

Growth and Stand Dynamics of Red Maple-Dominated Forests
in the Upper Great Lakes Region, USA

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Justin Luke Pszwaro

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Anthony W. D'Amato, Ph. D.

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Abstract

Red maple (*Acer rubrum* L.) was historically a common but not abundant tree species in North American temperate forests. Over the last several decades it has increased in abundance on upland sites across most of its range and today is perhaps the single most abundant tree species in eastern North America. With climate change and associated impacts on forest dynamics, red maple is expected to increase in relative importance in the Upper Lake States and New England. However, red maple lacks commercial importance and has thus received little attention in growth and yield studies and little is known of the dynamics of previously rare red maple-dominated stands. The objectives of this thesis were to 1) quantify the effects of stocking level and stand age on overall patterns of red maple stand productivity, 2) evaluate how these relationships vary across different geographic locations and climatic conditions, and 3) describe the composition dynamics of pure red maple-dominated forest stands.

To accomplish these objectives, this study used long-term measurements from a growth and yield study established by the USDA Forest Service in 1979 across 52 sites in northern Wisconsin and Michigan to examine the growth and compositional responses of even-aged red maple stands to various levels of thinning. Future stand-level red maple basal area of these areas was modeled as a function of stand and plot characteristics, as well as climatic variables, using linear mixed effects modeling. One climatic variable, total precipitation during the growing season, and its interaction with initial red maple basal area were significant predictors of stand-level growth; however, they only collectively reduced RMSE by 0.22% relative to a base model containing solely stand and plot factors. Model projections indicated there was little difference in predicted future basal area for the range of growing season precipitation (426-656 mm) experienced by these stands highlighting the wide tolerance of moisture conditions for this

species across the region. Pre-treatment patterns in overstory community composition across the 52 stands also reflected the wide ecological amplitude of red maple with overstory communities ranging from wet-site red maple-ash-elm forests to more mesic red maple-sugar maple systems. Post-thinning compositional development of these areas indicated an increasing abundance of shade-tolerant species in these stands; however, the relatively constant levels of red maple ingrowth and low overstory mortality rates observed for this species over the 30-year study period suggest long-term red maple dominance in these areas. Given the projected increases in the abundance of this species for the upper Great Lakes region, results from this network of plots can be used to inform future management regimes aimed at maintaining red maple stand productivity and achieving compositional objectives in these relatively novel systems.

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Chapter One: Introduction

Land-use and forest management practices in the centuries following European settlement in the eastern United States have had broad, deep, and lasting impacts on contemporary forest development, structure, and community composition (Foster *et al.*, 1998; Foster *et al.*, 2003; Schulte *et al.*, 2007). For many tree species, the concurrent introduction of non-native plants, insects, and diseases have greatly impacted native tree populations and compounded the effects of broad scale anthropogenic disturbance on forest communities (Lovett *et al.*, 2006). Climate change impacts are expected to interact synergistically with these disturbances and stressors to generate novel ecosystem conditions that present considerable challenges to the long-term sustainable management of forest ecosystems (Hobbs *et al.*, 2006).

One often-noted consequence of these changes throughout the eastern US has been the increased prevalence of red maple (*Acer rubrum* L.). The ability of this species to reproduce following disturbance and its wide ecological amplitude have given red maple a competitive advantage in a wide variety of ecosystems and geographic, edaphic, and climatic settings (Abrams, 1998). The result has been a significant increase in the abundance of red maple in nearly every part of its range including New England and New York (Lorimer, 1984; Abrams, 1998), the mid-Atlantic (Nowacki and Abrams, 1992), the southeast (Christensen, 1977) and south (Cain and Shelton, 1995), and the Lake States (Larsen, 1953; Palik and Pregitzer, 1992). This species, although historically abundant largely in swamps and lowlands with minor representation in upland sites (Abrams, 1998), now garners near “invasive” status as the bane of many land managers across a wide variety of ecological settings where it often thrives at the expense of more valued species. While nearly pure forests stands dominated by red maple were

typically only found in swamps and lowlands, they have increasingly become established on upland sites.

Despite the documented increases in red maple abundance over at least the last several decades (Abrams, 1998; Fei and Steiner, 2007), including in the upper Lake States region (Pugh, 2010; Perry, 2011), there is little information on the growth, yield, and forest structural and successional dynamics of red maple-dominated forests presumably due to the historically low commercial value of this species (Walters and Yawney, 1990; Strong *et al.*, 2006) and lack of perceived ecological importance. Given the projected increases in the abundance of this tree species and forest type owing to climate change, there is a great need to develop an understanding of the range of compositional conditions characterizing these communities, as well as their response to different thinning intensities both in terms of stand growth and community dynamics. In addition, in light of the recognized importance of climatic variation in affecting patterns of tree growth across the Lake States (Graumlich, 1993), and the documented sensitivity of maple growth to climate patterns (Reed *et al.*, 1992b; Carter, 1996; Fekedulegn *et al.*, 2003; Dombroskie *et al.*, 2010), efforts to model the response of these forests to management should account for the influence climate may have on stand growth and yield.

Based on these information needs, the overall objective of this thesis was to evaluate the long-term growth and dynamics of even-aged second-growth hardwood forests dominated by red maple within the upper Great Lakes region over a range of site conditions and geographic locations. To accomplish this, this study takes advantage of a unique, long-term series of study plots established by the USDA Forest Service in 52 red maple-dominated stands across northern Wisconsin and northern Michigan. These areas were thinned to a range of stocking levels (9.2, 13.8, 18.4, 23.0, 27.6, or 32.2 m² per hectare—or a no harvest control) in 1980 and remeasured in 1985, 1990, 1996, 2000, and 2011. The second chapter of this thesis applies these long-term data collections to quantifying the effects of stocking level and stand age on overall patterns of stand

productivity, in terms of basal area growth, across different geographic locations and climatic conditions. Results from whole-stand basal area projection models suggest that the climatic variation across the study region has significant but minor influence on basal area growth, and, in keeping with the site flexibility of the species, its productive potential is maintained across a wide variety of conditions. Basal area growth was best predicted by stand and plot-level conditions, including basal area at the beginning of a growth interval, which is consistent with the production ecology of other tree species.

The third chapter of this thesis documents the range of community composition of stands dominated by red maple across a variety of site types and their subsequent successional and mortality patterns following thinning. The results of this study indicated that species associates in red maple-dominated stands reflected the range of conditions in which it grows, from wet-mesic to mesic and poor to rich soils, and while management has some influence over stand compositional trajectory, red maple is likely to remain a dominant component in these stands for some time given its ability to reproduce following thinning on these sites and longevity of canopy trees.

The fourth and final chapter of this thesis presents conclusions related to results from all chapters of this document. Specifically, management recommendations are given based on results indicating the primary factors effecting growth potential and conditions favoring either maintenance or exclusion of red maple. This final chapter also includes a section on study limitations and future research recommendations intended to point out key observations that can be made by continued monitoring of the study sites.

Chapter Two: Stand basal area growth of thinned and unthinned red maple (*Acer rubrum* L.) forests in the upper Great Lakes region, USA.

Introduction

Red maple (*Acer rubrum* L.) is one of the most widespread tree species in North America in terms of both geographic range and ecological amplitude (Walters and Yawney, 1990). Historically it was only a minor component of the forests of the eastern US (Abrams, 1998) but has been increasing in abundance over at least the last several decades (Abrams, 1998; Fei and Steiner, 2007) and now ranks seventh in highest average importance value (IV) for tree species in the eastern US (east of the 100th meridian) based on recent national inventories (Prasad et al., 2007-ongoing). At localized scales, the magnitude of this increase in abundance is often much greater. For example, within the upper Lake States, summaries of recent Forest Inventory and Analysis (FIA) data indicate that in both Michigan and Wisconsin, red maple is second only to sugar maple in terms of wood volume (Pugh, 2010; Perry, 2011). In Michigan, red maple now accounts for 116 million m³ of standing wood volume (12.7 cm dbh and larger) and 72 million m³ in Wisconsin. Between just the last two complete FIA surveys for Minnesota, a significant increase (>60%) in red maple relative abundance (dbh \geq 2.54cm) has also been observed (Fei and Steiner, 2007). During the same period in the northeastern US, red maple sawtimber volume has more than tripled and now comprises nearly one quarter of growing stock volume between 12.7 and 27.7 cm dbh (Alderman et al., 2005).

Current stand structures and demographics of this species suggest that the pattern of increasing red maple abundance will continue. Within every state in its range for which there is data, red maple diameter distributions follow a reverse “J” distribution with high recruitment rates into larger size classes, suggesting it will continue to increase in abundance over at least the next

generation (Fei and Steiner, 2007). Furthermore, in many forest forecasting models that attempt to predict forest response to climate change, red maple is predicted to increase in abundance in parts of its range. Modeled growth and yield over the next 80 years in eastern Canada suggests red maple would respond positively to future climate under both current climate and a projected climate change scenario (Dombroskie *et al.*, 2010). Similarly, the USDA Forest Service Climate Change Atlas indicates that in the eastern US red maple could move up in overall IV rank to as high as number four and the area of the potential range for red maple could increase between 0 and 5.2 percent by the year 2100, depending on Global Circulation Model (GCM) and emissions scenario (Prasad *et al.*, 2007-ongoing). Under many GCM and emission scenarios, overall red maple importance in the eastern US is expected to decrease, particularly in the southeast; however, some regions could still see significant increases in red maple importance, particularly the Upper Lake States and northern New England.

Despite the current and projected future abundance and volume of red maple, growth and yield information is very limited for this species because it is often considered to be of poor quality and undesirable as a timber resource (Walters and Yawney, 1990; Alderman *et al.*, 2005; Strong *et al.*, 2006). A handful of studies have developed general management guidelines: red maple responds well to release (Erdmann *et al.*, 1985; Tift and Fajvan, 1999) and heavy thinning from below (9.2 to 18.4 m²/ha residual basal area) in even-aged stands has been shown to improve diameter and plot-level basal area growth for at least 14 years (Londo *et al.*, 1999). Thinning to an intermediate stocking level (16.1 to 18.4 m²/ha) has been recommended to improve diameter growth while limiting ingrowth of understory trees (Londo *et al.*, 1999; Strong and Erdmann, 2000).

Past growth modeling efforts with this species have largely focused either on diameter growth of individual trees (Hahn and Leary, 1979; Reed *et al.*, 1992a; Lessard *et al.*, 2001; Fekedulegn *et al.*, 2003) or stand-level growth in mixed forests where red maple is a minor

component of the overstory or occurs strictly in the understory (Solomon, 1977; Nowak, 1996). In many such examples the data from red maple has been combined with other species (e.g. silver maple) for analysis. Given the expected persistence of stands dominated by red maple (e.g. Eyre, 1980) and the potential for an increase in abundance of red maple in the northern parts of its range with climate change, a further understanding of growth in these forests is warranted.

Whole-stand growth and yield models are valued in forestry for their relatively low input requirements (e.g., stand basal area, site index, and age) which are already available for many forest stands or are otherwise easily and quickly obtained (Borders, 1989). Stand timber volume is often the primary attribute of interest as these models are developed, but basal area is also commonly examined both singularly and as one component of a comprehensive modeling system (Sun et al., 2007). Stand basal area observed across time provides a concise representation of forest stand development that includes survivor growth, ingrowth and mortality. It is simple to understand and inexpensive to measure and yet is strongly correlated with stand growth, yield, and mortality. Analysis of basal area change has thus been fundamental in the development of many forest growth and yield modeling systems and silvicultural prescriptions (Buckman, 1962; Clutter *et al.*, 1983; Burkhart and Tomé, 2012).

Since the earliest applications of variable-density yield equations (MacKinney and Chaiken as cited in Avery and Burkhart, 2002) stand projection models have employed a measure of initial stand density and stand age, and usually some measure of site productivity—most commonly site index—to predict stand growth. This is no less true of basal area projection equations (Clutter, 1963; Moser and Hall, 1969; Pienaar and Turnbull, 1973) where stand density may be represented as initial basal area (Knoebel *et al.*, 1986), number of stems per unit area (Pienaar and Shiver, 1986), or a stand density index derived from the combination of stem size and number relative to a theoretical maximum density (Candy, 1989). Additional independent variables are often included to explore stand basal area growth response to variation in environment or management

factors known or hypothesized to influence some dimension of tree or forest growth, or to allow for more accurate growth predictions based on such varied conditions. Such additions have included various indices of thinning intensity for managed stands (Bailey and Ware, 1983; Candy, 1989; Hasenauer *et al.*, 1997), stand average dominant height (Pienaar and Shiver, 1986), fertilization and weed control (Snowdon, 2002), pruned height ratio (Candy, 1989), climatic and edaphic variables (Woollons *et al.*, 1997) and indices of climatic variation (Snowdon, 2001).

Evidence from dendrochronology studies of individual tree growth has demonstrated that climate and site interact to influence diameter growth of many tree species and considerable research has explored the environmental effects on individual growth of red maple (Reed *et al.*, 1992a; Fekedulegn *et al.*, 2003). In modeling annual individual red maple diameter growth using a weekly time step in central Upper Michigan, air temperature degree days (base 4.4 deg C) through May, July soil potassium concentration in the upper 15 cm of mineral soil, and soil water holding capacity at a depth of 5-10 cm were found to be the predominant environment variables driving observed variation in diameter growth of individual red maple trees (Reed *et al.*, 1992a). Similar patterns were observed in examinations of stand-level biomass production in nearly pure, even-aged red maple stands where the highest levels of growth were on moderately well- to somewhat poorly-drained soils (Johnson *et al.*, 1987). Climate sensitivity of the species has also been demonstrated through provenance tests and resulting models, which suggest that a 4°C increase in mean annual minimum temperature could result in a height growth increase of 1.8-6.3% (Carter, 1996).

While recent experiments in red maple management have provided general management guidelines, there has been little consideration for how the stand-level growth response could be expected to vary by stand age or location. Given the documented influence of climatic and site conditions on red maple growth, it will be critical to account for these factors when forecasting the future dynamics of this species within a given region, such as the upper Great Lakes region

where there is a high degree of variation in site and climatic conditions. The objectives of this study are to evaluate the long-term basal area growth patterns of even-aged, red maple-dominated forests within the upper Great Lakes region over a range of site conditions and geographic locations. Specific objectives include: 1) quantifying the effects of stocking level and stand age on overall patterns of stand productivity in terms of basal area growth, and 2) evaluating how these relationships vary across different geographic locations and climatic conditions.

Methods

Study area

In 1979-1980, 52 study sites were established in even-aged, fully stocked red maple stands located throughout northern Wisconsin and Michigan, USA (**Error! Reference source not found.**), as part of a comprehensive red maple growth and yield modeling effort initiated by the US Forest Service North Central Research Station (now Northern Research Station). The study area locations range from the Chequamegon National Forest in northwestern Wisconsin, across the Upper Peninsula of Michigan, and south to the Huron-Manistee National Forest in the west of Michigan's Lower Peninsula (

Figure 1). Most study locations are in National Forests with nine sites located within state forests and two on privately owned commercial timberland. The climate of the study region is continental or humid continental with average January minimum temperature ranging from -17° C to -9° C and average July maximum temperature ranging from 24° C to 28° C. Total annual precipitation ranges from 65 to 82 cm across the study area. The soils types include a broad range from lacustrine and moderately well-drained glacial till soils to dry outwash and poorly drained glacial till soils (Haag, 1987).

Study plots were established in undisturbed, second-growth stands that established naturally following late 19th and early 20th century harvesting, and in which at least 75% of the overstory canopy was red maple (Erdmann *et al.*, 1981). Two to four plots were installed at each site, resulting in a total of 122 plots. Each plot was established as a 2000 m² rectangle surrounded by a 10 meter-wide isolation strip that received the same treatment as the interior of the plot. To improve marking uniformity for thinning treatments, each plot was subdivided into two square 1000 m² (31.6 x 31.6 m) half plots, the isolation strips were subdivided into four sections, and the residual density of each subdivision was controlled independently. Each tree ≥ 10 cm dbh was marked with a unique identifier to facilitate individual tree remeasurements.

In addition to red maple, common associate canopy tree species varied by site but included sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). Less common, but occasionally locally-abundant species included black cherry (*Prunus serotina*), paper birch (*Betula papyrifera*), eastern hemlock (*Tsuga canadensis*), black ash (*Fraxinus nigra*), and eastern white pine (*Pinus strobus*).

At the time of plot establishment, three to five dominant and codominant non-plot trees were felled for stem analysis at each site for the purpose of age and site index determination following the methods of Erdmann and Peterson (1982). Stand age was taken as the mean number of annual growth rings counted at ground-level for all stem analysis trees on each site adjusted from the time of felling to 1980. Similarly, site index was assumed to be the mean site index estimated from those trees. Stand age in 1980 ranged from 28 to 97 years old, and site index ranged from 12.6 to 22.9 m at a base age of 50 years (**Error! Reference source not found.**).

After the 1981 growing season, a harvest reduced the basal area of each plot to one of six randomly assigned residual stocking levels—9.2, 13.8, 18.4, 23.0, 27.6, or 32.2 m² per hectare—or a no harvest control with variable basal area. The study initially emphasized quality timber

production, so the plots were thinned from below to achieve the most uniformly-spaced stand of defect-free dominant and codominant red maple trees as possible. Poorly formed trees and species other than red maple were targeted for removal to increase the stocking percentage of quality red maple. Plots designated as control plots were left untreated.

Plots were measured for initial conditions in 1980 and remeasurement occurred in approximately 1985, 1990, 1996, 2000, and 2011, to determine tree- and stand-level growth response to thinning. If recorded, the actual date of measurement was used to determine stand ages and growth interval lengths, but where this information was missing the nominal measurement year was substituted. At each measurement period, the dbh and species of each live tree ≥ 10 cm dbh on every plot was recorded, including ingrowth trees. Every reasonable effort was made to locate all previously recorded trees. Those that had died were recorded as such, as were trees that could not be located. The exact year of harvest was not known for all sites, and post-harvest measurement did not occur until 1985, so growth observations for the 1980-1985 interval were excluded from the present analysis. One plot experienced significant wind damage in both 1983 and 1989 so only observations on that plot from 1996 onward were included. Some plots were harvested before the most recent measurement in 2011. In total, 452 growth observations were available for analysis.

Monthly climate variables at each site were estimated using thin plate spline smoothing algorithms (see McKenney *et al.*, 2011; 2013) and summarized as necessary to produce annual and seasonal estimates of climatic variables. These site-specific values were then averaged across all years of each growth interval specific to each site to test as predictors of basal area growth.

Basal Area Projection Modeling

The basal area of each tree was calculated from measured diameter and the basal area of all living trees on each plot was summed to determine total stand basal area at the time of

measurement. Plot basal areas were also determined by species. Since red maple accounted for an average of more than 80 percent basal area for all observations on all plots, and in order to focus the analysis on the red maple component, red maple basal area (m^2/ha) was used as the response variable in our analyses.

The factors most relevant to growth and yield (age, site quality, and stand density) combine multiplicatively in their influence over yield but are additive in their influence on the logarithm of yield (Clutter *et al.*, 1983; Avery and Burkhart, 2002), so the natural logarithm of red maple basal area at the end of the growth interval was selected as the response variable. Site index, various measures of time (age), stand density, and thinning intensity, were tested for inclusion in a basic regression model to describe red maple basal area growth. A partial list of variables considered during the fitting process is shown in (**Error! Reference source not found.**).

