Growth and Survival of *Picea glauca* following Thinning of Plantations Affected by Eastern Spruce Budworm

Anthony W. D'Amato, Stacy J. Troumbly, Michael R. Saunders, Klaus J. Puettmann, and Michael A. Albers

ABSTRACT

The effects of thinning treatments on growth and survivorship of white spruce (*Picea glauca* [Moench] Voss) plantations affected by recent eastern spruce budworm (SBW) outbreaks were examined over a 5-year period in northern Minnesota. Thinning treatments increased individual tree growth, live crown ratios (LCRs), and survival relative to unthinned stands. Overall, stands affected by SBW had lower rates of volume production than unaffected stands. In addition, individual tree volume growth was greater in thinned SBW-affected stands relative to unthinned SBW-affected stands. Across stand conditions, individual tree postthinning volume growth response was best predicted by the interaction of prethinning LCR and postthinning relative density (RD). In particular, at low stocking levels (RD = 0.20) higher live crown values resulted in the highest volume growth ratios. On the other hand, at higher stocking levels (RD 0.40–0.55) volume growth was fairly consistent, regardless of LCRs. Across all stocking levels, a minimum LCR of 40% appears to ensure high tree and stand growth rates and is also an indicator of a tree's ability to respond positively to thinning. This plasticity of white spruce suggests that stands maintained at these crown target levels can achieve high levels of stand and individual tree productivity as long as appropriate LCRs are maintained.

Keywords: white spruce, eastern spruce budworm, thinning, live crown ratio, mortality, relative density

Forest insect pests have become increasingly important disturbance agents within forested landscapes, affecting the ability to manage forest ecosystems and resulting in unprecedented levels of tree mortality and growth declines within many portions of North America (Tkacz et al. 2008). Dense, mature forest stands are particularly susceptible to insect pest outbreaks, largely because of higher levels of resource competition (McCullough et al. 1996, Magnussen et al. 2005, Fettig et al. 2007). These competitive conditions increase tree-level physiological stress (Manion 1981, Pedersen 1998) and decrease availability of resources for producing chemical defenses (Waring and Pitman 1985). As a result, higher levels of damage during pest outbreaks are generally observed within dense or overstocked stands (Carlson et al. 1985, Volney et al. 1999, Fettig et al. 2007).

Thinnings have been widely used to mitigate and reduce stand vulnerability to insect pests through increasing the growth and vigor of residual trees (Mitchell et al. 1983, Waring and O'Hara 2005, Dodds et al. 2007) and altering host structure (Liebhold et al. 1998). For example, thinning has led to increased vigor of lodgepole pine (Mitchell et al. 1983, Waring and Pitman 1985) and ponderosa pine (Larsson et al. 1983, Carlson et al. 1985) and to correspondingly decreased effects of mountain pine beetle attacks on stand growth and mortality within the western United States. Similarly, thinning combined with application of biological control agents, such as *Beddingia (Deladenus) siricidicola* Bed., have been used in Australia to combat outbreaks of the woodwasp, *Sirex noctilio* F. (Dodds et al. 2007). Although these and other studies have indicated that thinnings may serve as an alternative to insecticides for minimizing the impact of forest pests, the effectiveness of these treatments have varied within and across pest organisms and forest types (e.g., Liebhold et al. 1998, Sanchez-Martinez and Wagner 2002), highlighting the need for further evaluation of this approach.

The eastern spruce budworm (*Choristoneura fumiferana* Clemens; SBW) is one of the most widely distributed insect pests in eastern North America, with outbreaks causing significant mortality and reduced growth rates in balsam fir (*Abies balsamea* [L.] Mill.) and red, white, and black spruce (*Picea rubens* Sarg., *Picea glauca* [Moench] Voss, and *Picea mariana* [P. Mill.] B.S.P., respectively) throughout their ranges (Kucera and Orr 1981, Williams and Birdsey 2003, Fraver et al. 2007). White spruce is the most susceptible of the eastern spruce species, in part because of the high degree of synchrony between white spruce bud break and emergence of SBW larvae (MacLean and MacKinnon 1997, Nealis and Regniere 2004). SBW outbreaks have occurred at approximately 35-year

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This article uses metric units; the applicable conversion factors are: meters (m): 1 m = 3.3 ft; hectares (ha): 1 ha = 2.47 ac.

Table 1. Characteristics and locations of thinned white spruce plantations examined in northern Minnesota.

