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The Influences of Conventional and Low Density Thinning on Leaf Area, Growth, and Growing Space Relationships of Eastern White Pine (Pinus Strobus L.)

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THE INFLUENCES OF CONVENTIONAL AND LOW DENSITY THINNING ON LEAF AREA, GROWTH, AND GROWING SPACE RELATIONSHIPS OF EASTERN WHITE PINE (*Pinus Strobus* L.)

By

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An Abstract of the Thesis Presented
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Despite the commercial importance and widespread management of eastern white pine (*Pinus strobus* L.) in the Northeast, surprisingly little is known about the effects of thinning on even-aged stand development. To address this, patterns of leaf area, bole form, volume growth, and growth efficiency – defined as volume increment per unit leaf area – were examined over a 17-year period within a thinning study in central Maine designed to compare the conventional B-line and low density thinning regimes.

At the tree-level, many of the effects of thinning were as expected. Heavier, low density thinning resulted in significantly larger and deeper crowns with greater leaf area than equivalent trees in both the B-line and unthinned control treatments. These changes explained higher rates of diameter and volume growth. Thinning did not alter growth efficiency per se, but larger trees had slightly (but significantly) lower growth efficiency than smaller trees. Reconstruction of bole taper – quantified as Girard form class – showed that, surprisingly, B-line thinning produced more tapered butt-logs (first 5-meter)

than low density thinning, resulting from a thinning-induced growth response at breast height but not at the top of the butt-log.

At the stand-level, an annual record of leaf area index (LAI) attained by litterfall collection showed that leaf area in the control treatment was relatively constant or slightly declined over the study period. Thinning significantly reduced stand leaf area and thus gross volume growth, but the thinned treatments had nearly equal LAIs for the ten years following the initial thinning. This explained the similar gross volume growth rates and growth efficiencies of the thinning treatments. Following the re-entry harvest, B-line leaf area increased until the stands reached crown closure, while the low density treatment continued rates of crown expansion and LAI increase without reaching a peak. Due to greater LAI, B-line gross stand volume growth and growth efficiency were significantly higher during the latter growth period; low density stand growth efficiency was still no different from the control. Growth efficiency of the unthinned stands was found to be positively related to stand density.

Results of this study have important implications to managers of eastern white pine. The contention that thinning below B-line stocking has deleterious effects on stand yield was in general not supported. On the contrary, only a minor loss of gross stand volume growth was found by thinning to a low density. In addition, low density trees were larger, faster growing, and had better stem form than comparable B-line trees. Therefore, low density thinning was found to be a viable alternative to conventional management.

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Finally, a great deal of my gratitude goes to my fiancé, Julia Briedis, who introduced me to forestry field work, aided in my own data collection, and shared in the experience of grad school. Her support and ability to edit my writing helped this thesis immensely.

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INTRODUCTION

Since the time of European settlement, eastern white pine (*Pinus strobus* L.) has been a revered and iconic part of the New England forest (Howard 1986). Over the last 200 years up to today, the species has been an important contributor to New England's forest industry (McWilliams and others 2004). Pure stands of eastern white pine are common throughout the region (Widman and McWilliams 2004) as a result of agriculture land abandonment, yet white pine is also a prominent component of other northeastern forest types (Wendel and Smith 1990). When white pine trees reach larger sizes, they are both financially (Page and Smith 1994) and ecologically valuable (Rogers and Lindquist 1992), which is why foresters in New England often favor and actively regenerate eastern white pine.

When managing young pine stands, foresters are faced with a choice between two well-established silvicultural systems, the conventional B-line thinning regime and the low density thinning regime. Neither the research community nor experienced foresters have been able to provide clear consensus as to which system is more likely to meet the common management objectives of achieving rapid growth of individual trees while maximizing the use of available growing space to produce high stand yields. Both systems have their advocates, and a debate as to which regime best meets such objectives has been ongoing for nearly 40 years (Leak 2004; Seymour 2007).

Conventional B-line management follows the regional guidelines (Lancaster and Leak 1978) which state that stands should be maintained between the A- and B-lines on the white pine stocking guide (Philbrook et al. 1973), thus representing the "minimal stocking for full site utilization" (Lancaster and Leak 1978, p. 6). Lancaster and Leak (1978) warn that stand densities below the B-line will suffer from "diminished volume growth per acre." Low density management, therefore, challenges these notions since it is designed to fully isolate select crop trees through substantially heavier thinning than under conventional management. The initial design of low density regimes came from observations of extremely high growth rates on trees that were isolated by the 1938 hurricane (Smith and Seymour 1986; Page and Smith 1994). Recognizing that wide crowns resulting from the lack of competition defied the size-density metrics used in the conventional stocking guide, Seymour and Smith (1987) devised a new stocking guide that would aid in implementing low density rotations. Advocates of low density management assert that volume growth per acre will be sacrificed for increased monetary yield resulting from such high-value crop trees (e.g, Seymour 2007).

To date, there have been only two comparisons of these management regimes: one on Quabbin Reservoir lands in central Massachusetts, and the other on the University of Maine's Dwight B. Demeritt Forest in central Maine. The Quabbin thinning trial was meant to assess the different regimes in terms of growth and water-use through transpiration (Hunt and Mader 1970). Hunt and Mader (1970) found that low density thinning substantially increased diameter-at-breast-height growth over conventional thinning, and created stands that had lost less water to transpiration and were more tolerant of drought. After 20 years in these stands, Stone (1985) found that growth rates remained higher on the low density plots and board-foot volumes of low density trees were greatest. Economic analyses demonstrated that the low density plots had higher earnings on the most productive sites, while on the poorer site the conventional plots had slightly higher earnings (Stone 1985; Stone et al. 1986). Both Hunt and Mader (1970) and Stone (1985) concluded that low density thinning is a viable alternative to conventional management on watershed lands.

The study in central Maine, first described by Seymour (2007), showed that at the stand-level gross volume growth rates were similar between B-line and low density plots during the ten years following the initial thinning of the plantation. This finding was surprising, considering that the low density plots had roughly half the number of trees as the B-line plots. This thesis uses Seymour's thinning study to compare the growth rates and growing space relationships between the two silvicultural systems over the 17 growing seasons since its establishment in 1991. Ultimately, the results from this study will inform forest managers of the responses of eastern white pine to the differing thinning regimes.

Comparisons of the management regimes (Figure 1) will focus on the influences of the treatments on leaf area, volume growth, and growing space relationships. An understanding of how these ecophysiological characteristics have changed because of thinning has proven to enhance the efficacy of silvicultural prescriptions in other forest types (Long et al. 2004). Leaf area is used as a measure of site occupancy, but it is also directly related to the growth potential of trees and stands (Assmann 1970). Since leaf area is difficult to measure directly, we employ allometric equations to estimate its amount. The focus of Chapter 1 is to evaluate several allometric models in order to select the best equation for accurate and unbiased leaf area estimates that can then be employed in further analyses. Chapter 2 explores the effects of thinning on butt-log form and total stemwood volume growth. The butt-log (first 16 feet of the stem) receives particular attention because it both contains a substantial amount of the tree volume and accounts for a disproportionate amount of tree value. The form of the butt-log is important in timber sales as it directly relates to lumber yields (Husch et al. 2003). Surprising results in these analyses prompted an examination into taper equations that could account for the changes in stem form brought on by thinning. Again, it was important that an accurate and unbiased volume equation be employed to ensure fair and realistic comparisons between the thinning treatments. In Chapter 3, the patterns of leaf area and volume growth are used together to analyze the efficiency with which the trees utilize their leaf area and hence growing space. This study is the first of our knowledge to quantify these growth efficiency relationships in eastern white pine.

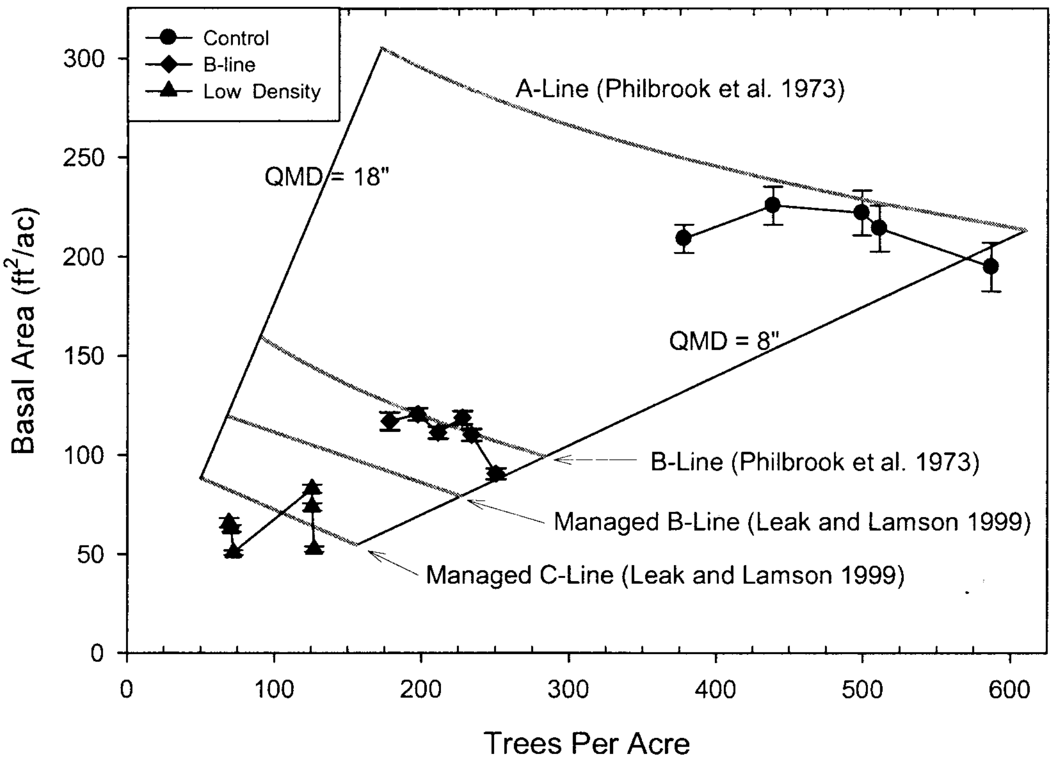

Figure 1. The eastern white pine stocking guide showing the development of the thinning treatments over the 17-year study period. Error bars are ± one standard error. QMD is quadratic mean stand diameter.

CHAPTER ONE

SEVENTEEN-YEAR PATTERNS OF PROJECTED LEAF AREA ACROSS CONTRASTING THINNING REGIMES OF EASTERN WHITE PINE (*Pinus strobus* L.): COMPARISON OF ALLOMETRIC LEAF AREA MODEL FORMS AND FITTING TECHNIQUES

ABSTRACT

Changes in tree leaf area following silvicultural treatments in eastern white pine (*Pinus strobus* L.) have not been well quantified, despite the commercial importance of the species. To address this, we used a 17-year record of leaf area index (LAI), attained by litterfall collections, to assist in evaluating six allometric leaf area prediction models. The models were fit using three different statistical fitting techniques to a sample of 51 eastern white pine trees, most of which are part of the thinning trial in central Maine where litterfall sampling is ongoing. Accuracy of the allometric model predictions was evaluated at both tree- and stand-levels. The best fitting technique depended on the model form, but stand-level leaf area predictions were always improved by weighting of the model primary covariate. Average absolute deviation of allometric-LAI predictions ranged from 0.321 to 1.777 among the models and fitting techniques. The best allometric model predicted leaf area from sapwood basal area and crown length; this form was the most robust among those tested as it was the least influenced by the different fitting techniques. The model was fit with weighted nonlinear mixed effects and applied to the study population without the input of the model random effects. Analyses on the

influences of thinning on leaf area in the 60-year-old eastern white pine stands revealed that 10 years following the initial harvest. and despite re-thinning, trees in the conventional (or B-line) thinning regime did not continue to increase leaf area because the stands had reached crown closure. This caused the LAI to be constant or slightly declining, a pattern similar to unthinned control plots. Low density thinning, on the other hand, resulted in increases of tree- and stand-level leaf area throughout the study period. We found no indication that the thinning treatments, if left unthinned, would ever achieve pre-harvest LAI levels.

INTRODUCTION

Canopy leaf area is important to consider in evaluations of silvicultural thinning treatments because it determines the productivity of trees and stands. Thinning reduces stand-level leaf area in the short-term until stands reach the point of crown closure, while at the tree-level, leaf area rapidly increases following thinning release through crown densification and elongation (Mainwaring and Maguire 2004). Such changes in stand structure and crown architecture may better explain the outcome of thinning than changes in stand density or tree size would alone (O'Hara 1988, 1989).

Thinning is commonly employed in even-aged eastern white pine (*Pinus strobus* L.) stands, yet to our knowledge no study has considered the effects of treatment on leaf area or how changes in crown structure alter growth response. For nearly 40 years, there has been an ongoing debate over the optimal management of white pine in the Northeast (see Seymour 2007). The silvicultural systems being employed and debated are thinning to the B-line and low density thinning. Studying the effects of thinning on leaf area could help inform this debate.

Since leaf area is difficult to measure directly, various methods of estimation have been developed. These include simple diameter-based (Kittredge 1944) and sapwood-based (Grier and Waring 1974) allometric equations, foliage litterfall sampling (Magwick and Olson 1974; Marshall and Waring 1986), and light interception methods (Pierce and Running 1988; Norman and Campbell 1989). Allometric equations, in particular, are widely available because of their ease of application and use of strong physiological relationships. For example, Valentine et al. (1994) developed equations to predict the cross sectional area at the base of the live crown, which is a surrogate for leaf area according to the 'Pipe Model Theory' (Shinozaki et al. 1964). In addition, Maguire and Bennett (1996) used a modified height-to-diameter ratio to approximate crown width. Most sapwood-based allometric equations utilize a nonlinear form to estimate sapwood taper below the live crown (Dean and Long 1986; Dean et al. 1988) and some integrate crown dimensions (Long and Smith 1988, 1989; Maguire and Hann 1989). Allometric models can also incorporate stand density and tree-competition metrics (Monserud and Marshall 1999).

Few studies have evaluated the error with which allometric equations predict leaf area when applied to a population. Such an analysis requires independent estimates of leaf area that are rarely available. Thus far in the literature, only a diameter-based allometric equation (Marshall and Waring 1986; Turner et al. 2000) and a fixed sapwood area-leaf area ratio (Dean et al. 1988) have been shown to yield biased results. Recently, however, Turner et al. (2000) found that results from the latter type of equation agreed with stand leaf area estimates obtained by litterfall sampling. Important aspects of developing allometric leaf area equations that researchers must consider are the model form, potential independent variables, and a variety of available statistical fitting techniques. Any of these could potentially add bias, especially where the model form is biologically naïve (Kershaw et al. 2009).

Our objectives were to (1) examine the effects of differing allometric model forms and fitting techniques through comparisons of allometric and litterfall LAI estimates from an eastern white pine thinning study in central Maine, and (2) evaluate the influences of B-line and low density thinning on canopy leaf area and crown structure. The former objective has the added benefit of aiding in the selection of an allometric leaf area prediction equation for further analyses of growth and growing space relationships within the thinning study.

METHODS

Study site and data collection

The study site is located in central Maine (44°55' N, 68°41' W) on the University of Maine's Dwight B. Demeritt Forest. It is a 0.96 ha eastern white pine plantation where, in 1991, the eastern white pine thinning study (WPTS) was initiated to evaluate tree and stand responses to two contrasting silvicultural systems for white pine. First described by Seymour (2007), the stand was originally an unreplicated spacing study planted in 1949 on somewhat poorly drained silt-loam soils of the Buxton series with an average site index of 19.8 m (base age 50; Frothingham 1914). It received no management until the first thinning in the fall of 1991 at age 42 yr and was subsequently re-thinned in 2001. The study consists of eight replicate blocks, each with three 0.04 ha (20 m x 20 m) plots blocked according to pre-treatment trees per hectare and basal area. Thinning treatments were assigned at random so that each block consists of a low density plot, a B-line plot, and an unthinned control plot. Crop trees in the low density treatment were marked prior to felling at approximately an 18-20 ft spacing according to the Seymour and Smith (1987) stocking guide and all non-crop trees were removed. Crop trees in the B-line treatment were marked identically to those in the low density treatment, and thinning was done in order to release them on 3-4 sides until the target residual basal area of the Philbrook et al. (1973) stocking guide was achieved. The 2001 re-entry harvest removed the least desirable low density trees and maintained the isolation of crop trees. On the B-line plots, the re-entry thinning was done to maintain B-line stocking, but since the initial left stocking below the B-line (Seymour 2007), the second entry was light on most plots. Analyses in the present study focus on four study blocks for which litterfall data were available (Table 1.1).

Data collection commenced prior to the 1992 growing season with plot tallies including diameter at breast height (DBH; nearest 0.25 cm; 1.37 m above the ground), total tree height (HT; nearest 0.05 m) and height to the lowest live whorl (HTLLW; having three or more live branches) for all trees in thinned treatments. Control trees were measured for DBH; however, only a subset (roughly equal to the per-plot number of trees on thinned plots) received the HT and crown measurements. Subsequently, these missing heights were estimated with plot-specific height-over-DBH regression equations. The inventories of 1999, 2001, 2006, and 2008 were conducted in August-September with

DBH, height, and crown measurements recorded for all living trees. Sapwood basal area (SBA) was measured on all living trees from increment cores extracted at breast height on the east and west sides in 2001 and on the north, southeast, and southwest sides in 2008. The sapwood-heartwood boundary was marked in the field prior to mounting the cores and later verified with a 10% ferric chloride ($FeCl_3$) solution (which stains the heartwood) prior to measuring the sapwood radii (nearest 0.1 mm). Coincident with increment coring, each tree was measured for bark thickness (nearest 0.1 cm) at breast height with a bark gauge. Sapwood basal area was calculated as the difference between inside bark basal area and the mean heartwood area (from individual sapwood radii minus inside bark radius).

Litterfall-based projected leaf area

Five litterfall collection traps were placed in each of six plots (two per treatment) in 1992. Additional traps were added to the control plots in 2001 and to two low density and two B-line plots in 2007. The traps are 50 cm x 50 cm (2500 cm^2) 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 corner. Litterfall is collected in October and June (for one-season's litterfall), placed in paper bags, dried at 65°C for at least one week, sorted, dried again, and massed to the nearest 0.01 gram. Plot-level leaf area index (LAI) is estimated as the mean of the trap-LAIs, which are calculated as

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

Table 1.1. Stand attributes of eastern white pine thinning study treatments during the study period. Values are means of four 0.4 ha plots per treatment; standard errors are in parentheses.

		Control	B-line	Low Density
1992 post-harvest				
	TPH	1550 (347)	594 (62)	313 (22)
	BA	45.8 (4.29)	20.2 (0.91)	12.7 (0.18)
	QMD[a]	21.7 (1.72)	21.7 (1.43)	23.3 (0.58)
	LAI[b]	4.7 (0.27)	2.0 (0.03)	1.9 (0.21)
2001 pre-harvest				
	TPH	1300 (236)	525 (34)	313 (22)
	BA	51.7 (3.90)	26.7 (1.18)	19.8 (0.46)
	QMD	24.8 (1.68)	26.4 (1.40)	29.1 (0.66)
	LAI	4.8 (0.27)	3.4 (0.11)	3.0 (0.12)
2001 post-harvest				
	TPH	1300 (236)	488 (44)	175 (10)
	BA	51.7(3.90)	25.3 (1.41)	11.8 (0.35)
	QMD	24.8 (1.68)	26.6 (1.43)	29.4 (1.23)
	LAI	4.8 (0.27)	3.3 (0.12)	1.9 (0.08)
2008				
	TPH	988 (142)	444 (19)	167 (6)
	BA	48.8 (2.37)	28.3 (1.68)	15.3 (0.47)
	QMD	27.1 (1.58)	29.0 (1.22)	34.1 (1.05)
	LAI	4.3 (0.16)	3.0 (0.18)	2.6 (0.06)

Note: TPH – trees per hectare; BA – basal area (m^2 ha^{-1});
QMD – quadratic mean stand diameter (cm);
LAI – leaf area index (m^2 m^{-2})
[a] QMDs are of upper crown class trees
[b] From two plots per treatment

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 length of time (in years) that needles stay on a given branch. Values for SLA and needle retention come from archived sample branch data (described below) as part of a larger white pine litterfall collection program on the University of Maine School Forests. For all litterfall traps in the WPTS, we applied the mean SLA for the site of 65.25 cm^2 g^{-1} because the treatments had no effect on SLA. Thinning was found to affect needle retention, and thus retention values of 2.37 years is applied to thinned plots and 2.207 years is applied to the control plots.

The senescence correction factor (SCF) is used to convert the dry weight of abscised needles collected in the trap to their approximate dry weight when alive. In short, the SCF integrates losses of dry weight resulting from the removal of nutrients and carbohydrates from the foliage prior to senescence (Vose et al. 1994), and potential decomposition within the trap prior to collection (decomposition is assumed to be minimal because trap bottoms are permeable and elevated at least 5 cm above the ground). The SCF was determined as the ratio of SLAs from 100 senesced (collected in litterfall traps)and oven-dried needles on 10 WPTS plots to the SLAs of 100 green and oven-dried needles from the same plots (the SLA procedure is described below). Senescent (dead) needles from the traps were found to have lost an average of 15.1% (ranging from 6 to 29%) of their dry weight per unit of surface area. Therefore, an SCF of 1.151 is used to convert the litterfall trap collections to their presumed dry mass when living.

Branch-level projected leaf area

Branch-level projected leaf area (PLA_{branch}) prediction models were fit to archived data from 48 eastern white pine trees sampled on the University of Maine Dwight B. Demeritt Forest (Table 1.2) (Barker 1998; Pace 2003; Rifkin 2005). Nineteen trees were located within the WPTS, including four B-line, seven control, and seven low density trees. The remaining trees were located within an approximately 100 ha area of the

Demeritt Forest. Sample trees from the control treatment come from an unthinned area adjacent to the study.

Table 1.2. Summary statistics for sample trees used to fit the PLA_{branch} and PLA prediction models. Data attributes include diameter at breast height (DBH), total stem height (HT), crown length to the lowest live branch (CL), sapwood basal area (SBA), total projected leaf area (PLA), and breast-height age.