The data includes unbalanced, irregularly spaced, longitudinal observations of plots grouped within stands. To account for this hierarchical and correlated structure, a linear mixed-effects modeling framework (Grégoire *et al.*, 1995) was applied. A variety of nonlinear mixed-effects model forms were also attempted, including common sigmoidal forms such as those from Schumacher (1939) and Chapman-Richards (Pienaar and Turnbull, 1973), but they generally lacked the flexibility to achieve convergence. This is probably at least in part because the dataset lacks observations in stands less than 30 years old, likely the age range that would include the inflection point in a sigmoidal yield curve.

To determine the ideal specification of the random effects structure, variance model, and autocorrelation structure, regressions were estimated by restricted maximum likelihood with different specifications for each, but including the same comprehensive set of all independent variables under consideration (Zuur *et al.*, 2009). Comparisons of the Akaike Information Criteria (AIC) were used to select the best performing structure from this set. Using this model structure and starting with two independent variables—the natural logarithm of initial red maple

basal area ($lnrmI$) and growth interval length (dt)—additional independent variables and interactions were incorporated into the regression and the results were evaluated for improvement. Once the model form and basic set of independent variables were selected, various climate variables were incorporated and tested for significance (**Error! Reference source not found.**). The R software program (R Development Core Team, 2012) and nonlinear mixed-effects (nlme) package (Pinheiro *et al.*, 2012) were used to estimate model parameters.

Results

Growth by stocking level

The 1982 thinning resulted in statistically distinctive stocking levels across treatments in 1985 (based on Analysis of Variance followed by Tukey's Studentized Range test, $P < 0.05$), with the exception of the most lightly thinned plots (target residual basal area of 32.2 m²/ha), which did not differ from the control plots in total basal area. Distinctive stocking conditions persisted for up to 18 years after thinning (

Figure 2a). By the 13th year following thinning, the control group and the two most lightly thinned groups had converged in terms of total stand basal area, and the other four more heavily thinned plots had begun to converge by the 29th year. Similarly, the four most heavily thinned plots retained different levels of red maple basal area after 18 years (

Figure 2b) with many groups converging by the 29th year. Total basal area annual increment generally had an inverse relationship with stocking (

Figure 2c), as did red maple annual basal area increment (

Figure 2d). A comparison between total stand basal area growth and red maple basal area growth indicated that red maple basal area generally followed the patterns of total stand basal area.

Periodic annual net basal area growth was lowest in the control and lightly thinned plots and increased with decreasing relative density (

Figure 3). Most of the control plots and some plots from the most lightly thinned treatments exhibited a net loss in basal area during the final growth interval. Periodic annual gross basal area growth (survivor growth plus ingrowth for the growth interval divided by the growth interval length) showed no strong relationship with density over the range covered by this data (not shown).

Linear mixed-effects regression

Based on basic stand- and plot-level conditions, the linear mixed effects regression model for predicting red maple basal area that provided the best fit took the form:

$$\ln \text{rm}2_{ij} = \beta_0 + \beta_1 \ln \text{rm}1_{ij} + (\beta_2 + b_i) dt_i + \beta_3 \text{inv. age}1_i + \beta_4 \text{pctrm}_{ij} + \beta_5 dq_{ij} + \beta_6 dt_i \\ \times \text{inv. age}1_i + \varepsilon_{ij}$$

where $\ln \text{rm}2_{ij}$ is the natural logarithm of total red maple basal area at the end of the growth interval on the j th plot in the i th stand, β_0 through β_6 are population-level fixed effects parameters, b_i is a stand-level random effects parameter, dt_i is the change in stand age (number of growing seasons) from the start to the end of the growth interval, $\text{inv. age}1_i$ is the inverse of initial stand age, pctrm_{ij} is the proportion of basal area comprised of red maple, dq_{ij} is the plot quadratic mean diameter for all trees greater than 10 cm, and ε_{ij} is the model error term, where $\varepsilon_{ij} \sim N(0, \mathbf{R}_{ij})$.

Stand density was represented in the final model form as the co-occurrence of initial red maple basal area and basal area proportion of red maple. Other density measures, such as relative density and stand density index, and site index either figured significantly and had unexpected

signs or caused unexpected signs to result on other variables and thus were not included in the final model. The number of stems per hectare was highly correlated with red maple basal area and quadratic mean diameter, and no index of thinning grade or intensity was found to be significant.

Parameter estimates from the fitted base model (**Error! Reference source not found.**) indicate initial red maple BA and percent red maple had positive effects on red maple growth, while stem density and quadratic mean dbh had negative effects on growth. Despite a negative parameter estimate for the inverse of initial age, when taken with its interaction with growth interval length this variable had a net positive effect, indicating higher red maple growth projections in younger stands (Figure 4b). For a given set of initial starting conditions, red maple basal area predictions are substantially higher for younger stands.

Mixed effects model performance relative to GLS

Models were initially fit with both plot-level and site-level random effects. Most of the variation between plots was described by the final combination of fixed effects in each model such that the plot-level random effects did not provide a significant improvement in the model fit. By contrast, the site-level random slope parameter on growth interval length (dt) in the base model remained highly significant indicating that site-level fixed effects did not sufficiently account for the variation between sites (**Error! Reference source not found.**). The influence of the random effect was greater for higher density plots (Figure 4b). For plots with an initial red maple component greater than 25 m²/ha basal area, the change in red maple basal area could range from nearly zero to over 3.0 m²/ha, depending on the estimated random effect for the stand.

Based on the parameter estimates, projections of red maple basal area growth in a hypothetical stand shows that basal area development can follow grossly different paths depending on the interval length applied in the projections (Figure 5a). Divergence is apparent

after only 20 years with longer growth intervals resulting in higher projected red maple basal area, and the differences become largest at roughly age 90 from which point the projections begin to converge again.

Climate effects on basal area projections

After testing many climate variables (**Error! Reference source not found.**) for inclusion in the base model, only the growth interval mean precipitation during the growing season (*precip3*) significantly improved the model fit, along with an interaction between mean growing season precipitation and the natural logarithm of initial red maple basal area. Including these terms altered the relationships such that the intercept term was no longer significant, and the resulting, final form was:

$$\ln m_{2ij} = \beta_1 \ln m_{1ij} + (\beta_2 + b_i) dt_i + \beta_3 \text{inv. age}_{1ij} + \beta_4 \text{pctrm}_{ij} + \beta_5 dq_{ij} + \beta_6 dt_{ij} \\ \times \text{inv. age}_{1ij} + \beta_7 \text{precip3}_i + \beta_8 \ln m_{1ij} \times \text{precip3}_i + \varepsilon_{ij}$$

where precip3_i is the mean precipitation during the growing season at the i th site for the growth interval and all other terms are as previously defined.

Climatic factors introduced only marginal improvements in model fit (MSE was reduced by only 2.1%) and local climate had only a minor influence on red maple basal area change. The parameter estimates reveal a density-dependent growth response to changes in precipitation. For a plot observation with average values for all included variables ($\text{age} = 76.9$ years, $\text{pctrm} = 0.81$, $dq = 24.1$ cm, and growth interval = 6.29 years) with initial red maple basal area of 24.8 m²/ha, the growth response is indifferent to variation in growing season precipitation. Such an “average” plot with a lower initial basal area would have a larger growth response with increasing

growing season precipitation, while an “average” plot with basal area greater than 24.8 m²/ha would have a lower growth response with increasing precipitation (Figure 6).

Discussion

Analysis of 26 years of stand-level red maple basal area development in second-growth red maple dominated stands has revealed that basal area growth in these systems is controlled by similar factors as for other species, including initial red maple basal area, stand age, and proportion of conspecific basal area. Despite the documented influence of climate on tree growth across our study region (Graumlich, 1993), and the sensitivity of individual red maple growth to climate (Reed *et al.*, 1992c; Carter, 1996; Fekedulegn *et al.*, 2003), we found only a modest improvement of predictions of stand-level basal area growth when accounting for climatic variation. This lack of relationship could reflect the wide ecological amplitude of the species and suggests factors more directly influenced by management, such as stocking and composition, are more important for projecting growth of this species.

Unlike most growth modeling studies which typically employ a total stand dimension as the response variable, this study used the component growth of an individual species.

Correspondingly, the primary predictor used here is initial conspecific basal area, which along with species proportion of basal area describes the level of competition in the stand. The highest basal area projections occurred in pure stands, which are representative of the lowest level of competition for a given conspecific basal area. A comparable result was obtained by Hasenauer *et al.* (1997), who developed a nonlinear model that included the loblolly pine proportion of basal area to project the basal area of the pine component in even aged plantations containing hardwood competition. Similar to observations summarized by the Langsaeter hypothesis regarding gross volume growth (Dean *et al.*, 2013), the mean annual basal area gross growth in

these stands does not appear to vary with stocking or density (data not shown). In contrast, net period annual basal area production decreased with increasing relative density and stocking (

Figure 3) which is reflective of the expected increase in competition and density-related mortality (Vanclay and Sands, 2009).

The results of this analysis demonstrate that red maple basal area growth decreases as stands grow older but because the response variable is not total stand basal area, direct conclusions cannot be made regarding the stand productivity-age relationship. Since growth and yield and ecological studies have almost universally documented a decline in tree and forest stand-level growth as stand age increases (Ryan *et al.*, 1997; Smith and Long, 2001), the observed trend in red maple basal area is likely the species-component corollary of age-related decline. In the case of tolerant species, as present in this study, other age classes may counterbalance this decline over time (O'Hara and Nagel, 2006).

Given differences between sites to support tree growth, many authors have noted the importance of accounting for site productive potential in growth models. Usually this is accomplished by taking observed tree height growth (site index) as a general indicator of site productive potential, despite the fact that it is often not well correlated with stand growth in dimensions other than height (Assmann, 1970; Skovsgaard and Vanclay, 2008; Skovsgaard, 2009) and the relationship may be further compromised by damage affecting tree height or mean stand height (Woods and Coates, 2013). We found little relationship between stand basal area growth and site index, which is consistent with the findings of other authors that have observed that site index may not be usefully correlated with basal area growth (Buckman, 1962; Payandeh and Wang, 1996; Snowdon, 2001). This is particularly true in mixed species stands, such as some of the stands in this study that contained higher proportions of species other than red maple.

Aside from height, other dimensions of past stand growth can be used to predict current or future growth. Skovsgaard (2009) recommended incorporating a pretreatment measure of site

productivity, specifically total volume production, for this purpose. Pretreatment mean annual basal area increment, which was selected (rather than total basal area) because of the wide range of stand ages in this data and because volume data was not available, did slightly increase the model fit. Nevertheless, inclusion of this variable in stand growth models requires knowledge of stand history that is often lacking in practice and therefore we did not include this variable in our final model forms. Additionally, as stand-level basal area growth is asymptotic, older stands may show a reduction of mean annual increment that is not characteristic of the stand's true productive potential. Finally, given this study sought to identify the drivers of these differences in growth and not simply to account for them we felt justified in excluding this variable from our models.

In examining the basal area growth of thinned and unthinned loblolly pine stands, Hasenauer *et al.* (1997) similarly concluded that it is necessary to account for the intensity of the thinning, not simply current stand density, to acquire consistent and unbiased growth projections. It would be expected that for stands of equal age, site index, and basal area, those that had a higher unthinned basal area were more productive and would subsequently support greater growth, a difference that would be captured in an index of thinning intensity. While such indices (Bailey and Ware, 1983; Hasenauer *et al.*, 1997) were marginally significant during preliminary analysis of our data, they did not prove to be helpful in the final model form. Given that red maple is a tolerant species, these natural-origin stands may not behave in the same manner as the even-aged plantations composed of intolerant species commonly examined in those and many other growth studies. It is apparent that as recruitment and ingrowth in these stands, especially heavily thinned ones, can make large contributions to basal area in a short time, differences in tree growth due to variation in thinning intensity may be quickly obscured by ingrowth.

A main objective of this research was to examine the influence of climatic variables on red maple basal area growth across our numerous site locations and conditions. Although we investigated a large number of climatic variables, precipitation during the growing season was the

only climate-related variable that improved model fit. The parameter estimate on precipitation during the growing season indicated increasing red maple basal area projections with increasing precipitation. The interaction with initial basal area reveals that the response to increased precipitation is positive for plots with initial red maple basal area below 24.8 m²/ha, but negative for higher density plots. Past work has suggested that insufficient moisture availability is limiting to individual red maple diameter growth (Reed *et al.*, 1992a; Fekedulegn *et al.*, 2003) but it is unclear whether trees would continue to respond to increasing moisture beyond a limiting threshold. The data from this study indicates that in low density stands where other resources are unlikely to be limiting to growth, increasing precipitation during the growing season does result in increased growth. It is possible that in more dense stands other resources are the limiting factors so as individuals take advantage of increasing precipitation, a resulting increase in competition-related mortality ultimately causes a reduction in stand-level basal area growth.

The apparently modest influence of climatic variation on stand-level basal area development of red maple in this region could reflect the broad ecological amplitude of the species. Red maple has successfully colonized sites of nearly every possible soil type and moisture regime in the eastern US and in many cases is highly competitive with more specialized species (Abrams, 1998; Saeki *et al.*, 2011). Even within a region, the species exhibits considerable variation in genetics, phenology, and ecological traits that likely contribute to this success. As an example, several experiments with red maple seedlings have shown that genotypes from different hydrologic habitats within the same region exhibit different growth response to changes in environmental variables (Abrams and Kubiske, 1990; Anella and Whitlow, 2000; Bauerle *et al.*, 2003a; Bauerle *et al.*, 2003b). Local populations seem to be adapted to site level-environmental conditions such that some interaction between soil type, genetics, and climate can be expected but difficult to determine or predict. Despite the species' flexibility, the significance of growing season precipitation in red maple basal area growth

corroborates other studies that have demonstrated the dependency of red maple growth and productivity on moisture availability (Johnson *et al.*, 1987; Reed *et al.*, 1992a).

Conclusion

The increasing abundance of red maple-dominated forests on the landscape has created a need for predictive models that describe growth and yield of this species across the wide variety of sites on which it occurs. Managers are eager to understand how the growth of individual species and forest communities will respond to future climatic conditions. In this context, the notable predicted success of red maple populations under forecasted climate conditions generates a particular interest in understanding how that species responds to environmental variation.

At the site level, basal area growth of red maple is well described by factors easily controlled for via management such as current stand density and age. The results from this study suggest that once red maple-dominated stands have established, the variation in climatic conditions as occurring across our study region do not result in large changes in stand-level red maple growth. There are growth differences between sites of similar age, quality, and management history that do not appear to be strongly related to regional variations in climatic conditions and highlight the productive potential of this species under a wide range of future climatic conditions. Red maple seems to be robust in growth across a range of climatic conditions such that, regardless of what climate change brings about, managers can expect it will be a reliable species for which to plan in the future.

Tables

Table 1. Initial conditions for 122 red maple dominated study plots across northern Wisconsin and northern Michigan in 1980.

Thinning Treatment	All plots	Control	9.2 m ² /ha	13.8 m ² /ha	18.4 m ² /ha	23.0 m ² /ha	27.6 m ² /ha	32.1 m ² /ha
n (# plots)	122	12	5	22	34	29	15	5
initial age (years)	66 (28-97)	70 (40-95)	46 (28-61)	56 (28-68)	65 (40-97)	71 (53-97)	69 (54-88)	76 (59-88)
site index (m)	17.2 (12.6-22.9)	16.7 (12.9-19.0)	16.3 (12.8-22.9)	17.5 (12.8-22.9)	17.3 (12.6-21.6)	17.1 (12.6-21.6)	17.6 (14.4-20.6)	17.4 (14.7-20.5)
initial basal area (m ² /ha)	30.7 (14.3-43.8)	30.9 (21.1-39.3)	19.1 (14.3-22.9)	26.2 (14.3-33.3)	30.1 (20.8-42.8)	33.1 (26.9-42.0)	34.4 (28.3-42.9)	37.4 (33.8-43.8)
red maple basal area (m ² /ha)	22.1 (4.6-35.5)	24.2 (11.8-32.1)	10.0 (4.6-18.1)	17.2 (7.3-30.1)	21.5 (10.7-31.9)	24.3 (14.0-35.0)	26.5 (16.6-35.5)	29.7 (26.3-33.8)
% red maple basal area	0.72 (0.23-0.98)	0.78 (0.56-0.97)	0.52 (0.23-0.79)	0.65 (0.35-0.96)	0.71 (0.46-0.96)	0.73 (0.51-0.95)	0.77 (0.5-0.98)	0.80 (0.73-0.95)
no. of trees per hectare	939 (510-1460)	835 (645-1250)	1104 (875-1355)	1022 (725-1400)	961 (565-1460)	907 (510-1340)	895 (585-1105)	833 (615-1195)
quadratic mean diameter (cm)	20.7 (13.6-30.8)	22.1 (16.0-26.1)	14.9 (13.6-15.7)	18.2 (13.6-23.4)	20.3 (15.2-26.3)	22.1 (16.5-30.8)	22.4 (18.1-27.0)	24.4 (21.6-27.1)
stand density index	647 (365-903)	638 (497-832)	466 (365-570)	585 (367-738)	645 (460-835)	684 (537-803)	707 (600-839)	746 (655-903)
relative density (% of max.)	0.64 (0.37-0.84)	0.62 (0.49-0.80)	0.46 (0.37-0.57)	0.58 (0.37-0.74)	0.63 (0.45-0.84)	0.67 (0.52-0.82)	0.69 (0.58-0.83)	0.72 (0.65-0.81)

Table 2. 1985 post-thinning conditions for 122 red maple dominated plots thinned to six levels of residual basal area or not thinned.

Thinning Treatment	Control	9.2 m ² /ha	13.8 m ² /ha	18.4 m ² /ha	23.0 m ² /ha	27.6 m ² /ha	32.1 m ² /ha
N (# of plots)	12	5	22	34	29	15	5
basal area (m ² /ha)*	32.8 (25.0-40.4)	13.0 (11.9-14.7)	16.9 (15.3-19)	21.1 (18.5-23.3)	25.6 (24.4-28.2)	29.9 (28.2-31.6)	34.0 (32.9-35.5)
red maple basal area (m ² /ha)	25.6 (14.7-34.2)	9.5 (7.3-11.8)	13.8 (6.5-16.5)	17.3 (13.2-21.8)	21.0 (14.1-26.1)	25.3 (16.4-31.3)	28.6 (26.3-32.9)
Age	76 (45-101)	51 (33-66)	61 (33-74)	71 (45-101)	76 (58-101)	74 (60-93)	81 (64-93)
no. of trees per hectare	808 (605-1215)	676 (560-900)	538 (235-1035)	546 (230-1075)	577 (225-1065)	643 (380-1045)	630 (505-820)
% red maple basal area	77.9 (58.2-96.5)	73.5 (49.3-95.1)	81.8 (39.0-98.7)	82.1 (59.6-100.0)	82.3 (54.1-100.0)	84.5 (54.8-99.0)	84.0 (76.4-97.2)
quadratic mean diameter (cm)	23.2 (17.2-27.0)	15.8 (14.4-16.8)	21.2 (14.3-29.6)	23.4 (16.1-32.7)	25.0 (17.7-37.4)	25.1 (18.8-31.4)	26.5 (22.9-29.2)
relative density (% of max.)	0.65 (0.57-0.81)	0.31 (0.29-0.35)	0.36 (0.29-0.47)	0.43 (0.33-0.53)	0.51 (0.41-0.61)	0.58 (0.51-0.65)	0.65 (0.62-0.70)
stand density index	665 (574-845)	313 (292-365)	364 (300-462)	436 (335-524)	514 (420-596)	596 (528-651)	660 (627-699)
basal area thinning ratio†	1 1-1	0.49 (0.40-0.64)	0.55 (0.41-0.96)	0.64 (0.43-0.88)	0.71 (0.54-0.9)	0.81 (0.64-0.98)	0.86 (0.74-0.95)

* Residual basal area was the target basal area for the thinning in 1982 which was not measured, while basal area in 1985 is the measured total basal area for all live trees ≥ 10 cm measured at that time.