Site	Age at thinning	Date thinned	Site index	SBW damage[a]	Location
AC	26	Fall 1999	77	O	47° 0′39.6″N, 93° 32′52.8″W
JL	38	Winter 2000	48	L	48° 5′20.4″N, 93° 40′55.2″W
LLS	32	Winter 2000	38	L	47° 46′37.2″N, 93° 24′40″W
PL	46	Winter 2000	54	L	48° 12′10.8″N, 93° 47′51.6″W
PR	30	Fall 1998	65	M	47° 42′38.3″N, 94° 2′7.7″W
SC	29	Fall 1999	60	L	47° 5′56.6″N, 93° 35′12.1″W
SWC	35	Summer 1999	65	L	47° 33′51.1″N, 94° 25′38.1″W
TT	41	Winter 2001	60	O	47° 8′29.6″N, 93° 13′49.5″W
WA	25	Winter 2002	69	O	47° 38′11.1″N, 93° 12′21.1″W
WSA	26	Summer 2002	64	O	48° 0′17.2″N, 93° 0′43.6″W

[a] Budworm damage rating (Fettes 1950): SBW, Eastern spruce budworm; O, no SBW damage; L, 0–33% SBW damage; M, >33–66% SBW damage.

intervals throughout eastern North America (Taylor and MacLean 2008) and continued for up to 15 years (Kucera and Orr 1981, Magnussen et al. 2005, Hennigar et al. 2007). In the past, pesticides and biological control agents were commonly used to maintain the productivity of infested sites (Mason and Paul 1996, Sheehan 1996); however, the minimal long-term success and the cost of these treatments have led to the search for less costly alternatives, such as thinning. Unfortunately, few studies have examined the effectiveness of thinning at minimizing mortality from SBW. Also, these studies have focused on the primary host species, balsam fir (Crook et al. 1979, Bauce 1996), leaving a limited understanding of the effectiveness of this approach for spruce-dominated systems. Furthermore, studies evaluating the effectiveness of thinning in reducing the impact of SBW have found varying results. For example, studies in young balsam fir stands have suggested that thinning treatments may elevate the severity of SBW by increasing host vigor (MacLean and Piene 1995). On the other hand, studies in older mixed conifer stands in the western United States have demonstrated that thinning may have beneficial effects in reducing western SBW populations in infested stands (Carlson et al. 1985).

There is a well-documented history of SBW outbreaks in eastern North America, with each lasting 7–17 years and separated by 30–60 years of no activity (Colson and Witter 1984). Interestingly, the most recent outbreak in Minnesota started in 1954 and has lasted across the forested landscapes in this region for over 55 years (Minnesota Department of Natural Resources [MNDNR] 2008). Potential explanations for the extended duration of this outbreak include an increased abundance of balsam fir due to the maturation of postlogging mixed aspen-balsam fir stands, as well as the fragmentation and homogenization of the landscape due to past land use (Sturtevant et al. 2004). In the 1990s, SBW began targeting white spruce, causing substantial top kill and mortality, particularly in white spruce plantations across Minnesota and other portions of the Lake States region (MNDNR 1996, Wisconsin Department of Natural Resources [WDNR] 2006). White spruce plantations cover over 72,000 ha of commercial forestland across the northern Lake States (Michigan, Minnesota, and Wisconsin; Rauscher 1984), suggesting a need to evaluate silvicultural strategies that might minimize effects of SBW outbreaks on stand productivity in a cost-effective manner. To address this need, this study investigates the relationships between thinning treatments applied to white spruce plantations affected by SBW and changes in individual tree and stand-level growth, canopy structure, and survivorship. Specific questions included the following: (1) Does thinning increase survivorship in stands affected by SBW? (2) Does thinning increase stand volume growth in stands affected by SBW through changes in foliage patterns (live crown ratio and foliage density)? (3) What factors are most important for predicting postthinning growth responses of individual white spruce in plantations affected by SBW?

