Long-Term Thinning Effects on the Leaf Area of *Pinus strobus* L. as Estimated from Litterfall and Individual-Tree Allometric Models

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Abstract: Canopy leaf area index (LAI) is important for predicting stand growth response to silviculture, but it is difficult to quantify because of high variability, time constraints, and limitations of nondestructive techniques. We used an uninterrupted 17-year record of litterfall in a 60-year-old *Pinus strobus* L. plantation in central Maine to quantify LAI in response to both B-line and low-density thinning and to evaluate individual-tree allometric leaf area prediction models fitted to data from 51 destructively sampled trees. Allometric model performance was inconsistent between the tree and stand levels; the most robust model at both scales predicted leaf area from sapwood basal area and crown length. The LAI of the control treatment declined gradually from 4.5 to 4, with interannual variability associated with disturbances to the canopy. Thinning reduced LAIs but not in proportion to the number of trees removed by thinning because LAIs were similar between the B-line and low-density treatments. At the tree level, differences between the treatments were substantial, with low-density tree leaf area increasing nearly fivefold over the study period, twice the response of comparable B-line trees. These results demonstrate the dynamic nature of leaf area, the difficulty in predicting it accurately, and the influence of silvicultural activities. FOR. SCI. 58(1):85–93.

Keywords: nonlinear least squares, nonlinear mixed effects, weighted models, eastern white pine

CANOPY LEAF AREA IS AN EFFECTIVE METRIC for evaluating the productivity of individual trees and entire stands. A primary goal of silvicultural thinning treatments is to maximize productivity, and, therefore, leaf area (LA) can be used to assess the outcome of different silvicultural treatments. In the short term, stand-level LA is reduced by thinning until stands regain crown closure (Long et al. 2004); however, at the tree level, LA rapidly increases after thinning through crown elongation (Weiskittel et al. 2007), increased crown width (Peterson et al. 1997), and crown densification (Mainwaring and Maguire 2004). Understanding the effects of such changes in stand structure and crown architecture may lead to improved predictions of outcomes from thinning compared with predictions based primarily on stand density or tree size (O'Hara 1988, 1989).

Eastern white pine (*Pinus strobus* L.) is an important species in the northeastern United States and represents 27% of the net volume of softwood sawtimber in Maine (McWilliams et al. 2003). Thinning is commonly used in even-aged stands of white pine to increase the growth of desirable trees and promote regeneration, but managers lack clear direction as to which silvicultural systems will best achieve their objectives. The two most common approaches are conventional B-line and low-density thinning. Conventional thinning follows regional guidelines (Lancaster and Leak 1978) that recommend maintaining stand densities close to the point of crown closure by thinning to the B-line on the Philbrook et al. (1973) stocking guide to achieve high stand-level growth rates and use all available growing space. Low-density thinning, in contrast, is meant to maximize crop tree growth by maintaining open stand structures with minimal crown competition.

To our knowledge, the effects of thinning on the LA of eastern white pine have not been studied, and thus we do not know how rapidly stands regain canopy cover after thinning and how such changes to canopy structure affect the growth response of individual trees and whole stands. An understanding of these outcomes would improve white pine silviculture (Long et al. 2004) and help solve a long-standing debate over whether conventional B-line or low-density thinning is optimal for even-aged stands of eastern white pine (Seymour 2007).

Because LA cannot be measured directly, various methods of estimation have been developed, including simple diameter-based (Kittredge 1944) and sapwood-based (Grier and Waring 1974) allometric equations, foliage litterfall sampling (Madgwick and Olson 1974, Marshall and Waring 1986), and light interception methods (Pierce and Running 1988, Norman and Campbell 1989). Although allometric equations are commonly used, few studies have evaluated the error with which they predict LA at the stand level, owing to a dearth of studies in which independent estimates of LA exist.

The few studies that have assessed the estimation error

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associated with allometric equations have demonstrated that results can be biased by the application of diameter-based equations (Grier et al. 1984, Marshall and Waring 1986, Bormann 1990, Turner et al. 2000) and a fixed sapwood area/LA ratio (Dean et al. 1988). Diameter-based allometric equations can be particularly inaccurate when applied to managed stands. For example, a diameter-based allometric equation showed a bias of −33 to 93% when applied to young fertilized Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands (Grier et al. 1984). Allometric equations that include sapwood area rather than diameter resulted in better agreement with stand leaf area index (LAI) estimates obtained by litterfall sampling (Turner et al. 2000).

The direct relationship between sapwood area and amount of foliage (Shinozaki et al. 1964) makes sapwood a biologically appealing predictor in allometric models. Sapwood-based equations, however, can be biased if within-stand variation (Dean et al. 1988) is not taken into account. Moreover, the measurement of sapwood area on standing trees can be imprecise owing to noncircularity of the bole and subjectivity in deciphering the sapwood-heartwood boundary on tree cores in some species. Additional information is needed in assessing whether sapwood measures are optimal for predicting LA.

The accuracy of an allometric equation depends on the model form, independent variables, and fitting technique. Any of these could potentially add bias, especially when the model form and independent variables do not reflect known biological relationships (Kershaw et al. 2009). Determining the best equation for a study is difficult because a good equation at the tree level may perform poorly when aggregated to the stand level (Weiskittel et al. 2010), which suggests that tradeoffs at both the tree and stand levels must be assessed when an equation is selected.