† Ratio of stand total basal area after the 1982 thinning harvests to stand total basal area before the thinning

Table 3. Summary of selected climatic variables for 52 site locations of even-aged red maple dominated forest stands used for red maple basal area projection modeling. Annual values were estimated for site locations using thin plate smoothing splines applied to the US National Weather Service Cooperative Observer Program weather observation data and additional sources (McKenney *et al.*, 2011), and averaged across years corresponding to the respective growth intervals at each site.

Growth interval	1985-1990	1990-1996	1996-2000	2000-2011
Number of plots	122	122	117	108
annual mean temp. (deg. °C)	4.7 (3.6-7.7)	4.5 (3.3-7.5)	5.1 (3.8-7.8)	5.3 (4.2-6.5)
annual mean precip. (mm)	770 (641-889)	813 (746-909)	774 (697-924)	793 (712-840)
start of the growing season (Julian day number)*	111 (99-117)	118 (106-121)	120 (106-125)	114 (107-121)
length of the growing season (days)	193 (171-222)	187 (170-212)	191 (169-215)	199 (174-212)
growing degree days during the growing season†	1559 (1424-2019)	1461 (1338-1912)	1570 (1458-1955)	1573 (1455-1812)
precipitation during the three months preceding the growing season	118 (75-154)	130 (107-163)	140 (111-161)	142 (113-171)
precipitation during the growing season (mm)	492 (426-645)	528 (469-624)	480 (431-576)	519 (477-612)
mean temp. during the growing season (degrees Celcius °C)	13.5 (12.5-15.2)	13.3 (12.6-14.6)	13.6 (13.1-14.8)	13.3 (12.6-14.6)

* The growing season is defined to start on the first day from March 1 on which the mean daily temperature has been 5° C or greater for 5 consecutive days, and to end from August 1 when the minimum temperature is -2° C or lower.

† For a growing season of length n days, each with minimum ($Tmin$) and maximum ($Tmax$) temperature, growing degree days = $\sum_{i=1}^n \frac{Tmax_i + Tmin_i}{2} - 5$.

Table 4. Restricted maximum likelihood estimates of β_0 through β_8 from the red maple basal area projection model*.

Parameter	Base model		Base + Climate	
	Estimate	Estimated SE	Estimate	Estimated SE
β_0	0.367399	0.0301506	---	---
β_1	0.881288	0.0072075	0.996235	0.0076846
β_2	-0.026293	0.0032446	-0.025146	0.0031923
β_3	-3.967345	1.1930352	-3.615232	1.1008237
β_4	0.124815	0.0157777	0.116558	0.0156584
β_5	-0.001557	0.0004291	-0.001191	0.0004034
β_6	2.694513	0.2662529	2.594156	0.2665845
β_7	---	---	0.000733	0.0000546
β_8	---	---	-0.000233	0.0000199
Index of fit†	0.95946852		0.9603028	
MSE‡	1.02406886		1.0029890	

* $\ln m_{2ij} = \beta_0 + \beta_1 \ln m_{1ij} + (\beta_2 + b_i) dt_i + \beta_3 \text{inv. age}_{1ij} + \beta_4 \text{pctrm}_{ij} + \beta_5 dq_{ij} + \beta_6 dt_{ij} \times \text{inv. age}_{1ij} + \beta_7 \text{precip}_{3ij} + \beta_8 \ln m_{1ij} \times \text{precip}_{3ij} + \varepsilon_{ij}$

†Index of fit = $\left(1 - \sum \frac{(\ln m_{2i} - \widehat{\ln m_{2i}})}{(\ln m_{2i} - \widehat{\ln m_{2i}})}\right)$, calculated using bias-corrected, back-transformed residuals based on the fixed effects in the mixed effects model.

‡MSE = $\frac{\sum (y_i - \hat{y}_i)^2}{n}$, calculated using bias-corrected, back-transformed residuals based on the fixed effects in the mixed effects model.

Table 5. Comparison of red maple basal area growth model selection statistics from regressions estimated with the fixed effects in equations 1 and 2 using restricted maximum likelihood with different structures for heteroscedasticity, autocorrelation, and hierarchical data. Note: comparisons of models with different fixed effects (i.e. between “Base” and “Climate” columns) fit using restricted maximum are not useful. See Table 6 for a comparison of the final “Base” and “Climate” models fit using maximum likelihood.

Model structure	Base Model			Climate Model		
	df	AIC	logLik	df	AIC	logLik
OLS	8	-1519.957	767.9785	9	-1486.361	752.1804
Heteroscedasticity	60	-1604.688	862.3438	10	-1547.876	783.9382
Autocorrelation	9	-1575.841	796.9206	62	-1639.123	881.5616
Heteroscedasticity and autocorrelation	61	-1664.239	893.1197	61	-1577.886	849.9430
Random effects and autocorrelation	10	-1674.972	847.4861	11	-1644.615	833.3076
Random effects and heteroscedasticity	61	-1722.490	922.2452	62	-1697.411	910.7057
Random effects, heteroscedasticity, and autocorrelation	62	-1737.742	930.8708	63	-1714.555	920.2776

Table 6. Model selection statistics for comparing the final base and climate models for red maple basal area projection fit using maximum likelihood.

	Model	df	AIC	BIC	logLik	L.Ratio	p-value
Climate	1	64	-1807.37	-1544.095	967.6853		
Base	2	63	-1796.78	-1537.618	961.3900	12.59055	4e-04

Figures

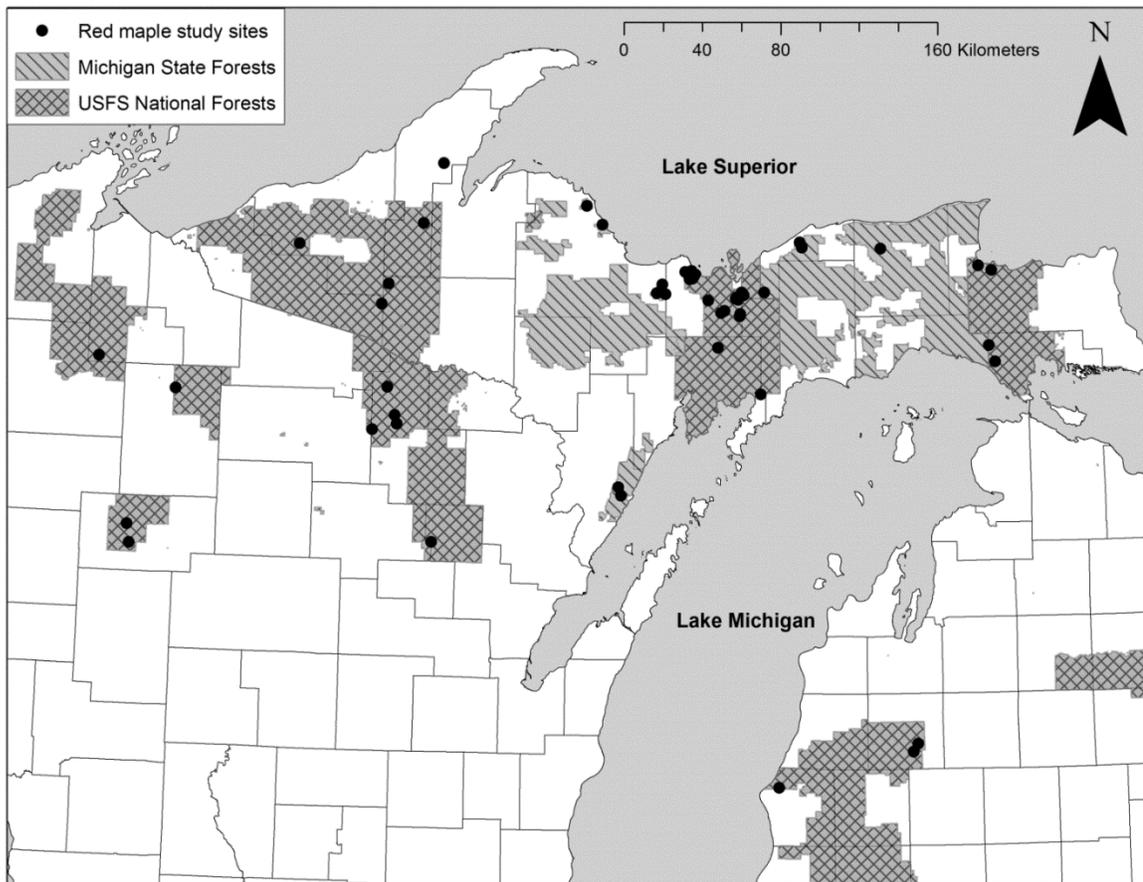


Figure 1. Locations of 52 red maple study sites across northern Wisconsin and northern Michigan used for red maple growth modeling.

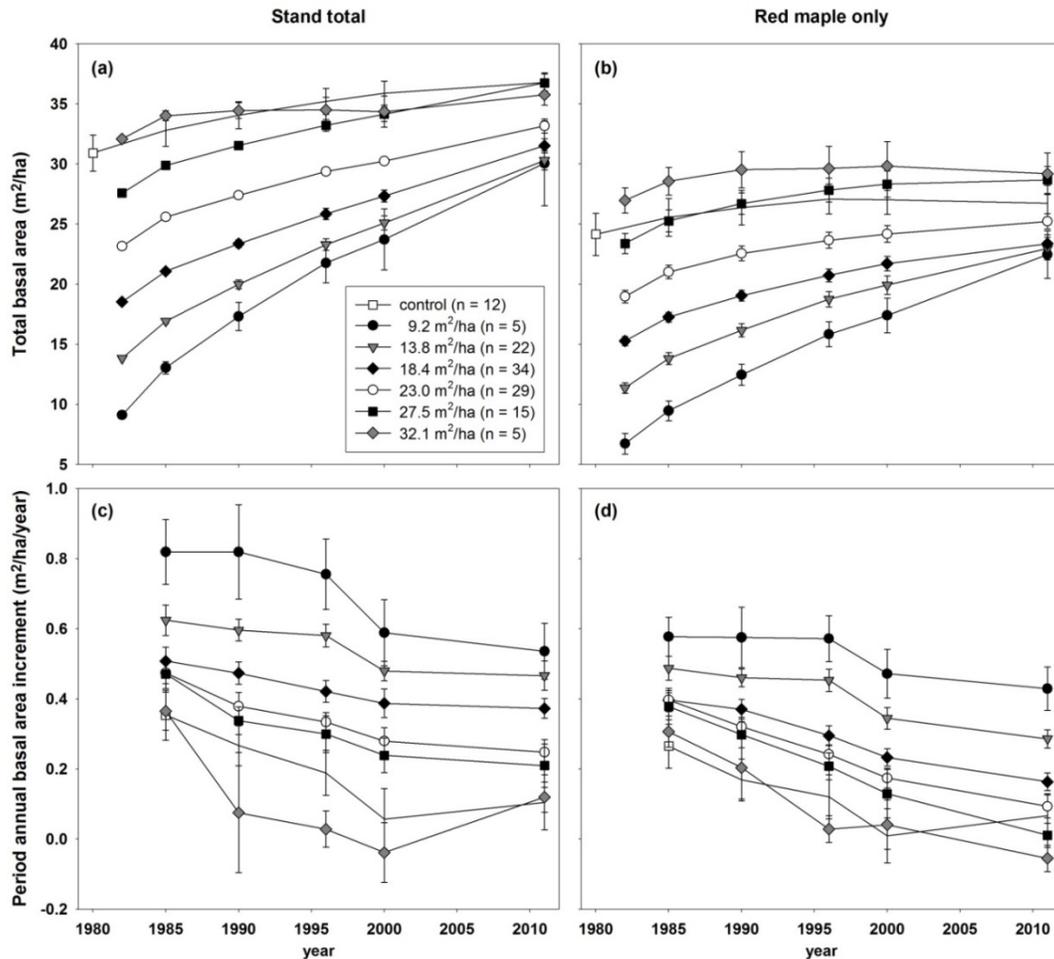


Figure 2. (a) Total stand and (b) red maple basal area development by 1982 target residual stocking level for trees greater than 10.0 cm dbh.in upper Lake States red maple forests. Plots were not measured immediately following the thinning so 1982 values were determined as the sum of the 1980 individual tree basal areas for all trees that were not recorded as cut in 1982. Measurement year is the nominal year of measurement; plots were measured up to one year before or after the stated year. (c) Total stand and (d) red maple period annual basal area increment by residual stocking level (total stand basal area). Period increment was calculated as the difference in total basal area for all red maple trees greater than 10 cm dbh (including ingrowth) from the previous measurement divided by the number of growing seasons since the last measurement for annual increment. Error bars are standard errors.

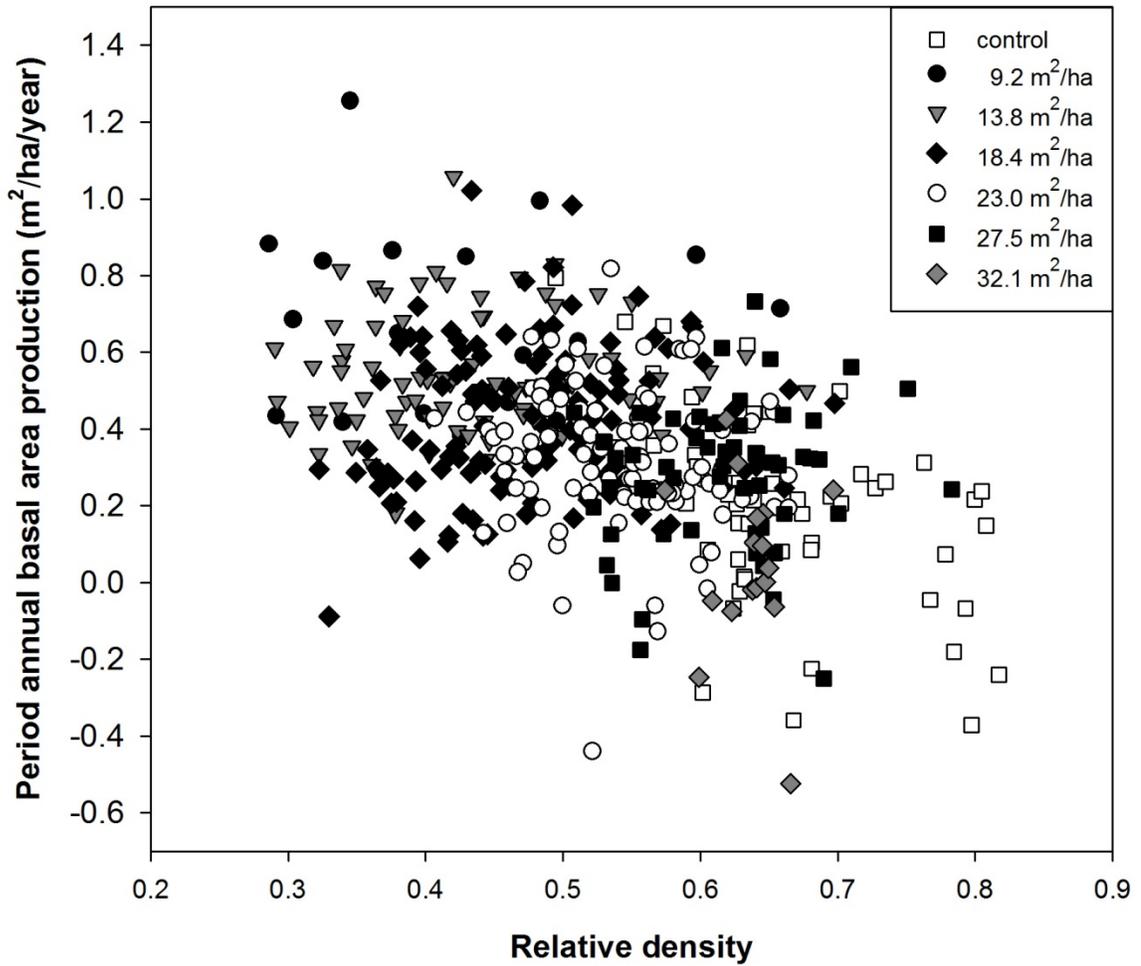


Figure 3. Basal area production as a function of stand stocking for red maple forests in the upper Lake States. Periodic annual net production was calculated from the difference in stand basal area for all trees greater than 10.0 cm dbh from the beginning to the end of the growth interval, divided by interval length. Relative density is proportion of Reineke's (1933) maximum SDI at the beginning of the growth interval, estimated using species wood specific gravity and equations from Woodall *et al.* (2005).

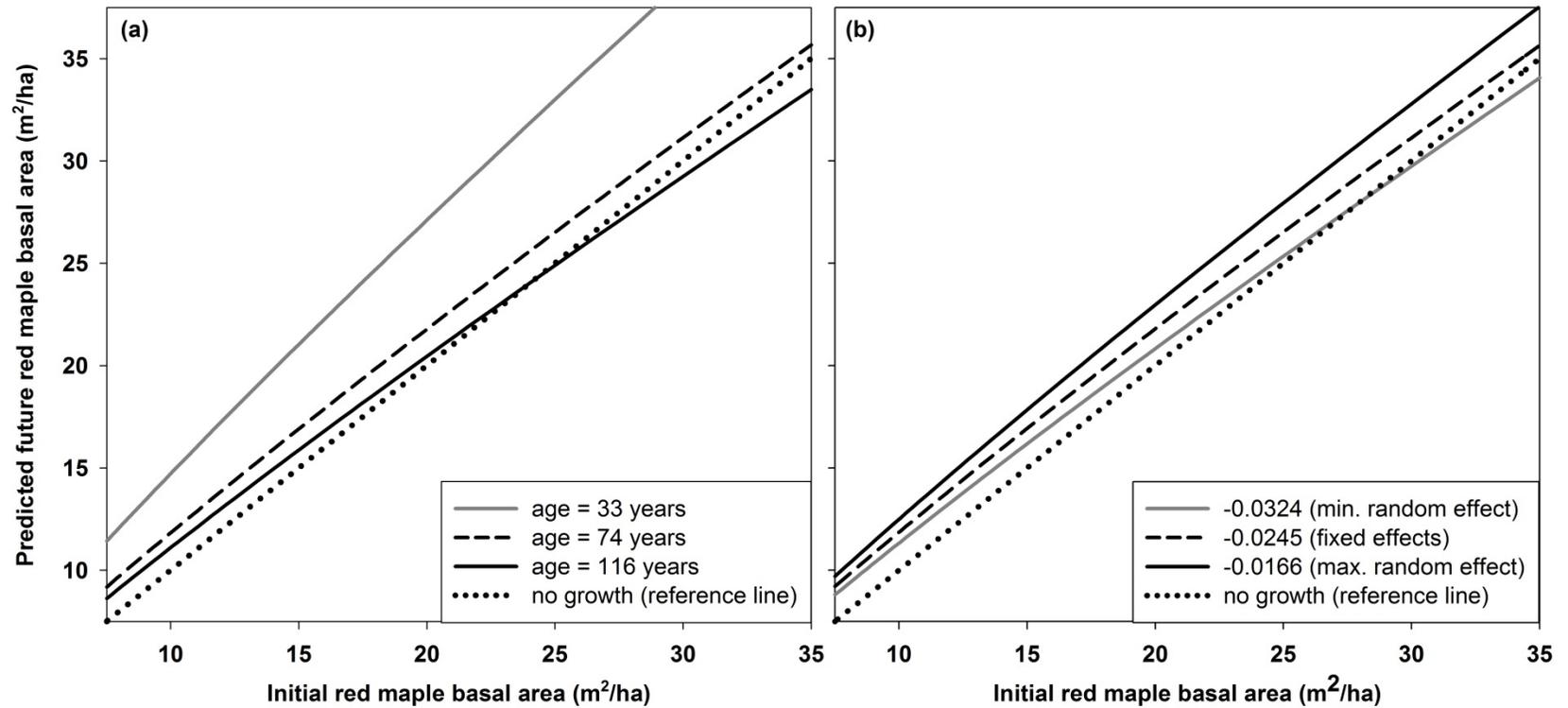


Figure 4. The influence of initial stand age on predicted red maple basal area (a) on predicted red maple basal area based on the results of fitting equation 2 using linear mixed effects regression. All other variables in the model were held fixed at the sample mean ($dt=6.2$ years, $dq = 24.1$ cm, $pctrm = 0.81$), and the influence of the interval length (dt) random slope parameter(b), where all variables took the values as in (a) and age = 77 years.

