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ARTICLE

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

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Abstract: Red maple (*Acer rubrum* L.), historically a common but not abundant tree species in North America, has increased in abundance throughout its range over the last several decades; however, it has received little attention in growth and yield studies. The objectives of this study were to (*i*) evaluate the effects of stocking level and stand density on overall patterns of red maple stand productivity and (*ii*) 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 the mean squared error 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.

Key words: Acer rubrum, basal area growth, climate, Great Lakes region.

Résumé : Historiquement l'érable rouge (*Acer rubrum* L.) était une espèce d'arbre commune mais peu abondante en Amérique du Nord. Malgré que son abondance ait augmenté partout dans son aire de distribution au cours des dernières décennies, cette espèce a suscité peu d'intérêt dans les études de croissance et de rendement. Les objectifs de cette étude étaient (*i*) d'évaluer les effets de la surface terrière et de la densité des peuplements sur la trajectoire de productivité des peuplements d'érable rouge et (*ii*) de quantifier ces relations pour une vaste gamme d'âge de peuplement, de qualité de station, de situation géographique et de conditions climatiques. Nous avons utilisé des mesures à long terme provenant de 52 stations au Wisconsin et au Michigan pour étudier la réaction de croissance de peuplements équiennes d'érable rouge soumis à différentes intensités d'éclaircie. À l'aide d'un modèle linéaire à effets mixtes, la future surface terrière de l'érable rouge à l'échelle du peuplement a été modélisée en fonction de caractéristiques des peuplements et des parcelles, ainsi que des variables climatiques. Les précipitations pendant la saison de croissance et leur interaction avec la surface terrière initiale de l'érable rouge étaient des variables prédictives significatives. Cependant, ces variables ont collectivement diminué l'erreur quadratique moyenne de seulement 2,1 % comparativement à un modèle de base ne contenant que des variables propres aux peuplements et aux parcelles. Les projections du modèle indiquaient que la future surface terrière qui a été prédite variait peu en fonction de la gamme de conditions climatiques observées dans ces peuplements, ce qui met en évidence la grande tolérance de l'érable rouge aux conditions environnementales de cette région. [Traduit par la Rédaction]

Mots-clés : Acer rubrum, croissance en surface terrière, climat, région des Grands Lacs.

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). Now it ranks seventh in highest mean importance value 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 diameter at breast height (dbh, 1.37 m) and larger), and in Wisconsin, it accounts for 72 million m^3 of standing wood volume. 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

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and Steiner 2007). During the same period in the northeastern USA, 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 that red maple would respond positively to future climate under both the 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% 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 red maple 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 on either 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 examples, red maple has been combined with other species (e.g., silver maple (*Acer saccharinum* L.)) 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%–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).

Although 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 in 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 that 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 that are widely known to affect tree growth (e.g., stocking, site quality, size, and age), climate data are 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 °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 the 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-drained 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). 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 (*i*) evaluating the effects of stocking level and stand density on overall patterns of stand productivity in terms of basal area development and (*ii*) quantifying these relationships across a wide range of stand age, site quality, geographic locations, and climatic conditions.