	DBH (cm)	HT (m)	CL (m)	SBA (cm^2)	PLA (m^2)	Age
Destructively-sampled trees (*n* = 48)						
Mean	17.88	15.02	6.10	126.75	49.96	41
Standard Error	1.80	1.00	0.47	22.66	14.04	4
Minimum	1.60	2.77	1.67	0.91	0.16	11
Maximum	61.30	29.63	17.14	830.94	604.78	128
Destructively-sampled plus climbed trees (*n* = 51)						
Mean	19.16	15.51	6.53	149.71	49.96	41
Standard Error	1.84	0.98	0.50	24.99	14.04	4
Minimum	1.60	2.77	1.67	0.91	0.16	11
Maximum	61.30	29.63	17.14	830.94	604.78	128

Sample trees were gently felled and measured for height and basal diameter of all live branches. Crowns were divided into three sections, with one sample branch randomly selected from each crown section. The SLA for each sample branch was determined from approximately 100 needles that were kept frozen until projected leaf area was measured to the nearest 0.0001 cm^2 using a high-resolution scanner (>1200 dpi) and the WinSeedle® program (Regent Systems, Inc.), then oven-dried at 65° C for 72 hours before massing to the nearest 0.0001 gram. SLA is calculated by dividing the projected leaf area by the dry weight. The remaining portions of the sample branches were dried for at least two weeks prior to sorting and massing both foliage and woody material to the nearest 0.01 gram. Total sample branch PLA_{branch} was determined as the product of the total foliage dry weight and the branch SLA (then converted from cm^2 to m^2).

Following initial screening of various published PLA_{branch} prediction models, the Maguire and Bennett (1996) Weibull model form was selected and fit to the sample of 143 branches (Table 1.3). The model form is expressed as

$$[2] \qquad PLA_{branch} = \left(\beta_0 BD^{\beta_1}\right) * \left(RelDINC^{(\beta_2-1)}\right) * e^{[-(\beta_3 * RelDINC^{\beta_2})]},$$

where BD is the branch basal diameter (cm), RelDINC is the relative depth of the branch into the crown (0 is at the top, 1 at the crown base), and β_is are parameters to be estimated by the model. The equation was fit with nonlinear mixed effects regression using the nlme library (Pinheiro et al. 2008) in R (R Development Core Team 2008). Random effects were added to the β_1 and β_3 parameters and account for the nested structure of the data at two levels: the type of thinning [NoThin (*n*=33), LightThin (*n*=5), HeavyThin (*n*=9), and Shelterwood (*n*=1)] and the individual sample tree. This technique created a tree-specific model while accounting for variation in crown form caused by stand density and thinning.

Table 1.3. Summary statistics for destructively sampled branches (*n*=143). Data attributes include branch basal diameter (BD), relative depth into the live crown (RelDINC), total branch leaf mass, specific leaf area (SLA), and branch-level projected leaf area (BLA).

Attribute	Mean	SE	Min	Max
BD (cm)	1.85	0.13	0.20	9.4
RelDINC	0.546	0.023	0.037	1.0
Leaf mass (g)	102.33	16.81	0.01	1374.16
SLA ($cm^2 g^{-1}$)	68.78	0.82	49.52	103.60
BLA (cm^2)	0.673	0.112	7.93E-05	9.416

Note: SE – standard error

Since heteroscedasticity was found in the residuals, various transformations and weights were tested. The best option was to use a variance power function (Pinheiro and Bates 2000),

[3] $$\mathrm{Var}(\varepsilon_i) = \sigma^2 |v_i|^{2\delta},$$

where σ^2 is the residual sum of squares, v_i is the primary covariate (branch basal diameter in this case), and δ is the variance function coefficient to be estimated by the model. The variance power function allows the model to find an optimal weight given the variance inherent in the data (Pinheiro and Bates 2000). Use of mixed effects with the weighting procedure resulted in a highly accurate fit of the PLA_{branch} model (Table 1.4).

Table 1.4. Parameter estimates and fit statistics for the PLA_{branch} model (eqn. [2]).

Equation	Parameter	Estimate	SE	δ	RMSE	R^2
[2]	β_0	0.5013	0.0554	1.3988	0.1292	0.9906
	β_1	1.8799	0.1341			
	β_2	1.8723	0.0925			
	β_3	1.7451	0.3930			

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

Tree-level projected leaf area

The branch-level model was applied to all live branches (n = 4306) on each sample tree and then summed for an estimate of the tree-level projected leaf area (PLA). In 2008, three more trees were added to the sample dataset to ensure better coverage of the larger trees present on the WPTS (Table 1.2). These trees were climbed and measured for heights and basal diameters of all live branches (n = 303), but no sample branches were collected. Equation [1] was then applied to each branch including the treatment random effects (but no tree effects).

Tree data used for the allometric-PLA models came from field measurements of DBH made prior to felling, and HT and HTLLW made with a logger's tape after felling. HTLLW 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 SBA 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 added trees.

Following initial screening of published PLA models, six forms were selected for further analysis (Table 1.5). All model forms are nonlinear because preliminary scatter plots indicated strong nonlinear relationships between PLA and the independent variables used in model fitting. In most cases, these 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 1.6) of each allometric-PLA model were attained through three statistical fitting techniques: nonlinear least squares (NLS); weighted nonlinear least squares (WNLS) using the generalized nonlinear least squares function (Pinheiro et al. 2008) 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 the improvement shown through the WNLS technique (see Discussion). 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 thinning type (same as for the PLA_{branch} model) (Table 1.7). Selection of the random parameter in each model was done by iteratively fitting each model using a different random parameter each time and finally choosing the option 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) and also just the fixed effects portion of the model (NLME-F).

Table 1.5. Selected model forms for estimating tree-level projected leaf area (PLA). 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), modified live crown ratio (mLCR), and live crown ratio (LCR). Live crown base is the lowest live whorl containing three or more live branches.

Model	Equation	Reference
SAP	$PLA = b_1 * SBA^{b_2}$	Espinosa Bancalari et al. 1987
SCL	$PLA = b_1 * SBA^{b_2} * CL^{b_3}$	Gilmore et al. 1996; Kenefic and Seymour 1999
MAG	$PLA = b_1 * CL^{b_2} * e^{(b_3 * \frac{DBH}{HT})}$	Maguire and Bennett 1996
SMAG	$PLA = b_1 * SBA^{b_2} * e^{(b_3 * \frac{DBH}{HT})}$	This study
VAL	$PLA = b_1 * (BA * mLCR)^{b_2}$	Modified from Valentine et al. 1994
DCL	$PLA = b_1 * DBH^{b_2} * CL^{b_3}$	This study

Table 1.6. Parameter estimates of the allometric-PLA equations. All estimates were significant at $P < 0.05$ unless otherwise indicated.

Model	Parameter	NLS	WNLS	NLME-F
SAP	b_1	0.1383	0.0845	0.1341
	b_2	1.1947	1.2735	1.1828
SCL	b_1	0.2236	0.0877	0.1027
	b_2	0.4806	0.6671	0.7541
	b_3	1.5379	1.4655	1.2538
MAG	b_1	0.6280	0.1934	0.2064
	b_2	2.3950	2.7811	1.6749
	b_3	0.0021*	0.1953*	1.5608
SMAG	b_1	0.1634	0.1145	0.1044
	b_2	1.1387	0.9426	0.8297
	b_3	0.1018*	0.9990	1.4615
VAL	b_1	0.9054	0.1112	0.1174
	b_2	0.8374	1.1842	1.1754
DCL	b_1	0.3970	0.0747	0.0645
	b_2	0.6149	1.0859	1.1497
	b_3	1.6450	1.6404	1.6286

* $P \geq 0.05$

Table 1.7. Random effects of NLME-R model fits specific to the WPTS. These values were added to the fixed effect (Table 1.7) of the respective parameter in each model.

Model	Random Parameter	Location	Thinning Type: Control	B-line	Low Density
SAP	b_2	-1.22E-09	-0.0551	-0.0043	0.0212
SCL	b_3	0.0179	-7.30E-09	6.66E-09	2.48E-09
MAG	b_2	0.2390	0.0410	0.1002	-0.0815
SMAG	b_2	8.47E-11	-0.0012	0.0554	0.0305
VAL	b_2	0.0246	-0.0008	0.0223	-0.0133
DCL	b_3	0.0043	-2.43E-07	1.87E-07	6.36E-08

Analyses

Tests for the effects of thinning on leaf area and tree-sizes used one-way analysis of variance and Tukey's HSD post-hoc mean separation test. Statistical significance was considered at the 95% level of confidence. Initial fits of the allometric-PLA models were evaluated from fit statistics, residual plot analyses, and estimates of bias. 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 original units (m^2) as

[4] $$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(\hat{Y}_i - Y_i)^2}{n}},$$

where $\hat{Y}_i$ is the predicted PLA from the model and Y_i is the PLA from branch summation (i.e. observed). Population estimates of PLA and LAI were made by applying the models to WPTS stand inventories; allometric-LAI was calculated by summing all tree PLAs for a given plot and year and dividing by the plot area. Allometric-LAI estimates were compared to litterfall-LAI estimates for each inventory year; however, models including SBA could only estimate leaf area for the years 2001 and 2008 because prior SBA measurements were unavailable. These comparisons were done both graphically and by calculating average absolute deviation (AAD) as

[5] $$AAD = \frac{\sum_{i=1}^{n} |\hat{Y}_i - Y_i|}{n},$$

where $\hat{Y}_i$ is the estimated allometric-LAI and Y_i is the litterfall-LAI. Comparisons for the years 2001 and 2008 used litterfall-LAI estimates from the years 2000 and 2007, respectively. The 2001 litterfall collection could not be used because it was confounded by thinning following the fall collection but before to the spring collection; trees removed in the thinning thus contributed only to the fall collections. The 2008 litterfall-LAI estimates could not be used because they were unavailable.

RESULTS

Seventeen-year patterns of litterfall-LAI and tree growth

Projected LAI from litterfall collections in the unthinned control treatment were relatively constant over the study period, staying generally between 4 and 4.5 $m^2\ m^{-2}$ with a few cases of temporarily reduced leaf areas (Figure 1.1). The sharp decline in 1998 was caused by a severe and region-wide ice storm that occurred in January and broke off tree tops, branches, and buds throughout the study site. The causes of reduction in 1994, 1997, and 2004 are unknown, but possibilities include foliage herbivore or climatic variation; allocation to seed production is unlikely because there is general lack of cone production on the site.

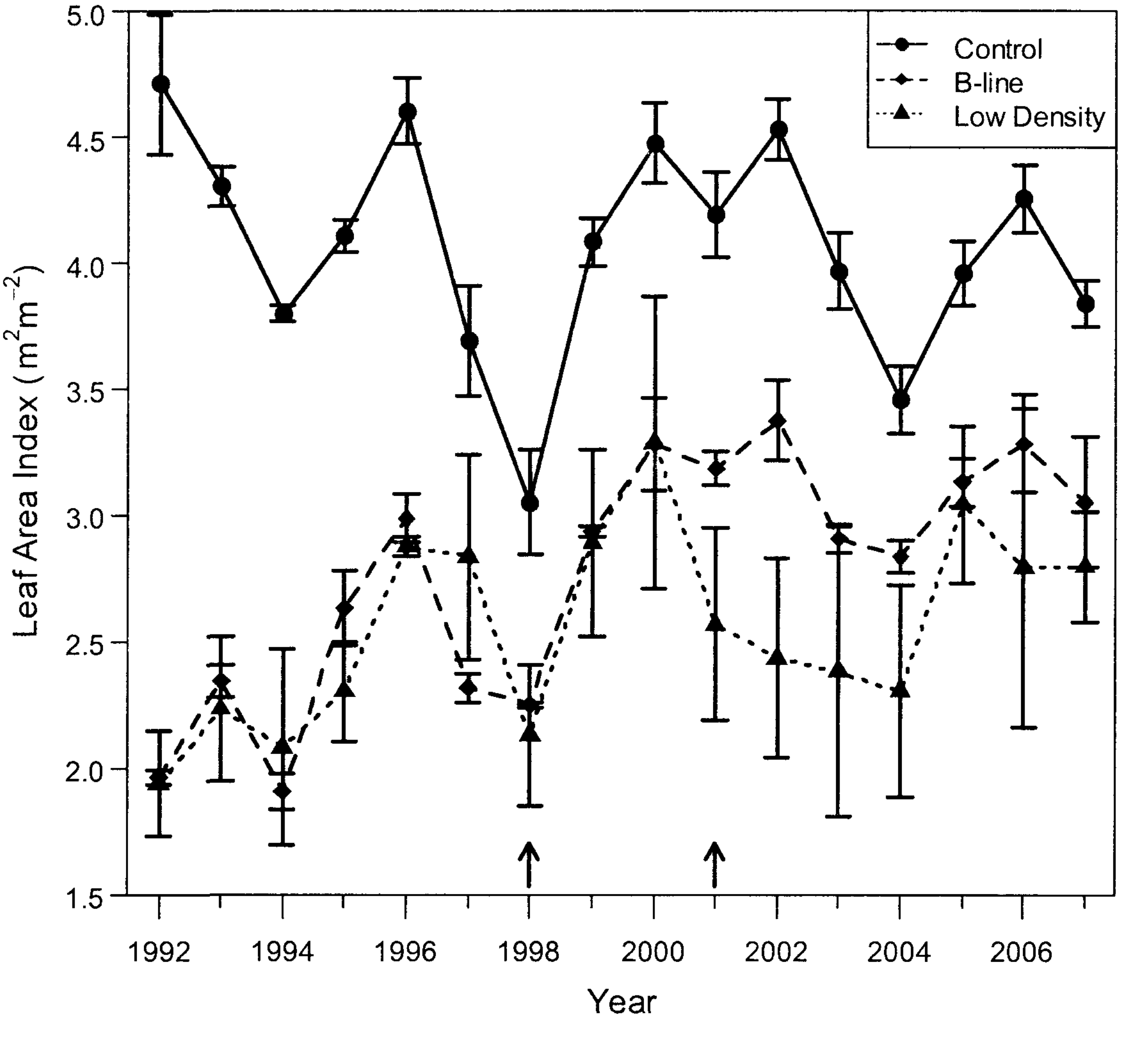

Figure 1.1. Projected leaf area indices (LAI) from litterfall sampling throughout the study period. Error bars are ± one standard error, and arrows along the bottom axis indicate the timing of the 1998 ice storm and the 2001 thinning entry.

Thinning significantly reduced LAIs throughout the study period ($P < 0.05$). The initial thinning entry in 1991 reduced LAIs from 4.75 $m^2\ m^{-2}$ to approximately 2 $m^2\ m^{-2}$ (60%) in both the B-line and low density treatments; the similarity between the LAIs of the thinned treatments is surprising because thinning was significantly heavier in the low density treatment than the B-line treatment ($P < 0.001$) (Table 1.1; Seymour 2007). From 1992 to 2001, LAIs generally increased in both thinning treatments. Throughout the final growth period (2001-2008), B-line LAIs remained fairly constant, while the low density LAI decreased until 2004 and then increased. Basal areas between the treatments were significantly different in 2008 ($P < 0.001$). Variability in the LAI estimates was highest in the low density treatment because of widely spaced and randomly located trees with respect to the five litterfall traps in each plot.

As expected, the effects of thinning on growth of upper crown class trees were largely to increase DBH and CL, especially in the low density treatment (Figure 1.2). Immediately following the initial thinning, the low density trees had significantly greater DBH and CL than the control treatment ($P < 0.01$), and they were similar to the B-line trees in terms of DBH ($P = 0.067$) but had longer crowns ($P = 0.007$); B-line trees were not different from the control ($P > 0.06$). Growth response in both the low density and B-line treatments caused significant differences in DBH and CL among all treatments ($P < 0.001$) for the remainder of the study period. Tree heights were mostly unaffected by thinning ($P > 0.05$). Sapwood basal area was not measured until 2001, at which point significant differences were apparent, which persisted for the rest of the study period ($P < 0.001$). Projected leaf area increased in all treatments between 1992 and 2001, at which point it remained relatively constant on B-line and control trees but kept increasing on

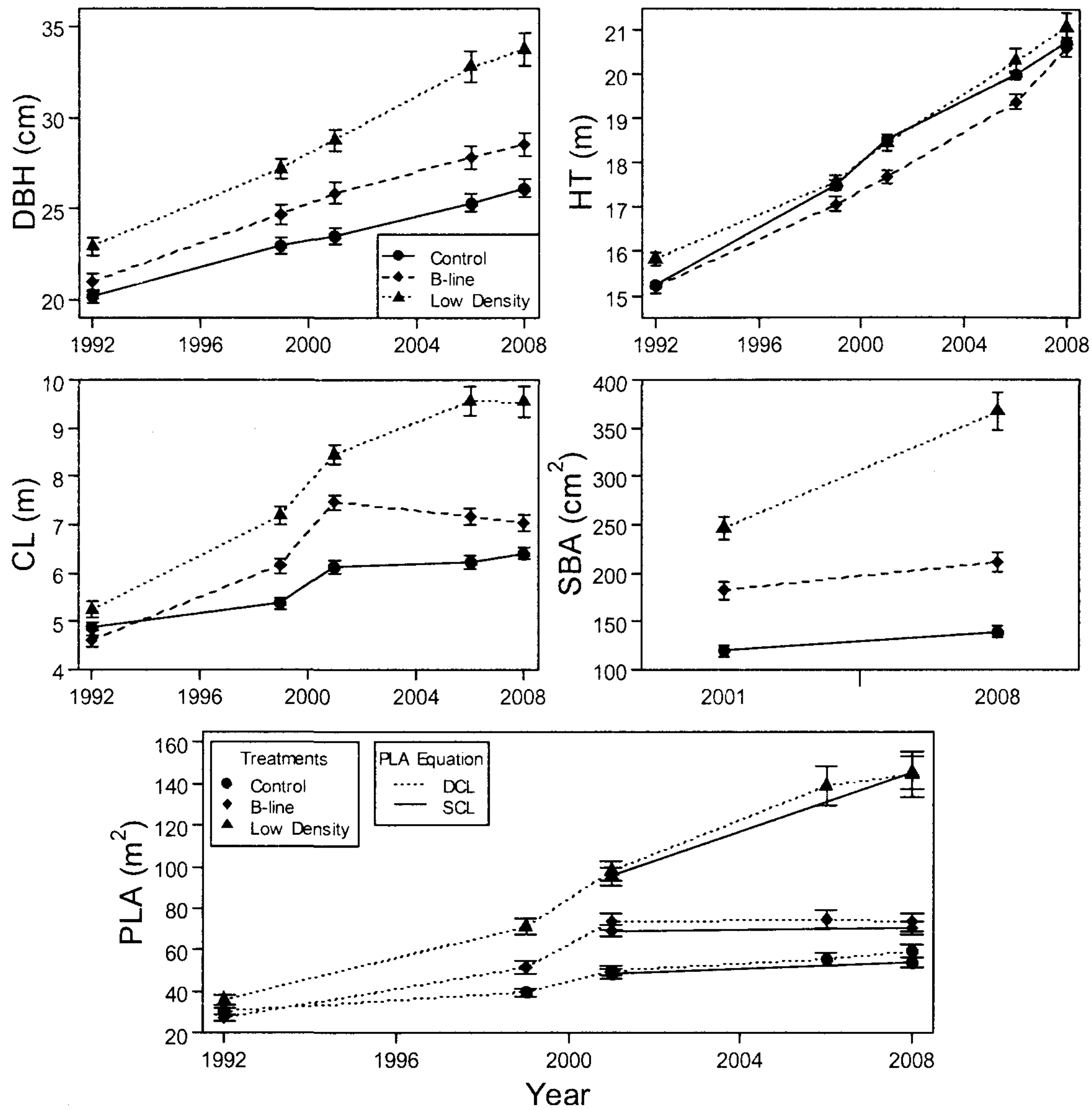

Figure 1.2. Patterns of tree growth among the WPTS treatments during the study period. Values are treatment means for dominant and codominant trees; error bars are ± one standard error. Fits of the DCL and SCL models came from the NLME-F and WNLS techniques, respectively (see Discussion for justification).

low density trees. In 1992, PLAs between the control and B-line trees were the same (P = 0.99) but the low density trees had greater leaf area than both treatments ($P < 0.049$). In 2001 and 2008, regardless of the estimation equation used, all treatments had significantly different PLA ($P < 0.002$).

Allometric-PLA model fits

The amount of error among the fitting techniques depended largely on the model form (Table 1.8). The RMSE of each model increased from the NLS technique to the WNLS; the increase was slight for the SAP and SCL models. The mixed effects procedure produced the lowest errors, while the application of only the fixed effects of the NLME fits resulted in the highest errors. The SAP and SCL models appeared to be the least influenced by the different fitting techniques; all others had substantially fluctuating RMSE values. Within each fitting technique, the SCL model had the lowest bias of the NLS, WNLS, and NLME-F techniques, while the VAL model had the lowest bias of the NLME-R procedure.

Residuals of the PLA predictions indicated that the NLME-F technique produced the greatest biases among the four techniques because they both underestimated the leaf area on mid-sized trees and substantially over-estimated the PLA on the largest sample tree (Figure 1.3). Negative bias was especially apparent with the MAG and SMAG models. The SAP and SCL models were best at predicting leaf area on the largest tree. Interestingly, the model form of the NLME-R technique had little effect on the predicted PLA of each sample tree.

Table 1.8. Root mean square error (RMSE) and Akaike's Information Criterion (AIC) for each PLA prediction equation and fitting technique.

Model	Weighted Variable	RMSE (m^2)				AIC		
		NLS	WNLS	NLME-R	NLME-F	NLS	WNLS	NLME-R
SAP	SBA	19.485	19.976	15.377	22.231	453.6	345.4	341.2
SCL	SBA	14.849	18.024	11.636	20.334	427.9	323.3	319.6
MAG	CL	17.284	30.717	10.422	46.005	443.4	380.0	354.5
SMAG	SBA	19.379	34.078	8.904	50.074	455.1	334.5	312.7
VAL	BA	19.013	51.298	8.191	50.091	451.1	309.1	291.7
DCL	DBH	15.680	27.128	8.889	34.012	433.5	318.6	317.7

According the AIC values in Table 1.8, the WNLS technique greatly improved the fit of each model from the NLS level. The mixed effects models were generally better than the WNLS, but significant improvements were only made for the MAG, SMAG, and VAL models. The best model within each fitting technique was the SCL for the NLS and the VAL for both the WNLS and NLME-R. The fit of the DCL model was similar to the best form under both the NLS and WNLS techniques.

