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Tree-level growth and survival following commercial thinning of four major softwood species in North America

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ABSTRACT

Thinning is commonly applied to increase the tree growth in forest stands by improving the availability of water, light, and nutrients. However, thinning also can increase soil evaporation and intensify wind penetration into residual stands, potentially increasing moisture stress and wind damage. To strengthen our understanding of tree-level responses to thinning, we used long-term measurements from three controlled, replicated thinning experiments for four commercially important softwood species in North America, including the shade-intolerant loblolly pine (*Pinus taeda* L.), moderately shade-tolerant Douglas-fir (*Pseudotsuga menziesii* Mirbel), and shade-tolerant red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.). The objectives of this study were to assess the long-term (13–24 years) pattern of individual-tree growth and survival after a variety of commercial thinning treatments. Our results showed that on average tree volume growth was 31% higher in thinned stands relative to unthinned stands irrespective of species and tree size. However, the rate of growth decreased over time following thinning for loblolly pine and Douglas-fir, while a curvilinear relationship was observed for red spruce and balsam fir. Tree size was important only for loblolly pine where growth increased linearly with the size of residual trees. Tree survival was also higher in thinned stands than unthinned stands across all species in the long-term, but a significant initial decrease in survival was found in balsam fir and red spruce immediately after thinning due primarily to windthrow and breakage. Stand relative age and total basal area at time of thinning were negatively related with growth for all tree species, which may indicate that the trees examined in this study had reached their maximum growth potential or had a period of suppression prior to thinning. The relatively minor influence (i.e., 5% of total R^2) of thinning intensity on growth may suggest that the timing of thinning (i.e., age of trees when thinned) and stand characteristics (species, tree age, and stand basal area) were more important in promoting individual-tree growth. However, a heavier intensity of thinning increased survival of loblolly pine and Douglas-fir trees. Overall, our results indicated that thinning can increase tree growth and survival across species of varying shade tolerance. To ensure the maximum benefits of thinning, the timing and intensity of the treatment needs to be adjusted for species characteristics, stand structure, and tree age.

1. Introduction

Commercial thinning is often applied as an effective means to extract timber in the short-term by selecting stems approaching imminent natural mortality. The long-term goal is generally to increase the growth of residual trees following thinning by decreasing the competition for available environmental resources (primarily light, nutrients, and water) (Kostler, 1956; Zeide, 2001). Despite its widespread use, results from thinning experiments have reported a wide range of outcomes, including increased mortality (e.g., Ruel et al., 2001; Ahnlund Ulvcrona et al., 2011; Kuehne et al., 2016) and growth stagnation of residual trees after thinning (Lagergren et al., 2008). However, the ultimate response to thinning is usually difficult to generalize because the growth and mortality of individual trees can vary substantially depending on the pre- and postthinning characteristics of the stand (i.e., stand age, density, and size distributions), site characteristics (i.e.,

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climate and soil), and thinning methods (Bose et al., 2014b; Giuggiola et al., 2015).

The post-thinning growth of an individual tree depends primarily on the neighborhood conditions created by the thinning operation (Scott and Mitchell, 2005; Canham et al., 2006). Neighborhood condition, tree age, size, and growth rate immediately prior to harvest have been shown to influence growth responses after thinning (Thorpe et al., 2007; Anning and McCarthy, 2013). These variables determine the ability of an individual tree to respond to reduced competition and greater availability of resources (Canham et al., 2004; Weiskittel et al., 2011). The position of the tree in the canopy prior to and after thinning is also crucial to understanding the mechanisms of competition after thinning (Anning and McCarthy, 2013; Bose et al., 2014a). Following release from competition, trees generally display an increased growth rate; however, the magnitude of responses may vary with tree size and light-use efficiency (Jones et al., 2009). For example, larger individuals may obtain a disproportionate share of resources and suppress the growth of smaller individuals (Berntson and Wayne, 2000). In addition, suppressed growth prior to thinning may also affect a tree's ability to respond to thinning, and slow growth rates before thinning have been associated with relatively modest growth increases (Thorpe et al., 2007; Baral et al., 2016).

Mortality of residual trees is another major concern of commercial thinning (Coates, 1997; Weiskittel et al., 2011). Residual trees can be physically damaged during thinning operations, increased wind penetration into residual stands can cause stem breakage or windthrow, and greater evaporative demand on residual trees can result in increased tree stress (Ruel et al., 2001). Previous studies have reported increased windthrow mortality of residual trees after commercial thinning (Ruel et al., 2001; Kuehne et al., 2016). However, low-intensity thinning primarily associated with the removal of weakened trees may also increase a stand's resistance to windthrow (Ruel et al., 2003; Kuehne et al., 2015).

Despite the prevalence of commercial thinning in North America and in other parts of the world, few studies have simultaneously examined and synthesized post-thinning tree-level growth and survival across multiple species and thinning treatments while also accounting for differences in prethinning stand and site conditions (Moulinier et al., 2015; Boivin-Dompierre et al., 2017). In addition, no study has evaluated the long-term (> 20 years) pattern of growth and survival for individual trees across species of varying shade tolerance to our knowledge. Consequently, a quantitative and comparative analysis of post-thinning growth and survival of commercially important species is fragmented. In this context, the primary objectives of this study were to assess the long-term (13–24 years) pattern of tree-level growth and survival following commercial thinning across stands containing four commercially important softwood species in North America (loblolly pine (*Pinus taeda* L.), Douglas-fir (*Pseudotsuga menziesii* Mirbel), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* L.)).

We addressed the following research questions in the analysis: (i) does tree size matter for growth responses to commercial thinning treatments, and how does that vary among species of varying shade tolerance and time since thinning, (ii) does thinning equally benefit all trees in the residual stand (i.e., variability in annual growth across residual trees) and how does the variability of tree growth change over time since thinning, (iii) which trees are more prone to mortality after thinning and how does that vary among species and time since thinning, and (iv) how are the pattern of tree growth and probability of survival influenced by stand-level and thinning characteristics. Similar to stand-level responses reported by Bose et al. (2018), we hypothesized that tree-level responses for all tree species examined would vary primarily with tree age and stand basal area at the time of thinning.

