LEAF AREA INDEX, DENSITY, AND AGE

RELATIONSHIPS OF EASTERN WHITE PINE *(Pinus Strobus* L.) IN MAINE

By

Adam Ross Bland

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B.S. Northern Arizona University, 2010

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Advisory Committee:

Robert S. Seymour, Curtis Hutchins Professor of Forest Resources, Advisor

Aaron R. Weiskittel, Assistant Professor of Forest Biometrics and Modeling

Brian E. Roth, Associate Director for the Cooperative Forestry Research Unit

THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Adam R. Bland I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine

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Robert S. Seymour, Curtis Hutchins Professor of Forest Resource December, 2012

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Thesis Advisor: Dr. Robert S. Seymour

An Abstract of Thesis Presented
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Pure stands of eastern white pine are common across New England as a result of agricultural abandonment; however a consensus on the optimal management regime has not been reached after nearly 40 years of debate (Leak, 2003; Seymour, 2007). To assist with developing thinning schedules, a density management diagram (DMD) was developed for eastern white pine using permanent and temporary plot data from self-thinning stands over 200 years of stand development. A maximum size-density relationship was fit to data from 72 plots using least squares regression which was independent of site quality. Using this biological maximum, relative density (RD) can be calculated for any stand as a proportion of this maximum. Data used to fit the self-thinning lines were well above A-line on the white pine stocking guide, suggesting these guides underestimate maximum density, and overpredict self-thinning. RD can be used to achieve a variety of objectives from maximizing stand-level growth to low density crop tree management and can be used to assess the relationship between stand density and growth.

Leaf area is highly correlated with volume growth (Gilmore and Seymour, 1996; Innes et al., 2005; Jose and Gillespie, 1997) and is commonly used to quantify canopy responses to silvicultural treatments. Relationships between leaf area index (LAI) and relative density (RD) were examined in even-aged stands of *Pinus strobus* (L.) using long-term litterfall measurements over a wide range of stand development in both natural and silviculturally treated stands. Projected LAI ranged from 0.7 to 7.2 over RDs of 0.14-1.0. RD alone was a poor predictor of LAI, but when combined with TOPHT (mean height of tallest 100 trees per hectare) and site index (SI), stand development patterns of LAI were effectively modeled using a linear mixed effects model. LAI reached a peak at a TOPHT of approximately 12 meters followed by a gradual decline. Data suggests a nonlinear increase in LAI with increasing RD. At a given RD, LAI was strongly and positively correlated with site index (SI). Stand development patterns of LAI have implications for establishing rotation lengths and implementing thinning schedules for white pine and can be used to estimate LAI for even-aged stands.

Leaf area is an important metric of growing space occupancy and is arguably the most important determinant of stemwood formation in trees and stands; however individual tree leaf area is difficult to measure directly. As a result, allometric equations using sapwood area have become the preferred predictor due to the strong physiological relationship between the conducting xylem and the amount of foliage a tree can support. Archived data from 61 destructively sampled trees was used to develop individual tree projected leaf area (PLA_{Tree}) prediction models using both sapwood and crown-based parameters. PLA_{Tree} models were tested at the stand-level by comparing allometric LAI (by summing up trees within the plots) to LAI obtained from litterfall. The Valentine model using a combination of basal area and modified live crown ratio performed the best at both the tree- and stand-level with the added benefit of not requiring destructive coring, however all models provided poor estimates of LAI when extrapolated to the stand-level. Tree-level models generally underpredict LAI in thinned stands and overpredict LAI in nonthinned plots likely due to a limited sample size of destructively sampled trees as well as a lack of larger trees in the dataset.

To address the error when summing up PLA_{Tree} equations to the stand –level a variety of stand-level models were developed by modifying tree-level equations and tested by estimating litterfall LAI for each plot. The best model predicted LAI as a function of sapwood area per hectare and crown length per hectare and reduced the bias from scaling up the PLA_{Tree} equations. These models provided more precise estimates of stand-level LAI across a wide range of stand age and density, but are less practical as they require destructive coring of all trees.

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CHAPTER ONE

A DENSITY MANAGEMENT DIAGRAM FOR EASTERN WHITE PINE (*Pinus strobus* L.) IN THE NORTHEASTERN U.S.

ABSTRACT

A stand-density management diagram (DMD) is presented for eastern white pine (*Pinus strobus* L.) stands in the northeastern US. The diagram was derived from permanent and temporary plot data from fully stocked stands in central Maine. A biological maximum size-density relationship was fit using the relationship between average tree volume and density. Relative density can be calculated using the maximum size-density equation and is applicable to thinned and nonthinned natural stands, or plantations. The DMD represents the average growth trajectory for both natural stands and plantations, with corresponding quadratic mean diameter and stand top height isolines provided for nonthinned stands. Data used to fit the self-thinning lines were well above A-lines on commonly used northeastern stocking guides, suggesting these guides underestimate maximum density, especially for smaller stems, and thus overpredict self-thinning. Three scenarios using permanent plot data were presented as example applications of the DMD and are compared to the stocking guide most commonly used in the region.

INTRODUCTION

In recent decades, white pine (*Pinus strobus* L.) has arguably become the single most important commercial tree species in Maine, second perhaps only to red spruce in commercial value. Although the standing sawtimber volume of white pine and red spruce (*Picea rubens*) are nearly equal, recent net growth of pine sawtimber in Maine exceeds spruce by 3.3 times, despite the fact that the white pine forest type (including pine-hemlock) covers only one-seventh the area of the spruce-fir type (McWilliams et al. 2005). Thinning is commonly recommended to accelerate growth of crop trees and capture mortality; however, consensus as to the optimal management regime for even-aged stands has not been reached after nearly 40 years of debate (Leak 2004; Seymour 2007).

Appropriate stocking levels for white pine in the Northeast have been strongly influenced by the publication of a Gingrich-style (1967) stocking guide (Philbrook et al., 1973) which defines a region of “full stocking” bounded below by the B line and above by the A line. These guides assume that once full stocking is achieved growth varies little over a wide range of increasing density, the so-called Langsaeter hypothesis. While much research has gone into the development and refinement of stocking guides (Lancaster and Leak, 1978), recent research has demonstrated that stands with a history of early management can reach crown closure at stocking levels well below the B-line (Leak and Lamson, 1999; Seymour and Smith, 1987). Furthermore, Leak (1981) and Schlagel (1971) found that eastern white pine growth continued to increase at densities well above the B line refuting the validity of the Langsaeter hypothesis (Gilmore et al., 2005). Research from a thinning trial in Maine found that resulting growth of thinned stands was not linearly correlated with the amount of basal area removed (Guiterman et al., 2011; Seymour, 2007).

Density management diagrams (DMDs) make it possible to quickly design and evaluate the consequences of alternative density management regimes including commercial and precommercial thinning (Jack and Long, 1996; Wilson et al., 1999). DMDs estimate the maximum possible density at a particular stage of development, which allow foresters to determine stocking or relative density (RD) for any stand. The use of RD as a measure of stocking allows various density management zones to be defined that are roughly analogous to the A and B lines on stocking guides. This paper presents a DMD and RD values for eastern white pine in Maine, which offers a more flexible and less prescriptive method of planning thinning schedules compared to the conventional stocking guide. Results of the DMD are compared with the commonly used Philbrook (1973)stocking guide and examples are provided to illustrate the use of the DMD. The DMD can be used to determine an "optimum" from volume growth data on permanent plots.

METHODS

The majority of data used in constructing the DMD came from long-term measurements of permanent single-cohort sample plots on the Dwight B. Demeritt Forest in central Maine (44°54' N, 68°38' W) between 1992 and 2011. In order to increase the utility of the diagram and anchor the upper end of the volume spectrum, additional temporary sample plots were established in the summer of 2011. Fixed-radius plots ranging from 0.01 to 0.04 ha were used for this study with DBH (4.5 feet above the ground), total tree height, lowest live branch (LLB) and lowest live whorl (LLW; defined as the lowest live whorl having three or more live branches) measured for all trees within the plot. Top height (TOPHT) defined as the mean height (ft) of the tallest 40 trees per acre and quadratic mean diameter (QMD, in) the diameter of the tree of average basal area were calculated for each plot and year combination (Table 1.1)

Table 1.1 Mensurational characteristics of the data used to construct the density management diagram. Average values with standard deviation are shown in the top row with ranges shown in parentheses below.

n	Density (trees ac^{-1})	Basal Area (ft^2)	QMD (in)	TOPHT (ft)	MeanVol (ft^3)	Vol (ft^3 ac^{-1})	SI (ft)
72	1391(1645)	243(39.5)	8.8(5.6)	68.3(23.5)	22(42.5)	4084(3009)	64.8(3.5)
	(81-7082)	(171-333)	(2.7-27.4)	(31.2-133.4)	(0.5-212)	(91-17,156)	(56-73.3)

All analyses were performed using R (R development core team, 2012). Standing stemwood volume inside bark was calculated using a regionally updated version of Honer's volume equation (Li et al. 2012; their equation 4).

[1] $$\text{VIB} = \frac{(\text{DBH})^2}{0.397+(\frac{410.15}{\text{Ht}})}$$

where VIB is total volume inside bark (ft^3), DBH is diameter (in) at 4.5 feet above the ground, and *Ht* is total height in feet.

In August of 2011, increment cores were extracted at breast height from every tree in the permanent plot network (n= 598) and most trees within the temporary plots. Breast height age was evaluated using WinDendro with missing rings near the pith estimated using transparences with concentric circles of different sizes (Applequist, 1958). Total age was estimated by uniformly adding 8 years to the age at breast height using a mean site index of 70 (Frothingham 1914. In the case of one plot where trees had established under overhead shade of a shelterwood, effective free-growth age was estimated by dividing the radius of the suppressed core before release by sthe average annual radial growth measured from the 4-year period after the overstory was removed in 1994 (Fajvan and Seymour, 1993). The estimated number of free-growth rings for the suppressed core was then added to the number of rings after the overstory removal.

Site Index

Plot-specific site index values were calculated from the trees used to estimate TOPHT using the Frothingham (1914) site index curve fit by Parresol and Vissage (1998, their equation 6). Permanent plot site indices were calculated using the measurement period where stand age was closest to the base age of 50. For the thinning study plantation, plot-specific site index values were estimated from the height of the dominant tree on each plot at age 50. Values for temporary plots where trees were not cored (n=6) were derived from a detailed soils map and a weighted average was applied to each stand based on proportion of each soil type within each stand polygon.

Data Collection

Only pure, fully stocked, self-thinning stands with no apparent history of silvicultural treatment were used to calibrate the maximum density and isolines for the DMD (n=72). Intermediate or suppressed trees were observed, a strong indication that temporary plots were undergoing competition-related mortality and could be included in the analysis. Permanent plots lacking signs of self-thinning were removed from the analysis as were stands with relative density values less than 0.55, the minimum threshold of self-thinning hypothesized by Drew and Flewelling (1979). The DMD consists of five related models: the maximum size-density, average stand trajectory, crown closure lines, TOPHT and QMD isolines.

Fitting the Maximum Size-density Line

Although many diagrams have been developed using the -3/2 self-thinning rule (Yoda et al., 1965), controversy about the generality of this rule has prompted a re-evaluation of its efficacy (Weller, 1987; Zeide, 1987). Recent analysis has shown that the species self-thinning line is dynamic rather than a universal law (Lonsdale, 1990; Weller, 1987; Zeide, 1985; Zeide, 1987) so in addition to estimating the slope, we tested the influence of site quality on both the slope and intercept and the influence of stand origin on the slope using the following equation

$$[3] \quad \mathrm{Log}\overline{Vol} = b_0 + b_1 * \mathrm{LogTPA} + b_2 * \mathrm{LogSI} + b_3 * \mathrm{Planted} + b_4 * \mathrm{LogTPA} * \mathrm{LogSI})$$

where Log$\overline{Vol}$ is the log (base 10) of average volume in ft^3, LogTPA is the log of trees per acre, LogSI is the log of site index (feet, base age 50), and Planted is an indicator variable for whether the plot origin was natural or planted, (0=natural, 1=planted).

Successive elimination of non-significant terms using stepwise regression resulted in the following parsimonious reduced model form:

$$[4] \qquad \mathrm{Log}\overline{Vol} = b_0 + b_1 * \mathrm{LogTPA}$$

RESULTS

Stochastic Frontiers Analysis (SFA, Aigner et al. 1977; Bi et al. 2000) has been used to statistically evaluate the maximum density line and incorporate other factors that might influence the line such as site quality and stand origin. After visual inspection and quantitative comparison, quantile regression was selected to represent the biological maximum size-density relationship as it provided an excellent fit to the data (Figure 1.1) and diagnostics statistics (σ^2 and γ, see Coelli, 1996 for details) indicated that stochastic frontier function was not warranted (Table 1.2). A primary consideration when developing a DMD is broad applicability across varying site conditions and the similarity between fitting methods supports our assumption that the maximum size-density relationship was independent of site quality.

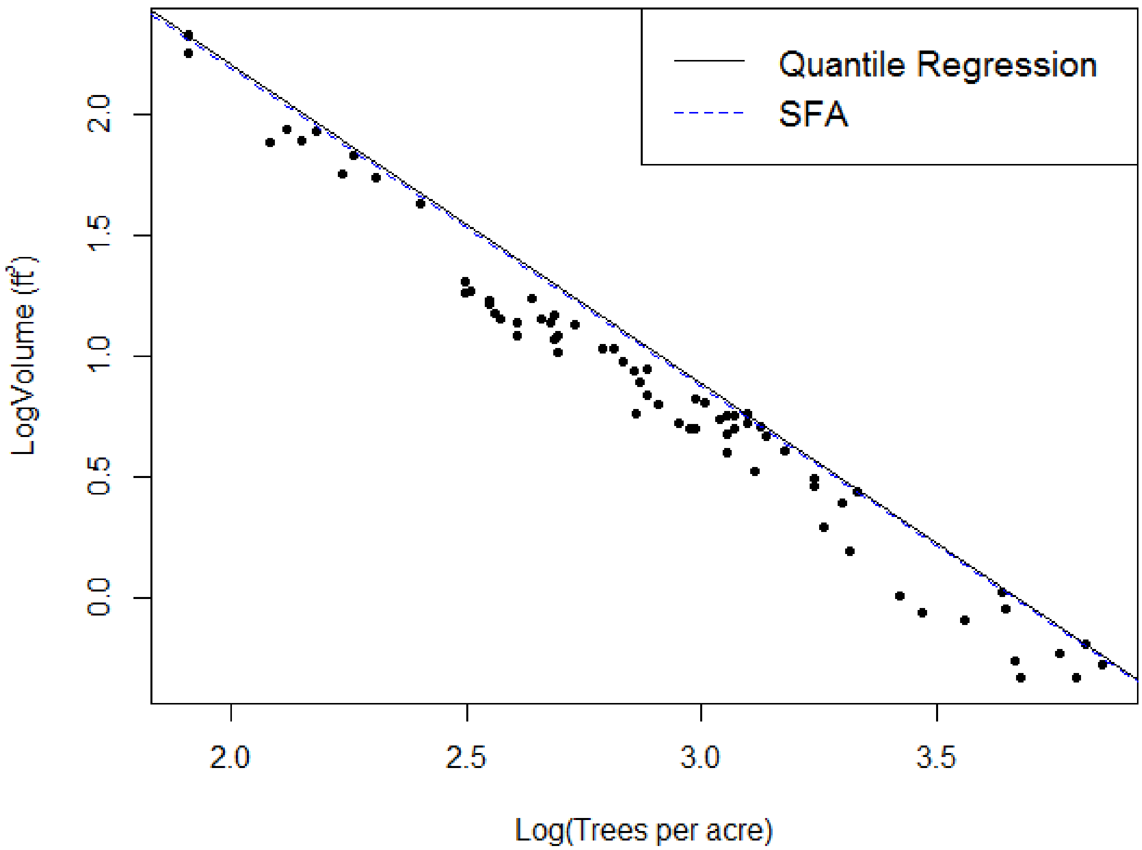

Figure 1.1. Graphical comparison of maximum density line fits using stochastic frontiers analysis (SFA) and ordinary quantile regression.

Table 1.2. Parameter estimates for the maximum density line fit using stochastic frontiers analysis (SFA) and ordinary least squares regression with standard errors shown in parentheses. σ^2 and γ are diagnostic statistics indicating the relevance of SFA with p-values of .55 and .13 respectively indicating that the use of SFA was not justified.

Model	b_0 (intercept)	b_1 (Slope)	σ^2	γ
SFA	4.80794	-1.311	0.0282	0.9858
	(0.733)	(0.1807)	(0.0474)	(0.656)
QR	4.83978	-1.3173	NA	NA
	(0.0499)	(0.016)		

Equations

Transforming the equation to the original units gives a negative exponential nonlinear model form typically given in DMD's:

$$\overline{Vol} = 10^{4.83978}\ \mathrm{TPA}^{-1.3173} \qquad [5]$$

The self-thinning or maximum size-density line in equation (3) represents a regionally estimated limiting relationship for eastern white pine that will, on average overestimate the potential stocking of a fully stocked stand. To estimate the average stand development, a second line parallel to equation (4) was fit through the geometric mean of the entire self-thinning data set (TPA =stems per acre , $\overline{Vol}$ = ft^3). This average-stand trajectory has the same slope as (4), but a lower intercept. The average stand trajectory corresponds to a relative density of approximately 0.74.

$$\overline{Vol} = 10^{4.66571}\mathrm{TPA}^{-1.3173} \qquad [6]$$

Equations predicting QMD and TOPHT were developed from the self-thinning data (n=72) using ordinary least squares (OLS) regression (Table 1.3).

$$\mathrm{QMD} = b_1(\overline{Vol}\,)^{b2}\mathrm{TPA}^{b3} \qquad [7]$$

$$\mathrm{TOPHT} = b_1(\overline{Vol}\,)^{b2}\mathrm{TPA}^{b3} \qquad [8]$$

Table 1.3. Coefficient estimates and fit statistics for QMD and TOPHT isolines including root mean squared error (RMSE), adjusted coefficient of determination (R^2), and Furnival's index (FI),(Furnival, 1961).

		Coefficient estimates					
Equation	*n*	b_1	b_2	b_3	RMSE	R^2adj	FI
QMD	72	6.4263 (0.9277)	0.3365 (0.0126)	-0.0802 (0.018)	0.2075	0.9986	0.212
TOPHT	72	10.4808 (3.4808)	0.3399 (0.0314)	0.1715 (0.0434)	3.9522	0.9705	4.037

Complete crown closure for white pine was determined using equations from Russell and Weiskittel (2011) relating diameter to crown width for eastern white pine in Maine. Maximum crown width for open grown white pine was estimated from equation 1 as:

[9] $$\mathrm{MCW} = 1.24\mathrm{DBH}^{0.585}$$

where MCW is maximum crown width (m) and DBHis diameter at breast height (cm). Largest crown width (LCW) was used to predict crown size for trees that are not able to reach their biological maximum because they are grown in denser forested stands using equation 2 as

[10] $$\mathrm{LCW} = \frac{\mathrm{MCW}}{\mathrm{DBH}^{0.147}}$$

where LCW and MCW and DBH are previously defined.