Methods

Study area

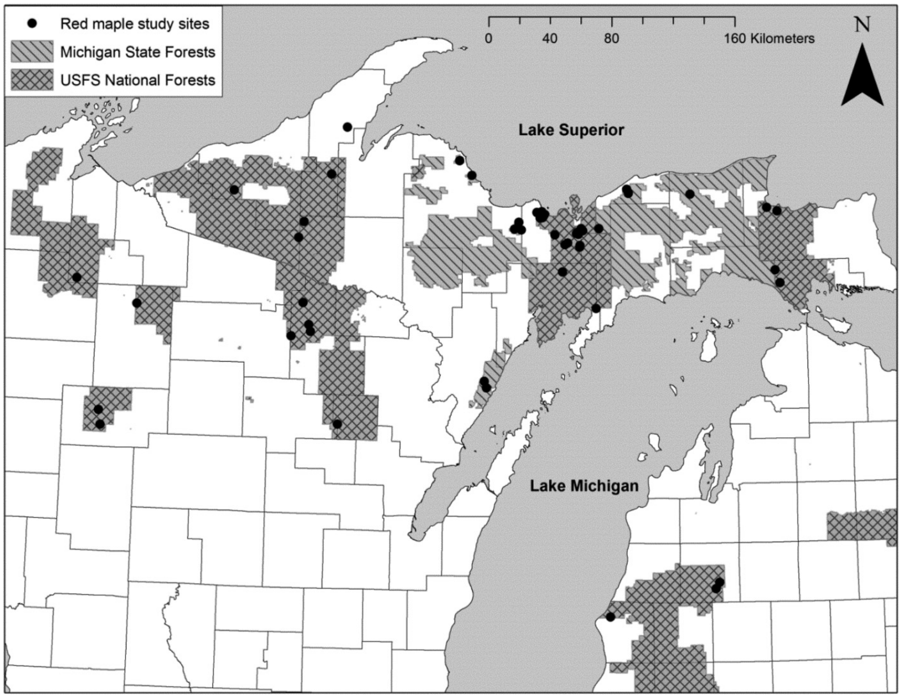
In 1979–1980, 52 study sites were established in even-aged, fully stocked red maple stands located throughout northern Wisconsin and Michigan, USA (Fig. 1), as part of a comprehensive red maple growth and yield modeling effort initiated by the USDA Forest Service North Central Research Station (now called 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 (Fig. 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 mean January minimum temperature ranging from –17 °C to –9 °C and mean 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).

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

Plot layout, treatment, and sampling

Study plots were established in undisturbed, second-growth stands in which at least 75% of the overstory canopy was red maple (Erdmann et al. 1981). All stands were 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

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



total of 122 plots. Each plot was a 2000 m² (31.6 m × 63.2 m) rectangle surrounded by a 10 m 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 1000 m² (31.6 m × 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 nonplot 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, either 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 $m^2 \cdot ha^{-1}$)or a no harvest control with variable basal area was used. In a few cases, strict random assignment was not possible due to low initial basal area. Additionally, because basal areas of 9.2 and 32.2 $m^2 \cdot ha^{-1}$ 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 1 year before or after the nominal year, was used to determine stand ages and growth interval lengths; however, 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. As the exact year of harvest was not known for all sites and postharvest 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 + ingrowth – mortality)·(growth interval length)$^{-1}$; 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 an analysis of variance (ANOVA) 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 + ingrowth for the growth interval)·(growth interval length)$^{-1}$; 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 stand density index 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.

Table 1. Mean initial conditions and range (in parentheses) across 122 red maple dominated study plots (thinned to six levels of residual basal area or not thinned (control)) in northern Wisconsin and northern Michigan in 1980.

	Residual target basal area						
Variable	Control	9.2 $m^2 \cdot ha^{-1}$	13.8 $m^2 \cdot ha^{-1}$	18.4 $m^2 \cdot ha^{-1}$	23.0 $m^2 \cdot ha^{-1}$	27.6 $m^2 \cdot ha^{-1}$	32.1 $m^2 \cdot ha^{-1}$
N (no. of plots)	12	5	22	34	29	15	5
Initial age (years)	70 (40–95)	46 (28–61)	56 (28–68)	65 (40–97)	71 (53–97)	69 (54–88)	76 (59–88)
Site index (m)	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 ($m^2 \cdot ha^{-1}$)	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 ($m^2 \cdot ha^{-1}$)	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 proportion of basal area	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	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)	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	638 (497–832)	466 (365–570)	585 (367–738)	645 (460–835)	684 (537–803)	707 (600–839)	746 (655–903)
Relative density (proportion of maximum)	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)

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. Because red maple, on average, accounted for more than 80% of basal area for all observations on all plots and to focus the analysis on the red maple component, red maple basal area ($m^2 \cdot ha^{-1}$) 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 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 3 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, with a complete list of climate variables in 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 (lnrm1) and growth interval length (dt), additional independent variables and interactions were individually added to the regression, and comparisons of AIC and mean squared error (MSE) 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 $m^2 \cdot ha^{-1}$), which did not differ from the control plots in total basal area. Distinctive stocking conditions persisted for up to 18 years after thinning (Fig. 2*a*). 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 (Fig. 2*b*), with most groups converging by the 29th year following thinning. Total basal area periodic annual increment generally had an inverse relationship with stocking (Fig. 2*c*), as did red maple basal area periodic annual increment (Fig. 2*d*). 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