2. Methods

2.1. Study sites

We considered four softwood species including planted loblolly pine (*Pinus taeda* L.) of southeastern US and Douglas-fir (*Pseudotsuga menziesii* Mirbel) of Pacific Northwest US as well as naturally regenerated red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* L.) of northeastern US. These species are commercially managed across a vast region of the US and Canada. Long-term datasets from three sources were used for this study: (1) Commercial Thinning Research Network (CTRN) for balsam fir and red spruce (Kuehne et al., 2018); (2) Stand Management Cooperative (SMC) for Douglas-fir (Maguire et al., 1991); and (3) Forest Modeling Research Cooperative (FMRC) for loblolly pine (Burkhart et al., 1985). For consistency, any measurement plot that had received prior treatments including precommercial thinning, pruning, fertilizer application, or herbicide spray was excluded from the analysis including 6.5%, 57.1%, and 32.9% of total number of plots from FMRC, CTRN, and SMC, respectively.

In the CTRN, seven treatments were applied and replicated in seven naturally regenerated sites across northern Maine. In addition to an unthinned control, thinning treatments included a factorial combination of thinning method (low, dominant, or crown) and intensities. The thinning treatments were assessed by the level of relative density (ratio of stand density index (SDI) and maximum SDI) reduction (33 or 50%). The low and dominant thinning treatments were defined as the removal of trees beginning at the lower or upper end of the diameter distribution, respectively, until the target reduction in relative density was achieved. In the crown thinning treatment, crop trees were selected at approximately one third average tree height apart, and then, dominant and codominant competitors around each crop tree were harvested until desired residual density was reached. The CTRN sites had not been subjected to any silvicultural treatments prior to the commercial thinning experiment. All sites were dominated by red spruce and balsam fir (> 92% of total stand volume). Measurement plots (n = 60) were 0.08 ha in size with a forwarder trail running through the plot center and in alignment with the plot's width (except the control treatment). These measurement plots were established in the center of each of the 0.37 ha treatment units. Following the treatment applications, diameter at breast height (DBH) of all live trees as well as newly established trees taller than 1.3 m were measured on an annual basis up to 13 years after establishment (Kuehne et al., 2016).

In the SMC, commercial thinning treatments were applied in three different types of installations. In the context of the present study, 190 measurement plots from 39 sites located along the coast of Pacific Northwest of US and Canada were used. For consistency, sites that received any thinning (commercial or precommercial) before 20 years of age (i.e., age of operational commercial thinning across Pacific Northwest for Douglas-fir) were excluded. These sites belong to three different types of experimental installation: (i) Type-I installations were established between 1986 and 1991 amongst a 1970s cohort of plantations when they were 7- to 15-years old. In these installations, seven measurement plots were established at each site as a common core that received predefined thinning treatments following Curtis' relative density (Curtis, 1982), (ii) Type-II installations were established between 1986 and 1991 in a cohort of 1950s plantations and naturally regenerated stands when they were 20–30 years old. In these installations, five measurement plots were established at each site as a common core that received pre-defined thinning treatments following the Curtis' (1982) relative density, and (iii) Type-III installations were planted in the mid-1980s. These installations received five different thinning treatments including an (i) unthinned control, (ii) thinning early with light intensity, (iii) thinning early with heavy intensity, (iv) thinning late with light intensity, and (v) thinning late with heavy intensity (Maguire et al., 1991). We considered 27, 8, and 4 sites from Type-I, II, and III, respectively. All SMC plots were 0.20 ha in size and measured

Table 1
Regression analyses of tree-level relative volume growth (RVG), Gini coefficient of growth, and probability of tree survival (PS) of four softwood species over time since thinning and various stand-level factors.

Analysis #	Research questions	Response variables	Explanatory variables
1	Effect of time since thinning, tree size and thinning treatments on individual tree-level RVG of four softwood species	Growth of thinned and unthinned stands of the four species	TST, log(TST), TRT, SPP, THP, TRT*TST*SPP, and TRT*THP*SPP
2	Effect of time since thinning and thinning treatments on Gini coefficient of individual tree-level RVG of four softwood species	Gini coefficient of growth of thinned and unthinned stands of the four species	TST, log(TST), TRT, SPP, and TRT*TST*SPP,
3	Effect of stand level factors on individual tree-level RVG of four softwood species	Growth of thinned stands	SPP, BA, BAR, RA, RSI, BA*SPP, BAR*SPP, RA*SPP, RSI*SPP, BA*BAR, BAR*RA
4	Effect of time since thinning, tree size and thinning treatments on individual tree-level PS of four softwood species	Survival of thinned and unthinned stands of the four species	TST, TRT, SPP, THP, TRT*SPP, TRT*THP, THP*SPP, and TRT*TST*SPP
5	Effect of stand level factors on individual tree-level PS of four softwood species	Survival of thinned stands	SPP, BA, BAR, RA, RSI, BA*SPP, BAR*SPP, RA*SPP, RSI*SPP, BA*BAR, BAR*RA

Note: TST = time since thinning or not thinning for unthinned stands (year), log(TST) = log transformed TST, TST^2 = squared TST, TRT = thinning treatments (two levels: unthinned and thinned), SPP = species (four levels: loblolly pine, Douglas-fir, red spruce and balsam fir), THP = tree height based percentile rank, BAR = basal area removal by harvesting (% of total), RSI = relative site index (ratio of plot site index to mean site index, calculated separately for each softwood forest type), BA = stand basal area at thinning ($m^2\ ha^{-1}$), and RA = relative age (ratio between stand age at thinning and age to reach maximum PAI (periodic annual increment), calculated separately for three forest types (the age to reach maximum PAI for loblolly pine, Douglas-fir, and red spruce-balsam fir were 15, 35, and 65 years, respectively)). The interaction terms among variables were indicated by a * (e.g., SPP*BA). Model selection or model comparison by AIC were used for the analysis 3 and 5.

every four years as well as before and after any treatment up to 24 years after establishment.

In the FMRC, measurement plots were established in the dormant seasons of 1980–81 and 1981–82 at 186 locations of plantations throughout the native range of loblolly pine across the southeastern US. Each plantation was at least eight years of age, had not been subject to any silvicultural treatments other than site preparation before plots were installed, free of evidence of heavy disease or insect attack, and contained from around 740 to 1730 planted pine stems per ha prior to thinning. At each location, three plots were established including an unthinned control, a lightly thinned from below (14.8–53.5% of total basal area removal), and a heavily thinned from below plot (22.3–60.6% of total basal area removal). Pretreatment site index, basal area, and stem density of plots at each location were required to be similar in order to minimize the plot-to-plot variation at time of treatment. The plots were randomly assigned to the three treatment categories and thinning treatments were applied at time of plot establishment. Plots were remeasured at three-year intervals through 21 years after establishment. A minimum buffer of at least two rows or 6 m was established around each plot, shielding it from all roads, windthrows, or other stand openings. The control plots were generally 0.04 ha in size, while the thinned plots ranged from 0.08 to 0.10 ha (Burkhart et al., 1985).