We sought to assess the influence of thinning on tree- and stand-level LA in a white pine plantation in central Maine, and this required that we first determine the best allometric LA equation to be used for both individual trees and stands. Our objectives were to (1) examine long-term trends in litterfall-derived LAI to evaluate thinning treatments and provide an independent standard of performance for validating individual-tree allometric models, (2) assess five allometric models for predicting tree-level projected LA using several different fitting techniques, (3) examine possible bias in the individual-tree models when summed to estimate stand-level LAI, and (4) compare conventional B-line and low-density thinning in terms of their effects on canopy LA and crown structure.

Methods

Study Design and Thinning Treatments

We conducted the study in a 1949-origin eastern white pine plantation in the Dwight B. Demeritt Forest of the University of Maine (44°55′ N, 68°41′ W). The site index is 20 m at a base age of 50 years (Frothingham 1914). In 1991, the white pine thinning study (WPTS) was initiated to examine tree and stand responses to conventional B-line and low-density thinning (Table 1). The study design consists of replicate blocks, each with three 0.04-ha (20 m × 20 m) plots blocked according to stand density (trees per hectare and basal area) before the initial thinning. We randomly assigned thinning treatments so that each block consisted of a B-line plot, low-density plot, and nontreated control plot. We selected crop trees at a 6-m spacing and then used crown thinning until B-line density was achieved on B-line plots or all non-crop trees were removed on low-density plots. In 2001, we thinned again to reestablish B-line density on B-line plots and removed less vigorous trees in competition with more desirable crop trees on low-density plots.

Data Collection

Before the 1992 growing season, we measured dbh (to 0.25 cm; 1.37 m above the ground), total tree height (to

Table 1. Stand attributes for each treatment of the eastern white pine thinning study.

Attribute	Control	B-line	Low-density
1992 postharvest			
Trees (ha^{-1})	1,550 (347)	594 (62)	313 (22)
BA (m^2 ha^{-1})	45.7 (4.3)	20.2 (0.9)	12.7 (0.2)
QMD (cm)	20.3 (0.7)	21.2 (1.6)	22.8 (0.7)
LCR (%)	32 (0)	30 (1)	33 (1)
2001 preharvest			
Trees (ha^{-1})	1,300 (236)	525 (34)	313 (22)
BA (m^2 ha^{-1})	51.7 (3.9)	26.7 (1.2)	19.8 (0.5)
QMD (cm)	23.2 (1.7)	25.6 (1.5)	28.5 (0.8)
LCR (%)	33 (1)	42 (1)	46 (1)
2001 postharvest			
Trees (ha^{-1})	1,300 (236)	488 (44)	175 (10)
BA (m^2 ha^{-1})	51.7 (3.9)	25.3 (1.4)	11.8 (0.4)
QMD (cm)	23.2 (1.7)	25.9 (1.5)	29.4 (1.2)
LCR (%)	33 (1)	42 (1)	46 (0)
2008			
Trees (ha^{-1})	988 (142)	444 (19)	167 (6)
BA (m^2 ha^{-1})	48.8 (2.4)	28.3 (1.7)	15.3 (0.5)
QMD (cm)	25.1 (1.6)	28.5 (1.5)	34.1 (1.1)
LCR (%)	31 (1)	34 (1)	45 (1)

Values are means of four 0.04-ha plots per treatment; SEs are in parentheses. BA, basal area; QMD, quadratic mean stand diameter; LCR, live crown ratio of upper crown class trees.

0.05 m), and height to the lowest live whorl (three or more live branches) for all trees in the thinning treatments. On the unthinned control plots, we measured all dbhs plus height and crown height on a subset roughly equal to the number of residual trees on the thinned plots and then applied plot-specific height-over-dbh regression equations to estimate the heights of nonmeasured trees. In subsequent inventories in the fall of 1999, 2001, 2006, and 2008, we measured dbh, height, and crown height on all surviving trees.

To measure sapwood basal area at breast height (SBA; cm²), we extracted increment cores from the east and west sides of each live tree in 2001 and from the north, southeast, and southwest sides of each live tree in 2008. We marked the boundary between the translucent sapwood and opaque heartwood in the field and later used a 10% ferric chloride solution to verify the boundaries before measuring the sapwood radii (to 0.1 mm). Coincident with increment coring, we measured bark thickness (to 1 mm) at breast height with a bark gauge. Finally, we calculated SBA as the difference between inside bark basal area and mean heartwood area.

Litterfall-Based Projected LA

Beginning in 1992, we collected litterfall in October and June of each year (for one season's litterfall) from five collection traps per plot. The litterfall traps have inner dimensions of 50 cm × 50 cm (2,500 cm), have 10-cm high wood sides that are beveled at the top to preserve the inner dimensions, have a floor of wire mesh, and sit approximately 10 cm above the ground. Collections between 1992 and 2001 consisted of six plots, two plots per treatment. In 2001, we added two control plots to the collection campaign, and in 2007 we added two low-density and two B-line plots. As of 2008, there were 12 plots with litterfall traps. We dried all collected material from the traps at 65 °C for 1 week to prevent decomposition and then selected white pine needles for drying to a constant mass before determining the final mass of white pine needles (to 0.01 g).

