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Analysis of stand basal area development of thinned and unthinned *Acer rubrum* L. forests in the upper Great Lakes region, USA.

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Abstract: Red maple (*Acer rubrum* L.) was historically a common but not abundant tree species in North America that has increased in abundance throughout its range over the last several decades, but nonetheless has received little attention in growth and yield studies. The objectives of this study were to 1) evaluate the effects of stocking level and stand density on overall patterns of red maple stand productivity and 2) quantify these relationships across a wide range of stand age, site quality, geographic location, and climatic conditions.

We used long-term measurements from 52 sites in Wisconsin and Michigan to examine growth responses of even-aged red maple stands to various levels of thinning. Using linear, mixed-effects modeling, future stand-level red maple basal area was modeled as a function of stand and plot characteristics and climatic variables. Growing season precipitation, and its interaction with initial red maple basal area were significant predictors; however, they only collectively reduced MSE by 2.1% 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 climate conditions experienced by these stands highlighting red maple’s wide tolerance of environmental conditions across the region.

Keywords: *Acer rubrum*, basal area growth, climate, Great Lakes region
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 USA (Abrams, 1998) but has been increasing in abundance over at least the last several decades (Fei and Steiner, 2007) and now ranks seventh in highest average importance value (IV) for tree species in the eastern USA (east of the 100th meridian) based on recent national inventories (Iverson et al., 2008). At localized scales, the magnitude of this increase in abundance is often much greater. For example, within the upper Lake States, recent Forest Inventory and Analysis (FIA) data indicate that among all tree species in both Michigan (Pugh, 2010) and Wisconsin (Perry, 2011), red maple is second only to sugar maple (Acer saccharum Marsh.) in terms of standing wood volume. In Michigan, red maple accounts for 116 million m$^3$ of standing wood volume (trees 12.7 cm dbh and larger) and 72 million m$^3$ in Wisconsin. Between the last two complete FIA surveys for Minnesota, a significant increase (>60%) in red maple relative abundance (dbh ≥ 2.54 cm) 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 of trees 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 into the future. Within every state in its range for which there is data, red maple population diameter distributions follow a reverse “J” distribution with high recruitment rates into larger size classes, suggesting it will continue to proliferate (Fei and Steiner, 2007). Furthermore, many forest models predict that red maple will increase in
abundance in parts of its range under various climate change scenarios. For example, growth
and yield models suggest red maple would respond positively to future climate under both
current climate and a projected climate change scenario over the next 80 years in eastern Canada
(Dombroskie et al., 2010). Similarly, the USDA Forest Service Climate Change Atlas indicates
that the potential range for red maple could increase between 0 and 5.2 percent by the year 2100,
depending on the Global Circulation Model (GCM) and emissions scenario used (Iverson et al.,
2008), even though red maple importance is projected to decrease in the southern portions of this
species range.

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 (Strong et al., 2006). Past growth modeling efforts
for this species have largely focused either on diameter growth of individual trees (Hahn and
Leary, 1979) or stand-level growth in mixed forests where red maple is a lesser component of the
overstory (Solomon, 1977) or occurs strictly in the understory (Nowak, 1996). In many such
e examples red maple has been combined with other species (e.g. silver maple) for analysis
(Lessard et al., 2001). After evaluating individual tree measurements across Michigan, Pokharel
and Froese (2008) observed that current and adjusted models of red maple diameter increment
were overpredicted by 8.0 to 17.6%, suggesting that errors could be amplified when scaling to
stand level values such as basal area. In contrast, growth and yield models may underpredict
diameter growth in stands with varied management histories (Kiernan et al., 2008).

While eastern North American forests now contain much higher proportions of red maple
than in the past, ecologists have acknowledged that such new species relative abundances can
still provide for ecological and social benefits if managed appropriately (Hobbs et. al, 2006).
Flexible species such as red maple may have particular value this regard. Given the expected persistence of stands dominated by red maple (e.g. Eyre, 1980), the potential for an increase in abundance of red maple in the northern parts of its range with climate change, and the resulting increased ecological and social roles the species may serve in future forests, a further understanding of growth for this species in managed stands 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). Analysis of basal area change has thus been fundamental in the development of many forest growth and yield modeling systems and silvicultural prescriptions (Clutter et al., 1983); however, to date such analyses have not been conducted with red maple.