Crown projection area (m^2) was calculated as:

[11] $$\mathrm{CPA} = \pi(\mathrm{LCW}*0.5)^2$$

The number of trees per hectare representing crown closure was determined by dividing the tree CPA into the area in a hectare ($10{,}000 m^2$). Corresponding average volume at a given QMD was determined from the QMD equation in Table 3. The resulting crown closure equation was converted into TPA and cubic foot volume and is as follows:

[12] $$\overline{Vol} = 10^{7.8061}\mathrm{TPA}^{-3.072}$$

This line corresponds to a RD of 0.05 at a $\overline{Vol}$ of 0.3 ft^3 (approximately 3 in. dbh), and rises to a RD of 0.5 at a $\overline{Vol}$ = 82 ft^3. The resulting DMD constructed from Equations (5), (6), (7), (8) and (12) is presented in Figure 2.

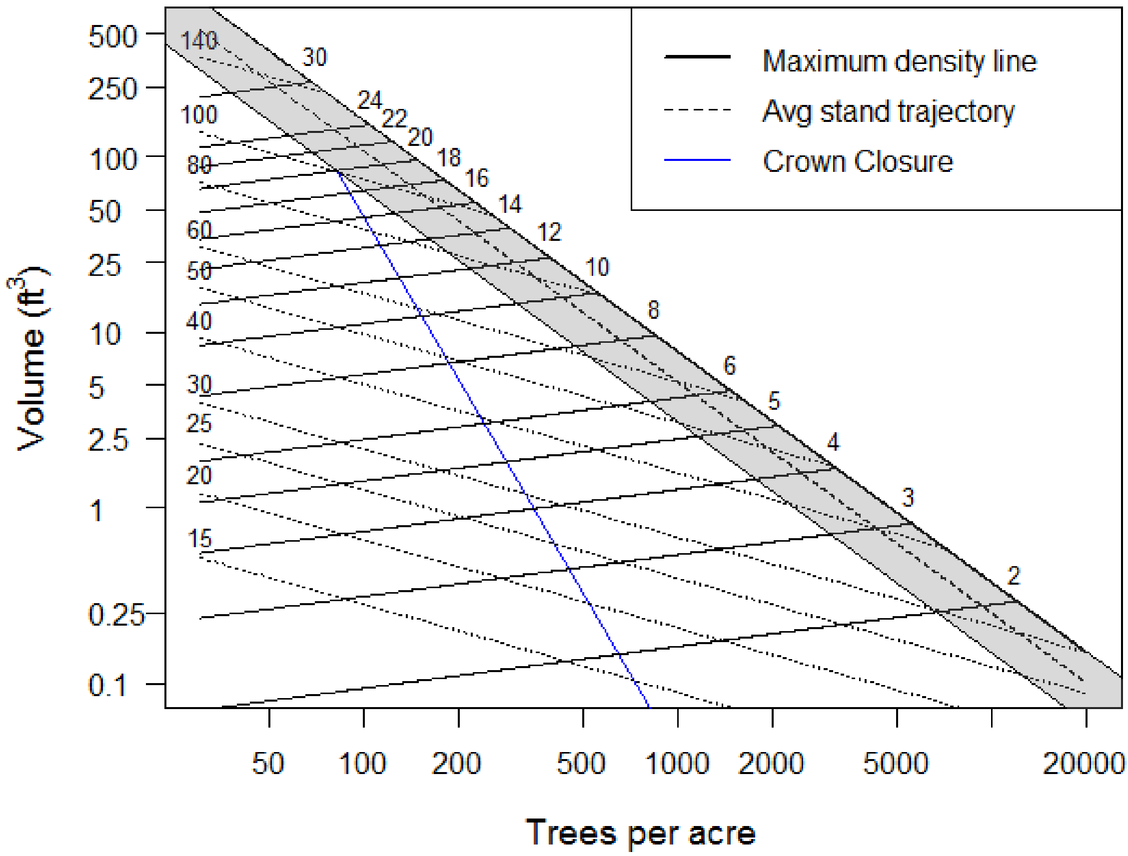

Figure 1.2. Density management diagram for eastern white pine including maximum density line, average stand trajectory, crown closure, QMD and TOPHT isolines. The highlighted area represents the range where isolines are considered accurate corresponding to relative density values of 0.5 to 1.

MANAGAMENT APPLICATIONS

The main advantage of a DMD is its ability to quickly design, display and evaluate alternative density management regimes. Average stand trajectories can be visually estimated directly from the diagram and tradeoffs between different thinning scenarios can be assessed. The inclusion of site or top height lines together with appropriate site index curves can be used to predict the age a stand will begin self-thinning, or plan timing of early thinning by estimating the TOPHT at which self-thinning will occur given stand density and using the site index curve to estimate the number of years to reach a given height. Harvest volumes from thinnings as well as the final harvest can be estimated from the diagram and constraints such as minimum harvest volumes or merchantability standards can be incorporated when planning thinning schedules. Managers can set a specific piece-size target for the end of the rotation and work backwards to the present stand condition, or thin to an “optimum zone” defined by researchers.

Data from a long-term thinning study in Old Town, Maine is used to demonstrate alternative stand development patterns of three different thinning scenarios. Summary stand statistics are presented in Table 4 and Figure 5 shows the stand trajectory of plotted on both the Philbrook stocking guide and the DMD developed in this study.

Stand Description

Permanent plot data from a 0.96 ha plantation on the University of Maine’s Dwight B. Demeritt forest near Orono, ME illustrates a typical application of the DMD. The eastern white pine thinning study (WPTS) first described by Seymour (2007) and more recently by Guiterman et al. (2011; 2012), was initiated to evaluate tree and stand responses to two contrasting silvicultural systems for white pine. The stand was an unreplicated spacing study planted at various densities from 2x2 to 8x8 foot spacing in 1949 on somewhat poorly drained silt-loam soils of the Buxton series with an average site index of 64.9 ft (base age 50; Frothingham 1914). Thinning treatments were assigned at random with each block consisting of a low density plot, a B-line and a nonthinned control plot based on similar initial densities. It was unmanaged until the first thinning in the fall of 1991 at age 42 and was subsequently re-thinned in 2001 and 2011.

Table 1.4. Stand attributes of thinning study permanent plot data from (1949-2011) for each inventory year, trees per acre (TPA), average tree volume in cubic feet ($\overline{Vol}$), basal area per acre (BA/Ac), TOPHT (TPHT), quadratic mean diameter (QMD), and relative density (RD).

	Control (B7)						B Line (A8)						Low Density (C7)					
Year	TPA	$\overline{Vol}$ (ft^3)	BA (ft^2)	TPHT (ft)	QMD (in)	RD	TPA	$\overline{Vol}$ (ft^3)	BA (ft^2)	TPHT (ft)	QMD (in)	RD	TPA	$\overline{Vol}$ (ft^3)	BA (ft^2)	TPHT (ft)	QMD (in)	RD
1949	1416	0.1	0.001	NA	NA	NA	1265	0.1	0.001	NA	NA	NA	1214	0.1	0.001	NA	NA	NA
1991	NA	NA	NA	NA	NA	NA	850	5.3	205.5	NA	6.6	0.64	911	4.8	208.1	NA	6.5	0.64
1992	941	5.03	222.4	56.5	6.6	0.68	253	7.1	79.12	56.5	7.6	0.24	152	8.3	56.6	55.2	8.3	0.16
1999	739	7.8	236.3	62.9	7.7	0.74	223	11.4	100.6	62.6	9.1	0.3	152	12.7	80.6	61.2	9.9	0.23
2001	718	8.7	244.1	65.8	7.9	0.79	223	13	112.2	64.5	9.6	0.34	152	15	90.7	63.8	10.5	0.26
2006	617	10.7	241.2	71.3	8.5	0.79	172	17.9	110.9	69.8	10.9	0.33	71	22.6	57.5	68.8	12.2	0.16
2008	496	12.2	211.6	73.9	8.9	0.70	172	20.2	115.6	74.9	11.1	0.36	71	25	61.2	72	12.6	0.18
2011	476	13.7	221.4	76.8	9.2	0.74	172	22	125.8	75.9	11.6	0.38	71	29.4	69.1	75	13.4	0.2

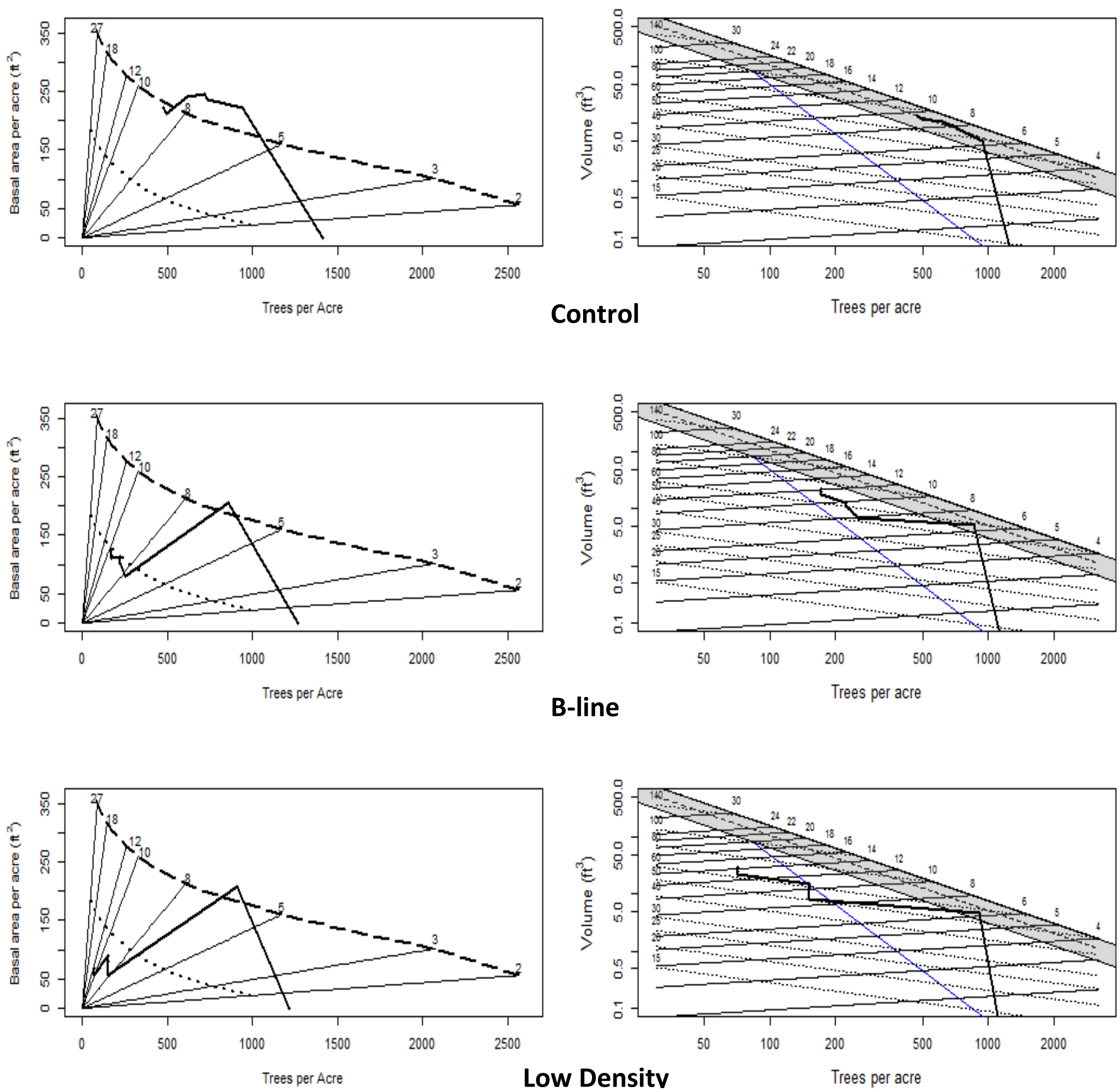

Figure 1.3. Stand trajectory of three plots within the white pine thinning study (WPTS) including a nonthinned control plot (upper), repeated thinnings to the B line (middle) and a low density crop tree approach (lower) displayed graphically on the white pine stocking guide (left) and the DMD (right).

Scenario 1: Natural Thinning Trajectory- Nonthinned Control

To effectively evaluate the influence of thinning, nonthinned controls were established to serve as a benchmark. Prior to 1992 the nonthinned stand experiences natural mortality, which reduced the density from 1416 in 1949 to 941 when it was measured in 1992. Between 1992 and 2011, the stand began self-thinning and moved upwards and to the left (Figure 1.3) along the average thinning trajectory line as competition-related mortality occurs. During this period, RD varied from 0.68-0.79 on the DMD (Table 1.4). In the absence of any harvesting, this stand is expected to continue along this trajectory. Natural stand development on the stocking guide show that the stand exceeds the A line early in stand development before eventually dropping below this point.

Scenario 2: Conventional B-Line Thinning

Repeated thinning to the B-Line on the Phibroook stocking guide is commonly recommended as the optimum method for growing maximum board foot volume of medium quality white pine (Leak, 1985) and is thought to be the minimum stocking where growth per acre is maximized (Lancaster et al., 1978). Similar to the nonthinned control, this plot had an initial density of 1416 TPA and was allowed to grow freely until 1992, during which time the density was naturally reduced to 850 TPA with an average tree volume of 5.3 ft^3 and a QMD of 6.6 inches (Table 1.4). In 1992, crop trees were marked and thinned to release them on 3-4 sides until the target residual basal area of the Philbrook (1973) stocking guide was achieved. The stand experienced some mortality despite RD values well below the self-thinning line, and continued to grow until 2001 when it was lightly rethinned and allowed to grow freely until it was remeasured in 2011. B-line thinnings reduced the RD from 0.64 to between 0.25 and 0.39 post-thinning (Table 4). The B line on the stocking guide is the theoretical crown closure line and the DMD suggests this plot is slightly above the minimum crown closure line, which is consistent with crown recession seen in these plots.

Scenario 3: Low Density/Crop Tree Approach

Low density crop tree management has recently come into favor with managers seeking to grow high value sawlogs rapidly on a relatively short rotation and recently numerous studies have supported this method as a viable management alternative (Desmarais and Leak, 2005; Guiterman et al., 2011; Page and Smith, 1994; Seymour, 2007). Similar to other scenarios, this plot had 1214 TPA in 1949 and was allowed to grow without intervention until 1992 when the density had self-thinned to 911 TPA with an average tree volume of 4.81ft^3 (Table 1.4). Crop trees in the low density treatment were marked for retention at an approximately 5.5-6.1 m (18-20 ft) spacing according to the Seymour and Smith (1987) stocking guide with all non-crop trees removed. Ten years later the stand was rethinned to a residual density of 71 TPA using a spacing to tree height ratio of 0.5. This reduced RD from 0.64 in 1992 prior to thinning to between 0.15 and 0.2 (Figure 1.3). Assuming no mortality the stand would naturally continue directly upward as trees accumulate volume. The trajectory on the stocking guide clearly shows the stand dropping well below the B line/crown closure line, and the DMD also suggests this stand remains below the lower limit of crown closure in 2001 post-thinning.

Hypothetical Scenario

Thinning to a Relative Density

A key step in designing a density management regime is deciding on upper and lower limits of relative density appropriate for particular stand management objective. This is similar to the concept of stocking guides which suggest an "optimum zone" which lies between the B and the A lines (Figure 1.5). The following section demonstrates how DMDs can be used to plan a series of thinnings to a RD of 0.2. For this example, we used pre-thinning plot data from the low density thinning study scenario to develop a hypothetical scenario consisting of repeated thinning to a relative density of 0.2 using an upper RD limit of 0.5 selected to minimize losses of merchantable volume due to competition-related mortality. Starting with the current stand conditions of a mean volume of 4.81 ft^3 at 911 TPA, initial RD is calculated using equation 5 based on the maximum number of trees per acre that can occur at a mean volume of 4.81 ft^3. Solving for TPA, we come up with 1432 trees per acre. RD is calculated simply by dividing the current TPA by the biological maximum 911/1433 = 0.64. Holding mean volume constant we locate the TPA that intersects with a RD of 0.2 which is 287 TPA (Table 1.5). Assuming no competition-related mortality, the density will remain constant and a new average volume is calculated for the upper RD limit corresponding to a volume of 16.08 ft^3. The residual TPA for this volume is once again estimated for the lower relative density limit and this procedure is repeated until a final average volume is reached. In this example, we grow the stand out until the average tree volume is 100 ft^3.

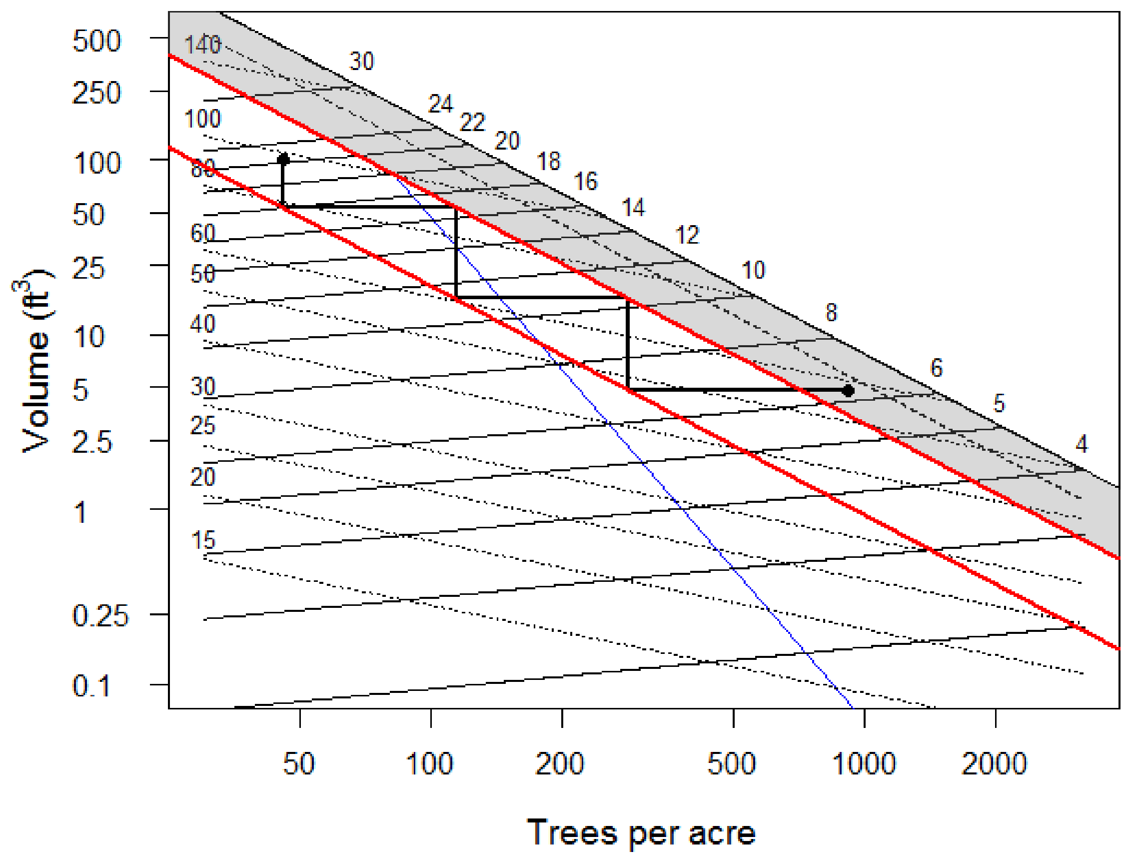

Figure 1.4. Hypothetical thinning scenario using RD plotted on the DMD. This scenario maintains a RD between 0.2 and 0.5.