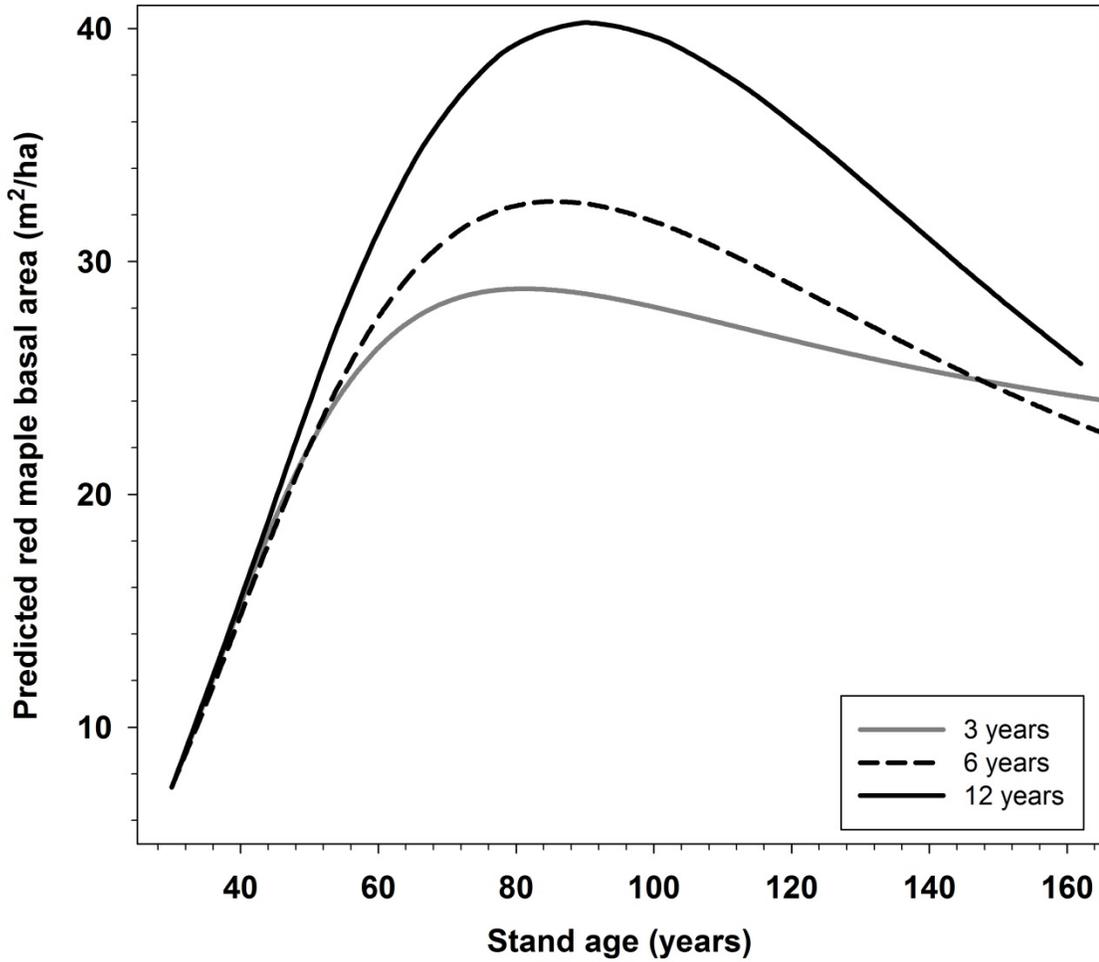


Figure 5. Red maple basal area projections using simulated data generated from the fitted base equation (Equation 1) for three different projection lengths (3, 6, and 12 years). Red maple basal area was initialized at 6.0 m²/ha and quadratic mean diameter (QMD) at 15 cm. QMD was recalculated from projected basal area assuming a constant 600 trees per hectare until projected basal area began to decline at which point QMD was held fixed at the projected maximum. The dataset contained observations out to 128 years of age and growth intervals ranging from 3 to 12 years.

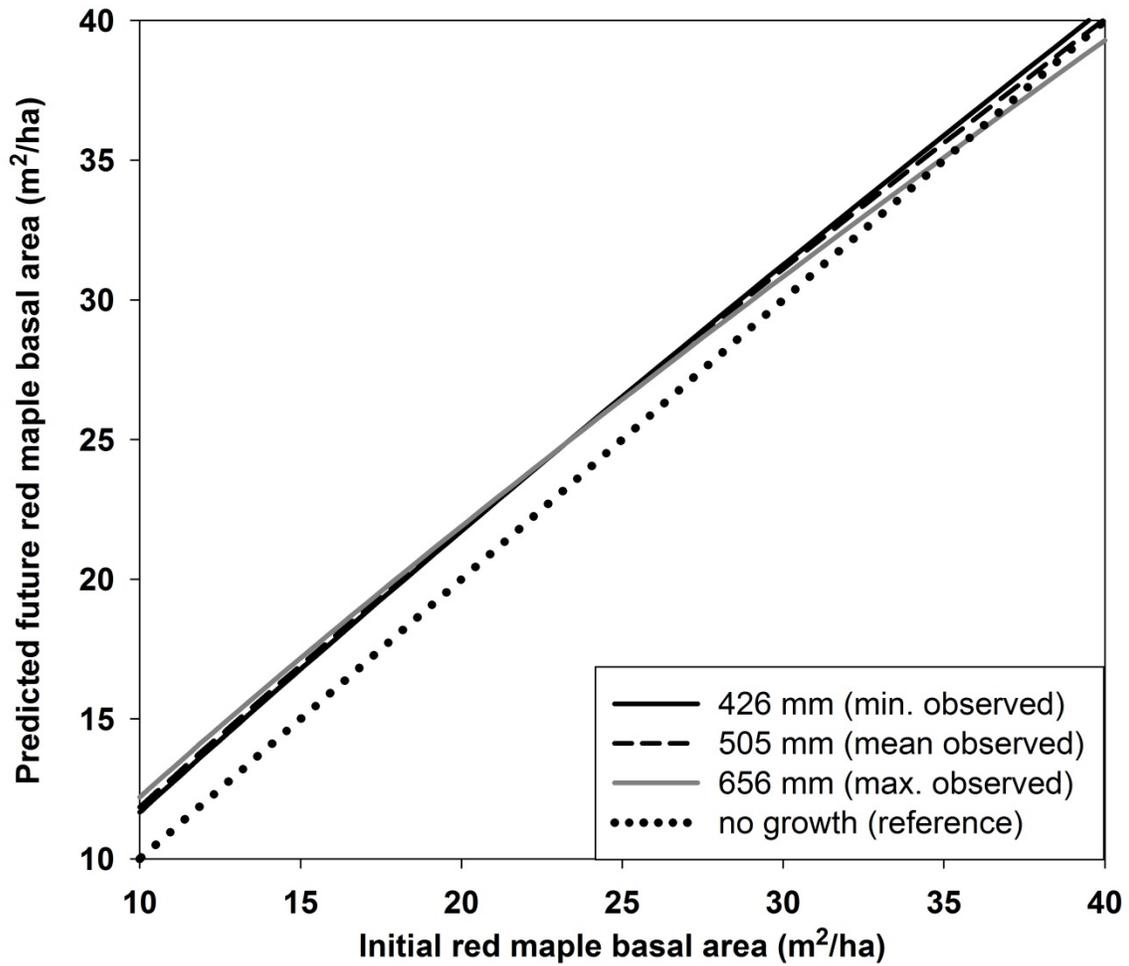


Figure 6. The influence of mean growing season precipitation on predicted red maple basal area based on the results of fitting equation 2 using linear mixed effects regression. All other variables in the model were held fixed at the sample mean ($dt = 6.2$, $dq = 24.1$ cm, $pctrm = 0.81$, $age = 77$ years).

Chapter Three: Tree community composition and dynamics of northern hardwoods stands dominated by red maple in the upper Great Lakes region, USA

Introduction

Over much of the last century, considerable research effort has been devoted to understanding forest stand development and successional pathways (Oliver and Larson, 1990). Based largely and necessarily on observations of ecosystems developing under historical environmental conditions, this research has been used to understand the structure and function of old-growth forest communities (Spies *et al.*, 1988; Fraver and Palik, 2012), quantify the historic range of variability of disturbance regimes (Frelich and Lorimer, 1991; D'Amato and Orwig, 2008) and subsequent community response, and develop management strategies to emulate such conditions (Franklin *et al.*, 2007). Given that forest ecosystems are constantly responding to an ever-increasing host of drivers which alter developmental pathways from what would be expected from historical patterns (Paine *et al.*, 1998), there is a need to broaden studies of stand development to include the relatively novel assemblages resulting from these combined effects.

Numerous factors have generated forest compositional and structural conditions that deviate from historic analogs for a given forest type. For example, land-use history has substantial influence over tree species composition and abiotic conditions that can influence forest development for centuries (Foster *et al.*, 1992; Foster *et al.*, 1998; Foster *et al.*, 2003). Similarly, climate change can alter species physiologic performance and competitive interactions, which in conjunction with the introduction of exotic species, can cause dramatic changes in community dynamics and structure (Woodall *et al.*, 2009). Of increasing importance is the role of exotic pests and pathogens, which may selectively remove canopy species giving rise to forest

systems with lower overall richness and dominance by species that were either historically absent or at lower abundance (e.g., *Betula lenta* following hemlock woolly adelgid infestations; Orwig and Foster, 1996; Ellison *et al.*, 2005). Any of these drivers alone or in combination can lead to the development of novel ecosystems (Hobbs *et al.*, 2006), creating considerable challenges for anticipating long-term forest dynamics under uncertain environmental conditions. Given the lack of historical analogs for these novel communities, management and conservation efforts are greatly hampered by an incomplete understanding of how these systems will develop over time and respond to future management interventions.

One such example of novel forest community development is the widely documented increase in red maple (*Acer rubrum* L.) abundance across eastern North America. Red maple is one of the most widespread tree species in North America in terms of both geographic range and ecological amplitude (Walters and Yawney, 1990). Historically it was only a minor component of the forests of the eastern US (Abrams, 1998) but over the second half of the last century, researchers and managers have noted its widespread abundance in the understories of various forest types (Palik and Pregitzer, 1992) and the subsequent increase in overstory importance (Alderman *et al.*, 2005; Fei and Steiner, 2007). The marked development of stands dominated by red maple prompted the Society of American Foresters to describe a previously unrecognized red maple coertype (Eyre, 1980). This increase in red maple abundance has been attributed to changes in historic disturbance regimes, land use, and the favorability of recent climate conditions for the establishment and growth of this species (Abrams, 1998; Woodall *et al.*, 2009). While the extent of communities dominated by red maple remains unknown, the species now ranks seventh in highest average importance value (IV) for tree species in the eastern US based on recent national inventories (Prasad *et al.*, 2007-ongoing).

A number of studies have investigated the dynamics of red maple as a lesser component of mixed forests (Tift and Fajvan, 1999; Rentch *et al.*, 2009), but none have considered the

dynamics of nearly pure, upland red maple stands. Moreover, the documented influence of climatic and site conditions on red maple growth (Reed *et al.*, 1992a; Fekedulegn *et al.*, 2003) highlight the importance of accounting for these factors when forecasting the future dynamics of this species within a given region. The objectives of this research are to 1) describe the range in species composition across red maple-dominated communities over the variety of site types on which they occur in the upper Lake States, 2) determine how environmental and stand conditions are related to these species associations, and 3) evaluate the degree of long term compositional and structural change within these communities, including patterns of ingrowth and mortality, as affected by management and environmental conditions.

Methods

Study area

The present study used data from 52 study sites established in 1979-1980 in even-aged, fully stocked red maple stands located throughout northern Wisconsin and Michigan, USA. The study area locations range from the Chequamegon National Forest in northwestern Wisconsin, across the Upper Peninsula of Michigan, and south to the Huron-Manistee National Forest in the west of Michigan's Lower Peninsula and are located on federal, state, and private land. The climate is continental or humid continental with average January minimum temperature ranging from -17° C to -9° C and average July maximum temperature ranging from 24° C to 28° C (McKenney *et al.*, 2011). Total annual precipitation ranges from 65 to 82 cm across the study area. The soils types include a broad range from lacustrine and moderately well-drained glacial till soils to dry outwash and poorly drained glacial till soils (Haag, 1987).

Study plots were established in undisturbed, second-growth stands that naturally established following late 19th and early 20th century harvesting, in which at least 75 percent of

the overstory canopy was red maple (Erdmann *et al.*, 1981). Two to four study plots were established in each of 52 stands for a total of 122 plots. Common associate canopy tree species varied by site but included sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). Less common, but occasionally locally-abundant species included black cherry (*Prunus serotina*), paper birch (*Betula papyrifera*), eastern hemlock (*Tsuga canadensis*), black ash (*Fraxinus nigra*), and eastern white pine (*Pinus strobus*). Stand age in 1980 ranged from 28 to 97 years old, and site index ranged from 12.6 to 22.9 m at a base age of 50 years.

After the 1981 growing season, a harvest reduced the basal area of each plot to one of six residual basal area stocking levels—9.2, 13.8, 18.4, 23.0, 27.6, or 32.2 m² per hectare—or a no harvest control with variable basal area, using thinnings from below to achieve the most uniformly-spaced stand of defect-free dominant and codominant red maple trees as possible. More detail about the study area and methods can be found in the methods section of Chapter 2 of this thesis.

Plots were measured for initial conditions in 1980 and remeasurement occurred in approximately 1985, 1990, 1996, 2000, and 2011, to determine tree- and stand-level growth response to thinning. At each measurement period, the dbh and species of each live tree ≥ 10 cm dbh on every plot was recorded. All 52 sites were used for initial community composition analysis. Of the 122 individual study plots established at the start of the study, 95 were measured in 2011 and used for the compositional change analysis.

Initial community composition

The basal area of each tree larger than 10 cm in diameter at breast height (dbh) was calculated from its measured dbh. Species relative abundance and relative dominance were calculated for each species at each site (for initial conditions), as well as on each plot (for

community change analysis). Relative abundance is the number of stems of the species divided by total number of all stems, and relative dominance is the total basal area of the species divided by total basal area. The mean of species relative abundance and relative dominance, termed the importance value (IV), was used for examining patterns in overstory tree community composition across sites.

Trees species that were present at fewer than three sites (about five percent) were dropped from the dataset to reduce noise in the analysis. Because all sites were dominated by red maple, the IV data was relativized across sites to balance the contribution of all species present and allow for the influence of under-represented species in the analysis.

Non-metric multidimensional scaling (NMS) ordination (Kruskal, 1964), using PC-ORD version 6.15 (McCune and Mefford, 2011), was used to examine the range in species tree species community composition (for trees ≥ 10 cm dbh) across red maple-dominated forests at the onset of the study before thinning treatments were applied. A matrix of Sørensen distances was calculated from the relativized species IV data and 250 runs with the real data were completed with each run stepping down from a six-dimensional solution to a one-dimensional solution, starting with randomly assigned axis scores, and limited to 500 iterations. The stress of the resulting configuration from each of these runs was calculated and the lowest stress for each dimensionality was compared to the corresponding stress values from an additional 250 Monte Carlo runs using random data. This comparison indicated a three-axis solution to be ideal, so the starting configuration that generated the lowest stress value for a three-dimensional solution using real data was used as the starting point for a single final run. The two axes representing the greatest proportion of variation are displayed. The strength of the relationship between species importance and the ordination solution axes was quantified with Kendall's tau rank correlation coefficient between each site's relativized species IV values and site axis scores.

Community compositional change

Patterns of compositional change from the 1982 thinning to the final measurement in 2011 using plot-level data were explored using nonmetric multidimensional scaling (NMS) ordination. While a measurement did not take place immediately following the thinning, the dataset was constructed from the initial conditions (1980) dataset by deleting all trees that were marked as “cut” following the thinning. Thus the data consisted of measurements from 1980 but only for those trees that remained following the 1982 thinning treatments. The same NMS ordination procedure described above was applied to this dataset, with the exception that the raw IV values were used instead of relativized values in order to focus the analysis on the change in relative importance of species within each plot rather than on the change in species importance across plots.

NMS axis scores for each plot (1982 and 2011 data) were used to determine the magnitude and direction of compositional shift during the measurement interval. The absolute magnitude of change plot in NMS score was tested for significance among treatments with analysis of variance (ANOVA). The uniformity of the mean direction of change for each treatment group was tested for significance using Rayleigh’s test of uniformity. Watson’s two sample test was used to test for differences between treatment group in terms of means direction of change.

Mortality, ingrowth, and ingrowth survivorship

Individual tree ingrowth, survivorship, and mortality were recorded for all trees at each remeasurement. Ingrowth was defined as trees that were smaller than the minimum diameter threshold (10 cm dbh) at the previous measurement and grew to a size larger than the diameter threshold during the growth interval. Density (stems per hectare) of ingrowth for the study period was summarized by treatment and species for all ingrowth stems that survived to the end of the study period (2011). Mortality (trees that were alive at the previous measurement but were dead

at the current measurement) was expressed as an annual rate of mortality for a given species and size class for all stems that were present at the initial inventory in 1980 (i.e., excluding ingrowth).

Rates were calculated as:

$$1 - \left(1 - \frac{M_1}{N_0}\right)^{\frac{1}{t}}$$

where M_1 is the number of stems that died during the sampling interval, N_0 is the total number of living stems in the previous sampling, and t is the number of growing seasons in the sampling interval. The mortality rate of each species \times size class group was calculated for each plot at each measurement year, and the mean of these rates by treatment was taken as the mean annual mortality rate for each species \times size class group. The influence of thinning treatment, time, and their interaction on ingrowth and annual mortality rates were examined using repeated measures analysis of variance following the SAS MIXED Procedure (SAS Institute, 2008). A SP (POW) covariance structure, which is an autoregressive error structure appropriate for the unequal spacing between measurement periods across all studies, was used for all models (Littell, 2006).