Methods

Study Area

The study was conducted in 10 white spruce plantations located in northern Minnesota, the region most affected by SBW in the state (Table 1). Sites were selected to reflect the variety of ages and SBW severity levels found in stands that had either been recently thinned or were scheduled to be thinned near the onset of this study. Care was taken to ensure all stands were fully stocked before thinning and had not received previous thinning treatments (Table 2). Planting densities across sites ranged from 1,482 to 3,212 stems ha^{-1}, which is representative of the range of planting densities for this species throughout the region (Rauscher 1984). Plantations are typically managed on 60–80-year rotations in the region, and thinnings are often considered around midrotation (MNDNR 1994, WDNR 2006). Each plantation was at least 4 ha in size, with each site assigned a control (unthinned) and treated (thinned) portion encompassing at least 1.2 ha each. Thinned and control areas bordered each other to ensure that each had similar microclimatic and site conditions, and they were separated by at least a 15.2-m unharvested buffer. Control areas were positioned at the edge of sites to minimize disturbance caused by the neighboring thinning treatments. The layout was solely determined by these logistical constraints, and there is no reason to believe that the assignments of control and treatment areas led to any consistent bias in terms of tree or stand conditions (Table 2). Treated areas were thinned through a combination of low and row thinning (for access lanes), allowing for operational limitations and using the suggested residual stand densities found in a preliminary white spruce density management diagram (Table 2; Saunders and Puettmann 2000).

Stand Measurements

Three plots were randomly located within each control and treatment area, totaling six plots per site with the exception of LLS, which had four plots in each treatment. Plot designs followed US Forest Service forest health monitoring protocols and were 0.016 ha in size and circular (Mangold 1997). Plots were established and measured prior to thinning, with the exception of JL, PL, WSA, and TT, for which stump measurements were taken during initial measurements and used to estimate prethinning density, tree size, and basal area. Even on these sites, measurements were taken before the growing season immediately following thinning. Equations for predicting dbh from stump diameter were developed from data collected across the other six plantations examined. Within each plot,

Table 2. Average stand conditions and associated standard errors (in parentheses) pre- and immediately postthinning for unthinned (C) and thinned (T) portions of each site.

Site	Treatment	$\mathrm{QMD}_{\mathrm{pre}}$[a]	$\mathrm{QMD}_{\mathrm{post}}$	$\mathrm{BA}_{\mathrm{pre}}$	$\mathrm{BA}_{\mathrm{post}}$	$\mathrm{RD}_{\mathrm{pre}}$	$\mathrm{RD}_{\mathrm{post}}$	$\mathrm{LCR}_{\mathrm{post}}$[b]	$\mathrm{FOL}_{\mathrm{post}}$[b]
		. . . .(cm)	. . . .	. . . . . .($\mathrm{m^2ha^{-1}}$)	. . . . . .			. . . .(%)	. . . .
AC	C	17.6 (0.07)		39.9 (5.29)		0.73 (0.07)		45.1 (5.6)	18.2 (1.3)
	T	18.6 (0.72)	20.4 (0.74)	47.7 (4.96)	25.5 (0.63)	0.84 (0.07)	0.53 (0.01)	47.2 (5.4)	20.9 (2.3)
JL	C	18.9 (0.18)		36.3 (4.20)		0.68 (0.06)		37.2 (4.3)	20.9 (0.3)
	T	17.6 (0.63)	21.3 (1.87)	56 (8.43)	31.7 (3.48)	0.94 (0.11)	0.54 (0.05)	40.0 (1.7)	17.1 (2.1)
LLS	C	11.2 (0.76)		20.8 (0.89)		0.43 (0.02)		42.8 (0.7)	26.7 (0.6)
LLS	T	13.7 (0.97)	14.5 (1.05)	18.2 (2.45)	9.81 (1.9)	0.39 (0.04)	0.24 (0.03)	47.7 (4.4)	18.7 (0.7)
PL	C	13.3 (0.79)		47.6 (4.94)		0.81 (0.07)		40.8 (0.8)	19.4 (1.3)
	T	14.3 (0.98)	16.7 (2.19)	48.3 (6.55)	21.7 (1.23)	0.83 (0.09)	0.46 (0.03)	47.2 (5.8)	17.2 (1.1)
PR	C	15.7 (0.25)		37.3 (4.77)		0.69 (0.06)		39.6 (3.0)	17.8 (0.5)
	T	18.1 (0.75)	19.6 (0.76)	41.2 (2.61)	18.1 (1.90)	0.75 (0.04)	0.41 (0.03)	42.2 (1.9)	14.9 (1.2)
SC	C	15.8 (0.19)		45 (1.51)		0.79 (0.02)		47.4 (3.7)	19.6 (0.2)
SC	T	14.6 (0.25)	17.9 (0.69)	36.5 (2.3)	16.0 (0.31)	0.67 (0.03)	0.37 (0.01)	41.5 (2.3)	19.2 (1.0)
SWC	C	19.1 (0.2)		40.1 (3.59)		0.74 (0.05)		34.7 (3.3)	16.1 (1.7)
	T	18.9 (0.82)	21.6 (0.93)	49.4 (2.14)	20.8 (0.76)	0.87 (0.03)	0.46 (0.01)	40.9 (0.7)	15.2 (0.5)
TT	C	19.5 (1.37)		29.4 (2.17)		0.59 (0.03)		36.4 (1.4)	16.3 (0.2)
	T	18.7 (0.95)	19.1 (0.51)	34.9 (5.39)	21.4 (2.70)	0.66 (0.08)	0.46 (0.04)	40.1 (3.4)	17.2 (0.7)
WA	C	18.6 (0.64)		54.2 (2.78)		0.93 (0.04)		38.9 (0.9)	16.6 (0.2)
WA	T	19.8 (0.96)	19.9 (2.07)	56.9 (3.11)	27.1 (2.88)	0.97 (0.04)	0.55 (0.05)	41.0 (1.8)	15.8 (0.7)
WSA	C	13.7 (0.63)		27.4 (4.5)		0.54 (0.07)		58.0 (1.7)	17.2 (0.7)
	T	13.2 (0.33)	15.2 (0.41)	31.3 (2.6)	12.9 (1.33)	0.59 (0.04)	0.31 (0.02)	65.8 (8.2)	16.2 (0.9)

