

2004

Leaf Area Index - Relative Density Relationships in Even-Aged Abies Balsamea - Picea Rubens Stands in Maine

Robert Justin DeRose

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**LEAF AREA INDEX - RELATIVE DENSITY RELATIONSHIPS IN EVEN-
AGED *ABIES BALSAMEA* – *PICEA RUBENS* STANDS IN MAINE**

By

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A.S. Salt Lake Community College, 1998

B.S. Utah State University, 2002

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

December, 2004

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AGED *ABIES BALSAMEA* – *PICEA RUBENS* STANDS IN MAINE**

By Robert Justin DeRose

Thesis Advisor: Dr. Robert S. Seymour

An Abstract of the Thesis Presented
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Relationships between leaf area index (LAI) and relative density (RD) were examined in even-aged stands of *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg. Twelve sites distributed across the Acadian forest in Maine were used to test conformance to three hypothesized models of LAI over RD: A) constantly increasing LAI over increasing RD, B) constant LAI with increasing RD, or C) decreasing LAI with increasing RD. Multivariate ordination suggested young, precommercially thinned (PCT), high-site-index (SI) *A. balsamea* stands should be analyzed separate from older, unspaced (NOPCT), lower-site *P. rubens* stands. All-sided *A. balsamea* LAIs ranged from 6.2 – 14.8 over RDs of 0.23 - 0.60, *P. rubens* LAIs ranged from 7.5 – 14.9 over RDs of 0.51 – 0.76. Data for both species suggested an increase in LAI with increasing RD. At a given RD, LAI was strongly and positively correlated with SI. Lack of data across a complete range of RDs for both stand types limited testing of any hypothesized relationship between LAI and RD; however, when LAIs were adjusted to a common SI, conformance to trend A was evident.

Volume increment (VINC) and growth efficiency (GE) were also studied for *A. balsamea* and *P. rubens* in the CTRN sites. Dominant and codominant trees were used to test for differences in GE by site quality. Young *A. balsamea* trees ($n = 205$) were pre-commercially thinned (PCT) 15 – 20 years ago while the older *P. rubens* trees ($n = 173$) were not. A model incorporating individual tree all-sided leaf area (ALA) and site index (SI) best predicted VINC. A monotonic decreasing pattern of GE over ALA was found for both species; GEs were higher overall for *P. rubens*. GE was used with previously reported LAIs from the same sites to calculate mean annual increments, periodic annual increments (PAI), and stand-level GE. These metrics showed all sites in this study have yet to achieve culmination of mean annual increment. Stand-level GEs were similar for both species, although *P. rubens* occurred on lower-quality sites. *P. rubens* were more productive when viewed in terms of PAI per unit of SI.

ACKNOWLEDGMENTS

I would like to begin by thanking my thesis advisor Bob Seymour for allowing and encouraging me to study a topic of my choosing. His knowledge, guidance and encouragement have helped me improve as a scientist. I also appreciate the guidance of my graduate advisory committee Jeremy Wilson and Bob Wagner for their involvement and help during my Masters program. Also thanks to Alan White for additional statistical advice. A very special thanks to the project collaborator, Spencer Meyer for running the field crew, providing helpful feedback and discussion since the inception of our projects. This project would not have been possible without the data and help from the Cooperative Forestry Research Unit Commercial Thinning Network via Dan McConville and our 2002 field crew; Joseph Little, Benjamin Waitman, Sarah Drew Grant, Nathan Gagnon, Rachel Auerbach, Brian Schuster, Wendy Sicard, Melissa Simon, Cailin O'Connor. Finally, thanks to my family and the many friends who helped support me during my stay in Maine; Isaac Annis, Andrew Moores, Andrew Reinmann, Erin Small, Kara Sylvester, Maggie Ward, David Ray, Kris Hoffman, Spencer Meyer and many other graduate students I met along the way.

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INTRODUCTION

Softwood logging has been an integral historical component in the northeast for over 200 years. With over two centuries of forestry experience in the area it is astonishing to note many forest landowners are still practicing diameter limit cutting. This method removes only the largest individuals on the site and ignores the benefits of intermediate silvicultural treatments and individual species silvical traits (Seymour et al. 1986).

Uncertainty of future returns on current investments may be one reason for this.

Approximately 30% of the forested land in Maine is stands of *Abies balsamea* (L.) Mill. - *Picea rubens* Sarg. (Laustsen et al. 2003). Many of these stands are young, vigorous forests which regenerated in response to the 1976-1984 *Choristoneura fumiferana* Clem. (spruce budworm) outbreak (Seymour 1992). Potentials for higher yield have increased interest in more refined silvicultural practices (Seymour 1993). Unfortunately in this region relatively little is known about the outcomes of these treatments. Knowledge of the benefits of precommercial thinning (PCT) and commercial thinning (CT) may help increase science-based intensive management. The topic of the most recent Maine Agricultural and Forest Experiment Station (MAFES) technical bulletin was prioritizing silvicultural research efforts using wood supply analysis (Wagner et al. 2003). The report emphasized the importance of research on silvicultural treatments specifically those with primary influence on increasing regeneration success, sustainable harvest levels and financial values.

With such a large percentage of the forested Maine land base in mixtures of *A. balsamea* and *P. rubens* we should take into consideration their silvical traits. These species are commonly considered one-in-the-same as a result of some seemingly similar

silvical properties such as shade tolerance and site utilization however, many more differences become apparent upon closer inspection of each species unique characteristics.

Abies balsamea is a very short-lived, shade-tolerant coniferous member of the true fir family. It is the only true fir to occur in the northeastern United States. It is arguably one of the most important northeastern trees because of its use in lumber, paper pulp and for Christmas trees (Frank 1990). It occurs on a very wide range of soil types and over a much larger geographic area than *P. rubens*. Prolific seeding gives it a competitive advantage over *P. rubens*, which has much less dependable seeding, on most sites. Moores (2003) found *A. balsamea* to be more responsive to canopy openness and thus more competitive in uneven-aged, mixed-species stands than *P. rubens*.

P. rubens is a long-lived, shade tolerant coniferous tree. It is also an important pulp species but can become highly valuable sawlogs or specialty soundboard if allowed to grow over longer time periods than conventional rotation lengths. Although it occurs with a variety of other tree species including *A. balsamea* it also independently occupies some unique sites in the state of Maine such as spruce flats and spruce slopes, sites where growth is unfavorable for its typical associates (Blum 1990). Both species take advantage of the ability to persist in the understory as advance regeneration however *P. rubens* will outlast *A. balsamea* by many decades (Cary 1899).

