

2003

# Effect of Stand Density on Behavior of Leaf Area Prediction Models for Eastern White Pine (*Pinus strobus* L.) in Maine

Micah D. Pace

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**EFFECT OF STAND DENSITY ON BEHAVIOR OF LEAF AREA  
PREDICTION MODELS FOR EASTERN WHITE PINE  
(*PINUS STROBUS* L.) IN MAINE**

By

Micah D. Pace

B.S. The Ohio State University, 2000

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine

May, 2003

Advisory Committee:

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An Abstract of the Thesis Presented  
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There is little debate within the forest science community that leaf area (LA, the surface area of live foliage) or leaf area index (LAI, the total surface area of live foliage per unit of ground area) are important variables, central to enhancing the understanding of forest growth and many forest ecosystem processes. The ability to accurately measure LAI has become a research priority and has resulted in various methods of estimation for a variety of species and regions. In this study LA estimation models for *Pinus strobus* L. were developed, tested, and compared across a wide range of densities for both thinned and unthinned stands in the Penobscot River Valley of central Maine. Test plots were located within a 52-year-old plantation.

Direct LAI estimations from litterfall were used to compare the indirect estimations of below-canopy light interception and various allometric models. Four tree-level models were developed through non-linear regression and compared at both tree-level and stand-level. Two models utilized sapwood area at breast height ( $SA_{bh}$ ) as a

predictor variable and two non-sapwood models were based on basal area and a modified live-crown ratio (BA\*mLCR). When compared to litterfall, LAI measurements from light interception data yielded underestimates and overestimates in thinned and unthinned sites, respectively. However, the treatment-specific bias was masked when pooling the data and a relatively strong relationship with litterfall existed ( $R^2 = 0.68$ ). Among the allometric models, the  $SA_{bh}$  models performed best showing no bias across stand densities. Estimations from BA\*mLCR were in agreement with both litterfall and sapwood models within unthinned sites, but were biased, providing overestimations for thinned plots. The apparent bias in LAI estimation from BA\*mLCR was caused by the model's high sensitivity to the limited range of large trees sampled for equation development. Basal area at breast height was particularly influential. However, when sapwood-derived coefficients were used, an adjusted BA\*mLCR equation performed well across the range of stand densities and provided accurate LAI estimations when referenced to litterfall and sapwood-based estimations.

## ACKNOWLEDGMENTS

Over the past two and a half years, I have received a great wealth of knowledge and character. Not least of which was aided by the hand of Bob Seymour, who was never afraid of letting me work independently, yet always ready to assist when needed. Bob's hands-off approach with me is testimony to his faith in my ability, to which I will always be grateful. A special thanks is also warranted for my thesis committee members: Alan White and Robert Shepard, who were willing to provide valuable time and insight to what seemed a never-ending project. My gratitude is also given to Bill Halteman for countless statistical assistance without which the summation of this research would not exist. I also wish to give thanks to the University of Maine, the Graduate School, and the Department of Forest Ecosystem Science for a fun yet, professional atmosphere in which to pursue an advanced degree. The Maine Agricultural and Forest Experiment Station, the Department of Forest Ecosystem Science, and the University of Maine Graduate School made funding available for this project.

It was a pleasure to study and work alongside both a brilliant and wonderful body of faculty and students. I appreciate both the encouragement and friendship of many people: Mike Saunders, Damián and Ale, Alex Elvir, the Bustos family, Shawn Fraver, Andrew Moores, Dawn Opland, and Isaac Annis just to name a few. The completion of this project and this stage of my life would have been impossible without the love and support of my family, and both old and new friends. The warmth of the UMaine community made the cold, long winters bearable and at times even pleasant. I will look upon my time both here in Maine and within the University with fond memories.

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## CHAPTER 1.

### INTRODUCTION

Leaf area (LA) has been described as the surface area available for the interception of radiant energy, the absorption of carbon dioxide, and the circulation of water between the foliage and the atmosphere (Margolis et al. 1995). LA is often expressed as a leaf area index (LAI), which is simply the area of leaves ( $m^2$ ) per unit of ground area ( $m^2$ ). Over the last two decades LA measurements have become major tools for forest ecosystem and silvicultural studies alike. Estimates may be used for a variety of studies ranging from light competition (Waring 1983), insect-forest interactions (Mitchell et al. 1983; Waring and Pitman 1985; Paine et al. 1990), and direct manipulative studies focused on LA response to thinning and fertilization (Brix 1983; Brix and Mitchell 1983; Binkley and Reid 1984; Vose and Allen 1988; Velazquez-Martinez et al. 1992). Three common methods for estimating LAI include below-canopy light interception measurements, litterfall collection, and allometric regression equations. LA may be estimated for individual trees or for whole stands depending on the method chosen.

#### **Light Interception Estimation**

Estimating stand LA from below-canopy light interception (or light transmission) measurements requires the use of either a sunfleck Ceptometer or an instrument such as the LAI-2000 plant canopy analyzer. Light interception measurements are based on the Beer-Lambert Law of light extinction and are used to develop relationships between projected LA and canopy transmittance of photosynthetically active radiation (PAR); the

range of the light spectrum between 380 and 710 nm utilized by plant cells for photosynthesis (Larcher 1980). The LAI-2000 has a 150° field-of-view lens seated over five concentric diffuse light-detecting silicon rings that receive radiation from five sky sectors between zenith angles 0° and 75°. Furthermore, a filter that eliminates light above 490 nm minimizes radiation scatter or reflectance from foliage and woody material (LICOR 1992). Measuring light transmission to the forest floor using the LAI-2000 requires two measurements, which determine the ratio between PAR under the canopy and PAR in a nearby opening (Lieffers et al. 1999). However, conversion factors are often required to convert the output generated from the system to the actual LAI (Barclay and Trofymow 2000).

Although the light extinction coefficient ( $k$ ) in the Beer-Lambert Law was originally assumed to be constant for a given species (Pierce and Running 1988), measured light interception appears to be a poor indicator of LAI across a range of stand structures because of subsequent variation in  $k$  (Smith et al. 1991). While some studies give contradicting results as to the relationship between LA and light interception (Smith et al. 1991; Smith 1993), preliminary studies for eastern white pine (*Pinus strobus* L.) in Maine show a strong correspondence between LA derived from measured light interception and that of litterfall (Seymour 2001). However, with variable stand densities the influences of stand structure on the light interception method may be significant.

## **Litterfall Estimation**

Litterfall also supplies a realistic estimate of stand LA, although estimates are time consuming and rely on season-specific collection. Leaf litter has a strong biological relationship to the total leaf area of a stand's canopy and in the case of conifers, relates

strongly to the average needle retention of the species of interest. Knowing the actual needle retention of the species of interest is essential for accurate LA estimation (Marshall and Waring 1986; Vose and Allen 1988). Using litterfall as an estimate for LA assumes that the foliar biomass of a tree and/or stand remains in a steady state when in reality LA does exhibit annual variation (Gholz et al. 1991, as cited in Margolis et al. 1995). However, litterfall is still a direct estimator of LA and may provide a more accurate estimation than allometric approaches (Turner et al. 2000; Seymour 2001).

### **Allometric Estimation**

Allometric approaches to the estimation of LA have aided much research over the past several decades. Interests in this method stems from the relative ease of data collection, such that measurements may be taken from only a few individuals and extrapolated to the stand and landscape level. The early allometric equations (Young et al. 1980) were based solely on diameter at breast height measurements; however, use of diameter-based equations later proved to be biased estimations of LAI (Marshall and Waring 1986; Smith et al. 1986). Over the past decade comparative studies have tested the dbh-based approach with that of other allometric equations only to show that sapwood area-based equations offer an alternative method of LA estimation, which lowers the standard error nearly in half and provides consistently lower estimations for larger diameter trees (Bormann 1990; Turner et al. 2000). Other studies have continued to provide support for the growing acceptance of the use of the cross-sectional area of the conducting sapwood as a means for determining LA (Waring et al. 1982; Dean and Long 1986; Coyea and Margolis 1992; Gilmore et al. 1996; Kenefic and Seymour 1999).

The use of the conducting sapwood area (SA) to predict the canopy LA of trees has its foundation in the “pipe model theory” popularized by Shinozaki et al. (1964a, 1964b). The theory proposes that a constant cross-sectional area of conducting tissue supports a given unit of foliage. Most studies utilizing SA did so with measurements at breast height (bh) (Waring et al. 1982; Marchand 1984; Marshall and Waring 1986; Gilmore and Seymour 1996; Turner et al. 2000). However, other studies have tested the SA at the base of the live crown (cb) as a more accurate measure of LA (Dean and Long 1986; Barker 1998; but see Kenefic and Seymour 1999 for contradictory results). Waring et al. (1982) and Dean and Long (1986) suggested that the taper of sapwood cross-sectional area between bh and cb be considered and incorporated to allow for more accurate LA estimations from  $SA_{bh}$ . While some sapwood taper models have been developed as a result (Maguire and Hann 1987; Ryan 1989) no such equations presently exist for eastern white pine (*Pinus strobus* L.) in the Northeast. In 1984 Whitehead et al. proposed their hydraulic model, which provided a theoretical basis for the relationship between LA and SA that is directly proportional to the sapwood permeability characteristics and water potential gradients of tree stems. Coyea and Margolis (1992) found LA-SA ratios in balsam fir to be positively influenced by sapwood permeability.

Valentine et al. (1994) developed a model that uses a tree’s basal area and modified live-crown ratio (mLCR) to serve as a surrogate for the cross-sectional area at crown base. The Valentine model is also based upon the pipe-model theory and stresses that the cross-sectional area of a tree at its crown base is proportional to the leaf area above it because the stem is generally composed of mostly sapwood at the crown base. Few studies have employed the mLCR technique (Gilmore et al. 1996; Barker 1998;

Kenefic and Seymour 1999; Barker-Plotkin and Seymour in preparation) and there still remains uncertainty as to its validity and/or applicability to stands outside of those from which it was derived. Gilmore et al. (1996) presented data for *Abies balsamea* (L.) that showed mLCR-based models to be inferior to sapwood-based models. Barker (1998) found the modified live crown ratio model performed nearly as well as sapwood-based tree-level models for *Pinus strobus* L., although it predicted negative leaf area for small diameter trees. Kenefic and Seymour (1999) found the Valentine model to perform as well as sapwood-based models for *Tsuga canadensis* L. Carr in the Acadian forests of east central Maine. In spite of contradicting results, the ease in obtaining the parameter measurements allows it to serve as a promising tool if proper adjustments can be made that enable the model to perform with acceptable accuracy.

## **Leaf Area and Stand Density**

It is widely accepted that leaf area is an invaluable forest ecosystem parameter. However, classifying appropriate and accurate measurement techniques is still debatable. Even more important is a clear understanding of how the available techniques or methods behave over changing stand conditions such as density. One of the earliest quantified observations of foliage across stand density described European beech (*Fagus sylvatica* L.) to have constant foliar mass with increasing density (Möller 1947). Since then other studies have shown constant foliage amounts across a wide range of densities for red pine (*Pinus resinosa* Ait.) (Satoo et al. 1955; Stiehl 1966), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Turner and Long 1975), and lodgepole pine (*Pinus contorta latifolia*) (Pearson et al. 1984; Jack and Long 1991).



Still, some studies disagree with the idea of stand foliage being independent of density. Baskerville (1965) showed balsam fir (*Abies balsamea* (L.) Mill.) foliage to be positively related to density. Foliage biomass of jack pine (*Pinus banksiana* Lamb.) also was shown to be positively correlated with density, although the results were described as dependent upon the type of density measurement chosen (Doucet et al. 1976). Data for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) from Jack and Long (1991) show LAI to increase with stand density. Explanations for a positive LA: density relationship were based upon ecophysiological differences attributed to relative shade tolerances of the species in question.

However, the above trends were all observed within closed canopy stands that had reached full site occupancy. Secondly, the early observations that helped shape the constant LA ideology were for relatively intolerant species. Therefore, examining foliage trends across density for a mid-tolerant species such as white pine, including stands less than fully occupied, may result in different trends altogether.

## **White Pine Silvics**

Eastern white pine (*Pinus strobus* L.) is an excellent candidate on which to examine leaf area methodology. White pine is present in many forest types of the Northeast and is one of the most valuable species utilized for sawlogs in this region. Its range also extends across the southern portions of Canada from southeastern Manitoba to Newfoundland and as far as the southern Appalachian mountains in northern Georgia. This important species has been labeled as a major component of 5 SAF forest cover types as well as a member of 23 other forest types. While white pine is intermediate in shade tolerance, maximum height growth increases as light conditions increase (Burns

and Honkala 1990). White pine is found in a variety of canopy positions. It may exist as an emergent species in stratified even-aged mixed-wood stands (Smith et al. 1997) and mixed conifer stands (Frajvan and Seymour 1993). However, in both cases transitions are made over many years with white pine first filling the role of a dominant before emerging above the canopy. The ability to emerge above the main canopy with time is owed to white pine's longevity and subsequent ability to continue growing in height long after its stand associates stop (Frajvan and Seymour 1993). White pine is a long-lived species frequently reaching ages over 200 years old with maximum ages reaching ca. 450 years (Burns and Honkala 1990). White pine can also exist in lower strata under faster growing intolerants (Stearns 1992) such as aspen and poplar; however, it will not thrive indefinitely and requires release in order to attain its full growth potential. Response to such releases, whether through shelterwood or other partial cutting techniques, depends on both the severity of the competition and the duration over which the pine has been overtopped (Burns and Honkala 1990).

White pine also has several ecological roles within the forest ecosystems of its range. It may function as a pioneer after land abandonment or fires; such is the case of old-field pine in New England (Barnes et al. 1998). It may function as a regional or site-specific climax species on sandy, xeric soils. It may function as a long-lived successional species, and it may exist in climax forests throughout its range (Burns and Honkala 1990). This large ecological amplitude may be a result of white pine inherent ability to survive on a variety of site conditions (Mader 1985; Kotar 1992), although its productivity generally increases on landforms and soils with greater moisture-holding capacity (Smith et al. 1996).

Determining effective leaf area measurement techniques will allow for both responsible and productive management of this species. While only a few studies have examined white pine leaf area in Maine (Barker 1998, Barker-Plotkin and Seymour in preparation), studies on leaf area dynamics over a wide range of densities for even-aged white pine stands are lacking. By holding species, age, and site characteristics constant, it is possible to isolate density as a target treatment variable and clearly investigate leaf area dynamics across variable stand structures.

## **Objectives**

This study's objectives were two fold: 1) to develop, test, compare, and evaluate multiple LA estimation methods for eastern white pine (*Pinus strobus* L.) and 2) depict trends in LA response to stand density/structure. Three distinct methods of estimation have been used for this study: below-canopy light interception, litter trap collection, and allometric regression equations. A total of four tree-level equations were developed and compared. In order to compare the allometric models, they were broadly grouped as either sapwood-based or nonsapwood-based (Valentine).