[a] QMD, quadratic mean diameter; BA, basal area; FOL, foliage density; LCR, live crown ratio.
[b] LCR and FOL were not measured on trees removed in thinnings; therefore, only postthinning stand-level values are reported.
"Pre" and "Post" subscripts correspond to pre- and postthinning values for a given attribute.

all trees were measured for dbh and locations mapped, whereas total tree height and height to the base of the live crown were recorded only for trees not scheduled for removal in thinning treatments. In addition, degree of damage from SBW was ocularly estimated for each tree based on Fettes (1950), and foliage transparency was ocularly determined for trees not being removed in thinning treatments (Mangold 1997). Individual tree volume was calculated using the equations in Scott (1981). All plots were measured annually at the end of each growing season through 5 years postthinning, but this study uses only measurements from the initial and final measurement periods (years 0 and 5, respectively). The average (±1 SE) number of trees in a plot was 31 ± 2 and 12 ± 1 trees for prethinned and thinned plots, respectively.

Analysis

The effect of thinning treatment and SBW damage on stand and individual tree characteristics, including survivorship (reductions in stem density), changes in individual tree live crown ratio and foliage density, and individual tree and stand-level volume growth, were examined using mixed model analysis of variance (ANOVA) in which thinning treatment and SBW damage were treated as fixed effects. Unfortunately, SBW activity, surprisingly, declined during the years of study installation (Blackford 2001), and we were unable to find sites with medium and high budworm damage. As such, SBW damage was treated as a binary variable in these analyses (i.e., visible damage and no damage). Because of the unbalanced distribution of affected and unaffected stands across stand conditions (e.g., site index and stand ages), data were analyzed at the plot level, and each mixed model ANOVA contained a random effect associated with plots nested within a given site. The statistical model used was

$$Y_{ijk} = T_i + \mathrm{SBW}_j + T \times \mathrm{SBW}_{ij} + \mathrm{Site}_k + \mathrm{Plot}_{l(k)} + e_{ijklm},$$

where T_i is the fixed effect for thinning treatment, SBW_j is the fixed effect for SBW, $T \times \mathrm{SBW}_{ij}$ is fixed effect for thinning by SBW interaction, Site_k is the random effect for site, $\mathrm{Plot}_{l(k)}$ is the random effect for plot nested within site, and e_{ijk} is the random experimental error. In cases with significant interactions between fixed effects, the statistical significance of a given factor at different levels of the other factor was obtained using the least square means SLICE option in PROC MIXED (SAS Institute, 2001). For all ANOVAs, significance was determined at $\alpha \leq 0.05$, and transformations were applied as necessary to meet normality assumptions of ANOVA. In addition, diameter distributions of trees that died over the measurement interval were compared between thinned and unthinned stands using Kolmogorov-Smirnov tests.