Management guidelines for mixtures of *A. balsamea* – *P. rubens* such as the recently published density management diagram (DMD) aid in scientifically based active management (Wilson et al. 1999). The DMD quantifies the maximum size-density relationship between the species of interest in a graphical form that is easily used by the

field forester. Further knowledge may be gained by examining the relationships between biologically meaningful variables and stand growth for the prediction of future yields. By using biologic variables to estimate future growth, independence of site specific data is achieved, and prediction accuracy increased. The use of leaf area (LA) as a biologic variable has seen increasing popularity because it is highly correlated with volume growth (Gilmore and Seymour 1996, Maguire et al. 1998, chapter two). Relative stand density (RD) is easily calculated from the DMD and, if found to be correlated with LA, may be used as its surrogate. Relationships between biomass and age in natural stands have been studied however; questions still exist as to whether these relationships hold when assessing LAI over RD. LAI and its relationship to RD in *A. balsamea* – *P. rubens* stands were examined in this study. The effect of site, species differences and age were investigated to reveal their effects on observed values of LAI. Further, incorporation of site quality differences in volume growth and LA between species was quantified and its effects on production were examined.

LITERATURE REVIEW

Leaf area

Foliage is an important variable in quantifying production potential of plants and is believed to be the most appropriate biologic variable in modeling tree and forest growth (Maguire and Bennett 1996). Foliage is of primary interest because of its role in the interception of light irradiance (Honda and Fisher 1978, Cannell 1989, Lieffers et al. 1999), which is a major determinant of forest growth (Vose and Swank 1990). As a measure of the photosynthesizing area of a tree it helps in characterizing growth and ecosystem functions. Foliage, or leaf area (LA), has also been largely cited as the primary variable dictating tree growth, and many published accounts of a strong relationship between foliage and volume increment exist (Long and Smith 1984, 1992, O'Hara et al. 1999, Seymour and Kenefic 2002).

The development of LA through time presents questions regarding the maximum amount of foliage on a given site and possible patterns with initial density and site index (SI, Long and Smith 1984, 1990). Water availability and local climate could potentially affect LA as well (Grier and Running 1977). Nutrient demand and site fertility (Brix and Mitchell 1983, Binkley and Reid 1984, Vose and Allen 1988) can also play a role in the amount and distribution of foliage in trees. Individual tree silvical traits can also affect site LA maximum (Smith and Long 1992). Many estimators of foliage area exist and are commonly referred to as 'leaf area'. Crown projection area (CPA) and crown surface area (CSA) were among the first measurements of tree foliage to be used in studies of forest science (Assmann 1970 p.109). CPA was correlated to a whole host of stand parameters such as density, volume, and growth but more recent work has shown varying degrees of

usefulness for CPA (Gilmore and Seymour 1996, Sterba and Amateis 1998). A more direct measure of leaf biomass and area is specific leaf area (SLA cm^2/g), the one-sided area of foliage per unit of weight (Marshall and Waring 1986). SLA accounts for the ratio of living 'wet' tissue to dead 'dry' tissue. If one multiplies this number by the dry weight of all foliage and sums over the total tree projected leaf area (PLA) is the result. This method abounds in the literature and is used in the following study. Differences in SLA from different heights within the crown have been found and should be accounted for (Kinerson et al. 1974, Keane and Weetman 1987). CSA and Crown volume (CV) have been widely used (Assmann 1970, Maguire and Bennett 1996, Kenefic and Seymour 1999) to assess LA and increment, but huge differences in within species crown morphology have made precise measurements difficult. Maguire and Bennett (1996) also noted variation in yearly foliage production makes CSA and CV problematic for growth prediction. Perhaps the most common measure of LA at the plot or stand level is leaf area index (LAI), this measure takes the sum of the plot or stand projected leaf area over ground area ($\text{m}^2 \text{m}^{-2}$, O'Hara 1988). Generally LAI in conifers > hardwoods (Smith and Long 1992), and shade tolerant species > intolerant species (Kaufmann and Troendle 1981, Parker and Long 1989). Magnussen et al. (1986) found LAI linearly related to aboveground drymatter production in *Pinus banksiana* Lamb. Due to their relative contributions to economic value, LA of coniferous trees is studied far more than hardwoods; however, examples exist in the literature (Marks and Bormann 1972, Madgwick and Olsen 1974, Waring et al. 1977, Rogers and Hinckley 1979).

There are a number of ways to estimate leaf area; First, below canopy light interception based on the Beer-Lambert law of light extinction, Second, litterfall

collection (Kinerson et al. 1974, Vose and Allen 1988) which is commonly thought of as the most accurate method because annual variation in leaf area is largely accounted for (McShane et al. 1983), third, allometric relationships with simple static measures such as diameter at breast height (DBH) and basal area at breast height (BA) and fourth, mechanistic relationships such as the pipe model theory (Shinozaki et al. 1964a, b) which notes each unit of foliage weight is supported by a proportional unit of conducting tissue, or xylem. In their original works Shinozaki et al. (1964a, b) assumed cross-sectional area at the crown base (CBSA) was entirely composed of conducting 'pipes' and this principle has been used to examine the relation between conducting area or, sapwood area (SA), where it is easier to measure, breast height (1.3 m) and tree LA. Studies of the relationship between CBSA and SA have consistently found sapwood taper to occur (Long et al. 1981, Espinosa Bancalari et al. 1987) such that a given unit of SA at breast height contains only a percentage of the 'pipes' at crown base (Waring et al. 1982, Dean and Long 1986, Maguire and Hann 1987, Mäkelä et al. 1995). Although SA is highly correlated with LA, further investigations revealed the permeability of the sapwood in question could help explain more variation in the relationship (Whitehead et al. 1984, Thompson 1989, Coyea and Margolis 1992, Mencuccini and Grace 1995). In an early examination of allometric variables, Kittredge (1944) assessed foliage weight predicted from DBH and suggested differences in predicted weights with varying stand density. Gholz et al. (1976) used DBH to estimate LA, which was later found to be biased. Kendall Snell and Brown (1978) found SA predicted LA much more accurately than DBH in seven western conifers. Significant correlations were found between all methods except static tree allometrics by Marshall and Waring (1986). Smith et al. (1991) found

sapwood area and light interception were not related in stands of *Pinus contorta* var. *latifolia* Engelm. Pace (2003) found reasonable correlations between four methods of LAI estimation. Allometric relations including the pipe-model theory were used in this study and the discussion of LA measurement techniques will be limited to these methods.