The null hypotheses for this study were: 1) that sapwood and nonsapwood-based models are equivalent predictors for stand leaf area and 2) that stand density and subsequent crown structure does not influence overall stand leaf area. The results of this study are aimed at improving silvicultural prescriptions by advancing both the knowledge and use of leaf area mensuration.

## CHAPTER 2.

# LEAF AREA MODELS FOR *PINUS STROBUS* L. IN MAINE AND THE EFFECTS OF STAND DENSITY ON MODEL BEHAVIOR

### Introduction

Since the development of early leaf biomass models in the 1980's (Young et al. 1980), forest researchers have become increasingly interested in the use of leaf area (LA) as a means of describing processes and relationships within forest ecosystems. These early allometric equations predicted leaf area or weight solely from diameter at breast height (dbh). However, early use of these equations proved the models to be biased estimators of LA and more recent comparative studies have refuted the accuracy of the dbh-based approach, favoring alternative mensurational methods (Marshall and Waring 1986; Smith et al. 1986; Bormann 1990; Robichaud and Methven 1992; Turner et al. 2000). One alternative that has gained growing acceptance is the use of the cross-sectional area of the conducting sapwood. Sapwood is defined by the "living" xylem tissue inside the stem of a tree that transports water and nutrients from the roots to the living foliage within the crown (Chalk et al. 1964). The use of sapwood area is justified by the "pipe model theory" popularized by Shinozaki et al. (1964a, 1964b). The theory proposes that a constant cross-sectional area of the conducting tissue supports a given unit of foliage. Most studies utilizing sapwood area did so with measurements at breast height (bh) (Waring et al. 1982; Marchand 1984; Marshall and Waring 1986; Gilmore and Seymour 1996; Turner et al. 2000). However, other studies have tested whether the

sapwood area at the base of the live crown, or crown base (cb) is a more accurate measure of LA (Dean and Long 1986; Barker 1998).

Other available methods of estimation include the collection of foliage, or litterfall, from ground or tree-based collectors and below-canopy light interception measurements through one of several techniques including: radiometers, photosensitive paper or chemicals, hemispherical canopy photographs, and the plant canopy analyzer (LAI-2000). Lieffers et al. (1999) provide a thorough review of the accuracy, costs, efficiency of use and use limitations for these techniques with respect to northern and boreal forests. Litterfall is the only direct measurement of leaf area apart from complete destructive sampling. It also has a strong biological relationship to total stand leaf area, and in the case of conifers, relates to species-specific needle retention. Preliminary data have shown consistent values within respective thinning treatments, indicating litterfall as a valid estimation method (Seymour 2001). Although estimates are time consuming and rely on season-specific collection, litterfall supplies a realistic estimate of stand LA. Estimating stand LA from below-canopy light interception (or light transmission) measurements is based on the Beer-Lambert Law of light extinction. Measurements can be used to develop relationships between projected LA and canopy transmittance of photosynthetically active radiation (PAR).

Few studies, however, have tested multiple estimation methods (Marshall and Waring 1986; Chason et al. 1991; Smith et al. 1991) and even fewer studies have tested leaf area estimation methods across a variety of quantified stand structures (Long and Smith 1988, 1989, 1990; Jack and Long 1991; Robichaud and Methven 1992; Smith

1992). More specifically, eastern white pine (*Pinus strobus* L.) lacks detailed research in leaf area dynamics relating to stand density influences.

Based upon previous research detailing differential LA response to stand density (Baskerville 1965; Pearson et al. 1984; Jack and Long 1991) it is possible to assume at least one of two hypothetical trends. First, LA may have a constant linear increase with density (Trend A) or secondly, LA may initially increase at a similar rate as in Trend A, but then level off, remaining relatively constant after reaching an optimum level (Trend B) (Figure 2.1). The cause of these patterns and how they may be altered is not well established, although differential shade tolerance and levels of site occupancy have been offered as explanations (Baskerville 1965; Jack and long 1991). While most studies have reported foliage responses following either Trend A or Trend B, a few chronosequence studies of LA reported a possible third trend (Trend C) whereby, stands achieve a maximum level of foliage and then gradually decline over time (Gholz and Fisher 1982; Tadaki 1986). Trend C may be observed in cases where there is weak differentiation between individual trees at narrow spacing, such that the entire stand stagnates as crown abrasion and recession results in shrinking crown areas (cf. Figure 8.1 Oliver and Larson 1996). Ultimately, the response of LA to density has not been fully investigated for all species or stand densities. More specifically, LA responses to density are currently unknown for eastern white pine. Therefore, the goal of this research was to develop multiple allometric leaf area equations and compare their respective estimates of leaf area with estimations from both direct litterfall and below-canopy light interception methods and assess LA response across a wide variety of stand densities.

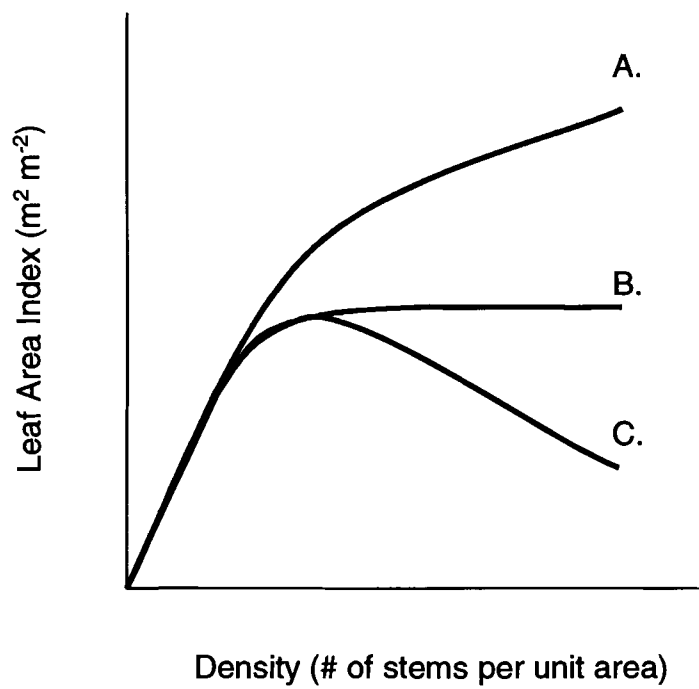


Figure 2.1: Hypothetical trends for Leaf Area Index over stand density.

## Methods

### Study Site

Data were collected from a 52-year-old even-aged white pine plantation located in the Dwight B. Demeritt Forest at the University of Maine (Orono, Maine, 44°54' N, 68°38' W). Study plots were segregated by density (trees per hectare (tph)), which ranged from approximately 300 to 3,000 tph as a result of an ongoing thinning study established in 1991. Thinning plots were set up as 20 m x 20 m (400 m<sup>2</sup>) plots and then grouped by comparable initial density and quadratic mean dbh into blocks consisting of three plots each. Eight blocks were created in which one plot was thinned to the b-line according to an eastern white pine stocking guide (Lancaster and Leak 1978), another plot was thinned to a low density by crop tree selection, and finally one plot in each block was left unthinned to serve as a control. As a consequence of this design there were eight replicates of two thinning treatments or eight treatment triplets including the unthinned controls. Furthermore, a high-density control block with 0.61 m (two-foot) spacing was also established with three 100-m<sup>2</sup> plots that remained unthinned.

The density range for each treatment was 275-375 tph, 425-625 tph, 750-1775 tph, and 2800-3400 tph for crop, b-line, unthinned, and unthinned dense treatments, respectively. Relative densities calculated using a white pine (plantation) density management diagram (Smith and Woods 1997) ranged from the lowest value of 0.23 in the crop tree treatment to 1.21 in the unthinned dense treatment. Basic tree-level statistics for the four treatments are given in Tables 2.1 and 2.2. In some analyses, treatments were pooled in order to compare two distinct treatment types: thinned and unthinned. Study plots were pure white pine with an average site index of 62 feet (base



age 50) for sampled stands. Stand-level data, including LAI estimates (methods discussed below) are compiled in Table 2.3.

## **Data Collection**

### **General Mensuration**

All living trees on the permanent plots were measured for dbh, height to crown base (both lowest live branch and lowest live whorl), total height, and live crown ratio (LCR) between June and August of 2001. All diameters were taken to the nearest millimeter (mm) using d-tapes and heights to the nearest 1/100 m using a Haglöf™ Vertex III hypsometer. Two cores oriented at 180° from one another were extracted at breast height (1.37 m) to determine sapwood area at breast height ( $SA_{bh}$ ). In the field, cores were held to the sun to differentiate between the translucent sapwood and opaque heartwood. Cores were also treated with ferric chloride ( $FeCl_3$ ) to determine sapwood-heartwood boundaries before sanding. Sapwood boundaries were marked on the cores themselves as well as the boards in which they were glued.

Table 2.1: Basic statistics<sup>1</sup> for crop and b-line treatments including: the range (min/max), average, and standard errors for both treatments respectively.

	<b>Crop</b>				
	<b>N of cases</b>	<b>Minimum</b>	<b>Maximum</b>	<b>Mean</b>	<b>Std. Error</b>
TL_HT	98	8.47	20.45	17.41	0.19
HT_LLБ	98	3.17	11.47	8.45	0.16
HT_LWH	98	3.63	11.92	9.25	0.15
DOB_BH	98	10.16	40.89	27.37	0.49
DOB_CB	20	12.50	26.20	19.25	0.84
CL	98	3.69	14.39	8.96	0.18
MLCR	98	0.29	0.86	0.56	0.01
REL_HT	98	0.42	1.00	0.89	0.01
BA_BH	98	81.07	1313.18	606.90	20.60
BA_CB	20	122.72	539.13	301.43	26.11
SAP_BH	98	40.74	434.11	210.68	7.67
SAP_CB	20	81.92	284.49	154.18	10.69

	<b>B line</b>				
	<b>N of cases</b>	<b>Minimum</b>	<b>Maximum</b>	<b>Mean</b>	<b>Std. Error</b>
TL_HT	185	10.73	20.12	17.12	0.13
HT_LLБ	185	2.99	13.02	9.29	0.12
HT_LWH	185	5.76	13.58	10.15	0.11
DOB_BH	185	9.14	41.91	24.04	0.42
DOB_CB	29	4.40	25.40	15.92	0.96
CL	185	1.71	14.87	7.83	0.14
MLCR	185	0.16	0.90	0.49	0.01
REL_HT	185	0.54	1.07	0.89	0.01
BA_BH	185	65.61	1379.51	479.02	15.52
BA_CB	29	15.21	506.71	219.25	24.12
SAP_BH	185	13.31	437.62	157.44	5.07
SAP_CB	29	8.01	236.79	109.42	10.48

<sup>1</sup>Where TL\_HT is the total height, HT\_LLБ is the height to lowest live branch, HT\_LWH is height to lowest live whorl, DOB\_BH and DOB\_CB are diameter outside bark at breast height and crown base respectively, CL is crown length, mLCR is a modified live crown ratio, REL\_HT is relative height, BA\_BH and BA\_CB are basal area at breast height and crown base respectively, and SAP\_BH and SAP\_CB are sapwood area at breast height and crown base, respectively.

Table 2.2: Basic statistics<sup>1</sup> for unthinned and unthinned dense treatments including: the range (min/max), average, and standard errors for both treatments respectively.

	<b>Unthinned</b>				
	<b>N of cases</b>	<b>Minimum</b>	<b>Maximum</b>	<b>Mean</b>	<b>Std. Error</b>
<b>TL_HT</b>	298	9.17	21.76	17.86	0.12
<b>HT_LLB</b>	298	5.55	15.67	11.51	0.10
<b>HT_LWH</b>	298	6.10	15.67	12.25	0.10
<b>DOB_BH</b>	298	6.60	43.18	22.06	0.37
<b>DOB_CB</b>	31	7.10	24.20	13.63	0.82
<b>CL</b>	298	0.83	11.64	6.35	0.13
<b>MLCR</b>	298	0.07	0.65	0.38	0.01
<b>REL_HT</b>	298	0.44	1.00	0.84	0.01
<b>BA_BH</b>	298	34.21	1464.38	413.18	13.60
<b>BA_CB</b>	31	39.59	459.96	161.65	19.16
<b>SAP_BH</b>	298	14.51	415.42	117.84	4.26
<b>SAP_CB</b>	31	23.13	215.82	86.64	9.20

	<b>Unthinned Dense</b>				
	<b>N of cases</b>	<b>Minimum</b>	<b>Maximum</b>	<b>Mean</b>	<b>Std. Error</b>
<b>TL_HT</b>	95	12.86	20.33	17.05	0.18
<b>HT_LLB</b>	95	9.02	15.21	12.66	0.12
<b>HT_LWH</b>	95	10.17	15.21	13.13	0.11
<b>DOB_BH</b>	95	7.11	23.62	14.74	0.37
<b>DOB_CB</b>	15	3.60	14.80	7.37	0.84
<b>CL</b>	95	0.73	7.35	4.38	0.15
<b>MLCR</b>	95	0.06	0.42	0.27	0.01
<b>REL_HT</b>	95	0.63	1.00	0.87	0.01
<b>BA_BH</b>	95	39.70	438.18	180.46	9.05
<b>BA_CB</b>	15	10.18	172.03	50.36	11.86
<b>SAP_BH</b>	95	11.29	157.40	58.61	3.53
<b>SAP_CB</b>	15	6.78	109.25	30.52	7.38

<sup>1</sup>Where TL\_HT is the total height, HT\_LLB is the height to lowest live branch, HT\_LWH is height to lowest live whorl, DOB\_BH and DOB\_CB are diameter outside bark at breast height and crown base respectively, CL is crown length, mLCR is a modified live crown ratio, REL\_HT is relative height, BA\_BH and BA\_CB are basal area at breast height and crown base respectively, and SAP\_BH and SAP\_CB are sapwood area at breast height and crown base, respectively.