LAI (m² projected LA per m² ground surface area) of each plot was calculated as the average of the five trap LAIs that we determined using the equation

$$
\text{LAI} = \left(\frac{\text{needle mass} \cdot \text{specific leaf area} \cdot}{\text{trap area}} \right) \cdot \begin{array}{c} \text{needle} \\ \text{retention.} \end{array} \quad (1)
$$

Specific leaf area (SLA) and needle retention were estimated from the destructively sampled trees used to fit the individual-tree allometric models (below). SLA averaged

65.25 ± 0.91 cm² g⁻¹ (±SE) and was unaffected by thinning treatments. Thinning did affect needle retention slightly, averaging 2.37 ± 0.04 years on thinned plots and 2.21 ± 0.05 years on the control plots.

Following Martin and Jokela (2004), we developed the senescence correction factor to convert dry weight of abscised needles collected in a trap to their approximate dry weight when live. The factor integrates losses of dry weight resulting from the removal of nutrients and carbohydrates from foliage before senescence (Vose et al. 1994) and decomposition by endophytic fungi after senescence (Deckert et al. 2001). We assumed that decomposition within litterfall traps was minimal because trap bottoms were permeable and elevated above the ground. The senescence correction factor is the ratio of average SLA from 100 senesced and oven-dried needles on 10 WPTS plots to the SLA of 100 green and oven-dried needles from the same plots. Because senescent needles from the traps lost an average of 15.1 ± 2.3% of their dry weight per unit of surface area, we used 1.151 as a multiplier in Equation 1 for all plots and years.

Allometric Model-Based Projected LA

Tree-level LA was developed by the two-step branch-summation method based on data largely from 48 destructively sampled trees; 33 of these were taken from the thinning study itself on two occasions, whereas the remainder were from nearby pure white pine stands of various ages and management histories. Archived data on LA, branch diameter, and crown position from 144 sample branches (3 per tree) were used to fit the Weiskittel et al. (2009) branch-level equation (Guiterman 2009). Sapwood widths were measured on 6 radii of breast-height sample disks and were used to calculate SBAs. In 2008 three large trees on low-density plots in the WPTS were climbed to measure the diameter and location of all living branches in situ. The branch equation was solved for all live branches on the 51 sample trees and summed to provide tree-level projected LAs, the dependent variable in the tree-level model-fitting described below (Table 2).

We fit five different nonlinear allometric models (Table 3) to 51 sample trees by using three statistical fitting techniques: nonlinear least squares (NLS), weighted nonlinear least squares (WNLS), and weighted nonlinear mixed effects (NLME). In the weighted equations, the primary independent variable was used for weighting. For the NLME fits, we added random effects to one parameter that accounted for the different stands ($n = 7$) and management

Table 2. Descriptive statistics for the sample tree data set ($n = 51$) used to fit allometric tree-level LA equations.

Attribute	Mean	SE	Minimum	Maximum
dbh (cm)	19.2	1.8	1.6	61.3
ht (m)	15.5	1.0	2.8	29.6
CL (m)	6.5	0.5	1.7	17.1
SBA (cm²)	149.7	25.0	0.9	830.9
LA (m²)	50.0	14.0	0.2	604.8
Age (yr)	41	4.0	11	128

ht, total tree height; CL, live crown length; SBA, sapwood basal area; LA, tree-level leaf area.

Table 3.   Selected model forms for estimating tree-level projected LA.

Model name	Equation	Reference
Sapwood-only	$LA = b_1 \cdot SBA^{b_2}$	Espinosa Bancalari et al. (1987)
Sapwood-crown length	$LA = b_1 \cdot SBA^{b_2} \cdot CL^{b_3}$	Gilmore et al. 1996, Kenefic and Seymour 1999
Maguire and Bennett	$LA = b_1 \cdot CL^{b_2} e^{b_3 \cdot (dbh/ht)}$	Maguire and Bennett 1996
Valentine et al.	$LA = b_1 \cdot BA \cdot mLCR^{b_2}$	Modified from Valentine et al. 1994
Diameter-crown length	$LA = b_1 \cdot dbh^{b_2} \cdot CL^{b_3}$	This study

Independent variables include SBA (cm^2), live crown length (CL, m), dbh (cm), basal area at breast height (BA, cm), total stem height (ht, m), modified live crown ratio (mLCR), and live crown ratio (LCR). Parameters to be estimated are indicated as b_i.

histories ($n = 4$) within the sample data. We selected the parameter for random effects by iteratively fitting each model and changing the randomized parameter; ultimately, we chose the option with the lowest Akaike information criterion (AIC). Because NLME models estimate the population trend (fixed effects) and each tree's deviation from the population (through random effects; Pinheiro and Bates 2000), we evaluated both the full mixed-effects model (NLME-R) and the fixed-effects version of the same model (NLME-F).

Analyses

We used repeated-measures analysis of variance and Tukey's honestly significant difference test to evaluate the effects of thinning on LAI and tree-level LA and report statistical significance at the 95% level of confidence. In tree-level comparisons, we analyzed the plot mean LA of dominant and codominant trees only, so that lower crown class trees present in the control and B-line treatments would not skew the results.