Results

Initial community composition

Tree community composition of the unmanaged red maple-dominated stands in 1980 was explained by a three-dimensional non-metric multi-dimensional scaling solution (Final stress= 17.711, $r^2 = 0.669$, and instability= 0.000). The wide distribution of stands along the two primary ordination axes suggests a gradient in compositional conditions across red maple stands, as opposed to distinct, red maple-dominated communities. Most of the variation in overstory tree composition was explained by axis one (33.5%), which ranged from wet-site tree species in the negative portion of this axis to more mesic species in the positive portion (Figure 1; Table 1). In particular, wet-site associates such as black ash (*Fraxinus nigra*), green ash (*Fraxinus*

pennsylvanica), American elm (*Ulnus americana*), and yellow birch (*Betula alleghaniensis*) were all significantly, negatively correlated with this axis, whereas sugar maple had a positive, significant correlation with axis one (Table 1). Environmental variables positively associated with axis one included mean annual precipitation (map) and precipitation during the three months preceding the growing season (pp1). The longitudinal geographic location of plots (long) was also significantly positively correlated with axis one reflecting the westerly distribution of stands in this portion of axis one. Mean temperature of the growing season (mt3), growing season precipitation (gsp), growing degree days of the growing season (gdd3), July maximum temperature (julmax), and annual maximum temperature (maxat) were all significantly negatively correlated with axis one (Figure 7).

The distribution of plots along axis two, which explained 20.0 % of the variation in the data, ranged from red maple communities with a greater abundance of conifer species, including eastern hemlock, white pine, northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), and white spruce (*Picea glauca*) in the negative region to plots with mixed red maple-hardwood communities containing sugar maple, white ash (*Fraxinus americana*), and aspen (*Populus tremuloides* and *P. grandidentata*) in the positive portion of this axis (Figure 1, Table 1). None of the environmental variables included were significantly correlated with axis two. Of the 19 species included in the main data matrix, only red maple, black cherry, and American beech were not significantly correlated with plot scores along either axis.

Community compositional change

Patterns in compositional change in red maple communities between 1982 and 2011 were best explained by a three-dimensional ordination ($r^2 = 0.946$, final stress = 10.285, and final instability = 0.000). Since raw species IV was used as the abundance metric, red maple IV was the primary driver of the final solution with percent red maple the most strongly correlated

variable with axis one (Figure 2; Table 2). The concentration of plots from 1982 in the negative portion of axis one reflects the application of initial thinning treatments to maximize the importance of red maple in all thinned plots. Twenty-nine years after thinning, the majority of plots dispersed from the central point of axis two and shifted toward the positive end of axis one by 2011, which was associated primarily with an increased abundance of mid-tolerant and shade-tolerant species, including sugar maple, American elm, white spruce, black ash, balsam fir, American basswood, eastern hemlock, and yellow birch (Figure 2; Table 2).

With the exceptions of the control group and plots thinned to the lowest residual basal area ($9.2 \text{ m}^2/\text{ha}$, of which there were only four), all treatment groups had a significantly uniform direction of change (based on Rayleigh's test of uniformity with $P < 0.05$; Table 3). This is reflected by the direction of compositional shift in ordination space (Figure 2), which although somewhat variable, has a general trend of increasing toward the negative end of axis two with decreasing thinning intensity. The species driving this directional shift—yellow birch, eastern hemlock, black ash, white spruce, paper birch, aspen, American beech, and white pine—cover a wide range of moisture and light requirements. Only the stands thinned to $13.8 \text{ m}^2/\text{ha}$ residual basal area had a significantly different direction than any other group and were statistically different from stands thinned to $23.0 \text{ m}^2/\text{ha}$ or higher, including the control plots (Table 3). This treatment had a relatively high percentage of plots that shifted positively along axis two (Figure 2), which is strongly correlated with sugar maple importance value, whereas plots maintained at higher densities primarily shifted in the negative direction of axis two. The mean absolute magnitude of change was not significantly different for any treatment group (Table 3, based on ANOVA with $P > 0.05$).

Mortality, ingrowth, and ingrowth survivorship

Ingrowth (based on number of stems) of species other than red maple across study plots was influenced by growth interval but not by thinning treatment (ANOVA $F=1.03$ for treatment; $F=23.57$ for year; $P < 0.05$). All treatment groups had an uptick of ingrowth in the final growth interval, but the increase over previous levels within each treatment was not significant for the control group and the plots thinned to $9.2 \text{ m}^2/\text{ha}$ (Figure 3). Ingrowth in the heavily thinned plots declined after 10 years post-thinning while ingrowth in plots thinned to higher levels of residual basal area generally increased over time. Red maple ingrowth was significantly impacted by treatment, time, and the interaction between treatment and time, and was greatest early in the study in the most heavily thinned treatment group and consistently declined with both increasing residual density and increasing time since thinning across the thinned treatments. Control group plots had significantly lower ingrowth than the plots thinned to $9.2 \text{ m}^2/\text{ha}$ at the 1985, 1990, and 1996 samplings, and lower ingrowth than plots thinned to $13.8 \text{ m}^2/\text{ha}$ in just the 1985 sampling (based on ANOVA with $P < 0.05$). Across the entire study period and all tree species, the most heavily thinned treatment group had higher ingrowth density than all other treatments (based on ANOVA with $P < 0.05$; Figure 4). The control group had significantly lower ingrowth density than the 9.2 and $13.8 \text{ m}^2/\text{ha}$ residual basal area treatment groups, but was not different from the other treatments. Ingrowth in the $13.8 \text{ m}^2/\text{ha}$ treatment group was significantly greater than the $23.0 \text{ m}^2/\text{ha}$ treatment, but was similar to all other treatments. Total study period ingrowth density across all treatment groups had a general trend of decreasing ingrowth density with increasing residual basal area but no other differences were significant (Figure 4).

Over the duration of the study a total of 5635 ingrowth trees were recorded across all plots. Of these ingrowth trees, 300 (5.3 percent) were subsequently recorded as mortality at or before the final measurement. The largest fraction of ingrowth was balsam fir (33.3 percent) followed by red maple (21.4 percent), sugar maple (15.3 percent), and American beech (12.4 percent) (Figure 4). Together these four species accounted for 82.4 percent of all recorded ingrowth.

Most species followed a trend of decreasing ingrowth stems per hectare with increasing residual basal area, but American beech ingrowth stems was higher in the higher residual density treatments (Figure 4).

Red maple ingrowth recorded across all plots in 1985 accounted for 29.8 percent (360 stems) of all red maple ingrowth for the study period. Fifteen percent (54 stems) of these initial ingrowth stems did not survive to the end of the study. A relatively high fraction of the 1985 red maple ingrowth occurred on heavily thinned plots (Figures 3 and 4) with survival rates ranging from 84-90% for the three lowest density treatments (Table 4). Mean diameter increment for the 26 year growth period (1985-2011) for all 1985 red maple ingrowth was 3.89 cm (*std. err.* = 0.158, *n* = 360), while mean diameter increment of those trees that survived to 2011 was 4.39 cm (*std. err.* = 0.168, *n* = 306). Considering all of the red maple ingrowth recorded before the 2011 measurement, 692 (90.3 percent) remained alive in 2011 with a mean diameter of 14.0 cm.

Within the thinned plots, mean tree mortality rates for all tree species combined increased with increasing residual basal area (based on ANOVA, $P < 0.05$), ranging from 0.1 percent/year in the plots thinned to 9.2 m²/ha to 1.0 percent per year in the plots thinned to 32.2 m²/ha (Figure 5). The control group and highest density thinned plots had the highest overall mean annual mortality rates and there was no statistical difference between mortality rates in these two treatments. There was also no difference in overall mortality rates between the 9.2 m²/ha and 13.8 m²/ha, 18.4 m²/ha and 23.0 m²/ha, and 23.0 m²/ha, 27.6 m²/ha, and 32.2 m²/ha plots, respectively. Mortality rates were not consistent across size classes in any treatment group (Figure 5). Plots thinned to 9.2 m²/ha had high mortality in the 14 cm size class and a very sharply monotonically decreasing curve thereafter. For residual thinning densities above 9.2 m²/ha, mortality rates by size class generally followed a U-shaped curve with higher mortality rates among the smallest and largest trees and relatively low mortality rates among mature mid-sized trees. With few exceptions, red maple mortality rates were lower than the combined

mortality rates of all other species for a given treatment group and size class (Figure 5). The consistently highest red maple mortality rates occurred in the 14 cm size class where they ranged from 0.02 in the 18.4 and 32.2 m²/ha treatment groups, to nearly 0.05 in the 9.2 m²/ha residual basal area group.

Discussion

Red maple is a species that is ubiquitous across a wide gradient of soil conditions in forest ecosystems across eastern North America, yet the composition and dynamics of red-maple-dominated forests have not been described beyond the relatively common red maple swamps found throughout much of this region (Golet and Allen, 1993). The long-term, repeatedly measured network of study plots examined in this study provided a unique opportunity to document the composition and dynamics of this burgeoning community type across a broad geographic area and wide variety of site conditions. Although each stand was dominated by red maple, co-associates ranged from obligate wetland to mesic canopy tree species reflecting the wide ecological amplitude of this species and its ability to dominate a wide variety of sites (Abrams, 1998). Shifts in stand composition following the application of thinning treatments indicate these systems will increase in the abundance of other shade-tolerant species, including American beech, sugar maple, and balsam fir; however, the persistent (albeit low in dense plots) ingrowth of red maple and low mortality rates for this species suggest it will remain dominant on these sites for the foreseeable future. Given the projected increases in abundance of red maple and red maple-dominated systems for much of the upper Great Lakes region (Prasad *et al.*, 2007-ongoing), the understanding gained from this work regarding successional dynamics and patterns of mortality will be valuable to decision-making as managers increasingly encounter this community type on their land base.

Pre-treatment patterns in overstory community composition across the 52 stands reflected the wide ecological amplitude of red maple with overstory communities ranging from wet-site red maple-ash-elm forests to more mesic red maple-sugar maple systems. The ability of red maple to occur on a wide range of site types as individual or small groups of trees is well-documented (Brush *et al.*, 1980; Abrams, 1998); however, this is the first work to our knowledge to describe the characteristics and dynamics of red maple-dominated forests spanning this range. As would be expected, the canopy species co-occurring with red maple across site types were reflective of individual species site requirements, with species such as American elm and black ash occupying canopy positions on wet sites and sugar maple and black cherry on more mesic to xeric sites. These patterns are consistent with past descriptions of the forest communities in which red maple forms a minor component (Abrams and Kubiske, 1990); however, in the case of this study, red maple was the dominant overstory tree. In addition, the stands we examined were at a higher latitude than previous work examining this species and as such documented red maple-dominated mixedwood communities (Reinikainen *et al.*, 2012) that included boreal conifer species, such as balsam fir and white spruce.

The application of thinning treatments to the sites we examined was focused on reducing the abundance of tree species other than red maple and improving stand quality from a timber perspective. These treatments not only created relatively uniform overstory compositional conditions immediately following treatment, but also resulted in a relatively uniform trajectory of compositional change across sites over the subsequent 29 years following thinning, as evidenced by significantly uniform direction of movement in ordination space (Figure 2). This shift was reflective of an increasing shade-tolerant component across stands, and the differences in compositional change between stands were largely influenced by site moisture conditions and, to a lesser degree and judging by the gradient due to conifer species importance, nutrient availability. These findings are consistent with other thinning studies that have documented an

increased development of shade tolerant regeneration following the application of thinning treatments (Bailey and Tappeiner, 1998; Ares *et al.*, 2010; Olson *et al.*, 2013); however, the range of species recruiting across these sites was much broader given the range of site types on which red maple can occur. Red maple is somewhat unique in that it is not particularly exacting in requirements for moisture or nutrients but is also shade tolerant and reproduces prolifically. Other species have equal or greater tolerance of wide ranges of moisture and nutrient availability (e.g. paper birch, aspen), but are very intolerant of shade. The species that are equally or more shade tolerant (e.g. sugar maple, American beech; Franklin *et al.*, 1993) tend to also be more exacting in moisture or nutrient requirements. As a result, the compositional shifts observed across communities were towards an increasing admixture of the shade-tolerant species narrowly adapted to the given site conditions red maple was dominating (i.e., sugar maple and American beech on more mesic sites and balsam fir, eastern hemlock, and white spruce on wetter sites).

Although post-thinning compositional development of these areas indicated an increasing abundance of other shade-tolerant species in these stands, the relatively constant levels of red maple ingrowth and low overstory mortality rates observed for this species over the 30-year study period suggest long-term red maple dominance in these areas. The ability of red maple to perpetuate on these sites is reflective of the range of establishment mechanisms it employs. In particular, past work in second-growth forests in the upper Lake States documented that the red maple component of the first cohort of post-disturbance stands establishes primarily from stump sprouts, while a second cohort establishes from seed beginning approximately 30-35 years after stand initiation and continuously thereafter (Palik and Pregitzer, 1992). It is highly unlikely that the ingrowth observed at the 1985 measurement period were sprout-origin individuals from the thinning treatments just three years prior. More likely they were seed-origin advance regeneration established in the understory (Palik and Pregitzer, 1992) that were not cut or damaged during the thinning operations. It is not possible therefore to judge whether the

observed pattern of red maple ingrowth in 1985 reflects the suitability of stand conditions for tree recruitment or is simply an artefact of the mechanics of the thinning.

The long-term stability of red maple dominance on these sites was largely related to severity of overstory thinning treatments, as stands thinned to very low residual basal areas had the greatest levels of red maple ingrowth and the lowest levels of overall mortality of any treatment, whereas higher residual densities limited the ingrowth of red maple without substantially limiting ingrowth of other tolerant species such as American beech, sugar maple, and balsam fir. This is in contrast to red maple compositional responses in Appalachian hardwoods forests, where more moderate thinning intensities (75% relative density, roughly comparable to 17.0 m²/ha basal area) resulted in the greatest levels of retention of red maple in the upper canopy and decreased mortality of dominant and codominant individuals over a 20-year period (Rentch *et al.*, 2009). This difference is reflective of the greater abundance mid-tolerant canopy tree species in these Appalachian forests, namely oak species, which are favored over red maple when heavier thinning treatments (65% of relative density, approximately 14.3 m²/ha basal area) are applied (Rentch *et al.*, 2009).

Although red maple has often been classified as a mid-successional species that is ultimately replaced by later successional species, such as sugar maple and eastern hemlock (Canham *et al.*, 1994), the low mortality rates documented for red maple canopy trees and ingrowth suggest a greater level of persistence on the sites we examined than suggested by most studies. Regardless of thinning treatment, the 26-year survival of red maple ingrowth recorded in 1985 was quite high ranging from 67-100%, which is consistent with survival rates documented for this species in central hardwood forests in southern New England (Lorimer, 1984). In contrast, work examining red maple sapling survival in the understory of northern hardwood stands dominated by American beech, sugar maple, and hemlock indicated relatively low levels of survival for red maple saplings (Canham *et al.*, 1994). These differences in survival are likely

related to the higher levels of understory light transmission in the red maple-dominated systems examined in this study relative to sites dominated by other late-successional species (Canham *et al.*, 1994). Despite these differences, the u-shaped patterns of mortality rates across size classes and overall mortality rates for all thinning treatments were similar to those documented for second-growth and old-growth northern hardwood systems in the upper Lake States (Lorimer *et al.*, 2001) and reflected a low rate of mortality for red maple across size classes relative to other canopy species. Collectively, these patterns underscore the ability of red maple to not only maintain canopy dominance for high rates of overstory tree survival, but to persist over the long-term on these sites via recruitment under closed canopy conditions.

Conclusion

Given the projected increases in the abundance of red maple for the upper Great Lakes region, results from this network of plots can be used to inform future management regimes aimed at maintaining red maple stand productivity and achieving compositional objectives in these relatively novel systems. Heavy thinning (to 9.2 m²/ha residual basal area) favors continued recruitment of red maple and minimizes red maple mortality and is likely to maintain red maple dominance at the highest levels. This could serve as a useful strategy to maintain stand productivity in some situations, for example on wet-mesic sites where many of the other predominant species are currently (e.g. American elm, due to Dutch elm disease) or potentially will be (e.g. ash species, due to emerald ash borer) difficult to maintain. On the other hand, maintaining stands at higher densities minimizes red maple recruitment in favor of more shade tolerant species and would gradually diversify the stand with more shade-tolerant species.

Environmental and biotic stressors are high on many tree species across large areas within the natural range of red maple (e.g. due to emerald ash borer and beech bark disease causing high mortality rates in ash species and American beech, respectively) but maintaining stand

productivity remains essential for achieving carbon sequestration and biomass production targets, maintenance of wildlife habitat, recreation and aesthetics, and other ecosystem services. In these situations there is potential for managers to leverage the flexibility of red maple to increase available options for meeting stand objectives. Although this species has historically been viewed negatively from a timber production standpoint, its broad flexibility in site conditions and recruitment strategies may represent ecologically important characteristics for sustaining forest functioning across a wide range of site conditions in the face of climate change and other associated stressors. Given the relatively young age of the stands examined in this study, the long-term monitoring of these areas will be critical for evaluating the longevity and persistence of red maple on these sites, particularly as the effects of environmental change become more apparent.

Tables

Table 1. Kendall's tau rank correlation coefficient between relativized species IV and site scores from NMS ordination of data taken in 1980 from 52 unmanaged, red maple-dominated stands across the upper Lake States. Axis scores for species where IV is significantly correlated with plot axis scores ($P < 0.05$) are in bold.

Tree species			Species axis scores (Tau-b p-value)	
Symbol	Latin name	Common name	Axis 1	Axis 2
ACSA	<i>Acer saccharum</i>	sugar maple	0.399 (<.0001)	0.279 (0.0036)
FRAM	<i>Fraxinus americana</i>	white ash	-0.355 (0.0011)	0.312 (0.0042)
TIAM	<i>Tilia americana</i>	American basswood	-0.316 (0.0055)	-0.027 (0.8103)
BEAL	<i>Betula alleghaniensis</i>	yellow birch	-0.286 (0.0033)	-0.236 (0.0149)
ACRU	<i>Acer rubrum</i>	red maple	-0.104 (0.2762)	0.131 (0.1697)
TSCA	<i>Tsuga canadensis</i>	eastern hemlock	-0.307 (0.0018)	-0.499 (<.0001)
BEPA	<i>Betula papyrifera</i>	paper birch	-0.551 (<.0001)	-0.059 (0.5755)
ULAM	<i>Ulmus americana</i>	American elm	-0.414 (0.0002)	0.113 (0.3129)
PRSE	<i>Prunus serotina</i>	black cherry	0.198 (0.056)	-0.096 (0.3526)
FRNI	<i>Fraxinus nigra</i>	black ash	-0.445 (<.0001)	-0.033 (0.7639)
ABBA	<i>Abies balsamea</i>	balsam fir	-0.26 (0.0081)	-0.353 (0.0003)
POTR	<i>Populus tremuloides</i> and <i>Populus grandidentata</i>	Quaking aspen and bigtooth aspen	-0.455 (<.0001)	0.278 (0.0072)
FAGR	<i>Fagus grandifolia</i>	American beech	0.172 (0.0964)	-0.048 (0.6391)
AMSP	<i>Amelanchier spp.</i>	Juneberry	-0.071 (0.5137)	-0.278 (0.0101)
THOC	<i>Thuja occidentalis</i>	northern white cedar	-0.355 (0.0012)	-0.303 (0.0057)
PIGL	<i>Picea glauca</i>	white spruce	0.12 (0.2692)	-0.296 (0.0064)
PIST	<i>Pinus strobus</i>	eastern white pine	0.096 (0.3731)	-0.412 (0.0001)
FRPE	<i>Fraxinus pennsylvanica</i>	green ash	-0.335 (0.0031)	0.153 (0.1778)

Table 2. Kendall's tau rank correlation coefficient between species IV and site scores from NMS ordination of 1982 and 2011 compositional data from 95 thinned and unthinned red maple-dominated study plots across the upper Lake States. Axis scores for species where IV is significantly correlated with plot axis scores ($P < 0.05$) are in bold.