Table 2.3: Per hectare density and LAI values by plot and treatment in 2001

Plot ID	Stems per ha	BA per ha (m <sup>2</sup> )	RD	QMD (cm)	Litterfall LAI (m <sup>2</sup> m <sup>-2</sup> )			LICOR LAI (m <sup>2</sup> m <sup>-2</sup> )	Allometric LAI (m <sup>2</sup> m <sup>-2</sup> )				
					1999	2000	2001		SA <sub>bh</sub>	SA <sub>bh</sub> + mLCR	Valentine	Val Sapwood	
Unthinned Plots													
Unthinned	B2	750	45.8	0.58	27.9	4.02	4.47	4.37	5.41	3.94	3.93	5.79	4.61
Unthinned	B7	1775	56.2	0.95	20.1	3.84	4.16	3.94	4.57	4.13	3.72	4.30	4.10
Unthin Dense	D1	2800	45.0	0.93	14.3	3.34	3.55	3.42	4.78	3.53	3.00	2.54	2.80
Unthin Dense	D2	3400	60.1	1.21	15.0	3.66	3.94	3.50	4.33	4.72	4.16	3.69	3.95
Unthin Dense	D3	2800	58.3	1.19	16.3	4.11	4.71	3.94	4.15	4.84	4.30	3.85	4.01
Thinned Plots													
Crop	C1	300	18.6	0.23	28.1	2.94	3.48		3.79	2.58	2.53	2.39	1.93
Crop	C7	375	20.7	0.27	26.5	2.27	2.44		2.07	2.27	2.31	2.86	2.31
B-line	A8	550	25.5	0.37	24.3	2.77	3.21		3.61	2.88	2.78	2.81	2.40
B-line	C2	425	30.1	0.35	30.0	2.55	2.68		3.35	3.08	3.16	4.39	3.39

## **Tree Processing for Model Development**

Methods for the destructive sampling of plot trees closely followed those methods implemented by Gilmore et al. (1996), Maguire et al. (1998), Barker (1998), and Kenefic and Seymour (1999). The timing of this project coincided closely with the 10-year thinning interval for the on going thinning project. Therefore, the next thinning operation was scheduled and sampling from 22 harvested trees occurred in August of 2001. When selecting which trees to process, attempts were made to cover the full range of crown sizes and diameters represented by the entire population. Trees were not felled in the unthinned controls in order to preserve their integrity for the original thinning project. Therefore, 12 trees were chosen from an unthinned stand nearby that represented similar age and site quality.

All harvested trees were measured for total height and height to the base of the live crown (both lowest live branch and lowest live whorl). All live branches in the crown were measured for basal diameter and crown position (relative height). Cookies (1/2 – 1” thick) were sectioned at the stump, breast height, crown base, 2-meter intervals between breast height and crown base, and every meter between crown base and the terminal. Sapwood boundaries were marked in the field as with increment cores. Upon sectioning of the stem, outside-bark diameters and bark thickness were measured at meter-intervals with d-tapes and bark gauges, respectively. All cookies and cores were air dried and sanded before radial increments and sapwood widths were measured using a high-resolution scanner and the WinDendro image analysis system.

Following the felling process, the crown area was divided into three segments: top half and two bottom quarters. A branch at a random distance within each segment was selected for subsequent determination of branch LA and specific leaf area (SLA). Each branch was cut-up and placed into paper bags to be dried. Needle retention was visually estimated by observing distal shoots of the sampled branches to assess the proportion of third-year needles remaining. Both the number of attached third-year fascicles with at least one live needle and total number of third-year fascicle scars were recorded. The proportion of 3<sup>rd</sup> year needles present was calculated by dividing the number of 3<sup>rd</sup> year needles observed by the total number of possible needles. The proportion was then added to 2.0 assuming that all 1<sup>st</sup> and 2<sup>nd</sup> year needles were present. To determine SLA, 100-200 needles were removed from the sampled branches in proportion to their occurrence by needle age class, placed into plastic bags by branch, and stored in a cooler in the field until they were placed in a freezer at the end of the day. All frozen needle samples were analyzed using Seedle<sup>®</sup> image analysis software and high-resolution scanning equipment; the one-sided projected leaf area (PLA) was obtained for each sample. After frozen samples were analyzed, they were placed in a drying oven where they were left at 65° C for approximately one week. Once samples were dried they were weighed to the nearest 0.01-gram. Needle weight measurements were then used to calculate SLA for the respective sampled branches by dividing the one-sided PLA of each needle sample by its oven-dried weight. Branch biomass values were multiplied by the derived SLA values to obtain individual branch LA. Linear regression was used to develop a relationship between needle biomass, basal branch diameter and relative crown position for all

remaining live branches. Individual branch LA was converted to total tree LA by summing individual branch values.

### **Leaf Area Estimation**

Leaf area (LA) was determined by 2 or 3 different years of litterfall data, four allometric equations, and canopy gap fraction (below-canopy light interception).

Because litterfall represents the most biological and direct method for canopy leaf area measurement (assuming needle retention is accurately measured or known), estimation models were compared by treatment, using litterfall estimates for 1999, 2000 and 2001 as the benchmark. Utilizing a series of bar graphs, allometric models were compared to one another and to treatment/year-specific litterfall LAI. Litterfall from 2001 was only valid for unthinned controls and could not be used for thinning treatment plots because collected trap samples contained some needles from harvested trees that fell prior to the September 2001 thinning.

Ongoing collections and measurements of litterfall have occurred since 1992 on six of the original 16 400-m<sup>2</sup> study plots (four thinned and two unthinned). Five 0.5 m x 0.5 m (.25 m<sup>2</sup>) litter traps were constructed and systematically distributed through out each chosen plot in an "X" shape: one in the center with the remaining four traps at the midpoint of the diagonal between the center and each of four corners (approximately seven m from center). Two more traps were placed in each of the three high-density control plots. Litter has been collected twice a year (late October after second-year needles fall, and late spring before budbreak) including the most recent collection in June 2002 for the past 10 years. Prior to the 2001 growing season, five traps were placed into

each of four additional control plots selected in order for unthinned plots to span across all density ranges.

Once leaf litter was collected, it was placed into paper sacks labeled by both trap number and plot number and taken to a drying room where samples were dried at 65°C for at least one week. Each trap sample was then sorted by plot into pine needles, woody material, reproductive material, deciduous foliage, and miscellaneous debris. The sorted materials were dried again for at least two days and finally weighed recording weight to the nearest 0.01 gram. Treatment-specific specific leaf areas (SLA) and measured needle retention rates were utilized to calculate canopy LA (Table 2.4). First, fallen needle weights from one year's sample, which consists of two collections, one in late October and one in late April) were converted to areas by multiplying by the appropriate SLA, then converted to a canopy value by multiplying by the treatment-specific retention rate for 2001 samples.

Table 2.4: Specific leaf area (SLA) and needle retention rates by treatment for 2001

	Crop	B-line	Unthinned
SLA (cm <sup>2</sup> /g)	65.22	65.51	69.59
Needle Retention (yr)	2.36	2.45	2.30

Canopy gap fraction was measured in August of the 2001-growing season during overcast conditions in order to get a diffuse light estimate on all litter trap plots using a LAI-2000™ plant canopy analyzer. A base station or open-sky sensor was set-up in a nearby 12-acre overstory-removal cutting and synchronized with a roving sensor.



Measurements were taken with the roving sensor at the mid-point of the southern boundary of each plot. Five readings, one over each plot litter trap, were recorded at 30-second intervals. A 25 % mask was used in order to cover the sensor's southern hemisphere and to block out the operator. Light data used for all analyses encompassed a sky view of 28° from vertical (inner 2 rings of the LICOR sensor).

Tree allometric equations were developed using weighted non-linear regression analysis with Systat statistical software version 10 (Systat 2002). Thirty destructively sampled trees from across all treatments were used to develop predictive equations. Eight trees came from the Barker (1998) study while the remaining 22 trees were sampled during the present study. Sub-sampled needle biomass and treatment-specific SLAs were utilized to calculate individual branch leaf areas for sub-sampled branches. Through linear regression, relationships developed between needle biomass, basal branch diameter and relative crown position facilitated the calculation of leaf areas for all branches. Branch values were finally converted to whole crown values by summing all branches. Weighted non-linear regression analyses between observed leaf area of the thirty destructively sampled trees and tree variables such as sapwood area at breast height ( $SA_{bh}$ ), and modified live crown ratio (mLCR) (crown length / (total height – 1.3m) provided equation coefficients and predictive equations to determine projected leaf area (PLA) for all trees on the study site. Four PLA models were tested and compared to estimates from litterfall (Table 2.5). Two models were sapwood-based while the remaining two models relied upon a surrogate measurement of the cross-sectional area at crown base ( $BA_{bh} * mLCR$ ) (Valentine et al. 1994). Equations were weighted to avoid violation of the assumption for variance homogeneity. Models (1) ( $SA_{bh}$ ) and (2)

( $SA_{bh} + mLCR$ ) were weighted by the inverse of the  $SA_{bh}^2$  and model (3) (Valentine) was weighted by the inverse of  $BA_{bh} * mLCR^2$ . Model (4) (Val Sapwood) was developed by using the PLA values from model (2) as actual leaf area observations. Equation coefficients were derived as with the first three models and individual PLA values calculated by using the same equation as model (3). Model (4) was not weighted because its coefficients were derived not from data but from predictions of the weighted sapwood model. Individual tree values were summed for each respective plot and then converted to a per unit ground area or leaf area index (LAI).

LAI from allometric models were also compared to each other and to litterfall estimates in order to depict trends in LAI response to density. LAI values for litterfall from both 2000 (all plots) and 2001 (unthinned controls) and models (2) and (3) were plotted against three density variables (trees per hectare, basal area at breast height, and relative density) at the stand-level in order to display trends in LAI as influenced by density. Trends were shown by using a scatterplot with distance weighted least squares (DWLS) smoothing lines, which fit a line through each set of points by least squares in order to determine the shape of the function. Tension was set at 0.9 to control the amount of local flex between data points. Tested patterns in LAI were compared to those expected from the hypothetical trends displayed in Figure 2.1. All comparative tests were tested at significance level  $\alpha = 0.05$ .

Table 2.5: Allometric leaf area prediction model equations

Model	Independent Variable(s)	Dependent Variable	Equations	Weight	R <sup>2</sup>
(1) (SA <sub>bh</sub> )	Sapwood Area @ Breast Height	LA predicted from branch summation	$0.073 * SA_{bh}^{1.283}$	$SA_{bh}^{-2}$	0.938
(2) (SA <sub>bh</sub> mLCR)	Sapwood Area @ Breast Height + Modified Live Crown Ratio	LA predicted from branch summation	$0.144 * SA_{bh}^{1.212} * mLCR^{0.384}$	$SA_{bh}^{-2}$	0.949
(3) (Valentine)	Basal Area * Modified Live Crown Ratio	LA predicted from branch summation	$0.138 * (BA * mLCR)^{1.123}$	$(BA_{bh} * mLCR)^{-2}$	0.928
(4) (Val Sapwood)	Basal Area * Modified Live Crown Ratio	LA predicted from model (2)	$0.305 * (BA * mLCR)^{0.947}$	Not Weighted	0.881

## Results

### Plot-level LAI

#### Litterfall

After a decade of litterfall data collection across treatments, litter trap values showed consistency, or relatively constant LAI within each thinning treatment, indicating litterfall is not only a stable estimation method, but also a valid source of comparison for allometric models and other forms of LA estimation (Figure 2.2). As expected, both the b-line and crop treatment LAI values were reduced following thinning in 1991. Thinning treatment LA was elastic and reached nearly 70 percent of control values five years post-thinning. The 1998 ice storm, however, lowered leaf area across all treatments and slowed recovery of LAI values for both thinning treatments. Thinning in 2001 is shown by the reduction of LAI values within the thinning treatments. However, the 2001 values overestimate the post-thinning LAI because the June to October collection contained some needles from trees later removed in the 2001 thinning. The average projected LAI value for thinned plots in 1999 was  $2.63 \text{ m}^2 \text{ m}^{-2} (\pm 0.103)$  and  $2.95 \text{ m}^2 \text{ m}^{-2} (\pm 0.169)$  for 2000. For the unthinned treatment, the 2000 average projected LAI was  $4.19 \text{ m}^2 \text{ m}^{-2} (\pm 0.110)$ . The average projected LAI values for 1999 and 2001 were nearly equal at  $3.82 \text{ m}^2 \text{ m}^{-2} (\pm 0.082)$  and  $3.83 \text{ m}^2 \text{ m}^{-2} (\pm 0.099)$ .

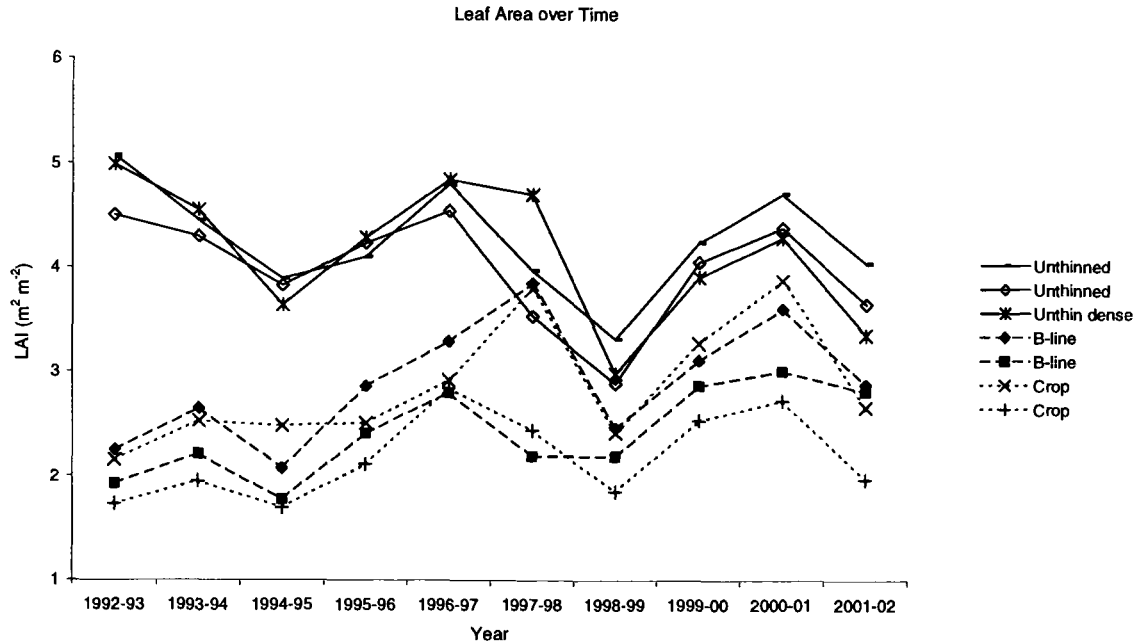


Figure 2.2: Annual plot average LAI from litter traps across thinning treatments for a 10-yr period. Thinning plots show positive LA response and after ten years are reaching control values. Unthinned plots are essentially stable with a slight reduction in LA as a result of self-thinning and crown abrasion.

Analysis of variance (ANOVA) between 2000 litterfall and allometric equations (1), (2), and (3) displayed no significant difference in plot-level average LAI ( $P = 0.737$ ) (Table 2.6). LA means ranged between  $3.26 \text{ m}^2 \text{ m}^{-2}$  and  $3.57 \text{ m}^2 \text{ m}^{-2}$  (Table 2.7). The interaction between estimation method and treatment was not significant ( $P = 0.810$ ) (Figure 2.3). The significant treatment effect ( $P = 0.000$ ) was not surprising since differences in average LAI are inherent in the removal of approximately 50% of the LA in thinned plots.