Beyond the stand and tree-level factors widely known to affect tree growth (e.g., stocking, site quality, size, and age), climate data is increasingly being integrated into growth and yield models to account for temperature and precipitation effects on long-term dynamics (Crookston et al., 2010). Evidence from dendrochronology studies of red maple indicate that climate and site attribute strongly interact to influence diameter growth (Fekedulegn et al., 2003). Past work in Upper Michigan has shown that air temperature degree days (base 4.4 deg C) through May, soil potassium concentration in the upper 15 cm of mineral soil, and soil water holding capacity at a depth of 5-10 cm are predominant environmental variables driving observed variation in diameter growth of individual red maple trees (Reed et al., 1992). 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 to 6.3% (Carter, 1996).

Given the documented influence of climatic and site conditions on red maple growth, it may 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 were 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) evaluating the effects of stocking level and stand density on overall patterns of stand productivity in terms of basal area development, and 2) quantifying these relationships across a wide range of stand age, site quality, 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 (Figure 1) 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-Nicolet 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). Study locations are in National Forests (n=41), state...
forests (n=9) and privately owned commercial timberland (n=2). 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 soil 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).


**Plot layout, treatment, and sampling**

Study plots were established in undisturbed, second-growth stands in which at least 75 percent of the overstory canopy was red maple (Erdmann *et al.*, 1981). All stands established naturally following late 19th and early 20th century harvesting (Erdmann *et al.*, 1981). Two to four plots were installed in each stand, resulting in a total of 122 plots. Each plot was a 2000 m² (31.6 x 63.2 m) 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 divided 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 subsequent individual tree remeasurements.
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 (Table 1).

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 m$^2$ ha$^{-1}$—or a no harvest control with variable basal area. In a few cases strict random assignment was not possible due to low initial basal area. Additionally, since 9.2 and 32.2 m$^2$ha$^{-1}$ basal area are at the respective low and high extremes of what would remain following a silvicultural thinning in practice, assignment of those levels was limited to six plots (with only five of each utilized in the present study) (Appendix, Table A1). 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 of quality red maple.

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, which was up to one year before or after the nominal year, 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. Trees that had died were recorded as such, as were trees that
could not be located. Plots were not measured immediately following the thinning so 1982
values, when required for analysis, were determined as the sum of the 1980 individual tree basal
areas for all trees that were not recorded as cut in 1982. Since the exact year of harvest was not
known for all sites, and post-harvest measurement did not occur until 1985, 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 stand-level basal area growth observations were available for analysis.

**Basal area development**

Total stand basal area development and periodic annual basal area production (survivor
growth plus ingrowth minus mortality, divided by the growth interval length)(Avery and
Burkhart, 2002), as well as red maple basal area development and red maple periodic annual
basal area production were compared to determine whether red maple basal area development
follows similar patterns to whole stand basal area. The effects of residual basal area and
measurement year on total stand basal area and red maple basal area were evaluated using
analysis of variance followed by Tukey’s studentized range test (alpha=0.05). The influence of
stand density on patterns of periodic annual gross basal area growth (survivor growth plus
ingrowth for the growth interval divided by the growth interval length)(Avery and Burkhart,
2002) and periodic annual basal area production were both graphically assessed. Stand density
for these mixed-species stands was quantified as relative density—the 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). Because measurements of tree
heights were not available, analysis of stand volume growth was not possible.

**Basal area projection modeling**

Linear regression models were used to investigate the influence of stand and site factors on
red maple basal area development. 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 plot
basal area at the time of measurement. Since red maple accounted for an average of more than
80 percent of basal area for all observations on all plots, and in order to focus the analysis on the
red maple component, red maple basal area (m²ha⁻¹) was used as the response variable in our
analyses.

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 younger than 30 years, likely the age range that would include the
inflection point in a sigmoidal yield curve.

Because the factors most relevant to growth and yield (stand age, site quality, and stand
density) combine multiplicatively in their influence over yield but are additive in their influence
on the logarithm of yield (Avery and Burkhart, 2002), 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, time since thinning, etc.), stand density, and thinning intensity, were
tested for inclusion in a basic regression model to describe red maple basal area development. A partial list of variables considered during the fitting process is shown in Table 2 with a complete list in the Appendix (Table A2).

To account for the effects of climatic conditions on basal area growth of red maple, numerous climate variables that have been demonstrated to influence tree or stand growth in red maple or other species, or that can be logically hypothesized to be important factors governing red maple growth, were considered. These include annual mean temperature and precipitation, growing season length and precipitation, growing degree days, precipitation during the three months preceding the start of the growing season, and timing of the start of the growing season. The mean and range of these climate variables for each growth interval across all sites is provided in Table 3, and a complete list of climate variables considered is in the Appendix (Table A2). Monthly climate variables at each site were estimated using thin plate spline smoothing algorithms (McKenney et al., 2011) 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 additional predictors of basal area growth.