Taking increment cores to determine SA has been widely used for LA estimations and is thought to be fairly accurate (Long and Smith 1988, 1989, Gilmore et al. 1996, Maguire et al. 1998, Kenefic and Seymour 1999, Turner et al. 2000). The difficulty with the SA - LA allometry is that initial destructive sampling is required to establish a baseline relationship. Appropriate felling and sectioning of representative trees must be conducted and needles collected representatively from the crowns. Dean et al. (1988) found within-stand variability was not taken into account by this relationship suggesting the importance of how LA is measured. They suggested some measure of stand structure, live crown ratio (LCR), defined as the length of the crown divided by total tree height, or the vertical midpoint of LA should be included with SA prediction models. Inter-annual variation also exists in LA levels of forest stands (Vose and Swank 1990) and must be considered when sampling. Evidence exists for both linear (Marchand 1984, Schuler and Smith 1988, Robichaud and Methven 1992, Coyea and Margolis 1992,) and non-linear SA - LA relationships (Dean and Long 1986, Long and Smith 1988, 1989, Thompson 1989). Long and Smith (1988) argue in support of non-linear SA – LA models because constant, or linear, relationships may remove the effect of stand density on the relationship. A suitable surrogate for SA, modified live crown ratio (MLCR), was developed by Valentine et al. (1994). MLCR uses cross sectional area at breast height, or basal area (BA), with tree height and crown length to estimate leaf area. This simple

model is obviously easier to measure in the field, as it non-destructively predicts cross-sectional area at crown base, through approximation of stem taper, which has been shown to affect the SA – LA relationship (Coyea and Margolis 1992, Maguire and Bennett 1996).

Growth efficiency

Although leaf area is used to assess a multitude of tree and forest attributes it must be combined with some measure of efficiency to evaluate production. Growth efficiency (GE, volume increment divided by leaf area, leaf weight or its surrogate) provides an index with which to compare productivity and vigor of forest trees and stands. Indeed, many studies exist which use GE to assess vigor (Waring et al. 1980, Mitchell et al. 1983, Blanche et al. 1985). A number of different GE surrogates are reported in the literature (Gilmore and Seymour 1996, Sterba and Amateis 1998). Perhaps the first measure, CSA, was reported by Assmann (1970 p.120), who cited Toma (1940) and also examined R. Mayer's dissertation, which uses CPA in *Quercus petraea* (Mattuschka) Liebl. and was subsequently tested in *Pinus taeda* L. by Sterba and Amateis (1998). GE allows appropriate consideration of stand structure when applying thinning treatments and may more accurately reflect growth potential of individual thinned trees (O'Hara 1988). Different patterns of GE - PLA are discussed in the literature and the affect of species shade tolerance, stand structure, cultural treatment and age have all been used to support these trends. We could benefit by discussing each of these subjects in turn.

In early papers (Waring et al. 1980, 1981) assessment of the GE - LA relationship at the stand-level found that tree growth decreased as LAI increased, i.e. net assimilation decreased with increasing LAI in stands of *Pseudotsuga menziesii* (Mirb.) Franco

Furthermore, they found that GE peaked near half the maximum observed LAI. A different relationship was found by Oren et al. (1987) in *Pinus ponderosa* Dougl. ex. Laws. stands. A negative exponential curve best described GE over LAI. They also noted increases in LAI started to plateau at higher LAIs (their Fig. 3), which provided evidence of no pattern in GE over LAI. O'Hara (1988) provides evidence for a monotonically increasing trend in GE over LAI in uneven-aged stands. Maguire et al. (1998) studied uneven-aged stands of *P. rubens* and found a decreasing trend of GE with LAI. The use of an index of suppression did not change the relationship. Sterba and Amateis (1998) found GE decreased with increasing LAI. Roberts and Long (1992) proposed the conceptual model that GE increases with LAI to some peak and then decreases with LAI like that found by Waring et al. (1981). They provide further support for the argument that increasing respiratory demands result in the decrease of GE. They cited the most efficient trees were nearly the tallest and had ~ 67% of maximum LA. O'Hara (1988, 1989) cites potential methodological problems in earlier studies that could lead to different observed patterns. Gilmore and Seymour (1996) found model choice determined what pattern of GE over PLA resulted.

In a comparison between tolerant and intolerant species, Roberts et al. (1993) suggested GE depends on the amount of carbon fixed by foliage and amount allocated to stemwood growth, citing stand structure as the balance between these. They attempt to reconcile two different patterns of GE over LAI with this conceptual argument.

Structure has been discussed at length as a possible determinant of GE in forest trees. O'Hara (1988) found GE increased with increasing tree height, which helps explain why large trees from unthinned controls exhibit similar GEs to medium-sized trees from

thinned plots. Roberts and Long (1992) found increases in LAI were generally correlated with greater height (HT) which further suggests a close relationship between LAI and GE. O'Hara (1988) provided evidence in support of thinning to desired structures rather than densities, since the most growth efficient trees, codominant (C) and dominant (D) trees were found to account for the majority of stand-level growth. In a study assessing crown position influences on GE Gilmore and Seymour (1996) found suppressed trees were less efficient than the other crown classes. Jack and Long (1992) found that as mean crown size increases GE decreases. They make the argument that trees at high densities are more GE because they have a smaller "bare inner core" (Assmann 1970, p.111). In contrast, Ford (1982) found smaller trees were less efficient in growth per unit of BA (surrogate for LA) than large trees in *Picea sitchensis* (Bong.) Carr. In uneven-aged stands Seymour and Kenefic (2002) found D stratum GEs were much higher than B stratum for *P. rubens* and *Tsuga canadensis* (L.) Carr. In a comparison of even-aged to uneven-aged stands Kollenberg and O'Hara (1999) found higher GE in even-aged stands but higher LAI in uneven-aged stands. They found stand volume increment was only weakly correlated to LAI and noted that crown position was a more important determinant of GE than age, but their study only included trees up to 160 years old.

