10.31 (0.37)	33.1
Quercus alba	9.38 (0.21)	9.30 (0.29)	8.50 (0.41)	8.44 (0.16)	15.4

Table 2. The 23-year and annual mortality rates for original trees planted in 1990.

Species	Number of Original Trees Measured in 2013 (% of Population)	% Mortality Since 1990	Average Annual Mortality
Tilia americana (basswood)	14 (1.4)	17.65	0.84
Prunus serotina (black cherry)	3 (0.3)	0.00	0.00
Juglans nigra (black walnut)	235 (24.3)	36.31	1.94
Quercus macrocarpa (bur oak)	160 (16.5)	29.82	1.53
Ostrya virginiana (ironwood)	18 (1.9)	28.00	1.42
Quercus rubra (northern red oak)	14 (1.4)	47.62	1.54
Acer rubrum (red maple)	60 (6.2)	16.67	0.79
Acer saccharum (sugar maple)	68 (7.0)	54.97	3.41
Fraxinus americana (white ash)	271 (28.0)	28.12	1.43
Quercus alba (white oak)	113 (11.7)	44.61	2.54
Prunus americana (wild plum)	11 (1.1)	72.50	5.46
Total	967 (100)	35.79	1.91

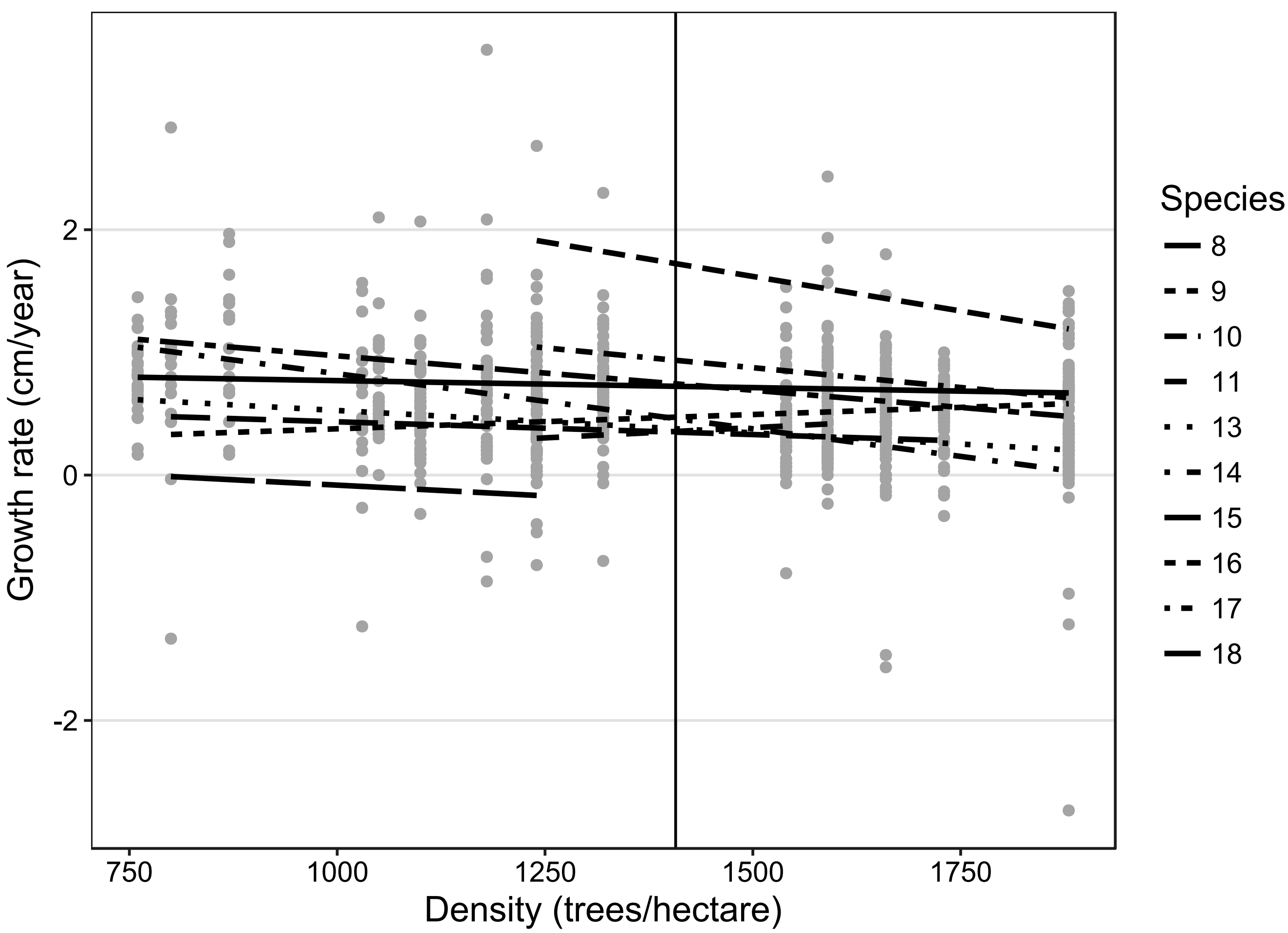


Figure 4. Tree growth rate was significantly reduced (multiple linear regression analysis, $F_{20,668} = 9.68$, $p < 0.001$) as density increased and varied with tree species. Growth rates are shown at centered (average) density indicated by the vertical line. The slopes of the horizontal lines indicate the rate of decrease in growth with density. When compared with the reference species, *Fraxinus americana* (8), growth rates decreased more with density in *Juglans nigra* (14) ($t = -4.25$, $p < 0.001$) and *Quercus alba* (16) ($t = -2.41$, $p < 0.05$). Other species are *Acer saccharum* (9), *Quercus rubra* (10), *Ostrya virginiana* (11), *Quercus macrocarpa* (13), *Acer rubrum* (15), *Tilia americana* (17), and *Prunus americana* (18).