Model construction followed the methodology described by Zuur et al. (2009). To determine an appropriate specification of the random effects structure, variance model, and autocorrelation structure, regressions that included the same comprehensive set of all independent variables under consideration (including climatic variables and interactions) were estimated by restricted maximum likelihood. These models differed only in how each component of the variance structure was specified, and 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 \((\ln rm1)\) and growth interval length \((dt)\)—additional independent variables and interactions were individually added to the regression and comparisons of AIC and mean squared error were used to gauge improvement in the fitted models. Once the model form and base set of independent variables were selected, the climate variables were similarly incorporated individually and the fitted models evaluated for significant improvement (Table 3). Logically plausible interaction terms that included climate variables were likewise evaluated for relevance.

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

Basal area development

The 1982 thinning resulted in statistically distinctive stocking levels across treatments in 1985, with the exception of the most lightly thinned plots (target residual basal area of 32.2 m²ha⁻¹), 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. The four most heavily thinned groups retained different levels of red maple basal area after 18 years (Figure 2b) with most groups converging by the 29th year following thinning. Total basal area periodic annual increment generally had an inverse relationship with stocking (Figure 2c), as did red maple basal area periodic annual increment (Figure 2d). A comparison between total stand basal area development and red maple basal area development indicated that red maple basal area generally followed the patterns of total stand basal area. Periodic annual basal area production 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 plots exhibited a net loss in basal area during the final
growth interval. Periodic annual basal area gross growth showed no strong relationship with
density over the range covered by this data (not shown).

**Basal area projection modeling**

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:

\[
\ln(\text{BA}_2)_{ij} = \beta_0 + \beta_1 \ln(\text{BA}_1)_{ij} + (\beta_2 + b_i) \Delta t_i + \beta_3 A_i^{-1} + \beta_4 \text{pctrm}_{ij} + \beta_5 \text{dq}_{ij} + \beta_6 \Delta t_i \times A_i^{-1} + \varepsilon_{ij}
\]

where \(\ln(\text{BA}_2)_{ij}\) and \(\ln(\text{BA}_1)_{ij}\) are the natural logarithm of total red maple basal area on the \(j\)th
plot in the \(i\)th stand at the end and the beginning of the growth interval, respectively, \(\beta_0\) through
\(\beta_6\) are population-level fixed effects parameters, \(b_i\) is a stand-level random effects parameter, \(\Delta t_i\)
is the change in stand age (number of growing seasons) from the start to the end of the growth
interval, \(A_i^{-1}\) is the inverse of initial stand age, \(\text{pctrm}_{ij}\) is the proportion of basal area comprised
of red maple, \(\text{dq}_{ij}\) is the plot quadratic mean diameter for all trees greater than 10 cm, and \(\varepsilon_{ij}\) is
the model error term, where \(\varepsilon_{ij} \sim N(0, R_{ij})\) and \(R_{ij}\) is the variance-covariance matrix for the
model error term.

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. Inclusion of other density measures—
such as relative density and stand density index—and site index either resulted in unexpected
signs or caused unexpected signs for other variables and thus were not included in the final
model. Geographic location of each site, represented by latitude and longitude, did not improve
the model fit. 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 a
significant predictor.

Parameter estimates from the fitted base model (Table 4) indicate initial red maple BA and
percent red maple had positive effects on red maple basal area projections, while stem density
and quadratic mean dbh had negative effects on projections. 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.

Models were initially fit with both plot-level and site-level random effects (by nesting plots
within sites to specify random effects). However, 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. 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 m$^2$ha$^{-1}$ basal area, the change
in red maple basal area could range from nearly zero to over 3.0 m$^2$ha$^{-1}$, depending on the
estimated random effect for the stand.

**Climate effects on basal area projections**

After testing many climate variables for inclusion in the base model (Table 3), only the
growth interval mean precipitation during the growing season 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:

\[
\ln(BA_{ij}) = \beta_1 \ln(BA_{1ij}) + (\beta_2 + b_i)dt_i + \beta_3 A_i^{-1} + \beta_4 \text{prec}rm_{ij} + \beta_5 dq_{ij} + \beta_6 dt_i \times A_i^{-1} + \beta_7 \text{precip}3_i
\]

\[+ \beta_8 \ln(BA_{1ij}) \times \text{precip}3_i + \epsilon_{ij}\]

where \text{precip}3_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.