Tree species			Species axis scores (Tau-b p-value)	
Symbol	Latin name	Common name	Axis 1	Axis 2
ACSA	<i>Acer saccharum</i>	sugar maple	0.428 (<.0001)	0.596 (<.0001)
FRAM	<i>Fraxinus americana</i>	white ash	-0.162 (0.0053)	-0.043 (0.4583)
TIAM	<i>Tilia americana</i>	American basswood	0.139 (0.0183)	0.011 (0.8566)
BEAL	<i>Betula alleghaniensis</i>	yellow birch	0.12 (0.0226)	-0.252 (<.0001)
ACRU	<i>Acer rubrum</i>	red maple	-0.818 (<.0001)	0.076 (0.1215)
TSCA	<i>Tsuga canadensis</i>	eastern hemlock	0.155 (0.0049)	-0.366 (<.0001)
BEPA	<i>Betula papyrifera</i>	paper birch	0.009 (0.8727)	-0.198 (0.0005)
PRSE	<i>Ulmus americana</i>	American elm	0.215 (0.0001)	0.107 (0.0551)
FRNI	<i>Prunus serotina</i>	black cherry	0.027 (0.6384)	-0.055 (0.3416)
ABBA	<i>Fraxinus nigra</i>	black ash	0.306 (<.0001)	-0.477 (<.0001)
OSVI	<i>Abies balsamea</i>	balsam fir	0.162 (0.0062)	-0.014 (0.8064)
POTR	<i>Populus tremuloides and Populus grandidentata</i>	Quaking aspen and bigtooth aspen	0.057 (0.3341)	-0.204 (0.0005)
FAGR	<i>Fagus grandifolia</i>	American beech	0.019 (0.7163)	-0.161 (0.0024)
AMSP	<i>Amelanchier spp.</i>	Juneberry	0.05 (0.4029)	-0.048 (0.417)
THOC	<i>Thuja occidentalis</i>	northern white cedar	0.017 (0.7778)	-0.106 (0.0726)
PIGL	<i>Picea glauca</i>	white spruce	0.193 (0.0007)	-0.33 (<.0001)
PIST	<i>Pinus strobus</i>	eastern white pine	-0.008 (0.8843)	-0.145 (0.0114)
FRPE	<i>Fraxinus pennsylvanica</i>	green ash	0.047 (0.4269)	0.066 (0.2615)

Table 3. Mean direction and magnitude (distance) of the compositional change of red maple sites by treatment based on the ordination scores for 1982 and 2011 data (Figure 2). The direction is clockwise in degrees with zero degrees corresponding to positive change along axis one and zero change along axis two. Superscripted letters indicate significant differences in direction between groups using Watson two-sample test of homogeneity ($p < 0.05$). The control and lowest residual basal area treatments were not included in statistical comparisons since they do not have uniform directionality. There was no difference in mean absolute distance between treatments.

Treatment (residual basal area)	n	Mean direction (Rayleigh's test statistic p-value)	Mean absolute distance (standard error)
Control	8	51.58 (0.123)	0.3926 (0.2150)
9.2 m ² /ha	4	37.95 (0.977)	0.7482 (0.3041)
13.8 m ² /ha	18	16.29 (0.000) ^a	0.7784 (0.1433)
18.4 m ² /ha	28	24.77 (0.000) ^{ab}	0.9002 (0.1149)
23.0 m ² /ha	20	39.12 (0.000) ^b	0.6838 (0.1360)
27.6 m ² /ha	13	49.16 (0.015) ^b	0.7700 (0.1687)
32.2 m ² /ha	4	50.64 (0.023) ^b	0.7482 (0.3041)

Table 4. Total number of red maple ingrowth stems recorded across all plots in 1985 by treatment group, along with survivorship to the end of the study period.

Treatment	Red maple ingrowth stems in 1985	Ingrowth surviving to 2011	% survival
Control	16	12	75%
9.2 m ² /ha	82	69	84%
13.8 m ² /ha	143	129	90%
18.4 m ² /ha	76	65	86%
23.0 m ² /ha	34	23	67%
27.6 m ² /ha	6	5	83%
32.2 m ² /ha	3	3	100%

Figures

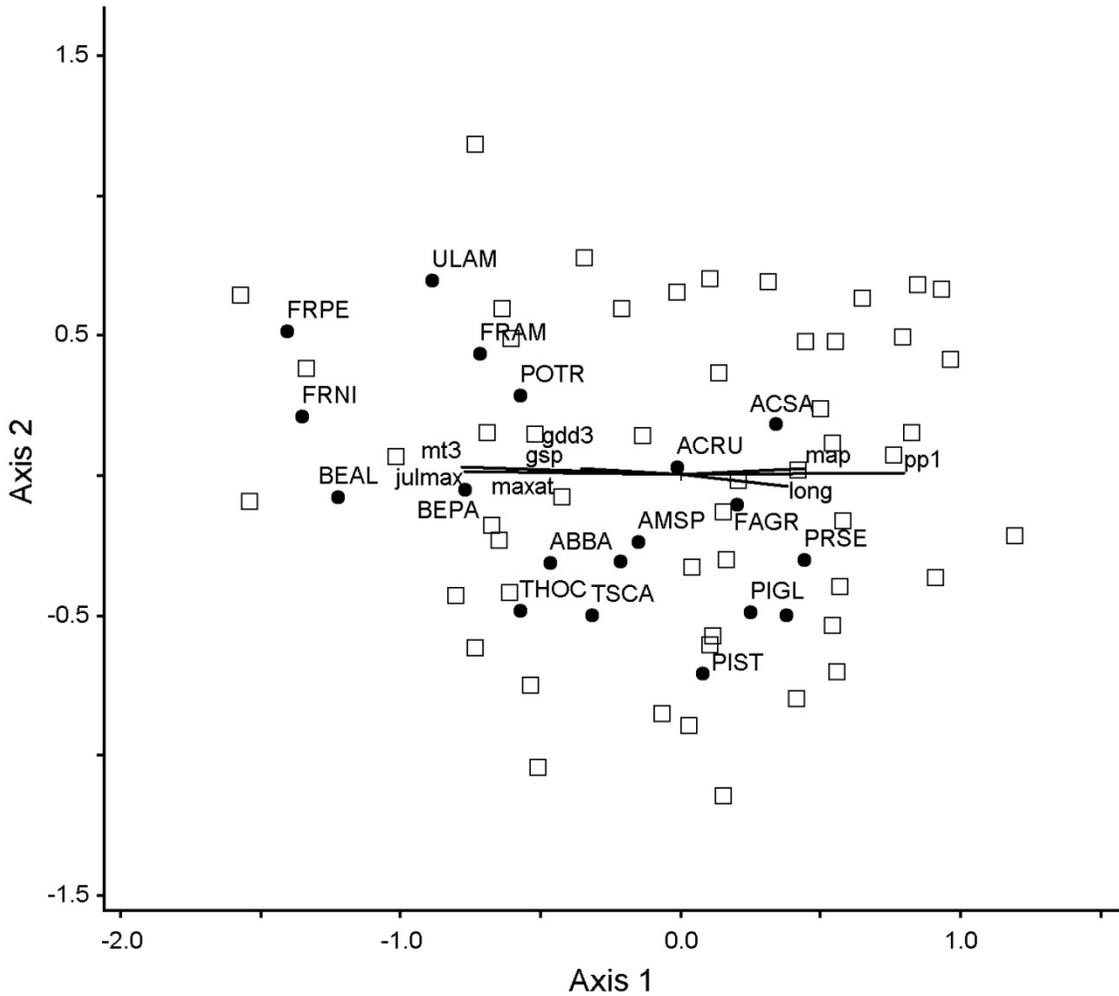


Figure 7. Two-dimensional graph of NMS ordination of initial stand conditions (1980) for 52 unmanaged red maple-dominated stands in the upper Lake States. Stand scores are indicated by hollow squares and species scores are shown as solid circles. Only species where site-level importance value has a significant correlation ($P < 0,05$) with the site ordination score of either axis are labeled and locations are based on weighted averages. Vector length represents explanatory power of climatic variables in describing the distribution of stands with only variables with $r^2 > 0.2$ displayed. See Appendix 1 and 2 for definitions of abbreviations used for species and climatic variables, respectively.

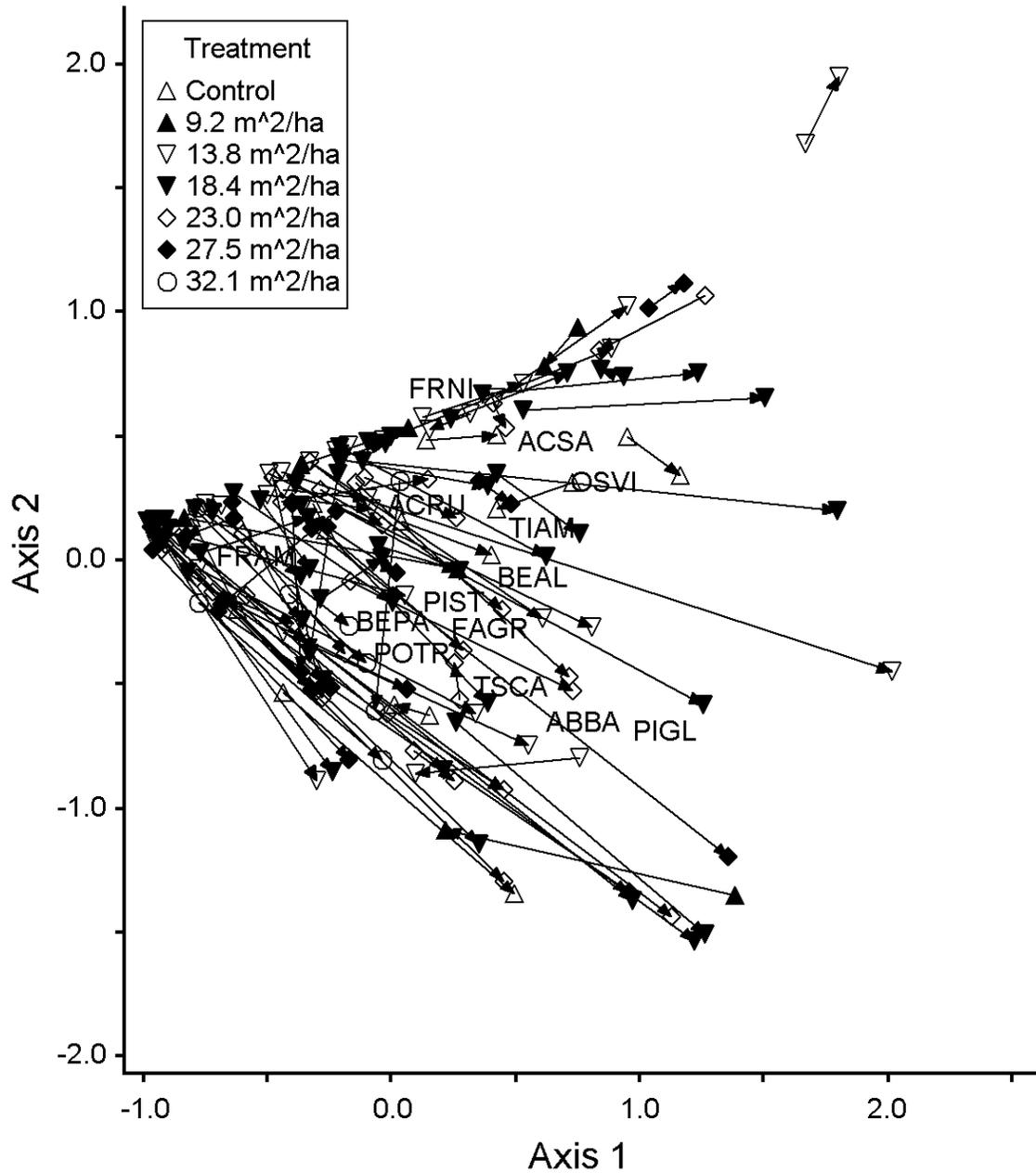


Figure 8. NMS ordination of tree species compositional change from 1985 to 2011 of 95 thinned and unmanaged red maple-dominated study plots in the upper Lake States. Species locations are based on weighted averages and vectors indicate the compositional shift in ordination space. Species locations are approximately indicated by the location of the abbreviated species name;

only species for which plot-level importance value has a significant correlation with the plot ordination score of either axis are labeled.

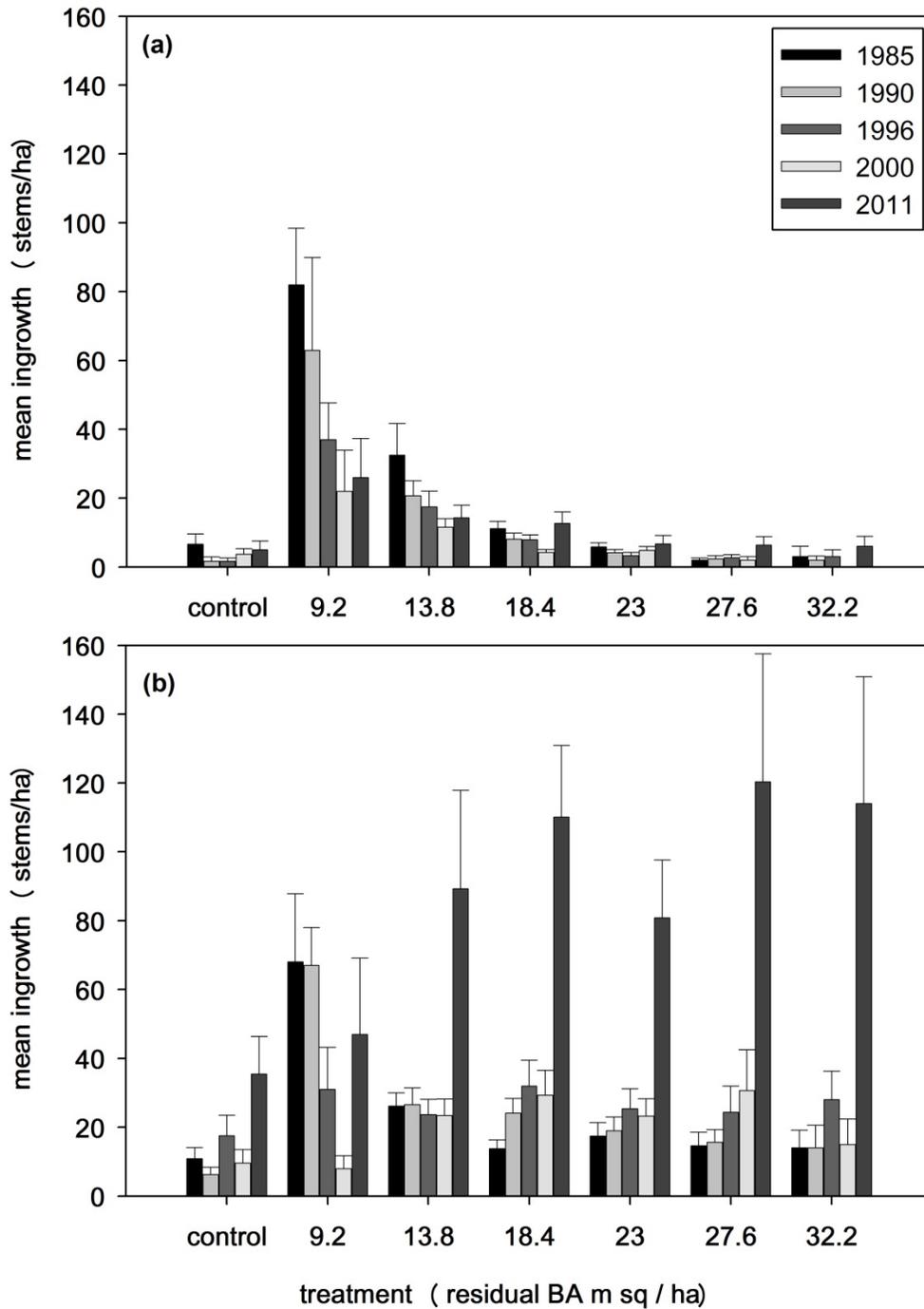


Figure 9. Mean (a) red maple ingrowth and (b) ingrowth of all tree species other than red maple for 122 thinned and unthinned (control) study plots in red maple dominated forest stands in the upper Lake States by thinning treatment target residual basal area and growth period.

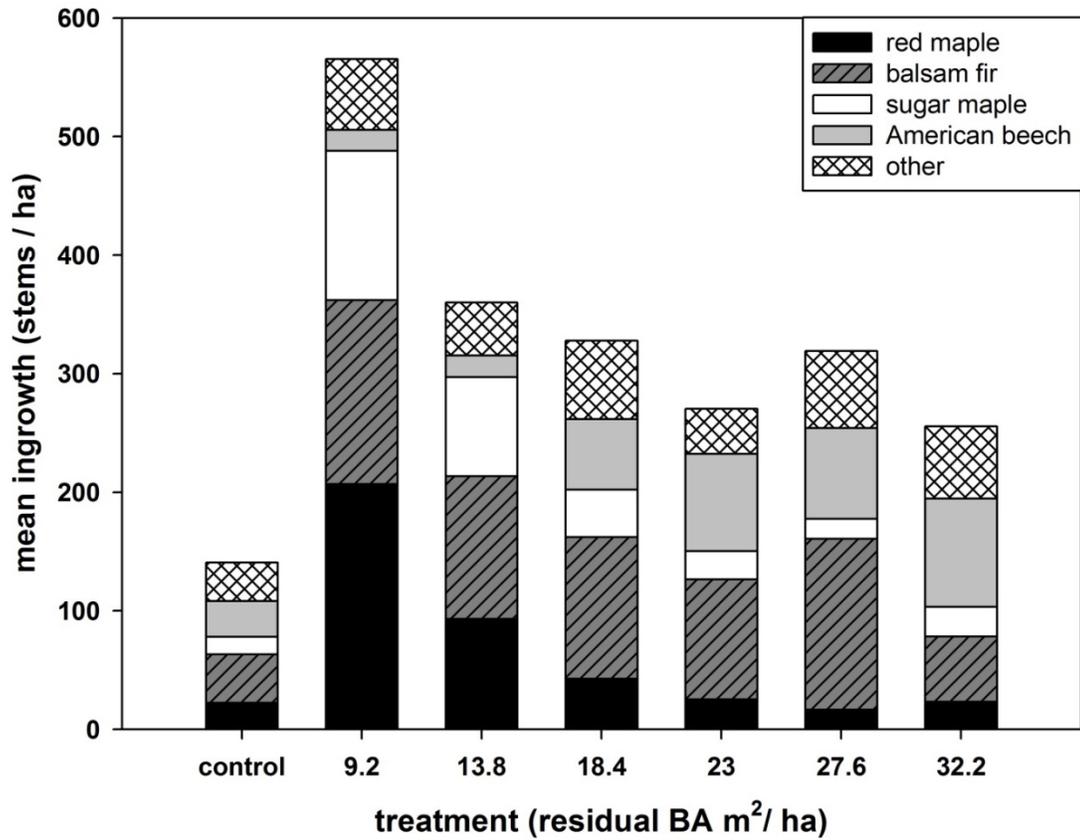


Figure 10. Mean study period ingrowth by species and treatment group for 95 thinned and unthinned (control) study plots in red maple dominated forest stands in the upper Lake States. Only ingrowth that survived to the final measurement in 2011 is included. Species included in the “other” category in order of decreasing quantity include eastern hemlock, white spruce, yellow birch, eastern white pine, black cherry, eastern hophornbeam, and nine additional species each represented by fewer than ten ingrowth stems per hectare.