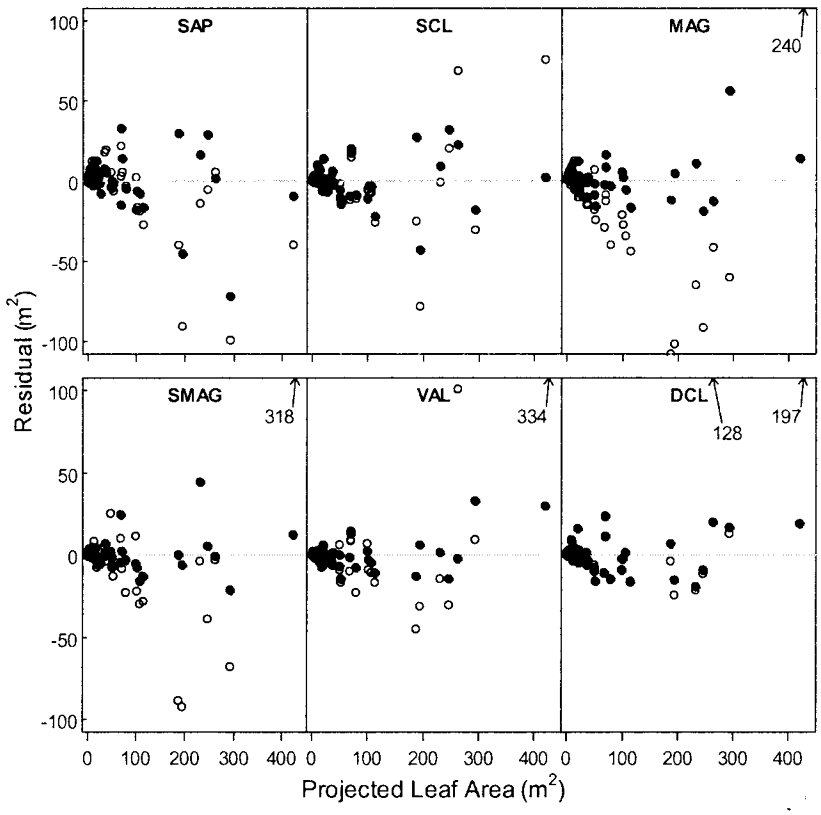

Figure 1.3. Residual plots for NLME model fits of each allometric-PLA equation. The x-axes are observed PLA (from branch summation). Filled symbols are NLME-R and hollow symbols are NLME-F. Arrows indicate a value that plots outside the plot region (the number is the value of the residual); all of which are from NLME-F predictions. Residuals are predicted minus observed.

Allometric-LAI estimation

Contrary to errors at the tree-level, comparisons of stand-level LAI estimates from the allometric models and litterfall showed that the WNLS procedure was often better than NLS fitting, and application of NLME-R fits increased error for most model forms (Table 1.9). Furthermore, performance of the NLME-F technique was better than the NLS and NLME-R, but similar to or slightly worse than the WNLS fits. The most accurate LAI predictions were made by the SAP and SCL models; in the 2001 comparison, these models had similar AAD values, which were less than half the other model forms. While not as substantially different in the 2008 comparisons, these two models still had the lowest AADs.

Much of the error in the NLME-F predictions was generated in the LAI estimates of the unthinned control plots (Figure 1.4). The models were better at predicting the LAIs of the low density treatment, where there is less leaf area.

DISCUSSION

Allometric-PLA model selection and assessment

The research objectives of the WPTS require a leaf area prediction equation that is robust, accurate, and unbiased. Assessing these attributes required an independent estimate of leaf area within the WPTS; the litterfall collections provided an ideal resource for the evaluations. Furthermore, the long-term record of litterfall revealed that using just a single season's collection could have had a substantial impact on the model evaluations because LAI was found to have reductions of around 20% four times during the study period due to both known and unknown factors (Figure 2.1) that would not have been

Table 1.9. Average absolute deviations (AAD) of allometric-LAI estimates compared to litterfall-LAI estimates.

	1992 (6 plots)				2001 (6 plots)				2008 (12 plots)			
Model	NLS	WNLS	NLME-R	NLME-F	NLS	WNLS	NLME-R	NLME-F	NLS	WNLS	NLME-R	NLME-F
SAP	-	-	-	-	0.638	0.387	0.498	0.389	0.730	0.541	0.321	0.563
SCL	-	-	-	-	0.445	0.679	0.458	0.393	0.446	0.513	0.405	0.366
MAG	0.657	1.088	1.576	0.895	1.003	0.628	2.867	1.004	0.645	0.394	1.308	0.763
SMAG	-	-	-	-	0.734	0.796	1.477	1.019	0.770	0.554	0.827	0.585
VAL	1.079	0.648	0.798	0.637	1.734	1.064	1.777	1.074	1.238	0.686	1.159	0.700
DCL	0.390	0.683	0.591	0.607	1.208	0.739	0.886	0.858	0.918	0.649	0.739	0.721

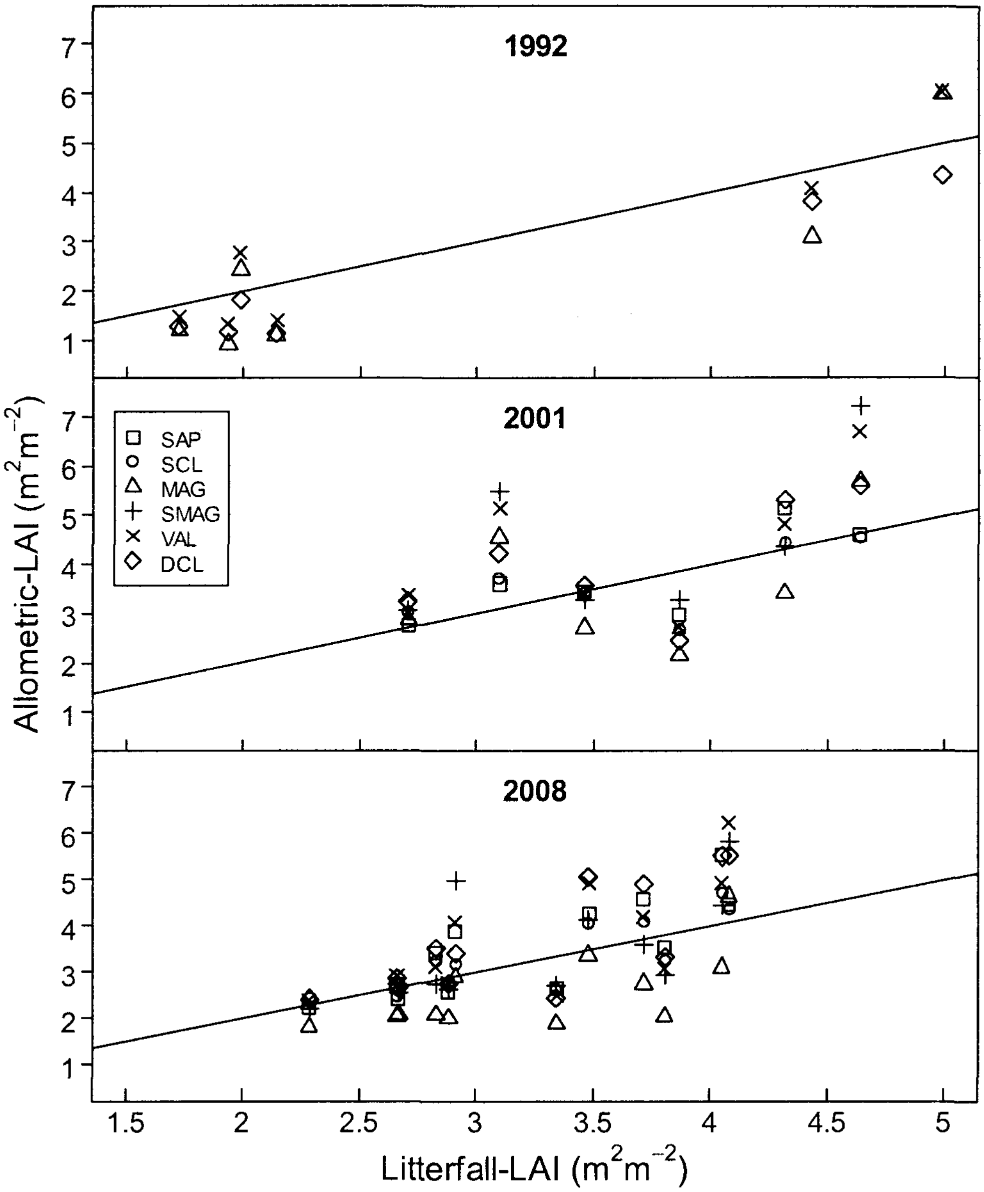

Figure 1.4. Comparison of projected LAI estimates from the NLME-F allometric equations and litterfall collections. The SAP, SCL, and SMAG model LAI estimates were not made for 1992 because SBA was not measured at that time. Diagonal lines represent perfect correspondence.

accounted for by the allometric equations. Comparisons of the litterfall-LAI and allometric-LAI estimates were done for years without anomalous variation.

In the end, the SCL model, using the NLME-F fit, was chosen as the best model for future studies in the WPTS. With no clearly superior allometric model form and fit, the choice was somewhat subjective. However, the decision was based on the consistent accuracy of the equation at both the tree and stand levels. While the SAP model predicted LAI slightly better, it was inconsistent between years and fitting techniques. This variability, present in other forms as well, indicates a lack of a robust relationship within the model, such that small changes in the parameter estimates (Table 1.6) can have a large impact on the predictions.

Evaluations of the six model forms showed that, for some, the fitting technique had a substantial impact on the accuracy of the PLA predictions. The effect of weighting the models was to improve the fit to the small trees in the sample. This had the further impact of making the predictions worse for large trees. Because the large trees simply carry far greater leaf area than the smaller ones, increased error in predicting their leaf area had a great impact on RMSE (Table 1.8). AIC, as a measure of how well the model fits the data (Burnham and Anderson 2002), rewarded the weighting procedure because most of the sample trees were small, and thus the weighted models were more accurate in terms of fitting more of the data, without consideration for the magnitude of the predictions or their error. These weighted models in turn predicted LAI more accurately because of the prevalence of small trees in the WPTS, in particular on unthinned control plots.

The NLME-R technique generated the best overall estimates at the tree-level because it included the benefits of the weighting procedure described above while also accounting for variation in the allometric relationships by site, and resulting from thinning (as designated by the multi-level random effects). This allowed for the predictions of the large trees to be more accurate than with WNLS because their deviation from the overall trend was known; therefore, the tree predictions were similar among all model forms using the mixed effects approach (Figure 1.3). For the models where AIC did not show significant improvement between the WNLS and NLME-R techniques, all sample trees were predicted quite well by WNLS and the random effects were close to zero (Table 1.7). The NLME-R models were among the worst in application to the WPTS because the within-group variation of the selected random levels did not account for actual variations between sites and thinning treatments. In other words, the random effects did not extract well to the population. This was the result of having relatively few sample trees within each group; greater sampling (particularly within the WPTS) may have improved the application of these models.

In the NLME-F technique, the model random effects were ignored. Applications of the allometric models with this technique had similar accuracy to the WNLS (Table 1.9) because of the influence of weighting alone; in this case, estimating the parameters with maximum likelihood and least squares had similar results. Had the random effects been better estimates of the population, as noted, the fixed effects would have likely performed better. As it was, the fixed effects reflected the trends within the sample dataset better than the WPTS as a whole and thus applied just as well as the WNLS technique.

In estimating leaf area, forest managers may prefer an equation that does not require sapwood measurements because of the labor required in taking increment cores and potential for defects to the bole; in addition, non-SBA models utilize basic forest mensuration data. Of the non-SBA models we evaluated, the DCL (using the WNLS technique) performed the best, and is thus recommended if sapwood measurements are unavailable. The VAL and MAG models, as noted, have strong theoretic and empirical foundations that rely upon surrogates for leaf area (Valentine et al. 1994; Maguire and Bennett 1996), but despite favorable fits to the sample trees (Table 1.8) produced unrealistically high LAI estimates. These biased tree PLA predictions accumulated into LAI estimates for the control plots that were above 5 m^2 m^{-2}, which may be within the range of published LAIs for unmanaged eastern white pine stands (Table 1.10), but is well outside of reasonable confidence intervals of the litterfall estimates over the 17-year study period (Figure 1.1).

When applying the SCL equation, it is important to recognize the potential error associated with measuring SBA accurately. We tried to minimize this error by measuring SBA close to the time of peak leaf area (Vose and Swank 1990; Vose et al. 1994) from two to three radii per tree using increment cores. Up to six radii, however, may be required to estimate SBA with only 20% error (Seymour, unpublished data). Further research is required to determine the exact amount of error involved when measuring SBA from any number of radii, and if there is additional error associated with measuring it from increment cores.

Despite this shortcoming, sapwood basal area is commonly used as a surrogate for leaf area (e.g., O'Hara 1988, 1989). However, we advise caution in using SBA alone with

Table 1.10. Published estimates of projected LAIs from unmanaged white pine stands.

Reference	Location	BA	TPH	Age	SLA	Retention	LAI	Method
1	NH	31.5	469	94	48.32	2.32[a]	1.0	Litterfall
1	NH	82.1	445	121	48.32	2.32[a]	2.4	Litterfall
1	NH	44.7	1124	39	48.32	2.32[a]	2.4	Litterfall
2[b]	NC	7.3–23.4	1790–1760	10–15	75.40[c]	na	1.7–3.2[d]	Allometric
3	ME	56.0	1775	62	65.25	2.207	4.1, 4.4	Litterfall, Allometric
4	ME	45.9	750	62	65.25	2.207	4.5, 4.6	Litterfall, Allometric
5[a]	NC	50.1	1154	32	na	na	5.3[e]	Light Interception
6	WI	41.8	1180	29	na	na	7.1, 8.5[f]	Allometric, Light Interception
7[a]	WI	44.1[g]	1248[g]	28	76 ± 5	3	7.4	Litterfall
8[a]	WI	65.1	1250	27	na	na	7.4[h]	Allometric

References: 1 – Innes et al. (2005); 2 – Swank and Schreuder (1973); 3 – This study, block 1control in 2001; 4 – This study. block 7 control in 2001; 5 – Vose and Swank (1990); 6 – Gower and Norman (1991); 7 – Gower et al. (1993); 8 – Bolstad and Gower (1990) **Notes:** BA – Basal area (m^2 ha^{-1}); TPH – trees per hectare; SLA – specific leaf area (cm^2 g^{-1}); Retention – needle retention (yrs); LAI – leaf area index (m^2 m^{-2}). [a] Values are study means; [b] Data from re-measured plots and re-fit allometric equations over a 5-yr period; [c] Estimated from Swank and Schreuder [1974, eqn. (4)] assuming 1/5 of a 100 mg fascicle converted to projected area using a divisor of 3.14 (Grace 1987); [d] Converted from all-sided LAI to projected LAI using a divisor of 3.14 (Grace 1987); [e] Reported season peak (late July); [f] Estimated from Fig. 1b; [g] From Son and Gower (1991); [h] Also reported light interception LAIs of 7.1 and 8.2

eastern white pine because it may not account for changes in crown structure resulting from silvicultural thinning or natural self-thinning. This is best demonstrated by plotting SBA and leaf area indices over common measures of stand density (Figure 1.5). From Figure 1.5, it is clear that sapwood basal area is linearly related to stand density across the WPTS treatments, while the SCL equation produces LAI estimates with an asymptote at LAIs between 4 and 5 m^2 m^{-2}, just as is present with the litterfall-LAI estimates. The asymptote likely occurs at the maximum LAI of the site, where with increasing density, LAIs remain fairly constant owing to the plasticity of crowns that are affected by crown recession and abrasion (Jack and Long 1991a, 1991b; Smith and Long 1992). The non-linear form of the SCL model (Dean et al. 1988) along with the integration of CL as a metric for localized stand density and competition (Weiskittel et al. 2007a) helped to capture the influence of crown structure on the SBA-PLA relationship.

Influence of thinning

The annual record of LAIs from litterfall collection presented here showed that when short-term fluctuations due to disturbances or climatic influences (Gholtz et al. 1991) are excluded, the unthinned control plots had relatively stable or slightly declining leaf areas throughout the 17-year study period (Figure 1.1). This pattern is consistent with litterfall records for slash pine (*Pinus elliottii*) (Gholtz and Fisher 1982; Gholtz et al. 1991). As noted, the stable LAIs were related to the effects of crown closure on individual trees (Smith and Long 1989), where crown recession maintained constant CL and PLA as the trees grew taller (Figure 1.2).

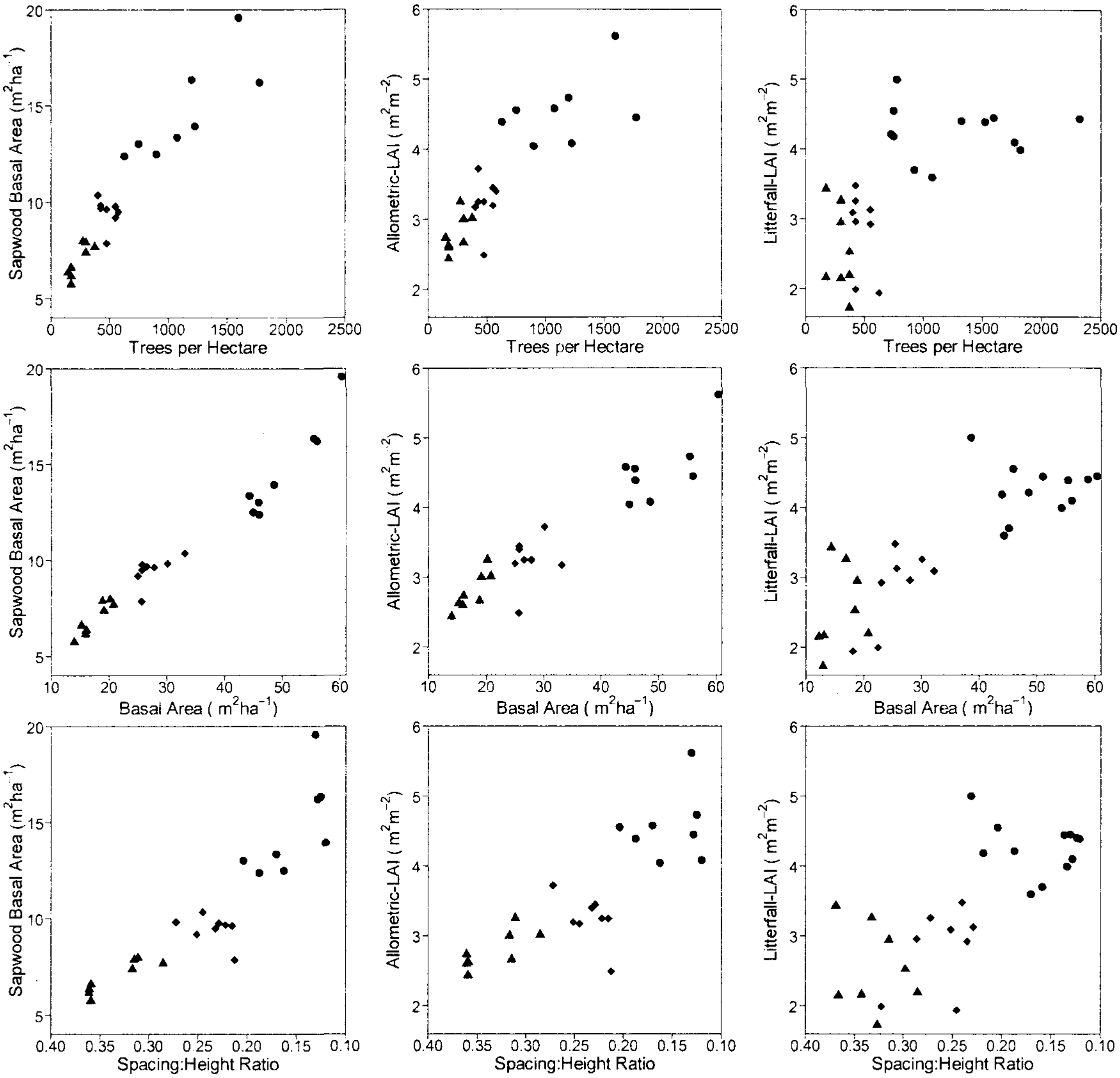

Figure 1.5. Sapwood basal area (SBA), allometric-LAI (from the SCL model using the NLME-F technique), and litterfall-LAI plotted over three measures of stand density including: trees per hectare, basal area, and Wilson's (1946) spacing-to-height ratio (using Lorey's height). WPTS treatments are indicated by a circle for the control, diamond for the B-line, and triangle for low density. Each graph includes all observations of LAI, SBA, and density throughout the study period.

Following the initial thinning, the response of trees was as expected. Much of the observed DBH growth in the B-line and low density treatments was associated with increases in CL, SBA, and thus PLA (Figure 1.2). With respect to CL, the implementation of the low density thinning was successful as the wide spacing is largely meant to retard crown recession (Seymour and Smith 1987; Seymour 2007) and build leaf area per tree. The increase in leaf area on thinned trees was likely concentrated in the lower portion of the crown (Brix 1981; Maguire and Bennett 1996; Medhurst and Beadle 2001) because the primary effect of thinning on crowns is to increase the size (Weiskittel et al. 2007a) and longevity (Weiskittel et al. 2007b) of lower branches. Between 2006 and 2008, the CL and PLA of low density trees was relatively stable, indicating some crown recession which is explained by shading as the lowest branches had begun to touch those of neighboring trees; this happened roughly 4 years before low density thinning schedules predicted (Seymour and Smith 1987).

At the stand-level, thinning significantly reduced LAI, but reasons for the surprising similarity in LAIs between the thinning treatments are unclear; one cause could have to do with the implementation of the thinning treatments. Crop-tree selection was done identically in each treatment, and B-line stocking was achieved by leaving small codominants and intermediates, while all non-crop trees were removed in the low density treatment (Seymour 2007). It is plausible that these small B-line trees did not contribute greatly to the overall leaf area of the stands and the LAIs are then more reflective of the larger crop trees. The direct effect of this similarity in LAIs may have been to produce the nearly equal stand-level volume growth rates of these treatments during the same time period (Seymour 2007; and see Chapter 2).

While both thinning treatments began to recover leaf area rapidly following the initial treatment, after 2001 the B-line LAI remained relatively constant for the rest of the study period. This stability coincided with decreased CL, slightly increasing SBA, and constant PLA because the stands reached crown closure. In their review, Long et al. (2004) stated that full recovery of pre-harvest LAI by thinned stands depended on the intensity of thinning and site quality. The patterns of tree and stand leaf area presented here indicate that thinned stands will in fact never recover the full amount of pre-harvest LAI, even if left unthinned (which is not part of the management plan for the WPTS) because of canopy structural changes that occur following crown closure.