In an assessment of resource availability, Velazquez-Martinez et al. (1992) found that fertilization increased GE but did not differentiate whether it increased LAI, efficiency or both. However, Fig. 3 in Velazquez-Martinez et al. (1992) suggests the effect of density reduction created efficient trees with small crowns that do not have maximum LA but still contribute to stand growth. Binkley and Reid (1984) also found that reduced density created higher tree GE. In a comparison between precommercially thinned (PCT) stands

and controls Phillips (2002) found GE of *A. balsamea* and *P. rubens* trees of similar size, age and origin to be statistically similar.

Kaufmann and Ryan (1986) found GE declined with age but their results were confounded with PLA. Seymour and Kenefic (2002) provided the first account to separately test age and mean tree PLA influences on GE in uneven-aged *T. canadensis* and *P. rubens* stands. Their results suggest a pattern of decreasing GE with increasing age, independent from tree LA. They also provide an excellent review of the published patterns in GE relationships.

Relative density

Relative density (RD) as defined by Curtis (1970) quantifies maximum size-density relationships in stands of trees, and is commonly used to help design and guide commercial thinning (CT), PCT and other intermediate treatments. RD can be calculated by simply taking the number of observed trees of average size per unit area and divide by the maximum number possible for the site. This procedure assumes the site and species maximum has been pre-determined. For the establishment of site and species maximums one must sample from a large sample of geographically representative stands determined to be currently undergoing self-thinning (Hutchings and Budd 1981, Westoby 1984, McCarter and Long 1986, Wilson et al. 1999). RD is an effective measure of site occupancy or stocking because it is independent of site and age in self-thinning stands and is supported by the self-thinning rule (Yoda 1963, Drew and Flewelling 1977, Curtis 1982, Long 1985, Jack and Long 1996, Wilson et al. 1999).

Self-thinning, or the $-3/2$ rule, is defined as competition-induced death of the less vigorous individuals during the stem-exclusion stage of stand development (Oliver and

Larson 1996, p.152). Intervening before this process allows silviculturists to favor vigorous stems based on observable characteristics such as crown class (Smith et al. 1997, p.30, Nyland 2002 p.387) and LCR (Long 1985). Simplified explanations of stand development use RD to describe changes in stand structure over time (Long and Smith 1984, Jack and Long 1996). Similarly, many relationships between measures of size, density and growth are well understood at both the stand and tree level (Long 1985, Smith et al. 1997). These relationships are supported by three assumptions; first, there is a maximum possible number of stems of mean tree size per unit area, second, that self-thinning occurs at some percentage of maximum density and third, the size-density relationship adequately describes competition (Westoby 1977, 1984, Jack and Long 1996). Even-aged stands are commonly used to exemplify the relationships between size and density for the sake of simplicity (Jack and Long 1996). Size-density relationships in uneven-aged stands are more difficult to assess and consequently less is known about them (Westoby 1984, Woodall et al. 2003). The application of density measures in uneven-aged stands typically treat the different cohorts as individual, even-aged groups within a stand and apportion measures of density proportionally across the cohorts (Long 1996, O'Hara 1996, Shaw 2000, O'Hara et al. 2001). Part of the difficulty in assigning measures of RD, which is based on a mean tree value, is that stands with large variations in individual tree size need growing space occupancy accurately portrayed. This can potentially lead to biased estimates of density and subsequently growth potential. It has been suggested that some measure of tree growing space occupancy would better describe growth potential (Assmann 1970, sec. C-II, O'Hara 1988, 1996). Individual tree leaf area is an appropriate variable to characterize growing space occupancy because of

its relation to stand density (Dean and Long 1985, 1986). Westoby (1977) found mean LA over density yields the self-thinning line. Furthermore, Hutchings and Budd (1981) found LAI remained constant as thinning proceeded in *Trifolium pretense* L. suggesting a biologic mechanism whereby mean tree LA drives stand density.

Structure

Stand structure is commonly portrayed as the horizontal and vertical arrangement of foliage on tree stems. Assessment of structure in silviculture is important because the varying objectives of different types of thinning; crown, dominant and low thinning each remove trees from combinations of different crown class positions (Smith 1997, chpt. 5), which, by definition have different arrangements of foliage that affect light interception. Growth is influenced by the distribution of leaf area on tree stems, and the distribution of those stems over the available growing space (Assmann 1970, p.101, O'Hara 1989). In a study of three pine species, Dean (2004) showed not only leaf area but its associated vertical distribution best predicted basal area increment. Since it is known that distribution of leaf area between trees is not independent of relative density (Jack and Long 1991a), and mean tree leaf area must vary with density and age if it is to remain stable over wide ranges of either variable (Jack and Long 1991b). It would be of benefit to consider the potential differing displays of individual tree leaf area within a stand.

Leaf area, density and growth efficiency relationships

Foliage has been used as an index, much like site index, of site quality or potential for volume growth. McLeod and Running (1988) found LAI correlated well with stem volume increment but varied with stand density. O'Hara (1996) also found a strong linear relationship between all-sided leaf area and stand density index (SDI) in *P. ponderosa*. In

contrast Long and Smith (1990) found LAI was independent of stand density in mature *P. contorta*. Grier and Running (1977) found LAI was as closely related to net primary productivity as site water balance, suggesting stand level LAI is controlled by water availability. The ability of LA to predict site productivity may be due to the inherent capability of better sites to produce more LA per unit area. RD also affects LA relationships since denser stands take less time to reach their site dictated maximum LA (Long and Turner 1975). Long and Smith (1988) found mesic *P. contorta* sites hold 30% more LA than xeric sites. In a study of stand-level GE, O'Hara (1989) corroborated the earlier findings of Binkley and Reid (1984) who found no relationship with GE and LAI at the stand-level. Long and Smith (1990) assessed the influence of density and site on GE and found LAI weakly correlated with SI, and GE unrelated to LAI in mature *P. contorta* stands. The implication of this study was that site quality affects the amount of LA but not the efficiency. Smith and Long (1991) further corroborate this in *Abies lasiocarpa* (Hook) Nutt.- *P. contorta* mixtures where similar GEs were reported for two very dissimilar species with different LAIs. Knowledge of these relationships has lead to increasing use of LAI to guide management and stocking relationships for a number of coniferous species (O'Hara 1996, 2001). Like LAI, GE is a biologically meaningful measure of growing space efficiency in forest stands and its relationship to LAI warrants increased attention.