We evaluated goodness of fit in the allometric LA models by comparing fit statistics, residual plot analyses, and estimates of error. Final model selection was based on AIC and root mean squared error. We considered an AIC reduction of 10 units to be statistically significant (Burnham and Anderson 2002). We estimated stand LAI from the allometric models as the sum of all tree LAs for each plot and in each inventory year, divided by the plot area. We assessed the bias in applying allometric equations by comparing allometric LAI estimates with litterfall LAI estimates. Our chosen metric for these comparisons was the average absolute deviation (AAD) because it preserved the differences in the estimates by eliminating the potential for a balancing effect of positive and negative values to average to zero. The AAD is defined as

$$AAD = \frac{\sum_{i=1}^{n} |\hat{Y}_i - Y_i|}{n}, \qquad (2)$$

where $\hat{Y}_i$ is the allometric LAI and Y_i is the litterfall LAI. We used litterfall LAI estimates from the year 2000 to compare with the allometric LAI estimates of 2001. The 2001 litterfall collection was confounded by thinning after the fall collection but preceding the spring collection, and thus trees removed by thinning contributed only to the fall collection.

Results

Litterfall LAI

The pattern of litterfall-based projected LAI from 1992 to 2008 shows the variable nature of canopy LA (Figure 1). The control treatment had the most interannual variability with marked departures in 1994, 1998, 2004, and possibly 2008. For all other years of the study period, however, control LAIs generally remained between 4 and 4.5 m^2 m^{-2}. Repeated-measures analysis of variance showed that thinning significantly reduced LAIs throughout the study period ($P < 0.01$). The initial thinning entry in 1991 reduced LAIs from 4.75 to approximately 2 (a 60% reduction) in both the B-line and low-density treatments, despite significantly more trees being removed from the low-density stands than the B-line stands (Table 1).

Over the study period, the B-line and low-density LAIs were somewhat different ($P = 0.06$), owing primarily to large differences from 2001 to 2004. In 2008, the two thinning treatments were not statistically distinguishable. High SEs in the low-density LAIs until 2007 were due to the difference between the two sample plots, and thus the addition of two more plots in 2007 reduced the estimation error.
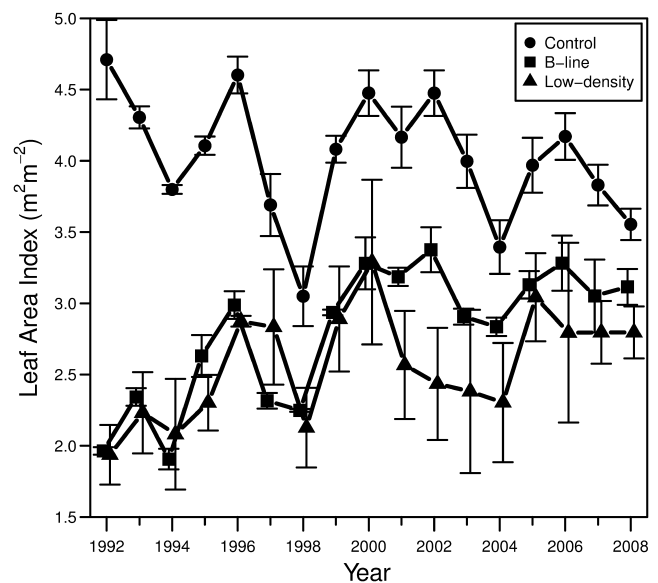

Figure 1.   Projected LAIs from litterfall sampling throughout the study period. Error bars are ± 1 SE. For clarity, data points for the B-line and low-density treatments were slightly offset along the abscissa.

Allometric Model Performance

All fits to each allometric LA model were significant, with only one parameter in the Maguire and Bennett (1996) model being insignificant in two of the three fitting techniques (Table 4). We evaluated the tree-level performance of the model fits by comparing their predictions with the known LA quantities of the 51 sample trees (Figure 2A). The prediction errors were lowest with use of the NLME-R; the WNLS and NLME-F techniques had the highest amount of error. In contrast, AIC scores revealed that weighting the models greatly improved their performance (Figure 2B); only two models showed an improvement when fit by NLME-R versus WNLS. The overall best performing allometric equation at the tree level was the Valentine et al. (1994) model when the NLME-R technique was used. However, the WNLS and NLME-F versions of this model had the highest estimation errors.

At the stand level, the model form, rather than the fitting technique of the allometric equations, was important in determining prediction bias relative to litterfall-based LAIs (Figure 3). Contrary to tree-level performances, however, biases with the NLME-R technique were among the highest. The best tree-level model, the Valentine et al. (1994) equation, performed relatively poorly at the stand level. There is clearly no superior model form or fitting technique, but overall the sapwood-crown length model was the least biased, with estimates consistently within ½ unit of LAI. Of the fitting techniques we evaluated for the sapwood-crown length model, the NLME-F fit appears most suited for application. Of the models that do not rely on sapwood area, the Maguire and Bennett model (fit by WNLS) was the best performer.