CHAPTER TWO

INFLUENCE OF CONVENTIONAL AND LOW DENSITY THINNING ON THE VOLUME GROWTH AND BOLE TAPER OF EASTERN WHITE PINE (*Pinus strobus* L.)

ABSTRACT

Thinning eastern white pine (*Pinus strobus* L.) stands is common throughout the northeast, yet foresters lack clear information as to whether conventional B-line thinning or low density thinning will better achieve their management objectives. To inform this debate, we compared the thinning regimes with each other and unthinned controls with a focus on two practical and important aspects of white pine management: bole taper (quantified as Girard form class) and stemwood volume growth. Over the 17-year study period, Girard form class increased among all treatments from an overall average of 0.77 to 0.82. Surprisingly, B-line thinning produced more tapered butt-logs than low density thinning, resulting from a thinning-induced growth response at breast height but not at the top of the butt-log. Low density thinning, on the other hand, resulted in substantially larger, less tapered logs with significantly higher growth rates at breast height and the top of the butt-log. These findings have important implications for financial returns from management practices such as pruning.

Comparisons of stemwood volume estimates using the Honer (1967) equation and two taper equations (Li and Weiskittel 2009) revealed that the Kozak (2004) "Model 02"

variable-exponent taper equation provided the most accurate volume estimates. Results from the Kozak equation showed that low density trees grew at more than 50% the volume growth rate of B-line trees and 100% more than control trees. Thinned stands grew at 50 – 80% of the gross volume growth rate of the control treatment. Growth rates between the thinning treatments, however, were generally similar despite significant reductions in stand density between the B-line and low density thinning regimes. These findings reveal the remarkable growth potential of low density eastern white pine stands and have important implications for forest management in the region.

INTRODUCTION

Eastern white pine (*Pinus strobus* L.) is a significant component in many forest types throughout the northeastern U.S. (Widmann and McWilliams 2004). Pure stands of white pine are common in the region as a result of agricultural land abandonment and the widespread use of shelterwood regeneration systems. White pine trees can be highly valuable once they reach a large diameter and volume; therefore, thinning treatments are widely recommended and often implemented to hasten growth rates. A consensus as to optimal residual densities, however, has not been reached after nearly 40 years of research on the topic (Leak 2004; Seymour 2007).

Many studies in white pine stands have documented patterns of increased growth rates in response to thinning. Della-Bianca (1981) reported a 20% increase in DBH growth rates on thinned trees and higher gross volume growth over 8 years in a thinned versus an unthinned stand, despite differences in site quality. Likewise, Burger et al.

(2003) showed a 54% increase in the 6-year annual volume increment due to thinning a 17-year-old white pine plantation in Virginia. Projected to the final harvest at age 30, thinning would account for a 31% increase in the value of the stand (Burger et al. 2003).

Potential for even greater growth response under substantially heavier thinning than previously tested was first documented on mature white pines isolated by the 1938 hurricane (Smith and Seymour 1986; and reviewed by Seymour 2007). This led to the idea of low density management, which was first evaluated by Hunt (1968) and Hunt and Mader (1970) and led to a new stocking guide that incorporated the growth of large crowns produced by heavily releasing young crop trees (Seymour and Smith 1987). In the last two decades, the number of proponents and practitioners of low density management has grown.

Low density thinning involves retaining only those pines with the best form and/or the highest growth potential at an unconventionally wide spacing. Seymour (2007) suggested that Wilson's (1946) spacing: height ratio should be kept between 0.4 and 0.5; in other words, trees should be spaced to half of the stand height. Thinning entries are then timed to prevent crown recession and will ultimately result in about 75 trees per hectare (30 trees per acre). Hunt and Mader (1970), and subsequently Stone (1985), concluded that low density thinning is an attractive alternative to conventional thinning because low density trees have substantially higher diameter growth rates than their counterparts in conventionally thinned and unthinned stands, which amounted to similar basal area and board-foot volume growth rates between the treated stands. Desmarais and Leak (2005) reported that low density thinning in a roughly 40-year-old white pine stand in New Hampshire had a 20% increase in quadratic mean stand diameter over 10 years.

During this growth period the stand more than doubled board-foot volume which caused stumpage value to triple (Desmarais and Leak 2005).

Low density thinning, however, challenges the regional guidelines for white pine management, which recommend maintaining optimal stand-level gross volume growth through repeated thinning to the B line on the Philbrook et al. (1973) stocking guide (Lancaster and Leak 1978). Lancaster and Leak (1978) state that B-line thinning maintains high growth rates because the stand is neither under- nor over-stocked. However, several comparisons of growth rates of stands thinned to different densities either at or well below B-line stocking have indicated that stand growth losses may actually not be incurred below the B-line (Leak 1982; Stone 1985; Seymour 2007) and that the highest stand-level growth is actually well above B-line stocking in unthinned stands (Schlaegel 1971; Leak 1981; Seymour 2007). Therefore, gross volume increment in white pine stands is linearly related to stand density (Innes et al. 2005), and no evidence has been shown of an optimal level of growth around B-line stocking (Seymour 2007). This has prompted some to believe that perhaps the regional guidelines should be re-evaluated.

An update of management guidelines should consider those attributes of management that foresters focus their attention on in the field. In the case of white pine, thinning is done to increase growth rates, which will in turn reduce the time to attain target piece size of crop trees. Since the 5-meter butt-log portion of a white pine tree contains much of the total stemwood volume and a disproportionate amount of the value, the effects that thinning has on butt-log growth and form are important. Often foresters estimate the Girard form class (GFC; Girard 1933) of crop trees prior to a timber sale because GFC, as a measure of bole taper, is highly related to both cubic and board foot volumes (Husch et al. 2003). Thinning can substantially decrease GFC, increasing log taper, due to disproportionate growth in the lower bole (Larson 1963), which may lower the value of the log. As such, if low density thinning were to result in the degradation of butt-log quality, foresters might be better served by maintaining higher stand densities.

Other important aspects of management include stemwood volume and volume growth, and obtaining accurate and unbiased volume estimates is essential for making objective comparisons among different management regimes. Because thinning intensity can influence bole form, it is essential that a volume prediction equation accounts for these differences. At present, there are two types of volume equations for white pine in this region: the widely used Honer (1967) allometric model, and taper equations (Li and Weiskittel 2009). Honer's equation was used previously by Innes et al. (2005) and Seymour (2007) in their analyses of the relationship between gross volume increment and stand density. No study has applied the taper equations to date, but Li and Weiskittel (2009) found that their best model reduced bias in volume estimation by 45% compared to Honer's equation.

The objectives of this paper were to: (1) explore the influence of thinning on Girard form class and butt-log growth; (2) assess the accuracy of the two best Li and Weiskittel (2009) taper equations in the Seymour (2007) white pine thinning study (WPTS); (3) compare the volume predictions and volume growth results of the taper equations to the Honer (1965) equation; and (4) analyze the influence of thinning on total stemwood volume growth over 17 years in the WPTS.

METHODS

Study site and data collection

The study site is located in central Maine (44°55' N, 68°41' W) on the Dwight B. Demeritt Forest of the University of Maine. It is a 0.96 ha eastern white pine plantation where, in 1991, the eastern white pine thinning study (WPTS) was initiated to evaluate tree and stand responses to two contrasting silvicultural systems for white pine. First described by Seymour (2007), the stand was originally an unreplicated spacing study planted in 1949 on somewhat poorly drained silt-loam soils of the Buxton series with an average site index of 19.8 m (base age 50; Frothingham 1914). It received no management until the first thinning in the fall of 1991 at age 42, and was subsequently re-thinned in 2001. The study consists of eight replicate blocks, each with three 0.04 ha (20 m x 20 m) plots blocked according to pre-treatment trees per hectare (tph) and basal area. Thinning treatments were assigned at random so that each block consists of a low density plot, a B-line plot, and a control plot. Crop trees in the low density treatment were marked prior to felling at approximately an 18-20 ft spacing according to the Seymour and Smith (1987) stocking guide; all non-crop trees were removed. Crop trees in the B-line treatment were marked identically to those in the low density treatment, and thinning was done in order to release them on 3-4 sides until the target residual basal area of the Philbrook et al. (1973) stocking guide was achieved. The 2001 re-entry harvest removed the least desirable low density trees and maintained the isolation of crop trees. On the B-line plots, the re-entry thinning was done to maintain B-line stocking, but since the initial thinning left stocking below the B-line (Seymour 2007), the second entry was light on most plots. Analyses presented here focus on four study blocks (Table 2.1).

Data collection commenced prior to the 1992 growing season with plot tallies including diameter at breast height (DBH; nearest 0.25 cm; 1.37 m above the ground), total tree height (HT; nearest 0.05 m), and height to the lowest live branch (HTLLB) for all trees in thinned treatments. Control trees were measured for DBH; however, only a subset (roughly equal to the per-plot number of trees on thinned plots) received the HT and crown measurements. Subsequently, these missing heights were estimated with plot-specific height-over-DBH regression equations. The inventories of 1999, 2001, 2006, and 2008 were conducted in August-September with DBH, height, and crown measurements recorded for all living trees.

Girard form class

In 2008, 63 trees were selected for reconstructing Girard form class (GFC; Girard 1933) over the study period. Crop trees in the low density stands were paired with equivalent trees in the B-line and control stands based on 1992 DBH, crown ratio (CR), and crown class; in addition, only unthinned trees with desirable bole form were selected to ensure compatibility with thinned crop trees. In effect, the sample represented 21 individual crop trees grown for 17 years in three different density management regimes. Each tree was climbed to 5.27 m and measured for diameter outside bark and bark thickness (nearest 0.1 cm), then increment bored through the center of the entire bole (i.e. two cores at 180°). The cores were mounted to wooden boards in the field and later sanded with increasingly finer grit sandpaper to clearly expose ring boundaries under

Table 2.1. Stand attributes of the eastern white pine thinning study treatments during the study period. Values are means of four 0.4 ha plots per treatment; standard errors are in parentheses.

		Control	B-line	Low Density
1992 post-harvest				
	TPH	1550 (347)	594 (62)	313 (22)
	BA	45.8 (4.29)	20.2 (0.91)	12.7 (0.18)
	QMD[a]	21.7 (1.72)	21.7 (1.43)	23.3 (0.58)
	LAI[b]	4.7 (0.27)	2.0 (0.03)	1.9 (0.21)
2001 pre-harvest				
	TPH	1300 (236)	525 (34)	313 (22)
	BA	51.7 (3.90)	26.7 (1.18)	19.8 (0.46)
	QMD	24.8 (1.68)	26.4 (1.40)	29.1 (0.66)
	LAI	4.8 (0.27)	3.4 (0.11)	3.0 (0.12)
2001 post-harvest				
	TPH	1300 (236)	488 (44)	175 (10)
	BA	51.7(3.90)	25.3 (1.41)	11.8 (0.35)
	QMD	24.8 (1.68)	26.6 (1.43)	29.4 (1.23)
	LAI	4.8 (0.27)	3.3 (0.12)	1.9 (0.08)
2008				
	TPH	988 (142)	444 (19)	167 (6)
	BA	48.8 (2.37)	28.3 (1.68)	15.3 (0.47)
	QMD	27.1 (1.58)	29.0 (1.22)	34.1 (1.05)
	LAI	4.3 (0.16)	3.0 (0.18)	2.6 (0.06)

Note: TPH – trees per hectare; BA – basal area (m^2 ha^{-1});
QMD – quadratic mean stand diameter (cm);
LAI – leaf area index (m^2 m^{-2})

[a] QMDs are of upper crown class trees

[b] From two plots per treatment in 1992

magnification. Ring widths were measured to the nearest 0.001 mm using the WinDendro program (Regent Instruments, Inc.) after scanning to 1200 dpi resolution. In order to estimate previous diameters, ring widths were scaled with the ratio of the full core length to half the measured inside bark diameter in 2008. Diameters inside bark at 5.27 m (scaling diameter) for the four stand inventories prior to 2008 were calculated as twice the average core radius for each year. GFC was then calculated as the ratio of inside bark diameter at 5.27 m and DBH from inventory data.

Stem taper equations

Stem taper equations predict diameter inside bark (dib) at any height along the stem (h) and can be numerically integrated to obtain an unbiased volume estimate (Gregoire et al. 2000). The numerical integration technique estimates the volume of 100 sections per tree using Smalian's formula, which assumes sections are frustra of parabloids (Husch et al. 2003). Li and Weiskittel (2009) fit various published taper equations to the white pine stem profile data of Honer (1967) as well as trees sampled from the WPTS. The best performing equations for dib and volume for eastern white pine were the Kozak (2004) "Model 02" and the Clark et al. (1991) models, respectively. Li and Weiskittel (2009) noted that including crown dimensions into the models resulted in improved volume estimates. Since crown variables were shown to adequately account for stand structural changes through time and from thinning when predicting projected leaf area in the WPTS (Chapter 1), we chose to use the Kozak model form that includes crown length (CL; [HT-HTLLB]) and the Clark model that includes crown ratio (CR; CL/ HT). The Kozak equation is defined as

[1] $$dib = \alpha_0 DBH^{\alpha_1} HT^{\alpha_2} X^{\beta_1 z^4 + \beta_2\left(\frac{1}{e^{DBH/HT}}\right) + \beta_3 X^{0.1} + \beta_4 (1/DBH) + \beta_5 HT^{Q} + \beta_6 X + \beta_7 CL},$$

where:

$X = \frac{1-(h/HT)^{1/3}}{1-p^{1/3}}$	$\alpha_0 = 1.055$	$\beta_3 = 0.305$
$p = \frac{1.3}{HT}$	$\alpha_1 = 0.991$	$\beta_4 = 4.978$
$Q = 1 - z^{1/3}$	$\alpha_2 = -0.027$	$\beta_5 = 0.112$
$z = \frac{h}{HT}$	$\beta_1 = 0.366$	$\beta_6 = -0.552$
	$\beta_2 = -0.824$	$\beta_7 = 0.002$

The Clark et al. (1991) equation was modified by Jiang et al. (2005; their eqn. 5) and is defined as

[2] $$dib = \left[I_S\left(DBH^2\left(1 + \frac{(1-h/HT)^{\beta_1} - (1-1.37/HT)^{\beta_1}}{1-(1-1.37/HT)^{\beta_1}}\right)\right) + I_B\left(DBH^2 - \left(\frac{DBH^2 - F^2((1-1.37/HT)^{\beta_4} - (1-h/HT)^{\beta_4})}{(1-1.37/HT)^{\beta_4} - (1-5.27/HT)^{\beta_4}}\right)\right) + I_T\left(F^2\left(\beta_6\left(\frac{h-5.27}{HT-5.27} - 1\right)^2 + I_M\left(\left(\frac{1-\beta_6}{\beta_6^{\,2}}\right)\left(\beta_5 - \frac{h-5.27}{HT-5.27}\right)^2\right)\right)\right) + \beta_7 CR \right]^{0.5}$$

where:

$I_S = \begin{cases} 1 & \text{if } h < 1.37 \\ 0 & \text{otherwise} \end{cases}$	$\beta_1 = 58.94088$ $\beta_4 = 1.941309$
$I_B = \begin{cases} 1 & \text{if } 1.37 < h < 5.27 \\ 0 & \text{otherwise} \end{cases}$	$\beta_5 = 0.720758$ $\beta_6 = 2.455252$
$I_T = \begin{cases} 1 & \text{if } h > 5.27 \\ 0 & \text{otherwise} \end{cases}$	$\beta_7 = -0.27982$
$I_M = \begin{cases} 1 & \text{if } h < 5.27 + \beta_5\,(HT - 5.27) \\ 0 & \text{otherwise} \end{cases}$	F = dib at 5.27 m

Clark et al. (1991) and Jiang et al. (2005) provide equations to predict F on standing trees, but in this study F was estimated as the product of DBH and the plot-average GFC for that year. Parameter estimates are given here because they were not reported by Li and Weiskittel (2009) for these particular model forms.

Taper model validation

Validation of the dib predictions from the Li and Weiskittel (2009) taper equations focused on possible treatment-related biases when the models were applied to WPTS data. The validation data includes 139 trees and 1,304 dib measurements (Table 2.2). Overall accuracy of dib and GFC predictions from the taper models was calculated as the average absolute deviation (AAD)

[3] $$AAD = \frac{\sum_{i=1}^{n} |\hat{Y}_i - Y_i|}{n},$$

where $\hat{Y}_i$ is the predicted dib or GFC and Y_i is measured dib or GFC.

Table 2.2. Means and ranges of the taper model validation dataset (*n* = 139). See text for variable definitions. These data include 52 control, 45 B-line and 42 low density trees.

	dib (cm)	h (m)	DBH (cm)	HT (m)	HTLLB (m)	CR
Mean	21.05	5.51	26.11	19.25	10.96	0.43
Minimum	0.60	0.15	15.24	15.21	6.13	0.20
Maximum	50.05	20.87	42.16	23.99	16.58	0.66

Analyses

Analysis of variance (ANOVA) was used to test for differences in GFC, DBH, and scaling diameters among the treatments. Volume growth rates were calculated with the Kozak, Clark, and Honer (1967) equations for two growth periods separated by the 10-year harvest entry in the thinning study; the growth periods were 1992-2001 (10 years) and 2001-2008 (7 years). ANOVA was then used to simultaneously test for differences among the treatments, volume equations, and for an interaction between these terms. Orthogonal contrasts were included to test for differences between the B-line and low density treatments, and between the unthinned control and the thinning treatments combined. Multiple comparisons of the ANOVA results were done using Tukey's HSD post hoc tests which maintained a 95% family-wise error rate. Statistical significance of all tests was considered at the 95% level of confidence.

RESULTS

Girard form class

Girard form class (GFC) increased in all treatments over 17 years from an overall average of 0.77 $\pm$ 0.006 ($\pm$ SE) to 0.82 $\pm$ 0.004 (Figure 2.1). Initially, there were no GFC differences among the treatments ($P > 0.66$); however, after 17 years, the B-line crop trees had significantly more taper (i.e. lower GFC) than comparable control trees ($P < 0.01$) and somewhat more taper than low density trees ($P = 0.12$). These patterns resulted from a significant thinning-induced diameter growth response at breast height ($P < 0.001$) for both treatments, while scaling diameters (dib at 5.27 m) in the B-line treatment remained nearly the same as the control, thus increasing butt-log taper relative to the control (Figure 2.2). Diameter growth rates at 5.27 m in the low density and B-line treatments were 97 $\pm$ 6 and 19 $\pm$ 8% greater than the control, respectively.

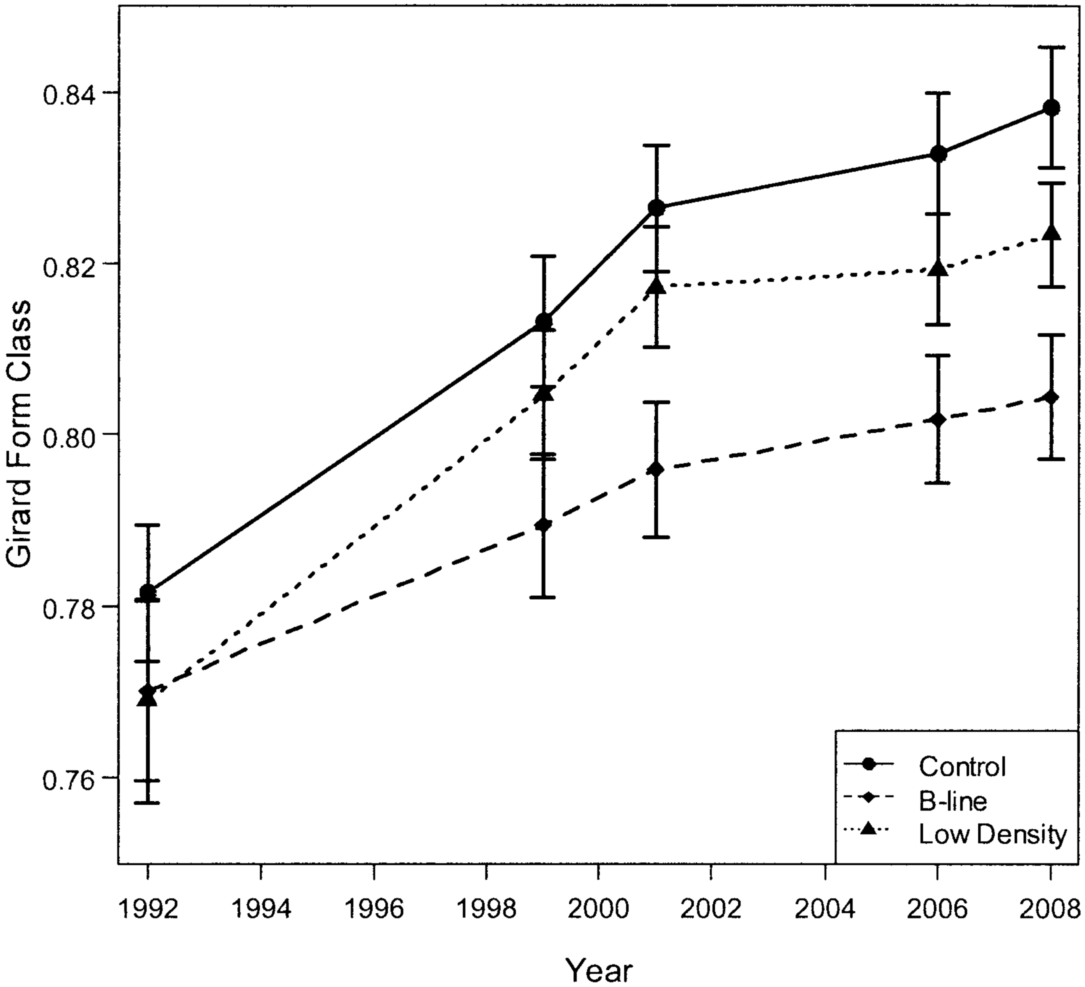

Figure 2.1. Mean Girard form classes for each treatment throughout the study period. Error bars are ± 1 standard error.