Although the addition of precipitation in the model improved the fit significantly based on an AIC difference of more than 10 (Table 5), the gain was marginal—MSE was reduced by only 2.1 percent—and local climate had only a minor influence on red maple basal area projections (Figure 5). The parameter estimates reveal a density-dependent growth response to changes in precipitation. For a plot observation with average values for all included variables (\textit{age} = 76.9 years, \textit{pctrm} = 0.81, \textit{dq} = 24.1 cm, growth interval = 6.29 years) with initial red maple basal area of 24.8 m\(^2\)ha\(^{-1}\), 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 m\(^2\)ha\(^{-1}\) would have a lower growth response with increasing precipitation (Figure 5).

**Discussion**

**Effects of stand characteristics on growth**

The long-term stand-level red maple basal area development in the second-growth stands we examined highlights that basal area growth in these systems is controlled by similar factors as for other species, and included 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
(Fekedulegn et al., 2003), we found only a minor improvement of projections of stand-level
basal area when accounting for average climatic variation (namely precipitation) over a given
growth interval. This lack of relationship could reflect the wide ecological amplitude of the
species and suggests site factors and stand structural characteristics, such as stocking and
composition, are more important for projecting growth of this species. Nonetheless, the
documented sensitivity of this species to inter-annual variability in climate conditions (Zhang et
al., 2014) argues for the consideration of climate variables when predicting future growth of this
species. An apparent reduction in basal area increment is evident in Figure 2(c and d) for the
1996-2000 growth interval which could be attributed to a climatic variable not included in our
analysis, as there was no strong correlation between basal area annual increment and any
climatic variable that we considered. The reduction in increment seems to be most pronounced
in the control plots and those thinned to low residual basal area, but further analysis would be
required to determine if this is linked to climate.

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—albeit dominant—
species. Correspondingly, the primary predictor used here was initial basal area in red maple
stems which, along with the proportion red maple basal area, describes the level of competition
in the stand. The highest basal area projections occurred in pure red maple stands. 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 periodic annual basal area gross growth in these stands does not appear to vary with stocking
or density (data not shown). In contrast, periodic annual basal area production decreased with
increasing relative density and stocking (Figure 3) which reflects 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. Although the response variable we examined is not total stand basal area, the
observed trend in red maple basal area is likely the species-component corollary of age-related
decline universally documented for tree and forest stand-level growth as stand age increases
(Smith and Long, 2001). In the case of tolerant species as present in this study, other age classes
may counterbalance this decline over time as multi-aged structures develop and younger, more
efficient cohorts contribute to stand-level red maple growth (O’Hara and Nagel, 2006).

Given differences between sites in their ability 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 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) 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). This is particularly true in mixed species stands (Payandeh and Wang, 1996), 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 have been used to model 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, did slightly increase the model fit. Nevertheless, inclusion of this variable in stand projection 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 yield 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) demonstrated the importance of accounting for the intensity of the thinning, not simply current stand density, to acquire consistent and unbiased growth projections. While an index of thinning intensity (e.g. Bailey and Ware, 1983) was marginally significant during preliminary analysis of our data, its inclusion was not justified in the final model form. Given that red maple is classified as a tolerant species in this portion of its range, these natural-origin stands may not behave in the same manner as the even-aged plantations composed of intolerant species commonly examined in many forest growth studies. It is apparent that as recruitment and ingrowth can make large contributions to stand basal area over a short time frame, especially in heavily thinned stands, differences in tree growth due to variation in thinning intensity may be quickly obscured by ingrowth.

Effect of climatic conditions on basal area development
A main objective of this research was to examine the influence of climatic variables on red maple basal area development 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 m²ha⁻¹, 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., 1992), 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.

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 USA and in many cases is highly competitive with more specialized species (Abrams, 1998). 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 (Bauerle et al., 2003). 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 can be difficult to determine or predict. Despite the species’
flexibility, the significant effect of growing season precipitation on 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).

Conclusion
The increasing abundance of red maple-dominated forests on the landscape in the eastern
USA has created a need for 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 predicted future climate
conditions (Dombroskie et al., 2010) generates a particular interest in understanding how this
species responds to environmental variation.

At the site level, basal area growth of red maple is well described by factors easily
controlled for by management such as 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.