Table 3. Number of individuals and percent of each tree species as a colonizing (col) species and combined with original trees to become all trees. Percent of original trees in 1990 is given to indicate how species composition has changed.

Species	Field 1 Col Trees	Field 2 Col Trees	% of All Col Trees	Field 1 All Trees	Field 2 All Trees	% of All Trees in 2013	% of All Trees in 1990
Ulmus americana	9	21	6.0	16	21	2.5	0
Acer ginnala	6	17	4.6	6	18	1.6	0
Populus tremuloide	14	4	3.6	14	4	1.2	0
Tilia americana	3	23	5.2	17	23	2.7	1.4
Prunus serotina	2	4	1.2	5	4	0.6	0.3
Juglans nigra	3	5	1.6	67	176	16.6	24.3
Acer negundo	36	36	14.4	36	36	4.9	0
Quercus macrocarp	8	1	1.8	145	24	11.5	16.5
Ostrya virginiana	15	1	3.2	26	1	1.8	1.9
Quercus rubra	30	14	8.8	44	14	4.0	1.4
Acer rubrum	0	1	0.20	0	61	4.2	6.2
Acer saccharum	5	3	1.6	38	38	5.2	7.0
Fraxinus americana	3	192	39.1	103	363	31.8	28.0
Quercus alba	12	4	3.2	103	26	8.8	11.7
Prunus americana	0	27	5.4	5	33	2.6	1.1
Total	146	353	100	625	842	100	100
Trees/ha	232	420	–	992	1002	–	–

average diameters greater than 8 cm. The remainder of the species, average diameters smaller than 6 cm, included *A. negundo, Q. macrocarpa*, *U. americana*, *F. americana*, *A. saccharum*, *A. ginnala, P. tremuloides, O. virginiana,* and *P. americana.*

Dissimilarities indices quantifying the change in species composition between fields from 1990 to 2013, using the presence/absence of species, showed Field 2 was more dissimilar to the original forest than was Field 1 based on a 2-sample t-test ($t_{12} = -3.32$, $p = 0.006$ Bray-Curtis index, $t_{12} = -3.29$, $p = 0.006$ Jaccard index, Table 4). However, when using the relative abundance of species, we did not see a difference between fields in species composition change from 1990 to 2013 using the Jaccard and Bray-Curtis dissimilarity indices (Table 4).