CHAPTER ONE: LEAF AREA INDEX - RELATIVE DENSITY
RELATIONSHIPS IN EVEN-AGED *ABIES BALSAMEA* – *PICEA RUBENS*
STANDS IN MAINE

ABSTRACT

Relationships between leaf area index (LAI) and relative density (RD) were examined in even-aged stands of *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg. Twelve sites distributed across the Acadian forest in Maine were used to test conformance to three hypothesized models of LAI over RD: A) constantly increasing LAI over increasing RD, B) constant LAI with increasing RD, or C) decreasing LAI with increasing RD. Multivariate ordination suggested young, precommercially thinned (PCT), high-site-index (SI) *A. balsamea* stands should be analyzed separate from older, unspaced (NOPCT), lower-site *P. rubens* stands. All-sided *A. balsamea* LAIs ranged from 6.2 – 14.8 over RDs of 0.23 - 0.60, *P. rubens* LAIs ranged from 7.5 – 14.9 over RDs of 0.51 – 0.76. Data for both species suggest an increase in LAI with increasing RD. At a given RD, LAI was strongly and positively correlated with SI. Lack of data across a complete range of RDs for both stand types limited testing of any hypothesized relationship between LAI and RD; however, when LAIs were adjusted to a common SI, conformance to trend A was evident.

INTRODUCTION

The trade-off between individual tree growth and stand growth has been discussed extensively in the literature (Long and Smith 1984, Long 1985, Jack and Long 1996). One can balance these by controlling stand stocking, which regulates tree and stand leaf area (LAI, $\text{m}^2 \text{m}^{-2}$). Arguably the most ecologically sound method by which to measure stocking is relative density (RD), defined as the number of observed trees of average size per unit area divided by the biological maximum number possible for the site. This metric relies on the self-thinning rule (Yoda 1963, Drew and Flewelling 1977), a pattern that has been found in many plant populations. Easily measured, RD may be a potentially useful predictor of LAI, but only if its relationship with LAI is understood and quantified.

Forest stands occurring on mesic sites with $\text{RD} < 25\%$ are commonly characterized as having maximum individual tree growth, but below potential maximum stand growth. At such low densities, crown closure has not been achieved and the site is still on a trajectory toward its maximum LAI. After reaching $\sim 25\%$ RD, individual tree growth increases at a decreasing rate (Long 1985). Likely a result of the beginning of competitive interaction between trees, and the start of branch-shedding and differentiation in even-aged stands or stratification among species in mixed stands (Long and Smith 1984, Jack and Long 1996). Wilson et al. (1999) found crown closure to occur between 11% and 32% of RD in stands of *A. balsamea* – *P. rubens*. Foliage biomass, as a corollary to LAI, has been observed to reach its maximum soon after crown closure, depending on initial stand density (Turner and Long 1975, Meng and Seymour 1992). Once LA has reached its maximum, where differentiation of even-aged stands into crown classes is well underway, stand growth is at its maximum potential (Long and Smith

1984) and self-thinning is evident (Dean and Long 1985). Active intervention before the onset of self-thinning (<50% RD) is one goal of production silviculture.

A common pattern of relatively constant foliage biomass over time after canopy closure has been well-documented (Turner and Long 1975, Jack and Long 1991a). Such studies require observing many stands of differing ages as a chronosequence to interpolate possible changes through time. Less is known about the behavior of LAI with increasing RD beyond self-thinning. If foliage is described by LAI and RD increases with time three similar trends can be hypothesized (Fig. 1.1).

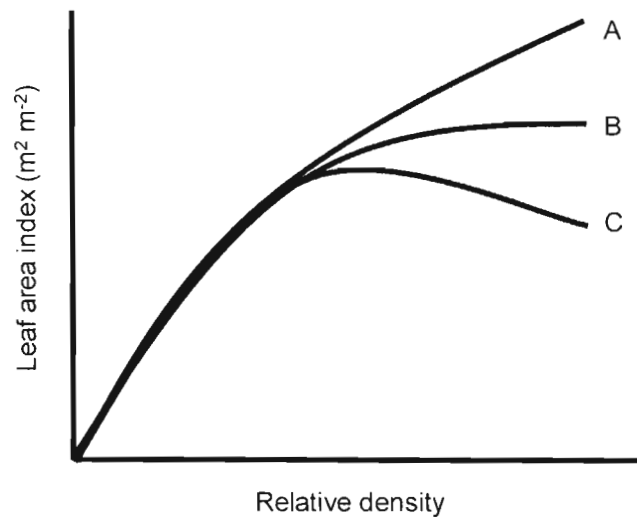


Fig. 1.1. Hypothesized relationship between all-sided leaf area index (LAI) and relative density (RD)

Limited evidence exists for the behavior of LAI or foliage at increasing RDs. Baskerville (1965) found a positive relationship between foliage biomass and stand density (stems per hectare) for 41 yr old *A. balsamea* in New Brunswick, evidence of Trend A. Jack and Long (1991a) also found trend A for *Abies lasiocarpa* (Hook.) Nutt. and *Pinus contorta*

var. *latifolia* Engelm. when LAI was plotted over relative stand density index. However, LAI of fully stocked stands in the latter species was only marginally higher in high density stands, possibly displaying trend B (their Fig. 2). O'Hara (1996) found trend A in uneven-aged, thinned stands of *Pinus ponderosa* Dougl. ex Laws. in Montana and Oregon (his Fig. 7). Doucet et al. (1976) provide evidence of low foliage amounts in high density stands when compared with low density stands in even-aged *Pinus banksiana* Lamb. in Quebec, suggesting trend C. A possible cause of lower observed LAI in high density stands is crown abrasion (Long and Smith 1992). This loss of foliage due to crown interactions may explain trend C.

It has been postulated that maximum LAI is governed by the species' tolerance of shade (Jack and Long 1991a, Smith and Long 1992, Roberts et al. 1993). This reasoning suggests shade-tolerant species, able to persist in more vertically diverse structures, maintain more LAI at higher stocking (trend A). In a similar fashion inherent species differences like crown architecture and structure have been used to explain the difference in LAI over stocking observed between species (Long and Smith 1990, Jack and Long 1991a, Smith and Long 1992, Robert et al. 1993). Total foliage has been shown to be related to site quality (Moller 1947, Assmann 1970, p.36, Long and Smith 1989) suggesting higher quality sites support more foliage than those of lower quality. Implications of LAI varying with site can be graphically portrayed as a shift of the hypothesized relationships up or down on the y-axis (Fig. 1.1).