Table 2.6: Analysis of variance table for plot-level LAI estimation methods: 2000 Litterfall vs. allometric models (1), (2), and (3) in Table 2.5)

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
METHOD	0.56	3	0.19	0.43	0.737
TRT	12.76	1	12.76	28.89	0.000*
METHOD*TRT	0.43	3	0.14	0.32	0.810
Error	12.36	28	0.44		

\* Indicates significant P values at significance test  $\alpha=0.05$

Table 2.7: Least squares means and standard errors for LAI methods

LAI Method	LS Mean	SE
Litter	3.56	0.22
SA <sub>bh</sub>	3.47	0.22
SA <sub>bh</sub> + mLCR	3.26	0.22
Valentine	3.57	0.22

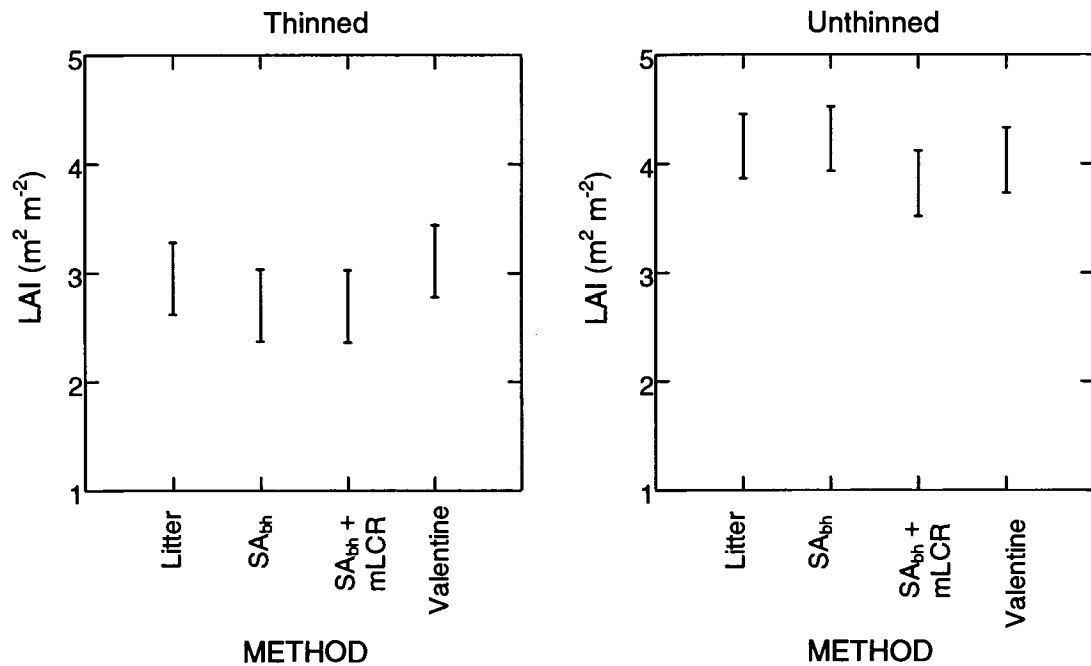


Figure 2.3: Interaction plots between estimation method and thinning treatment.

Interaction was not significant, although the patterns appear somewhat different.

### Allometric Models

Although no method effect was demonstrated with ANOVA testing, regression analyses of individual models against litterfall revealed differences that were apparently masked by the ANOVA (Table 2.8). Perfect agreement between estimation methods would result in a linear regression with a slope of 1.0 and a  $R^2$  of 1.0. Estimates from models (1) and (2) were closely related ( $R^2 = 0.71$  and  $0.70$  respectively) to estimates from 2000 litterfall. These results agree with those from Marshall and Waring (1986) who also found no statistical difference between estimates from sapwood allometrics and litterfall. However, estimates from model (3) and litterfall were poorly related ( $R^2 =$

0.23) with the slope not significantly different from 0 ( $P = 0.196$ ). The confidence intervals of  $\Xi_1$  for both sapwood models included 1.0 while the upper-end of the confidence interval for the Valentine model fell beneath 1.0 and included negative values (Figure 2.4). Because estimates from neither sapwood model were significantly different, data from both sapwood models were then pooled, which resulted in a relatively good fit with litterfall estimates ( $R^2 = 0.68$ ) (Table 2.9, Figure 2.5). Assuming litterfall as a standard, allometric models that incorporate sapwood at breast height appeared to be good predictors of stand LAI across the range of stand densities and structures sampled. On the other hand, the Valentine model appeared to be a poor predictor.

Table 2.8: Regression analysis table for allometric models against 2000 litterfall. Sapwood models had significant slopes.

Model	Coefficient	Std Error	t	P (2 Tail)
SA <sub>bh</sub>	0.71	0.17	4.14	0.004*
SA <sub>bh</sub> +mLCR	0.88	0.22	4.02	0.005*
Valentine	0.33	0.23	1.43	0.196

\* Indicates significant P values at significance test  $\alpha=0.05$



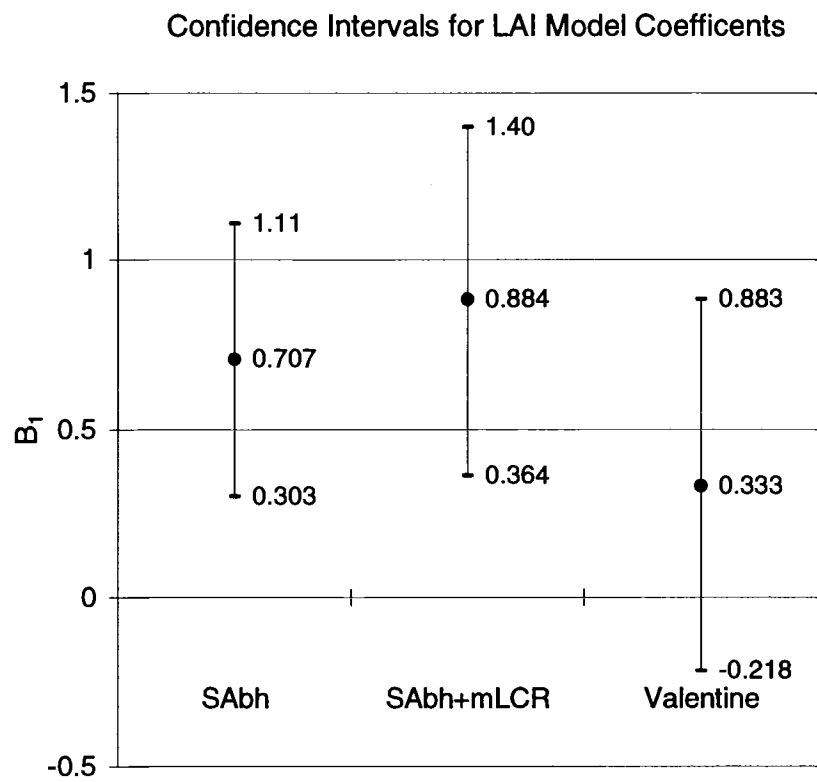


Figure 2.4: Confidence intervals of

Table 2.9: Regression analysis table for pooled sapwood data and Valentine model against 2000 litterfall. Sapwood model had a significant slope.

Model	Coefficient	Std Error	t	P (2 Tail)
Pooled Sapwood	0.76	0.13	5.84	0.000*
Valentine	0.33	0.23	1.43	0.196

\*Indicates significant P values at significance test  $\alpha=0.05$

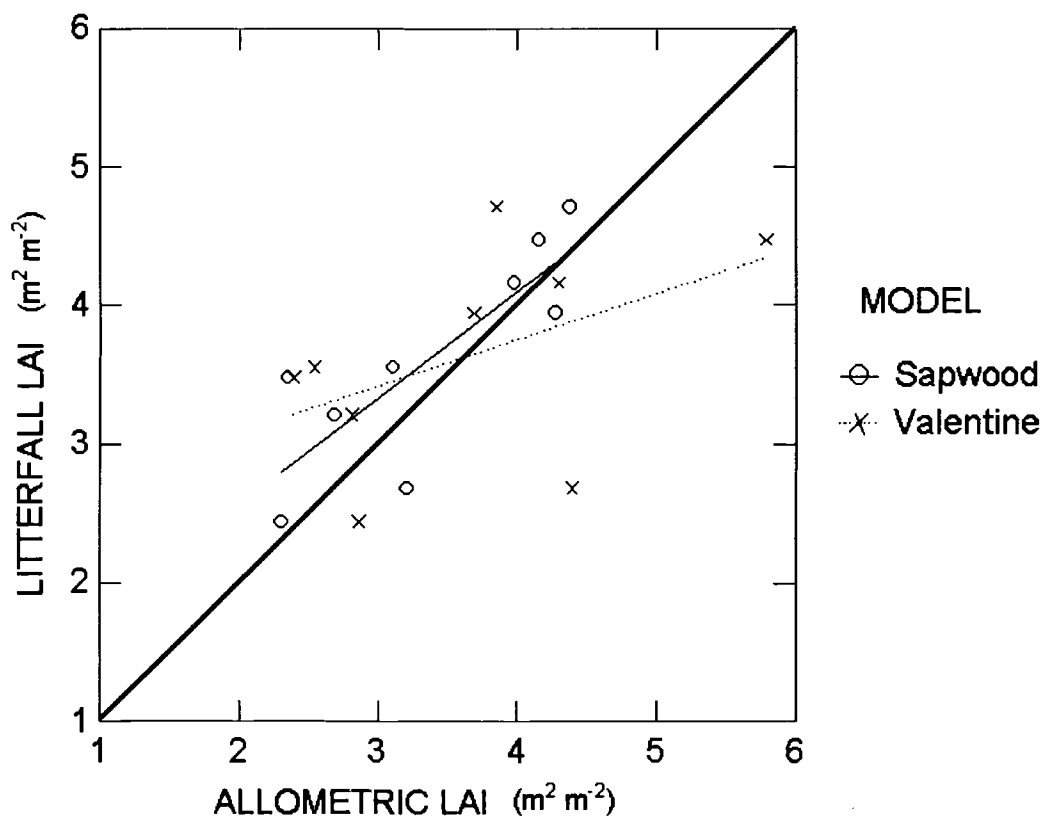


Figure 2.5: Regression line for pooled sapwood model and Valentine model against litterfall. Dark solid line is 1:1 line.

## **Tree-level PLA**

Unlike the plot-level ANOVA results, average tree-level (N = 697) one-sided PLA differed significantly among models (P = 0.000) (Table 2.10). The Valentine model estimates were the largest across all treatments with approximately 15% greater estimates than sapwood models (Figure 2.6). The least squares means for individual PLA across treatments ranged between 43.5 m<sup>2</sup> and 52.0 m<sup>2</sup> (Table 2.11). Gilmore et al. (1996) presented data for *Abies balsamea* (L.) that also showed mLCR-based models to be inferior to sapwood-based models. Barker (1998), however, found the modified live crown ratio model to perform nearly as well as sapwood-based tree-level models for *Pinus strobus* L., although a smaller sample size (N = 16) may have limited the range of crown sizes over which the equations were developed in. A significant interaction term (P > 0.023) suggests that model (3) has more bias in thinned plots than unthinned (Figure 2.7).

Table 2.10: Analysis of variance table for PLA models at tree-level: SA<sub>bh</sub> (1), SA<sub>bh</sub>+mLCR (2), and Valentine (3) allometric models

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
MODEL	30232.87	2	15116.44	14.95	0.000*
TRT	481810.01	1	481810.01	476.64	0.000*
MODEL*TRT	7649.00	2	3824.50	3.78	0.023*
Error	2043952.82	2022	1010.86		

\* Indicates significant P values at significance test  $\alpha=0.05$

Table 2.11: Least squares means and standard errors for PLA models

PLA Model	LS Mean	SE
SA <sub>bh</sub>	43.9	1.24
SA <sub>bh</sub> + mLCR	43.5	1.24
Valentine	52.0	1.24

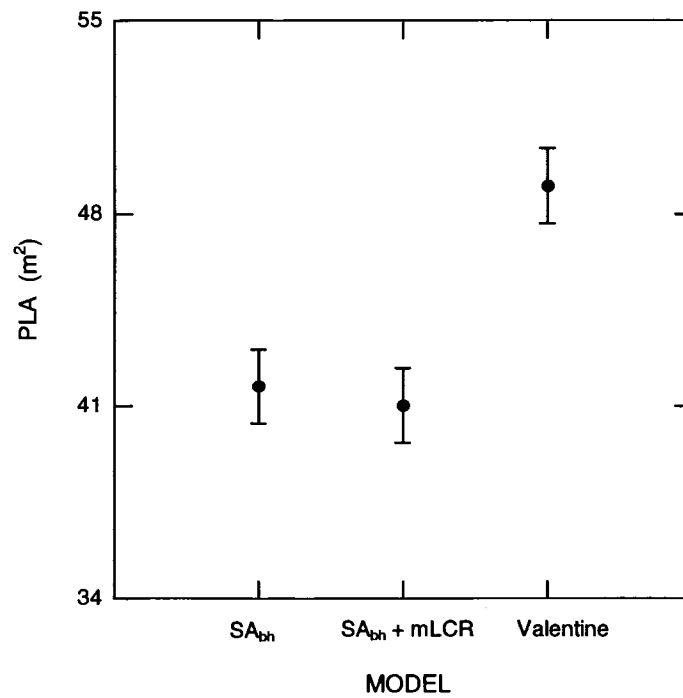


Figure 2.6: Least squares means for tree-level PLA models. Average PLA estimates from Valentine model (3) were significantly larger than sapwood models (1) and (2).

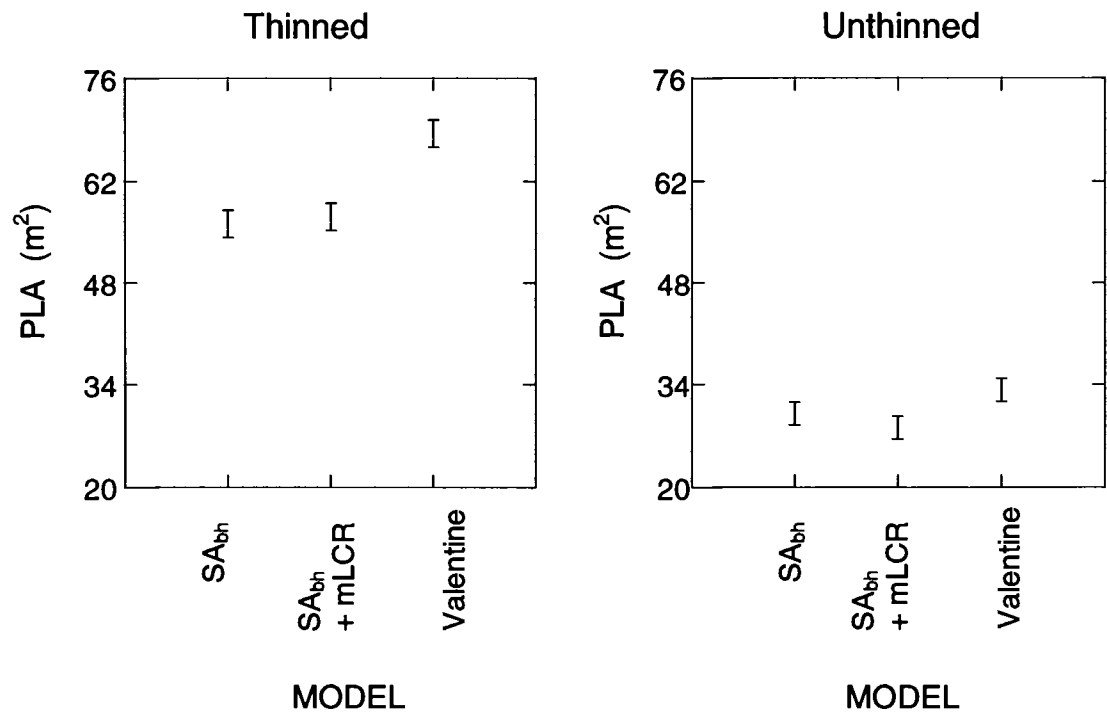


Figure 2.7: Interaction plots between allometric models and thinning treatment.