Tree Response to Thinning

To assess the effects of thinning at the tree level, we applied the two best allometric models to upper crown class trees in each treatment (Figure 4). From 1999 to 2008, the low-density trees had more LA than the control and B-line trees ($P < 0.01$), but B-line and control trees were equivalent ($P = 0.26$). In 2008, the average low-density tree had 96% more LA than the average B-line tree.
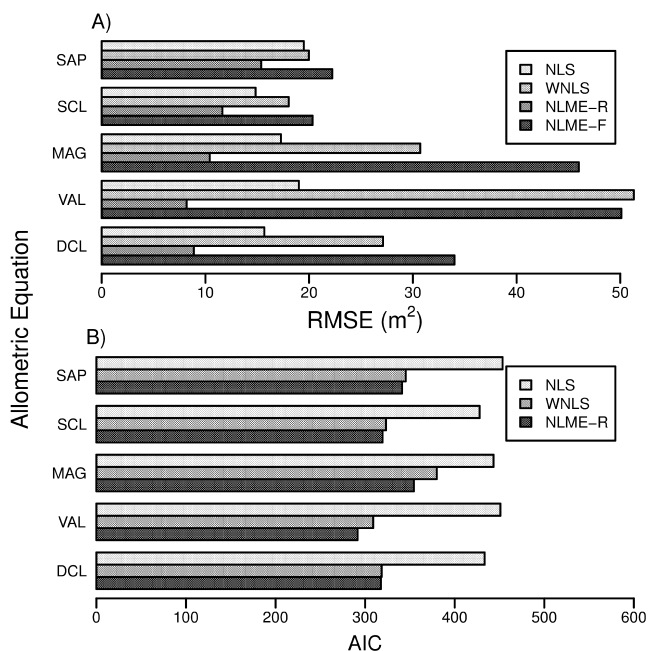

Figure 2. Tree-level performance of the five allometric LA equations (sapwood [SAP], sapwood-crown length [SCL], Maguire and Bennett 1996 [MAG], Valentine et al. 1994 [VAL]; and diameter-crown length [DCL]) fit by NLS, WNLS, and NLME. NLME-R indicates that the random effects were used, and NLME-F indicates that only the fixed-effects parameter estimates were used. RMSE, root mean squared error of the predictions in original units.

Discussion

Patterns of LA and Influences of Thinning

Our results demonstrate the variability of LA in a white pine plantation over nearly two decades. Such variability in the litterfall LAI record is associated with known and unknown disturbances and climatic variation (Gholz et al. 1991). The largest disturbance to affect the study site was the 1998 ice storm that broke off branches, tree tops, and dormant buds. This reduced production of new needles during the 1998 growing season but by 1999 much of the lost LA had been recovered. The causes of LAI reduction in 1994, 1997, and 2004 are unknown, but possibilities include
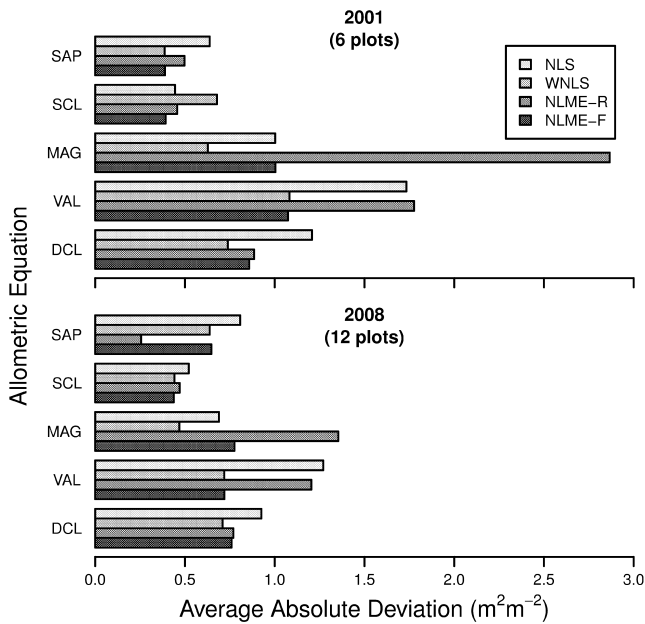
Table 4.   Parameter estimates of the allometric LA equations.

Model name	Parameter	NLS	WNLS	NLME-F
Sapwood-only	b_1	0.1383 (0.0437)	0.0845 (0.0193)	0.1341 (0.0274)
	b_2	1.1947 (0.0505)	1.2735 (0.0425)	1.1828 (0.0440)
Sapwood-crown length	b_1	0.2236 (0.0538)	0.0877 (0.0133)	0.1027 (0.0150)
	b_2	0.4806 (0.1180)	0.6671 (0.0970)	0.7541 (0.0787)
	b_3	1.5379 (0.2521)	1.4655 (0.2603)	1.2538 (0.2075)
Maguire and Bennett	b_1	0.6280 (0.1594)	0.1934 (0.0432)	0.2064 (0.0397)
	b_2	2.3950 (0.1695)	2.7811 (0.2640)	1.6749 (0.2268)
	b_3	0.0021 (0.1304)*	0.1953 (0.3443)*	1.5608 (0.2669)
Valentine et al.	b_1	0.9054 (0.1875)	0.1121 (0.0078)	0.1174 (0.0117)
	b_2	0.8374 (0.0309)	1.1842 (0.0163)	1.1754 (0.0261)
Diameter-crown length	b_1	0.3970 (0.1096)	0.0747 (0.0087)	0.0645 (0.0102)
	b_2	0.6149 (0.2032)	1.0859 (0.0968)	1.1497 (0.1181)
	b_3	1.6450 (0.2437)	1.6404 (0.1676)	1.6286 (0.1660)

SEs are in parentheses. All estimates had $P < 0.05$ unless otherwise indicated.
* $P > 0.05$.