2.2. Response variables

Tree volume was estimated using the available allometric taper and volume equations. Total tree-level volume of red spruce and balsam fir were estimated by using the taper equations of Li et al. (2012), while for Douglas-fir and loblolly pine trees were estimated by using the equations of Hann (2011) and Tasissa et al. (1997), respectively. The required height and height to crown base of all trees, which were partly missing in the datasets for Douglas-fir, balsam fir, and red spruce, were estimated from species-specific DBH-height relationships determined from the data, while considering the associated plot within site-specific random effects using the nonlinear mixed effect modelling approach described by Kuehne et al. (2016). Covariates besides DBH considered in these modeling approaches included basal area, basal area in larger trees, and site index.

Tree growth was defined by the periodic relative volume growth between two successive measurement periods by an individual tree, and was quantified using the following equation:

$$Growth = \frac{Stem\ volume\ at\ measurement\ period_j - Stem\ volume\ at\ measurement\ period_i}{Stem\ volume\ at\ measurement\ period_i} \tag{1}$$

where i = measurement 1 … n − 1, and j = measurement i + 1…n.

This variable was chosen to better assess the relative differences between the various species and treatments being examined as well as measure the dynamics following thinning. For consistency, the growth was annualized for the three experiments by dividing the observed periodic growth by the measurement interval. Although this can result in biased predictions, all measurements were relatively consistent and short (≤4 years) so the effect on the findings was likely minimal. Probability of tree survival was quantified as a binary variable (1 if alive, 0 otherwise). For consistency, we use 'growth' and 'survival' instead of 'relative volume growth' and 'probability of survival', respectively, throughout the manuscript.

2.3. Data analysis and explanatory variables

For the first analysis (i.e., effect of tree size on growth response as influenced by time since thinning and species shade tolerance), growth was modelled as a function of time since thinning, log transformed time since thinning, thinning treatment (two levels: thinned and unthinned), species (four levels: loblolly pine, Douglas-fir, red spruce, and balsam fir), tree height based percentile rank (increasing ranks indicating decreasing tree size relative to maximum height per plot), and interactions among those predictor variables (see details in Table 1). The shade intolerant loblolly pine was considered as a reference level in the regression analysis, and tested with other species. The posttreatment (thinned or unthinned) observation length (number of years of inventory measurement since the treatment establishment) varied across the three experiments (FMRC, SMC, and CTRN), which were 13, 21, and 24, years for CTRN, FMRC, and SMC, respectively.

For the second analysis (i.e., change of growth response variability over time), the growth variability was quantified in terms of Gini coefficient (Gini, 1921). The Gini coefficient was modeled as a function of time since thinning, log transformed time since thinning, thinning treatment (two levels: thinned and unthinned), species (four levels: loblolly pine, Douglas-fir, red spruce, and balsam fir), and interactions among those predictor variables (see details in Table 1).

For the third analysis (i.e., factors affecting the growth in thinned stands), we considered various stand-level factors including % basal area removal (% of total basal area) by harvesting, stand basal area at thinning ($m^2\ ha^{-1}$), relative age at thinning (years), and relative site index. Due to inherent differences in species potential productivity, we created a relative site index, which was the ratio between the mean site index of an experiment (three experiments: FMRC (loblolly pine), SMC (Douglas-fir), and CTRN (red spruce and balsam fir) and the site index of a specific plot. Site index was estimated using the available density management diagram for CTRN sites (Wilson et al., 1999) and available site index equation for the SMC sites (Flewelling et al., 2001), while mean dominant height of the 10 tallest trees per plot at the age of 20 years was used for FMRC sites. The relative age was quantified separately for each experiment and was defined as a ratio between the observed stand age and the age of maximum periodic annual increment (PAI) for that particular species. We considered 15, 35, and 65 years for loblolly pine, Douglas-fir, and red spruce-balsam fir, respectively as the age of maximum PAI (Meyer, 1929; Curtis et al., 1981; Borders et al., 1990). For this research question, we formed a list of candidate models (Table S.1 of Supplementary material) based on existing biological understanding to interpret the effects of stand-level factors on growth of the four-softwood species (see details in Table 1).

A similar approach was taken for the survival analysis. Survival was first modelled as a function of time since thinning, thinning treatment, species, tree height based percentile rank, and interactions among those predictor variables (see details in Table 1). The shade intolerant loblolly pine was again considered as a reference level to compare with the three other species. Finally, for the fifth analysis (i.e., factors affecting the survival in thinned stands), stand-level factors including % basal area removal by harvesting, stand basal area at thinning (m^2 ha^{-1}), relative age at thinning (years), and relative site index as well as selected interaction terms were considered (see details in Table 1). Formulation of candidate models was based on existing biological knowledge (Table S.2 of Supplementary material).

2.4. Statistical analysis

Effects of explanatory variables on growth and Gini coefficient of growth were assessed by linear mixed-effect models using the function *lme* in the *nlme* package (Pinheiro et al., 2014) in R (R Development Core Team, 2014). Fixed effects of the five analyses are presented in Table 1. Plots nested within sites, and sites nested within region (northeast, Pacific Northwest, and southeast) were treated as random effects. In addition, the random effects associated with repeated measurements were plots nested within measurement periods, measurement periods nested within sites, and sites nested within region were also incorporated into the model. The random effects structure of the final model was based on preliminary analyses, which compared models with different structures of random effects by Akaike weights (AICc) and residual plots. The Gini coefficient was quantified by using the function *gini* of the R package *ineq* (Zeileis et al., 2009).

A similar approach was taken for the survival analysis, except the modeling approach was nonlinear. A logistic function of the following form was used to model the probability of individual tree survival:

$$PS = (1 + exp(-(X\beta)))^{\frac{1}{YIP}} \tag{2}$$

where **Xβ** is the model-specific explanatory variable design matrix (see Table 1) with the associated estimated parameters and YIP is years in period to account for the varying inventory cycles across the studied experiments. Models were derived and evaluated using the function *nlme* of the *nlme* package.