Interaction was significant; the Valentine model appears to overestimate LA more in thinned plots than in unthinned.

All bias between models was eliminated when estimates from model (2) were used to refit the Valentine model (Val Sapwood). ANOVA analysis between models (1), (2), and (4) showed no statistical difference ( $P < 0.873$ ) in least squares means of the three models (Table 2.12). Both Table 2.13 and Figure 2.8 illustrate agreement of mean PLA across models.

Table 2.12: Analysis of variance table for PLA models at tree-level:  $SA_{bh}$  (1),  $SA_{bh}+mLCR$  (2), and Val Sapwood (4) allometric models

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
MODEL	213.23	2	106.62	0.14	0.873
TRT	397886.82	1	397886.82	508.92	0.000*
MODEL*TRT	789.22	2	394.61	0.51	0.604
Error	1580867.09	2022	781.83		

\* Indicates significant P values at significance test  $\alpha=.05$

Table 2.13: Least squares means and standard errors for PLA models

PLA Model	LS Mean	SE
$SA_{bh}$	43.9	1.09
$SA_{bh} + mLCR$	43.5	1.09
Val Sapwood	43.1	1.09

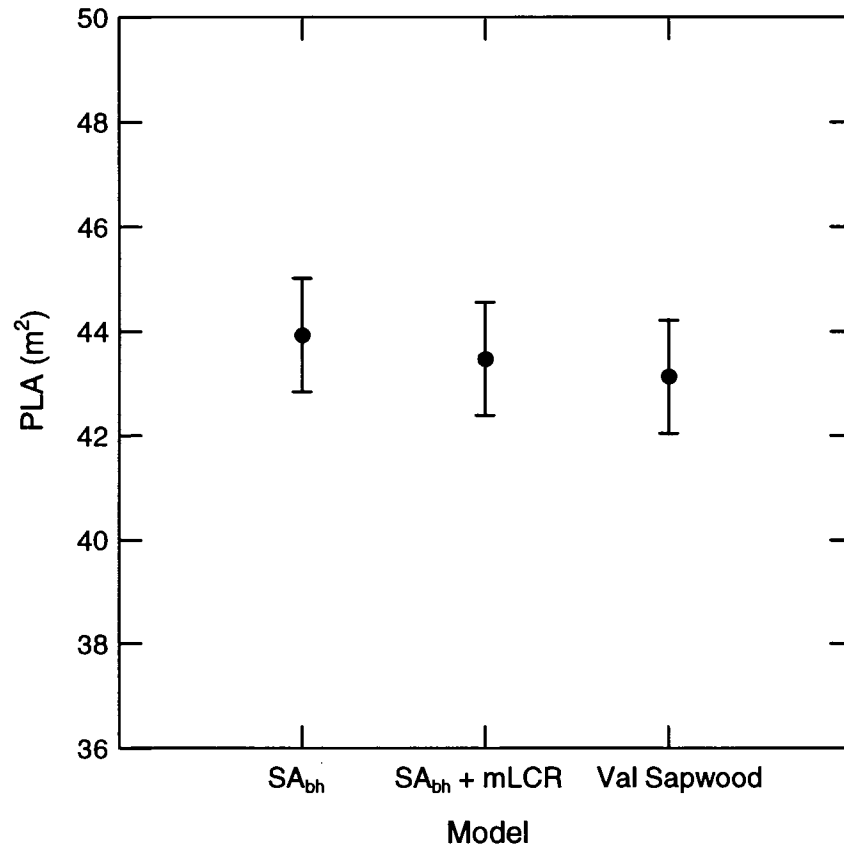


Figure 2.8: Least squares means for tree-level PLA models (1), (2), and (4).

There were no statistical differences between average model estimates.

## **Light Interception**

There was a relatively strong relationship ( $r^2 = 0.68$ ) between data from light interception and 2000 litterfall (Table 2.14); however, the confidence interval for  $\Xi_1$  ( $0.562 \pm 0.13$ ) did not include 1.0, suggesting bias. LICOR-2000 measurements appeared to underestimate LAI in the lower-half of the data range and overestimate in the upper-half (Figure 2.9). Chason et al. (1991) reported underestimates of LAI from the LAI-2000 of nearly 45 % from natural mixed-age oak-hickory stands in Tennessee. Similarly, comparisons for old-growth Douglas-fir (*Pseudotsuga mensiezii* [Mirb.] Franco) in Oregon also showed underestimations from PAR (Marshall and Waring 1986), confirming a general underestimation from light interception.

Table 2.14: Regression analysis table for light interception and litterfall methods. LAI estimation from treatment pooled below-canopy light interception data had a relatively strong relationship with litterfall ( $R^2 = .68$ ) with a significant slope ( $P = 0.000$ ).

Effect	Coefficient	Std Error	t	P (2 Tail)	R <sup>2</sup>
CONSTANT	1.279	0.268	4.776	0.000	
LICOR	0.562	0.066	8.583	0.000*	0.68

\*Indicates significant P values at significance test  $\alpha = .05$



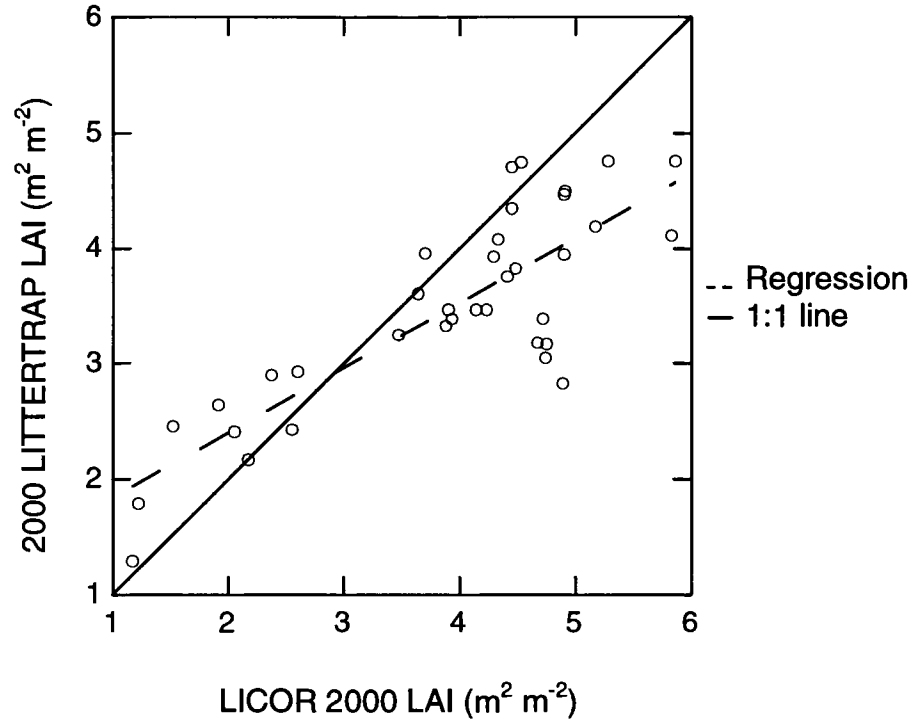


Figure 2.9: Regression line for pooled LICOR-2000 estimates and LAI estimates from 2000 litterfall data.

While previously published comparisons of light interception and litterfall did not test over a wide range of densities, treatment-specific regression analysis helped to distinguish different trends for thinned and unthinned treatments in the present study. Data within thinned plots had significant slopes ( $P = 0.000$ ) while unthinned data were not statistically different from 0 ( $P = 0.083$ ) indicating a poor fit with litterfall data (Table 2.15). The LICOR-2000 plant canopy analyzer generally underestimated LAI within the thinned plots and overestimated within unthinned plots (Figure 2.10). In general, LAI estimation from below-canopy light interception did not provide consistent results comparable to litterfall estimation when taken across a range of stand structures.

Table 2.15: Regression analysis table for light interception and litterfall methods. LAI estimation from treatment-specific below-canopy light interception data showed a relatively good fit to individual litter trap estimates ( $R^2 = .61$ ) for thinned sites with a significant slope ( $P = 0.000$ ).

\* Indicates significant P values at significance test  $\alpha = .05$

Effect	Coefficient	Std Error	t	P (2 Tail)	$R^2$
Thinned: CONSTANT	1.45	0.30	4.81	0.000	
LICOR	0.47	0.09	5.32	0.000*	0.61
Unthinned: CONSTANT	2.38	0.93	2.56	0.023	
LICOR	0.36	0.20	1.87	0.083	0.20

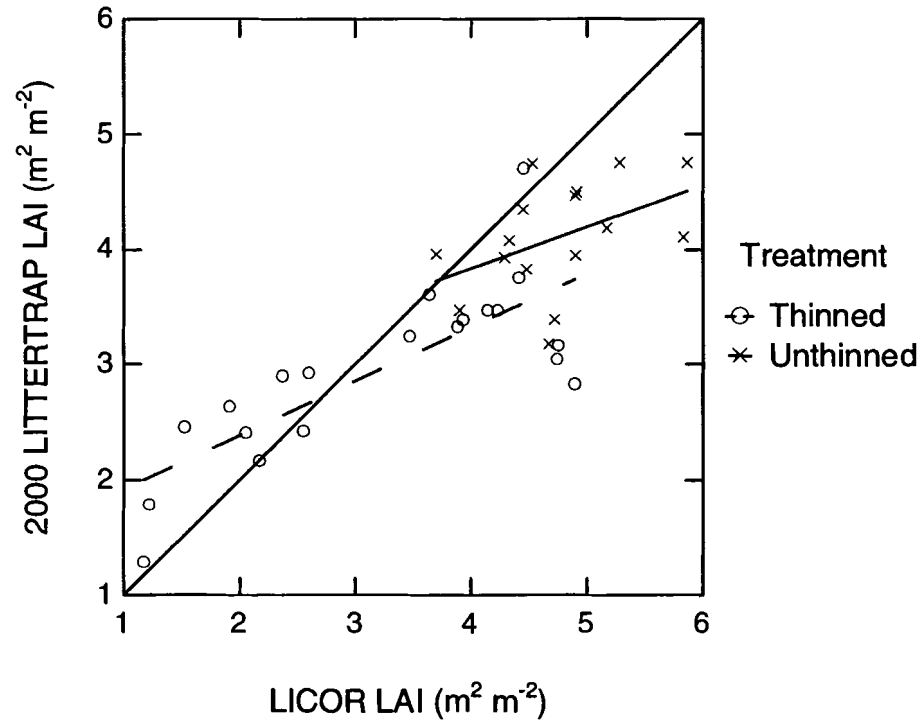


Figure 2.10: Regression lines for treatment-specific analyses of LICOR-2000 data and individual litter trap values from year 2000. Thinned data had a relatively good fit to 1:1 line, although underestimations and overestimations occurred at the lower and upper end of data range respectively. Data for unthinned sites generally overestimated.

## **Comparison to Alternate Litterfall Years**

When the average plot-level LAI estimations from all four models within the thinned treatment were referenced to the average LAI from litterfall for multiple years, bias in the Valentine model was apparent (Figure 2.11). Both sapwood models and the Valentine model adjusted with sapwood-based coefficients showed close agreement with one another as well as with the litterfall estimate from 1999. The Valentine estimate was similar to the average 2000 litterfall line, yet this reference line appears to be an unusually high yearly average. This claim was supported by the fact that the yearly average for both the 1999 and 2001 litterfall estimates were nearly identical within the unthinned treatment, while the interval year value from 2000 was approximately 10% higher. Unfortunately, this comparison could not be made directly for the thinned treatment since litter trap collections for 2001 were not taken prior to thinning in the fall and were therefore invalid for direct reference. Graphical analysis between all four models and litterfall within the unthinned treatment showed consistent agreement across all models indicating that lower estimates from the Valentine model may be structurally influenced (Figure 2.12).

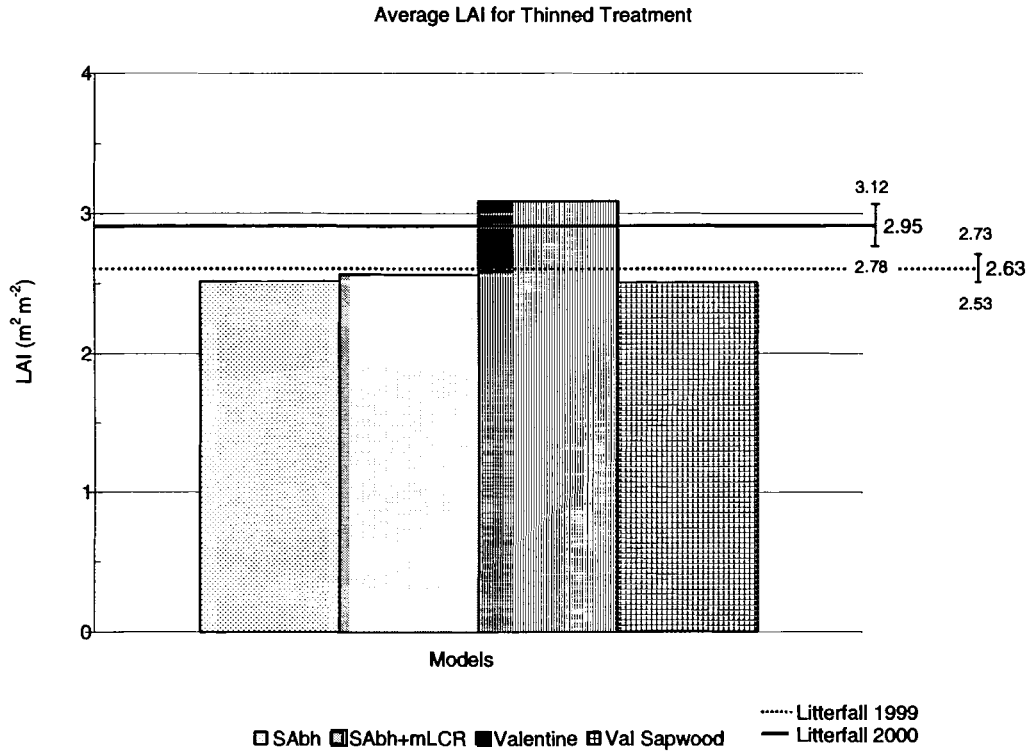


Figure 2.11: Average stand-level LAI for thinned treatment plots from four tree-level models. Model values are referenced to the average litterfall LAI for two consecutive years and their respective standard errors. Sapwood models and Val Sapwood model have general agreement with 1999 litterfall reference.