Mixed model linear regression was used to test specific a priori hypotheses regarding the influence of factors such as live crown ratio and thinning intensity (postthinning relative density [RD]) on postthinning volume growth of individual trees in thinned plots. Because we were interested in explaining the variation in individual volume growth beyond those expected because of differences in size, we used volume growth ratio (Vol*r*), calculated as

$$\mathrm{Vol}r = \frac{\mathrm{Vol}_5 - \mathrm{Vol}_0}{\mathrm{Vol}_0}.$$

where Vol_0 and Vol_5 are individual tree volumes immediately after thinning and 5 years postthinning, respectively. Using the corrected Akaike Information Criterion (AICc; Akaike 1974), we constructed and evaluated candidate models based on a priori hypotheses regarding how initial individual tree and stand conditions (such as prethinning live crown ratio [LCR] and foliage transparency [prethinning], initial SBW damage [0 or 1], and immediate postthinning RD at the plot level) affected volume growth ratio. Plot-level postthinning RDs and individual tree-level prethinning LCRs and foliage transparency were used within our candidate models. All logical interactions between predictors, as well as random-site and plot-nested within-site effects were also included in these models. AICc

Table 3. Summary of type 3 test results from mixed effects ANOVAs for 5-year survivorship rates, changes in individual tree live crown ratio (LCR) and foliage density, and stand-level and individual tree-level volume growth for white spruce plantations experiencing thinning treatments and affected by eastern spruce budworm (SBW).

Source of variation	df	Mortality		Change in LCR		Change in foliage density		Stand-level volume growth		Tree-level volume growth	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
		(%)						($m^3ha^{-1}year^{-1}$)			
Thinning	1	12.60	**0.0008**	33.71	**<0.0001**	0.04	0.8351	1.91	0.1726	127.37	**<0.0001**
SBW	1	4.83	**0.0320**	0.53	0.4705	0.42	0.5184	27.68	**<0.0001**	9.51	**0.0031**
Thinning × SBW	1	1.15	0.2885	1.56	0.2163	2.57	0.1150	0.79	0.3763	12.74	**0.0007**

Boldface *P* values are statistically significant at $P < 0.05$. df, degrees of freedom.

Table 4. Average (standard errors in parentheses) survival rates, changes in individual tree LCR and foliage density, and stand- and individual tree-level volume growth for thinned and unthinned and SBW affected and unaffected white spruce plantations in northern Minnesota. Results are based on mixed-effects ANOVAs.

	Thinned	Unthinned	SBW	No SBW
Five-year survival rate (% of stems that died)	5.7 (1.4)^a	14.0 (1.4)^b	11.2 (1.4)^a	6.5 (1.3)^b
Five-year change in LCR (%)	6.0 (1.4)^a	−6.0 (1.9)^b	0.9 (1.7)^a	−2.2 (2.4)^a
Five-year change in foliage density (%)	−3.0 (3.7)^a	−5.9 (3.0)^a	−10.2 (5.3)^a	−2.8 (2.6)^a
Stand-level volume growth ($m^3ha^{-1}year^{-1}$)	6.89 (0.66)^a	7.07 (0.45)^a	5.44 (0.29)^a	10.65 (0.53)^b
Individual tree volume growth ($m^3ha^{-1}year^{-1}$)	0.61 (0.05)^a	0.29 (0.02)^b	0.37 (0.03)^a	0.66 (0.08)^b

^{a,b} Different letters indicate statistically significant differences ($P \leq 0.05$).

takes into consideration lack of fit and model complexity (Weisberg 2005), and models are ranked according to the difference between the AICc value for a given model ($AICc_i$) and the lowest AIC_c value in a given set of models ($AICc_{min}$): $\Delta_i = AICc_i - AICc_{min}$. A null model containing an intercept, random-site and plot-nested within-site effects, and an error term was also included within this set to determine whether the best approximating models were significantly better than other unmeasured factors (Anderson et al. 1998). A likelihood ratio test R^2 was calculated for each model and used as an additional measure of goodness of fit (Magee 1990). In addition, Δ_i values were used to calculate Akaike weights (*W*), which are an approximation of the probability of a model being the best in a given set (Burnham and Anderson 1998). To meet linearity assumptions, natural log transformations were applied to the response variable, Vol*r*, as well as the predictor variables postthinning RD and prethinning LCR to provide the best linear fit (Sabin and Stafford 1990). A variance component error structure was assumed for each model.

Results

Thinning and SBW Effects on Stand-Level Productivity and Survival

Thinning had a positive effect on survivorship, as survival was higher in thinned plots relative to unthinned areas (Tables 3 and 4). In contrast, there were no differences in stand-level volume growth between thinned and unthinned stands (Tables 3 and 4). SBW damage significantly affected stand-level responses in thinned and unthinned stands, with lower survival occurring in stands affected by SBW and greater levels of stand-level volume growth occurring in stands without SBW (Table 4).

Size distributions of trees that died in thinned and unthinned plots over the 5-year period were significantly different (Kolmogorov-Smirnov test, $D = 0.4146$, $P < 0.0001$). In particular, unthinned sites experienced mortality primarily within the smaller diameter classes, most likely because of natural self-thinning of suppressed or overtopped trees (Figure 1). In contrast, mortality was more evenly distributed across size classes within thinned sites (Figure 1).