Candidate models (Tables S.1 and S.2 of Supplementary material) were compared by the AICc, and the model average estimates were used for prediction (Burnham and Anderson, 2002; Mazerolle, 2006). Model comparisons were performed using the AICcmodavg package in R (Mazerolle, 2011). We visually verified the assumptions of normality and variance homogeneity of the residuals. We also tested for potential multicollinearity among explanatory variables of a model using the variance inflation factor (VIF), which was quantified using the *vif* function of package *car* in R. The R^2 for fixed and random effects and for fixed effects only were calculated using the function *r.squaredGLMM* of *MuMIn* package in R (Bartoń, 2013). For the models of *survival*, a receiver operator curve (ROC) was constructed and area under the curve (AUC) computed (Hein and Weiskittel, 2010) using the R package *pROC* (Robin et al., 2011).

Finally, the relative importance of predictor variables for growth were quantified by decomposing the total variance explained (R^2) in a multiple linear regression by averaging sequential sum of squares over all orderings of the predictor variables. This analysis was implemented using the '*relaimpo*' package in R (Gromping, 2006). This analysis overcomes the usual problem of correlation among predictor variables, and thus has advantage over the use of R^2 from univariate regressions (Gromping, 2006).

3. Results

Overall, tree growth was higher for loblolly pine and Douglas-fir than for balsam fir and red spruce. Tree growth was also higher in thinned stands than unthinned stands among the four tree species. Relative to unthinned stands, the number of dead trees was higher in thinned stands for red spruce and balsam fir, but lower in thinned stands for Douglas-fir and loblolly pine. The relative dead tree density (relative to total number of trees) was less than 5% across species and thinned and unthinned stands, except unthinned stands of loblolly pine (Table 2).

3.1. Growth response

Tree growth was significantly higher in thinned stands relative to unthinned stands irrespective of species and tree size. However, this was negatively correlated with time since thinning for loblolly pine and Douglas-fir, while the relationship was curvilinear for red spruce and balsam fir. The growth decreased during the first five years after thinning for red spruce and balsam fir, but increased during five to thirteen years since thinning (Fig. 1A). Tree size was important only for loblolly pine where growth increased linearly with increasing size of residual trees, which was true for both thinned and unthinned treatments (Fig. 1B). Shade intolerant loblolly pine and moderately shade tolerant Douglas-fir had higher growth than shade tolerant red spruce and balsam fir irrespective of the thinning treatment (Fig. 1).

Trees in unthinned stands for all species had greater variability (Gini coefficient) in growth than trees in thinned stands. However, trees of red spruce and balsam fir had higher variability than trees of loblolly pine and Douglas-fir. The variability decreased over time since thinning for red spruce and balsam fir, but increased for loblolly pine and Douglas-fir (Fig. 2).

The most complex model, which included all explanatory variables considered in the analysis, had the greatest support of AICc weight (Table S.1 of Supplementary material). Stand age and total basal area at the time when stands were thinned had strong negative relationships with growth irrespective of species (Fig. 3A and C). Tree growth responses to thinning intensity and site index were dependent on species (i.e., interaction was significant). For example, thinning intensity had no significant effect on growth of Douglas-fir and balsam fir, but had negative effects on growth of red spruce and loblolly pine (Fig. 3E). Relative site index was negatively correlated with growth of balsam fir, but positively correlated with growth of the other three species (Fig. 3G).

The relative contribution to the model R^2 indicated that stand basal area at thinning and species were the most influential predictor variables for tree growth, and that the magnitude of importance remained stable with increasing time since thinning. The effect of thinning intensity on tree growth decreased in importance with time since thinning (Fig. 4).

Table 2
Descriptive statistics of response and predictor variables of thinned and unthinned treatments across the four softwood species.

Species		Relative volume growth (RVG)	Gini coefficient of RVG	Absolute dead tree density (stems ha^{-1})*	Relative dead tree density (relative to total)*	Stand basal area at thinning (m^2 ha^{-1})*	Basal area removal (% of total)*	Relative age at thinning*	Relative site index at thinning*
Douglas-fir									
Unthinned	Mean ± 1 SD	0.08 ± 0.05	0.19 ± 0.07	40.9 ± 50.8	4.3 ± 4.3	25.8 ± 9.5	0	0.7 ± 0.1	1.0 ± 0.1
	Range	0.94, −1.00	0.52, 0.06	326.2, 0.0	21.9, 0.0	44.1, 5.8	0, 0	1.1, 0.6	1.2, 0.7
Thinned	Mean ± 1 SD	0.10 ± 0.08	0.19 ± 0.08	9.9 ± 17.5	1.6 ± 2.6	22.9 ± 5.2	38.4 ± 10.4	0.7 ± 0.2	1.0 ± 0.1
	Range	2.45, −0.65	0.51, 0.09	118.6, 0.0	19.7, 0.0	32.1, 4.9	75.4, 5.3	1.5, 0.6	1.2, 0.7
Loblolly pine									
Unthinned	Mean ± 1 SD	0.08 ± 0.08	0.28 ± 0.07	96.4 ± 100.3	7.8 ± 8.1	25.9 ± 8.7	0	1.0 ± 0.3	1.0 ± 0.1
	Range	0.95, −0.21	0.53, 0.08	1210.8, 0.0	84.5, 0.0	53.9, 5.6	0, 0	1.5, 0.5	1.5, 0.7
Thinned	Mean ± 1 SD	0.11 ± 0.09	0.21 ± 0.07	17.7 ± 43.1	2.4 ± 5.3	16.3 ± 6.0	35.0 ± 10.2	1.0 ± 0.3	1.0 ± 0.1
	Range	1.37, −0.16	0.49, 0.07	867.6, 0.0	86.5, 0.0	36.7, 3.5	77.5, 15.2	1.5, 0.5	1.5, 0.7
Red spruce									
Unthinned	Mean ± 1 SD	0.02 ± 0.06	0.60 ± 0.13	108.7 ± 158.3	2.6 ± 3.0	42.6 ± 6.7	0	0.6 ± 0.2	0.9 ± 0.2
	Range	2.58, −0.53	0.86, 0.29	765.3, 0.0	12.7, 0.0	53.9, 31.9	0, 0	1.1, 0.5	1.2, 0.7
Thinned	Mean ± 1 SD	0.03 ± 0.05	0.47 ± 0.13	48.6 ± 94.3	4.0 ± 6.8	20.4 ± 5.4	54.7 ± 12.9	0.7 ± 0.2	1.1 ± 0.2
	Range	2.77, −0.75	0.83, 0.13	715.9, 0.0	45.2, 0.0	29.8, 8.8	80.6, 23.1	1.1, 0.5	1.2, 0.7
Balsam fir									
Unthinned	Mean ± 1 SD	0.04 ± 0.07	0.58 ± 0.12	108.7 ± 158.3	2.6 ± 3.0	42.6 ± 6.7	0	0.6 ± 0.2	0.9 ± 0.2
	Range	1.58, −0.90	0.92, 0.24	765.3, 0.0	12.7, 0.0	53.9, 31.9	0, 0	1.1, 0.5	1.2, 0.7
Thinned	Mean ± 1 SD	0.06 ± 0.08	0.35 ± 0.18	48.6 ± 94.3	4.0 ± 6.8	20.4 ± 5.4	54.7 ± 12.9	0.7 ± 0.2	1.1 ± 0.2
	Range	2.41, −0.96	0.86, 0.00	715.9, 0.0	45.2, 0.0	29.8, 8.8	80.6, 23.1	1.1, 0.5	1.2, 0.7