It is unclear which trend even-aged stands of *A. balsamea* and *P. rubens* in Maine might exhibit and whether site quality or species composition play a role in the relationship. Thus, the purposes of this research were to 1) assess the potential of RD to

predict LAI, 2) explore the relationship between LAI and RD in even-aged *A. balsamea* - *P. rubens* stands in Maine and 3) evaluate whether site quality or species composition play a role in the LAI – RD trend. Specifically, the hypotheses were: 1) RD can be used to predict stand-level LAI in even-aged *A. balsamea* - *P. rubens* stands in Maine, 2) the LAI – RD relationship follows trend A in even-aged stands of *A. balsamea* and *P. rubens* (Fig. 1) and 3) site quality and/or species composition affect the LAI – RD relationship.

METHODOLOGY

Study sites

The Cooperative Forestry Research Unit (CFRU) Commercial Thinning Research Network (CTRN) sites were used for this study. These sites were selected for treatment, measurement and assessment of a number of forest management activities including intensive silviculture, harvest practice effects, forest growth and economic return. Sites are dominated by either *Picea rubens* Sarg. or *Abies balsamea* (L.) Mill. but also include *Picea glauca* (Moench) Voss., *Tsuga canadensis* (L.) Carr. and *Pinus strobus* L. All CTRN sites fall within the Acadian Forest Region (Tables 1.1 – 1.6, Rowe 1972). Sites were naturally regenerated by even-aged silvicultural methods. Six sites have a history of PCT in the early 1980s and are dominated by *A. balsamea* (Table 1.6) while the other six sites have no history of precommercial thinning (NOPCT) and are dominated by *P. rubens* and *A. balsamea* (Table 1.5).

Table 1.1. Site names, identification and geographic locations for the Cooperative Forestry Research Unit Commercial Thinning Research Network (CTRN)

Name (Site ID)	Latitude (N)	Longitude (W)	County	Township
Alder Stream (AS)	45°22'21"	69°47'50"	Somerset	Squaretown
Golden Road (GR)	45°43'21"	68°40'31"	Penobscot	Grindstone
Harlow Road (HR)	45°38'44"	67°50'29"	Washington	Danforth
Lake Macwahoc (LM)	45°47'58"	68°17'11"	Aroostook	T 2 R 4 WELS
Lazy Tom (LT)	45°43'33"	69°27'28"	Piscataquis	Spencer Bay
Penobscot Experimental Forest (PE)	45°51'17"	63°38'07"	Penobscot	Bradley
Ronco Cove (RC)	45°40'51"	69°38'06"	Piscataquis	Days Academy Grant
Rump Pond (RR)	45°11'36"	71°01'11"	Oxford	Parmachenee
Sara's Road (SR)	44°49'10"	70°54'41"	Oxford	Magalloway Plantation
School Bus Road (SC)	44°50'28"	70°46'45"	Oxford	Richardsontown
St. Aurelie (SA)	46°15'32"	70°09'43"	Somerset	T 7 R 19 WELS
Weeks Brook (WB)	46°13'11"	68°31'24"	Penobscot	T 7 R 6 WELS

Table 1.2. Site index (SI) for each site predicted from Steinman (1992) equation in Wilson et al. (1999).

NOPCT			
Site	Mean age ^a	Species ^b	Site index ^c
GR	52	<i>P. rubens</i>	14.9
HR	76	<i>P. rubens</i>	12.2
RR ^d	39	<i>A. balsamea</i>	15.8
		<i>P. rubens</i>	17.4
SA	33	<i>A. balsamea</i>	19.2
SC	62	<i>P. rubens</i>	14.0
SR	53	<i>P. rubens</i>	13.7
PCT			
AS	26	<i>A. balsamea</i>	21.9
LM	38	<i>A. balsamea</i>	17.7
LT	27	<i>A. balsamea</i>	20.1
PE	29	<i>A. balsamea</i>	20.2
RC	21	<i>A. balsamea</i>	22.9
WB	28	<i>A. balsamea</i>	20.1

Note: ^a Average age at breast height of dominant (D) trees, ^b Species used for site index calculation, ^c Site index (m) base age 50 calculated for each dominant (D) tree of major species composition using the equation;

$$S = [b_0(HT - 4.5)^{b_1}] [1 - \exp(b_2 \text{ AGE})]^{(b_3(HT - 4.5)^{b_4})}$$

where S = site index (SI m) and HT = height (m) from Wilson et al. (1999, Appendix A, equation 9) then averaged, ^d Two site indices reported as a result of nearly 50:50 species composition, NOPCT - plots that received no precommercial thinning, PCT - sites that received precommercial thinning, sites as in Table 1.1.

Table 1.3. Ranges of leaf area index (LAI m² m⁻²), relative density (RD), mean height of the tallest 100 trees per hectare (TOPHT m), basal area (BA cm²) and trees per hectare (TPHA) for each study site

NOPCT					
Site	LAI (m ² m ⁻²)	RD	TOPHT (m)	BA (m ²)	TPHA
GR	(8.6 – 11.3)	(0.51 – 0.56)	(15.0 – 16.0)	(14.4 – 15.6)	(2323 – 3842)
HR	(7.5 – 9.4)	(0.54 – 0.67)	(17.4 – 18.1)	(13.9 – 17.3)	(1664 – 2446)
RR	(10.3 – 14.9)	(0.55 – 0.73)	(13.3 – 14.4)	(15.7 – 21.0)	(3929 – 8117)
SA	(10.2 – 14.8)	(0.47 – 0.60)	(12.2 – 13.4)	(14.1 – 18.5)	(4188 – 8228)
SC	(7.9 – 9.1)	(0.66 – 0.76)	(16.2 – 17.1)	(17.5 – 20.0)	(3002 – 4448)
SR	(9.6 – 11.0)	(0.52 – 0.63)	(14.3 – 16.0)	(14.7 – 17.8)	(2286 – 5498)
PCT					
AS	(9.0 – 13.7)	(0.23 – 0.35)	(11.6 – 12.4)	(8.3 – 12.0)	(1063 – 1569)
LM	(8.4 – 11.1)	(0.29 – 0.40)	(13.8 – 14.6)	(9.3 – 12.6)	(939 – 1829)
LT	(9.7 – 12.6)	(0.31 – 0.37)	(12.3 – 12.8)	(10.2 – 12.1)	(1495 – 2236)
PE	(6.2 – 11.7)	(0.23 – 0.34)	(12.1 – 13.6)	(7.7 – 10.8)	(1297 – 1643)
RC	(9.6 – 12.1)	(0.25 – 0.33)	(10.3 – 10.9)	(8.8 – 11.9)	(1396 – 2162)
WB	(10.3 – 12.5)	(0.34 – 0.39)	(12.6 – 13.3)	(10.9 – 12.3)	(1754 – 2718)

Note: NOPCT – stands with no history of precommercial thinning, PCT – stands with a history of precommercial thinning, sites as in Table 1.1.