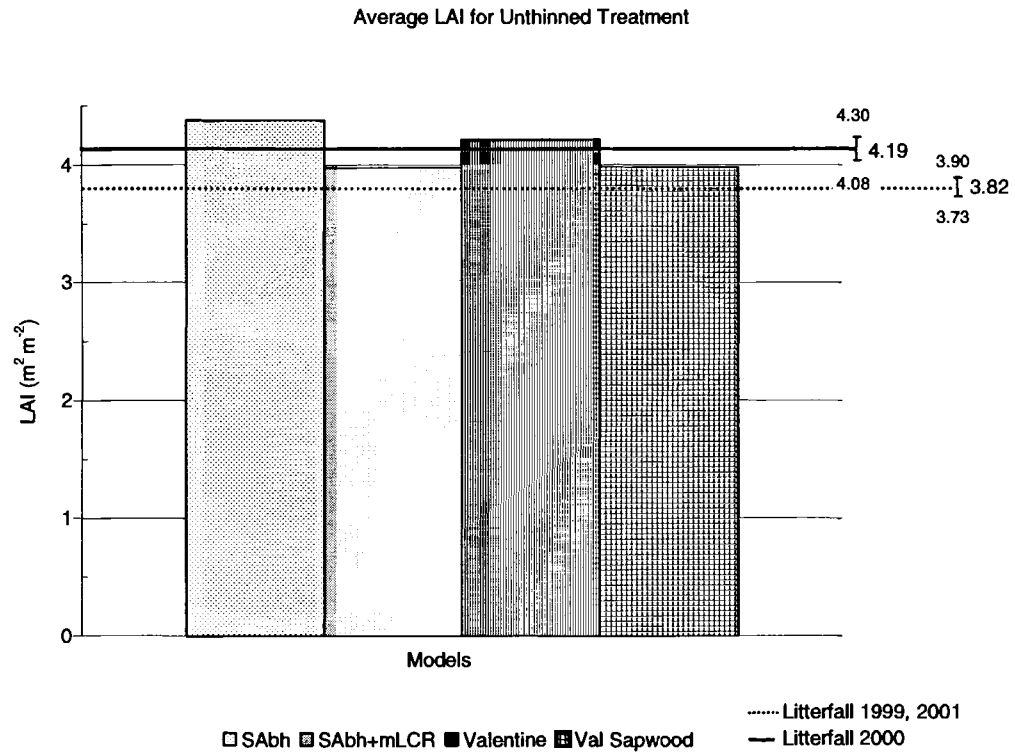


Figure 2.12: Average stand-level LAI for unthinned treatment plots from four tree-level models. Model values are referenced to the average litterfall LAI for three consecutive years and their respective standard errors. There was general agreement between all models and litterfall. Note that 1999 and 2001 litterfall was essentially identical.

## **Relationship Between LAI and Density**

The relationship between the Valentine model and the sapwood models was variable across treatment, shown by the significant interaction term in Table 2.10 and the variability between bar charts in Figures 2.11 and 2.12, suggests an interaction effect between stand density and methods used to estimate LAI. LAI estimates from 2000 (all plots) and 2001 (unthinned controls) litterfall and model (2) in both thinned and unthinned treatments leveled off at densities around 1500 tph and then remained relatively constant, following Trend B (Figure 2.1) and indicating little if any effect at all from density (Figure 2.13). Litterfall and model (2) LAI estimates again showed similar trends when plotted against basal area, although both increased linearly with BA conforming to Trend A (Figure 2.14). Trends related to relative density were more similar to those from absolute density (tph), rising initially at lower density before relatively leveling off around 0.7, thus following the expected pattern from Trend B and supporting the idea that LA estimates from litterfall and sapwood-based models are independent of stand density (Figure 2.15).

When estimates from Model (2) and Model (3) were compared across density for both thinned and unthinned treatments patterns were quite different. The density effect on model (3) behavior was clearly shown by declining LAI with density, at densities > 800 tph (Figure 2.16). Although model (3) behaved similar to model (2) at lower densities, overall it was strongly influenced by density and most closely resembled pattern C.

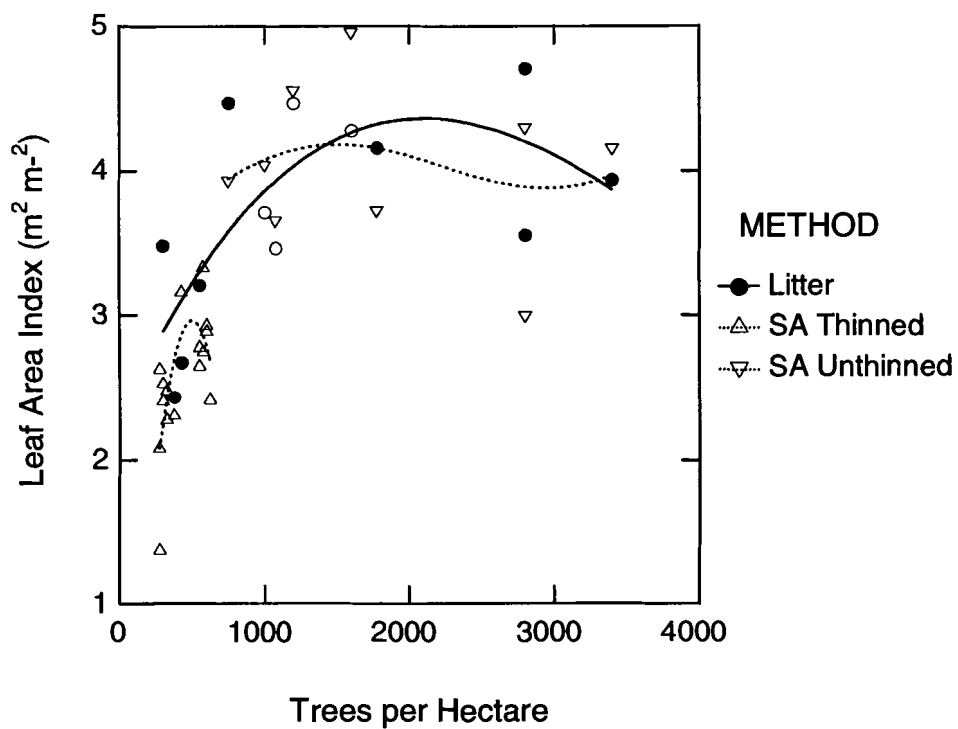


Figure 2.13: Comparison of trends in plot-level LAI across density (trees per hectare) for litterfall and Model (2). Litter fall data includes 2000 estimates for all plots ● and 2001 estimates for all unthinned controls ○. Both litter and Model (2) estimates appear to reach an optimum level and then remain fairly constant across density. Curves fitted by DWLS smoothing algorithm.



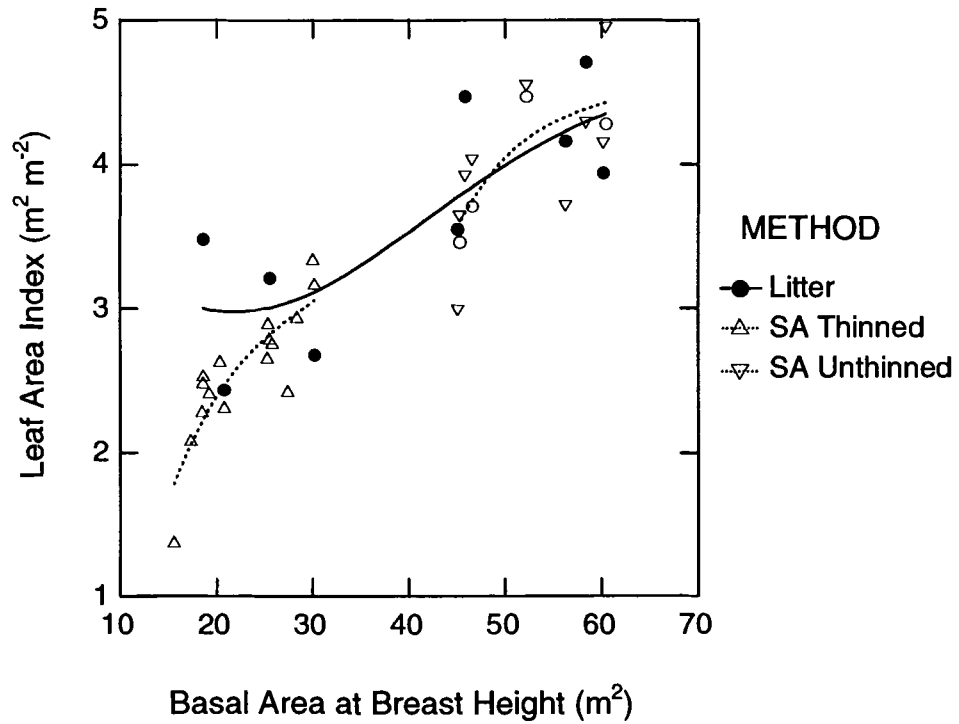


Figure 2.14: Comparison of trends in plot-level LAI across density (basal area at breast height per hectare) for litterfall and Model (2). Litter fall data includes 2000 estimates for all plots ● and 2001 estimates for all unthinned controls ○. Both litter and Model (2) estimates appear to increase linearly across density. Curves fitted by DWLS smoothing algorithm.

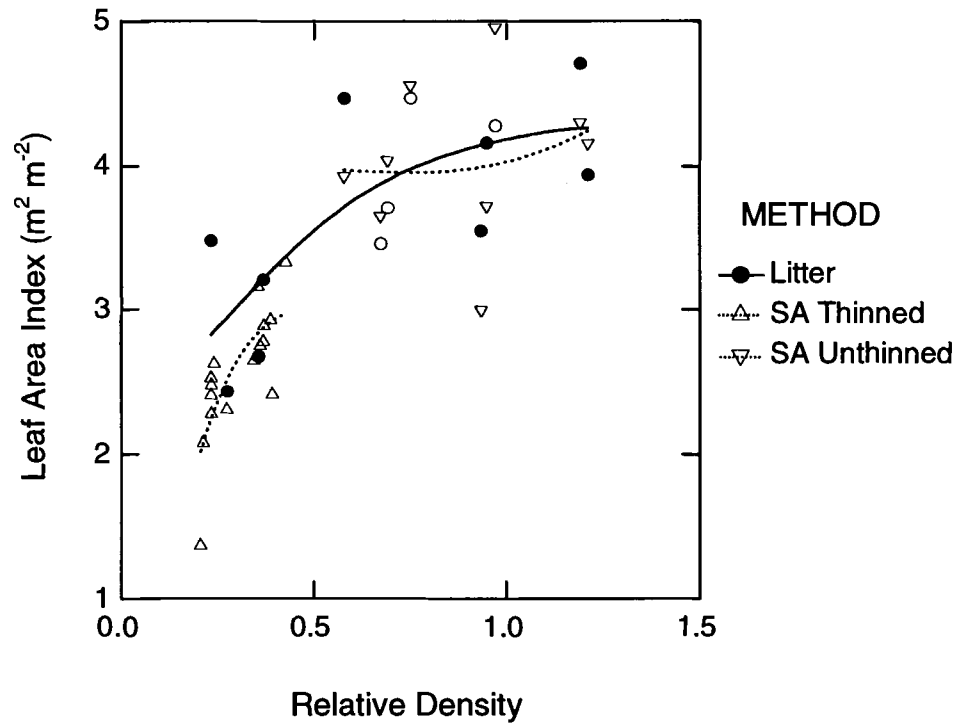


Figure 2.15: Comparison of trends in plot-level LAI across density (relative density) for litterfall and Model (2). Litter fall data includes 2000 estimates for all plots ● and 2001 estimates for all unthinned controls○. Both litter and Model (2) estimates show a tendency to level off as density increases. Curves fitted by DWLS smoothing algorithm.

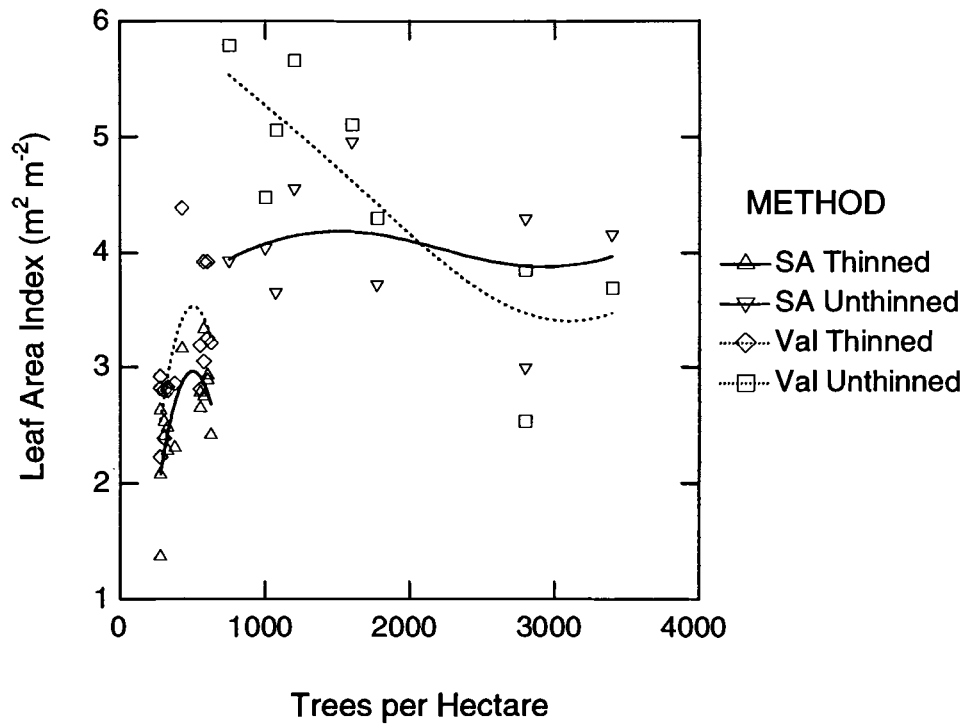


Figure 2.16: Leaf area index from Model (2) and Model (3) plotted against trees per hectare by treatment. Model (2) estimates show a constant LAI while Model (3) estimates decline with density. Curves fitted by DWLS smoothing algorithm.

## Discussion

### Light Interception

Estimation of LAI by below-canopy light interception using the Plant Canopy Analyzer LAI-2000 did not provide consistent measurement across the range of densities in this study. Two major assumptions of this method were that the foliage within the canopy is horizontally displayed in a random pattern and is considered to be optically black, having maximum absorption and therefore minimizing significant scatter of light transmission (Nilson 1971; Lang et al. 1985; Perry et al. 1988; Campbell and Norman 1989; Nuemann et al. 1989). In fact, underestimations relative to litterfall were reported to be due to clumping of foliage in *Quercus* and *Carya* spp in Tennessee (Chason et al. 1991).