Acknowledgements

We would like to C. Kern, D. Kastendick, and R. Cook for assisting with various aspects
of the study, as well as F. Falzone, K. Gill, N. Bolton, and M. Reinikainen for assisting with field
work. D. McKenney and P. Papadopol provided modeled climate data for the study site
locations. Financial support for this research was provided by the USDA Northern Research Station and the Minnesota Agricultural Experiment Station.

**Literature cited**


Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46 (7), 627-638.


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### Table 1.

Average initial conditions and range (in parentheses) across 122 red maple dominated study plots in northern Wisconsin and northern Michigan in 1980.

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>9.2 m²·ha⁻¹</th>
<th>13.8 m²·ha⁻¹</th>
<th>18.4 m²·ha⁻¹</th>
<th>23.0 m²·ha⁻¹</th>
<th>27.6 m²·ha⁻¹</th>
<th>32.1 m²·ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>n (# of plots)</td>
<td>12</td>
<td>5</td>
<td>22</td>
<td>34</td>
<td>29</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>initial age (years)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>70</td>
<td>46</td>
<td>56</td>
<td>65</td>
<td>71</td>
<td>69</td>
<td>76</td>
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<tr>
<td>(40-95)</td>
<td>(28-61)</td>
<td>(28-68)</td>
<td>(40-97)</td>
<td>(53-97)</td>
<td>(54-88)</td>
<td>(59-88)</td>
<td></td>
</tr>
<tr>
<td>site index (m)</td>
<td>16.7</td>
<td>16.3</td>
<td>17.5</td>
<td>17.3</td>
<td>17.1</td>
<td>17.6</td>
<td>17.4</td>
</tr>
<tr>
<td>(12.9-19.0)</td>
<td>(12.8-22.9)</td>
<td>(12.8-22.9)</td>
<td>(12.6-21.6)</td>
<td>(12.6-21.6)</td>
<td>(14.4-20.6)</td>
<td>(14.7-20.5)</td>
<td></td>
</tr>
<tr>
<td>initial basal area</td>
<td>30.9</td>
<td>19.1</td>
<td>26.2</td>
<td>30.1</td>
<td>33.1</td>
<td>34.4</td>
<td>37.4</td>
</tr>
<tr>
<td>(m²·ha⁻¹)</td>
<td>(21.1-39.3)</td>
<td>(14.3-22.9)</td>
<td>(14.3-33.3)</td>
<td>(20.8-42.8)</td>
<td>(26.9-42.0)</td>
<td>(28.3-42.9)</td>
<td>(33.8-43.8)</td>
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<tr>
<td>red maple basal area</td>
<td>24.2</td>
<td>10.0</td>
<td>17.2</td>
<td>21.5</td>
<td>24.3</td>
<td>26.5</td>
<td>29.7</td>
</tr>
<tr>
<td>(m²·ha⁻¹)</td>
<td>(11.8-32.1)</td>
<td>(4.6-18.1)</td>
<td>(7.3-30.1)</td>
<td>(10.7-31.9)</td>
<td>(14.0-35.0)</td>
<td>(16.6-35.5)</td>
<td>(26.3-33.8)</td>
</tr>
<tr>
<td>red maple proportion of basal area</td>
<td>0.78</td>
<td>0.52</td>
<td>0.65</td>
<td>0.71</td>
<td>0.73</td>
<td>0.77</td>
<td>0.80</td>
</tr>
<tr>
<td>(0.56-0.97)</td>
<td>(0.23-0.79)</td>
<td>(0.35-0.96)</td>
<td>(0.46-0.96)</td>
<td>(0.51-0.95)</td>
<td>(0.5-0.98)</td>
<td>(0.73-0.95)</td>
<td></td>
</tr>
<tr>
<td>no. of trees per hectare</td>
<td>835</td>
<td>1104</td>
<td>1022</td>
<td>961</td>
<td>907</td>
<td>895</td>
<td>833</td>
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<tr>
<td></td>
<td>(645-1250)</td>
<td>(875-1355)</td>
<td>(725-1400)</td>
<td>(565-1460)</td>
<td>(510-1340)</td>
<td>(585-1105)</td>
<td>(615-1195)</td>
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<tr>
<td>quadratic mean diameter (cm)</td>
<td>22.1</td>
<td>14.9</td>
<td>18.2</td>
<td>20.3</td>
<td>22.1</td>
<td>22.4</td>
<td>24.4</td>
</tr>
<tr>
<td></td>
<td>(16.0-26.1)</td>
<td>(13.6-15.7)</td>
<td>(13.6-23.4)</td>
<td>(15.2-26.3)</td>
<td>(16.5-30.8)</td>
<td>(18.1-27.0)</td>
<td>(21.6-27.1)</td>
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</table>