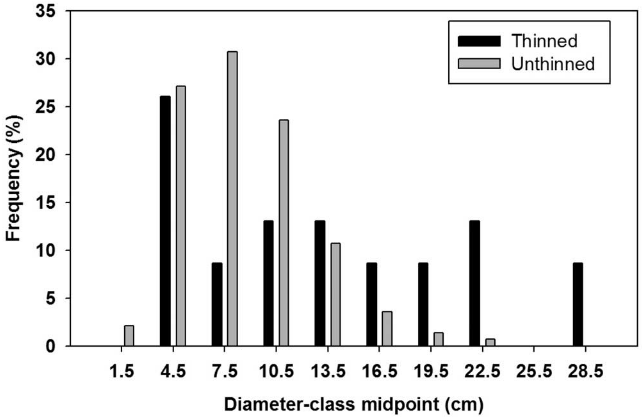

Figure 1. Frequency distribution of killed trees by diameter class in (a) thinned (number of dead trees = 23) and (b) unthinned sites (number of dead trees = 140).

Thinning and SBW Effects on Individual Tree Growth and Foliage Patterns

LCRs and individual tree volume growth increased in thinned plots relative to unthinned areas (Tables 3 and 4). In addition, SBW damage interacted with thinning to affect individual tree volume growth (Table 3). Comparisons between thinning treatments indicated that thinning resulted in higher volume growth rates in stands affected by SBW relative to trees in unthinned stands. Similarly, volume growth was greater in thinned stands without SBW versus those with SBW. There was no significant effect of thinning or SBW on 5-year changes in individual tree foliar transparency ($P > 0.05$; Table 3).

Factors Related to Individual Tree Postthinning Volume Growth

The most important factors affecting postthinning volume growth were prethinning LCR and postthinning RD. The best model (i.e., lowest AICc value) for predicting postthinning volume growth ratio included both these variables and their interactions

Table 5. Model rankings for linear regression models predicting postthinning individual volume growth ratio (Vol*r*). Only the top two models and the null model are presented due to the low level of support for the remaining models (i.e., Δ > 4; Burnham and Anderson 1998).

Model: Vol$r(x)^a$	AICc	Δ_i^b	W^c	R^2
RD, LCR, RD × LCR	−487.7	0	0.87	0.34
RD, FOL, LCR, SBW, LCR × FOL, LCR × RD, LCR × SBW, FOL × RD, FOL × SBW, LCR × FOL × SBW	−482.4	5.3	0.06	0.23
Null model	−434.0	53.7	<0.01	

[a] LCR, prethinning LCR (%); FOL, prethinning foliage transparency (%). RD is after thinning. SBW damage: 0, no damage; 1, visible damage.
[b] Difference between model AICc value and minimum AICc value.
[c] Probability of model being the best in a given set.
R^2 values are based on likelihood ratio tests (Magee 1990), and variables in boldface are significant predictors ($P < 0.05$).

Table 6. Parameter estimates, 95% confidence intervals (in parentheses), and test statistics for the best approximating model for predicting individual tree volume growth ratio (Vol*r*). The model with the lowest AICc in Table 5 was chosen as the best approximating model.

	Parameter estimate	*t* statistic	*P* value
B_0	−1.643 (−2.478, −0.809)	−3.87	0.0001
B_{RD}	3.299 (1.331, 5.267)	3.30	0.0011
B_{LCRi}	0.496 (0.275, 0.716)	4.42	<0.0001
$B_{\mathrm{RD}\times\mathrm{LCRi}}$	−0.874 (−1.396, −0.352)	−3.29	0.0012

Model: $\ln(\mathrm{Vol}r) = B_0 + B_{\mathrm{RD}}(\ln(\mathrm{RD})) + B_{\mathrm{LCR}}(\ln(\mathrm{LCR})) + B_{\mathrm{RD}\times\mathrm{LCR}}(\ln(\mathrm{RD}) \times \ln(\mathrm{LCR}))$, where Vol$r$ = volume growth ratio, B_0 = model intercept, B_{RD} = effect of postthinning RD, B_{LCR} = effect of prethinning LCR, and $B_{\mathrm{RD}\times\mathrm{LCR}}$ = interaction between RD and LCR.