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

	Residual target basal area						
Variable	Control	9.2 m²·ha⁻¹	13.8 m²·ha⁻¹	18.4 m²·ha⁻¹	23.0 m²·ha⁻¹	27.6 m²·ha⁻¹	32.1 m²·ha⁻¹
N (no. of plots)	12	5	22	34	29	15	5
Basal area (m²·ha⁻¹)	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 (m²·ha⁻¹)	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 (years)	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 proportion of basal area	0.78 (0.58–0.97)	0.74 (0.49–95.1)	0.82 (0.39–0.99)	0.82 (0.60–1.00)	0.82 (0.54–1.00)	0.85 (0.55–0.99)	0.84 (0.76–0.97)
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 (proportion of maximum)	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)

Note: Residual basal area (column heading) was the target basal area (not the true value) for the thinning in 1982, whereas basal area (row heading) in 1985 is the measured total basal area for all live trees ≥ 10 cm (including ingrowth) measured at that time. The basal area thinning ratio is the 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.

	Growth interval			
Variable	1985–1990	1990–1996	1996–2000	2000–2011
No. of plots	122	122	117	108
Annual mean temperature (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 precipitation (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 (mm)	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 temperature during the growing season (°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)

Note: 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. The growing season is defined to start on the first day after 1 March on which the mean daily temperature has been ≥ 5 °C for 5 consecutive days and to end after 1 August 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, the growing degree days $= \sum_{i=1}^{n} \frac{T_{\max_i} + T_{\min_i}}{2} - 5$.

thinned plots and increased with decreasing relative density (Fig. 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

$$(1)\qquad \ln(\mathrm{BA}_2)_{ij} = \beta_0 + \beta_1 \ln(\mathrm{BA}_1)_{ij} + (\beta_2 + b_i)\mathrm{dt}_i + \beta_3 \mathrm{A}_i^{-1} + \beta_4 \mathrm{pctrm}_{ij} + \beta_5 \mathrm{dq}_{ij} + \beta_6 \mathrm{dt}_i \mathrm{A}_i^{-1} + \varepsilon_{ij}$$

where $\ln(\mathrm{BA}_2)_{ij}$ and $\ln(\mathrm{BA}_1)_{ij}$ 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, β_0–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, A_i^{-1} 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 $\varepsilon_{ij} \sim \mathrm{N}(0, \mathbf{R}_{ij})$ and $\mathbf{R}_{ij}$ is the variance–covariance matrix for ε_{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. Inclusion of other density measures e.g., 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 that initial red maple basal area and percent red maple had positive effects on red maple basal area projections, whereas 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 (Fig. 4*b*). For a given set of initial starting conditions, red maple basal area predictions are substantially higher for younger stands.

Refinement of the variance structure during the modeling procedure produced significant improvement for both the base and

Fig. 2. Basal area development for the (*a*) stand total and (*b*) red maple only and the annual basal area increment for the (*c*) stand total and (*d*) red maple only, by 1982 target residual stocking level, for trees greater than 10 cm dbh in red maple forests in the upper Lake States. Error bars are standard errors.