Note: Stands have not been received precommercial thinning, pruning, fertilizer, and herbicide spray were considered in the analysis. Relative site index = ratio between the mean site index of a forest type and the site index of a specific plot, relative age = ratio between stand age at thinning and age to reach maximum PAI (periodic annual increment), calculated separately for three forest types (the age to reach maximum PAI for loblolly pine, Douglas-fir, and red spruce-balsam fir were 15, 35, and 65 years, respectively).

* These stand-level attributes are same for balsam-fir and red spruce because they both are from same experiment.

3.2. Probability of tree survival

Tree survival was higher in thinned stands relative to unthinned stands for all species in the long term, but a significant initial decrease in survival was found for balsam fir and red spruce immediately after thinning (Fig. 1C, Table S.3 of Supplementary material). However, survival of thinned balsam fir and red spruce recovered over time and exceeded survival of trees in unthinned stands approximately twelve and eight years after thinning, respectively. We found a strong positive effect of tree size on survival with larger trees having higher survival for all species irrespective of the thinning treatment. This effect was most pronounced in unthinned loblolly pine and Douglas-fir (Fig. 1D).

Thinning intensity was positively correlated with tree survival of thinned loblolly pine and Douglas-fir, though to a lesser extent (Fig. 3F). In contrast, a reverse effect of thinning intensity was observed for balsam fir and red spruce, with survival decreasing with increasing thinning intensity. With the exception of Douglas-fir, tree survival was lower when a relatively older stand was thinned, and the negative effect of stand age at thinning was most pronounced in loblolly pine and balsam fir (Fig. 3B). Higher basal area at the time of thinning was negatively related with tree survival for loblolly pine and Douglas-fir, but positively related with tree survival for balsam fir (Fig. 3D). Site index was not significant (Table S.3 of Supplementary material), and hence the most complex candidate model (which included all explanatory variables such as site index) did not have the highest support of AICc weight (Table S.2 of Supplementary material).

4. Discussion

The results of our synthesis analysis across four commercially important species showed that tree growth can be ~31% higher after commercial thinning irrespective of species, site, and thinning treatment. However, the response of trees to commercial thinning can vary with thinning intensity, time since the last thinning, species' shade tolerance, stand structure, stand age, and site condition. Consequently, the timing of a commercial thinning treatment needs to account for species' shade tolerance in that a stand with shade intolerant species (e.g., loblolly pine) should probably be treated earlier than shade tolerant species (e.g., spruce-fir). Heavy intensity thinning should be used cautiously in order to minimize windthrow induced tree mortality in sites associated with high ground water table and shallow tree root network.

4.1. Effect of time, tree size and thinning treatment on tree growth

Our results indicated that the effect of thinning on tree-level volume growth can vary with time since thinning. The negative trend of growth of loblolly pine and Douglas-fir may indicate that trees of these two species were approaching maturity, and hence their growth (i.e., relative to previous years) was decreasing with time. For example, loblolly pine may reach its maximum growth potential at approximately age ten (Daniels et al., 1986) and may display a negative relationship between age and biomass assimilation from age 14 (Drake et al., 2010). Therefore, although thinning increased the magnitude of annual increment for loblolly pine and Douglas-fir, it did not prolong the age for maximum growth potential relative to trees of unthinned stands. Our results may suggest that to achieve maximum benefit from commercial thinning, the treatments should be applied earlier than the stands examined in this study (i.e., average age of thinning for loblolly pine and Douglas-fir were 15.0 ± 3.8 and 25.6 ± 6.6 years, respectively) (Bose et al., 2018).

Although thinning increased the growth of balsam fir and red spruce relative to unthinned stands, it did not change the pattern of growth over time since thinning. The initial growth decline in thinned and unthinned stands may be due to increased wind exposure during those years (Kuehne et al., 2016). Trees of both balsam fir and red spruce may allocate a large proportion of their carbon in below-ground tissues to increase the mechanical strength against windthrow (Bose et al., 2014b). However, trees of both species recovered from initial decline and maintained a positive growth trend during six to thirteen years