Table 1.5. Summary statistics for hypothetical thinning scenario including trees per acre (TPA), average volume($\overline{Vol}$), and harvest volume estimated from the DMD.

RD Scenario		
TPA	$\overline{Vol}$ (ft^3)	Harvest Volume (ft^3)
911	4.81	
287	4.81	3001.4
287	16.08	
115	16.08	2765.8
115	53.77	
46	53.77	3710.1
46	100	4600

DISCUSSION

Stocking Guides

In the Northeast, the Philbrook (1973) stocking guide is the most common tool used to evaluate stocking in even-aged white pine stands. Stocking guides are two-dimensional nomograms, which depict various combinations of basal area and trees per acre (and thus, quadratic mean diameter) that define certain biological thresholds. The A Line defines the upper limit of stocking, whereas the B Line is meant to represent the lower limit of complete crown closure. The definition for the C line varies, but generally expresses 10 years until a stand reaches crown closure. In response to criticism that the B-line underestimates potential stocking in managed stands, the revised white pine stocking guide (Leak and Lamson, 1999) has two sets of B and C Lines in recognition of the fact that the exact densities that define crown closure are not fixed, but depend on the stand's past history of thinning (Seymour and Smith, 1987). When data used to estimate the self-thinning line in this study are displayed on the white pine stocking guide, a majority of the data fall well above the A line (Figure 1.5) suggesting that the Philbrook (1973) stocking guide underestimates potential stocking of younger eastern white pine stands in Maine (<10 inches dbh).

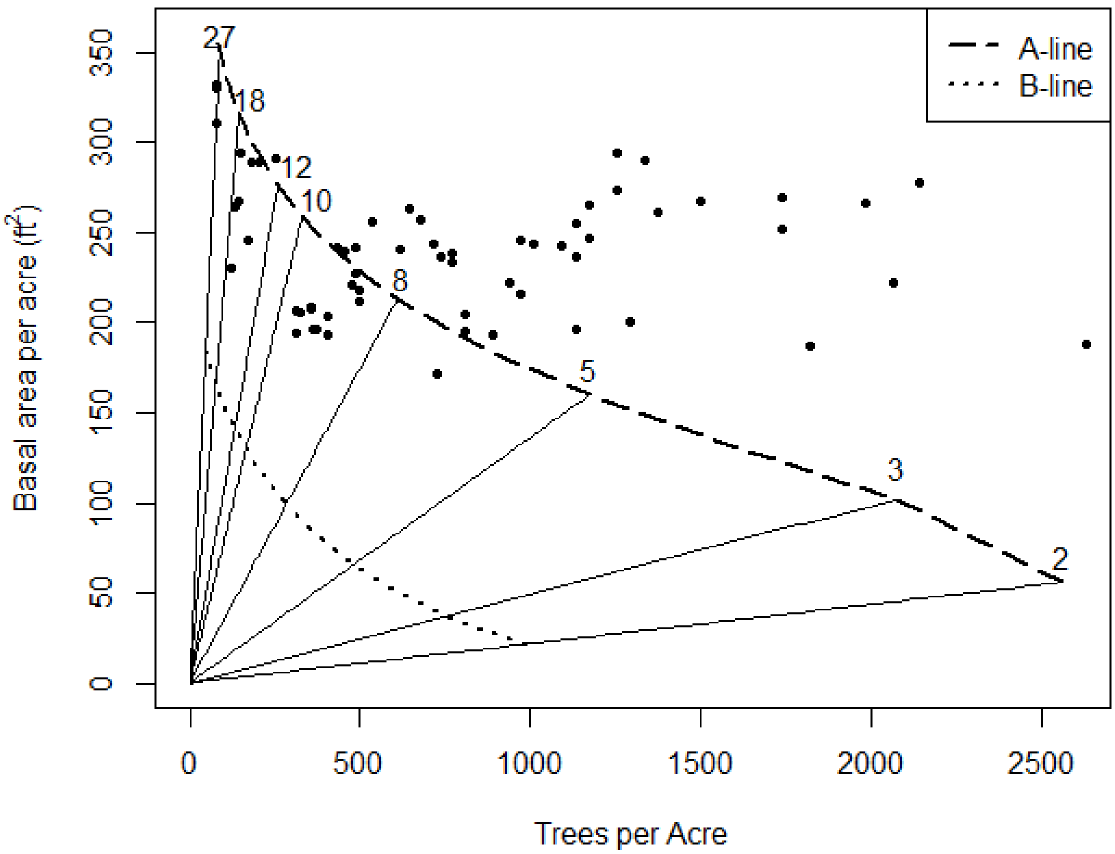

Figure 1.5. Data used to construct DMD data plotted on the Philbrook (1973) eastern white pine stocking guide.

Maximum Size-Density

The biological basis of the DMD is the -3/2 “self-thinning rule”, which defines the maximum possible density a stand can achieve at a particular stage of development. For eastern white pine, Smith and Woods (1997) and Innes et al. (2005) found slopes of -1.73 and -1.51 in Ontario and New Hampshire, respectively. When these maximum density relationships are plotted over the self-thinning data used in this study, many of the data points at high densities lie above the maximum self-thinning line (Figure 1.6). This suggests that, like the stocking guide, these maximum density relationships slightly overestimates the maximum potential stocking for older/larger stands while grossly underestimating younger/smaller stands when basal area is used as a metric of stocking. Slopes shallower than -1.5 have been found for other northeastern conifers including -1.24 for balsam fir (Sprugel, 1984), and -1.21 for spruce-fir stands in Maine (Wilson et al., 1999).

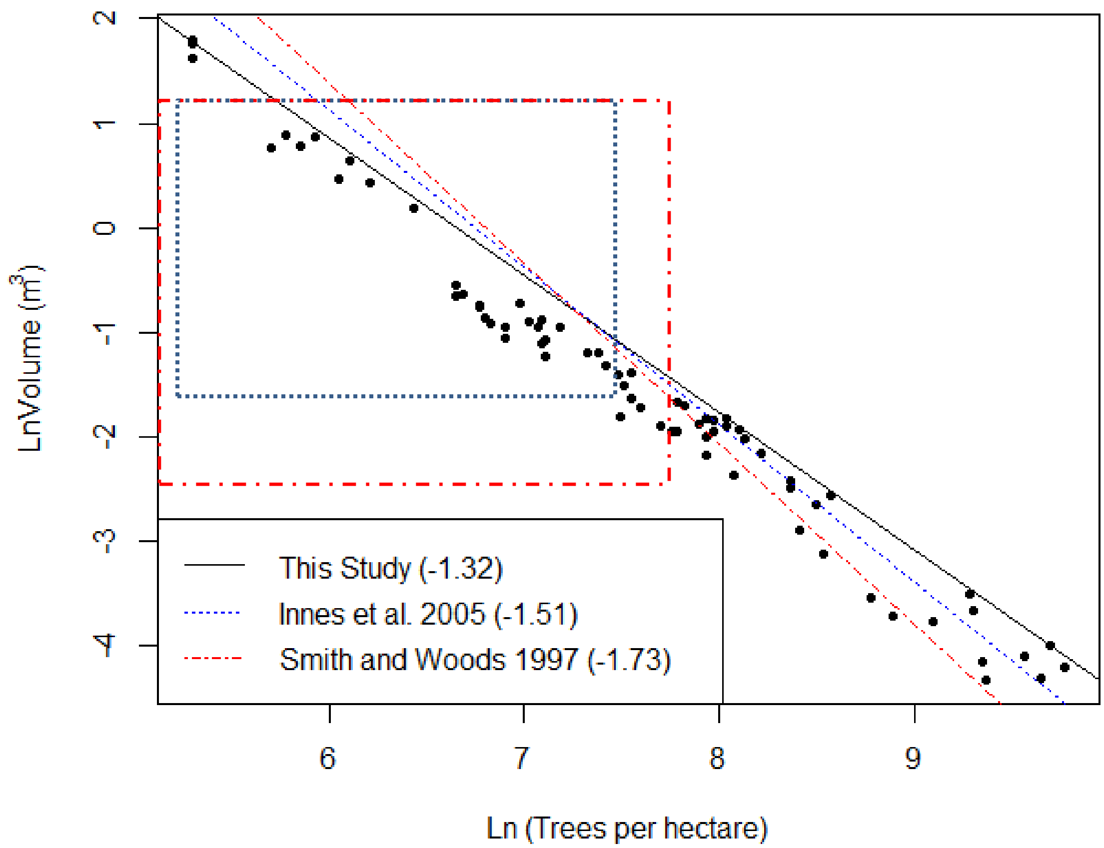

Figure 1.6. Comparison of eastern white pine maximum density lines from the literature including New Hampshire (Innes et al. 2005), Ontario (Smith and Woods 1997) and this study. The maximum size-density relationship for this study was calculated using natural log to allow direct comparison with other studies. Boxes correspond to the range of density and average volume used in each study with slopes included in the legend.

Additional Considerations

This DMD provides an objective, quantitative framework for developing density management prescriptions in even-aged eastern white pine stands and are an improvement over stocking guides. Determining appropriate stocking levels involving biological and economic factors specific to a particular management objectives. While the self-thinning lines are assumed to be independent of initial stand density and can be used to predict mortality and RD of any stand, the QMD and TOPHT isolines are only accurate for nonthinned stands. Heavily thinned stands will have a larger QMD and higher average volume at a given TOPHT and will therefore most likely underestimate average volume for stands at a given TOPHT, therefore the use of isolines is only recommended for stands within the highlighted region corresponding to RD values between 0.5 and 1.

CHAPTER TWO

PATTERNS OF LEAF AREA INDEX OVER STAND DEVELOPMENT FOR EVEN-AGED EASTERN WHITE PINE (*PINUS STROBUS* L.): AN ANALYSIS FROM LONG-TERM LITTERFALL MEASUREMENTS

ABSTRACT

Leaf area index (LAI) is an important metric of growing space occupancy and is arguably the most important determinant of wood production in forest trees and stands. To test the hypothesis that a combination of relative density (RD), site index (SI) and stand top height (TOPHT, surrogate for age), can accurately predict LAI, long-term litterfall measurements were used to quantify and evaluate LAI over an eastern white pine (*Pinus strobus* L.) chronosequence in central Maine composed of 14 locations spanning nearly 200 years of stand development. LAI peaked when dominant trees reached a top height of 11.7 meters or at approximately 30 years and declined gradually at a given relative density (RD). LAI increased nonlinearly with RD, but the relationship varied with history of thinning. Maximum LAI was highly and positively related to site index (SI). When analyzed simultaneously, stand top height, RD and SI are strong predictors of LAI in even-aged stands and can be used to indirectly manage LAI.

INTRODUCTION

Leaf area index (LAI) is the primary biophysical parameter used in forest productivity modeling and carbon sequestration studies, and is commonly used to quantify canopy responses to silvicultural treatments (Gower et al., 1999; Guiterman et al., 2012; Landsberg and Waring, 1997) because canopy foliage or leaf area is highly correlated with volume growth (Gilmore and Seymour, 1996; Innes et al., 2005; Jose and Gillespie, 1997). Innes et al. (2005) found that a combination of site index (SI) and relative density (stand density index) were significant predictors of LAI for eastern white pine (*Pinus strobus* L.) in New Hampshire and integrating age-related trends into a model can allow for more precise inferences about patterns of LAI through stand development. It is well established that productivity of forest stands declines with age and the magnitude of this decline is directly related to the amount and efficiency of leaf area (Long and Smith, 1992; Ryan et al., 1997). Peak production and its subsequent decline are associated with changes in canopy architecture, growth efficiency and the structure of developing forest stands (Smith and Long, 2001). Quantifying the influence of density and site quality on age-related patterns of leaf area can provide the scientific underpinnings to understand growth and development of even-aged white pine stands as they age.

Age

The development of LAI through time is related to mean annual increment and influences rotation lengths for even-aged stands, thus understanding this relationship is of paramount importance for timber production and carbon sequestration. Two primary age-related leaf area patterns have been reported in the literature; namely a peak followed by a constant LAI and a peak early in stand development followed by a progressive decline. Aplet et al. (1989) found that LAI reached a plateau in 200-700 year old Rocky Mountain spruce-fir stands although these estimates were based on sapwood regression equations. Needlefall collections found a similar pattern of constant LAI after a peak for loblolly (*Pinus taeda*) and slash pine (*Pinus elliottii*), although these were measured over a relatively short rotation (16 years) (Figure 3, Jokela and Martin 2000). Long and Smith (1992) were the first to suggest age-related decline in leaf area for *Pinus contorta* var. *latifolia,* hypothesizing that this decline was caused by crown abrasion as trees grow taller and sway more in the wind (Rudnicki et al., 2003). Perhaps the most convincing evidence for age-related decline in LAI comes from a meta-analysis of 12 chronosequence studies by Ryan et al. (1997), which demonstrated a peak, followed by a progressive decline in 11of 12 species. In contrast, In a number of eastern white pine chronosequence studies, leaf area index reaches a peak LAI between 15 (Peichl and Arain, 2006; Vose and Swank, 1990), and 20 years (Barker, 1998) followed by a gradual decline.

Density

Early studies suggested that LAI reached a plateau around the time of crown closure and that increasing density had no effect on LAI (Long and Smith, 1984; MarMoller, 1947). This idea is the basis of many stocking guides derived from the Langsaeter (1941) hypothesis, which asserts that there is a range in density where volume growth is independent of density. In contrast, Baskerville (1965) and Jack and Long (1991) found LAI to be positively related to RD for even-aged stands of *Abies balsamea* L. and *Abies lasiocarpa* (Hook.) Nutt., respectively. Kenefic (2000) found a similar pattern for multi-aged, mixed species conifer stands in central Maine. Many other studies also support the general positive relationship between LAI and density in stands managed at densities below self-thinning (Dean and Baldwin, 1996; DeRose and Seymour, 2010; O'Hara, 1996).

Site Quality

Site quality has been shown to be related to maximum LAI (DeRose and Seymour, 2010; Long and Smith, 1989; MarMoller, 1947) with higher quality sites supporting more foliage than those of lower quality (Assmann, 1970). In plantation studies, manipulation of site quality through fertilization have resulted in corresponding increases in stand-level leaf area and stand growth in both loblolly pine and slash pine (Albaugh et al., 1998; Colbert et al., 1990; Jokela and Martin, 2000; Vose and Allen, 1988; Will et al., 2002). Similar results were reported in with natural stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) by Gower et al. (1992). Innes et al. (2005) found that a combination of SI and density (SDI) accurately estimated LAI (R^2=0.66) for even-aged stands of eastern white pine.

To test the hypothesis that a combination of relative density (RD), site index (SI) and stand top height (TOPHT), can accurately predict LAI, we used permanent plot data with corresponding litterfall LAI measurement over a wide range of stand ages and silvicultural treatments. Understanding how age-related patterns of leaf area quantity is influenced by density and site quality will aid in developing age-specific silvicultural thinning schedules for even-aged white pine stands. Results from this research will inform ecologically based management of this species from timber production to carbon sequestration and will provide the foundation for future research on the production ecology of eastern white pine.

METHODS

Study Site and Data Collection

Study sites are located within the University of Maine's Dwight D. Demeritt Forest (Orono, Maine, 44°54' N, 68°38' W). We used thirteen previously established permanent plots representing a wide range of both natural and silviculturally treated even-aged white pine, with uninterrupted litterfall collection ranging from 1 to 20 years (Table 2.1). Six of these were naturally regenerated permanent plots representing fully stocked self-thinning pure or nearly pure (>80% BA) white pine stands over a range of stand development stages from young saplings to old-growth. The remainder of the plots was silviculturally thinned to various densities.

Table 2.1. Stand attributes of permanent plot network within the Demeritt Forest including stand name, age at breast height in 2011 (BH Age) , mean height of tallest 40 trees per acre (TOPHT), relative density (RD), site index (SI), projected leaf area index values from average of litterfall traps (LAI), year of first collection (First Collection), number of traps per plot, plot size (in hectares).

Stand	BH Age (2011)	TOPHT (m)	RD	SI (m)	Litterfall LAI	First Collection	No of Traps	Plot Size (ha)
Nonthinned								
1990	18	(5.7-11.4)	(0.17-1)	21.5	(1.0-7.3)	2001	6	0.01
1970	42	(12.5-19.6)	(0.61-1)	20.3	(4.1-4.8)	1996	4	0.01
Control	65	(16.2-24.3)	(0.32-0.83)	19.1	(3.4-4.7)	1992	20	0.04
HD	65	(15.4-22.7)	(0.65-0.97)	19.1	(3.2-5.0)	1992	6	0.03
BlueSpr	80	29.4	0.93	21.4	4.1	2011	5	0.04
MM	108	34.5	0.94	22.2	(3.4-4.6)	2010	5	0.04
Nutting	203	(37-40.7)	0.94	19.8	(3.4-4.7)	2002	5	0.04
Early PCT								
2x2	19	(6.1-12.1)	(0.1-0.45)	21	(1.6-6.1)	1998	2	0.01
2x2New	20	(7.3-13)	(0.12-0.4)	23.2	(4.6-5.7)	2002	5	0.01
3x3	22	(11-14.2)	(0.18-0.4)	22.8	(5.1-6.8)	1998	5	0.01
LightThin								
Old-Field	62	(18.9-25.4)	(0.64-0.89)	19.5	(4.0-5.0)	1992	5	0.04
Low								
LD	65	(17.1-23.2)	(0.15-0.25)	18.7	(1.7-3.4)	1992	20	0.04
1970-LD	42	16.3	(0.11-0.16)	19.4	(0.4-2.4)	2008	5	0.04
B-Line								
B-line	65	(16.1-23.6)	(0.23-0.4)	18.7	(1.9-3.9)	1992	20	0.04

Fixed-radius plots ranging from 0.01 ha to 0.04 ha were established within each stand with trees numbered and remeasured approximately every 5 years. Within each plot, diameter at breast height (DBH, 4.5 feet above the ground), total tree height, lowest live branch (LLB) and lowest live whorl (LLW; defined as the lowest live whorl having three or more live branches) were measured on all trees.