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<table>
<thead>
<tr>
<th>stand density index</th>
<th>638</th>
<th>466</th>
<th>585</th>
<th>645</th>
<th>684</th>
<th>707</th>
<th>746</th>
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<tbody>
<tr>
<td></td>
<td>(497-832)</td>
<td>(365-570)</td>
<td>(367-738)</td>
<td>(460-835)</td>
<td>(537-803)</td>
<td>(600-839)</td>
<td>(655-903)</td>
</tr>
<tr>
<td>relative density</td>
<td>0.62</td>
<td>0.46</td>
<td>0.58</td>
<td>0.63</td>
<td>0.67</td>
<td>0.69</td>
<td>0.72</td>
</tr>
<tr>
<td>(proportion of max.)</td>
<td>(0.49-0.80)</td>
<td>(0.37-0.57)</td>
<td>(0.37-0.74)</td>
<td>(0.45-0.84)</td>
<td>(0.52-0.82)</td>
<td>(0.58-0.83)</td>
<td>(0.65-0.81)</td>
</tr>
</tbody>
</table>
Table 2. 1985 post-thinning conditions for 122 red maple dominated plots thinned to six levels of residual basal area or not thinned.

<table>
<thead>
<tr>
<th>Residual Target Basal Area</th>
<th>Control</th>
<th>9.2 m²ha⁻¹</th>
<th>13.8 m²ha⁻¹</th>
<th>18.4 m²ha⁻¹</th>
<th>23.0 m²ha⁻¹</th>
<th>27.6 m²ha⁻¹</th>
<th>32.1 m²ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (# of plots)</td>
<td>12</td>
<td>5</td>
<td>22</td>
<td>34</td>
<td>29</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>basal area (m²ha⁻¹)</td>
<td>32.8</td>
<td>13.0</td>
<td>16.9</td>
<td>21.1</td>
<td>25.6</td>
<td>29.9</td>
<td>34.0</td>
</tr>
<tr>
<td>(1)</td>
<td>(25.0-40.4)</td>
<td>(11.9-14.7)</td>
<td>(15.3-19)</td>
<td>(18.5-23.3)</td>
<td>(24.4-28.2)</td>
<td>(28.2-31.6)</td>
<td>(32.9-35.5)</td>
</tr>
<tr>
<td>red maple basal area (m²ha⁻¹)</td>
<td>25.6</td>
<td>9.5</td>
<td>13.8</td>
<td>17.3</td>
<td>21.0</td>
<td>25.3</td>
<td>28.6</td>
</tr>
<tr>
<td>(14.7-34.2)</td>
<td>(7.3-11.8)</td>
<td>(6.5-16.5)</td>
<td>(13.2-21.8)</td>
<td>(14.1-26.1)</td>
<td>(16.4-31.3)</td>
<td>(26.3-32.9)</td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>76</td>
<td>51</td>
<td>61</td>
<td>71</td>
<td>76</td>
<td>74</td>
<td>81</td>
</tr>
<tr>
<td>(45-101)</td>
<td>(33-66)</td>
<td>(33-74)</td>
<td>(45-101)</td>
<td>(58-101)</td>
<td>(60-93)</td>
<td>(64-93)</td>
<td></td>
</tr>
<tr>
<td>no. of trees per hectare</td>
<td>808</td>
<td>676</td>
<td>538</td>
<td>546</td>
<td>577</td>
<td>643</td>
<td>630</td>
</tr>
<tr>
<td>red maple proportion of basal area</td>
<td>0.78</td>
<td>0.74</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>0.85</td>
<td>0.84</td>
</tr>
<tr>
<td>(0.58-0.97)</td>
<td>(0.49-0.95)</td>
<td>(0.39-0.99)</td>
<td>(0.60-1.00)</td>
<td>(0.54-1.00)</td>
<td>(0.55-0.99)</td>
<td>(0.76-0.97)</td>
<td></td>
</tr>
<tr>
<td>quadratic mean diameter (cm)</td>
<td>23.2</td>
<td>15.8</td>
<td>21.2</td>
<td>23.4</td>
<td>25.0</td>
<td>25.1</td>
<td>26.5</td>
</tr>
<tr>
<td>(17.2-27.0)</td>
<td>(14.4-16.8)</td>
<td>(14.3-29.6)</td>
<td>(16.1-32.7)</td>
<td>(17.7-37.4)</td>
<td>(18.8-31.4)</td>
<td>(22.9-29.2)</td>
<td></td>
</tr>
<tr>
<td>relative density (proportion of max.)</td>
<td>0.65</td>
<td>0.31</td>
<td>0.36</td>
<td>0.43</td>
<td>0.51</td>
<td>0.58</td>
<td>0.65</td>
</tr>
<tr>
<td>(0.57-0.81)</td>
<td>(0.29-0.35)</td>
<td>(0.29-0.47)</td>
<td>(0.33-0.53)</td>
<td>(0.41-0.61)</td>
<td>(0.51-0.65)</td>
<td>(0.62-0.70)</td>
<td></td>
</tr>
<tr>
<td>stand density</td>
<td>665</td>
<td>313</td>
<td>364</td>
<td>436</td>
<td>514</td>
<td>596</td>
<td>660</td>
</tr>
</tbody>
</table>