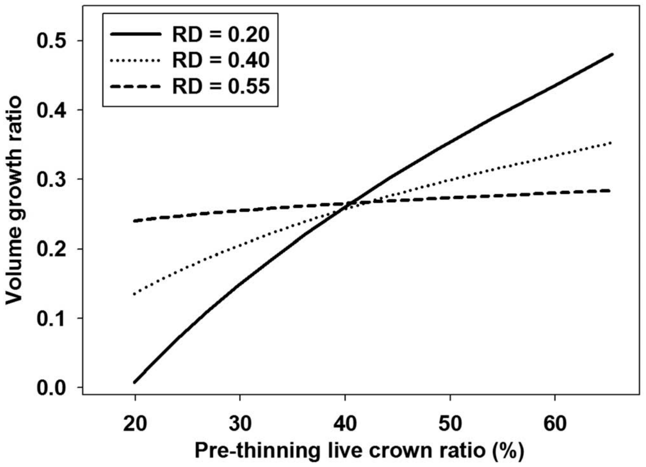

Figure 2. Relationship between volume growth ratio of individual white spruce and prethinning LCR for several postthinning RDs based on the best model in Table 5.

(Table 5). Other candidate models received very little support (i.e., Δ > 4); however, all models were better supported by the data than the null model, indicating that the tree- and stand-level characteristics included in model testing were important to the volume growth of white spruce in these stands. Nonetheless, the relatively low R^2 values for these models suggest that other, unmeasured factors are also affecting the patterns of volume growth within these systems (Table 5).

On the basis of the best approximating model, individual volume growth was positively related to prethinning LCR and postthinning RD and negatively affected by the interaction between these two variables (Table 6). To examine interactive effects of LCR and RD, we generated visualizations of model predictions holding different postthinning RDs constant (Figure 2). Overall, volume growth ratio increased as LCR increased, particularly in stands at low stocking levels (RD = 0.20), but also at stocking levels corresponding to the lower bound of optimum stocking (Saunders and Puettmann 2000, RD = 0.40; Figure 2). In addition, individuals with LCRs less than 40% had the highest volume growth ratios within stands at RD = 0.55, whereas trees with LCRs above this level had the greatest volume growth ratios within the lower stocking levels (Figure 2). Overall, volume growth ratios were relatively constant across LCRs for individuals in stands at RD = 0.55 (Figure 2). There were no detectable trends in scatter plots of volume growth ratio versus individual tree volume or dbh (data not shown), suggesting that these predicted relationships were not confounded by differences in individual tree size.

Discussion

Forest pest outbreaks are capable of causing significant economic losses to managed forests. The application of silvicultural treatments has been suggested as a means to minimize these effects, as well as building stand- and landscape-level resistance (Waring and O'Hara 2005, Dodds et al. 2007, Fettig et al. 2007). In white spruce plantations in the Lake States, eastern SBW has become a persistent and common forest pest (MNDNR 1996), and we evaluated the effectiveness of thinning treatments at increasing the productivity of plantations affected by this insect. Our findings indicate that thinning treatments may serve to increase or maintain the productive capacity of trees in stands affected by SBW through increases in LCR and volume growth rates. Also, thinning increased overall levels of tree survival. In addition, our findings highlight the importance of prethinning LCR and residual stand stocking in determining the responsiveness of individual trees to thinning treatments within white spruce plantations. Collectively, these findings lend support to the notion that thinning treatments can serve to increase the levels of resources available for growth and secondary defense compounds (Mitchell et al. 1983, Waring and O'Hara 2005), thus serving to increase tree and stand resistance to low levels of SBW infestation. Future work in stands more heavily affected by SBW will highlight the applicability of these treatments during high levels of infestation.

The application of thinning treatments to forest stands, particularly low thinning, typically results in lower overall levels of mortality due to the removal of suppressed and overtopped trees otherwise lost to self-thinning mortality (Marshall and Curtis 2002, Davis et al. 2007). In the unthinned stands examined in this study, mortality was concentrated on the lower diameter classes, suggesting that many of the trees killed during the course of this study were suppressed individuals; this finding is consistent with other studies comparing mortality in thinned and unthinned stands across various species (Pothier 2002, Makinen and Isomaki 2004, Fleming et al. 2005). Nonetheless, mortality in stands affected by eastern and western SBW is often initially concentrated on smaller diameter individuals because of the inability of suppressed trees to survive defoliation events relative to larger trees (e.g., Alfaro et al. 1982, MacLean and Ostaff 1989, Filip et al. 1993). In addition, measurable levels of SBW-related mortality have been observed in stands experiencing even low to moderate SBW defoliation (Pothier and Mailly 2006). Thus, it is likely that the lower survival levels that we observed in unthinned stands were at least partially reflective of

SBW damage, with thinning treatments reducing levels of mortality.