While no evidence exists to support the claim that non-random distribution of canopy foliage is a significant factor here, another possible explanation for the observed relationship between litterfall and LICOR estimates is a changing proportion of both live and dead branches to leaf area with increasing density. In other words, does the ratio of total branch mass to leaf area increase or decrease with density? It is reasonable to believe that at lower densities there might be more live branch mass per LA because of more growing space and the better opportunity for branches to expand laterally than at higher densities where lateral growth is limited by neighboring competitors (Horn 1971; cf. Figure 3.13 Oliver and Larson 1996). On the other hand fewer dead branches would be present at lower densities due to a lack of shading from above, as well as, from the sides. The relationship between the presence of dead branches and density is related to species-specific branch retention ability, which in the case of pine is relatively high.

If these assumptions are valid, it seems likely then that overestimations in the unthinned treatment have resulted from a larger proportion of intercepted light coming from non-photosynthetic material. The explanation for the underestimation of LAI from below-canopy light interception in the thinned treatment is less clear, but may result from high levels of light reaching the canopy floor from the sides or from the overlapping of branches in the upper crown, which have responded to the available growing space, with those in the lower portion of the canopy, thus limiting the instrument's ability to recognize total LA.

### **LAI and Density**

The results from the preceding section discussing the relationship between LAI and density showed average plot-level LAI from litterfall and the sapwood model to level off after an initial increase and become fairly stable across stand density, resembling hypothetical Trend B (Figure 2.13). Stable leaf area for *Pinus contorta* var. *latifolia* Engelm. in Utah and Wyoming (Long and Smith 1990; Jack and Long 1991) was explained by the plasticity of mean tree-level PLA across densities. One explanation given for this trend in *P. contorta* was the species ability to alter crown architecture (i.e. rapid crown expansion at low density) in order to compensate for changes in density (Jack and Long 1991). Relative shade tolerances were considered as controlling factors arguing that shade intolerant pioneer species such as *P. contorta* are more highly sensitive to competition than highly tolerant, late successional species like *Abies lasiocarpa*, which exhibited a linear increase in LAI with stand density and resembled patterns for Trend A. Linear increases with density was also reported for *Abies balsamea* another late successional, highly shade tolerant species (Baskerville 1965). While *P.*

*strobis* may be classified as mid-tolerant, it behaves more like intolerant species in that it commonly pioneers sites and its crown is highly sensitive to density changes. Therefore, it is not surprising that its LAI patterns agree with those for *P. contorta*.

The trends observed in Figure 2.14 reflect a strong relationship between basal area and LA. Basal area is known to be highly correlated with sapwood area, which is highly correlated to LA and is the underlying force of the observed linearly increasing relationship between LAI and basal area. However, BA may not accurately depict the true relationship between LAI and density, when considering the high correlation of basal area to diameter and that diameter, which is known to be a poor predictor of LA. The LAI trend with relative density, agrees with that of absolute density, providing further evidence that stable leaf area across density is a valid trend when LAI is estimated from either litterfall or sapwood-based prediction models for eastern white pine (Figure 2.15).

Studies have reported that tree-to-tree variation in the leaf area-sapwood area ratio contributes to overall model bias across stand densities for sapwood-based equations (Dean and Long 1986). Model corrections involving the inclusion of the distance from breast height to the mid-point of the live crown eliminated bias related to both density and site quality in non-linear predictive equations for lodgepole pine and subalpine fir (Dean and Long 1986; Long and Smith 1988, 1989). Variations in the leaf area-sapwood area ratio were reported to be related to the permeability of sapwood to water flow (Whitehead et al. 1984; Coyea and Margolis 1992) and furthermore, this relationship has been described to be influenced by stages of stand development (Pothier et al. 1989).

However, the derived sapwood models for this study performed well across the range of densities sampled. On the other hand, the nonsapwood-based, unadjusted

Valentine model clearly expressed differential behavior across the stand densities tested (Figure 2.16). Also seen graphically by its relation to both litterfall and sapwood estimates in thinned versus unthinned treatments (Figures 2.11 and 2.12). The bias is within the thinned treatment, while there is general agreement between the Valentine model and both litterfall and sapwood estimates over the entire range of densities sampled for the unthinned treatment. However, when distinguishing between unthinned and unthinned dense treatments, Valentine estimates performed poorly at lower density unthinned controls, but improved at extremely high density (~2800 tph) (Figure 2.15). There are no studies, however, where this alternative method of leaf area estimation was tested across a range of quantified densities either alone or in conjunction with other allometric models and therefore, direct comparisons for support or explanation are unavailable.

### **Sampling and Model Bias**

In order to determine causes of bias in, or explain the behavior of the Valentine model, several key variables were tested using a two-sample t-test between the 30 trees from which the equations were derived (Processed trees) and the entire population (Applied trees) (Table 2.16). Among the important variables that were significant was basal area at breast height and the Valentine estimator ( $BA * mLCR$ ). These differences were important to model behavior and identifying them helped to underline sampling inconsistencies. However,  $SA_{bh}$  was not significantly different between applied and processed trees, which allowed for estimations from sapwood models to remain stable across density.

Table 2.16: Comparison of key variables between the processed (equation trees) and the applied trees.

Variable	Sample Type	N	Min	Max	Mean	Standard Error
*DBH (cm)	Processed	32	4	31.1	18.9	1.1
	Applied	654	6.6	43.1	22.4	0.2
*BA <sub>bh</sub> (cm <sup>2</sup> )	Processed	32	12.5	759.6	316.6	35.7
	Applied	654	34.2	1464.3	429.2	9.4
*BA <sub>cb</sub> (cm <sup>2</sup> )	Processed	32	1.7	444.8	138.7	21.5
	Applied	73	10.1	539.1	211.6	16.1
*SA <sub>cb</sub> (cm <sup>2</sup> )	Processed	32	0.9	202.6	75	10.5
	Applied	73	6.7	284.4	104.7	7.2
*BA <sub>m</sub> LCR	Processed	32	2.8	422.2	137.3	20.6
	Applied	654	7.5	951.7	182.2	5.4
*Pct SA <sub>cb</sub>	Processed	32	0.42	0.80	0.57	0.02
	Applied	73	0.25	0.72	0.53	0.01
*Stem Taper (cm <sup>2</sup> /m)	Processed	32	1.7	38.6	18.7	1.7
	Applied	73	5.3	75.4	27.5	1.7
SA <sub>bh</sub> (cm <sup>2</sup> )	Processed	32	1.6	271.5	116.8	13.8
	Applied	654	11.3	437.6	134.1	3.2
mLCR (%)	Processed	32	0.20	0.58	0.38	0.02
	Applied	654	0.06	0.72	0.38	0.01
TI Ht (m)	Processed	32	9.2	20.4	17.1	0.5
	Applied	654	8.5	21.8	17.5	0.1
HLLB (m)	Processed	32	6.2	14.4	11.0	0.4
	Applied	654	3.0	15.7	10.6	0.1
SA Taper (cm <sup>2</sup> /m)	Processed	32	0.1	8.5	4.5	0.4
	Applied	73	-0.7	22.0	5.1	0.5

\* Denotes significant difference between processed and applied trees at P = .05



Values of  $BA_{bh}$  were significantly larger ( $P = .002$ ) for the applied trees throughout the entire study site (Figure 2.17). While mLCR was not statistically different between the processed and applied trees, both  $BA_{bh}$  and mLCR values were higher for applied trees within thinned treatments (Figures 2.18 and 2.19). Logically higher estimates of the two key variables of a model would result in higher estimates of leaf area. This agrees with the observed overestimations within the thinned treatment. Another way to explain the bias is that the applied trees also contained significantly more  $BA_{bh}$  at any given unit of the Valentine estimator in both unthinned and thinned treatments (Figures 2.20 and 2.21).

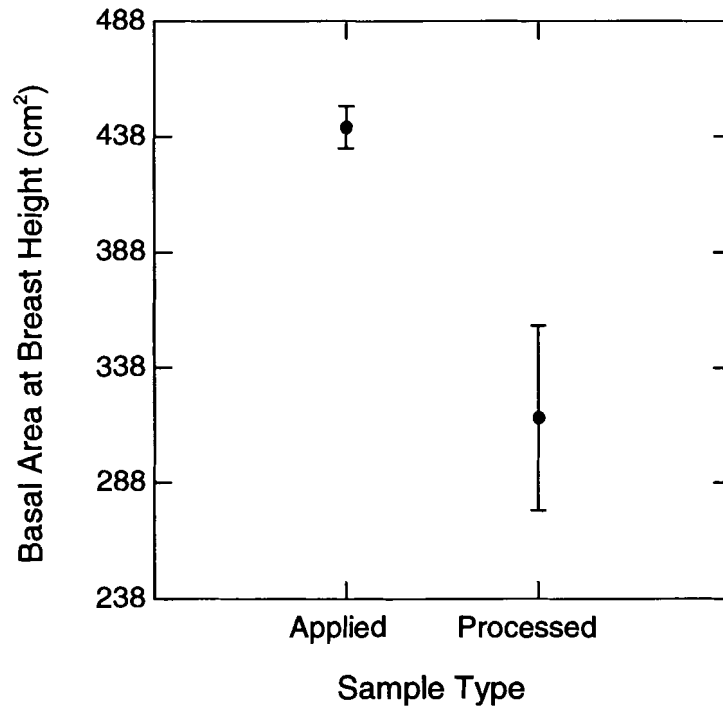


Figure 2.17: Comparison of BA<sub>bh</sub> between the processed and applied trees. The applied trees had significantly higher basal area.

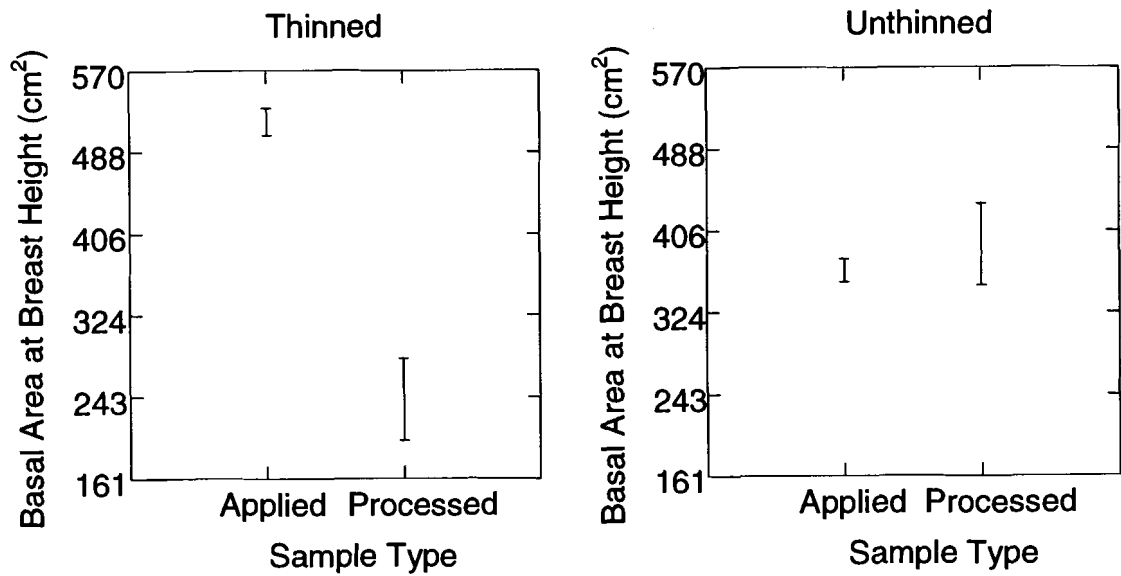


Figure 2.18: The interaction between BA and sample type across treatments.  
Larger trees existed within the thinned applied trees.

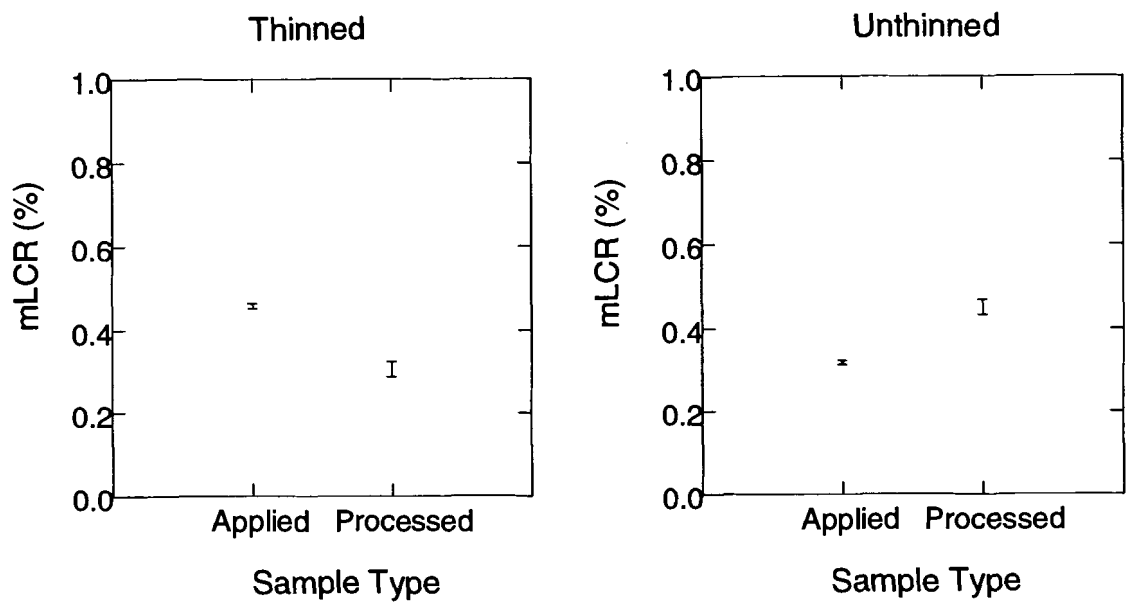


Figure 2.19: The interaction between mLCR and sample type across treatments.  
Trees with larger crowns existed within the thinned applied trees.