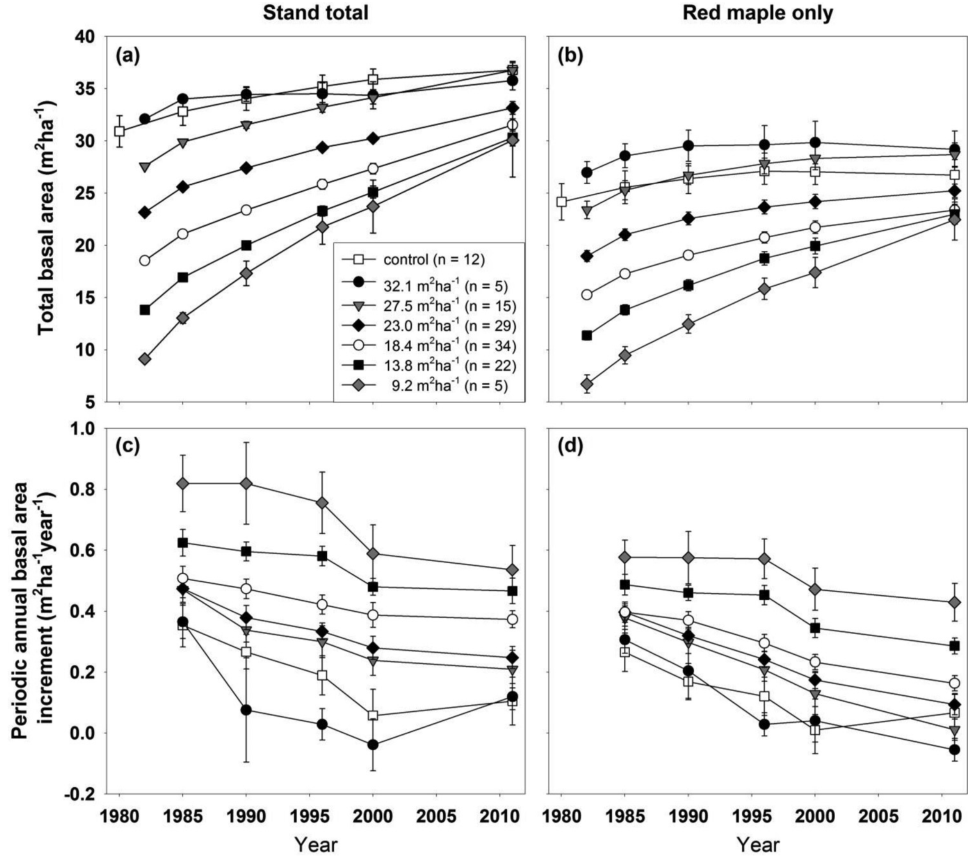


Fig. 3. Basal area production as a function of stand stocking for red maple forests in the upper Lake States.

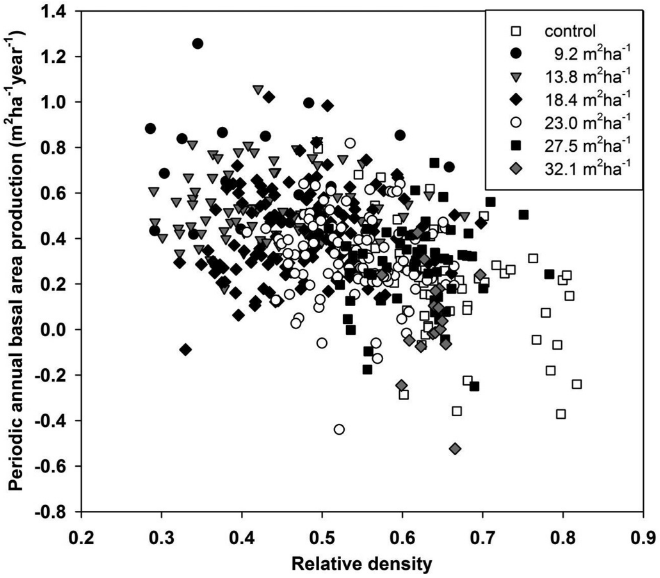


Table 4. Restricted maximum likelihood estimates (SE) of β_1–β_8 from the red maple basal area projection model.