Site Index

At least two increment cores per tree were extracted at breast height using a 24 volt cordless power drill and 16 inch increment borer. Trees less than 16” DBH were double cored straight through the pith providing two cores 180 degrees apart. Trees larger than 16” had at least one age core extracted approximately 120 degrees with additional cores extracted in the case of missing pieces or indistinguishable rings due to rot. The cores were glued into grooved boards in the field, dried at room temperature and sanded to aid in identifying the ring boundaries in subsequent lab analysis.

Plot-specific site index values were calculated from the trees used to estimate TOPHT using the Frothingham (1914) site index curve fit by Parresol and Vissage (their equation 9b, 1998). Permanent plot site indices were calculated using the measurement period where stand age was closest to the base age of 50. When possible, plot-specific site index values were estimated from the height of the dominant tree on each plot at age 50. Values for temporary plots where trees were not cored (n=6) were derived from a detailed soils map with a weighted average applied to each stand based on proportion of each soil type within each stand polygon.

Litterfall-LAI

Litterfall has been monitored continuously using five 0.25 m^2 traps per plot providing up to 20 years of uninterrupted litterfall data. The traps are spatially arranged in an "X" pattern with one trap at plot-center and the others located half way along the diagonals from plot-center to the outside boundaries. Litterfall has been collected twice annually: in late October, following senescence and drop of the two-year needles, and in late May, just prior to bud-break. Samples were dried at 60 degrees C, sorted, and weighed to the nearest 0.01 gram. Plot-level leaf area index (LAI) was estimated as the mean of the trap-LAI, calculated as:

[1] $$\text{LAI} = \left(\frac{\text{Needle Mass} * \text{SLA} * \text{SCF}}{\text{Trap Area}}\right) * \text{Needle Retention}$$

where SLA is specific leaf area (cm^2 needle leaf area per gram needle mass), SCF is a senescence correction factor, and needle retention is the average number of years that needles stay on a given branch.

A senescence correction factor of 15.1 ± 2.3% (SE) was used to convert the dry weight of the abscised needles collected in the trap to their approximate dry weight when alive based on a subsample of branches collected within the University Forest (Guiterman et al., 2012). Values for SLA and needle retention come from archived sample branch data as part of the white pine litterfall collection program on the University of Maine School Forests. SLA was calculated using an archived database of 135 destructively sampled tree branches within the study area. Preliminary analysis suggested that mean SLA for the youngest stand was significantly different from all others; however this difference was nullified when two abnormally high SLA values from very small tree (<2cm DBH) were removed from the data set. After removing outlying trees, SLA values were relatively constant among stands, regardless of stand age or density and a mean SLA value of 66.12 (cm^2 g^{-1}) ± 0.75(±SE) (n=135) was applied to all plots.

Due to variable needle retention (e.g. 2.21-2.37 years) for eastern white pine, litterfall collections two years post overstory measurements were used to evaluate LAI for inventory years prior to 2010. For plots measured in 2010 and 2011, concurrent litterfall data was used as 2012 and 2013 data was not yet available. To reduce the inherent variability in leaf litter, a loess smoothing function was fit to the litterfall data for each plot as a function of year (Figure 2.1). This polynomial spline was fit using R (R Development Core Team, 2012) with number of knots defined as 1- the degrees of freedom. This had the effect of reducing the influence of anomalous LAI values caused by measurement error, climatic events such as ice storms or a substantial cone crop and elucidated average LAI trends within plots.

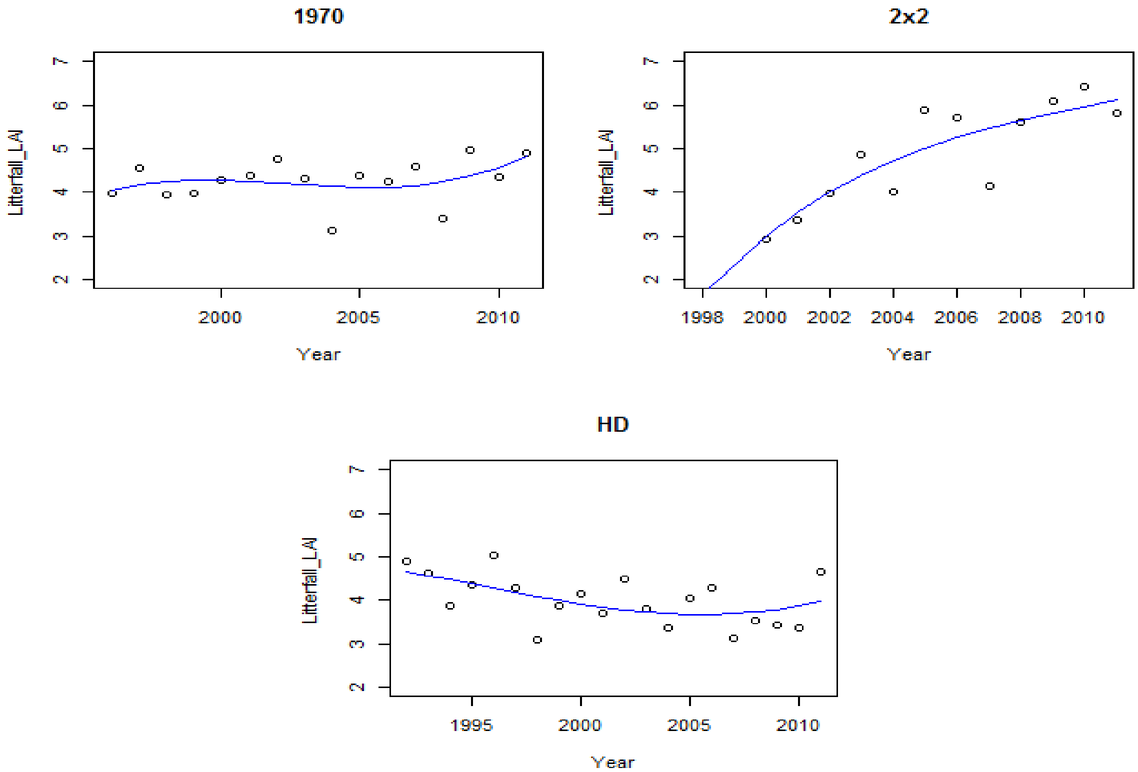

Figure 2.1. Projected Litterfall LAI for three permanent plots with fitted spline shown.

Analysis

To quantify hypothesized LAI developmental patterns, various linear and nonlinear models were assessed using different independent variables: RD, calculated using equations from density management diagram (Chapter 1); TOPHT (m) and SI (m base age 50), calculated using Parresol and Vissage (equation 9b, 1998) from increment cores extracted in 2011 (Table 2.1). A generalized additive mixed model (GAMM) was used to assess the relationship between the model parameters and the independent variable (Wood, 2006). Several statistical methods and model forms were assessed before deciding on a linear mixed effect model using plot as a random effect. Akaike's information criterion (AIC), root mean squared error (RMSE), mean absolute bias (MAB) and generalized coefficients of determination R^2 (Kvalseth 1985), and were used to assess model fits. An AIC reduction of 10 units was considered statistically significant (Burnham and Anderson, 2002). RMSE was calculated in the original units.

RESULTS

Preliminary scatterplots suggested nonlinear relationships between LAI and all independent variables analyzed. A generalized additive mixed model (GAMM) was fit to the data to analyze the degree of smoothness between TOPHT, relative density and site index. The result is a loess smooth function showing differences with respect to the mean for all independent variables (Figure 2.2). LAI showed a peak early in stand development at a TOPHT of less than 15 meters followed by a decline. LAI increased linearly until a RD of 0.5 with a curvilinear relationship thereafter. Similarly, LAI appeared to increase nonlinearly through the range of SI values present in this study.

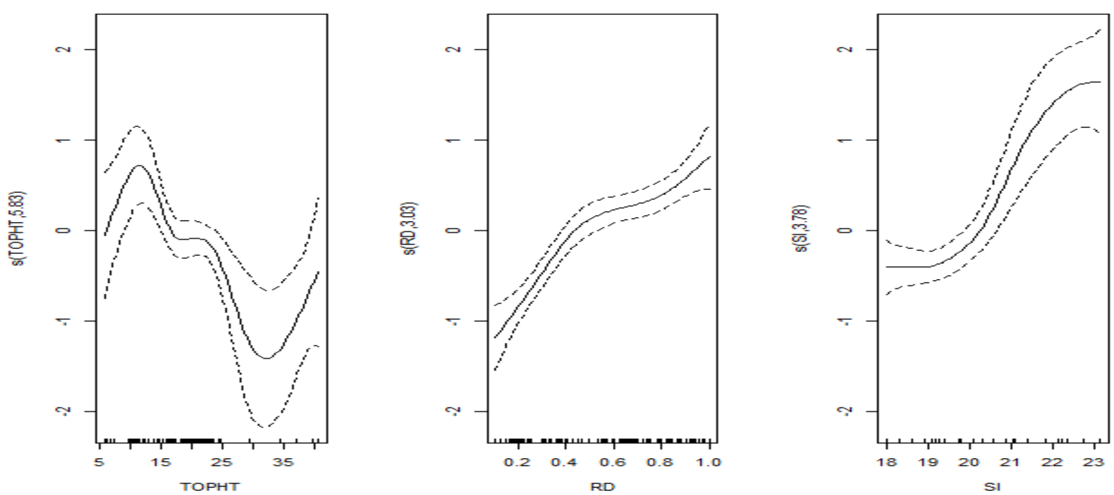

Figure 2.2. Generalized additive model showing difference from the mean for stand top height (TOPHT), relative density (RD), and site index (SI). The dashed lines represent a confidence envelope.

A variety of models were tested from the literature including models developed by Innes and Ducey (2005), DeRose and Seymour (2010) and well as linear mixed effect model developed for this study (Table 2.2).

Table 2.2. Model forms for estimating leaf area index (LAI) of permanent plots. Summary includes model number, equation, reference and random effects if included.

Model	Equation	Reference
1	LAI=$b_1 + b_2$log(RD) + $b_3$log(SI)	Innes et al. (2005)
2	LAI= $b_1 + b_2$log(SDI) + $b_3$log(SI)	Innes et al. (2005)
3	LAI=b_1*RD^{b2}*SI^{b3}*b_4*TOPHT$^{(b4-1)}$exp(-[(TOPHT/b_5)^{b4}])	DeRose and Seymour (2010)
4	LAI=b_1*RD^{b2}*SI^{b3}*b_4*TOPHT$^{(b4-1)}$exp(-[(TOPHT/b_5)^{b4}])	DeRose and Seymour (2010)
5	LAI= b_1+ b_2TOPHT+$b_3$log(TOPHT) + $b_4$log(SI) + b_5RD	This Study
6	LAI= b_1+ b_2TOPHT+$b_3$log(TOPHT) + $b_4$log(SI) + $b_5$log(RD)	This Study
7	LAI= b_1+ b_2TOPHT+$b_3$log(TOPHT) + $b_4$log(SI) + b_5SDI	This Study
8	LAI= b_1+ b_2TOPHT+$b_3$log(TOPHT) + $b_4$log(SI) + $b_5$log(SDI)	This Study

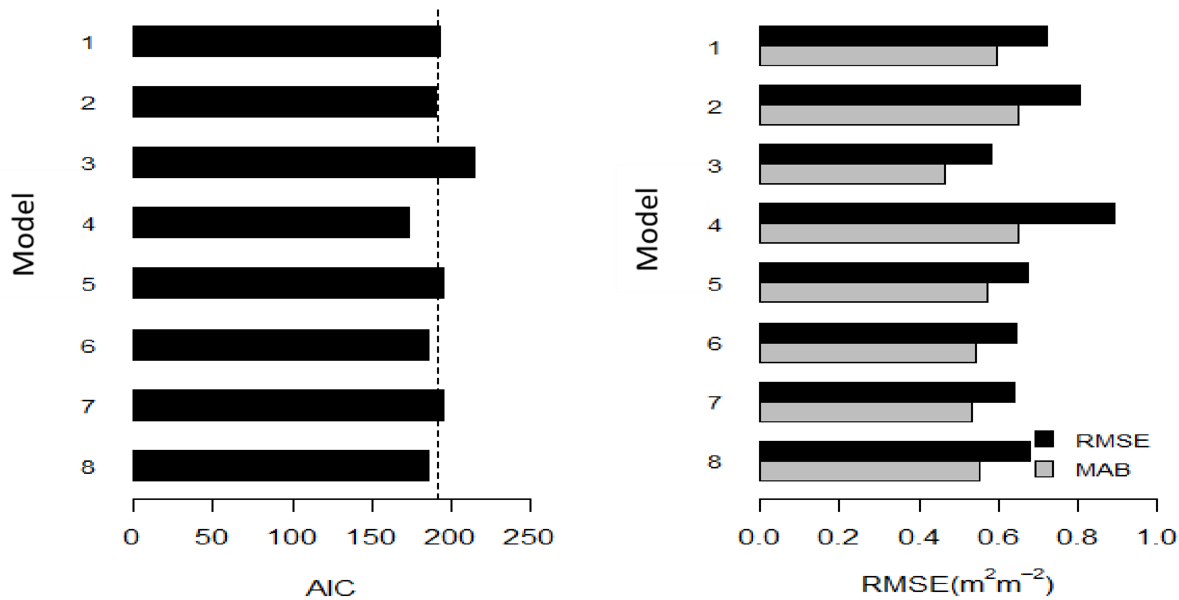

Figure 2.3. Barcharts of fit statistics for LAI model including Akaikes information criterion (AIC), root mean squared error (RMSE) and mean absolute bias (MAB) in original units. The dotted line represents average AIC for all models tested.

Although Model 4 had a significantly lower AIC value than all other models, the b_1 parameter was non-significant and it had the highest error and bias so it was disregarded (Table 2.3, Figure 2.3). When stand attributes were analyzed simultaneously, the best fit was from a linear mixed effects model showing LAI as a function of TOPHT, RD, and SI (Model 6, Table 2.3), where log is base 10 and RD, TOPHT, and SI are previously defined. Model 6 was selected based on low RMSE, MAB and FI values) as well as the significant parameter estimates (Table 2.4).

Table 2.3. Fit statistics for LAI models including Akaike's information criterion (AIC), Furnival's Index (FI), Root mean squared error (RMSE, m^2/m^{-2}), mean absolute bias (MAB, m^2/m^{-2}), and R^2 index of fits. The statistics presented here are for models employing fixed effects only.

Model	AIC	FI	RMSE	MAB	R^2	R^2 adj	Parameter significance	Comments
1	193.2	0.383	0.723	0.594	0.922	0.887	0.001	
2	190.2	0.393	0.804	0.649	0.917	0.880	0.001	
3	214.6	0.592	0.580	0.467	0.756	0.747	0.05	b_1 nonsignificant
4	173	0.359	0.894	0.649	0.929	0.895	0.05	b_1 nonsignificant
5	195	0.395	0.672	0.574	0.916	0.877	0.001	
6	184.9	0.378	0.644	0.544	0.923	0.887	0.05	
7	195.4	0.368	0.642	0.534	0.928	0.893	0.05	
8	185.1	0.379	0.681	0.552	0.923	0.886	0.001	

Table 2.4. Parameter estimates for final LAI model including standard error (SE) and significance values for each of the coefficients.

Model	Parameter	Estimate	SE	p-value
6	b_1	-29.87	6.62	0.000
	b_2	-0.13	0.04	0.001
	b_3	3.55	1.64	0.034
	b_4	25.42	4.38	0.000
	b_5	2.56	0.4	0.000

This model effectively predicted LAI over a wide range of ages in both nonthinned and silviculturally treated stands, while still accounting for much of the variance due to silvicultural treatment. Residual analysis showed this model to be unbiased with respect to all independent variables. At a given RD and SI, LAI peaked over TOPHT. Specifically, LAI increased until peaking at a TOPHT of ~12 m followed by a gradual decline (Figure 2.4). LAI demonstrated a positive and nonlinear increase with increasing RD and SI.

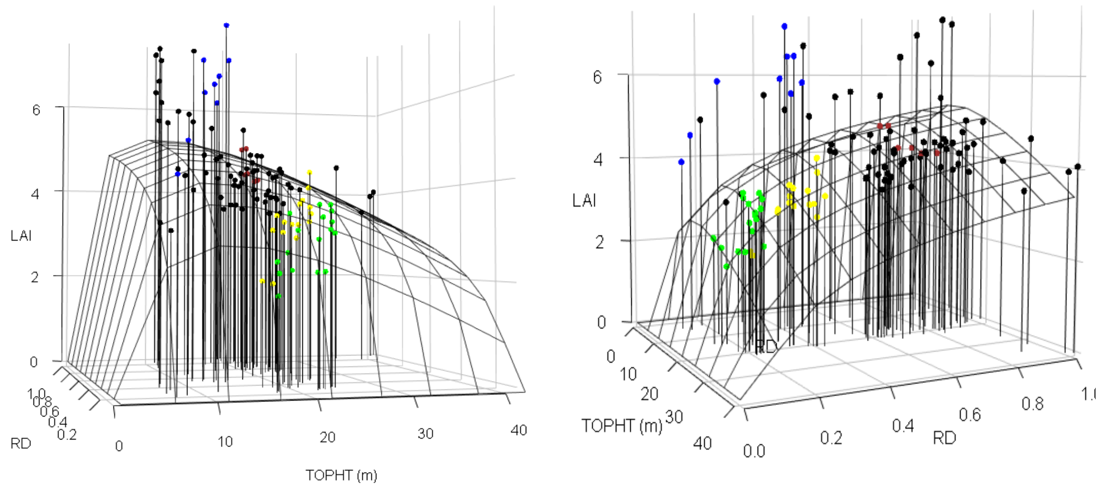

Figure 2.4. Three-dimensional plot showing projected leaf area index (LAI), stand top height (TOPHT), and relative density (RD) displayed from two different angles. The mesh represents the fitted model 6 (holding SI = 19.68).

LAI-TOPHT Relationships

Self-thinning eastern white pine stands in this study demonstrate an age-related LAI development pattern similar to 12 of the 13 chronosequence studies evaluated by Ryan et al. (their figure 5, 1997). These results support the conceptual models of Long and Smith (1992) and DeRose and Seymour (2010) with LAI reaching a maximum early in stand development (~12 m) followed by a gradual decline (Figure 2.5). The cause of this decline is likely physical due to crown abrasion as trees grow taller and sway in the wind (Long and Smith, 1992; Rudnicki et al., 2003) leading to a reduction in photosynthesis. This reduction in quantity of foliage as stands age appears to coincide with physiological effects including reduced stomatal conductance and hydraulic conductivity which can lead to declines in photosynthesis and productivity (Binkley et al., 2002; Hubbard et al., 2001; Ryan et al., 1997; Ryan et al., 2004).