1) N represents the number of plots.
<table>
<thead>
<tr>
<th>index</th>
<th>(574-845)</th>
<th>(292-365)</th>
<th>(300-462)</th>
<th>(335-524)</th>
<th>(420-596)</th>
<th>(528-651)</th>
<th>(627-699)</th>
</tr>
</thead>
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<tr>
<td>basal area</td>
<td>1</td>
<td>0.49</td>
<td>0.55</td>
<td>0.64</td>
<td>0.71</td>
<td>0.81</td>
<td>0.86</td>
</tr>
<tr>
<td>thinning ratio†</td>
<td>(1-1)</td>
<td>(0.40-0.64)</td>
<td>(0.41-0.96)</td>
<td>(0.43-0.88)</td>
<td>(0.54-0.9)</td>
<td>(0.64-0.98)</td>
<td>(0.74-0.95)</td>
</tr>
</tbody>
</table>

* Residual basal area (column headings) was the target basal area (not the true value) for the thinning in 1982, while basal area in 1985 is the measured total basal area for all live trees ≥10 cm (including ingrowth) measured at that time.

† Ratio of stand total basal area after the 1982 thinning harvests to stand total basal area before the thinning (i.e., the proportion of basal area retained).
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 data from additional sources (McKenney et al., 2011), and averaged across years corresponding to the respective growth intervals at each site.

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

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

† For a growing season of length $n$ days, each with minimum ($T_{min}$) and maximum ($T_{max}$) temperature, growing degree days $= \sum_{i=1}^{n} \frac{T_{max_i} + T_{min_i}}{2} - 5$. 
Table 4. Restricted maximum likelihood estimates of $\beta_0$ through $\beta_8$ from the red maple basal area projection model*.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Base model</th>
<th>Base + Climate</th>
</tr>
</thead>
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<tr>
<td></td>
<td>Estimate</td>
<td>Estimated SE</td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>0.367399</td>
<td>0.0301506</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>0.881288</td>
<td>0.0072075</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>-0.026293</td>
<td>0.0032446</td>
</tr>
<tr>
<td>$\beta_3$</td>
<td>-3.967345</td>
<td>1.1930352</td>
</tr>
<tr>
<td>$\beta_4$</td>
<td>0.124815</td>
<td>0.0157777</td>
</tr>
<tr>
<td>$\beta_5$</td>
<td>-0.001557</td>
<td>0.0004291</td>
</tr>
<tr>
<td>$\beta_6$</td>
<td>2.694513</td>
<td>0.2662529</td>
</tr>
<tr>
<td>$\beta_7$</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>$\beta_8$</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

Index of fit† 0.959  0.960
MSE‡ 1.024  1.003

*\(\ln rm2_{ij} = \beta_0 + \beta_1 \ln rm1_{ij} + (\beta_2 + b_i) dt_i + \beta_3 \text{inv.age1}_{ij} + \beta_4 \text{pctrm}_{ij} + \beta_5 d_{qij} + \beta_6 d_{tij} \times \text{inv.age1}_{ij} + \beta_7 \text{precip3}_{ij} + \beta_8 \ln rm1_{ij} \times \text{precip3}_{ij} + \varepsilon_{ij}\)

†Index of fit = \(1 - \sum \frac{(\ln rm2_i - \ln rm2_j)}{(\ln rm2_i - \ln rm2_j)}\), calculated using bias-corrected, back-transformed residuals based on the fixed effects in the mixed effects model.

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

Table 5. Model selection statistics for comparing the final base and climate models for red maple basal area projection fit using maximum likelihood.