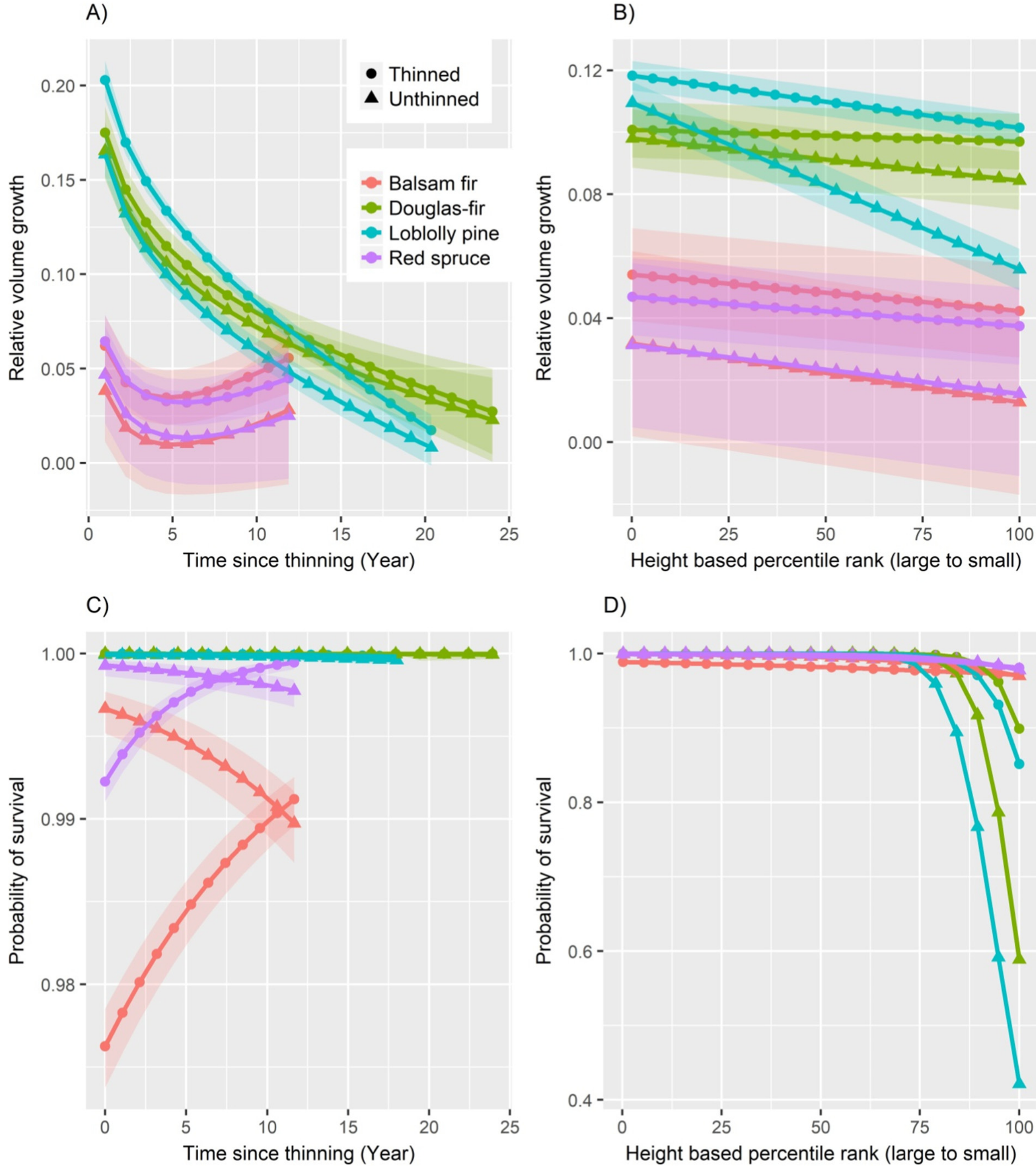

Fig. 1. Predicted tree-level relative volume growth (relative to the previous year) and probability of survival for trees in thinned and unthinned treatments across the four species examined over time since thinning and tree height based percentile rank (increasing ranks indicating decreasing tree size relative to maximum height per plot). Shaded areas represent mean ± 95% confidence interval.

after thinning. This results may due to reduced neighborhood competition from windthrow events, which apparently benefited the residual individuals of both species. In addition, some studies have indicated that shade tolerant species can exhibit a longer-lasting growth response to canopy opening than shade intolerant species (Wiser et al., 2005; Jones et al., 2009). Tree size or age can be relatively less important for shade tolerant species because of their ability to stagnate growth under unfavorable growing conditions and to wait for increased availability of resources, which often is a result of a canopy opening (Messier et al., 1999; Jones et al., 2009). Findings from our study indicate that vigorous and healthy residual trees of shade tolerant species can respond to canopy opening irrespective of their size. Shade-intolerant loblolly pine displayed an improved tree-level growth with increased size of residual trees. This may indicate that the response of loblolly pine to greater availability of resources was size symmetrical, which means that an individual's access to resources is proportional to its size (Schwinning and Weiner, 1998). A similar result has also been documented for several other shade intolerant species, such as for *Populus tremuloides* in boreal mixedwood forests of western Quebec, Canada (Bose et al., 2014a) and in interior British Columbia, Canada (Coates et al., 2009) as well as for *Pinus sylvestris* in boreal forests of Finland (Mäkinen and Isomäki, 2004).

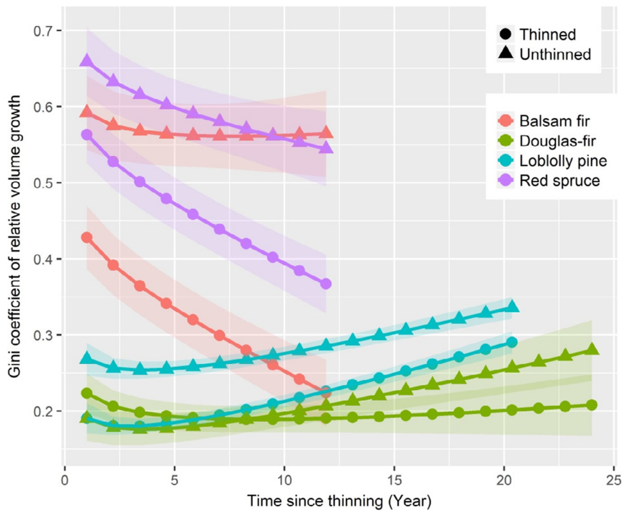

Fig. 2. Predicted Gini coefficient of tree-level relative volume growth (relative to previous year) with thinned and unthinned treatments across the four softwood species examined. Shaded areas represent mean ± 95% confidence interval.

4.2. Effect of stand characteristics on tree growth

Total basal area and stand age at thinning were the most important predictor variables for tree-level growth of thinned stands. The negative effect of total basal area suggests that trees from highly stocked stands passed through a phase of suppressed growth that effectively inhibited or slowed the response to canopy openings after thinning. The negative effect of suppression on tree growth response to canopy opening has been reported for various forest types, such as northern hardwoods to partial harvesting in eastern Canada (Baral et al., 2016) as well as Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) to variable density thinning in US Pacific Northwest (Roberts and Harrington, 2008), and black spruce (*P. mariana* (Mill.) Bong) to diameter limit cutting in boreal Canada (Thorpe et al., 2007).