Litterfall LAI values were highest in our young, high site stands regardless of density (Figure 3). The most recent litterfall measurements for the youngest stands are at or near peak LAI (Table 1) and the pattern at heights less than 5 meters predicted by the model (a steep rise from 0 to 5 m) is somewhat speculative. It is not clear whether the PCT stands have reached maximum LAI as they have not yet begun to self-thin (RD=0.4) and have recently reached crown closure so the future trajectory is somewhat uncertain. It is possible that these stands will reach a maximum LAI at higher TOPHTs because of slower accumulation of LAI early in stand development.

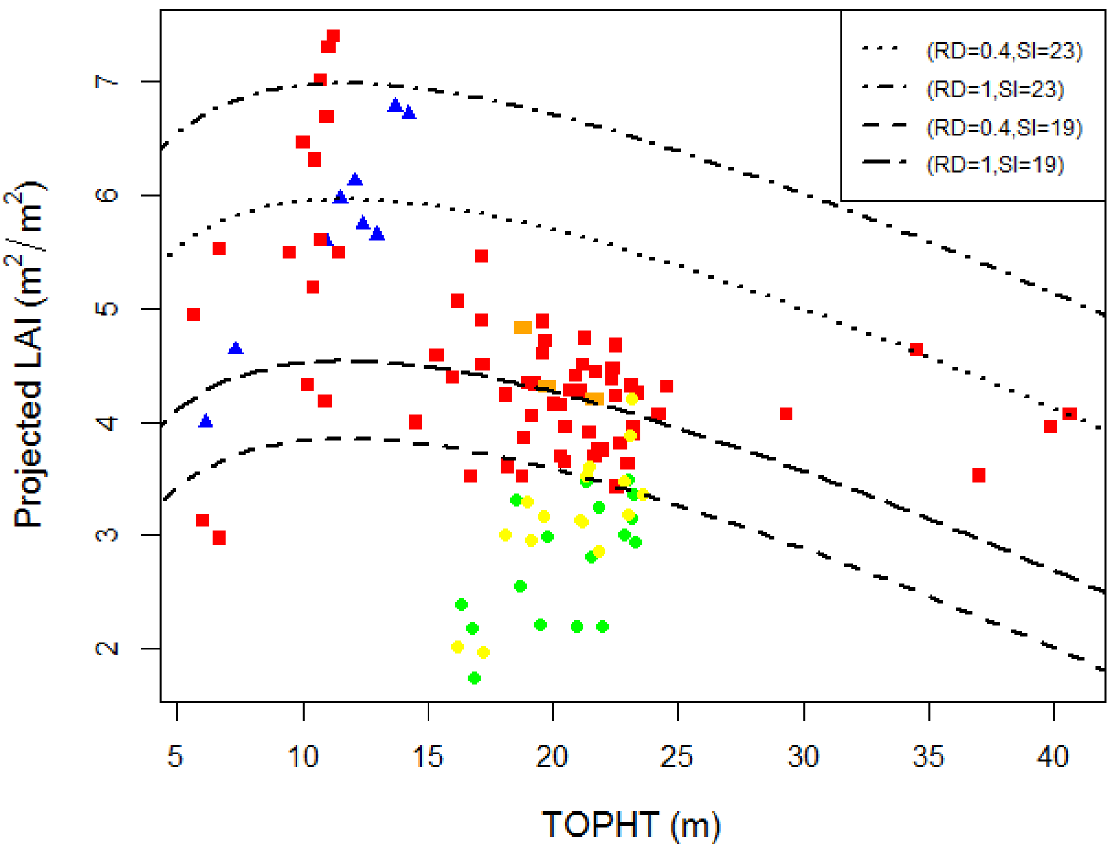

Figure 2.5. Scatterplot of LAI plotted over TOPHT. Squares represent nonthinned plots, triangles represent PCTd stands and circles represent stands thinned to the B-line and low density.

LAI-RD Relationships

LAI rises nonlinearly with increasing RD consistent with the findings of (Baskerville 1965; DeRose and Seymour, 2010, Jack and Long, 1991, *Abies lasiocarpa*; Kenefic, 2000) (Figure 2.6). These results refute the idea that post crown closure LAI reaches an equilibrium with increasing density having no effect on LAI (Jack and Long, 1991; Marks and Bormann, 1972; MarMoller, 1947; Tadaki, 1966; Turner and Long, 1975). As with DeRose and Seymour (2010), LAI of high site quality precommercially thinned stands increased more rapidly with RD for stands where RD was relatively low (<0.4) and not yet self-thinning, however silviculturally thinned stands showed a post-thinning recovery of LAI that did not appear to return to pre-thinning equilibrium.

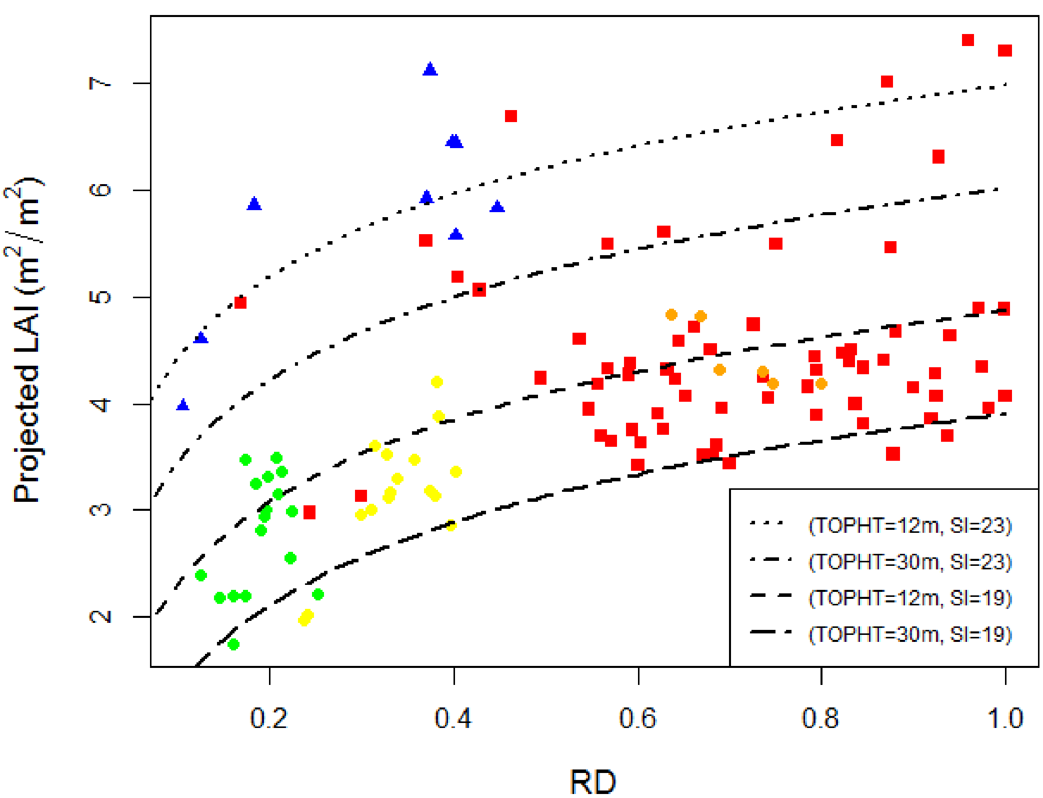

Figure 2.6. Scatterplot of LAI plotted over RD. Squares represent nonthinned plots, triangles represent PCTd stands and circles represent stands thinned to the B-line (yellow) and low density (green).

LAI-SI Relationships

LAI was strongly and positively related to SI over the range of RD and TOPHT values found in this study (Figure 2.7). These results support those found by Assman (1970) and Long and Smith (1989) over natural site gradients as well as experimental manipulation of site quality in southern pine plantations (Colbert et al., 1990; Dalla-Tea and Jokela, 1991; Jokela and Martin, 2000; Vose and Allen, 1988).

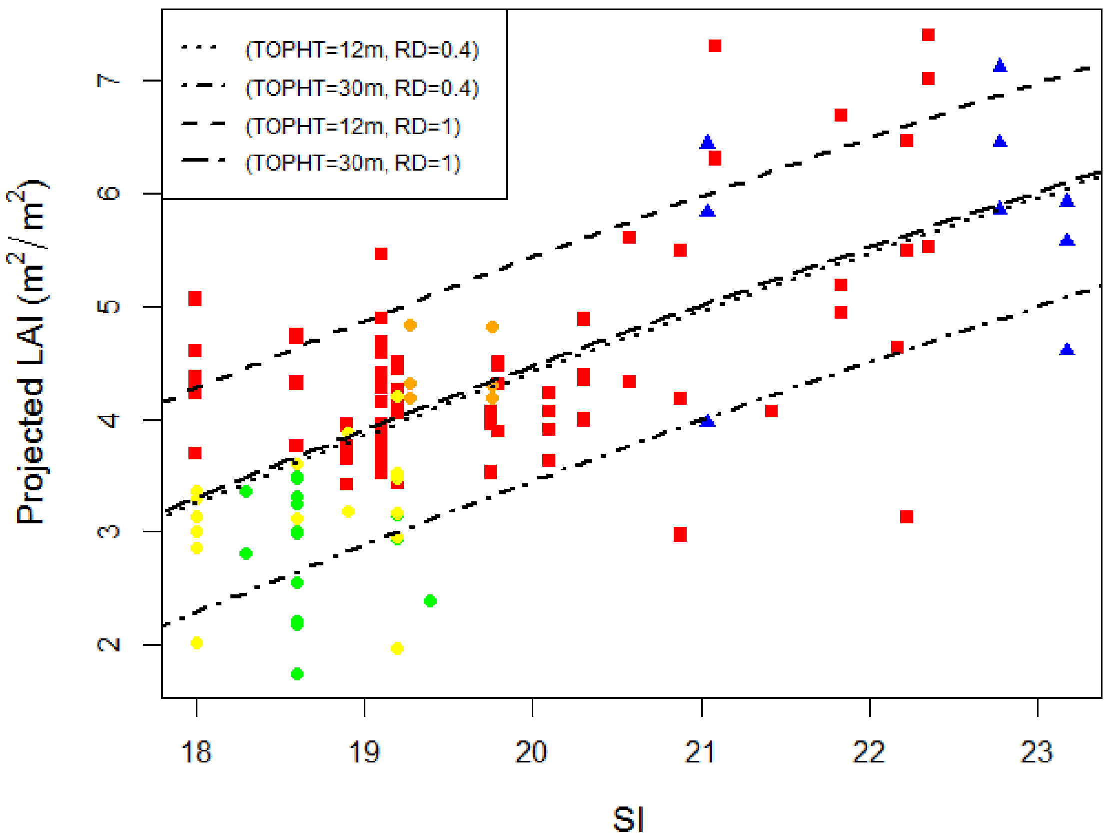

Figure 2.7. LAI plotted over SI. Squares represent nonthinned plots, triangles represent PCTd stands and circles represent stands thinned to the B-line (yellow) and low density (green).

DISCUSSION

LAI values for this study ranged from less than 1 to just over 7 with the highest LAI nearly three times larger than litterfall LAI values found by Innes et al. (2005) in New Hampshire. The difference is likely attributable to substantially lower SLA values (36.8%) used for their study (48.32 vs. 66.12 in this study). Recently thinned stands experience a period of reduced LAI followed by a gradual recovery for many years post-thinning to some percentage of the previous LAI (Guiterman et al., 2012) . Much of the error in the LAI predictions comes from slight bias at the lower and upper ends of the litterfall LAI values (Figure 2.8).

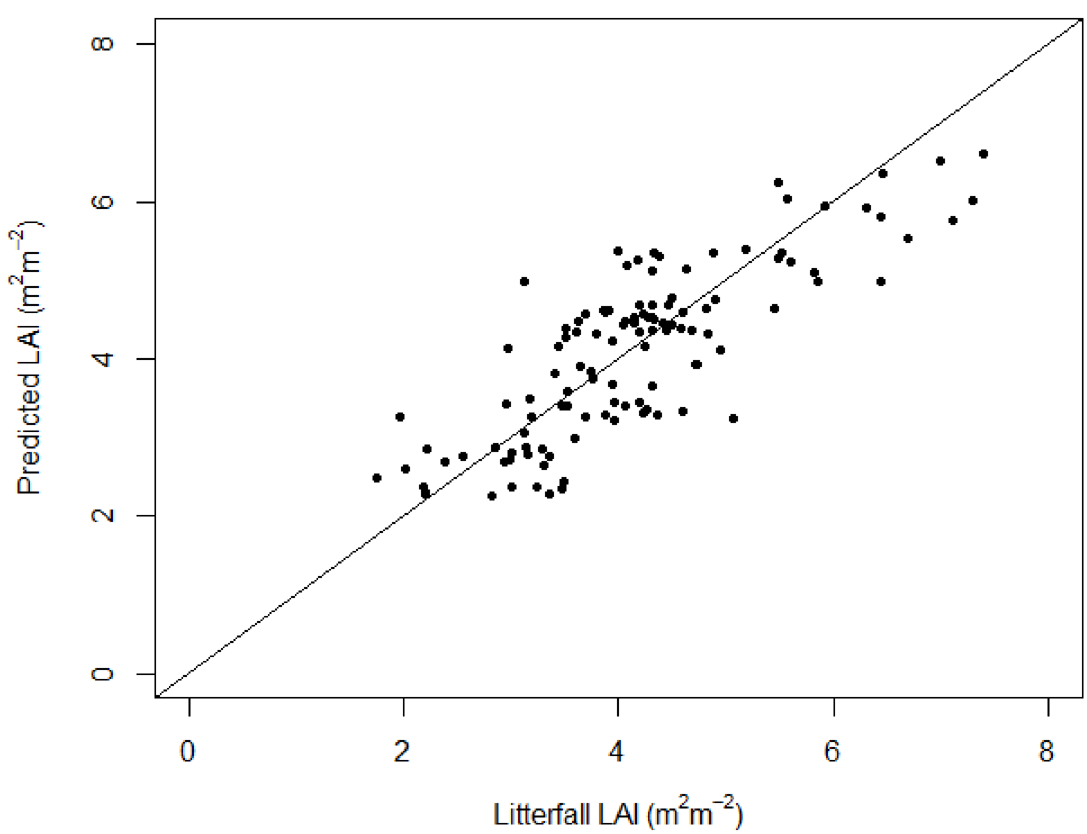

Figure 2.8. Comparison of projected LAI estimates from the LME model and litterfall collections.

RD alone without including TOPHT and SI is a relatively poor predictor of LAI, however when these three variables were analyzed simultaneously, patterns of LAI through stand development were effectively modeled using a linear mixed effects model. As with other studies of conifers, LAI was strongly and positively correlated with SI (Assmann, 1970; DeRose and Seymour, 2009; Long and Smith, 1990). Self-thinning stands exhibited an increasing pattern of LAI with increasing density rather than a post-crown closure plateau as suggested by Long and Smith (1984) and Aplet et al. (1989), however this relationship depends on history of treatment. The young stands that were precommercially thinned currently have RD values of approximately 0.4 despite having nearly the same LAI as similar aged fully stocked stands (Figure 2.4). Future research will determine how growth efficiency (growth per unit leaf area) of trees and stands is influenced with age and density which will have implications for establishing rotation lengths for managed even-aged white pine stands.

CHAPTER 3
INDIVIDUAL TREE AND STAND-LEVEL ALLOMETRIC LEAF AREA EQUATIONS FOR EASTERN WHITE PINE IN CENTRAL MAINE

ABSTRACT

Leaf area is perhaps the most important determinant of growing space occupancy and productivity and managing its amount and distribution requires accurate, unbiased equations to estimate foliage of trees and stands. We used a 20-year record of litterfall-based leaf area index (LAI) to assist in evaluating various allometric leaf area prediction models at both the individual tree and stand level. At the tree-level, nonsapwood projected leaf area (PLA) equations using diameter and crown length performed equally as well as the best sapwood-based model using sapwood area at breast height (SBA). However, when tree leaf area predictions were summed to the stand-level, sapwood-based equations performed only marginally better than non-sapwood equations. Modifying tree-level equations by analyzing tree and crown attributes at the stand-level demonstrated substantial improvements over stand-level leaf area estimates derived from summing individual tree leaf area equations. Incorporating crown length and stand top height (TOPHT) showed further improvements in model fit. Results demonstrate that individual allometric equations demonstrate bias with respect to density variability due to silvicultural thinning, and to a lesser extent, age. For even-aged eastern white pine stands, TOPHT and stand-level sapwood area at breast height (SBA) were effective predictors of LAI.

INTRODUCTION

Leaf area regulates light interception, carbon uptake and is ultimately the variable that management operates upon. Managing LAI can become more feasible by using allometric equations developed from easily obtained tree attributes. Leaf area has been cited as the primary variable driving stand-level growth (Innes et al., 2005; Ryan et al., 1997) and manipulating stand density indirectly modifies the quantity and distribution of foliage (Guiterman et al., 2012; Innes et al., 2005; McDowell et al., 2007). The use of leaf area in managing stand structure requires an efficient and accurate method of estimating quantity of foliage in trees and stands and the value of these models can be strengthened by using an independent measure of LAI such as litterfall.

Despite its obvious potential for guiding management, high variability, time constraints, and limitations of non-destructive sampling techniques make leaf area difficult to measure accurately over a large population. As a result, estimation methods have been developed, including light interception (Norman and Campbell, 1989; Pierce and Running, 1988), foliage litterfall sampling (Guiterman et al., 2012; Kinerson et al., 1974; Madgwick and Olson, 1974; Marshall and Waring, 1986; Vose and Allen, 1988) and sapwood-based allometric equations (Grier and Waring, 1974; Kenefic and Seymour, 1999; O'Hara and Valappil, 1995), which are briefly described below.

Light interception methods are based on the Beer-Lambert Law of light extinction and are used to develop relationships between projected leaf area (PLA) and canopy transmittance of photosynthetically active radiation (PAR);(Larcher, 2003). LAI estimates using this method requires an accurate estimate of the light extinction coefficient, and the devices generally measure all plant material and not just foliage. A primary source error when indirectly estimating LAI is clumping of foliage which commonly occurs in eastern white pine (Jonckheere et al., 2004). For eastern white pine, Pace (2003) found this method to underestimate LAI of thinned stands and overestimate LAI for nonthinned stands.

Litterfall traps are excellent predictors of leaf area when needle retention is known. Fortunately, these values have been well documented for eastern white pine in Maine (Guiterman et al., 2012). Leaf litter is directly related to the amount of foliage in the canopy and can provide accurate and reliable estimation of stand-level LAI (Marshall and Waring 1986; Vose and Allen 1988).

Allometric equations using sapwood area have become the preferred predictor due to the close biological relationship between the conducting xylem and the foliage it supports. Sapwood equations that include attributes such as crown length have shown improvements over models with sapwood alone (Gilmore and Seymour, 1996; Guiterman et al., 2012; Kenefic and Seymour, 1999).