Figure 3. Stand-level performance of the allometric LA equations using litterfall-based LAI as the standard of accuracy (sapwood [SAP], sapwood-crown length [SCL], Maguire and Bennett 1996 [MAG], Valentine et al. 1994 [VAL]; and diameter-crown length [DCL]) fit by NLS, WNLS, and NLME. NLME-R indicates that the random effects were used, and NLME-F indicates that only the fixed-effects parameter estimates were used. Average absolute deviation is defined in Equation 2.
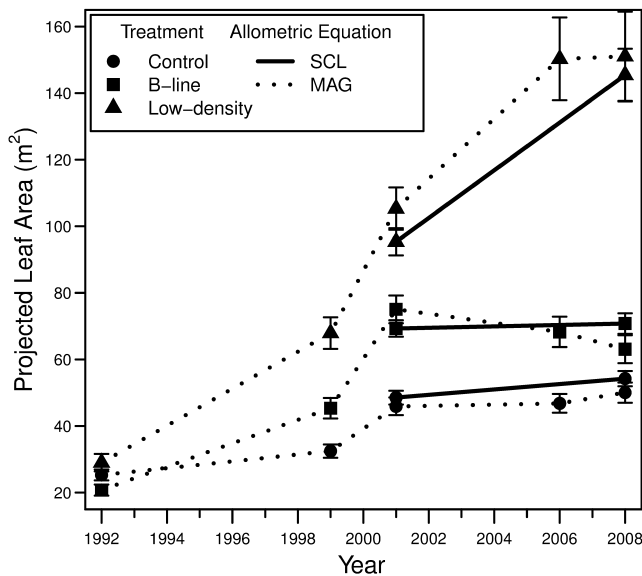

Figure 4. Mean projected leaf areas of dominant and codominant trees for each treatment throughout the study period. Tree-level projected LA estimates were made using the sapwood-crown length model (SCL) with the NLME-F parameters and the Maguire and Bennett (1996) model (MAG) with the WNLS parameters. Error bars are ±1 SE.

foliage herbivory, increased decomposition, or climatic variation. Allocation to seed production is an unlikely factor because cone production has been limited in these stands. Despite the overall variability in LA throughout the study period, there were clear differences in LAIs between the treatments and the control at both the tree and stand levels.

The LAI of the control treatment decreased slightly throughout the 17-year study period, as is illustrated in the progressive lowering of interannual peaks in Figure 1. This decline should be expected over time, given the combined effects of competition, age, crown abrasion, and canopy disturbance on a closed-canopy, even-aged stand (Oliver and Larson 1996). As opposed to stand-level LAI, the tree-level LA in the control treatment increased minimally throughout the study period. The increase in LA is small because, as the trees grow taller and build LA vertically, there is recession of the crown base due to the low-light conditions of a closed canopy stand (Weiskittel et al. 2007). The pattern of decreasing LAI with stable or slightly increasing tree LA observed in the control treatment is a consequence of self-thinning, as the site-maximum LAI is distributed among fewer individuals.

The B-line and low-density silvicultural systems we evaluated were designed to stimulate crop tree growth through release and to mitigate the negative effects of stand development that were observed in the control treatment. Our expectation before thinning was that residual LAIs would be proportional to the residual stand densities. This, however, was not the case. The thinning treatments expressed nearly the same LAI for much of the study period. A possible explanation for this similarity is the method by which the silvicultural systems were implemented. The crop tree selection process was identical in both treatments, with the difference between treatments being that small codominants and intermediates were left on the B-line plots to achieve the desired stocking, whereas only the crop trees remained on the low-density plots (Seymour 2007). We postulate, therefore, that the small codominant and intermediate B-line trees do not contribute greatly to the overall LA of the stands; instead the large crop trees that dominate both thinned treatments comprise the majority of the LAI. In a study of the volume growth of white pine on this experimental site, the thinned treatments similarly expressed nearly equal stand-level gross volume growth rates from 1992 to 2001 (Seymour 2007, Guiterman et al. 2011), as one might expect, given the known high correlation between volume growth and LAI. From 2001 to 2008, however, the B-line stands grew at a significantly higher rate than the low-density treatment stands, which is not reflected by a similar difference in the LAIs of these stands. It is plausible that the B-line treatment benefited from a greater number of trees and/or a more efficient canopy architecture composed of smaller-crowned trees (Assmann 1970).

The greatest differences between the B-line and low-density treatments are at the tree level. Low-density thinning clearly results in large-crowned crop trees with an increasing LA through time, especially after the 2001 thinning entry. B-line thinning, on the other hand, produced a moderate increase in tree LA, but after 2001 the average LA remained constant. These results illustrate the inability of B-line thinning to release crop trees enough to stimulate a rapid and sustained canopy response. This lack of a canopy response translates directly to tree-level volume growth rates similar to those of control trees (Guiterman et al. 2011). An opposite pattern is present in the low-density

treatment for which increases in tree LA drive high tree-level growth rates.