Table 4. Jaccard and Bray Curtis dissimilarity indices with standard deviation (SD) for the change in species composition in each field from 1990 to 2013. The binary method accounts for presence/absence of species, while the regular method is based on relative abundance of species. Values of 0 indicate no change in species composition, and values of 1 indicate complete change in composition. Field 2 was more dissimilar to the original forest than Field 1 according to a 2-sample *t*-test based on the binary method ($t_{12} = -3.29$, $p < 0.05$ Jaccard index, $t_{12} = -3.32$, $p < 0.05$ Bray-Curtis index). The difference between fields in species composition change from 1990 to 2013 was not significant using relative abundance.

	Jaccard Mean (SD)	Binary Jaccard Mean (SD)	Bray-Curtis Mean (SD)	Binary Bray-Curtis Mean (SD)
Field 1	0.441 (0.059)	0.281 (0.053)	0.292 (0.050)	0.169 (0.035)
Field 2	0.524 (0.041)	0.473 (0.025)	0.361 (0.037)	0.313 (0.023)
p-value	0.274	0.0064*	0.274	0.0061*

The Shannon and Simpson diversity indices showed that Field 1 had greater species diversity than Field 2 in 1990 and in 2013 (Table 5). The species richness and diversity increased in both fields from 1990 to 2013. Diversity of the entire restoration was 0.84 (Shannon) and 0.82 (Simpson) in 1990, and increased to 0.95 (Shannon) and 0.84 (Simpson) in 2013. The overall diversity in 2013 was significantly greater than in 1990 when Simpson indices were compared with a two-sample t-test ($t_{\infty} = 2.431$, $p < 0.05$).

Discussion

Growth and Mortality

Although the dominant forest type in southeastern Minnesota today is maple-basswood forest, early tree growth in this restoration study showed that northern *Q. rubra, Q. alba, T. americana,* and *F. americana* were the dominant and larger species in both height and diameter after 23 years (Figure 2). Height of these species increased more than ten-fold and diameter increased more than five-fold over twenty-three years. All species grew from initial mean heights of 0.3–0.8 m to mean heights of 9–12 m in the taller species and 2–6 m in the shorter species. The larger canopy species in maple-basswood forests in this region generally included *Ulmus* spp., *Quercus spp., T. americana, A. saccharum,* and *Fraxinus* spp. (Daubenmire 1936). In

Table 5. Shannon and Simpson species diversity indices for the entire restoration area in 1990 and 2013, and for Fields 1 and 2. Values for the year 1990 include originally planted trees, and values for the year 2013 include originally planted trees and new colonizing trees. When Simpson indices were compared with 2-sample t-tests, Field 1 was significantly more diverse than Field 2 in 1990 ($t_\infty = 5.19$, $p < 0.05$) and 2013 ($t_\infty = 7.90$, $p < 0.05$). The entire restoration area was more diverse in 2013 than in 1990 ($t_\infty = 2.431$, $p < 0.05$).

	1990		2013	
Species Diversity Index	Field 1	Field 2	Field 1	Field 2
Shannon (H′)	0.82	0.69	0.96	0.83
Simpson (Ds)	0.81	0.75	0.86	0.77
Entire Restoration Shannon (H′)	0.84		0.95	
Entire Restoration Simpson (Ds)	0.82		0.84	

this study, the open field conditions enhanced the growth of *Q. alba*, *Q. rubra*, and *F. americana*, while *A. saccharum* was much shorter and had slower growth rates (Figure 3). These growth patterns are consistent with findings that *A. saccharum* saplings grow well in mature forest gaps (Bray 1956), and that *A. saccharum* is considered very tolerant of shade, while oaks and ash are intermediate in shade tolerance (Baker 1949).

The height growth curves for the five more common species in this study *(F. americana, Q. alba, Q. macrocarpa, A. saccharum,* and *J. nigra*) showed a similar general pattern for all species (Figure 3). A simple exponential model was found to be the best fit in analyses of growth curves in these trees after 20 years (Eisinger et al. 2011). After growing at the same rate for the first five years, *F. americana* and *Q. alba* started growing faster and *Q. macrocarpa, J. nigra* and *A. saccharum* continued growing at slower rates. All these species are expected to continue growing from a current height of 6–12 m up to a mature tree height of 30 m (Burns and Honkala 1990). Multiple regression analysis showed growth rate varied among species and with density. The decrease in growth rates as tree density per transect increased (Figure 4) suggests increased competition for resources, such as light and water (Bazzaz 1979, Kobal et al. 2015).