Thinning in white spruce plantations increased individual tree growth and LCR, which is consistent with the findings of numerous studies examining conifer postthinning growth response (e.g., Peterson et al. 1997, Makinen and Isomaki 2004, Guan et al. 2008). In stands affected by SBW, individual tree growth was greater in thinned than in unthinned plots, a finding consistent with similar comparative studies evaluating growth of western conifer species infested by western SBW (Wickman et al. 1992). In addition, the levels of individual and stand-level volume growth response that we observed were influenced by SBW damage, as damaged stands had average stand-level and individual tree volume growth rates that were 96 and 78% lower, respectively, than uninfested stands (Table 4). This is similar to the patterns observed in Douglas-fir plantations thinned in response to Swiss needle cast (*Phaeocryptopus gaeumannii* [T. Rohde] Petr.) infestation in which infested stands showed positive growth responses to thinning, although at lower rates compared with uninfested stands (Mainwaring et al. 2005). Nonetheless, these observed trends in volume growth may also be partially reflective of the higher site quality of two of our uninfested sites (sites WA and AC, Table 1).

LCR has long been recognized as a coarse index of the general vigor and photosynthetic capacity of trees (Zarnoch et al. 2004). It has been used for setting target conditions to time thinnings and select crop trees (Smith et al. 1997). Despite the widespread occurrence of white spruce plantations in the Great Lakes region, formal live crown targets for scheduling thinning treatments in these systems do not exist (Rauscher 1984). As a result, many stands, such as those examined in this study, are managed for LCRs recommended for other conifer species, such as red pine (e.g., $> 30\%$ LCR; Gilmore and Palik 2006). Our results suggest that trees with small LCRs cannot take advantage of the improved growing conditions the first 5 years after thinning. On the other hand, LCRs above 40% elicited the highest levels of postthinning growth response (Figure 2), suggesting that these values might represent more reasonable targets for sustaining high levels of individual tree growth in white spruce plantations and are indicative of trees that are able to respond to thinning treatments.

Beyond LCR, individual volume growth ratios in thinned stands were also related to residual stocking level (based on RD). Consistent with the predictions of Long (1985), the highest predicted level of individual tree volume growth was for trees within the lowest stocking levels examined ($\text{RD} = 0.20$, Figure 2) when LCRs were greater than 40%. Nonetheless, stands at this low stocking level represent a compromise in terms of individual tree and stand-level volume production (Drew and Flewelling 1979, Long 1985). The relatively comparable levels of growth predicted for the RDs corresponding to the lower and upper limits for the zone of maximum stand production (0.40 and 0.55, respectively; Saunders and Puettmann 2000) confirm the value of these thinning targets for maintaining high levels of stand and individual tree productivity in these systems. In contrast, the low levels of individual volume growth observed on trees with low LCRs at $\text{RD} = 0.20$ may partially be related to greater physiological stress at these low densities (Donner and Running 1986), as individuals with similar LCRs had greater levels of growth at higher stocking levels (Figure 2). In addition, this relationship may also reflect the fact that some of the stands with low postthinning RDs were on poorer quality sites. Based on the relationships between LCR and stocking level for other conifer species (Long 1985, Dean and Baldwin 1996, Jack and Long 1996), it is likely that stands maintained at RDs between 0.40 and 0.55 will contain average LCRs favorable for white spruce volume growth (i.e., $>40\%$).

Conclusions

Thinning has long been recommended as a strategy for minimizing losses to insects and diseases, as well as for increasing tree and stand vigor. Nonetheless, little empirical data exist for the effectiveness of this strategy for white spruce plantations affected by SBW, despite the prevalence of this insect pest and these stand types in the Lake States. Although the findings of this work are from a relatively short time period and during low levels of SBW infestation, our results suggest that thinning treatments applied to stands affected by SBW can serve to increase levels of survivorship while also promoting productivity through increases in LCR and individual volume growth rates. The relationships between growth response of trees in thinned stands, postthinning RD, and LCR suggest that thinning regimes in white spruce plantations should be frequent enough to maintain a LCR of at least 40% on residual trees. This level appears to provide for optimal growth under higher residual stocking (RD from 0.40 and 0.55) and also indicates the tree's ability to respond to thinning by increasing growth. Thus, stands managed for these targets would be more responsive to future thinning entries and may also be more resistant to future outbreaks of SBW.

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