Table 1.4. Pre-thinning tree-level mean \pm standard deviation (SD), minimum, maximum and sample size (n) for quadratic mean diameter (QMD cm), height (HT m), modified live crown ration (MLCR [(HT-LLB)/(HT-1.3)]), individual tree projected leaf area (PLA $\text{m}^2 \text{m}^{-2}$) and sapwood area (SA cm^2).

Attribute	Mean \pm SD	NOPCT		
		Minimum	Maximum	n
QMD (cm)	11.5 \pm 5.31	0.254	64.8	13 441
HT (m)	10.3 \pm 3.58	1.43	26.5	13 441
MLCR	0.43 \pm 0.16	0.086	1.22	485
PLA ($\text{m}^2 \text{m}^{-2}$)	10.0 \pm 14.9	0.0002	512.4	13 441
SA (cm^2)	48.9 \pm 42.9	1.04	263.8	485
Attribute	Mean \pm SD	PCT		
		Minimum	Maximum	n
QMD (cm)	14.1 \pm 4.17	0.762	40.9	5742
HT (m)	10.5 \pm 1.98	1.92	19.5	5742
MLCR	0.75 \pm 0.13	0.353	1.13	300
PLA ($\text{m}^2 \text{m}^{-2}$)	26.8 \pm 18.1	0.016	163.9	5742
SA (cm^2)	63.8 \pm 35.4	1.57	161.4	300

Note: Plot data at site PE were not taken as a result of Forest Service Continuous Forestry Inventory guidelines against increment core sampling.

Table 1.5. Species composition as a percentage of plot basal area (BA m²) for sites that received no precommercial thinning (NOPCT). Pre-treatment data were used.

Site	Species	CR33	CR50	Control	DOM33	DOM50	LOW33	LOW50
GR	BF	26.4	17.9	12.2	24.1	47.6	19.8	29.6
	EH	0.9	0.6	0.4	6.8	8.4	0.0	1.0
	NC	1.8	0.0	0.2	4.0	16.1	0.2	0.4
	RS	60.5	72.0	76.7	59.1	26.5	75.0	64.8
	WP	10.4	9.5	10.6	6.1	1.4	5.0	4.2
HR	BF	0.0	0.0	0.0	0.0	0.7	0.0	0.0
	EH	0.3	0.0	0.1	0.3	0.0	0.0	0.0
	NC	0.0	4.3	2.9	2.6	2.5	2.2	2.1
	RS	92.4	95.2	87.1	94.8	86.5	96.0	91.0
	WP	7.3	0.0	8.9	2.3	10.3	1.7	7.2
	WS	0.0	0.5	1.0	0.0	0.0	0.2	0.7
RR	BF	52.7	48.4	43.2	55.7	45.3	53.7	45.9
	NC	6.5	12.8	4.2	16.3	1.3	9.7	9.9
	RS	40.8	37.7	52.6	28.0	53.4	36.6	44.2
	WS	0.0	1.1	0.0	0.0	0.0	0.0	0.0
SA	BF	90.0	87.4	84.2	87.7	91.7	94.4	89.9
	NC	9.1	2.8	11.1	4.7	2.1	0.7	1.7
	RS	1.0	9.8	4.7	7.6	6.2	5.0	8.4
SC	BF	1.7	1.0	5.1	3.4	3.0	4.7	2.3
	NC	1.5	0.5	4.6	4.5	0.1	1.2	0.3
	RS	78.1	87.6	79.4	73.1	71.7	90.5	74.9
	WP	18.7	10.9	10.9	19.0	25.3	3.6	22.6
SR	BF	0.1	0.5	0.5	1.6	0.5	0.0	0.7
	EH	1.9	0.0	0.0	0.0	0.0	0.0	0.0
	NC	0.2	0.6	0.0	2.0	0.1	0.0	0.3
	RS	91.3	90.2	90.1	79.0	79.5	86.0	77.0
	WP	6.5	8.6	9.5	17.3	19.9	14.0	21.9

Note: See Table 1.1 for site definitions. BF – *Abies balsamea*, EH – *Tsuga canadensis*, NC – non-commercial hardwood species, RS – *Picea rubens*, WP – *Pinus strobus*, WS – *Picea glauca*. CR33 – crown thin to 33% density, CR50 - crown thin to 50% density, DOM33 - dominant thin to 33% density, DOM50 - dominant thin to 50% density, LOW33 – low thin to 33% density, LOW50 - low thin to 50% density.

Table 1.6. Species composition as a percentage of plot basal area (BA m²) for sites that received no precommercial thinning (PCT). Pre-treatment data were used.