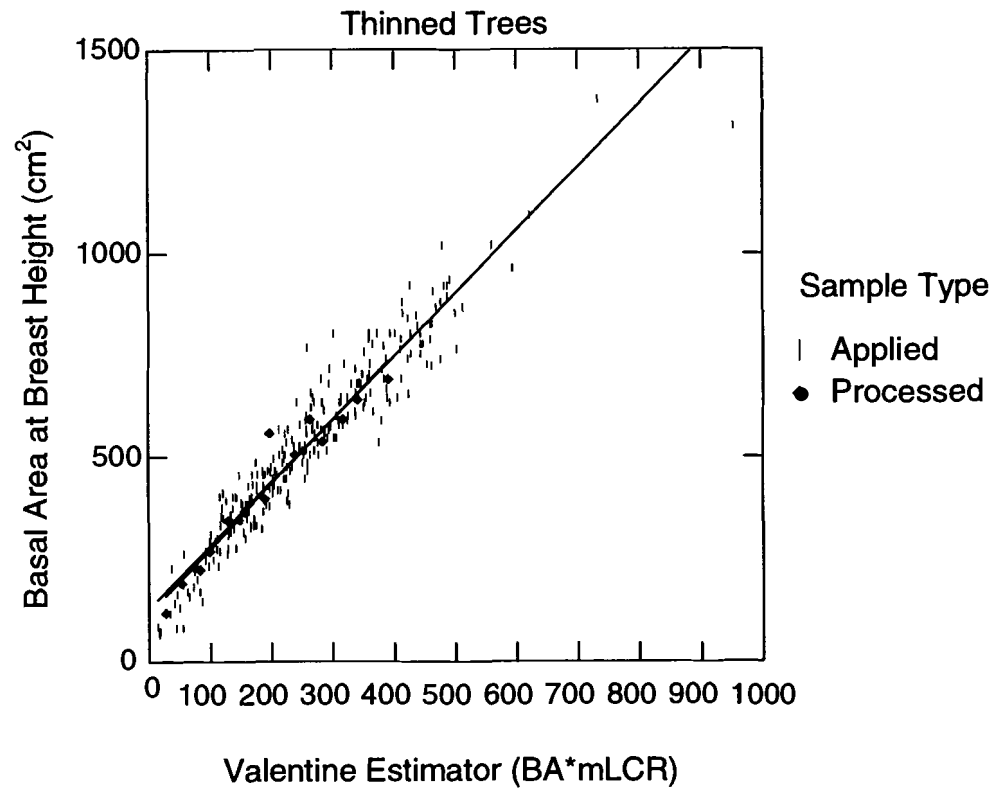


Figure 2.20: Basal area at breast height plotted against the Valentine estimator for processed and applied trees within the thinned treatment. Applied trees had larger basal areas at any given unit of the Valentine estimator.

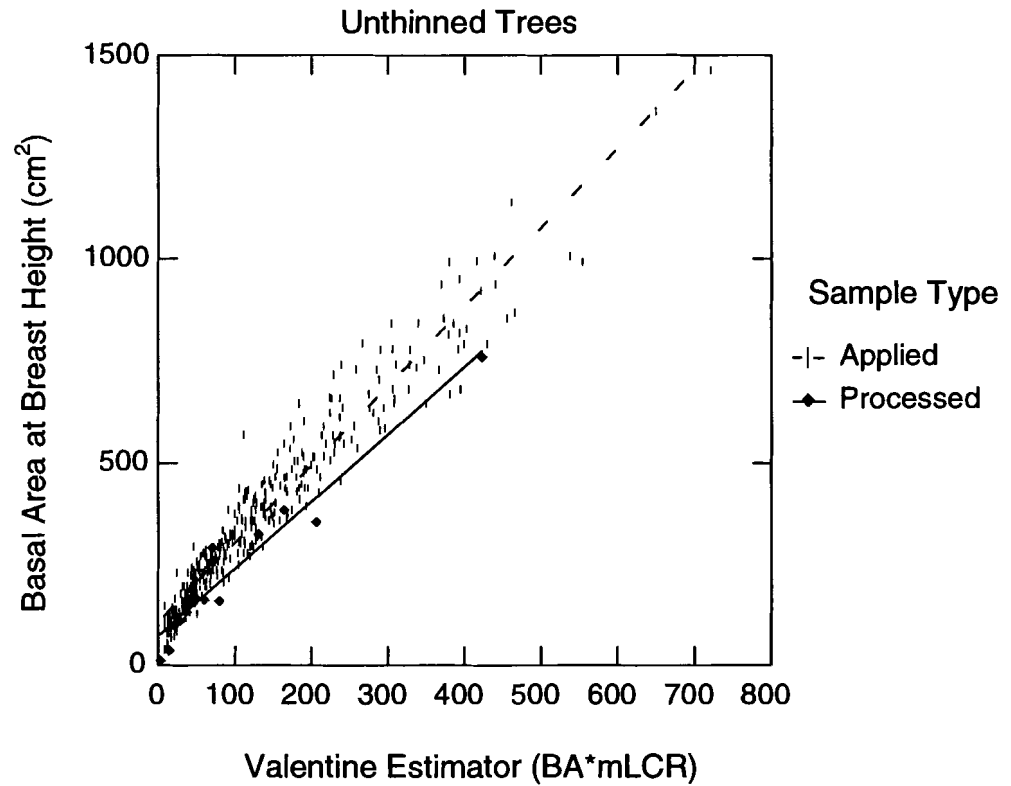


Figure 2.21: Basal area at breast height plotted against the Valentine estimator for processed and applied trees within the unthinned treatment. Applied trees had larger basal areas at any given unit of the Valentine estimator.

While the tests between the two sampling types illustrates the differences in the means of influential variables, perhaps more important is the significant difference in the range of values for these variables rather than the means themselves. For example, when plotting PLA from  $SA_{bh}$  against both  $BA_{bh}$  and the Valentine estimator, the apparent deficiency in large trees (as noted by the abundance of applied tree data points to the right of the largest processed tree data point) within the processed sample type is explicit (Figures 2.22 and 2.23). The Valentine model was strongly influenced by these variations across the study site and perhaps is just more sensitive to range of sampling than sapwood-based models when extrapolating to the stand level. However, if  $SA_{bh}$  was significantly different between the sample types, bias may have existed for the sapwood models as well. It is for this reason also that no bias existed for the adjusted Valentine model. In either case, it seems that thorough sampling across the entire represented population might be the key to eliminating model bias across variable stand structures.

For practical management use it may require little more than a true representation of the entire stand to be sampled when developing the equations. This may be achieved by simply ensuring that at least one individual from every dbh class present in the stand be used in building the model. In the case of the Val Sapwood model it would require much fewer cores at breast height to be taken, relative to the true sapwood models. This offers promise for managers avoiding leaf area measurements because of the laborious efforts known to exist with such measurements in the past.

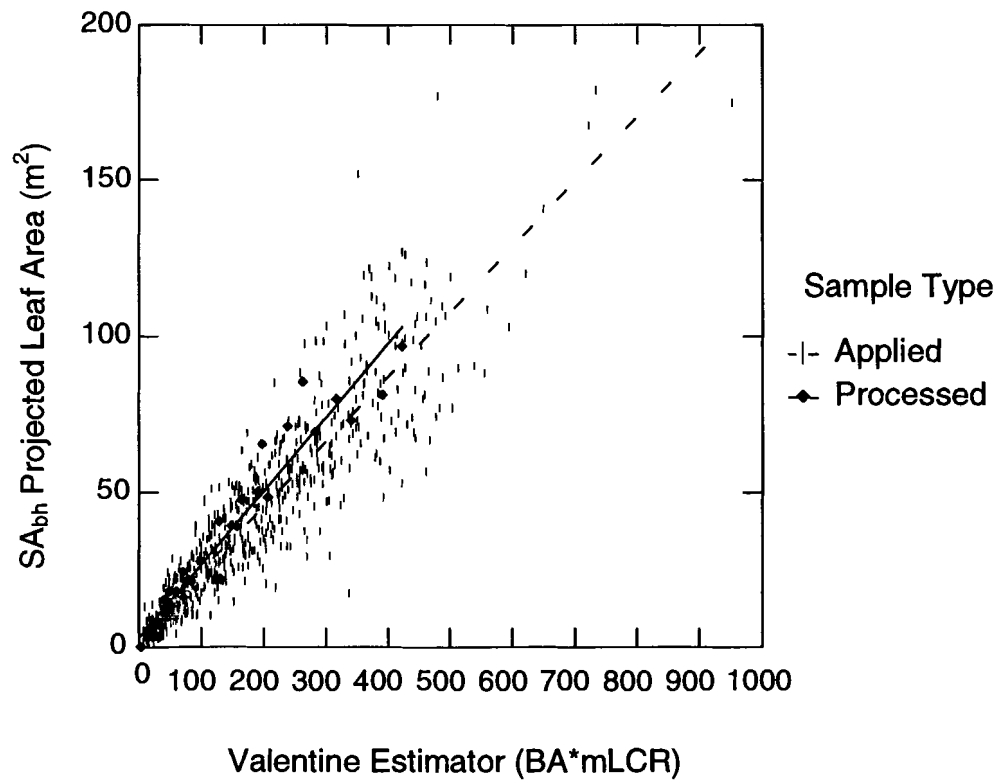


Figure 2.22: PLA from SA<sub>bh</sub> plotted against the Valentine estimator for processed and applied trees across treatment.

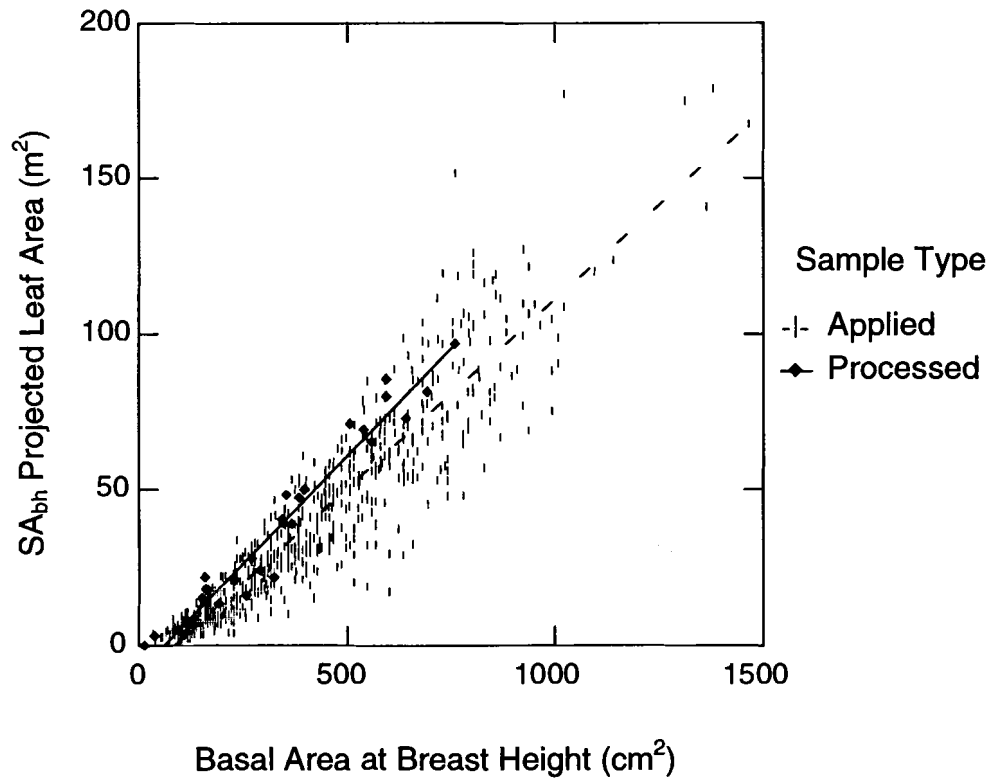


Figure 2.23: PLA from SA<sub>bh</sub> plotted against basal area at breast height for processed and applied trees across treatment.



## **CHAPTER 3.**

### **CONCLUSION**

Researchers and managers alike have regarded proper measurement of leaf area in forest ecosystems as a key variable to understanding forest productivity as well as physiological processes such as gas exchange and water cycles. However, the availability of multiple leaf area estimation techniques has caused confusion as to which method of estimation offers the most accurate assessment of live foliage, which method is the easiest to utilize, and which method is most cost-effective. Certainly any manager or person attempting to model forest growth or evaluate any of several important forest ecosystem relationships could benefit from the answers to these questions.

The results from the present research have focused on three methods of estimation (litterfall, below-canopy light interception and allometric regression models) in order to develop a reliable leaf area mensuration tool for eastern white pine. The apparent underestimation of leaf area from below-canopy interception is in agreement with previous studies (Marshall and Waring 1986; Chason et al. 1991) and explained perhaps in part by changes in the proportion of branch mass to LA due to variations in canopy architecture across densities. Comparative analyses of allometric models showed that sapwood-based models offer the most consistent indirect estimations across variable stand densities when referenced to direct estimations from litterfall, while the non-sapwood-based Valentine model was biased across stand density resulting in overestimations for thinned sites. Adjustments to the Valentine model seemed to eliminate all bias with respect to stand density and provided agreement with both litterfall and sapwood model estimates.

However, detailed tests examining differences between the trees used to develop the models and all remaining trees in the study provided evidence that equation derived trees were not representative of the entire site with respect to several important variables. In particular, basal area at both breast height and crown base was among the significant variables. This may explain the Valentine model's lack of consistent estimation with respect to stand density and in light of the apparent sampling problem, illustrates the difficulty in developing site appropriate models. These results suggest the importance of having knowledge of both stem and canopy parameters of the stand in which you wish to estimate leaf area before developing the predictive models, to insure proper sampling across the entire range of the population. Because sapwood area at breast height was considered representative of the entire population, the sapwood-based models remained consistent across stand density and were less sensitive than the Valentine model to sampling inconsistencies.

Perhaps it is too soon to regard the Valentine model as less superior to sapwood-based approaches for eastern white pine leaf area estimation, even though it has been reported as inferior by Gilmore et al. (1996) for balsam fir in Maine. Improving the Valentine model should be a research priority because of its relative ease in estimation. Providing an accurate and time-efficient method of leaf area estimation would help both public and private land managers to not only make more informed decisions about when and how much to cut, but would enable them to have a better tool for examining stand growth response after various cultural practices. While the methods employed here may be valid elsewhere, particularly for *Pinus spp.*, local equations must be developed for best predictive ability.

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Micah Pace was born in Cleveland, Ohio in October of 1976. He was raised in Richfield, Ohio and attended Revere High School in the same town. Micah graduated from high school in 1995, and from The Ohio State University, in Columbus, Ohio with a B.S. degree in Natural Resource Management (emphasis in Forestry) in June of 2000. Throughout his career at Ohio State, he was certified as an Ohio Nurseryman and worked as Property Manager/Chemical Specialist for a landscaping and horticultural firm. He also received his Wildland Firefighting Certification in 2000. Micah was fortunate enough to get a position working with Dr. Robert S. Seymour and began his graduate studies at the University of Maine in September of 2000. Micah is a student member of the Society of American Foresters. His research was on display in poster format at the 2002 Eastern CANUSA Forest Science Conference held at the University of Maine. His love of New England is tied to the natural beauty of the landscape and the abundant recreational opportunities, as well as family heritage. In February of 2003 Micah will move to Ecuador to work as a Forestry Extensionist while serving with the Peace Corps. Micah Pace is a candidate for the Master of Science degree in Forestry from The University of Maine in May, 2003.