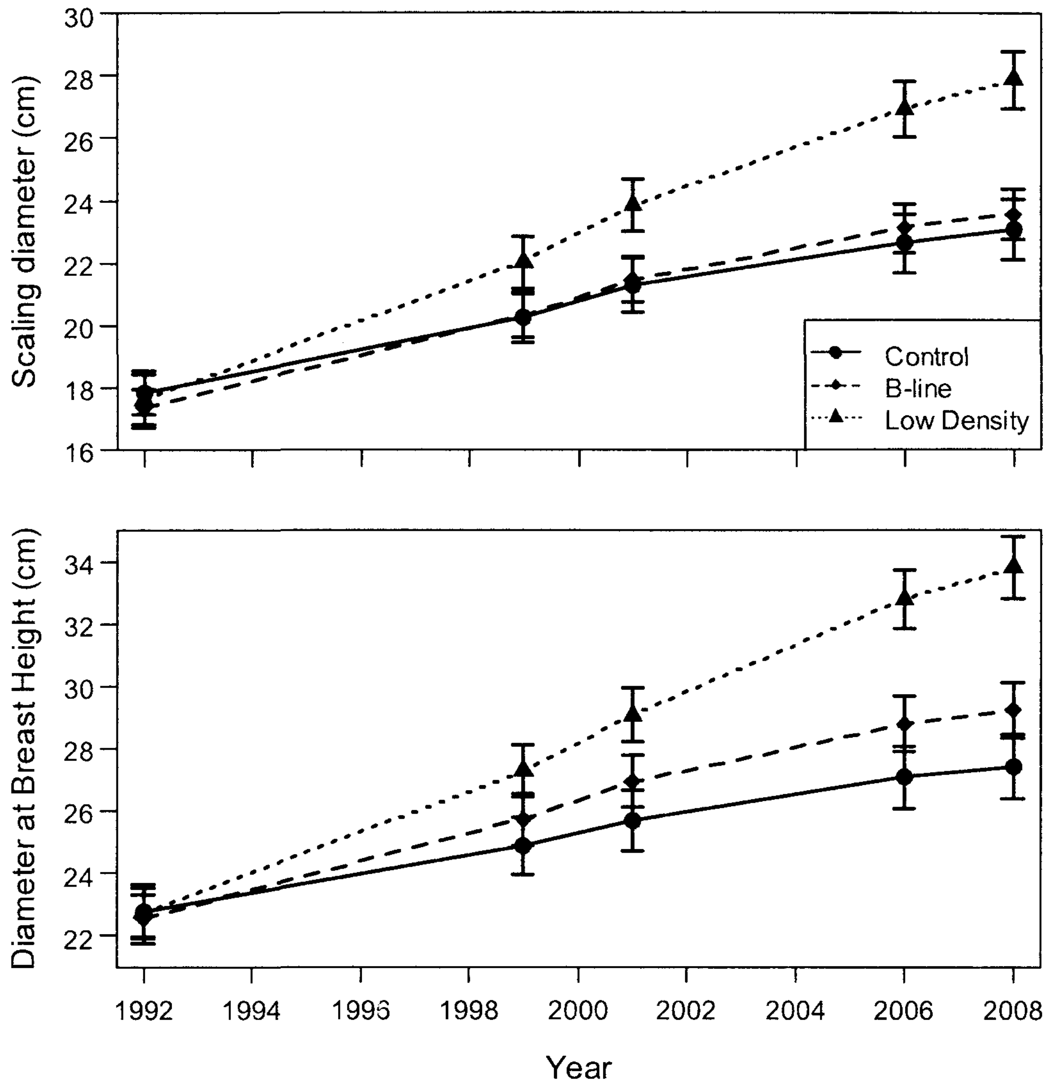

Figure 2.2. Mean diameters at breast height (DBH) and scaling diameters (at 5.27 m) of the GFC-analyzed trees throughout the study period. Error bars are ± 1 standard error.

Taper model validation

The Li and Weiskittel (2009) taper models predicted dib measurements from the WPTS with less than 10% error on average (Table 2.3). The Kozak model produced more accurate estimates of dib than the Clark equation. Whether the equations could replicate the patterns of butt-log taper presented above was assessed through biases of dib predictions at breast height, 5.27 m, and overall GFC. The Kozak equation was closer to breast-height dib and GFC, but the Clark equation was a better predictor of scaling diameter. The latter result is a consequence of inputting scaling diameter directly into the model as the F variable. Residuals of the dib estimates showed no apparent treatment-related bias (Figure 2.3), but the Clark equation exhibits more bias below 5.27 m for all treatments. Both equations predicted dib accurately throughout the middle and top portions of the trees.

Table 2.3. Average absolute deviations (AAD) of the Li and Weiskittel (2009) taper equation predictions compared to dib and Girard form class of the validation dataset.

Model	All Trees (*n* = 139) dib	GFC-analyzed trees (n = 63)		
		dib at breast-height	dib at 5.27 m	Girard form class
Kozak	1.0767	0.8697	0.8051	0.0322
Clark	1.4821	2.8021	0.1775	0.0709

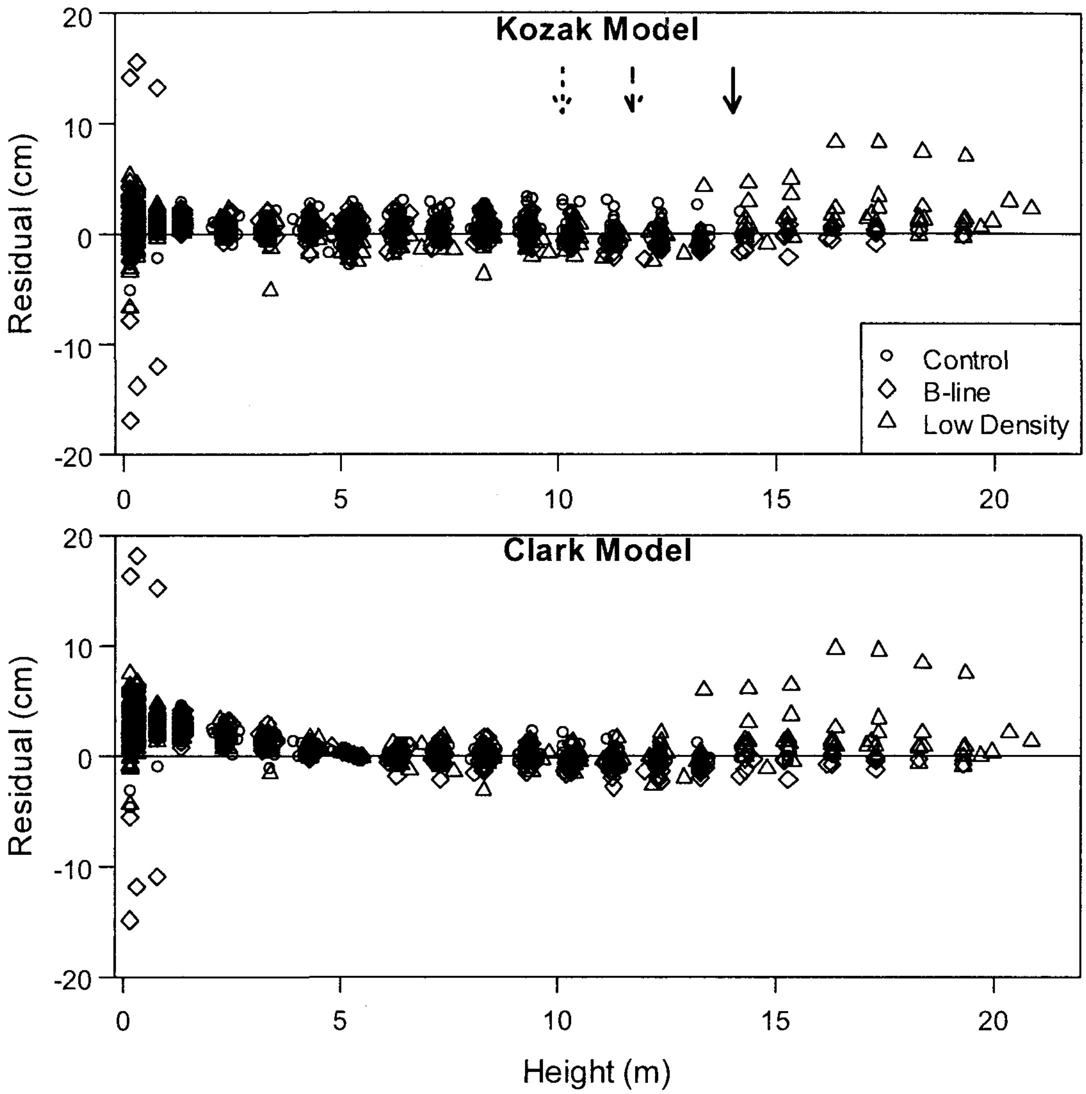

Figure 2.3. Residuals (predicted – observed) of dib estimates made by the Li and Weiskittel (2009) Kozak and Clark taper equations. Arrows indicate the mean crown base in 2008 for the control (solid), B-line (dashed), and low density (dotted) treatments.

Volume growth

As expected, heavier thinning in the low density treatment resulted in greater tree volumes than the other treatments throughout the study period (Figure 2.4). Volume predictions made by the Honer (1967), Kozak, and Clark equations were similar for B-line and control trees; however, the Clark equation added substantial volume to low density trees. The Honer equation estimated the lowest volumes in all treatments.

Regardless of the equation used, tree-level periodic annual increments (TVINC; $dm^3\ yr^{-1}$) of dominant and codominant trees were significantly different among all treatments during both growth periods (Tables 2.4 and 2.5). Volume growth estimates for the B-line and control treatments were equal among the prediction equations. For the low density treatment, however, volume growth estimates of the Clark equation were significantly higher than both other equations during the first growth period (1992-2001) but only differed from the Honer equation during the second period (2001-2008). According to the Kozak equation, during the first period the low density trees grew 96% more volume than the control and 47% more than the B-line trees; during the second period the low density trees grew 181% more than the control and 75% more than the B-line trees.

Stand-level volume growth estimates made by each equation showed the same general patterns throughout the study period (Figure 2.5). Again, the Honer estimates were the lowest for each treatment, and the Clark estimates were higher than the others for the low density treatment. Volume growth per hectare (SVINC; $m^3\ ha^{-1}\ yr^{-1}$) during the first growth period did not differ between the B-line and low density treatments [as was reported previously by Seymour (2007)] but during the second period, the B-line grew significantly more volume (Table 2.5). This resulted from a 28% increase in B-line SVINC while the low density stand SVINC was constant between growth periods (as estimated by the Kozak equation; Table 2.4). The control plots grew significantly more volume than both thinning treatments during each period.

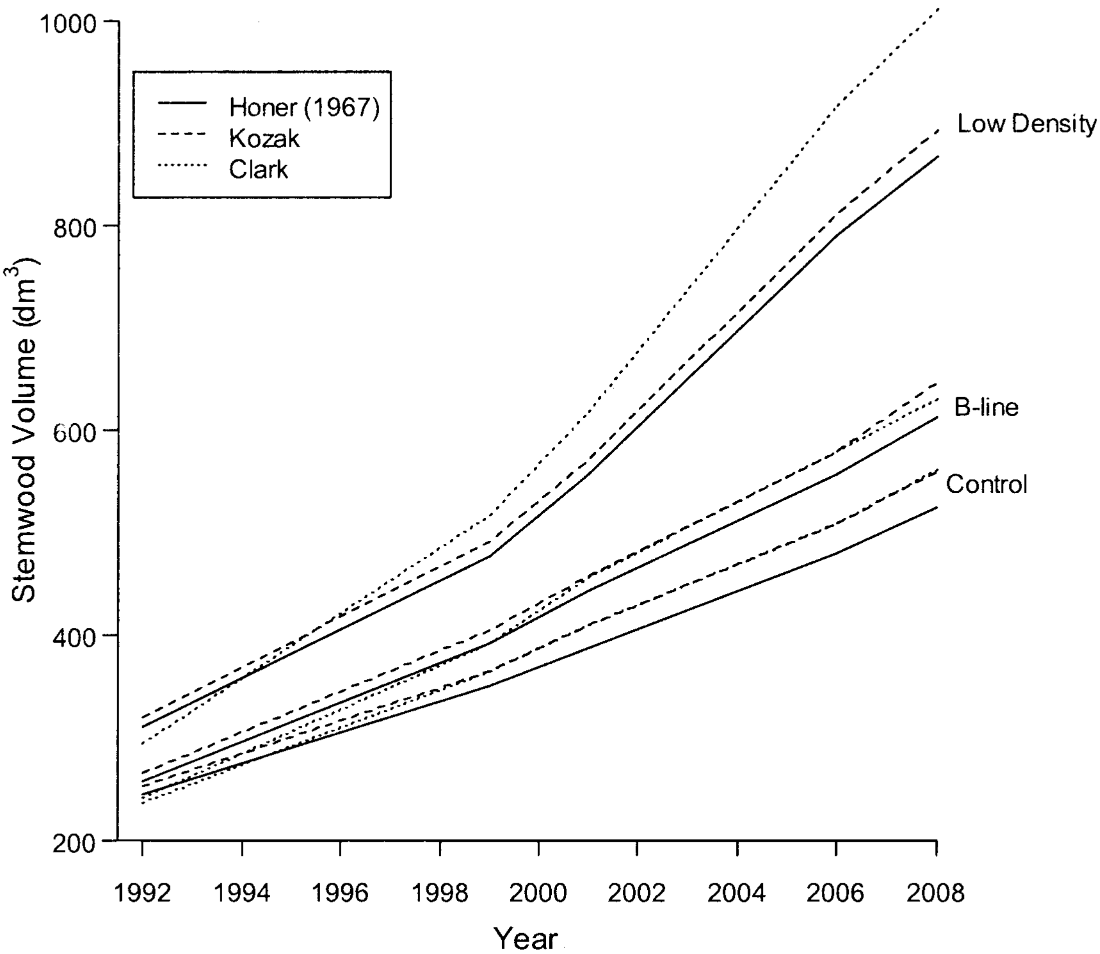

Figure 2.4. Mean stemwood volumes of dominant and codominant trees for each treatment throughout the study period.

Table 2.4. Mean periodic annual volume growth estimates by equation and treatment. Standard errors are in parentheses; units are $dm^3\ yr^{-1}$ for tree-level growth and $m^3\ ha^{-1}\ yr^{-1}$ for stand-level gross growth. Only dominants and codominants are included in the tree-level estimates, and stand-level values are gross volume growth.

Equation	Control	B-line	Low Density
1992-2001 Growth Period			
Tree-level			
Honer	11.4 (0.50)	16.5 (0.91)	24.6 (1.13)
Kozak	12.8 (0.57)	17.1 (0.90)	25.1 (1.16)
Clark	14.3 (0.86)	19.3 (1.44)	32.3 (1.86)
Stand-level			
Honer	12.2 (1.19)	8.0 (0.47)	7.3 (0.30)
Kozak	13.8 (1.52)	8.3 (0.38)	7.4 (0.36)
Clark	15.7 (0.94)	9.3 (0.99)	9.7 (0.42)
2001-2008 Growth Period			
Tree-level			
Honer	13.8 (0.68)	22.3 (1.24)	41.5 (2.96)
Kozak	15.6 (0.78)	24.9 (1.34)	43.7 (2.99)
Clark	14.3 (1.05)	22.3 (1.66)	52.1 (3.97)
Stand-level			
Honer	11.5 (0.64)	9.5 (0.69)	7.0 (0.15)
Kozak	13.0 (1.08)	10.6 (0.91)	7.4 (0.18)
Clark	11.9 (0.63)	9.4 (1.17)	8.8 (0.29)

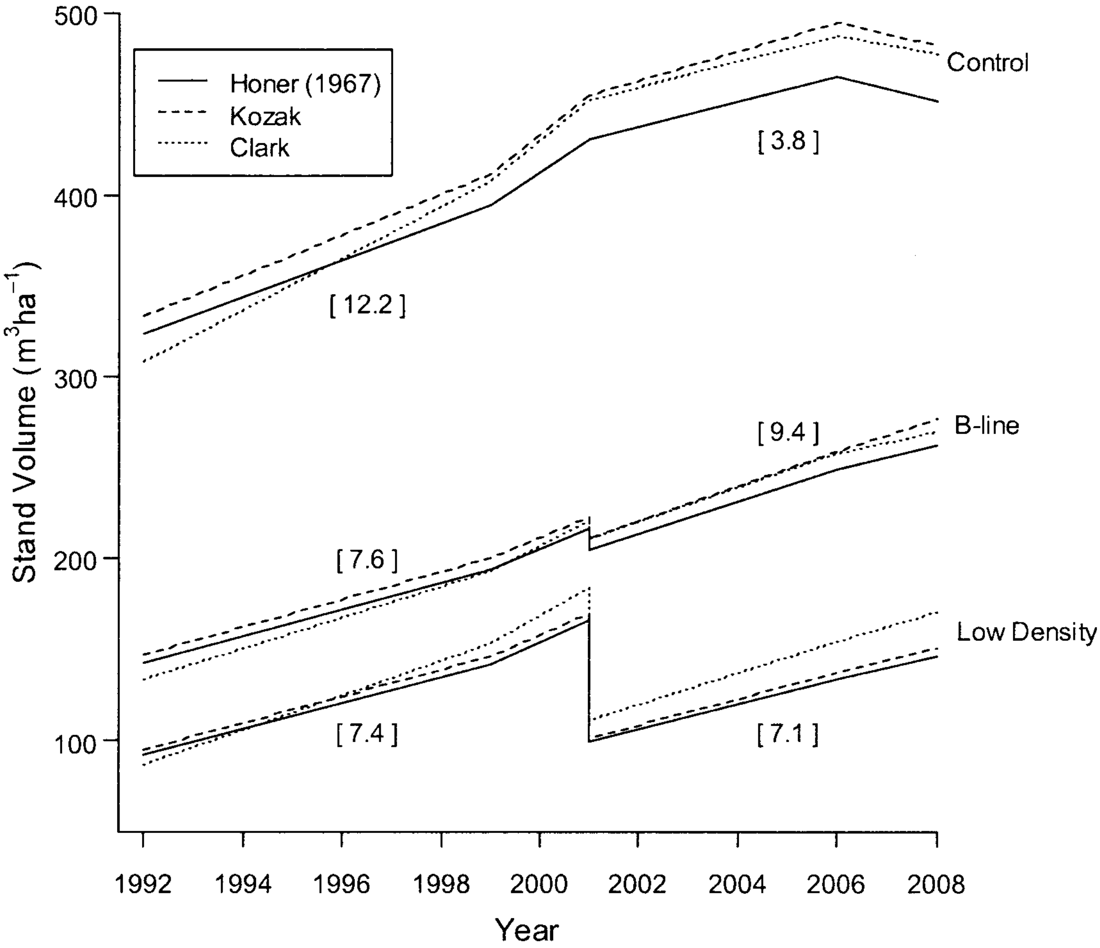

Figure 2.5. Mean volumes per hectare for each treatment throughout the study period. Numbers in brackets are Kozak estimates of net volume growth (m^3 ha^{-1} yr^{-1}) corresponding to the two growth periods. The 2001 thinning removed 24 ± 6.8 m^3 ha^{-1} (mean ± SE) from the B-line treatment and 63 ± 5.7 m^3 ha^{-1} from the low density treatment.

Table 2.5. Analysis of variance results for tests of differences in volume growth rates among the treatments as calculated by the Kozak, Clark, and Honer (1967) equations. The treatment parameter was divided into orthogonal contrasts between the B-line (B) and low density (LD) treatments and between the two thinning treatments combined (Thin) and the unthinned control (C). Only dominants and codominants are included in the tree-level comparisons.

Parameter	df	SS	*F*-value	*P*-value	R^2	RSE	Parameter	df	SS	*F*-value	*P*-value	R^2	RSE
1992-2001 Growth Period													
Tree-level							Stand-level						
Block	3	5026	21.933	< 0.001	0.317	8.740	Block	3	21.457	3.144	0.044	0.851	1.508
Treatment	2	21765	142.471	< 0.001			Treatment	2	249.302	54.795	< 0.001		
B vs. LD	1	4798	62.811	< 0.001			B vs. LD	1	0.861	0.378	0.544		
C vs. Thin	1	16967	222.130	< 0.001			C vs. Thin	1	248.441	109.212	< 0.001		
Equation	2	2007	13.137	< 0.001			Equation	2	35.019	7.697	0.003		
Trt:Eqn	4	724	2.370	0.051			Trt:Eqn.	4	5.833	0.641	0.638		
Residual	834	63704					Residual	24	54.596				
2001-2008 Growth Period													
Tree-level							Stand-level						
Block	3	3687	9.6847	< 0.001	0.463	11.265	Block	3	25.215	6.270	0.003	0.831	1.158
Treatment	2	65105	256.5084	< 0.001			Treatment	2	117.005	43.643	< 0.001		
B vs. LD	1	1161	9.150	0.003			B vs. LD	1	26.685	19.907	< 0.001		
C vs. Thin	1	63943	503.866	< 0.001			C vs. Thin	1	90.320	67.379	< 0.001		
Equation	2	539	2.125	0.1203			Equation	2	6.691	2.496	0.104		
Trt:Eqn.	4	1687	3.324	0.1203			Trt:Eqn.	4	9.178	1.712	0.180		
Residual	648	82235					Residual	24	32.171				

Note: df - degrees of freedom; SS - sum of squares; RSE - residual standard error

DISCUSSION

Girard form class

Initially, we expected that changes in Girard form classes (GFC) in the WPTS would follow the stem form development patterns reviewed by Larson (1963). These would suggest that in the control and B-line treatments, GFC would increase as crowns receded due to crowding and age, and that the low density treatment would greatly decrease GFC due to long crowns on widely spaced crop trees (Chapter 1; and Figure 2.3). While control trees supported this hypothesis, we were surprised to find that B-line trees had more taper than low density trees 17 years after thinning (Figure 2.1).

Investigation into the growth trends of each component of the GFC ratio elucidated the possible causes of this result. Diameter growth along the butt-logs analyzed in this study conformed to the "passive" and "stimulatory" growth concepts of Larson (1965). Passive growth occurs when the upper stem increases in diameter while the lower stem does not; this happens on trees that do not experience substantial wind sway, such as those in dense stands (Larson 1965) or that are experimentally guyed (Jacobs 1954). Stimulatory growth is a response to stresses in the lower bole caused primarily by wind sway; growth concentrates within the stressed areas to build greater support. This type of growth has been observed relatively high on stems. For example, Jacobs (1954) found a stimulatory growth response up to 4.57 m high on heavily thinned, fee-swaying *Pinus radiata*. In the present study, control trees grew more at the top of the first log (5.27 m) relative to growth at breast height, which may have resulted from reduced sway in these dense stands and thus a higher ratio of passive to stimulatory growth. Thinning around B-line crop trees caused them to sway somewhat more than controls and thus experience greater diameter growth at breast height. Apparently, the wind sway was not sufficient enough to also increase growth at 5.27 m (Figure 2.2), and therefore, the B-line trees had greater bole taper (lower GFC) than the control trees. Wind exposure was certainly greatest for low density trees, which also had larger crowns that both catch wind and add weight to the top of the trees; the resulting sway increased the amount of stimulatory growth up to at least 5.27 m.