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>AIC</th>
<th>BIC</th>
<th>logLik</th>
<th>L.Ratio</th>
<th>p-value</th>
</tr>
</thead>
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<tr>
<td>Climate</td>
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<td>64</td>
<td>-1807.37</td>
<td>-1544.095</td>
<td>967.6853</td>
<td></td>
</tr>
<tr>
<td>Base</td>
<td>2</td>
<td>63</td>
<td>-1796.78</td>
<td>-1537.618</td>
<td>961.3900</td>
<td>12.59055</td>
</tr>
</tbody>
</table>
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 and (c) total stand and (d) red maple periodic annual basal area increment, by 1982 target residual stocking level, for trees greater than 10 cm dbh in upper Lake States red maple forests. 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.

Figure 4. (a) The influence of initial stand age on projected 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, $pctrm = 0.81$). (b) The influence of the interval length ($dt$) random slope parameter, where all variables took the values as in (a) and age = 77 years.

Figure 5. The influence of mean growing season precipitation on projected red maple basal area based on equation 2. 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).
Figures

Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
### Appendix

**Table A1. Distribution of plots across initial basal area conditions for each target residual basal area.**

<table>
<thead>
<tr>
<th>Initial basal area (m²ha⁻¹)</th>
<th>Control</th>
<th>9.2</th>
<th>13.8</th>
<th>18.4</th>
<th>23.0</th>
<th>27.6</th>
<th>32.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;20</td>
<td>---</td>
<td>2</td>
<td>2</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>20-25</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>6</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>25-30</td>
<td>2</td>
<td>---</td>
<td>8</td>
<td>12</td>
<td>10</td>
<td>2</td>
<td>---</td>
</tr>
<tr>
<td>30-35</td>
<td>5</td>
<td>---</td>
<td>6</td>
<td>9</td>
<td>11</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>35-40</td>
<td>2</td>
<td>---</td>
<td>---</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>&gt;40</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
Table A2. List of independent variables that were evaluated for inclusion in red maple basal area projection modeling.

<table>
<thead>
<tr>
<th>Stand and site characteristics:</th>
</tr>
</thead>
<tbody>
<tr>
<td>• red maple basal area at the start of the growth interval</td>
</tr>
<tr>
<td>• red maple proportion of stand basal area</td>
</tr>
<tr>
<td>• stand age at the start of the growth interval</td>
</tr>
<tr>
<td>• growth interval length</td>
</tr>
<tr>
<td>• basal area thinning ratio (the ratio of basal area after the thinning)</td>
</tr>
<tr>
<td>• site index</td>
</tr>
<tr>
<td>• relative density</td>
</tr>
<tr>
<td>• quadratic mean diameter (QMD)</td>
</tr>
<tr>
<td>• stand density index</td>
</tr>
<tr>
<td>• trees per hectare</td>
</tr>
<tr>
<td>• initial basal area (1980)</td>
</tr>
<tr>
<td>• time since thinning</td>
</tr>
<tr>
<td>• age at time of thinning</td>
</tr>
<tr>
<td>• quadratic mean diameter of removed trees</td>
</tr>
<tr>
<td>• QMD of the stand before the thinning</td>
</tr>
<tr>
<td>• ratio of QMD of cut trees to QMD of the stand before the thinning</td>
</tr>
<tr>
<td>• difference in relative density before and after thinning (1980-1982)</td>
</tr>
<tr>
<td>• ratio of number of trees cut to the number present before thinning</td>
</tr>
<tr>
<td>• pretreatment mean annual basal area increment</td>
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</table>

<table>
<thead>
<tr>
<th>Climatic variables:</th>
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<tbody>
<tr>
<td>• growing season length</td>
</tr>
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<td>• growing season degree days</td>
</tr>
<tr>
<td>• Julian day of the start of the growing season</td>
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<tr>
<td>• annual precipitation</td>
</tr>
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<td>• precipitation during the three months preceding the growing season</td>
</tr>
<tr>
<td>• precipitation during the growing season</td>
</tr>
<tr>
<td>• mean temperature during the growing season</td>
</tr>
<tr>
<td>• mean temperature during the wettest three month period</td>
</tr>
<tr>
<td>• mean temperature during the driest three month period</td>
</tr>
<tr>
<td>• maximum temperature of the warmest period (the highest temperature of any monthly maximum temperature)</td>
</tr>
<tr>
<td>• latitude</td>
</tr>
<tr>
<td>• longitude</td>
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</table>

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Table A3. 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.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>Base Model</th>
<th>Climate Model</th>
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