Parameter	Base model	Base + climate model
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*	0.959	0.960
MSE†	1.024	1.003

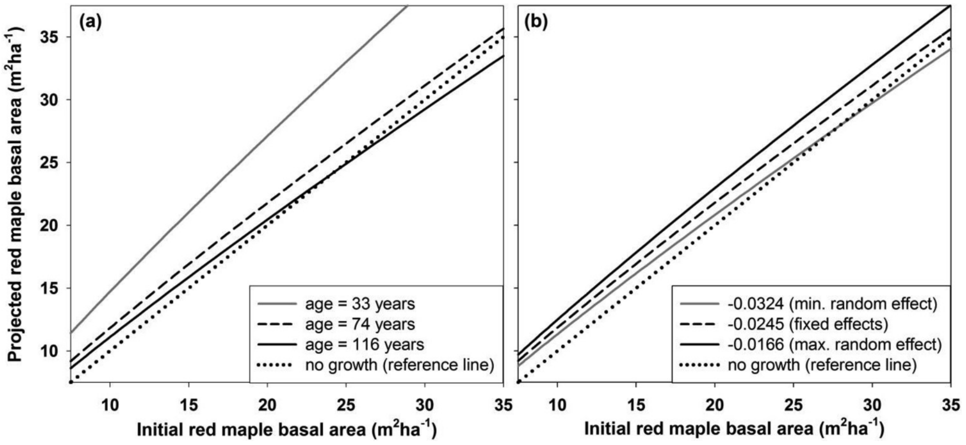
Note: The projection model is as follows: $\mathrm{lnrm2}_{ij} = \beta_0 + \beta_1\mathrm{lnrm1}_{ij} + (\beta_2 + b_i)\mathrm{dt}_i + \beta_3\mathrm{inv.age1}_{ij} + \beta_4\mathrm{pctrm}_{ij} + \beta_5\mathrm{dq}_{ij} + \beta_6\mathrm{dt}_{ij}\mathrm{inv.age1}_{ij} + \beta_7\mathrm{precip3}_{ij} + \beta_8\mathrm{lnrm1}_{ij}\mathrm{precip3}_{ij} + \varepsilon_{ij}$ SE, standard error of the parameter estimate.

*Index of fit $= \left[1 - \sum\frac{(\mathrm{lnrm2}_i - \widehat{\mathrm{lnrm2}_i})}{(\mathrm{lnrm2}_i - \overline{\mathrm{lnrm2}})}\right]$, 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.

climate model performance (Appendix Table A3). 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 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 (Fig. 4*b*). For plots with an initial red maple component greater than 25 m²·ha⁻¹ basal area, the change in red

Fig. 4. (*a*) The influence of initial stand age on projected red maple basal area based on the results of fitting eq. 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 dt random slope parameter, where all variables took the values as in (*a*) and age = 77 years. dt, growth interval length; dq, plot quadratic mean diameter; pctrm, proportion of basal area comprised of red maple.



maple basal area could range from nearly zero to more than 3.0 $m^2 \cdot ha^{-1}$, 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

$$(2)\qquad \ln(BA_2)_{ij} = \beta_1 \ln(BA_1)_{ij} + (\beta_2 + b_i)dt_i + \beta_3 A_i^{-1} + \beta_4 pctrm_{ij} + \beta_5 dq_{ij} + \beta_6 dt_i A_i^{-1} + \beta_7 precip3_i + \beta_8 \ln(BA_1)_{ij}\, precip3_i + \varepsilon_{ij}$$

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.

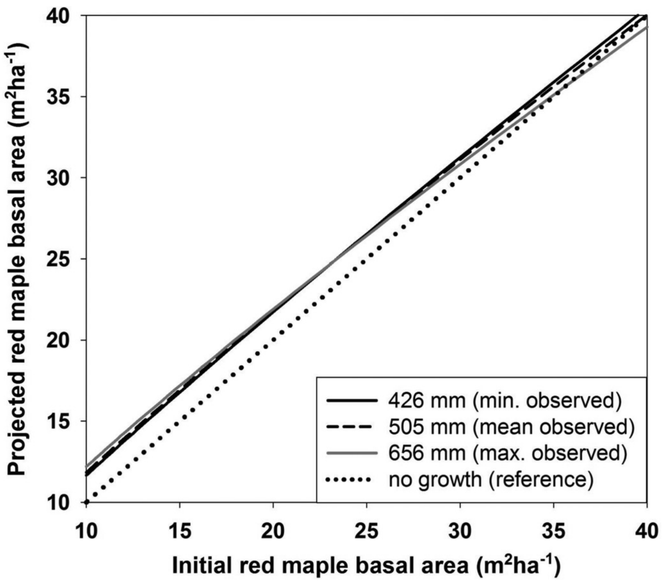
Although the addition of precipitation in the model improved the fit significantly based on an AIC difference of more than 10 (Table 5), the gain was marginal (MSE was reduced by only 2.1%), and local climate had only a minor influence on red maple basal area projections (Fig. 5). The parameter estimates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