Allometric Model Assessment

Performance of the allometric LA equations that we tested varied considerably between the tree and stand levels, fitting technique, and model forms. The sapwood-crown length model was consistently the most accurate one using all fitting techniques (Figure 3). Small variations in its parameter estimates appear to be unimportant, making this model form the most robust in predicting LA on trees of markedly different sizes (Figure 4). The Maguire and Bennett (1996) model achieves comparable accuracy when fitted using WNLS and is recommended if SBA is not available. It should be noted, however, that the b_3 parameter estimate for this model fit was not significant, which caused the model to be a slightly modified power function of crown length. Overall, we judge the Maguire and Bennett model to be less robust than the sapwood-crown length because other methods of fitting it produce much larger errors. Although the Valentine et al. (1994) model performed well at the tree level, it is clearly less accurate when summed to predict stand LAI, especially when fitted with a mixed-model approach.

In applying the sapwood-based equations, it is important to recognize the potential error associated with measuring SBA accurately. We tried to minimize this error by measuring SBA close to the time of peak LA (Vose and Swank 1990, Vose et al. 1994) from two to three radii per tree. Up to six radii, however, may be required to estimate SBA with only 20% error (R.S. Seymour, School of Natural Resources, University of Maine, 2006). Further research is required to determine the exact amount of error in measuring SBA from any number of radii and whether there is additional error associated with measuring it on increment cores.

Despite this shortcoming, SBA is commonly used as a surrogate for LA (e.g., O'Hara 1988, 1989). However, we advise caution in using SBA alone with eastern white pine because it may not account for changes in crown structure resulting from silvicultural thinning or natural self-thinning. This limitation is best demonstrated by plotting SBA and LAI over stand density (Figure 5). Note that the relationship of SBA to stand density is nearly linear, whereas LAIs estimated from our best equation (sapwood + crown length) and from litterfall approached an apparent asymptote at between 4 and 5. The sapwood-only LA equation also gave a linear relationship to density, but the diameter-crown length equation produced an asymptote (not shown). At densities greater than 700 trees ha^{-1} or a basal area of approximately 40 m^2 ha^{-1}, sapwood continues to increase whereas LAI remains constant (Figure 5), probably owing to the plasticity of crowns that are affected by crown recession and abrasion during self-thinning (Jack and Long 1991a, 1991b, Smith and Long 1992). The nonlinear form of the sapwood-crown length model (Dean et al. 1988)
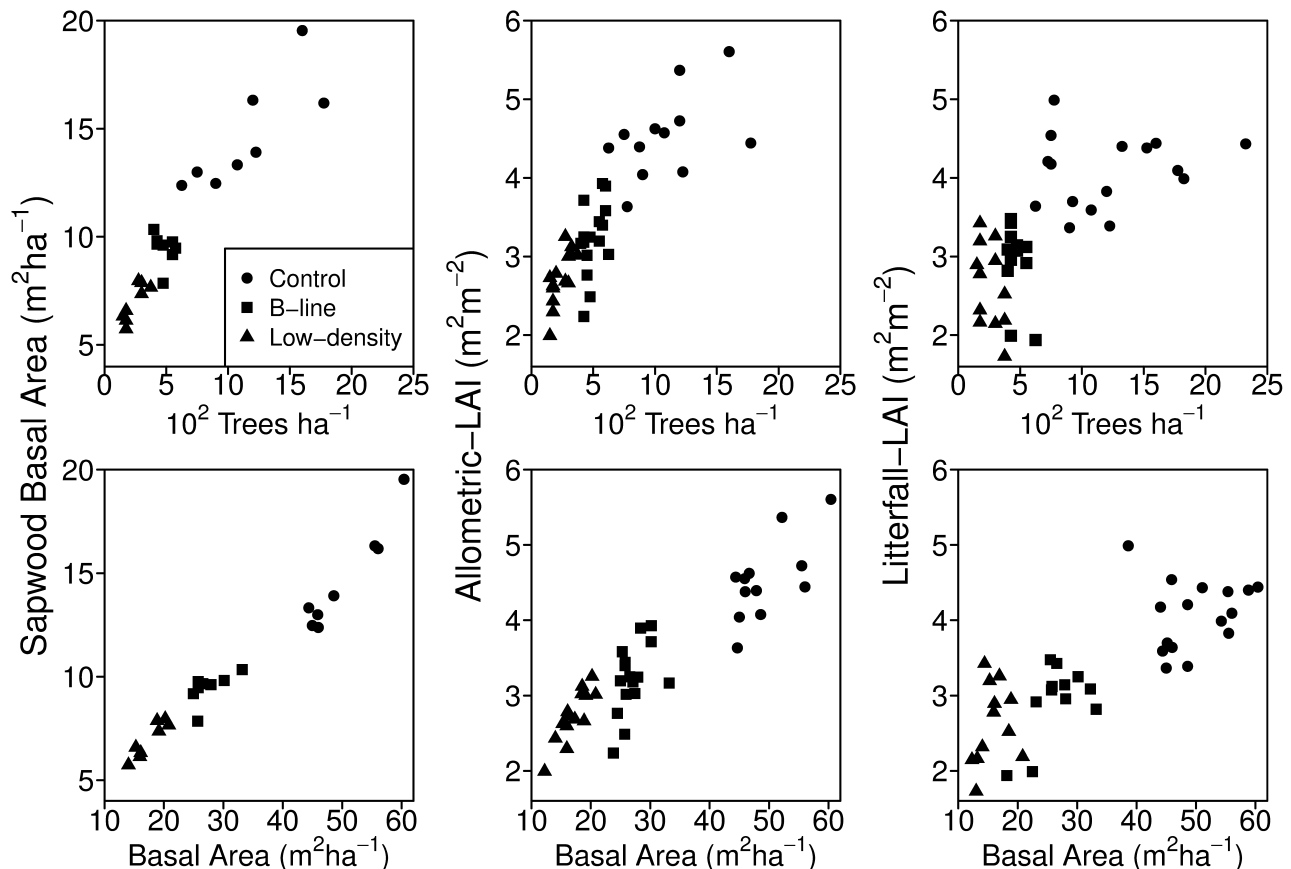