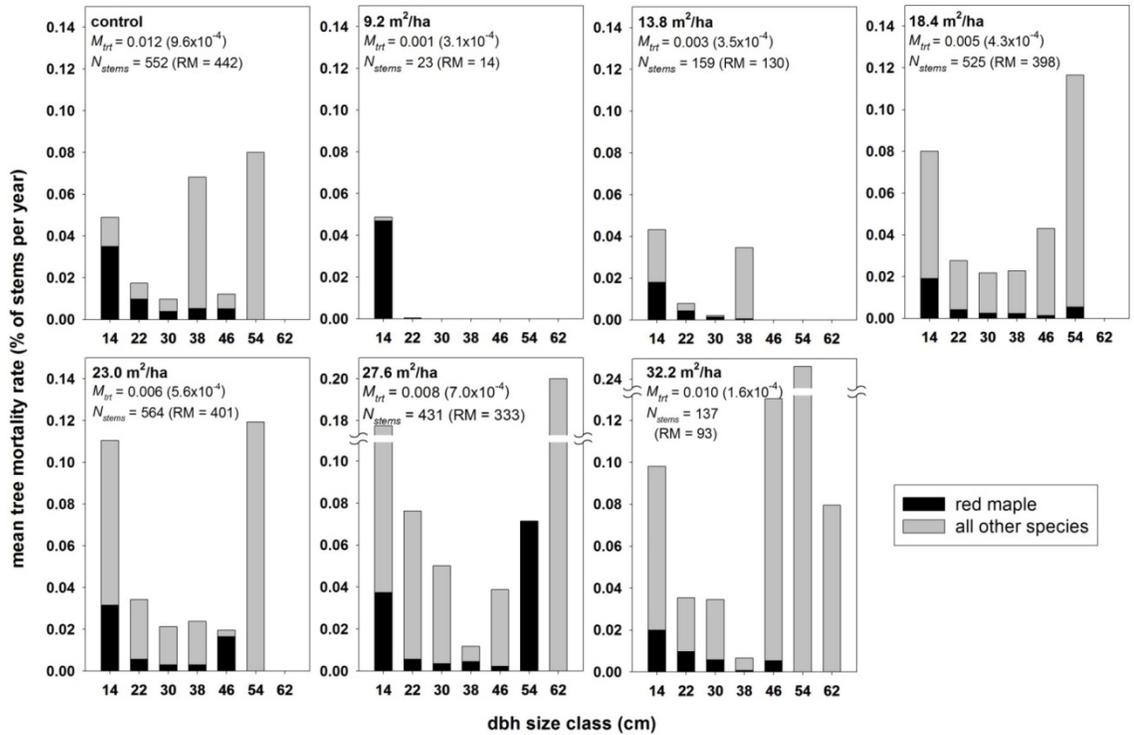


Figure 11. Study period annual tree mortality rates by species (red maple and all other species) and size class for 122 study plots in red maple dominated forest stands in northern Wisconsin and northern Michigan. Each panel represents a different thinning treatment residual basal area or unthinned control. Only stems that were ≥ 10 cm dbh at the initial inventory in 1980 are included. Size classes span 8 cm and are labeled by the class mid-point (e.g. size class 14 includes trees between 10 and 17.9 cm dbh). M_{trt} is the mean mortality rate for all trees in the treatment with standard error in parenthesis. N_{stems} is the total number of mortality stems recorded in the treatment with red maple mortality stems in parenthesis.

Chapter 4: Conclusions

The ecological traits and behavior of red maple, especially seedlings and saplings, have been well studied over the last 50 years. The findings of this thesis builds upon previous work that has documented the widespread distribution of this species as individuals or minor components of mixed stands and demonstrates that mature forest communities dominated by red maple can also develop on and occupy the range of site types on which red maple is known to occur. As with other forest species, basal area development of these stands was largely related to stocking level and age with the greatest levels of growth occurring in younger and heavily thinned stands. Although the influence of local climate on stand-level growth was demonstrated, it was not as great as might be expected given past research and the large positive influence climate change is forecasted to have on red maple abundance and distribution. The sampled stands spanned a relatively wide climatic gradient and the relative unimportance of climate in explaining patterns in stand-level growth across these conditions is further confirmation of the wide tolerance of moisture and temperature conditions for this species.

Red maple forms a minor component of many northern forest communities; however, this thesis is the first study to describe the dynamics and successional patterns in red maple dominated communities in upland settings. Despite historically being viewed as a mid-successional canopy tree species, the low levels of overstory tree and ingrowth mortality and the constant levels of red maple recruitment observed over the 31 years of this study indicate that red maple can persist for extended period on sites in which it is dominant. Nevertheless, successional dynamics on these sites following thinning treatments reflected an increase in shade-tolerant species with greater site-specificity with the long-term development of these areas trending towards mixed red maple-beech-sugar maple and mixed red maple-balsam fir communities. The persistence of red maple

in these second-growth hardwood stands illustrates the previously documented ability of this species to recruit in the understory across a range of developmental stages (Palik and Pregitzer 1992).

Management implications

The lack of information on red maple-dominated communities owes to the lack of historic commercial importance of this species. While many managers continue to develop management regimes to eliminate and reduce the red maple components in forest stands, the complex of stressors and disturbances threatening the future health of forest ecosystems in the upper Great Lakes region requires consideration of the potential beneficial role red maple may play in our future forests. In particular, when focusing on the supporting and regulating ecosystem services forests provide, such as carbon storage and water filtration, a key to long-term sustainability of these services is maintaining forested conditions in a region, regardless of the commercial importance of its constituent species. Other work has demonstrated the importance of novel forest ecosystem assemblages in maintaining these services after other species have been impacted by climate change or introduced insect pests or diseases (Mascaro et al. 2011) and the broad ecological amplitude demonstrated by red maple in this and other studies suggests it can play a similar role across a wide range of forest types. In addition, the mixed species stands developing over time on the sites followed by this study provide a high degree of flexibility and management options concerning stand-level growth and stand dynamics, and highlight the stability of stand-level growth over this range of site conditions and the stability of red maple dominance over this time period. Although management regimes will continue to favor species of higher commercial value, the maintenance of red maple as a stand component may provide the opportunity for greater resilience to future environmental changes given its ability to respond to disturbance and changes in the environment.

Study limitations

The thinning treatments applied in this study were designed to maximize the stocking of dominant and codominant red maple which doubtlessly influenced the compositional trajectory of these stands. Different outcomes may be expected when prescriptions are designed to meet other objectives, including regeneration harvests aimed at regenerating even-aged or multi-aged stands. Although red maple ingrowth and recruitment was documented across sites, appropriate regeneration methods for maintaining these stand conditions have not been examined.

Past work in the same stands used in this study explored the relationship between soil physical and chemical properties and past stand productivity and found a strong relationship between soil drainage class and site quality for red maple in terms of total biomass production and site index (Haag thesis, Johnson et al., 1987). A logical extension to these efforts would be to incorporate detailed soils information into the analysis of growth and dynamics observed through time, as this would help clarify the connection between red maple community dominance and site productive potential. In addition, integration of this information would further refine our understanding of the factors driving the levels of compositional variability observed across red maple-dominated communities.

This research focused exclusively on the growth and dynamics of the community of trees larger than 10 cm dbh as can be deduced from measures of diameter alone. To obtain a broader understanding of the long-term dynamics of these systems the seedling and sapling stages must be considered, particularly as it relates to the long-term dominance of red maple on these sites relative to other shade-tolerant species. Similarly, the mature tree measurements employed in this study, although temporally rich, were relatively limited and future analysis of tree height, stem volume, canopy size, and canopy class dynamics could provide insights into stand growth and

mixed species interactions over time in these systems. Furthermore, there are a host of ecological attributes that have important implications for long-term stand productivity, wildlife habitat, and other ecosystem services, and are necessary components of a complete characterization of system functioning. These include site-level nutrients, the abundance, distribution, and residence time of dead wood, and other stand structural properties. Indeed, changes in nutrient cycling and water distribution have already been suggested as possible effects of red maple dominance (Alexander et al., 2010).

Recommendations for future research

Even though the increasing abundance of red maple has been documented throughout its range, the same mechanisms are not likely driving this change on every site. This is especially true given the high degree of site flexibility exhibited by red maple in this and many other studies. The current study was conducted in the Upper Great Lakes region in northern hardwoods stands where high proportions of red maple established, likely from seed, following widespread removal of pre-settlement vegetation and often subsequent burning (Palik and Pregitzer, 1992). In other regions and coartypes the establishment of stands dominated by red maple has often been the result of proliferation of this species in the seedling and sapling layer of mature forests with the exclusion of fire during the 20th century (Abrams, 1998). The growth and dynamics of the stands present in this study cannot be assumed to hold in other regions and on other site types. Even within this region, although this study included some sites described as excessively-drained sandy sites as well as some poorly-drained sites (Johnson et al., 1987), sites at the extremes/limits of the range of red maple's moisture tolerance were not well represented.

While the 31-year duration of this study provides a necessary first look at the dynamics of mature stands dominated by red maple, long-term continued monitoring of these plots is necessary to gain a more complete understanding of the growth and dynamics and the

permanence of red maple dominance, especially considering that the maximum life span of red maple is in excess of 200 years. This is shorter than many of red maple's associates on these sites (sugar maple, American beech, white spruce) but longer than many others (paper birch, aspen species).

Given that an increase in red maple stocking is not always the desired result, further research should include treatments more likely to produce other outcomes. Researchers have begun to explore treatments that may limit red maple regeneration and recruitment in central hardwoods stands dominated by oak and hickory species (Green et al., 2010; Hutchinson et al., 2005; Alexander et al., 2008), but substantial knowledge gaps remain concerning the conversion of mature red maple-dominated stands to other covertypes.

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Appendices

Appendix 1. List of tree species, species codes and abbreviations for all species sampled in this study.

Study code	Common name	Latin name	Abbreviation
1	sugar maple	<i>Acer saccharum</i>	ACSA
2	white ash	<i>Fraxinus americana</i>	FRAM
3	Basswood	<i>Tilia americana</i>	TIAM
4	yellow birch	<i>Betula alleghaniensis</i>	BEAL
5	red maple	<i>Acer rubrum</i>	ACRU
6	Eastern hemlock	<i>Tsuga Canadensis</i>	TSCA
7	paper birch	<i>Betula papyrifera</i>	BEPA
8	American elm	<i>Ulnus americana</i>	ULAM
9	black cherry	<i>Prunus serotina</i>	PRSE
10	black ash	<i>Fraxinus nigra</i>	FRNI
11	Northern red oak	<i>Quercus rubrum</i>	QURU
12	balsam fir	<i>Abies balsamea</i>	ABBA
13	ironwood (Eastern hophornbeam)	<i>Ostrya virginiana</i>	OSVI
14	aspen (bigtooth and trembling)	<i>Populus tremuloides and Populus grandidentata</i>	POTR
15	American beech	<i>Fagus grandifolia</i>	FAGR
16	juneberry	<i>Amelanchier spp.</i>	AMSP
17	Northern white cedar	<i>Thuja occidentalis</i>	THOC
18	white spruce	<i>Picea glauca</i>	PIGL
19	Eastern white pine	<i>Pinus strobus</i>	PIST
20	pin cherry	<i>Prunus pensylvanica</i>	PRPE
22	green ash	<i>Fraxinus pennsylvanica</i>	FRPE
24	mountain ash	<i>Sorbus americana</i>	SOAM
25	striped maple	<i>Acer pensylvanicum</i>	ACPE

Appendix 2. Climatic and edaphic variables for each site that were included in the secondary matrix for NMS ordinations.

Variable name	Variable definition	Units
long	Longitude	
lat	Latitude	
elev	Elevation	m
mat	mean annual temperature	° C
janmin	January minimum temperature	° C
julmax	July maximum temperature	° C
map	mean annual precipitation	mm
dsgs	Julean day of the start of the growing season	Julean day
degs	Julean day of the end of the growing season	Julean day
gsd	growing season length in days	days
pp1	precipitation of period 1	mm
gsp	growing season precipitation	mm
gdd3	growing degree days during the growing season	growing degree days
minat	minimum annual temperature	deg C
maxat	maximum annual temperature	° C
mt3	mean temperature of the growing season	° C
clay	percent clay in the soil profile	%
d_mottle	depth to mottling	cm
d_root	depth of roots	cm
si_c_spod	percent silt and clay of the spodic horizon	%
si_c_arg	percent silt and clay of the argic horizon	%
si_c_c	percent silt and clay of the c horizon	%
tkn_tot	total potassium and nitrogen in the forest floor	kg/ha
tkn_site	total potassium and nitrogen on site	kg/ha

Appendix 3. Comparison of FVS-modeled diameter and basal area growth with observed growth in northern hardwoods stands dominated by red maple.

The Forest Vegetation Simulator (FVS) (Stage, 1973; Wykoff *et al.*, 1982; Dixon, 2002) is one of the most commonly applied forest growth modeling systems in the United States (Robinson and Monserud, 2003; Crookston and Dixon, 2005). FVS is an individual-tree distance-independent growth model that relies on regional variants to project tree- and stand-level growth. The Lake States variant (FVS-LS) is based on the Lakes States variant of the TWIGS growth model (Miner *et al.*, 1988), but most model components have been updated within FVS such that only the large tree diameter growth component remains unchanged from the original TWIGS system (Dixon and Keyser, 2008 (revised 2012)).

The red maple study plots were measured for initial conditions in 1980. Residual basal area (40, 60, 80, 100, 120 and 140 ft²/acre, and un-thinned control) thinning treatments were applied in 1982, and subsequent measurements were taken in 1985 (the first post-treatment measurement), 1990, 1996, 2000, and 2011. To simulate this with modeled growth, the initial stand conditions were used as input data into LMS and the trees were grown for two years. Then all trees that were marked as “cut” in 1985 were deleted from the dataset, and the result was used as the input data to model growth for each of the other corresponding years (i.e. after the first two-year cycle, subsequent cycle lengths were three, five, six, four and eleven years, consecutively, and projected tree attributes were used as input data for the next cycle). Only plots that remained intact through the 2011 (31 year) remeasurement were included in the model comparison (n=95). Following Guertin and Ramm (1996), ingrowth was ignored. For all plots, only site index for red maple was included in the input data; site index for other species is calculated from a series of equations relating site index of various species to one another.

Mean error, or bias, is defined as the predicted value minus the observed value so positive values indicate over-estimation of growth (Guertin and Ramm, 1996). The mean error of FVS-projected diameter was calculated for all trees for each projection interval and separately for the most common species for each interval. Projected diameter mean error was also calculated by size class for all trees and for red maple trees for the first two projection intervals. For all species for each interval, and separately for the most common species, plot-level basal area (m^2/ha), basal area increment, and trees per hectare mean error were calculated. Finally, plot-level basal area and trees per hectare mean error by size class were calculated for the first two projection intervals for all species and for all intervals for red maple.

In making this comparison I discovered some data entry errors. I deleted records with extreme values for bias for the following summary (i.e. bias < -3.6 cm for the 5 year projection removed eight records, etc.) since these were due to the data entry errors, but did not run FVS again with corrected data.

The Landscape Management System (LMS) is the TWIGS interface used for this comparison. LMS relies on variants of FVS to model tree growth. The Lake States variant was applied here, which originally used the LS-TWIGS growth models. However, most of the model components from LS-TWIGS were reformulated for FVS-LS in 2006—only the large tree diameter growth component remains unmodified from LS-TWIGS (Dixon and Keyser, 2008).

Results

Expansion Factors

For 2000 m^2 plots, the initial expansion factor for every tree was 2.023 trees per acre. By year 2000 TWIGS had reduced the expansion factor of 178 trees to less than one per acre and by year 2011, 668 (6% of all trees) were thus afflicted (Figure 1 shows the distribution of fractional

expansion factors at year 31 and Figure 2 shows the distribution of their diameters). Of those, 10 had reached zero by 2000 and 41 had reached zero by 2011. However, most of the factors less than one were close to one, and most of the trees represented were small pole-sized trees.

Individual Tree Diameter Growth

Tables

Table shows error summaries of individual tree growth in centimeters for all trees by year and also by species for the most common species. In general, FVS-LS slightly over-predicted diameter increment starting at the first 5-year period with errors increasing with time, as could be expected. Tables

Table contains individual error summaries for each species.

Individual Tree Diameter Bias by Size Class

Individual tree diameter bias (projected tree diameter minus observed diameter) was calculated for each tree and averaged by size class and year for all species combined and each species separately. The results are summarized in Table 2. As judged by mean percent error, errors were smaller for large trees (> 5 inches diameter) than for small trees through the second projection cycle (10-year projection) when all trees were combined. For red maple trees, this is true even for the 31-year projection, and by year 31 large mean percent error is only 11 percent.

Plot-Level Bias by Species

Mean plot-level bias for basal area (m²/ha), basal area increment (m²/ha) and number of trees per hectare was calculated by year and by species. Results for all trees and the four most

common species (red maple, sugar maple, American beech and yellow birch) are summarized in Table 3.

Plot level projected BA for red maple was negative for the first projection cycle and positive for every following interval, increasing with time, but remained below 10 percent mean error to the end of the 31-year projection. Mean percent error for basal area increment was much higher, and positive for every interval. Bias for projected red maple trees per acre was negative for every projection interval but remained below 10 percent. FVS under-predicted trees per hectare but over-predicted BA and BA increment: mortality is over-estimated and growth on remaining trees is also over-estimated, but total stand basal area remains reasonable to the end of a 31-year projection. Errors for other species were generally much larger but also more variable.

Plot-level Bias by Species and Size Class

Trees were classified by size correlating to sapling, pole, small sawtimber and large sawtimber and aggregated by plot to summarize plot-level BA bias and trees per hectare bias. Results for all trees and individually for the four most common species for the first two projection intervals are tabulated in Table 4. Results for all five projection intervals for red maple only are shown in Table 5.

In most cases, basal area bias was largest for trees in the smallest size class, and increased with time for all size classes. For red maple, basal area mean percent error for trees in the middle two size classes, which accounted for most trees, remained under one percent for the first two projection intervals (out to 10 years) and remained below ten percent for the 31 year projection.

Conclusion

FVS/TWIGS comparison

At least two STEMS/TWIGS/FVS validators have documented that TWIGS projections of red maple growth have lower error than those of other species. Here also, red maple seems to be quite predictable, however in this case red maple also represents a large majority of the trees and the only species for which site quality was provided directly. With over 8000 red maple trees, the relatively favorable results may simply be an artifact of this being really the only species for which there is an appropriate sample size. Only 1100 sugar maple trees were represented, and less than 200 of every other species. I would not be confident that summaries of those species, especially when aggregated by plot and separated by size class, are representative of model performance.

The 2006 FVS/TWIGS model seems to over-predict tree diameter growth for most species (also consistent with what validators have found) and also over-predicts tree mortality. The net result is that for a 5-year growth projection stand basal area is under-predicted, but excessive tree growth (in spite of over-predicted mortality) results in over-predictions of stand basal area for the longer projections. As expected, errors and variance almost universally increase with longer projections.