The tallest trees in the forest were *F. americana* and *Q. alba* (Figure 3, Table 1). The likely death of *F. americana* in response to the expected emerald ash borer invasion will create significant openings in the canopy allowing different species to dominate. These openings may enable *A. saccharum* to take a more prominent role in the canopy since it is a dominant species in maple-basswood forests, and a specialist at colonizing gaps (Bray 1956). Canopy height varied significantly by field section with Field 1 South having a taller canopy height than the other three sections. Measurements of canopy coverage of 96% showed near canopy closure in most parts of the restoration, except for the northwestern part of Field 2 where coverage was 73%. Strong growth of grasses and *S. canadensis* in more open areas may make it difficult for new tree seedlings to become established.

After an initial period of higher mortality, trees became established and causes of early mortality, such as competition from ground cover plants and deer browsing, were reduced, resulting in an overall mortality rate of 35.79% (1.91% per year) since 1990 (Table 2). Of the future canopy trees, *A. saccharum* had the highest overall mortality rate (55%), followed by *Q. alba* and *Q. rubra* (45–48% respectively). These rates are higher than the 31% mortality in *Q. rubra* saplings after 8 years found by Lantagne (1996) and may be due to preferential browsing by *Odocoileus virginianus* (white-tailed deer), animals known to browse on *Q. rubra* and commonly seen in the forest restoration (Stange and Shea 1998, Cote 2004).

Colonization Effects

Because of colonization, the tree density in 2013 was about the same as the original planting density. With an overall mortality of 35.79% since 1990, the original tree density decreased to 658 trees/ha. Colonizing trees (399 tree/ha) made up approximately 34% of the current density of 998 trees/ha. The tree density in this restoration is similar to the tree density in sites Daubenmire (1936) surveyed. The Northfield Daubenmire site (8 km from this study site) had 852 trees/ha that were 2.5 cm (one inch) or larger DBH and the Minnetonka site (64 km north) had 968 trees/ha.

However, the species composition of the restoration is still quite different from what would be considered mature maple-basswood forest in this region. In two Minnesota sites (Northfield and Minnetonka, 56 km north of Northfield), Daubenmire (1936) found 56–64% of the trees were *A. saccharum*, 16% *T. americana*, 7% *Q. rubra*, 7% *O. virginiana*, and 9–10% *Ulmus* spp. In the Northfield site, green ash (*Fraxinus pennsylvanica), C. cordiformis*, and *Q. macrocarpa* were also found in small numbers. Surveys of Nerstrand-Big Woods State Park (24 km southeast of Northfield) found the most abundant species to be *T. americana*, *Carya* spp, *Q. alba*, *Q. rubra, A. saccharum*, *F. pennsylvanica, O. virginiana,* and *Populus grandidentata* (bigtooth aspen [Minnesota Department of Resources 1983]). In the restoration described in this paper, *A. saccharum* and *T. americana* made up fewer than 10% of the trees, and *F. americana, J. nigra,* and *Q. alba* were the most common species.

The two most common colonizing species added to the restoration sites were *F. americana* (39%) and *A. negundo*

(14% [Table 3]). Seeds likely came from forest fragments located within 30 m of the restoration on the northeast side (Figure 1), as well as observed internal seed production. *Fraxinus americana* has played a major role in the overall species and canopy composition from the beginning. *Acer negundo* seedlings have germinated and grown quickly in openings, but seedlings will likely be reduced after a few years in shaded understory areas (Smith 2008). Another colonizing species, *P. tremuloides,* reproduces quickly through clonal growth, likely leading to an increase in the size of *P. tremuloides* patches, especially in more open areas where more light resources are available (Uva 1997). *Quercus alba, T. americana*, *Q. rubra*, and *J. nigra* were the four largest colonizing species by height and DBH, while *F. americana* and *A. negundo* were smaller and more numerous (Table 3).

Field 2 had a greater number of colonizing trees per transect than did Field 1, and over half of them were *F. americana* (Table 3). Field 2 changed more from the original 1990 forest than Field 1 did (Table 4) over the period from 1990 to 2013 based on binary (presence/absence of species) Jaccard and Bray Curtis dissimilarity indices (Dyer 1978). Because there was not a significant difference between the two fields (Table 4) when comparing differences in the relative abundance of species (regular Jaccard and Bray-Curtis indices), results suggest that the addition/subtraction of species is contributing more to community change than changes in the relative abundance of species.