Our results showed higher growth rates among trees of younger stands compared to trees of older stands across the four species, which generally agrees with the well-known phenomenon that tree growth decreases with age (Ryan et al., 1997). The reduced growth with increasing age may be due to reduced stomatal conductance from increasing limitation to water transport (Ryan and Yoder, 1997), reduced leaf area and sap flow per unit of leaf area (Ryan et al., 2004), increased below-ground biomass allocation for maintaining the increased non-photosynthate biomass (Gower et al., 1996), and reduced nutrient availability, particularly the availability of nitrogen with stand development (Martinez-Vilalta et al., 2007).

Thinning intensity and relative site index were not important predictor variables for tree-level growth throughout the evaluation period examined in this analysis (Fig. 4). This result is consistent with stand-level responses (Bose et al., 2018), and may indicated that an increased availability of resources through greater thinning intensity does not always proportionally increase tree growth. Released individuals must have the ability to utilize the improved growing conditions after commercial thinning. Loblolly pine and Douglas-fir plantations appeared to have been too mature to fully utilize the benefits of thinning, while windthrow events complicated the interpretation of the effects of thinning intensity and site index on growth of balsam fir and red spruce.

4.3. Variability in relative volume growth

The growth variability among residual trees was lower in thinned stands when compared to trees in unthinned stands. Commercial thinning treatments applied in our stands likely reduced structural heterogeneity or tree size variability relative to unthinned stands, creating more uniform interspecific growing conditions for trees in thinned stands than for trees in unthinned stands (Kuehne et al. 2018). Unlike some other thinning experiments (e.g., Thomas et al., 1999; Work et al., 2004; Bose et al., 2015), our commercial thinning studies did not have any ecological objectives, such as improving the structural complexity for wildlife habitats, natural regeneration of ecologically important species, and biodiversity of understory vegetation.

Even in the naturally regenerated spruce-fir, thinning decreased the variability in growth across individuals, but it still remained quite high when compared to the Douglas-fir and loblolly pine plantations. This finding is at least partly attributable to the variety of thinning methods implemented in spruce-fir compared to the prevailing low thinning treatments in loblolly pine and Douglas-fir. Thinning in spruce-fir effectively modified the spatial arrangement of trees from fully random to a more clustered (removal of dominant and codominant individuals) or a more regular distribution (removal of intermediate and suppressed individuals). As a result, reduced stand structural heterogeneity and lower spatial variability in tree-level basal area growth were observed in the low and dominant thinning treatments (Kuehne et al., 2018). The results from this analysis suggest the same patterns would also hold for volume growth.

4.4. Probability of tree survival after thinning

Natural self-thinning of loblolly pine and Douglas-fir in unthinned stands occurred primarily in small-sized trees of suppressed and intermediate crown classes. In addition, self-thinning in loblolly pine stands might be triggered by the attacks of southern pine beetle (*Dendroctonus frontalis* Zimm) (Daniels et al., 1979; Burkhart et al., 1986; Nowak et al., 2015). Mortality amounted to 7.8% and 4.3% of the total number of live and dead trees for loblolly pine and Douglas-fir, respectively, over the entire evaluation period (i.e., 21 and 24 years for loblolly pine and Douglas-fir, respectively). The commercial thinning treatments essentially replaced self-thinning of suppressed stems, thus decreasing stem mortality (Fig. 1C and Table 2) in plantations of these two species.

Thinning was also effective at reducing long-term tree mortality in red spruce and balsam fir. During the years immediately after treatment (Fig. 1C), thinning increased mortality from windthrow and stem breakage (Kuehne et al., 2016). Besides species-specific characteristics (shallow rooting patterns in either species and proneness to stem rot in balsam fir) and site specifics such as shallow soils and a high seasonal groundwater table (Seymour, 1992), greater exposure to wind and snow damage after thinning (Coates, 1997) may have contributed to this finding. The location and surroundings of treated stands, such as areas adjacent to large openings (e.g., clearcut) can also influence windthrow events (Ruel et al., 2003). Although tree size has been reported as a strong predictor of blowdown and/or snapping where the vulnerability to windthrow increases with greater tree size (Canham et al., 2001; Rich et al., 2007), we detected no significant effect of tree size on the survival of thinned balsam fir and red spruce (Fig. 1D). Among the two species, balsam fir exhibited lower survival levels than red spruce, agreeing with other studies that compared windthrow mortality levels of balsam fir and spruce species (Ruel, 2000; Canham et al., 2001). Balsam fir also has a tendency to develop significant internal decay and is considered vulnerable to decay when compared to other species (Frank et al. 2018), which may increase susceptibility to windthrow and ultimately, long–term survival.

Mortality across the three forest types and four species examined was apparently stochastic, and not driven by stand characteristics examined in our analysis (Fig. 4 and Appendix 3 of Supplementary material). Thinning intensity and basal area at thinning appeared to be the most influential stand-level predictor variables among those studied here, confirming the significance of stand density and its effect on tree