Growth of trees smaller than 5 inches diameter (here the smallest size class) is estimated by a different set of equations than the larger size classes, and the small size class equations have been modified from the original TWIGS formulation while the large tree model remains unchanged. Presumably it had been recognized that the large tree model performed better than the small tree model and so did not require reformulation. With this data, the small tree model still performed more poorly than the large tree model.

Figures

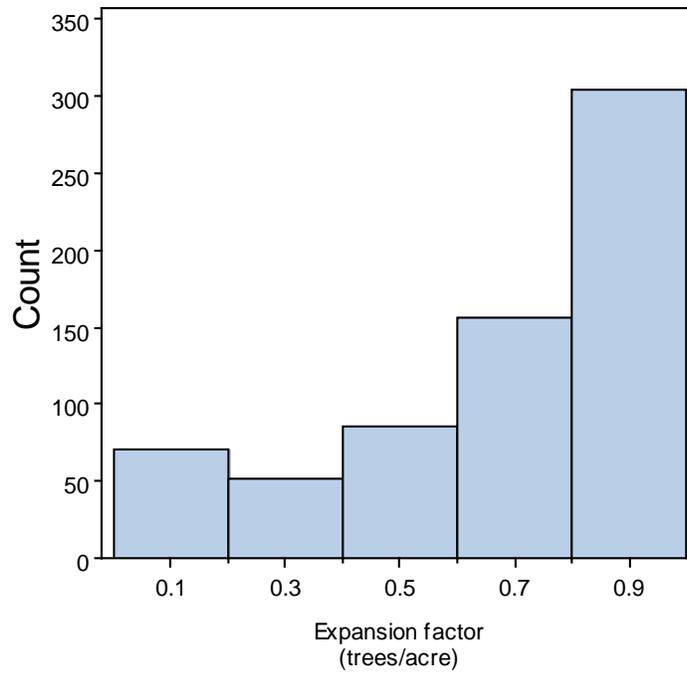


Figure 1. Distribution of FVS-modeled tree expansion factors for all trees with a tree expansion factor <1 at 31 years.

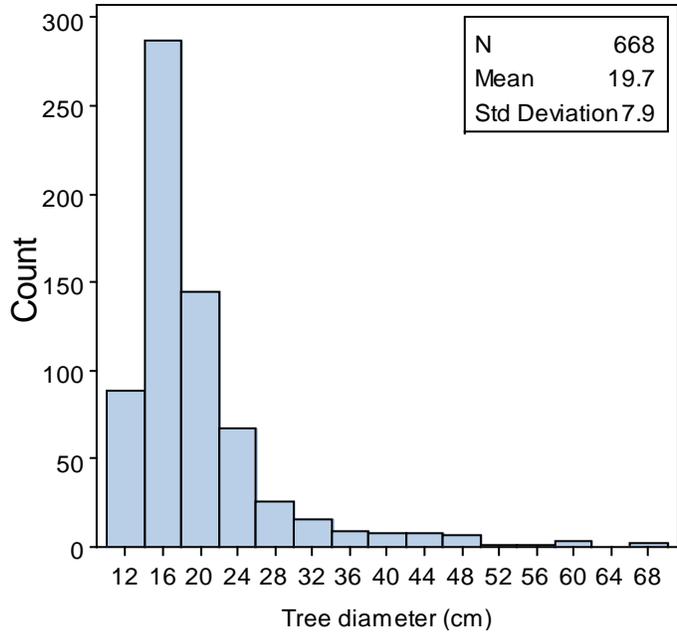


Figure 2. The distribution of FVS-modeled tree diameter for trees where expansion factor < 1 at year 31 (2011).

Tables

Table 1. Mean tree-diameter BIAS (projected minus observed diameter—negative values indicate under-prediction—as defined by Gribco and Wait (1992)) and standard deviation (SD) of bias, minimum, and maximum bias by year for all trees and by the four most common species.

All trees						Red maple			
YEAR	N	BIAS	SD	MIN	MAX	YEAR	N	BIAS	SD
1985	10883	0.20	0.70	-3.56	3.05	1985	8783	0.20	0.69
1990	10566	0.61	1.25	-4.83	5.41	1990	8566	0.59	1.22
1996	10213	1.16	1.90	-6.66	7.98	1996	8297	1.14	1.83
2000	9911	1.59	2.31	-9.55	9.72	2000	8070	1.58	2.21
2011	8955	2.64	3.50	-19.31	14.42	2011	7339	2.60	3.32

Sugar maple				American beech				Yellow birch			
YEAR	N	BIAS	SD	YEAR	N	BIAS	SD	YEAR	N	BIAS	SD
1985	1197	0.37	0.66	1985	170	0.11	0.67	1985	165	0.10	0.67
1990	1185	1.05	1.16	1990	166	0.16	1.18	1990	154	0.33	1.33
1996	1146	1.93	1.78	1996	165	0.02	1.97	1996	146	0.56	1.72
2000	1095	2.57	2.18	2000	163	0.18	2.41	2000	140	0.61	2.17
2011	968	4.46	3.22	2011	153	0.24	3.72	2011	121	0.65	3.01

Table 2. Individual tree diameter bias (projected tree diameter minus observed diameter), standard deviation, and percent error by size class, species, and year. Classification into size classes is based on diameter at the beginning of the projection cycle. Since after the first projection input data are projected diameters, the observed diameter and projected diameter of a tree are often in different size classes.

ALL SPECIES				
1985 -- 5 YEAR PROJECTION				
SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	1232	0.24	0.66	2.21
12.55 - 27.79 cm (5.0 - 10.99 in)	8096	0.19	0.69	1.09
27.80 - 43.03 cm (11.00 - 16.99 in)	1497	0.23	0.79	0.77
> 43.04 cm (> 17.00 in)	64	0.21	0.86	0.47
1990 -- 10 YEAR PROJECTION				
SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	584	0.44	1.16	4.37
12.55 - 27.79 cm (5.0 - 10.99 in)	8037	0.59	1.23	3.31
27.80 - 43.03 cm (11.00 - 16.99 in)	1863	0.75	1.33	2.44
> 43.04 cm (> 17.00 in)	91	0.52	1.88	1.30
1996 -- 16 YEAR PROJECTION				
SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	193	0.30	1.85	4.21
12.55 - 27.79 cm (5.0 - 10.99 in)	7539	1.06	1.84	5.99
27.80 - 43.03 cm (11.00 - 16.99 in)	2352	1.54	2.00	5.02
> 43.04 cm (> 17.00 in)	135	1.15	2.32	2.69
2000 -- 20 YEAR PROJECTION				
SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	56	-0.14	2.51	1.91
12.55 - 27.79 cm (5.0 - 10.99 in)	6695	1.40	2.21	7.95
27.80 - 43.03 cm (11.00 - 16.99 in)	2922	2.03	2.42	6.85
> 43.04 cm (> 17.00 in)	240	2.00	2.73	4.72
2011 -- 31 YEAR PROJECTION				
SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	22	-0.59	3.37	0.29
12.55 - 27.79 cm (5.0 - 10.99 in)	5521	2.13	3.32	11.79
27.80 - 43.03 cm (11.00 - 16.99 in)	3121	3.46	3.57	11.55
> 43.04 cm (> 17.00 in)	291	3.77	4.17	8.75

RED MAPLE**1985 -- 5 YEAR PROJECTION**

SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	883	0.30	0.63	2.68
12.55 - 27.79 cm (5.0 - 10.99 in)	6616	0.18	0.68	1.05
27.80 - 43.03 cm (11.00 - 16.99 in)	1248	0.22	0.77	0.73
> 43.04 cm (> 17.00 in)	36	0.09	0.96	0.26

1990 -- 10 YEAR PROJECTION

SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	393	0.60	1.09	5.63
12.55 - 27.79 cm (5.0 - 10.99 in)	6540	0.56	1.20	3.15
27.80 - 43.03 cm (11.00 - 16.99 in)	1577	0.73	1.29	2.37
> 43.04 cm (> 17.00 in)	56	0.70	1.68	1.67

1996 -- 16 YEAR PROJECTION

SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	96	0.89	1.44	8.58
12.55 - 27.79 cm (5.0 - 10.99 in)	6115	1.02	1.78	5.73
27.80 - 43.03 cm (11.00 - 16.99 in)	1995	1.51	1.94	4.91
> 43.04 cm (> 17.00 in)	91	1.32	2.17	2.99

2000 -- 20 YEAR PROJECTION

SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	11	1.44	0.92	13.30
12.55 - 27.79 cm (5.0 - 10.99 in)	5397	1.36	2.10	7.67
27.80 - 43.03 cm (11.00 - 16.99 in)	2483	1.99	2.35	6.69
> 43.04 cm (> 17.00 in)	179	2.19	2.56	5.10

2011 -- 31 YEAR PROJECTION

SIZE CLASS	N	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	3	1.58	0.85	13.74
12.55 - 27.79 cm (5.0 - 10.99 in)	4456	2.03	3.09	11.05
27.80 - 43.03 cm (11.00 - 16.99 in)	2657	3.41	3.43	11.29
> 43.04 cm (> 17.00 in)	223	4.14	3.81	9.47

Table 3. Mean plot-level bias for basal area (m²/ha), basal area increment (m²/ha) and number of trees per hectare for all species combined and for the four most common species. Basal area increment was calculated as the sum of the products of individual tree increment and expansion factor.

ALL SPECIES (n = 95)									
YEAR	BA (sq m/ha)			BA increment (sq m/ha)			Trees/ha		
	BIAS	SD	%	BIAS	SD	%	BIAS	SD	%
			ERROR			ERROR			ERROR
1985	-0.06	0.85	-0.07	0.33	0.70	21.33	-11.10	17.11	-1.65
1990	0.49	1.63	2.50	0.77	0.67	44.88	-15.44	36.21	-2.26
1996	1.16	2.22	5.35	1.15	0.73	60.85	-23.60	45.98	-3.47
2000	1.76	2.64	7.57	0.98	0.45	87.87	-27.99	48.39	-4.41
2011	3.07	3.73	12.48	2.36	1.04	78.80	-37.55	57.52	-6.53
RED MAPLE (n = 95)									
YEAR	BA (sq m/ha)			BA increment (sq m/ha)			Trees/ha		
	BIAS	SD	%	BIAS	SD	%	BIAS	SD	%
			ERROR			ERROR			ERROR
1985	-0.10	0.75	-0.43	0.25	0.61	20.67	-9.25	14.57	-1.70
1990	0.22	1.40	1.37	0.59	0.64	42.76	-14.15	26.10	-2.55
1996	0.68	2.06	3.73	0.91	0.77	61.18	-20.85	35.29	-3.85
2000	1.07	2.51	5.46	0.78	0.47	87.94	-25.18	38.77	-5.01
2011	1.99	3.66	9.61	1.83	1.21	78.78	-34.07	47.17	-7.51
SUGAR MAPLE (n = 75)									
YEAR	BA (sq m/ha)			BA increment (sq m/ha)			Trees/ha		
	BIAS	SD	%	BIAS	SD	%	BIAS	SD	%
			ERROR			ERROR			ERROR
1985	0.04	0.12	1.52	0.09	0.14	112.27	-2.14	3.48	-2.43
1990	0.19	0.32	8.21	0.18	0.19	258.37	-3.64	6.59	-3.46
1996	0.43	0.61	19.72	0.25	0.23	367.35	-4.33	11.21	-2.34
2000	0.64	0.90	62.41	0.20	0.18	680.13	-3.33	15.78	23.28
2011	1.21	1.30	113.88	0.61	0.53	1578.82	-2.50	20.70	27.66

AMERICAN BEECH

YEAR	BA (sq m/ha)			BA increment (sq m/ha)			Trees/ha		
	BIAS	SD	%	BIAS	SD	%	BIAS	SD	%
			ERROR			ERROR			ERROR
1985	0.05	0.28	6.91	0.02	0.07	27.95	-0.32	1.92	3.34
1990	0.09	0.46	-3.06	0.02	0.07	5.70	-0.54	3.56	-1.55
1996	0.04	0.51	-8.12	-0.01	0.08	-9.34	-1.42	4.34	-5.31
2000	0.10	0.74	-6.18	0.03	0.07	24.33	-1.82	5.47	-7.24
2011	0.12	1.05	-8.95	0.02	0.17	-3.27	-2.70	7.34	-13.65

YELLOW BIRCH

YEAR	BA (sq m/ha)			BA increment (sq m/ha)			Trees/ha		
	BIAS	SD	%	BIAS	SD	%	BIAS	SD	%
			ERROR			ERROR			ERROR
1985	-0.05	0.13	2.20	0.00	0.03	56.35	-0.60	2.77	0.45
1990	-0.05	0.26	2.30	0.01	0.07	106.11	-0.89	4.37	-3.45
1996	-0.09	0.39	-4.08	0.01	0.04	80.54	-2.01	5.89	-11.02
2000	-0.12	0.50	0.69	-0.01	0.04	148.12	-2.85	7.42	-13.63
2011	-0.29	0.77	-21.14	-0.03	0.12	-13.82	-4.63	10.41	-27.43

Table 4. Plot level basal area increment and trees per hectare mean bias by size class for all species and the four most common species for five- and ten-year projections..

1985 -- 5 YEAR PROJECTION

All trees combined

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	68	0.03	0.12	-1.35	-0.96	5.67	-2.07
12.55 - 27.79 cm (5.0 - 10.99 in)	95	-0.06	0.55	-0.36	-8.97	12.59	-1.87
27.80 - 43.03 cm (11.00 - 16.99 in)	91	-0.03	0.41	-0.34	-1.53	4.47	-1.51
> 43.04 cm (> 17.00 in)	32	0.03	0.30	3.08	0.07	1.47	1.34

Red maple

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	65	0.03	0.11	2.18	-0.40	5.00	-1.60
12.55 - 27.79 cm (5.0 - 10.99 in)	95	-0.07	0.50	-0.74	-7.54	10.90	-1.88
27.80 - 43.03 cm (11.00 - 16.99 in)	85	-0.05	0.35	-0.79	-1.59	3.96	-1.91
> 43.04 cm (> 17.00 in)	25	-0.01	0.18	-0.43	-0.06	1.03	-1.40

Sugar maple

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	30	0.00	0.05	-3.53	-1.76	2.52	-5.45
12.55 - 27.79 cm (5.0 - 10.99 in)	73	0.03	0.09	1.61	-1.34	2.06	-2.28
27.80 - 43.03 cm (11.00 - 16.99 in)	34	0.01	0.05	1.53	-0.28	0.28	-2.36
> 43.04 cm (> 17.00 in)	1	0.03		2.79	-0.11		-2.15

American beech

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	9	-0.01	0.03	-12.19	-0.05	1.83	-5.96
12.55 - 27.79 cm (5.0 - 10.99 in)	28	-0.01	0.04	-3.71	-0.58	0.83	-2.67
27.80 - 43.03 cm (11.00 - 16.99 in)	13	0.00	0.03	-0.55	-0.24	0.20	-2.71
> 43.04 cm (> 17.00 in)	5	0.44	0.61	27.91	1.82	2.77	22.32

Yellow birch

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	6	0.00	0.01	-4.29	-0.62	0.30	-7.21
12.55 - 27.79 cm (5.0 - 10.99 in)	31	-0.01	0.10	0.57	-0.18	2.93	0.05
27.80 - 43.03 cm (11.00 - 16.99 in)	25	-0.04	0.08	-3.97	-0.43	0.94	-4.69
> 43.04 cm (> 17.00 in)	8	-0.11	0.06	-8.66	-0.53	0.27	-8.83

1990 -- 10 YEAR PROJECTION

All trees combined

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	57	0.04	0.10	8.61	-0.05	7.12	0.91
12.55 - 27.79 cm (5.0 - 10.99 in)	95	0.27	1.10	1.79	-12.93	30.48	-2.84
27.80 - 43.03 cm (11.00 - 16.99 in)	92	0.14	0.78	3.30	-2.75	9.06	-0.91
> 43.04 cm (> 17.00 in)	43	0.15	0.64	11.72	0.41	2.84	7.46

Red maple

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	54	0.05	0.10	17.39	1.16	7.04	5.38
12.55 - 27.79 cm (5.0 - 10.99 in)	95	0.13	0.90	0.84	-11.88	20.61	-3.06
27.80 - 43.03 cm (11.00 - 16.99 in)	89	0.03	0.68	0.77	-3.23	8.15	-3.10
> 43.04 cm (> 17.00 in)	34	0.09	0.47	10.43	0.28	2.39	5.81

Sugar maple

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	24	-0.01	0.04	-3.30	-2.81	3.82	-10.18
12.55 - 27.79 cm (5.0 - 10.99 in)	73	0.14	0.24	8.36	-2.75	4.38	-3.10
27.80 - 43.03 cm (11.00 - 16.99 in)	40	0.10	0.19	8.66	-0.11	1.57	-2.00
> 43.04 cm (> 17.00 in)	2	0.04	0.03	4.28	-0.22	0.02	-4.37

American beech

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	8	-0.02	0.04	-18.54	-0.43	2.04	-12.38
12.55 - 27.79 cm (5.0 - 10.99 in)	28	-0.04	0.05	-8.12	-1.25	1.76	-5.75
27.80 - 43.03 cm (11.00 - 16.99 in)	17	0.10	0.26	4.60	0.74	2.73	1.66
> 43.04 cm (> 17.00 in)	6	0.40	0.62	22.96	1.37	2.61	15.35

Yellow birch

Size class	N (plots)	Basal area (sq m/ha)			Trees per hectare		
		BIAS	SD	% ERROR	BIAS	SD	% ERROR
10.00 - 12.54 cm (3.94 - 4.99 in)	5	-0.01	0.03	1.43	-0.01	0.03	1.43
12.55 - 27.79 cm (5.0 - 10.99 in)	30	-0.01	0.14	-2.08	-0.01	0.14	-2.08
27.80 - 43.03 cm (11.00 - 16.99 in)	27	-0.04	0.25	-11.95	-0.04	0.25	-11.95
> 43.04 cm (> 17.00 in)	8	-0.09	0.45	-18.77	-0.09	0.45	-18.77

Table 5. Plot level basal area (m²/ha) bias by size class and year for red maple.

Sapling: 10.00 - 12.54 cm (3.94 - 4.99 in)				
YEAR	N	BIAS	SD	% ERROR
1985	65	0.03	0.11	2.18
1990	54	0.05	0.10	17.39
1996	41	0.04	0.10	20.41
2000	16	0.03	0.09	76.10
2011	5	0.01	0.10	-84.09

Small saw: 27.80 - 43.03 cm (11.00 - 16.99 in)				
YEAR	N	BIAS	SD	% ERROR
1985	85	-0.05	0.35	-0.79
1990	89	0.03	0.68	0.77
1996	93	0.23	0.99	2.78
2000	94	0.45	1.31	4.37
2011	94	1.16	2.10	9.17

Pole: 12.55 - 27.79 cm (5.0 - 10.99 in)				
YEAR	N	BIAS	SD	% ERROR
1985	95	-0.07	0.50	-0.74
1990	95	0.13	0.90	0.84
1996	95	0.39	1.39	3.40
2000	95	0.55	1.52	5.52
2011	94	0.63	2.03	7.76

Large saw: > 43.04 cm (> 17.00 in)				
YEAR	N	BIAS	SD	% ERROR
1985	25	-0.01	0.18	-0.43
1990	34	0.09	0.47	10.43
1996	37	0.13	0.72	8.04
2000	52	0.13	0.74	7.46
2011	61	0.34	1.09	14.39