These growth trends have important management implications. For example, pruning dead branches from the butt-logs of select crop trees can substantially increase value (Smith and Seymour 1986; Page and Smith 1994) because white pine has a poor ability to shed dead branches naturally (Wendel and Smith 1990). Exposed branch knots or pruning wounds are considered log defects (Ostrander 1971) and, therefore, rapid occlusion of the pruning wounds is essential for recovering expenses and making a profit. Slow growth at 5.27 m on B-line trees would hamper occlusion, while low density trees will quickly begin growing valuable clear timber.

To our knowledge, the patterns of Girard form class presented here are unique in the literature because by pairing trees based on size (DBH and CR), crown class, and bole form immediately following thinning, the effects of thinning alone were able to be analyzed. Some studies have confounded the influences of tree size and thinning. For example, Hilt and Dale (1979) found that 11 to 12 years after thinning upland oaks (*Quercus spp.*) changes in GFC were attributable to initial form class and not to thinning; they concluded that thinning had no effect when in fact the trees they analyzed were not comparable. Similarly, Brinkman et al. (1965) reported that 10 years after thinning shortleaf pine (*Pinus echinata* Mill.), changes in GFC were again based on tree size where trees in the higher DBH classes had the greatest increase in form class. Trees in the lowest density stands had on average the highest GFC because they had the greatest number of large trees. Brinkman et al. (1965) thus concluded that thinning only indirectly affected GFC by increasing tree size and that unthinned trees were likely to have similar form class to heavily thinned trees once they reach the same size. In a one-time sample of repeatedly thinned loblolly pine (*Pinus taeda* L.), Shearin et al. (1985) found no differences in GFC among three thinning treatments and an unthinned control. However, when all trees less than approximately 24 cm were excluded, thinned stands had significantly higher GFC than unthinned stands (Shearin et al. 1985). Here again, despite the filtering of their data, they did not control for differences in crown class or initial form that could have influenced the array of bole forms present in the unthinned stands. Yet another study found Girard form classes in an eastern white pine thinning trial similar to ours (Stone 1985) were nearly the opposite of those presented in this study. Specifically, Stone (1985) found that conventionally thinned trees had the highest overall GFC, followed by low density trees and then unthinned control trees. The discrepancy between Stone's (1985) findings and ours is likely the result of Stone's tree selection, as with other studies, which was based on diameter class within each plot and not paired trees. Despite all of these different findings, what is consistent in the literature, and our results (Figure 2.1), is the finding that heavy thinning does not negatively influence Girard form class. It seems apparent, however, that tree selection is important for comparisons between thinned and unthinned stands because plot averages are unlikely to reflect the GFC on "would-be" crop trees that were never released in unthinned control stands.

Taper model selection

Both the Kozak and Clark taper equations predicted dib well, but the Kozak model was clearly more accurate. Because of its segmented polynomial form, biases of the Clark equation were caused by problems in the fit or form of the butt-log portion of the model. These over-predictions were surprising because Li and Weiskittel (2009) showed no such bias in their residual graphs. Li and Weiskittel (2009) also found that the Kozak equation was a better predictor of stem taper in their evaluations of eastern white pine, balsam fir (*Abies balsamea* L. Mill.), and red spruce (*Picea rubens* Sarg.). Similarly, Rojo et al. (2005), with maritime pine (*Pinus pinaster*Ait.) in Spain, found the Kozak model to be the best predictor of stem profile out of the 31 taper equations they compared. When predicting volumes, however, Li and Weiskittel (2009) found that the Clark model was the least biased. Similarly, Filho et al. (1996) found the Clark model best at predicting both stem profile and volume for loblolly pine in Brazil, and Filho and Schaaf (1999) demonstrated the accuracy of the Clark model by comparing volume estimates from several taper equations to those obtained by water displacement of slash pine (*P. elliotti* Engelm. var. *elliotti*). It should be noted that the Kozak equation was not tested by either Filho et al. (1996) or Filho and Shaaf (1999).

Despite the previous vindication of the Clark equation, its biased dib predictions make its volume estimates for the WPTS questionable. ANOVA of tree- and stand-level volume growth (Table 2.5) showed the potential for spurious conclusions from biased volume equations, such as the Clark model which estimated higher volumes for the low density treatment in particular. These likely resulted from the relatively large scaling diameters input into the model, combined with the elevated dib predictions in the lower bole. Differences between the Kozak and Honer (1967) predictions were less dramatic, but clear nonetheless. The Honer equation has long been the regional standard among researchers and foresters, and its predictions are usually trusted. Using much of Honer's (1967) data to fit their taper equations, Li and Weiskittel (2009) found that the Kozak model decreased absolute biases by 31% from the Honer equation. Given this result and the model's performance on our sample trees, the volume predictions made by the Kozak equation are likely to be more accurate than either other equation employed here. Furthermore, by including crown length in the model, it can account for crown structural changes following thinning (Weiskittel et al. 2007a; Chapter 1).

Influences of thinning on volume growth

Since the Kozak model is most likely to provide accurate volume predictions, further analyses here and for the WPTS will employ the Kozak equation. At the tree-level, we found low density trees to have significantly more volume and higher growth rates than either B-line or control trees. This trend was expected since heavily released or open-grown trees tend to be the largest in any given even-aged population, and low density trees in this study had significantly bigger crowns with greater leaf area than trees in either other treatment (Chapter 1). Most surprising was that B-line trees were not substantially (or significantly) larger than comparable trees in the control treatment (Figure 2.4). B-line TVINC, however, was significantly higher than the control during both growth periods, which seems to indicate a slow growth response from B-line thinning such that with more time, significant differences in mean tree volumes might arise.

Consistent with thinning studies in other regions (Assmann 1970; Zeide 2001), thinning reduced total stand gross volume growth in the WPTS. However, thinning to two different densities did not substantially affect SVINC during the first growth period, as was already reported by Seymour (2007). During the 2001-2008 growth period, the B-line growth rate increased nearly 30% over the first period, and became significantly higher than the low density treatment. This increase in SVINC was likely the result of an increase in leaf area between periods (Table 2.1) to the point of crown closure (Chapter 1) that was not augmented by thinning after the light re-entry harvest in 2001 (to re-establish B line stocking) (Figure 2.5). That SVINC of the low density treatment was equal between growth periods (Table 2.4) is remarkable because roughly half of the trees were removed in the 2001 thinning (Table 2.1).

CHAPTER THREE

PATTERNS OF TREE AND STAND GROWTH EFFICIENCY IN EASTERN WHITE PINE (*Pinus strobus* L.) STANDS MANAGED BY CONVENTIONAL AND LOW DENSITY THINNING

ABSTRACT

Despite the commercial importance of eastern white pine (*Pinus strobus* L.), its growing space relationships are largely unknown; these relationships have helped to improve silvicultural systems in many other North American forest types. This study was undertaken to inform a long-standing debate between conventional B-line and low density management of eastern white pine through analyses of tree and stand level growth efficiency (GE) – defined as the amount of stemwood volume growth per unit leaf area – over two growth periods spanning 17 years. Growth was measured between three stand inventories during the study period; leaf area was estimated from a power function of sapwood basal area and crown length at two times 7 years apart during the study period. Within each thinning treatment and the unthinned control, canopy position of individual trees did not GE. Also, thinning significantly increased leaf area and volume growth, but not differences in GE were found. At the stand-level, gross volume increment was positively and linearly related to leaf area index. Volume growth and growth efficiency of the B-line treatment were significantly higher than the low density treatment during the second growth period (but not the first); this coincided with canopy closure

and is thought to be temporary. In general, however, thinned plots had similar GE to unthinned plots, but with reduced variability. Variation in the GE of unthinned plots was more related to density (trees per hectare) than to the shape of the diameter distributions (stand structure); density was positively related to GE in the unthinned treatment. Contrary to expectations, low density thinning of eastern white pine did not sacrifice growing space efficiency at the tree- or stand-levels, and thus site utilization is not reduced by thinning below B-line stocking. Changes in the GE relationships between growth periods for the B-line treatment in particular emphasize the need for more long-term studies of production ecology.

INTRODUCTION

Growth efficiency (GE), the amount of annual stemwood volume increment per unit of leaf area (Waring et al. 1980), is an important component of forest production ecology because it defines how trees and stands utilize available growing space (Assmann 1970; Waring 1983). Growth efficiency was originally used as a simple measure of tree vigor (Waring et al. 1980), but advances in volume and leaf area estimation procedures have enabled wider application of GE studies in recent decades. Seymour and Kenefic (2002) identified three possible relationships of tree growth efficiency (TGE) and leaf area: (1) monotonic decreasing, where TGE decreases with crown size; (2) monotonic increasing, where TGE increases with crown size; and (3) sigmoid, where TGE peaks at an intermediate crown size. These patterns are influenced by tree size (Smith and Long 1989), shade tolerance (Webster and Lorimer 2003), stand density (Jack and Long 1991a), canopy position or strata (Gilmore and Seymour 1996; Kollenberg and O'Hara 1999), site quality (DeRose and Seymour 2009), and age (Seymour and Kenefic 2002).

Thinning can also have a strong influence on the GE of trees and stands. Following thinning, residual trees have been observed to increase their TGE due to an enhanced light environment until the negative effect of large crown size causes a reduction (Brix 1983; Jack and Long 1992). Thus, recently released intermediate-sized trees can have the highest TGEs (O'Hara 1988; Powers et al. 2009). Applied to the stand-level, this suggests that residual stands dominated by medium-sized trees can be most efficient and that more heavily thinned stands may result in less efficient use of the available space. Studies of various conifer species have resulted in both increased (Waring et al. 1981; Velazquez-Martinez et al. 1992) and relatively constant stand growth efficiency (SGE) following thinning (Binkley and Reid 1984; O'Hara 1989; McDowell et al. 2007). O'Hara (1989) attributed much of the variability in the SGEs of thinned Douglas-fir [*Psuedotsuga menziesii* (Mirb.) Franco.] stands to differences in stand structure, or the distribution of tree sizes within a stand (Smith et al. 1997).

For many North American tree species growing in both even- and uneven-aged forests, an understanding of production ecology has aided in the design and implementation of silvicultural systems that create optimal stand structures for utilizing growing space (e.g., O'Hara 1996). However, very little is known about the growth efficiency of eastern white pine (*Pinus strobus* L.), which is a component of many of the forest types in the Northeast (Wendel and Smith 1990) and frequently occurs in a dense, even-aged condition when growing in pure stands. White pine is also one of the fastest growing and most valuable species in the region (Widmann and McWilliams 2004), but foresters lack clear, quantitative direction on how to manage even-aged stands, owing to a long-standing debate within the forestry community (see Seymour 2007). Conventional management follows the Lancaster and Leak (1978) regional guidelines, which recommend repeated light thinning entries to the B-line on the white pine stocking guide (Philbrook et al. 1973; Leak and Lamson 1999). Others argue for substantially heavier thinning through a low density regime (e.g., Hunt and Mader 1970; Seymour and Smith 1987; Page and Smith 1994; Seymour 2007). With such contrasting density management approaches, understanding the efficiency with which thinned white pine trees and stands utilize the provided growing space will improve the efficacy of these systems (Long et al. 2004) while also helping to inform the debate. Therefore, the objective of this study was to model the relationships of growth efficiency for both thinned and unthinned eastern white pine stands to examine how this relationship is affected by thinning at both the tree- and the stand-levels.

METHODS

Study site and data collection

The study site is located in central Maine (44°55' N, 68°41' W) on the University of Maine's Dwight B. Demeritt Forest. It is a 0.96 ha eastern white pine plantation where, in 1991, the eastern white pine thinning study (WPTS) was initiated to evaluate tree and stand responses to two contrasting silvicultural systems for white pine. First described by Seymour (2007), the stand was originally an unreplicated spacing study planted in 1949 on somewhat poorly drained silt-loam soils of the Buxton series with an average site index of 19.8 m (base age 50; Frothingham 1914). It received no management until the first thinning in the fall of 1991 at age 42, and was subsequently re-thinned in 2001. The study consists of eight replicate blocks, each with three 0.04 ha (20 m x 20 m) plots blocked according to pre-treatment trees per hectare (TPH) and basal area. Thinning treatments were assigned at random so that each block consists of a low density plot, a B-line plot, and a control plot. Crop trees in the low density treatment were marked prior to felling at approximately an 18-20 ft spacing according to the Seymour and Smith (1987) stocking guide; all non-crop trees were removed. Crop trees in the B-line treatment were marked identically to those in the low density treatment, and thinning was done in order to release them on 3-4 sides until the target residual basal area (i.e., the B-line) of the Philbrook et al. (1973) stocking guide was achieved. The 2001 re-entry harvest removed the least desirable low density trees and maintained the isolation of crop trees. On the B-line plots, the re-entry thinning was done to maintain B-line stocking, but since the initial thinning left stocking below the B-line (Seymour 2007), the second entry was light on most plots. Analyses presented here focus on six study blocks (Table 3.1).

Data collection started prior to the 1992 growing season with plot tallies including diameter at breast height (DBH; nearest 0.25 cm; 1.37 m above the ground), total tree height (HT; nearest 0.05 m), height to the lowest live whorl (HTLLW; having three or more live branches) and height to the lowest live branch (HTLLB) for all trees in the thinned treatments. Control trees were measured for DBH; however, only a subset (roughly equal to the per-plot number of trees on thinned plots) received the HT, HTLLW, and HTLLB measurements. Subsequently, the missing heights were estimated

Table 3.1. Stand attributes of eastern white pine thinning study treatments during the study period. Values are means of six 0.4 ha plots per treatment; standard errors are in parentheses.

		Control	B-line	Low Density
1992 post-harvest				
	TPH	1450 (230)	608 (42)	312 (14)
	BA	44.6 (2.80)	20.2 (0.69)	12.3 (0.27)
	QMD[a]	22.0 (1.13)	21.6 (0.97)	22.7 (0.51)
	LAI[b]	4.7 (0.27)	2.0 (0.03)	1.9 (0.21)
2001 pre-harvest				
	TPH	1233 (157)	545 (25)	308 (15)
	BA	50.9 (2.61)	27.1 (1.00)	19.1 (0.51)
	QMD	25.3 (1.11)	26.2 (0.93)	28.6 (0.55)
	LAI	4.9 (0.20)	3.5 (0.11)	2.9 (0.09)
2001 post-harvest				
	TPH	1233 (157)	522 (26)	179 (7)
	BA	50.9 (2.61)	25.5 (0.69)	11.6 (0.29)
	QMD	25.3 (1.11	26.3 (0.95)	29.2 (0.85)
	LAI	4.9 (0.20)	3.4 (0.10)	1.9 (0.05)
2008				
	TPH	933 (97)	441 (12)	167 (5)
	BA	47.9 (1.64)	27.5 (1.24)	14.9 (0.63)
	QMD	27.9 (1.10)	29.0 (0.77)	33.7 (0.74)
	LAI	4.2 (0.15)	3.0 (0.13)	2.4 (0.11)

Note: TPH – trees per hectare; BA – basal area (m^2 ha^{-1});
QMD – quadratic mean stand diameter (cm);
LAI – leaf area index (m^2 m^{-2})

[a] QMDs are of upper crown class trees

[b] From two plots per treatment in 1992 only

with plot-specific height-over-DBH regression equations. In 2001 and 2008, stand inventories were conducted in August and September with DBH, HT, and crown measurements recorded for all living trees. Sapwood basal area was measured on all living trees during these inventories from increment cores extracted at breast height on the east and west sides in 2001 and on the north, southeast, and southwest sides in 2008. The sapwood-heartwood boundary was marked in the field prior to core mounting. Boundary marks were verified with a 10% ferric chloride ($FeCl_3$) solution that stains the heartwood prior to measuring the sapwood radii (nearest 0.1 mm). Coincident with increment coring, each tree was measured for bark thickness (nearest 0.1 cm) at breast height with a bark gauge. Sapwood basal area was calculated as the difference between inside bark basal area and the mean heartwood area (from individual sapwood radii minus inside bark radius).

Leaf area estimation

Tree-level projected leaf area (PLA, m^2) was estimated for the years 2001 and 2008 using an allometric equation based on sapwood basal area (SBA, cm^2) and live crown length (CL, m), with crown base as HTLLW. The PLA prediction equation is

[1] $$\mathrm{PLA} = 0.1027 * \mathrm{SBA}^{0.7541} * \mathrm{CL}^{1.2538},$$

where each variable is as defined. This model form was previously used by Gilmore et al. (1996) and Kenefic and Seymour (1999) for balsam fir (*Abies balsamea* L.) and eastern hemlock (*Tsuga canadensis* L.), respectively. Parameter estimates are fixed effects from a nonlinear mixed effects model fit. Projected leaf area index (LAI) predictions from Equation [1] were validated against an independent litterfall-LAI dataset on 12 of the same plots included here (Chapter 1). LAI (m^2 m^{-2}), or the total amount of PLA per unit ground area, is estimated using the allometric equation by summing tree PLAs on each plot and dividing by the plot area.

Stemwood volume estimation

The total stemwood volume of trees was estimated from the stand inventories. A stem taper equation was selected from those presented by Li and Weiskittel (2009) to predict diameter-inside-bark (dib) at any height (h) along the stem so that volume could be calculated by numerical integration; this procedure has been shown to provide unbiased estimates of volume given a robust taper equation (Gregoire et al. 2000). The Li and Weiskittel (2009) models were fit to the Honer (1967) regional eastern white pine dataset with some trees from the WPTS added. Results from Chapter 2 indicated that when applied to WPTS data, the best Li and Weiskittel (2009) model was the Kozak (2004) 'Model 02' variable exponent equation, which included crown length (here CL is HT-HTLLB):

[2] $$dib = \alpha_0 DBH^{\alpha_1} HT^{\alpha_2} X^{\beta_1 z^4 + \beta_2 \left(\frac{1}{e^{DBH/HT}}\right) + \beta_3 X^{0.1} + \beta_4 (1/DBH) + \beta_5 HT^{Q} + \beta_6 X + \beta_7 CL},$$

where:

$$X = \frac{1-(h/HT)^{1/3}}{1-p^{1/3}} \qquad p = \frac{1.3}{HT} \qquad Q = 1 - z^{1/3} \qquad z = \frac{h}{HT}$$

$\alpha_0 = 1.055$
$\alpha_1 = 0.991$
$\alpha_2 = -0.027$
$\beta_1 = 0.366$
$\beta_2 = -0.824$
$\beta_3 = 0.305$
$\beta_4 = 4.978$
$\beta_5 = 0.112$
$\beta_6 = -0.552$
$\beta_7 = 0.002$

Analyses

Patterns of tree and stand growth efficiency (TGE and SGE, respectively) were calculated by dividing volume growth by leaf area and were examined for two growth periods spanning the 17-year study. The first period includes the growth between the inventories of 1992 and 2001, the first 10 years after the initial thinning; the second period includes the growth from 2001 until 2008, the seven years following the second harvest entry. Periodic annual stemwood volume increment was calculated at the tree-level (TVINC; dm^3 yr^{-1}), and at the stand level as gross growth (SVINC; m^3 ha^{-1} yr^{-1}). Patterns of growth efficiency depend upon the relationship of volume growth to leaf area (Seymour and Kenefic 2002). For the three TGE patterns described above, there are two general mathematical forms of the TVINC-PLA relationship: a simple power function and a peaking function (often a cumulative Weibull distribution). Since there is no evidence of peaking TGE in our study (see Results), a power function was used to quantify patterns of growth efficiency as

[3] $$\mathrm{TVINC} = \beta_1 \mathrm{PLA}^{\beta_2},$$

where TVINC and PLA are as defined, β_1 is the constant, and β_2 is the exponent. Preliminary analyses tested the effects of including PLA estimates from the beginning, middle, and end of the growth period in equation [3]. Results showed substantial improvements in R^2, AIC, and statistical significance using the latter PLAs; thus, the period-end PLA or LAI was used in calculating TGE or SGE for each growth period.

Tree-level analyses focus on the TVINC-PLA and TGE-PLA relationships between crown classes within treatments and between treatments for upper crown class trees (dominant and codominant). Analyses of the differences in form and pattern of the TVINC-PLA relationship between crown classes or treatments used indicator variables for each respective factor in the model. Thus, the β_1 and β_2 parameters were modified by converting each parameter to an additive linear function which would then predict the constant and exponent for each factor in a single model. For example, to test for differences between thinning treatments the constant parameter in Equation [3] became

[4] $$\beta_1 = b_1 + a_1*B + a_2*LD,$$

where B and LD are indicator variables for the B-line and low density treatments, respectively, b_1 is the parameter for the control, and a_is are parameter estimates of the difference between the control parameter and the respective thinning treatment. Analyses of the differences between each factor's parameter estimates focused on the 95% confidence intervals (CIs) of each estimate where overlapping CIs indicated a non-significant difference and non-overlapping CIs were considered significantly different.

Stand-level analyses focus on the volume growth - leaf area index (SVINC-LAI) and SGE-LAI relationships between treatments for both growth periods. Analysis of covariance (ANCOVA) was used to test for the effect of thinning on SGE within each growth period using LAI as a covariate. Orthogonal contrasts were included to specifically compare the B-line and low density treatments as well as the unthinned control with the two thinning treatments combined. Statistical significance in the ANCOVA tests was considered at the 95% level of confidence.

Stand SGEs were also related to stand density (TPH) and stand structure. Structure was quantified as the shape parameter estimate of a Weibull probability density function (Husch et al. 2003)

[5] $$f(\mathrm{D}) = \frac{\mathrm{c}}{\mathrm{b}}\left(\frac{\mathrm{D}-\mathrm{a}}{\mathrm{b}}\right)^{1/\mathrm{c}} * e^{-[\frac{\mathrm{D}-\mathrm{a}}{\mathrm{b}}]^{\mathrm{c}}},$$

where f(D) is the probability density of each plot's DBH distribution, a is the location parameter (fixed at 2 cm, which is below the minimum population value), b is the scale parameter, and c is shape parameter. The Weibull model estimated the distribution of 1 cm diameter classes from the tree lists of each plot in 2001 and 2008. The shape parameter describes the general form of the distribution. For example, plots with a wide range of tree sizes will have a low estimate and plots with nearly uniform distributions will have a high estimate.

RESULTS

Unthinned control trees during the first growth period (1992-2001) had an increasing amount of TVINC with PLA, resulting in a monotonic decreasing TGE pattern (Figure 3.1). There were no differences in these relationships among the separate crown classes (Table 3.2; Figure 3.2). Likewise, when the crown classes were grouped into upper (dominant and codominant) and lower (intermediate and over-topped), no differences between the groups were found. In addition, during the second growth period (2001-2008) the crown classes were still similar; the same was true within each thinning treatment during both growth periods. Because there were very few or no lower crown class trees in the thinned treatments, further analyses focus on dominants and codominants only.