Non-sapwood equations are preferred because leaf area can be estimated from readily measurable tree attributes with no destructive increment coring required, however early allometric equations from diameter at breast height alone proved to be biased (Marshall and Waring, 1986; Smith Jr et al., 1986). Valentine (1994) developed a model that incorporates a tree's basal area and modified live-crown ratio (mLCR) to serve as a surrogate for the cross-sectional area at the crown base. Kenefic and Seymour (1999) found this equation performed as well as sapwood-based models for eastern hemlock in central Maine, although Gilmore et al. (1996) and Guiterman et al. (2012) found this model to be biased and less precise than sapwood-based models for balsam fir and eastern white pine, respectively. Allometric equations are useful due to their explanatory power and strong physiological relationships, but few studies have evaluated the error with which allometric equations predict leaf area when scaled up to the stand-level.

Objectives

The purpose of this research is to test previously developed individual tree allometric leaf area equations for eastern white pine in natural and silviculturally treated stands and assess their performance at the stand-level using long-term litterfall measures. Furthermore, we want to investigate how well modified individual tree leaf area equations work when applied to the stand-level by summing up tree-level attributes and fitting equations to litterfall LAI measurements.

Methods

Study Site and Experimental Design

The study site is located in Old Town, Maine (44°54' N, 68°38' W) on the 460 hectare (1137 acre) University of Maine's Dwight D. Demeritt Forest. Fourteen locations represent a chronosequence of even-aged white pine stands ranging from age 10 to nearly 200 years. Litterfall has been monitored continuously using five 0.25 m^2 traps per plot beginning at various dates, providing uninterrupted records of litterfall ranging from 1 to 20 years (Table 3.1). In each of these stands, samples come from fixed-area plots in which all trees have been measured for diameter at breast height, total height and crown dimensions on five-year or shorter intervals since plot establishment.

Table 3.1. Mensurational characteristics of long-term litterfall data collected within the Demeritt Forest including stand name, dominant age at breast height in 2011 (BH Age), treatment type, mean height of tallest 100 trees per hectare (TOPHT), range of litterfall leaf area index values from litter traps (LAI), site index in meters (SI base age 50), year of first collection (First Collection), and number of traps per plot. Mean values are provided with a range in parentheses.

Stand	BH Age	Treatment	TOPHT (m)	LAI	SI	First Collection	No of Traps
1990	18	NoThin	9.5(5.7-11.4)	5.1(1-7.3)	21.5	2001	6
2x2	19	Early PCT	9.9(6.1-12.1)	4.7(1.6-6.1)	21	1998	2
2x2New	20	Early PCT	10.9(7.3-13)	5.2(4.6-5.7)	23.2	2002	5
3x3	22	Early PCT	13(11-14.2)	6.1(5.1-6.8)	22.8	1998	5
1970	42	NoThin	17.3(12.5-19.6)	4.3(4.1-4.8)	20.3	1996	4
1970-LD	42	Low Density	16.3	1.2(0.4-2.4)	19.4	2008	5
Control	65	NoThin	20.2(16.2-24.3))	4.0(3.4-4.7)	19.1	1992	20
HD	65	NoThin	17.9(15.4-22.7)	3.9(3.2-5.0)	19.1	1992	6
B line	65	B line	20.7(16.1-23.6)	2.9(1.9-3.9)	18.7	1992	20
LD	65	LowDensity	20.8(17.1-23.2)	2.7(1.7-3.4)	18.7	1992	20
Old-Field	55	LightThin	22.3(18.9-25.4)	4.4(4-5.0)	19.5	1992	5
BlueSpr	80	NoThin	29.4	4.1	21.4	2011	5
MM	108	NoThin	34.5	4(3.4-4.6)	22.2	2010	5
Nutting	203	NoThin	39.3(37-40.7)	4.1(3.4-4.7)	19.8	2002	5

Data Collection

To measure sapwood basal area (SBA; cm^2), at least two increment cores per tree were extracted at breast height (4.5 ft) using a 24 volt cordless power drill and 16 inch increment borer in August of 2011. Coincident with increment coring, bark thickness was measured (to 1 mm) at breast height 180 degrees apart using a bark gauge. Trees less than 16" DBH were double cored straight through the pith providing two sapwood radii 180 degrees apart. Trees larger than 16" had at least three sapwood cores extracted approximately 120° apart. The cores were glued into grooved boards in the field where both bark and sapwood were marked with an indelible pencil to help with the identification of bark and sapwood boundaries in subsequent lab analysis. The cores were dried for approximately one week before a 10% ferric chloride solution was applied to verify the sapwood/heartwood boundary marked in the field and sapwood radii (to 0.1mm) were measured. Trees with high coefficient of variation (CV) between sapwood radii (>25%) were cored a second time for sapwood in late August. Cores with missing or indistinguishable pieces were removed from the analysis. Before performing any calculations the ring widths were adjusted for radial shrinkage by a factor of 3.14% (Forest Products Laboratory 1999). Sapwood area (SA, cm^2) for each tree was determined by subtracting each cores sapwood radii from diameter inside bark, averaging heartwood areas and subtracting that from averaged inside-bark basal areas. A subsample of the permanent plots were cored in 2001 and 2008 providing sapwood area estimates for these years (Guiterman et al., 2012). Increment cores were extracted 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.

Litterfall-based Projected Leaf Area

Litterfall has been continuously monitored on 14 plots using five 0.25 m^2 traps per plot. The traps are 50 cm x 50 cm (2500cm^2) arranged spatially in an "X" pattern with one trap at plot-center and the others located half way along the diagonals from plot-center to the outside corners. Littertraps were installed on two additional plots in 2010 and 2012 to allow for a more robust sample of LAI in older stands (Table 1.1). Littertraps have 10-cm high wood sides that are beveled at the top, a wire mesh floor, and sit approximately 10 cm above the ground. Litterfall is collected twice annually: in late October, following senescence and drop of the two-year needles, and in late May, just prior to bud-break. Samples are dried to a constant weight at 60 degrees C, sorted, and weighed to the nearest 0.01 gram. Plot-level projected leaf area index (LAI) is estimated as the mean of the trap-LAI, which is calculated as:

[1] $$\text{Projected LAI} = \left(\frac{\text{needle mass} * \text{specific leaf area} * \text{senescence correction factor}}{\text{Trap Area}}\right) * \text{Needle Retention}$$

where SLA is specific leaf area (cm^2 needle leaf area per gram needle mass), SCF is a senescence correction factor, and needle retention is the average number of years that needles stay on a given branch.

A senescence correction factor of 15.1 ± 2.3% was used to convert the dry weight of the abscised needles collected in the trap to their approximate dry weight when alive based on a subsample of branches collected within the University Forest. SLA was calculated using an archived database of 132 destructively sampled tree branches sampled within the study area. Tree SLA values from a previous study (Barker, 1998) were removed from the analysis due to issues caused by a poor resolution scanner which provided unreasonably high SLA values. Preliminary analysis suggested that mean SLA for the youngest stand were significantly different from all others; however this difference was nullified when two abnormally high SLA values from trees less than 2cm DBH were removed from the data set. After removing suppressed trees, we were confident that SLA values were relatively constant among stands regardless of stand age or density and a mean branch SLA value of 66.12 cm^2/g ± 0.75 (±SE) (n=135) was applied to all plots.

Needle retention for eastern white pine at this location is 2.2-2.37 years depending on stand age; thus the quantity of foliage collected in littertraps is not necessarily representative of current canopy leaf area. This is particularly true of recently thinned stands where canopy LAI is still recovering after thinning. Due to this delay in losing currently active foliage, comparisons of allometric LAI were made with litterfall LAI two years following tree attribute measurements, except for plot measurements made in 2010 and 2011 because only current litterfall measurements were available. Due to inter-annual variability in litterfall LAI, a piecewise polynomial spline was fit to reduce the influence of anomalous outliers caused by physiological stresses such as unknown climatic events or cone production.

Branch-level Projected Leaf Area

Branch-level projected leaf area was fit to a total of 61 destructively sampled trees from the Dwight B. Demeritt Forest including archived data from 48 trees (Table 3.2) (see Weiskittel et al. 2009 and Guiterman et al. 2012 for detailed description of these data sets). An additional 12 trees of various crown classes were added in 2011 from a young nonthinned stand within the study area.

Table 3.2. Summary statistics for sample trees used to fit the PLA_{branch} and PLA models. Date attributes include diameter at breast height (DBH), total stem height (HT), crown length to lowest live branch (CL), sapwood basal area (SBA), total tree projected leaf area (PLA), and breast-height age.

	DBH (cm)	HT (m)	CL (m)	SBA (cm^2)	PLA (m^2)	Age (yr)
Destructively-sampled trees (n=61)						
Mean	16.66	13.78	6.01	106.19	42.28	37.19
Standard error	1.49	0.85	0.38	18.56	9.2	3.02
Minimum	1.6	2.77	1.67	0.91	0.08	11
Maximum	61.3	29.63	17.14	830.94	429.94	128
Destructively-sampled plus climbed trees (n=64)						
Mean	17.73	14.23	6.36	125.45	52.18	37.98
Standard error	1.55	0.85	0.42	20.82	10.44	2.91
Minimum	1.6	2.77	1.67	0.91	0.08	11
Maximum	61.3	29.63	17.14	830.94	429.94	128

Sample trees were felled and measured for height and basal diameter of all live branches. Crowns were then divided into three or four vertical sections, with one sample branch randomly selected from each crown segment. Specific leaf area (SLA) for each sample branch was determined from approximately 100 needles that were kept frozen until the projected leaf area was measured to the nearest 0.0001cm^2 using a high-resolution scanner (>1200 dpi) and the WinSeedle® program (Regent Systems, Inc), then oven-dried before massing to the nearest 0.0001 gram. Branch SLA was calculated by dividing the projected leaf area by the dry weight. Remaining portions of the sample branches were dried to a constant weight prior to being sorted and massed to the nearest .01 gram. Total sample branch PLA was determined as the product of the total foliage dry weight and the branch SLA (then converted from cm^2 to m^2).

The Maguire and Bennett (1996) Weibull model form was fit to the destructively sampled (n= 184) branches (Table 3.3). The model form is expressed as:

$$[2] \qquad PLA_{Branch} = (b_0 BD^{b1})*(RDINC^{(b2-1)})*\exp^{((b3*RDINC\ b2)]}$$

where BD is the branch basal diameter (cm), RDINC is the relative depth of the branch into the crown (0 is at the top, 1 is at the crown base), and B_is are the parameters estimated by the model. Random effects were added to the B_1 and B_3 parameters to account for the nested structure of the data at two levels: the type of thinning [NoThin, LightThin, HeavyThin, and Shelterwood], and the individual sample tree. This technique creates a tree-specific model while accounting for variation in crown form caused by stand density and thinning.

Table 3.3. Summary statistics for destructively sampled white pine branches (n=184). Data attributes include branch basal diameter (BD), relative depth into the live crown (RDINC), total branch leaf mass, specific leaf area (SLA), and branch projected leaf area (BLA).

Attribute	**Mean**	**SE**	**Min**	**Max**
BD (cm)	1.86	0.11	0.20	9.4
RDINC	0.55	0.02	0.037	1
Leaf Mass (g)	92.69	13.26	0.01	1374.16
SLA (cm^2g^{-1})	68.18	0.83	48.73	103.6
BLA (cm^2)	6058.89	881.52	0.793	94157.44

Because heteroskedasticity was found in residuals the following variance power function was applied

$$[3] \qquad \mathrm{Var}(\textstyle\sum_i) = \sigma^2 |v_i|^{2\delta}$$

where σ^2 is the residual sum of squares, v_i is the primary covariate, (branch basal diameter), and δ is the variance function coefficient estimated from the model. This allows the model to find an optimal weight given the variance inherent in the data (Pinheiro and Bates, 2009). Using mixed effects with the weighting procedure resulted in a highly accurate fit of the PLA_{branch} model (Table 3.4).

Table 3.4. Parameter estimates and fit statistics for the PLA_{branch} model (equation [2]).

Equation	Parameter	Estimate	SE	δ	RMSE	R^2
[2]	B_0	0.4766942	0.0476498	1.514614	0.1637948	0.9829
	B_1	1.8626489	0.1097928			
	B_2	1.8792430	0.0854931			
	B_3	1.5784028	0.4722728			

Note: All parameters estimates are significant at P<0.001; SE – standard error; δ – coefficient of the variance power function (eqn [3]; RMSE – root mean squared error; R^2 – generalized coefficient of determination ((Kvålseth, 1985) for fixed + random terms

Tree-level Projected Leaf Area

Tree-level LA was estimated using the two-step branch-summation method. The branch-level model was applied to all live branches (*n* = 5391) on the sample trees and summed to estimate tree-level projected leaf area (PLA). In 2008, three trees were added to the sample dataset to ensure better coverage of the larger thinned trees present on one of the sample plots (Table 3.2). These trees were climbed and measured for heights and basal diameters of all live branches (*n* = 303), but no sample branches were collected. Equation [2] was then applied to each branch including the treatment random effects (but no tree effects).

Tree attributes used for the allometric-PLA models came from field measurements of DBH made prior to felling, and total height (HT) and height to lowest live branch (HTLLB) made with a logger's tape after felling. Height to lowest live branch HTLLB was used to calculate live crown length (CL), live crown ratio (LCR), and modified live crown ratio [mLCR; calculated as CL/(HT-1.37 m); Valentine et al. 1994]. Measurements of sapwood basal area on felled sample trees come from 6 measurements of sapwood radii on breast height cross-sections and from the 2008 increment cores on the three climbed trees.

Individual Tree PLA Models

Six PLA prediction model forms used by Guiterman et al. (2012) and two unique to this study were used to predict individual tree leaf area (Table 3.5). In most cases, variables approximate diameter or sapwood cross-sectional area at crown base by roughly modeling stem or sapwood taper below the live crown (Dean and Long 1986; Long and Smith 1988; Maguire and Hann 1989; Valentine et al. 1994; Maguire and Bennett 1996). The parameter estimates (Table 3.6) for each allometric-PLA model were generated through three statistical fitting techniques: nonlinear least squares (NLS); weighted nonlinear least squares (WNLS) using the generalized nonlinear least squares function (Pinheiro and Bates, 2009) where the primary covariate was weighted with the variance power function (eqn. [3]); and weighted nonlinear mixed effects (NLME). The NLME fits included the weighting function because of improvement shown through the WNLS technique. NLME fits also include one random parameter in each model that accounts for the tree's location (one of 7 within the Demeritt Forest) and whether the stand has been thinned (Thinned or NoThin). Selection of the random parameter was done by iteratively fitting each model using a different random parameter and choosing the one with the lowest Akaike Information Criterion (AIC; Akaike 1974). Since NLME models estimate the population trend (fixed effects) and each individual's deviations from the population (random effects) (Pinheiro and Bates 2000), we tested the differences of applying the models using the full mixed model (NLME-R) as well as just the fixed effects portion of the model (NLME-F)

Table 3.5. Selected model forms for estimating tree-level projected leaf area (PLA_{Tree}). Independent variables include sapwood basal area (SBA, cm^2), live crown length (CL, m), diameter at breast height (DBH, cm), basal area at breast height (BA, cm^2), total stem height (HT, m), and modified crown ratio (mLCR). Live crown base is the lowest live branch.

Model	**Equation**	**Reference**
SAP	$PLA = b_1 * SBA^{b2}$	(Bancalari et al., 1987)
SCL	$PLA = b_1 * SBA^{b2} * CL^{b3}$	(Gilmore and Seymour, 1996) (Kenefic and Seymour, 1999)
SMAG	$PLA = b_1 * SBA^{b2} * e(b_3 * \frac{DBH}{HT})$	(Guiterman et al., 2012)
DCL	$PLA = b_1 * DBH^{b2} * CL^{b3}$	(Guiterman et al., 2012)
MAG	$PLA = b_1 * CL^{b2} * e(b_3 * \frac{DBH}{HT})$	(Maguire and Bennett, 1996)
VAL	$PLA = b_1 * (BA * mLCR)^{b2}$	Modified from (Valentine et al., 1994)
SAP.MK	$PLA = b_1 * SBA^{b2} * (CL/SBA)^{b3}$	This Study
SMAG.MK	$PLA = b_1 * SBA^{b2} * (CL/SBA)^{b3} + (\frac{DBH}{HT})^{b4}$	This Study

Stand-level LAI

Stand-level LAI was estimated two ways: First, individual tree PLA equations were applied to all trees within the permanent plot network, summed to the plot level and divided by the plot area in meters^2 to estimate LAI. Second, to address potential error when summing up individual tree PLA equations to the stand-level, sapwood area, tree and crown attributes from the permanent plot data were expanded to a per hectare basis and modified versions of the individual tree PLA equations were fit to the litterfall data (Table 3.6). Sapwood basal area per hectare was most correlated with LAI so only models containing this factor were assessed. A modifier using stand top height (TOPHT, m) was included to incorporate the peaking pattern and subsequent decline of stand LAI found in chapter 2.

Table 3.6. Model forms estimating tree-level projected leaf area (PLA_{Tree}) and their modified forms to estimate stand-level leaf area index (LAI). Tree-level equations and independent variables are described in Table 5. Independent variables for stand-level models include sapwood basal area per hectare (SBA/Ha, m^2), Top Height (TOPHT, m), crown length per hectare (CL/Ha, m), diameter per hectare (DBH/Ha, cm), and total stem height per hectare (HT/Ha, m).