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

	Equation	df	AIC	logLik	L.Ratio	*p* value
Climate model	1	64	–1807.37	967.6853	—	—
Base model	2	63	–1796.78	961.3900	12.59055	4×10^{-4}

Note: df, degrees of freedom.

Fig. 5. The influence of mean growing season precipitation on projected red maple basal area based on eq. 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). dt, growth interval length; dq, plot quadratic mean diameter; pctrm, proportion of basal area comprised of red maple.



Discussion

Effects of stand characteristics on growth

The long-term, stand-level red maple basal area development in the second-growth stands that we examined highlights 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 (Fekedulegn et al. 2003), we found only a minor improvement of projections of stand-level basal area when accounting for mean climatic variation (namely precipitation) over a given growth interval. This lack of relationship could reflect the wide ecological amplitude of the species and suggests that 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 interannual 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 Figs. 2*c* and 2*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; however, further analysis would be required to determine if this is linked to climate.

Unlike most growth modeling studies that 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 (Fig. 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 that 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 Nage 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 that 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. Although 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 less than 24.8 $m^2 \cdot ha^{-1}$ but is 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 does 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.

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Appendix A

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

	Target residual basal area						
Initial basal area	Control	9.2 $m^2 \cdot ha^{-1}$	13.8 $m^2 \cdot ha^{-1}$	18.4 $m^2 \cdot ha^{-1}$	23.0 $m^2 \cdot ha^{-1}$	27.6 $m^2 \cdot ha^{-1}$	32.1 $m^2 \cdot ha^{-1}$
<20 $m^2 \cdot ha^{-1}$	—	2	2	—	—	—	—
20–25 $m^2 \cdot ha^{-1}$	2	3	6	6	—	—	—
25–30 $m^2 \cdot ha^{-1}$	2	—	8	12	10	2	—
30–35 $m^2 \cdot ha^{-1}$	5	—	6	9	11	6	1
35–40 $m^2 \cdot ha^{-1}$	2	—	—	6	6	6	3
>40 $m^2 \cdot ha^{-1}$	—	—	—	1	2	1	1

Table A2. List of independent variables that were evaluated for inclusion in red maple basal area projection modeling.

Stand and site characteristics

Red maple basal area at the start of the growth interval
Red maple proportion of stand basal area
Stand age at the start of the growth interval
Growth interval length
Basal area thinning ratio (the ratio of basal area after the thinning to basal area before the thinning)
Site index
Relative density
Quadratic mean diameter (QMD)
Stand density index
Trees per hectare
Initial basal area (1980)
Time since thinning
Age at time of thinning
Quadratic mean diameter of removed trees
QMD of the stand before the thinning
Ratio of QMD of cut trees to QMD of the stand before the thinning
Difference in relative density before and after thinning (1980–1982)
Ratio of number of trees cut to the number present before thinning
Pretreatment mean annual basal area increment

Climatic variables

Growing season length
Precipitation during the growing season
Mean temperature during the growing season
Mean temperature during the wettest three month period
Mean temperature during the driest three month period
Maximum temperature of the warmest period (the highest temperature of any monthly maximum temperature)
Latitude
Longitude

Table A3. Comparison of red maple basal area growth model selection statistics from regressions estimated with the fixed effects in eqs. 1 and 2 using restricted maximum likelihood with different structures for heteroscedasticity, autocorrelation, and hierarchical data.

	Base model			Climate model		
Model structure	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

Note: Comparisons of models with different fixed effects (i.e., between Base model and Climate model columns) fit using restricted maximum are not useful. See Table 5 for a comparison of the final Base and "Climate" models fit using maximum likelihood.