Figure 5. Comparison of stand densities with three estimates of canopy LA: sapwood basal area (a common surrogate for LA), allometric LAI estimates made with the sapwood-crown length equation and the NLME-F fit, and litterfall LAIs.

along with the integration of crown length as a metric for localized stand density and competition (Weiskittel et al. 2007) helped to capture the influence of crown structure on the sapwood-LA relationship.

When deciding among statistical fitting techniques for allometric equations, researchers must acknowledge the tradeoffs among different methods. Our results suggest that nonweighted least-squares techniques perform well in estimating the LA of large trees but overestimate for small trees. Weighting the models improved the fit to small trees but increased the error on large trees, and thus the overall error of the model increased (Figure 2). In application, the weighting reduced errors in LAI estimation because of the prevalence of small trees in the study stands, especially on control and B-line plots. Mixed-effects modeling had the most accurate fits to sample trees; however, applying NLME-R equations often resulted in the greatest bias (Figure 3). The fixed-effects models were similar in performance to the weighted model versions. This pattern might represent an inadequacy of our random effects to capture variability in the study population, where with greater sampling the NLME-R models (and the NLME-F versions) would probably be the best models to use. As it is, however, the use of mixed models would only be appropriate for analyses within the sample tree data set and not on our study population.

In this study, we used LAI estimates attained from litterfall sampling as the reference data from which to assess allometric models. Litterfall sampling, however, has its own set of potential errors. Because litterfall traps are located near the ground, there is potential for falling needles to drift between plots and for needles to be blown out of the traps. We tried to mitigate these potential errors by keeping traps approximately 5 m from plot edges, collecting needles in five traps per plot and by collecting needles shortly after needle senescence in October and new needle growth in May–June (the October collection comprises >90% of the total). Short of extreme wind events during needle fall, it is unlikely that needles would be blown from traps once they had landed because traps have 10-cm high side walls. Given the relatively wide spacing of trees on low-density plots, use of five traps might underestimate the actual LAI; however, there was good agreement in the LAI estimates between traps on all plots, with SEs usually <15%. Despite these limitations to litterfall sampling, our litterfall LAI estimates were comparable to values with our best independent allometric equations. Moreover, light interception estimates obtained with a LICOR LAI-2000 during the summer of 2001 (Pace 2003) nearly equaled our litterfall LAI estimates with an average difference of 1.5 ± 3.4% (AAD = 0.35 ± 0.12). Therefore, we feel confident that our litterfall LAI estimates were accurate and unbiased.

Conclusions

The optimal silvicultural system for even-aged stands of eastern white pine has been debated for decades. Our findings highlight the canopy responses of trees in each treatment. Conventional B-line thinning produces a minimal increase in crop tree LA due to competition from lower crown class trees, whereas the open structure of low-density stands enables rapid and sustained crown expansion until tree crowns begin to touch. The choice between the thinning regimes will depend on the manager's objectives. If crop tree attributes are desired, low-density thinning maximizes growth potential through sustained increases in tree LA and stand LAI but requires monitoring for the effects of crown closure that will slow or stop crown expansion and reduce growth. On the other hand, if periodic thinning entries that maintain a dense, closed canopy are desired, B-line thinning will maintain an "unmanaged" appearance and crown structure, while minimizing tree mortality and canopy gap formation. It is notable, however, that any thinning will reduce overall stand growth (Zeide 2001) because of a long-term reduction of LAI that will prevent full recovery to prethinning LAI levels.

In development of allometric LA equations, it is important that researchers be cognizant of tradeoffs in the accuracy of model forms and fitting techniques at both tree and stand levels. Mixed-effects modeling is a powerful tool, but if the sample is limited in depth or range, the random effects may be an inadequate representation of variability in the population. In such a case, applying the random effects may add bias, and the fixed parameters would be a better choice to use. Clearly, SBA is a robust predictor of LA, but some metric of stand density or competition (such as crown length) should be included to account for differences in crown structure, especially at high stand densities.

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