Model	**Tree-level Equation**	**Reference**	**Stand-level Equation**
SAP	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}$	(Bancalari et al., 1987)	$\mathrm{LAI} = b_1*\mathrm{SBA/Ha}^{b2}$
SAP.TOPHT	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}$		$\mathrm{LAI} = b_1*\mathrm{TOPHT}+b_2*\mathrm{logTOPHT}+\mathrm{SBA/Ha}^{b3}$
SAP.TOPHT.NLME	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}$		$\mathrm{LAI} = b_1*\mathrm{TOPHT}+b_2*\mathrm{logTOPHT}+\mathrm{SBA/Ha}^{b3}$
SCL	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*\mathrm{CL}^{b3}$	(Gilmore and Seymour, 1996) (Kenefic and Seymour, 1999)	$\mathrm{LAI}=(b_1*\mathrm{SBA/Ha}^{b2}*\mathrm{CL/Ha}^{b3})$
SCL.TOPHT	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*\mathrm{CL}^{b3}$		$\mathrm{LAI} = b_1*\mathrm{TOPHT}+b_2*\mathrm{logTOPHT}+(\mathrm{SBA/Ha})^{b3}*(\mathrm{CL/Ha})^{b4}$
SCL.TOPHT.NLME	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*\mathrm{CL}^{b3}$		$\mathrm{LAI} = b_1*\mathrm{TOPHT}+b_2*\mathrm{logTOPHT}+(\mathrm{SBA/Ha})^{b3}*(\mathrm{CL/Ha})^{b4}$
SMAG	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*\mathrm{e}(b_3*\frac{DBH}{HT})$	(Guiterman et al., 2012)	$\mathrm{LAI} = b_1*(\mathrm{SBA/Ha})^{b2}*\mathrm{e}(b_3*\frac{DBH/Ha}{HT/Ha})$
SMAG.TOPHT	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*\mathrm{e}(b_3*\frac{DBH}{HT})$		$\mathrm{LAI} = b_1*\mathrm{TOPHT}*b_2\,\mathrm{logTOPHT}*(\mathrm{SBA/Ha})^{b3}*\mathrm{e}(b_4*\frac{DBH/Ha}{HT/Ha})$
SMAG.TOPHT.NLME	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*\mathrm{e}(b_3*\frac{DBH}{HT})$		$\mathrm{LAI} = b_1*\mathrm{TOPHT}*b_2\,\mathrm{logTOPHT}*(\mathrm{SBA/Ha})^{b3}*\mathrm{e}(b_4*\frac{DBH/Ha}{HT/Ha})$
SAP.MK	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*(\mathrm{CL/SBA})^{b3}$	This Study	$\mathrm{LAI}\sim b_1*\mathrm{SBA/Ha}^{b2}*\frac{CL/Ha}{SBA/Ha}^{b3}$
SAP.MK.TOPHT	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*(\mathrm{CL/SBA})^{b3}$		$\mathrm{LAI}\sim b_1*\mathrm{SBA/Ha}^{b2}*\frac{CL/Ha}{SBA/Ha}^{b3}$
SAP.MK.TOPHT.NLME	$\mathrm{PLA}=b_1*\mathrm{SBA}^{b2}*(\mathrm{CL/SBA})^{b3}$		$\mathrm{LAI}\sim b_1*\mathrm{SBA/Ha}^{b2}*\frac{CL/Ha}{SBA/Ha}^{b3}$

Analyses

We evaluated goodness of fit in the allometric models from fit statistics, residual plot analyses, and estimates of bias. Statistical significance was considered at the 95% level of confidence. Final model selection was based on AIC and root mean squared error (RMSE). An AIC reduction of 10 units was considered statistically significant (Burnham and Anderson, 2002). RMSE was calculated from model predictions in the original units (m^2) as

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(\hat{y}_i - y_i)^2}{n}} \qquad [4]$$

where $\hat{y}_i$ is the predicted PLA from the allometric model and y_i is the PLA from the branch summation method (i.e. observed).

Models including SBA could only estimate leaf area for a subsample of plots in 2001, 2008 and 2011 because SBA measurements were unavailable for other years. These comparisons were performed both graphically and by calculating average absolute deviation (AAD) as

$$\text{AAD} = \frac{\sum_{i=1}^{n}|\hat{y}_i - y_i|}{n} \qquad [5]$$

where $\hat{y}_i$ is the estimated allometric-LAI and Y_i is the litterfall-LAI. The 2001 litterfall LAI estimates were confounded by thinning as trees removed contributed to the fall collection, but not the spring so the 2000 litterfall was used instead.

RESULTS

Allometric-PLA_{Tree} Model Fits

The amount of error among fitting techniques depended largely on the model form (Table 3.7). Similar to the findings of Guiterman et al. (2012), weighting the models increased RMSE; although the effect was minor for the SAP and DCL models. The mixed effects procedure in many cases produced the lowest errors with the exception of the SAP, MAG, and SMAG.MK, while applying only the fixed effects of the NLME generally resulted in the highest errors. All other models had fluctuating RMSE values depending on fitting technique.

Table 3.7. Root mean squared error (RMSE, m^2) and Akaike's Information Criterion (AIC) for each PLA_{Tree} prediction equation and fitting technique.

	Weighted	RMSE (m^2)				AIC		
Model	**Variable**	**NLS**	**WNLS**	**NLME-R**	**NLME-F**	**NLS**	**WNLS**	**NLME-R**
SAP	SBA	21.03	22.74	51.9	53.72	577.5	491.4	469.9
SCL	SBA	14.43	25.31	10.48	23.62	531.3	421.4	419.5
SMAG	SBA	19.96	30.97	11.19	26.75	572.8	445.7	435.6
DCL	DBH	14.43	19.18	11.06	16.32	531.3	404.3	407.5
MAG	CL	15.44	23.98	36.65	52.03	539.9	469.7	453.6
VAL	BA	15.89	27.51	16.93	28.97	570.5	371.2	368.1
SAP.MK	SBA	14.43	25.31	52.88	56.19	531.3	421.4	420.7
SMAG.MK	SBA	13.77	22.96	33.89	33.73	420.7	404.5	408.5

AIC and RMSE values show the weighting procedure improved the fit compared with the NLS fitting technique across all models (Figure 3.1, Figure 3.2). The mixed effects models were generally better with significant improvements in fit for all models with the exception of the DCL, VAL, and SMAG.MK. The best model was the DCL for the NLS and the VAL for both the WNLS and NLME-R (Table 3.7). Parameter estimates for all models are provided in Table 3.9.

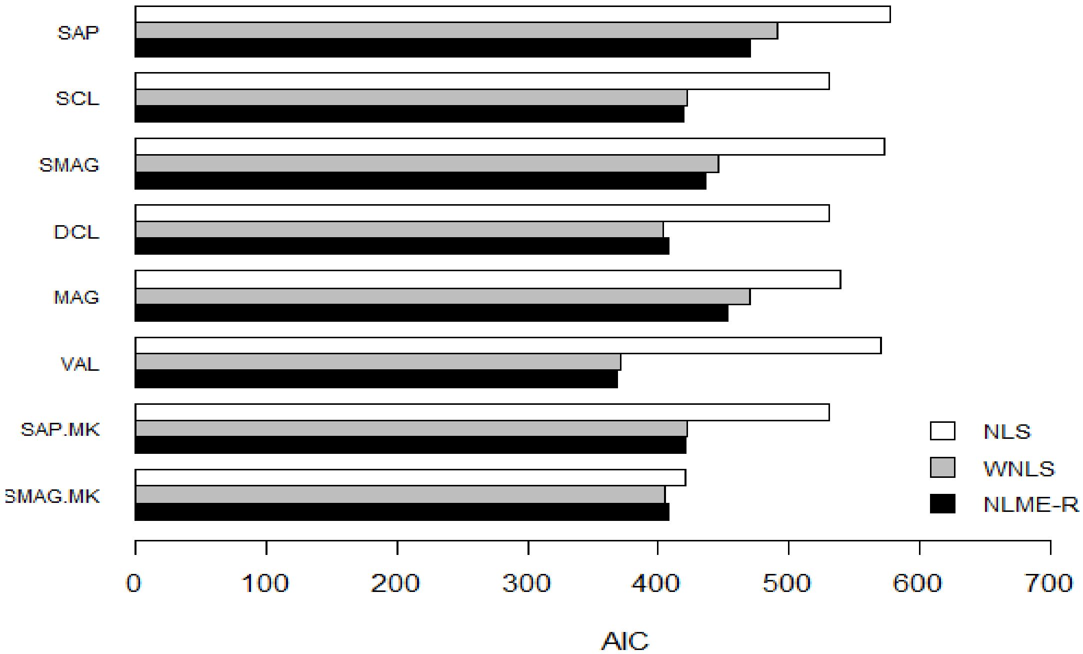

Figure 3.1. Barchart displaying Akaike's Information Criterion (AIC) for allometric LA equations fit by NLS, WNLS, and NLME. NLME-R indicates that random effects were used.

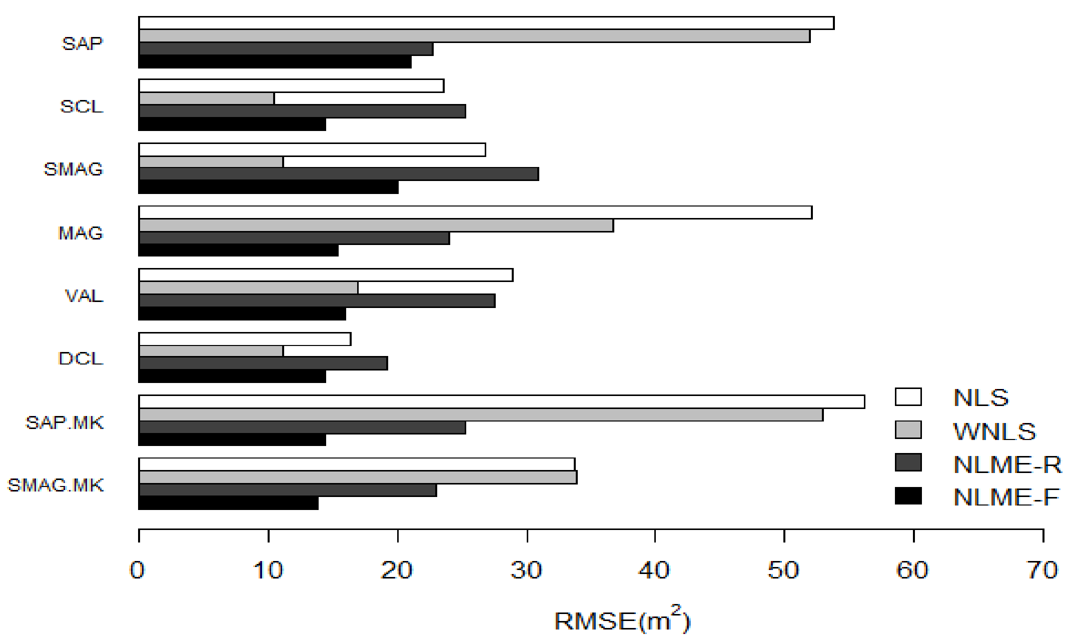

Figure 3.2. Barchart displaying root mean squared error (RMSE, m^2) the eight allometric LA equations fit by NLS, WNLS, and NLME. NLME-R indicates that random effects were used, and NLME-F indicates that only the fixed effects parameter estimates were used.

Table 3.8. Mean absolute bias for each PLA_{Tree} model form and fitting technique.

Model	Weighted Variable	MAB			
		NLS	WNLS	NLME-R	NLME-F
SAP	SBA	12.76	13.45	7.33	23.27
SCL	SBA	9.34	11.5	6.15	10.13
SMAG	SBA	12.44	13.19	6.03	10.75
DCL	DBH	9.71	9.51	6.28	8.17
MAG	CL	10.39	11.67	16.67	18.11
VAL	BA	12.96	12.0	6.79	9.94
SAP.MK	SBA	9.34	11.49	29.22	31.46
SMAG.MK	SBA	9.29	10.04	32.19	32.04

Table 3.9. Parameter estimates for allometric PLA_{Tree} equations. All estimates were significant at $P < 0.05$.

Model	Equation	Parameter	NLS	WNLS	NLME-F
SAP	$PLA = b_1 * SBA^{b2}$	b_1	0.1626	0.2532	0.1002
		b_2	1.1691	1.0845	1.2695
SCL	$PLA = b_1 * SBA^{b2} * CL^{b3}$	b_1	0.2312	0.0701	0.0703
		b_2	0.3432	0.3408	0.4857
		b_3	1.8547	2.3747	2.0269
SMAG	$PLA = b_1 * SBA^{b2} * e(b_3 * \frac{DBH}{HT})$	b_1	0.2856	0.1905	0.1754
		b_2	0.9728	0.7965	0.8267
		b_3	0.3670	1.2081	1.1346
DCL	$PLA = b_1 * DBH^{b2} * CL^{b3}$	b_1	0.1799	0.0624	0.0627
		b_2	0.7463	0.8776	1.0256
		b_3	1.6839	1.9238	1.6932
MAG	$PLA = b_1 * CL^{b2} * e(b_3 * \frac{DBH}{HT})$	b_1	0.1627	0.0964	0.0860
		b_2	3.0043	2.9174	2.0336
		b_3	-0.2808	0.1815	1.4830
VAL	$PLA = b_1 * (BA * mLCR)^{b2}$	b_1	0.5289	0.1199	0.1281
		b_2	0.8985	1.1300	1.1193
SAP.MK	$PLA = b_1 SBA^{b2} * (CL/SBA)^{b3}$	b_1	0.2312	0.0701	0.0709
		b_2	2.1979	2.7156	2.5972
		b_3	1.8547	2.3747	2.1746
SMAG.MK	$PLA = b_1 * SBA^{b2} * (CL/SBA)^{b3} + (\frac{DBH}{HT})^{b4}$	b_1	0.2070	0.0566	0.0565
		b_2	2.1755	2.7165	2.7174
		b_3	1.7923	2.3499	2.3512
		b_4	2.8878	4.3898	4.3900

The NLME-F technique generally produced the greatest biases among the four techniques (Table 3.8). Residual plot analyses show that all models tended to slightly underestimate tree PLA which became more pronounced for larger trees (Figure 3.3). This bias was particularly evident for the MAG, SMAG and to a lesser extent the SCL and VAL which were the two best tree-level models. Overall the DCL model was the least influenced by the fitting technique and had the lowest bias of any of the models which remained consistent among fitting techniques.

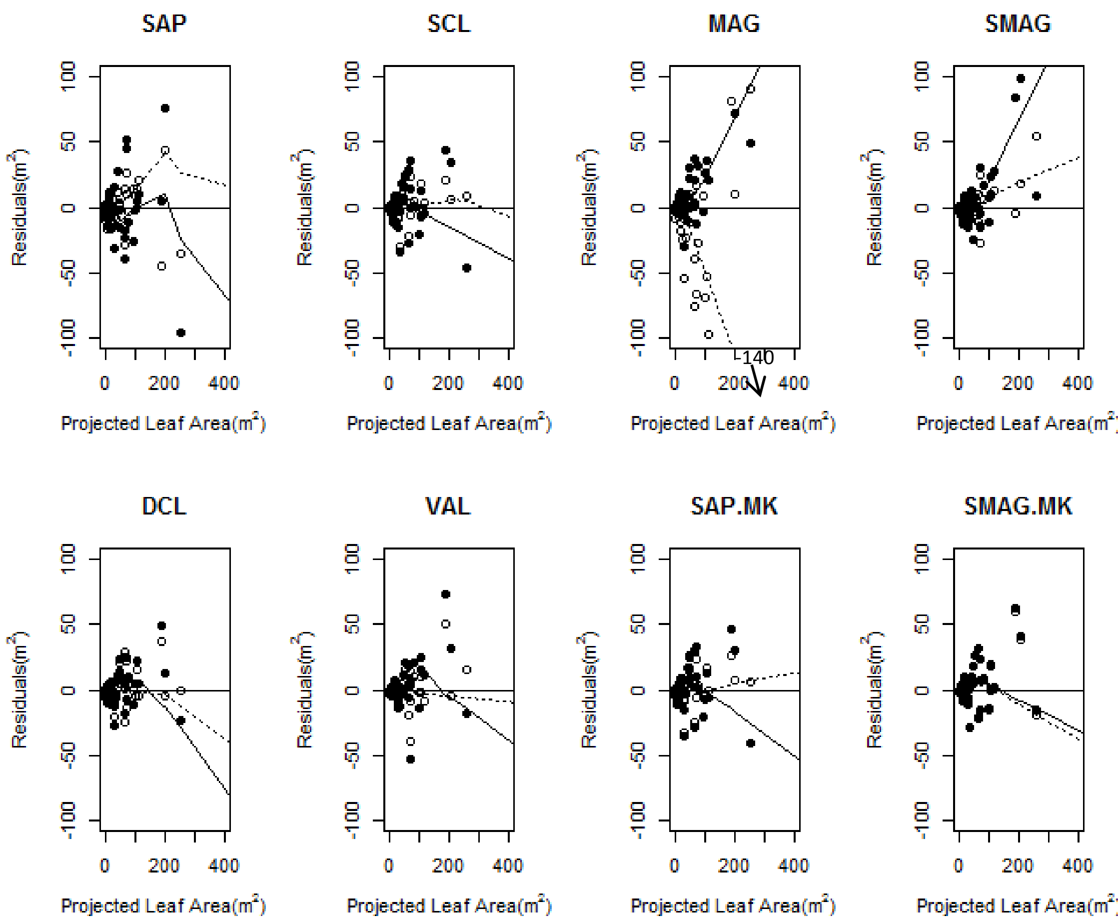

Figure 3.3. Residual plots for NLME model fits of each PLA_{Tree} equation. The x-axes are observed PLA (from branch summation). Filled symbols are NLME-R and hollow symbols are NLME-F. Loess smooth regression lines are included with solid line representing NLME-R and dotted line for NLME-F. An arrow indicates a value outside of the plot region (the number being the value of the residual). Residuals are predicted minus observed.

Allometric-LAI Estimation- Individual Tree Model Summation

Unlike the tree-level errors, comparisons of stand-level LAI estimates from allometric models and litterfall showed that the WNLS procedure was almost always better than the NLS fitting and the mixed effects fitting procedure marginally reduced the error for all models, except the SAP (Table 3.10,Figure 3.4).

Table 3.10. Average absolute deviation (AAD) of allometric-LAI estimates compared to litterfall-LAI estimates. Non sapwood models (MAG, VAL, DCL) consist of 81 plot measurements while sapwood equations (SAP, SCL, SMAG) have 27.

	AAD		
Model	NLS	WNLS	NLME-F
SAP	2.494	2.812	2.462
SCL	2.017	1.145	1.143
MAG	1.534	1.380	1.334
SMAG	1.513	2.291	2.054
VAL	2.111	1.129	1.124
DCL	1.595	1.267	1.260
SAP.MK	2.603	1.781	1.771
SMAG.MK	2.639	1.641	1.641

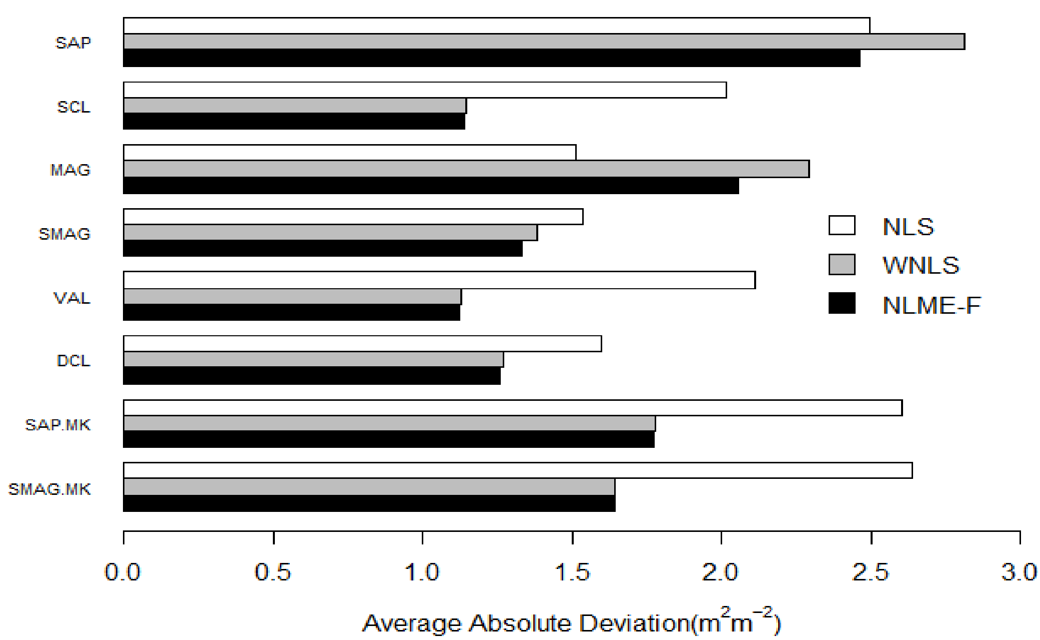

Figure 3.4. Barchart displaying average absolute deviation of allometric LAI obtained from summing PLA_{Tree} equations compared to Litterfall LAI.