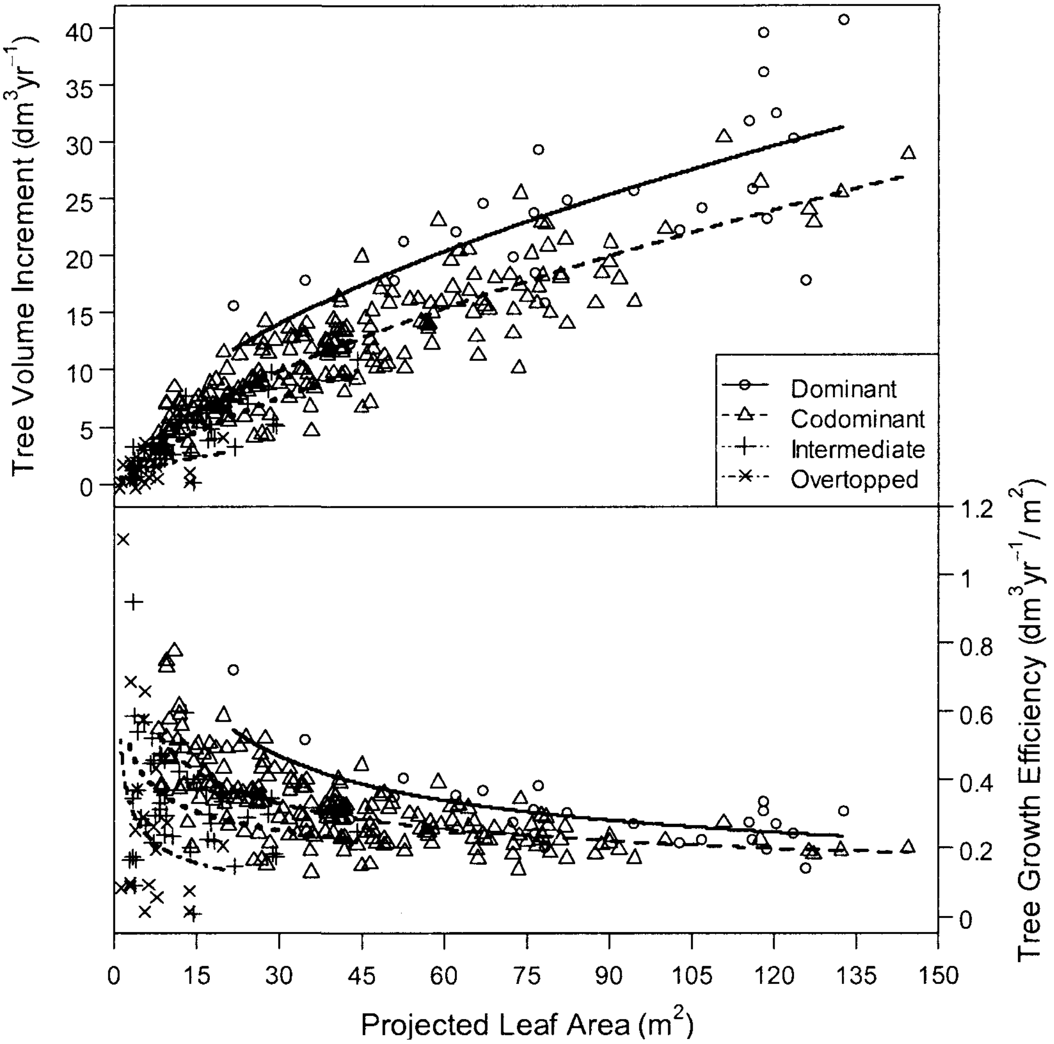

Figure 3.1. The relationships of stemwood volume growth (TVINC) and projected leaf area (PLA), and tree growth efficiency (TGE) and PLA for each crown class in the control plots during the 1992-2001 growth period. TVINC-PLA lines show the fits by crown class of the power function (Table 3.2); TGE-PLA lines were drawn by dividing the power function predictions by PLA.

Table 3.2. Nonlinear regression fit of the tree-level TVINC-PLA relationship by crown class for the control treatment during the 1992-2001 growth period. Parameter estimates for the dominant, intermediate, and over-topped crown classes are the difference between that crown class and the codominant estimate.

Parameter	Crown Class	Estimate	SE	*t*-value	*P*-value	R^2	RSE	df
Constant	Codominant	1.1291	0.1290	8.7516	< 0.0001	0.8706	2.7428	287
	Dominant	1.1233	0.6820	1.6472	0.1006			
	Intermediate	-0.4615	0.3159	-1.4608	0.1452			
	Over-topped	-0.6070	0.7446	-0.8151	0.4157			
Exponent	Codominant	0.6387	0.0281	22.6980	< 0.0001			
	Dominant	-0.1002	0.0710	-1.4120	0.1590			
	Intermediate	0.0737	0.1450	0.5084	0.6115			
	Over-topped	-0.0840	0.6398	-0.1314	0.8956			

Note: SE – standard error; RSE – residual standard error; df- residual degrees of freedom

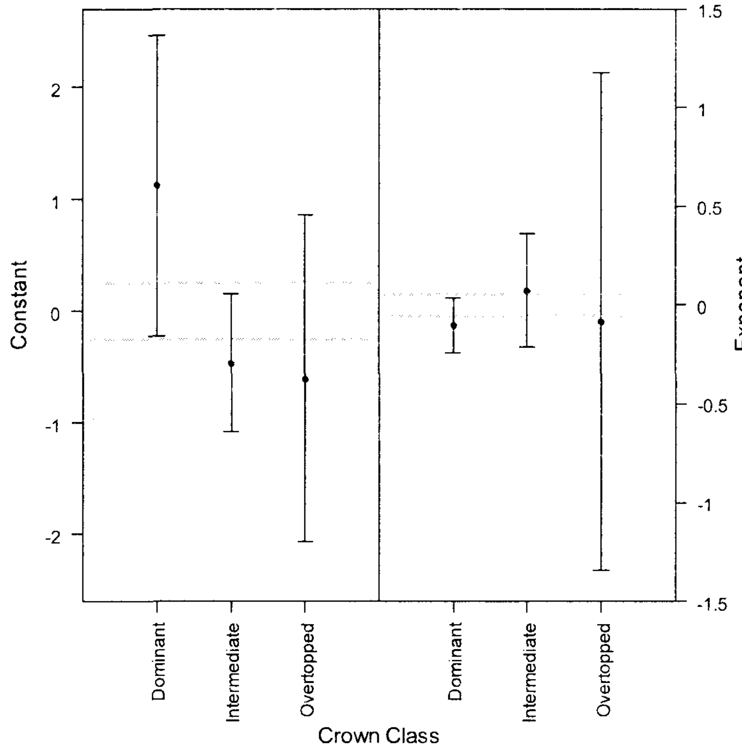

Figure 3.2. Comparison of the 95% confidence intervals of the constant and exponent parameter estimates of the nonlinear model for the control treatment during the 1992-2001 growth period (Table 3.2). Error bars are 95% confidence intervals of the parameter estimates. The grey dashed and dotted lines are the 95% confidence intervals for the codominant crown class.

The TVINC-PLA relationships for all treatments during both growth periods were significantly nonlinear (Table 3.3), resulting in a slight but significant decline in TGE with greater leaf area (Figures 3.3 and 3.4). There were no differences in the TVINC-PLA relationships between control and low density trees during either growth period. The TVINC-PLA relationship for the B-line treatment during the first growth period, however, was different from the control treatment (Table 3.3), but not from the low density treatment (Figure 3.5). By the end of the second growth period, there were no differences in the relationships of TGE among the treatments.

Table 3.3. Nonlinear regression fits of the tree-level TVINC-PLA relationship for each treatment during the 1992-2001 and 2001-2008 growth periods. Parameter estimates for the B-line and low density treatments are the difference between that treatment and the control estimate. Only dominants and codominants are included.

Parameter	Treatment	Estimate	SE	*t*-value	*P*-value	R^2	RSE	df
1992-2001 Growth Period								
Constant	Control	0.8734	0.1057	8.2606	< 0.0001	0.8377	3.3267	403
	B-line	-0.5417	0.1260	-4.3000	< 0.0001			
	Low Density	-0.1153	0.1882	-0.6125	0.5405			
Exponent	Control	0.7145	0.0286	24.9543	< 0.0001			
	B-line	0.2085	0.0540	3.8613	0.0001			
	Low Density	0.0427	0.0519	0.8226	0.4112			
2001-2008 Growth Period								
Constant	Control	0.8147	0.1542	5.2841	< 0.0001	0.8577	4.9320	303
	B-line	-0.1423	0.2088	-0.6817	0.4959			
	Low Density	-0.2376	0.2254	-1.0540	0.2927			
Exponent	Control	0.7610	0.0441	17.2750	< 0.0001			
	B-line	0.0709	0.0637	1.1128	0.2667			
	Low Density	0.0961	0.0706	1.3603	0.1747			

Note: SE – standard error; RSE – residual standard error; df- residual degrees of freedom

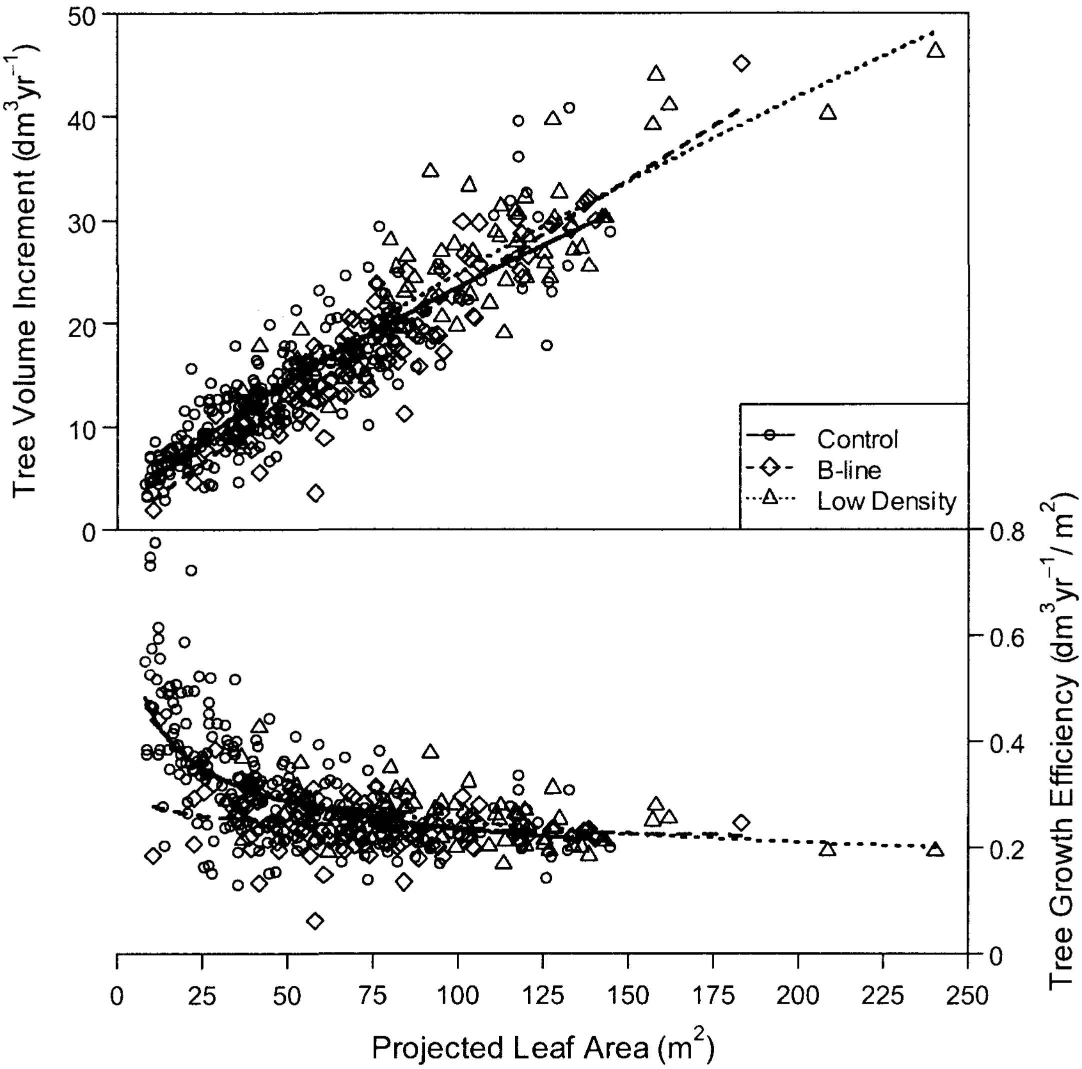

Figure 3.3. The relationships of stemwood volume growth (TVINC) and projected leaf area (PLA), and tree growth efficiency and PLA for each treatment during the 1992-2001 growth period. TVINC-PLA lines show the fits by treatment of the nonlinear regression model (Table 3.3); TGE-PLA lines were drawn by dividing the power function predictions by PLA.

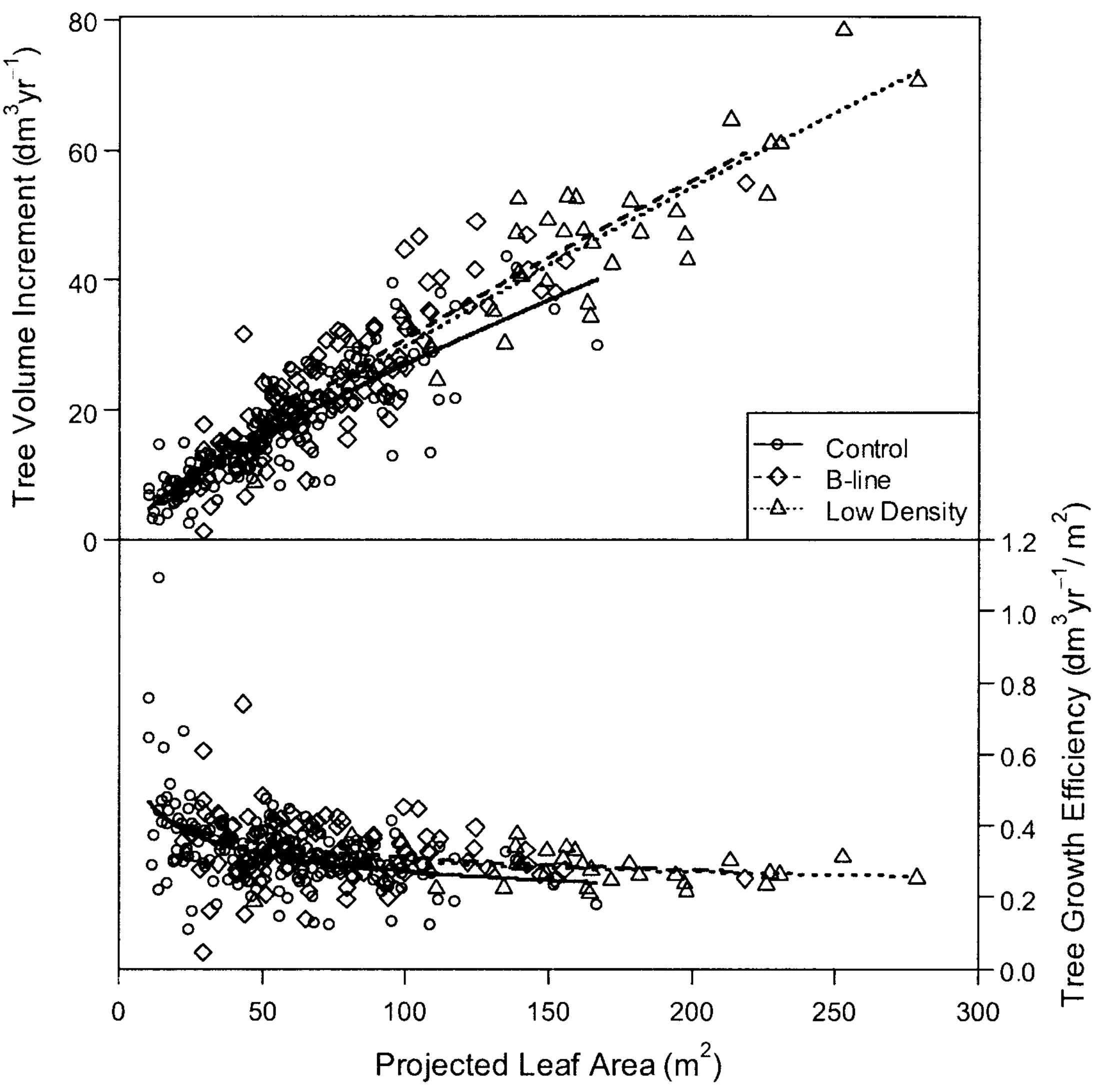

Figure 3.4. The relationships of stemwood volume growth (TVINC) and projected leaf area (PLA), and tree growth efficiency and PLA for each treatment during the 2001-2008 growth period. TVINC-PLA lines show the fits by treatment of the nonlinear regression model (Table 3.3); TGE-PLA lines were drawn by dividing the power function predictions by PLA.

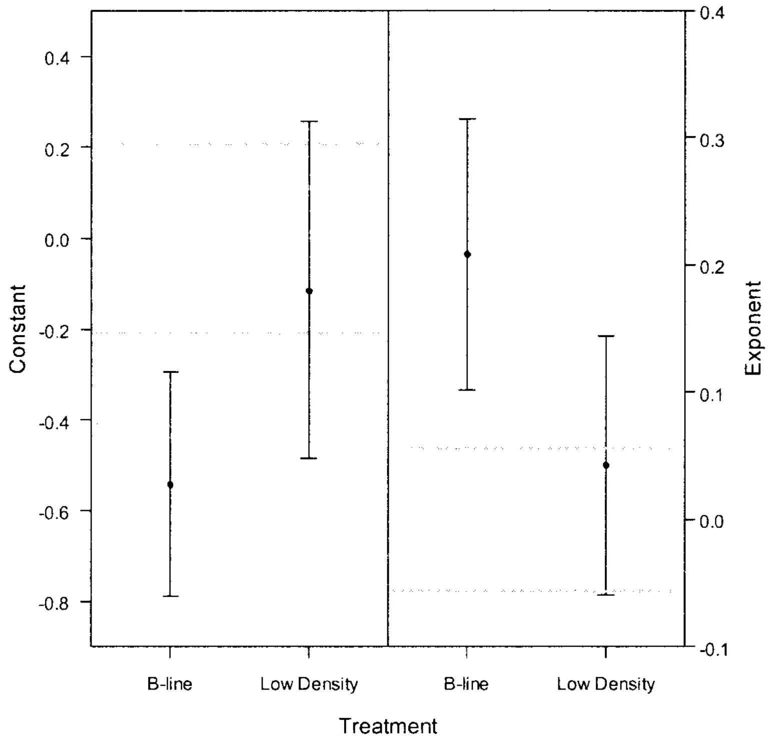

Figure 3.5. Comparison of the 95% confidence intervals of the constant and exponent parameter estimates of the nonlinear model for each treatment during the 1992-2001 growth period (Table 3.3). Error bars are 95% confidence intervals of the parameter estimates. The grey dashed and dotted lines are the 95% confidence intervals for the control treatment.

Gross stand volume growth (SVINC) during the 1992-2001 growth period was linearly related to leaf area index (LAI) (Figure 3.6). Surprisingly, the relationship of SVINC and LAI was stronger within the thinned treatments than it was for the control. SGE is quite variable for the control, despite similar LAIs among four of the plots. The ANCOVA showed that during this period there were no differences in SGE between the thinned treatments or between the unthinned control and the thinned treatments combined (Table 3.4).

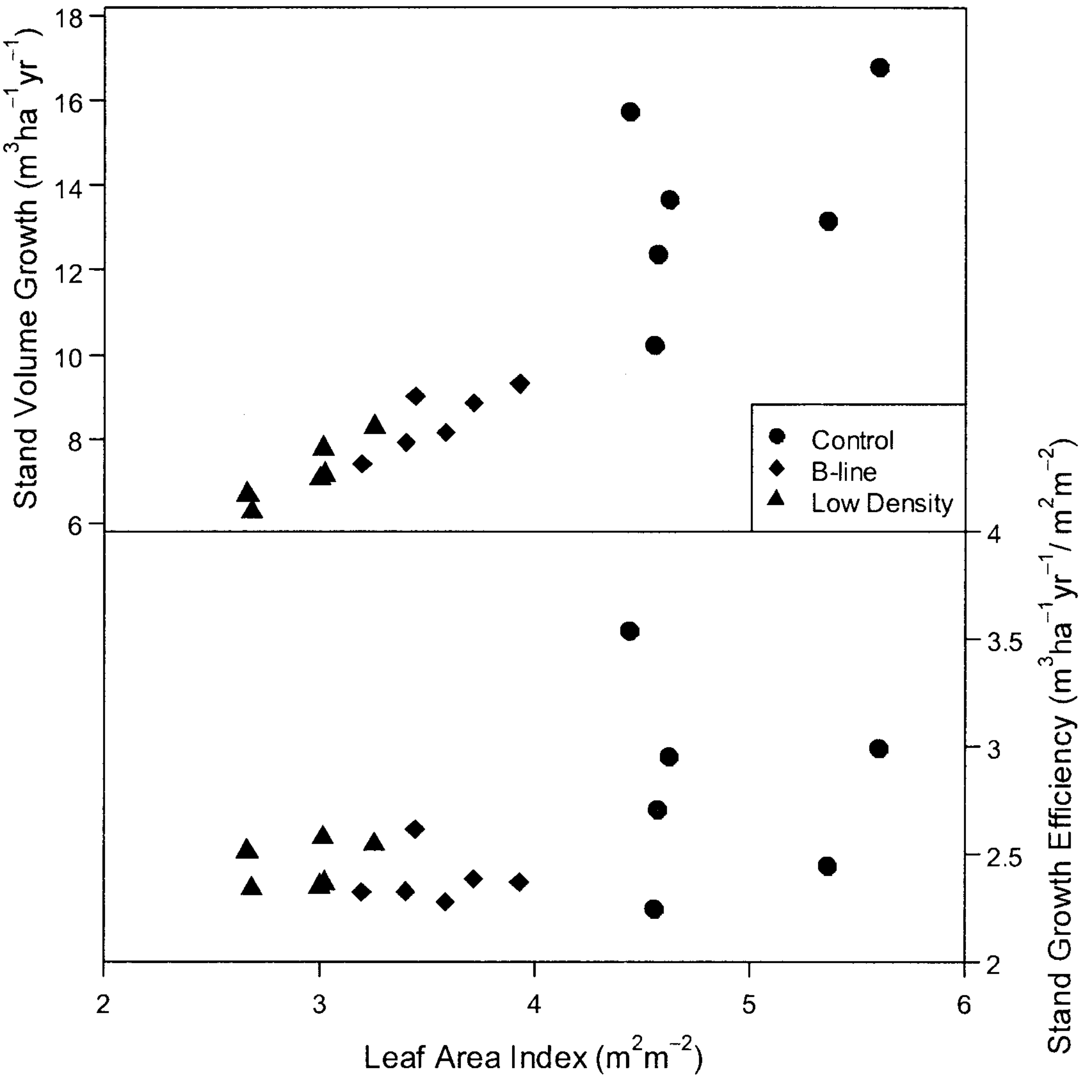

Figure 3.6. The relationships of leaf area index to volume growth and growth efficiency for the 1992-2001 growth period.