The overall diversity of the restoration increased from 1990 to 2013 (Table 5), showing the restoration is diversifying in species composition through colonization. Shannon and Simpson diversity indices demonstrate that Field 1 was more diverse than Field 2 in both 1990 and 2013. Field observations suggest there were fewer gaps for colonization in Field 1. Differences in species and colonization patterns recorded in this study suggest that different parts of the forest will likely reach alternative stable states, due to microhabitat differences in soil type, moisture availability, seed dispersal, and human disturbance (Suding and Gross 2006). *Quercus spp.* will continue to be more common in Field 1, which has less soil moisture, while *F. americana* and *J. nigra* will be more common in Field 2. Increases in diversity due to connectivity with other forest fragments will likely enhance resilience to climate changes (Timpane-Padgham, et al. 2017).

Future Recommendations and Conclusions

Tree growth patterns show that the species planted in 1990 have grown significantly and are likely to become part of a mature forest. In future restorations, more attention needs to be paid to environmental requirements of each species. For example, *Quercus spp.* should be planted in drier areas and *J. nigra* should be planted in areas of intermediate moisture and good soil fertility (Smith 2008). *Quercus* spp., *F. americana*, and *T. americana* did the best in the open field environment and our findings suggest that *A. saccharum* should be planted once other species of trees have become established enough to provide some shade.

This study links restoration and succession and provides specific information on composition and assembly that will be helpful in future restorations of northern deciduous forests. The data in this study support the initial floristic model (Egler 1954) in that all tree species can survive in the early successional environment of an open field, but show that some species clearly perform better than others. Restoration can be thought of as using successional concepts to better meet realistic restoration goals (Hobbs et al. 2007). Because reconstruction times for mature forests are not known (Zedler and Calloway 1999), and interannual variation makes it difficult to predict the time it will take for restoration, the sites in this study will continue to be monitored. Germination and growth of tree seeds and herbaceous understory plants will be enhanced as the understory accumulates more tree leaf litter. In nearby Nerstrand- Big Woods State Park (Nerstrand, Minnesota), an area was clear-cut for grazing from 1938–40 (Minnesota Department of Natural Resources 1983). After the area became part of the state park the canopy was reestablished in about 40 years, facilitated by connectivity with nearby forest fragments.

With two major disturbances on the horizon, *Agrilus planipennis* (emerald ash borer) and climate change, we can expect the forest's structure, composition, and productivity to shift as a result (Hufnagel and Garamvolgyi 2014, Ma et al. 2014). The loss of *Fraxinus* trees due to *A. planipennis* will create gaps that will change the dynamics of the forest, allowing other species such as *A. saccharum* and *A. negundo* to dominate the understory and canopy (Bray 1956, Herms et al. 2007). Current research (Herms et al. 2007) also suggests that this canopy gap-formation may facilitate the spread of invasive plants, such as *R. cathartica* or *Celastrus orbiculatus* (oriental bittersweet), which are already established in forests surrounding the restoration. Climate changes are likely to result in changes in tree growth rates and dominance patterns, leading to novel combinations of species (Hobbs and Cramer 2008). Future issues to address include planting more understory vegetation and the socioeconomic value of forest restoration (Wortley et al. 2013). These multiple past and potential environmental changes support our use of the "moving target" as compared to the "museum approach" (Frelich and Puettmann 1999). Ecological restoration needs to adapt to changes both in theory and restoration practice as the probability of returning to former states becomes increasingly less likely.

Discussion about whether a restoration is successful centers on whether initial goals have been achieved and whether the restoration is sustainable (Parker 1997, Hobbs and Harris 2001). The restoration project studied here is successful to date because the trees species planted had high survival rates (1.91% mortality per year), and in 23 years grew to create a closed canopy across much of the restored forest. Tree growth has created microenvironmental variation leading to an increase in species diversity as new species of trees have colonized the area since 1990. Although the restored forest is not yet mature, it represents a maple-basswood forest that will likely have variation in tree dominants in different sections depending on priority effects from the original planting as well as biotic and abiotic conditions that influence competition and colonization. The restoration provides important structural habitat for native plant and animal species, increases biodiversity, and acts as a carbon sink where agricultural fields once stood (Foley et al. 2005). It also provides information to guide future forest restoration projects.

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