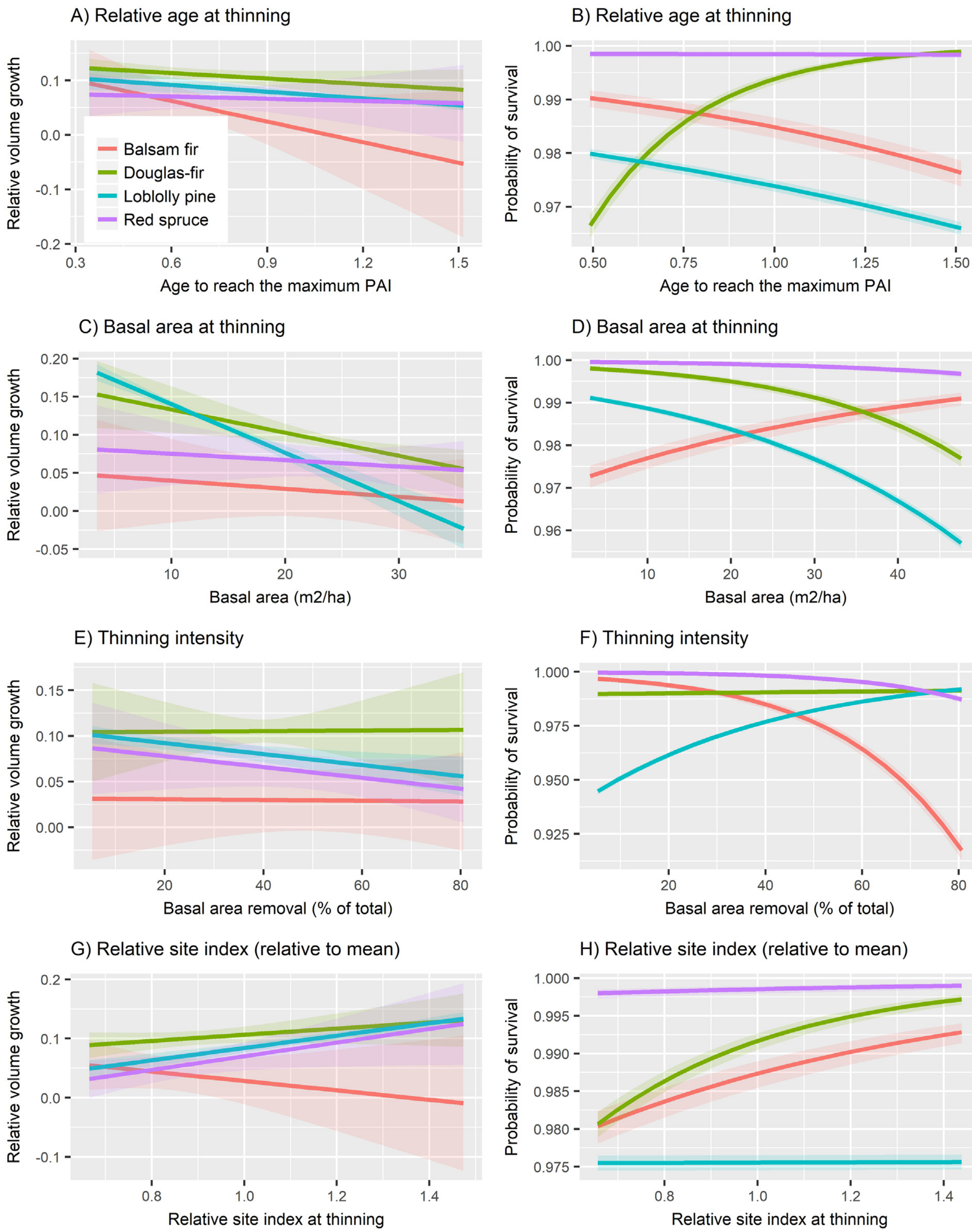

Fig. 3. Predicted tree-level relative volume growth (relative to the previous measurement) and probability of survival of the four softwood species of thinned stands as a function of relative stand age (ratio of observed age to the age of maximum PAI) at thinning, stand basal area at thinning, basal area removal at thinning, and relative site index. Shaded areas represent mean ± 95% confidence interval.

survival (Table S.3 of Supplementary material). The survival of balsam fir decreased with increasing thinning intensity, indicating vulnerability of this species to increased canopy openings that might concomitantly increase the wind penetration into residual stands (Ruel, 2000), while red spruce was unaffected from thinning intensity. An increased thinning intensity improved survival of loblolly pine, suggesting a greater removal of self-thinning prone individuals reduced the mortality of thinned loblolly pine stands. In addition to thinning intensity, crown ratio, inter-tree competition, and height ratio (total height : dominant height) can be other important variables for tree-level survival probability of loblolly pine (Avila and Burkhart, 1992).

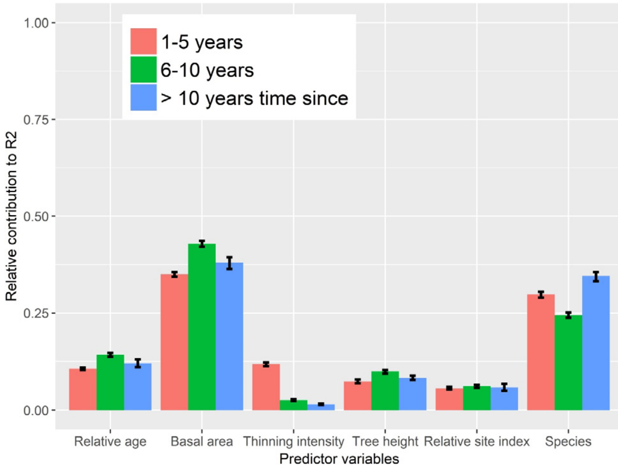

Fig. 4. Relative importance of predictor variables for relative volume growth (relative to previous year) of residual trees following commercial thinning treatments (data from unthinned plots excluded from analysis) of four softwood species. Bars represent means with 95% confidence intervals obtained from 1000 bootstrap replications (Gromping, 2006).

5. Summary and management implications

The results from our study indicated that commercial thinning treatments were effective in increasing the volume growth and probability of survival of residual trees across the four commercially important softwood species of North America. However, the timing of treatment application was likely too late for the shade intolerant loblolly pine and mid-tolerant Douglas-fir to attain the maximum benefits of the commercial thinning treatments. In addition, the probability of windthrow needs to be better incorporated in planning prior thinning applications for spruce-fir stands, particularly those dominated by balsam fir. Potential considerations would include items such as avoiding any adjacent harvested areas that could potentially intensify the wind penetration into residual stands, leaving residual trees in patches, and/or adjusting thinning prescriptions based on soil drainage as well as topographic exposure.

Despite some key findings to the long-term response of four commercially important softwood species to commercial thinning, the analysis has some important limitations that may limit the generality of these findings. These would include lack of direct measurements of key abiotic and biotic factors (e.g. climate, soil, disturbances), the large variability of the specific thinning treatments applied across the three experiments, and differences in method of stand establishment (spruce-fir sites were naturally regenerated, while the sites in two other experiments were planted). Future work should focus on better refining the understanding on relative contribution of tree-, stand-, and landscape-level site factors to growth and survival following commercial thinning, developing a more mechanistic understanding of tree response following thinning, and quantifying the effectiveness of additional treatments (e.g. fertilization) to help to maximize the benefits of commercial thinning treatments when stands are approaching their peak growth potential.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.06.019.

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