Consistent with the tree-level results, the VAL model was the best performing non-sapwood equation when applied to the stand-level. Unlike results at the tree-level, sapwood equations that included crown length performed better than non-sapwood equations at predicting stand-level LAI. Overall individual tree models tended to overpredict LAI of nonthinned stands and underpredict LAI of thinned stands (Figure 3.5).

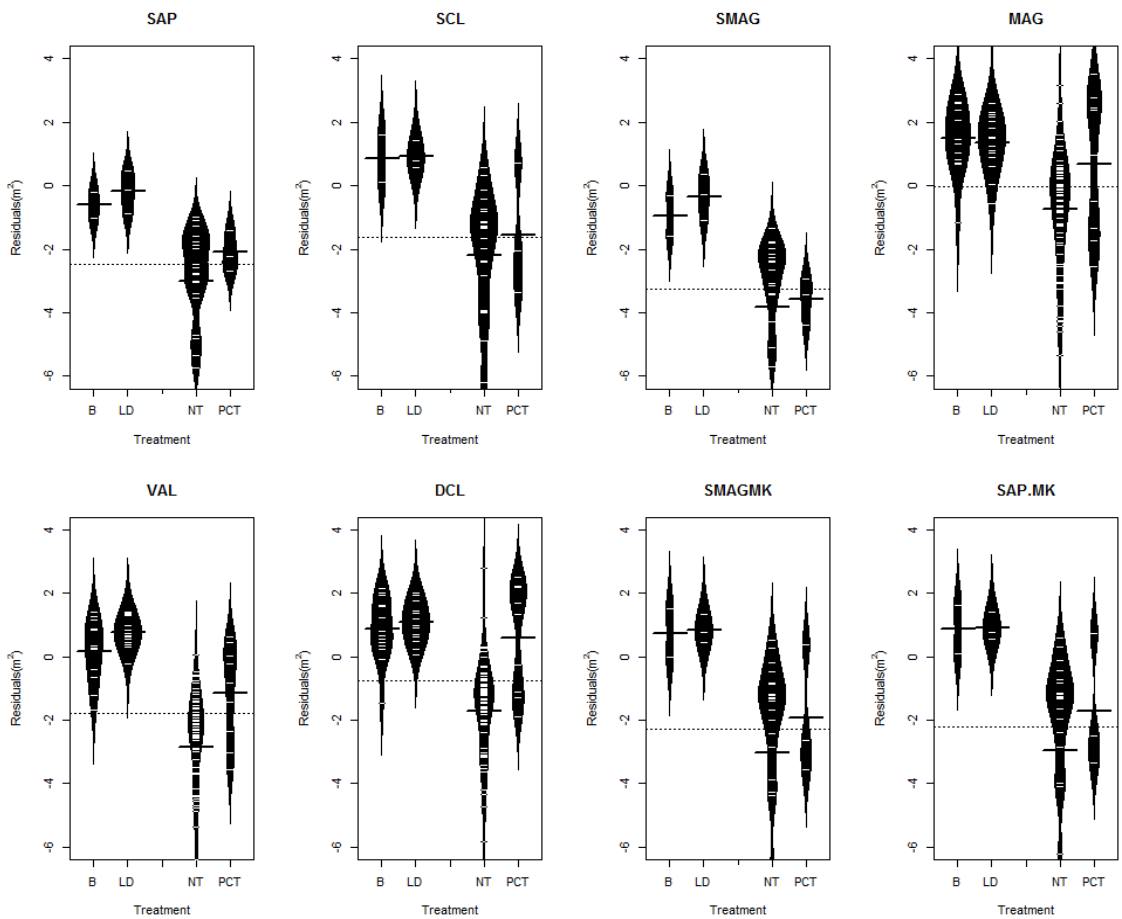

Figure 3.5. Residuals plotted over treatment for the allometric LAI equations. Residuals are observed minus predicted. Treatments include a B-line thinning (B), low density thinning (LD), no thin (NT), and precommercially thinned (PCT).

Allometric LAI Models from Stand-level Attributes

When stand-level equations were compared, the best model was the SCL.TOPHT model with plot included as a random effect as it had the lowest AIC, error and bias of all models tested (Table 3.11). Parameter estimates for all models are included in Table 3.12.

Table 3.11. Summary statistics of allometric LAI models including model name, random effect if included, Aikaike's information criterion (AIC), Furnival's index (FI), root mean squared error (RMSE), mean absolute bias (MAB), R^2, and adjusted R^2 as well as significance of parameter estimates. Predictions were made with fixed effects only.

Model	**Ranef**	**AIC**	**RSE-FI**	**RMSE**	**MAB**	R^2	**adj** R^2
SAP		75.87	0.56	0.34	0.16	0.82	0.81
SAP.TOPHT		68.70	0.51	0.31	0.15	0.85	0.84
SAP.TOPHT.NLMER	Plot|a2	62.57	0.25	0.31	0.15	0.98	0.92
SCL		54.91	0.43	0.26	0.12	0.89	0.89
SCL.TOPHT		45.13	0.38	0.23	0.11	0.92	0.91
SCL.TOPHT.NLMER	Plot|a3	42.31	0.26	0.23	0.11	0.97	0.86
SMAG		75.73	0.55	0.33	0.15	0.82	0.82
SMAG.TOPHT		49.86	0.40	0.24	0.12	0.91	0.90
SMAG.TOPHT.NLMER	Plot|a2	49.23	0.27	0.24	0.12	0.97	0.86
SAP.MK		75.73	0.55	0.33	0.15	0.82	0.82
SAP.MK.TOPHT		49.86	0.40	0.24	0.12	0.91	0.90

Table 3.12. Parameter estimates for stand-level allometric LAI models with standard errors provided in parentheses.

Model	Parameter	SAP	SAP.TOPHT	SAP.TOPHT.NLMEF
SAP	b_1	0.0084(0.0039)	0.0747(0.0277)	0.0966(0.0276)
	b_2	0.5188(0.0379)	5.3581(0.7542)	-6.0248(0.7627)
	b_3		0.1893(0.0043)	0.1933(0.0044)
SCL	b_1	0.0025**(0.0024)	0.0764(0.0216)	0.0790(0.0221)
	b_2	0.6868(0.1235)	7.9358(0.7603)	-8.3629(0.7774)
	b_3	-0.0882**(0.0616)	0.2827(0.0147)	0.2929(0.015)
	b_4		0.0921(0.0144)	-0.1015(0.0147)
SMAG	b_1	0.00086*(0.0005)	0.0872(0.0207)	0.0959(0.0228)
	b_2	0.6686(0.0404)	6.9486(0.6167)	-7.2291(0.6601)
	b_3	0.3994(0.0734)	0.1899(0.003)	0.1900(0.0031)
	b_4		0.1343(0.0206)	0.1474(0.0221)
SAP.MK	b_1	0.002478**(0.0024)	0.0764(0.0216)	0.0746(0.024)
	b_2	0.598628(0.0675)	7.9358(0.7603)	-8.4279(0.7905)
	b_3	-0.08818**(0.0616)	0.1905(0.0031)	0.1908(0.0031)
	b_4		0.0921(0.0144)	-0.1081(0.0146)

* P ≥ 0.05, ** P >0.1

DISCUSSION

The primary research objective was to develop an accurate and unbiased leaf area prediction equation that works over a range of stand age and structure. Assessing the performance of leaf area prediction models requires an independent estimate of leaf area for the stands investigated and long-term littertrap data provides an ideal benchmark for this purpose. Our results demonstrate the variability in performance of commonly used individual tree PLA models which were highly dependent on the fitting technique. Surprisingly, the basal area-modified live crown ratio (VAL) model performed marginally better than the diameter-crown length (DCL) and the sapwood area-crown length (SCL) models at the tree-level with the advantage of not requiring destructive coring of trees. This is similar to the results of Kenefic and Seymour (1999) who found the VAL model to be as accurate as equations including sapwood equations for eastern hemlock.

Despite previous research suggesting that equations including sapwood area can accurately estimate LAI for stands of varying density including both natural and silviculturally treated stands (Hein et al., 2008; Medhurst and Beadle, 2002; Waring and Schlesinger, 1985) results presented here do not support this for the tree-level equations. Despite measuring SBA in August near the time of peak leaf area (Vose et al., 1994; Vose and Swank, 1990) and recoring trees with high coefficient of variation, the best sapwood-based equation performed worse at the tree-level than either the VAL and DCL models. When PLA_{Tree} equations were summed to the plot-level, the VAL model still performed marginally better than the SCL model.

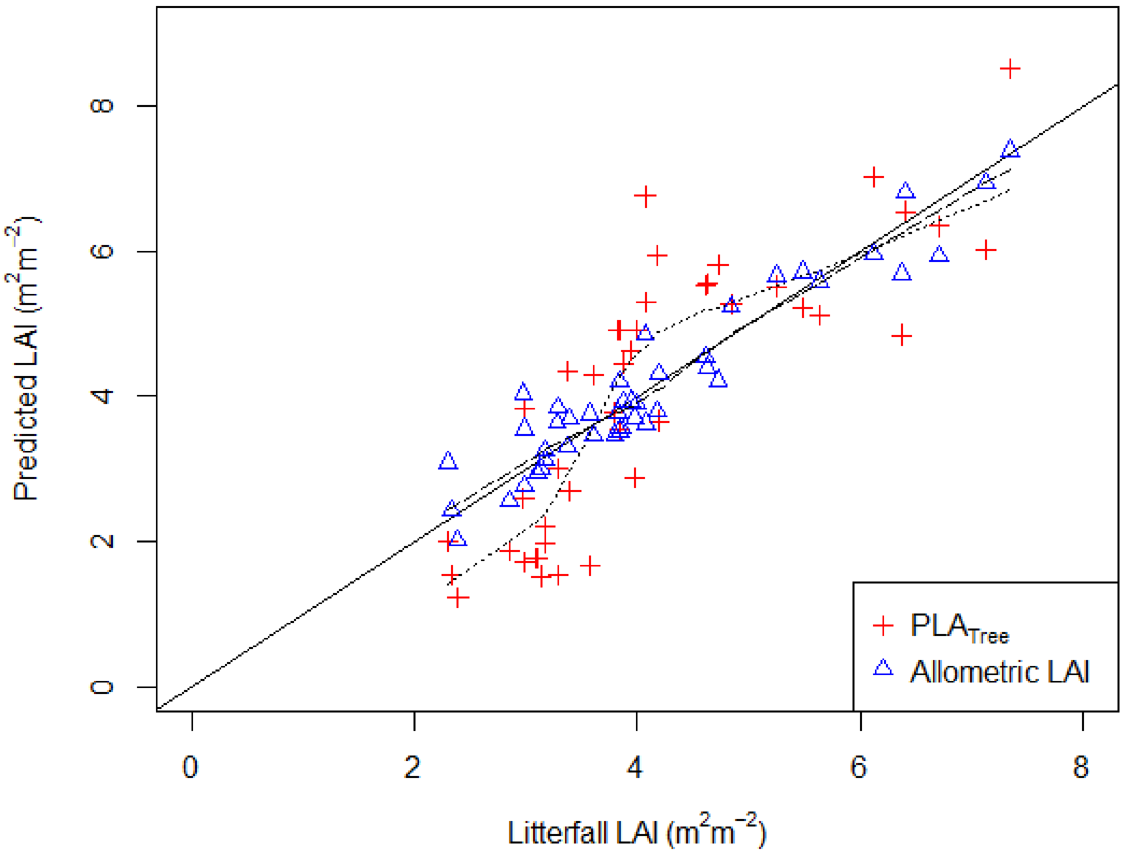

Figure 3.6. Allometric LAI plotted over litterfall LAI. The + symbol represents individual PLA_{Tree} equations summed to the stand-level and triangles are the stand-level LAI fit. Loess regression fits are included with dotted line showing PLA_{Tree} and long dash showing allometric LAI. Only plots with sapwood area calculated from cored trees are included.

At the stand-level, allometric LAI equations demonstrated marked improvements over the individual tree equations despite using essentially the same data (Figure 3.6). The difference is possibly due to crown differentiation in even-aged stands. Dominant trees within a stand carry a disproportionate amount of leaf area and individual tree sapwood were unable to account for these differences. These errors were exacerbated in stands that had been silviculturally thinned. Total sapwood area per hectare was highly correlated with LAI and the inclusion of crown length improved model fit for the stand-level allometric LAI equations. The sapwood-crown length equation has been an effective estimator of LAI for a silviculturally treated eastern white pine plantation (Guiterman et al., 2012), however results presented here demonstrate that when applied to a wide range in stand conditions, this model performs the best when applied directly to the stand-level. Despite the high correlation between sapwood area and leaf area, sapwood permeability could help explain some of the variation in this relationship (Coyea and Margolis, 1992; Mencuccini and Grace, 1995; Whitehead et al., 1984), although this was not explored for this study.

Allometric equations developed from sapwood have a number of issues. First, standard errors when estimating sapwood area from increment cores can be up to 20% even with 6 sapwood cores (Seymour unpublished data). Secondly, destructive coring of trees is time consuming and can cause defects to the bole. Error in predicting individual tree LA becomes compounded when summed to the stand-level so bias was a major concern. The best individual tree models, tended to overpredict LAI for nonthinned stands and particularly in the oldest (200 year) stand suggesting that these trees have less leaf area per unit of crown length than younger trees. Conversely the same equations generally underpredicted young and heavily thinned stands. This is likely due to crown densification (Mainwaring and Maguire, 2004) after thinning as crowns no longer recede and branches elongate. Further error in estimating leaf area is due to the lack of larger and heavily thinned trees in the destructively sampled database which can cause substantial errors when these equations are extrapolated to the stand-level.

Few studies have looked at applying allometric equations over a wide range of ages and stand structures and results presented here. Our data suggests that non-sapwood equations that include crown dimension in PLA models have the potential to explain much of the variation in individual tree PLA. Additional destructively sampled trees especially in larger size-classes will be necessary to improve the predictive ability of these equations in larger trees and thinned stands and a higher branch sampling intensity for destructively sampled trees could also improve the predictions. Perhaps the inclusion of growth effective age or crown projection area could account for differences among crown classes in dense stands as well as the observed higher mean tree leaf areas in heavily thinned stands.

Recommendations

Overall, our results suggest that sapwood area and crown attributes should be analyzed on a per hectare basis to most effectively estimate stand-level LAI (Figure 3.7). The inclusion of TOPHT improved predictions for all models and should be incorporated when testing these equations with other conifers. Overall, stand-level models using age, density and site quality (Chapter 2) or sapwood area and crown length fit much better when applied to a population.

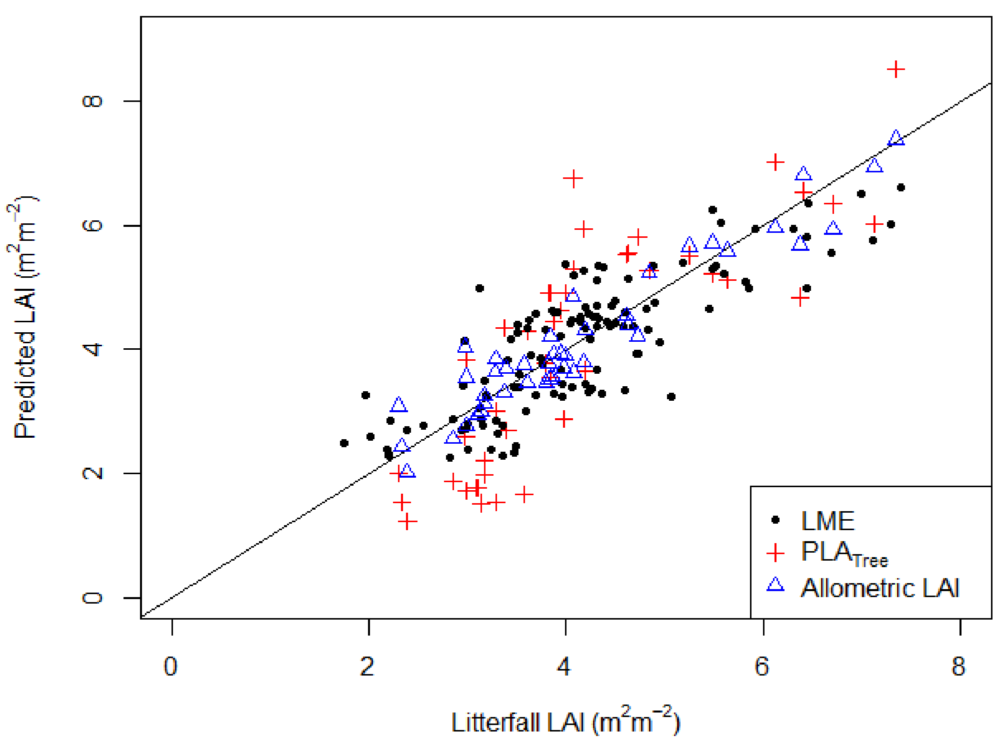

Figure 3.7. Allometric LAI estimated using three methods plotted over litterfall LAI. LME was estimated using Model 6 from chapter 2 using the mean height of tallest 100 trees per hectare (TOPHT, m), relative density (RD) and site index (SI). PLA_{Tree} was estimated by summing up individual tree leaf areas using the VAL equation using the WNLS fitting technique and dividing by the plot area. Allometric LAI was estimated using the SCL.TOPHT.NLMER model using fixed effects only.

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BIOGRAPHY OF THE AUTHOR

Adam Bland was born July 9th, 1985 in Tacoma, Washington. After moving to Arizona in 1996 he later attended high school in Gilbert, Arizona where he graduated in 2003. After graduating from Mesa Community College with an Associate of Science, Adam then attended Northern Arizona University in Flagstaff, Arizona where he graduated Cum Laude in 2010 with a Bachelor of Science in Forestry. During his undergraduate education Adam worked part time at the research greenhouse on campus and spent the summer assisting with research on the effects of fuel risk reduction treatments on carbon stock of ponderosa pine stands.

Throughout college, Adam was active in the cycling club and can be found on a bicycle year-round. Adam is currently a member of the Xi Sigma Pi, Forest Guild, and the Society of American Foresters. After his undergraduate studies, he came to Maine to study silviculture, stand dynamics and production ecology under the advisement of Dr. Robert S. Seymour. Adam is a candidate for the Master of Science degree in Forest Resources from the University of Maine, in December 2012.