Table 3.4. Analysis of covariance results for tests of the effects of thinning on SGE within each growth period. Specific contrasts were made between the B-line (B) and low density (LD) thinning treatments, and between these treatments combined (Thin) and the unthinned control (C).

Parameter	df	SS	*F*-value	*P*-value	R^2	RSE
1992-2001 Growth Period						
Block	5	0.603	1.886	0.192	0.686	0.253
LAI	1	0.453	7.089	0.026		
Treatment	2	0.203	1.586	0.257		
B vs. LD	1	0.104	1.628	0.234		
C vs. Thin	1	0.099	1.544	0.245		
Residual	9	0.576				
2001-2008 Growth Period						
Block	5	0.878	2.229	0.140	0.664	0.281
LAI	1	0.045	0.576	0.467		
Treatment	2	0.479	3.038	0.098		
B vs. LD	1	0.459	5.832	0.039		
C vs. Thin	1	0.019	0.244	0.633		
Residual	9	0.709				

Note: df - degrees of freedom; SS - sum of squares; RSE - residual standard error

During the 2001-2008 growth period, the SVINC-LAI relationship was somewhat more distinct among the treatments than during the first growth period, with the exception of two B-line plots that were similar to the low density plots (Figure 3.7). The overall SGE of the B-line treatment, however, was significantly different from the low density treatment, but not the control (Table 3.4). Likewise, the mean of the combined thinning treatments was not different from the control. SGEs among all treatments increased between growth periods (Table 3.5).

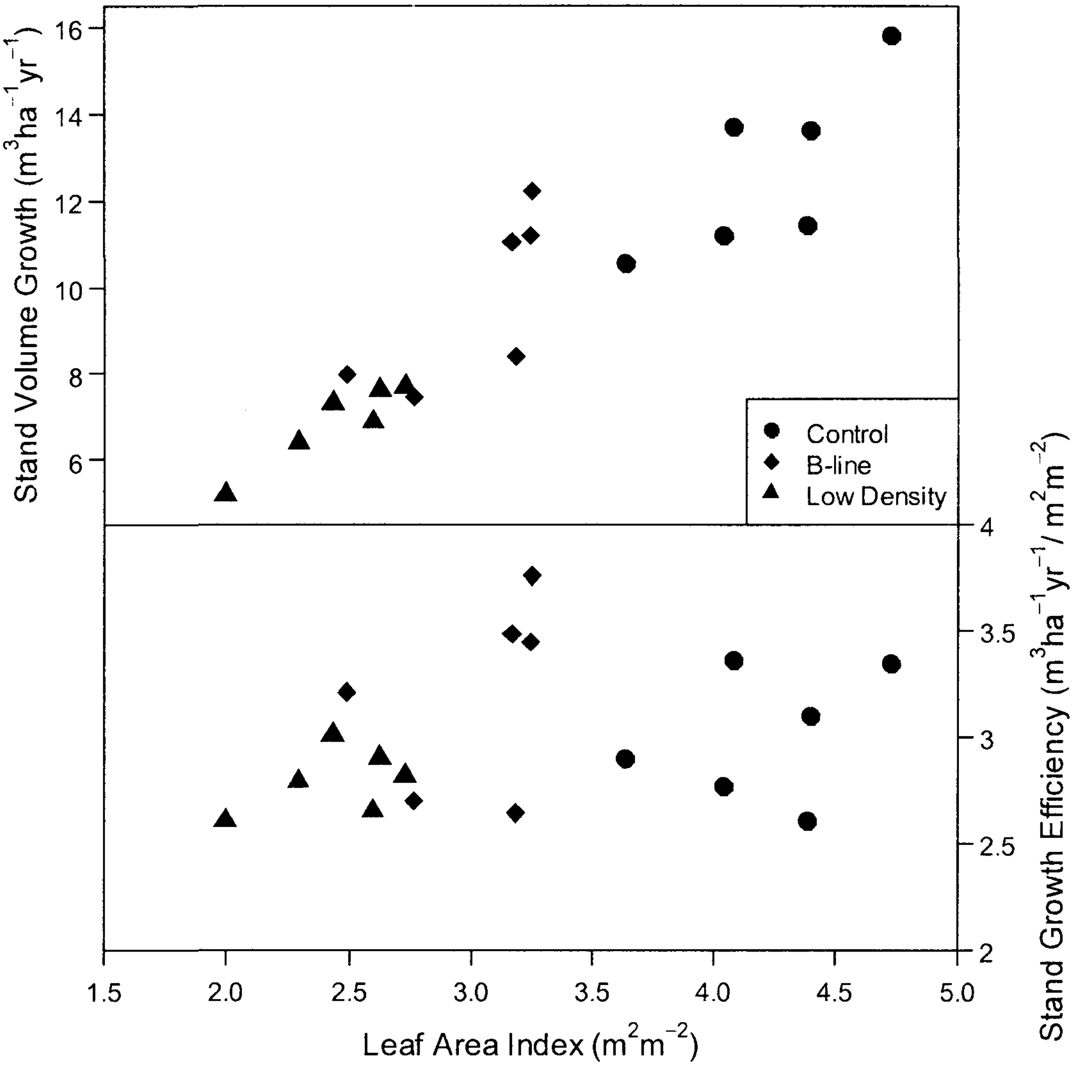

Figure 3.7. The relationships of leaf area index to volume growth and growth efficiency for the 2001-2008 growth period.

Table 3.5. Mean SGE of each treatment during the two growth periods; standard errors are in parentheses.

Growth Period	Control	B-line	Low Density
1992-2001	2.81 (0.187)	2.38 (0.049)	2.45 (0.044)
2001-2008	3.01 (0.126)	3.21 (0.184)	2.80 (0.062)

The Weibull shape parameters did little to explain the variability of SGE within the control plots during either growth period, as the shape parameters were similar among the plots (Figure 3.8). There was, however, a shift to higher shape parameter estimates between growth periods. The low density treatment showed that increasing uniformity (higher shape parameters) caused a slight decrease in growth efficiency. While the B-line treatment during the first growth period had constant or slightly decreasing SGE with increasing uniformity, there was no clear pattern during the second growth period. It should be noted that linear regressions of the shape parameters and SGE reflected the lack of a relationship ($P > 0.15$).

Stand density, expressed as trees per hectare (TPH), appears to explain the patterns of LAI, SVINC, and SGE better than the Weibull shape parameters (Figure 3.9). Both LAI and SVINC are positively and linearly or asymptotically related to density. While the treatments differentiate in terms of density, the overall relationships did not change as a result of thinning. The previously noted variability of the control treatment SGE was related to different stand densities, where higher densities were more growth efficient during both growth periods. Furthermore, adding the block numbers of each study plot to the graphs showed that the initial densities had an influence on SGE in that the higher initial densities (lower block numbers) were generally the most growth efficient plots after thinning.

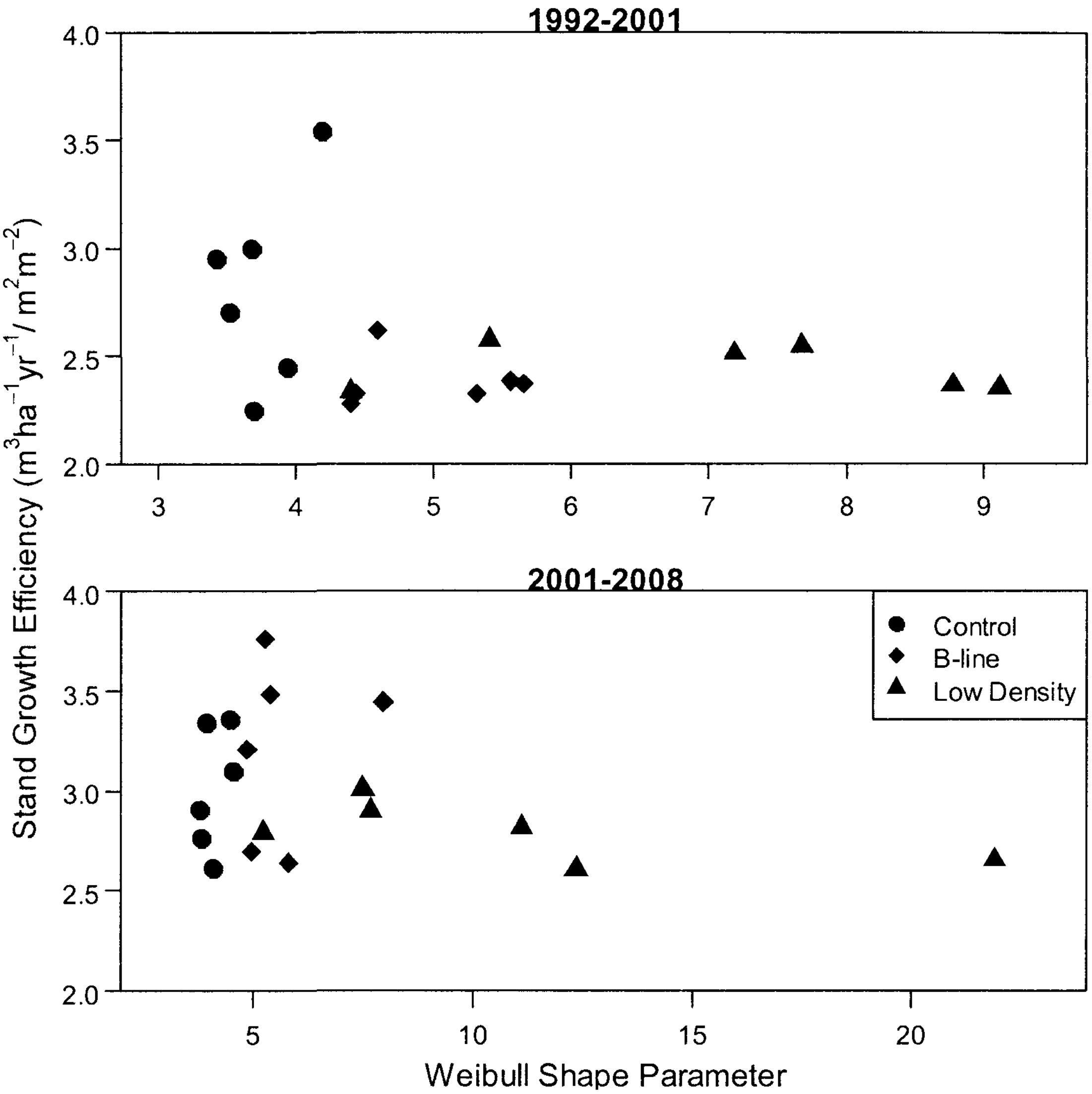

Figure 3.8. The relationship of Weibull shape parameter estimates to growth efficiency for the 1992-2001 and 2001-2008 growth periods. Note the change in scale of the x-axes between graphs.

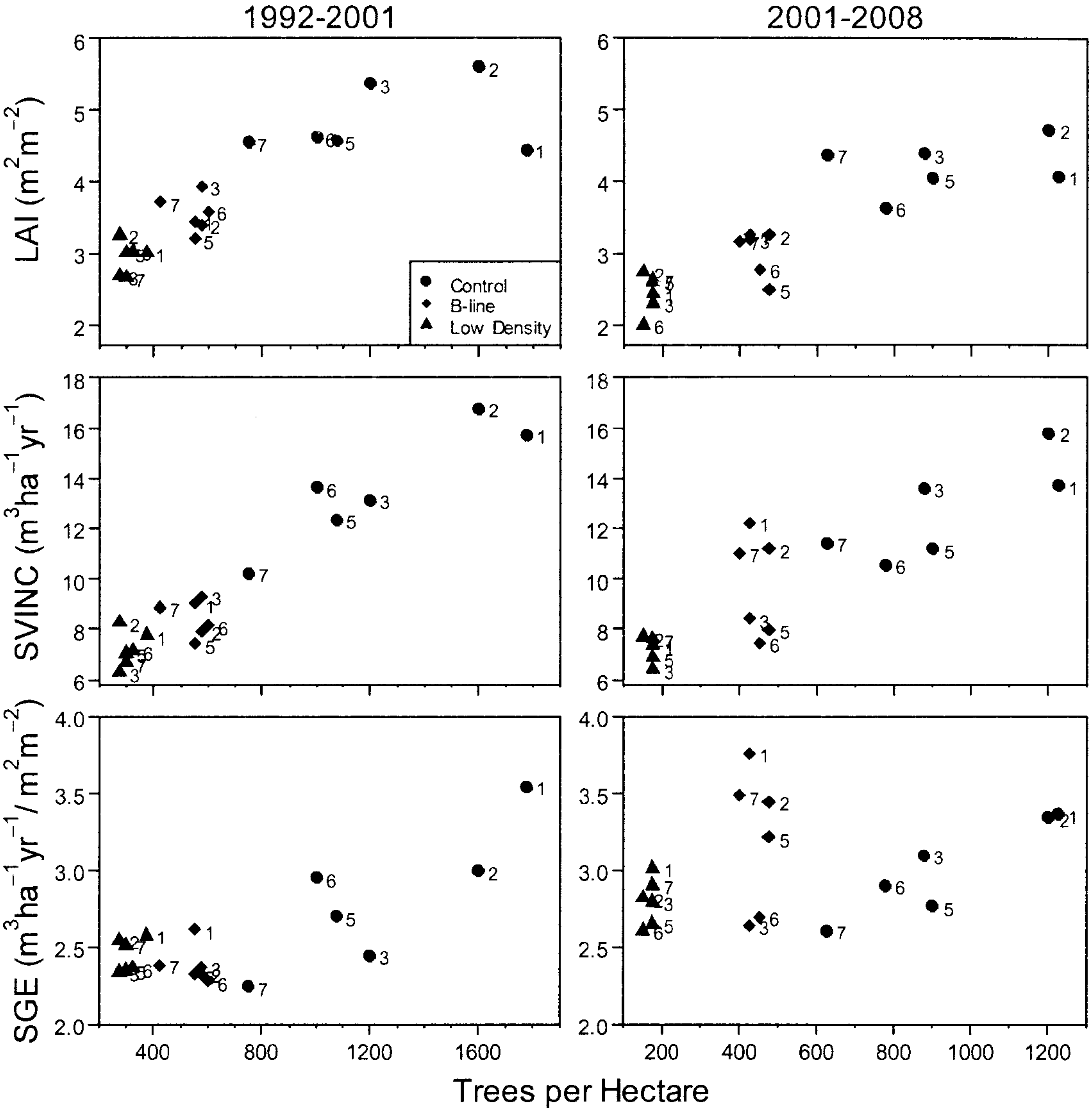

Figure 3.9. The relationship of stand density (trees per hectare) to leaf area index (LAI), annual volume increment (SVINC), and growth efficiency (SGE) for the 1992-2001 and 2001-2008 growth periods. Density and LAI values are for the end of the growth periods. Numbers adjacent to data points indicate the study block of that plot. Note that the scales of the x-axes change between growth periods.

DISCUSSION

Patterns of growth efficiency within the even-aged eastern white pine stands of the WPTS follow an asymptotic TVINC-PLA relationship across crown classes and thinning treatments. These results represent a monotonic decreasing pattern of TGE over leaf area and are consistent with patterns from even-aged stands of lodgepole pine (*Pinus contorta*) (Long and Smith 1990; Roberts et al. 1993; Kollenberg and O'Hara 1999), loblolly pine (*P. taeda* L.) (Sterba and Amateis 1998), red pine (*P. resinosa* Ait.) (Larocque and Marshall 1994; Powers et al. 2009), Douglas-fir (Velazquez-Martinez et al. 1992; Brunner and Nigh 2000), red spruce (*Picea rubens* Sarg.) (DeRose and Seymour 2009), black spruce (*Picea mariana* Mill.) (Groot and Saucier 2008), and balsam fir (*Abies balsamea* L.) (Gilmore and Seymour 1996; DeRose and Seymour 2009).

The most efficient trees in the WPTS had small to medium-sized crowns. Trees of this size are often found to be the most efficient following thinning (e.g., Assmann 1970; O'Hara 1988; Gilmore and Seymour 1996; Powers et al. 2009) but the exact mechanism for reduced efficiency in larger trees remains largely speculative (see Ryan et al. 2006). In this study, reductions in TGE were associated with increased PLA, and thinning was previously found to significantly increase tree PLA (Chapter 1). Although not measured, it is likely that the volume of the non-foliated "bare inner core" portion of the crown (Assmann 1970) increased from thinning because crown widths would have increased (Peterson et al. 1997). Jack and Long (1992) showed that TGE is negatively correlated with the size of the bare inner core. Lavigne (1991) found that foliage, branch, and stem growth were increased by thinning balsam fir; however, the growth of all aboveground components per unit of foliage weight was not affected by thinning. Our results were consistent with Lavigne's (1991) in that thinning did not alter TGE. Lavigne (1991) attributed the similarity between the efficiencies of thinned and unthinned stands to greater allocation of photosynthates in thinned trees to branch and (or) root respiration.

Given that larger trees are generally less efficient than comparable smaller trees, we initially hypothesized that thinning would alter the relationship of TVINC to PLA During the first growth period, the B-line trees had a more linear TVINC-PLA relationship than the other treatments and smaller B-line trees had the lowest TGEs. By the end of the second growth period, however, the B-line pattern shifted to one equal to the low density and control treatments. This shift can be attributed to a delayed response to the initial thinning for the smaller B-line trees. Originally, B-line stocking was achieved through crown thinning, which released selected crop trees on two to three sides and maintained enough basal area to meet the stocking guide target (Seymour 2007). These crop trees were mostly well-formed dominants and large codominants, with the remaining trees being small-crowned codominants or intermediates. As such, the smaller trees grew relatively less than the crop trees during the 1992-2001 growth period and caused the linear TVINC-PLA pattern for the B-Line treatment (Figure 3.3). By the end of the second growth period, however, all B-line trees had fully responded to thinning, and their TGEs were similar to low density trees. Therefore, we believe that B-line thinning did not truly reduce the TGE of smaller trees as was suggested by the GE pattern during the first growth period (Figure 3.3).

The TVINC-PLA pattern of low density trees changed little between growth periods and was not different than the control during either period. The effects of low density thinning, therefore, were to significantly increase leaf area (Chapter 1) and tree volume growth (Chapter 2) without substantially changing the patterns of growth efficiency. Any reduction in TGE in low density stands is related to the increase in tree sizes.

Gross volume growth (SVINC) within the WPTS during the first growth period was linearly related to LAI (Figures 3.7 and 3.8). This pattern has been shown previously for eastern white pine (Innes et al. 2005) and other conifers (Binkley and Reid 1984; O'Hara 1989; Smith and Long 1989; O'Hara 1996; Berrill and O'Hara 2007). The fact that thinning had little effect on SGE is surprising, because the literature suggests that the canopy architecture in low density stands, in particular, would be less efficient because of the prevalence of deep and wide crowns (e.g., Smith and Long 1989).

During the second growth period, half of the B-line plots had higher SGEs than the low density treatment. It was previously shown that the B-line treatment was thinned below actual B-line stocking in 1991(Figure 1) but reached the point of crown closure and a stable LAI shortly after the light thinning entry in 2001 (Chapter 1). Peak growth commonly occurs at canopy closure followed by a growth decline (Long and Smith 1992; Ryan et al. 1997; Smith and Long 2001; Ryan et al. 2004). This pattern implies that maintaining B-line stocking, and thus keeping the stand at the point of crown closure indefinitely (Philbrook et al. 1973), could be a means to maintain high SGE if growth rates continue to be high and LAI remains constant. However, thinning entries would have to be repeated often to prevent a decline in either growth or leaf area, and thus may not remove enough volume to be profitable. We believe that the increased B-line SGE is temporary because it coincides with canopy closure and is the result of increased growth rates on previously subordinate trees. Future inventories and analyses will test this hypothesis.

Thinning substantially reduced the variability in growth and growth efficiency evident on control plots. We originally hypothesized that this variability was related to stand structure (following the conclusions of O'Hara [1989]) since the control plots differed in their planting density which ultimately affects the array of tree sizes and timing of stand development (Oliver and Larson 1996). However, the shape of the diameter distributions had little or no relation to SGE (Figure 3.12). Stand density, however, was positively related to growth and SGE. This shows that there is a substantial contribution of each tree in dense eastern white pine stands to SVINC and SGE, despite having reached maximum LAI.

Results of this study emphasize a need for more research into the long-term patterns of some well-established trends in production ecology. For example, being able to investigate changes in the growth efficiency relationships of the B-line treatment in particular between growth periods allowed for more informed conclusions as to the effects of thinning.

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Christopher Guiterman was born on March 19, 1982, in New Haven, CT. He was raised in Orange, CT, and graduated from Amity Regional High School in 2000. He attended Bates College in Lewiston, ME where he received a B.A. in geology in 2005, graduating with departmental honors after conducting research on the structural geology of the alpine zone of Mount Washington, Presidential Range, NH. During college, Chris was very active with the Bates Outing Club, holding many of the club officer positions including president and vice president. He was also able to coordinate the Annual Entering Students Outdoor Program (AESOP) in 2003 for most of the class of entering first-year Bates students. Following graduation Chris worked briefly as a sternman on a lobster boat on Little Cranberry Island (Islesford), ME. Beginning in 2005, Chris worked for a contractor of the Forest Service in Joseph, OR, conducting stand inventories for the Forest Inventory and Analysis (FIA) and Current Vegetation Survey (CVS) programs. During the three seasons in Oregon and Washington, he also performed timber cruises on Forest Capital lands. Beginning in 2007, Chris came to the University of Maine to attend graduate school and work as a research assistant for Dr. Robert S. Seymour. Chris is a candidate for the Master of Science degree in Forest Resources from the University of Maine in December, 2009.