Site	Species	0.33	0.5	10a	10b	5a	5b	Control
AS	BF	88.4	67.6	95.5	79.6	89.9	86.4	62.9
	NC	0.0	0.0	0.4	1.0	0.0	0.0	0.2
	RS	4.0	14.5	4.1	16.9	2.1	3.1	7.9
	WP	0.0	4.9	0.0	0.0	0.0	0.0	0.0
	WS	7.5	13.1	0.0	2.4	8.0	10.5	29.0
LM	BF	81.3	93.1	86.4	88.5	92.3	77.4	89.9
	NC	18.7	6.9	13.6	9.7	7.7	22.6	10.1
	WS	0.0	0.0	0.0	1.8	0.0	0.0	0.0
LT	BF	73.4	59.0	81.5	63.8	65.2	82.2	55.8
	NC	7.1	2.3	0.1	4.3	1.7	0.5	14.5
	RS	4.8	36.4	18.4	31.4	16.5	17.3	11.0
	WS	14.7	2.2	0.5	0.5	16.6	0.5	18.7
PE	BF	84.9	70.3	60.0	39.8	64.0	52.7	66.4
	EH	3.2	3.4	1.1	0.5	0.3	1.1	8.3
	NC	7.7	13.6	8.2	10.6	8.5	5.4	6.6
	RS	1.3	12.2	27.6	45.1	24.3	39.5	10.4
	WP	0.5	0.5	0.5	3.8	2.7	1.3	0.5
	WS	2.8	0.5	3.1	0.8	0.2	0.5	8.3
RC	BF	86.1	97.4	99.2	96.7	98.7	98.5	94.7
	NC	0.6	2.4	0.8	0.8	0.6	0.5	2.1
	RS	13.3	0.2	0.5	2.5	0.7	1.5	3.2
WB	BF	95.9	88.3	77.7	90.5	85.4	88.4	81.0
	NC	2.9	0.2	8.8	7.0	6.6	3.7	10.2
	RS	1.2	10.9	4.3	2.5	8.0	7.9	6.3
	WS	0.5	0.6	9.1	0.5	0.5	0.5	2.5

Note: See Table 1.1 for site definitions. BF – *Abies balsamea*, EH – *Tsuga canadensis*, NC – non-commercial hardwood species, RS – *Picea rubens*, WP – *Pinus strobus*, WS – *Picea glauca*. 0.33 – 33% density reduction, 0.50 – 50% density reduction, 5a, 10a, 5b, 10b – plots to receive 33% reduction (a) or 50% reduction (b) in five (5) or 10 years (10).

Commercial Thinning Research Network experimental design

The study design involves two studies, each with six sites, arrayed in a randomized-complete-block design with replications. Sites serve as blocks and treatments are arranged in a 2 X 3 factorial design; including two levels of relative density reduction (33% and 50% reduction) and three thinning methods (crown, dominant and low, Smith 1997, chpt. 5) for NOPCT, or timing of entry (0, 5 or 10 years) for PCT, with an untreated control. Seven 0.37 ha (61 m x 61 m) treatment plots with nested 0.08 ha (26.6 m x 30.5 m) measurement plots were established at each site. Measurement plots were further divided into subplots of 0.02 ha (13.2 m x 15.2 m) to aid data collection in extremely dense stands. For trees taller than 1.37 m and greater than 5.1 cm DBH, pre-treatment DBH and species were recorded. Height (HT) and HT to base of live crown were measured on sub-plots and used to predict height of unmeasured trees on each site. On PCT sites, 2.4 m radius subplots were established on each plot corner to tally each tree taller than 1.37 m and smaller than 5 cm DBH. On the NOPCT sites all trees were tallied by species and diameter class.

Plot measurements

Sites were measured for this study the summer after plot treatment, prior to any detectable response. Five plots per site were chosen from the NOPCT stands, the dominant and low thinning 33% and 50% reduction plots to maximize potential treatment contrasts, and the control. Four plots per site were chosen from the PCT stands: the two treated stands (33% and 50% reduction) and the two remaining untreated stands with the highest RD. A total of 49 plots were measured. To accurately represent the range of variability in each site, the 2002 post-thinning plot measurements were stratified into 5.1

cm DBH (1.0 in = 2.54 cm) classes by three live crown ratio (LCR, crown length / tree HT) classes and grouped according to quartiles, class 1 = 0-25%, class 2 = 25-75%, class 3 = 75-100%. This division was selected to represent the entire range in LCR. The LCR classes were calculated relative to the range of LCR for the untreated control at each site. The remaining plot trees were assigned a LCR class based on this range. One in ten trees was randomly selected from each cell in the DBH - LCR array. Individual tree measurements taken on each plot include: DBH, measured with a metal D-tape to the nearest 0.1 cm at 1.3 m above the ground; bark thickness, measured to the nearest mm with a bark gauge at breast height on the north and east sides of the tree; and height (HT) and HT to lowest live branch (LLB) were measured to the nearest 0.1 m with a Haglof© Vertex II hypsometer. Crown class (CC) designations were given to each tree as follows (Smith 1997 p.30, Nyland 2002 p.387), dominant (D), co-dominant (C), intermediate (I) or overtopped (O). Care was taken to instruct field workers of appropriate characteristics to take into account when defining crown class (Nicholas et al. 1991). Two increment cores for each tree were taken 90° apart at breast height using a cordless power drill and increment borer. Sapwood was determined immediately in the field by holding the core to light and marking the boundary between the translucent sapwood and opaque heartwood. They were then placed into grooved boards where both bark and sapwood were marked with an indelible pencil to help with the identification of bark and sapwood boundaries in subsequent lab analysis.

Stem analysis

Seven or eight trees from each site covering a range of DBH and CCs were chosen from the plot buffers, directly outside the measurement plots but within the treatment plots. *A.*

balsamea trees were sampled on PCT sites and site SA, *P. rubens* trees were sampled on NOPCT sites. In total, 94 trees were measured for height and marked on the bole at 1.3 m. The trees were then felled with care to damage as few branches as possible. True tree height was measured and one meter increments marked along the bole. Random sample branches at three positions within the crown, one from the upper half and one each from the two lower quartiles. The crown was divided as such to compensate for the biologic necessity of lower larger branch foliage to recede as it nears mortality (Maguire and Bennett 1996) and to account for known differences in specific leaf area (SLA) with crown depth (Keane and Weetman 1987). Branch basal diameters (BRD) were measured to the nearest 0.1 cm using digital calipers and their associated height was measured from a tape stretched along the bole. Approximately 100 needles were taken from across the range of needle ages for each branch. Needles were immediately placed in plastic bags and put in a cooler. Upon return from the field the needle samples were stored in a freezer until analysis. Sample branches were placed in large paper bags and moved to a drying room.

Sapwood area measurement

The core boards collected during plot sampling were scanned and analyzed using WinDendro 2003a. Prior to scanning core boards were sanded to aid in the distinction between early and latewood cells. North core ring widths from the pith outward were measured for age and sapwood widths (to the nearest 0.001 mm.). East core ring widths were measured from the sapwood mark outward. Any cores with missing pieces, indistinguishable rings or of an obviously older age class were eliminated from the analysis. Sapwood areas (SA) for each tree were determined by subtracting the north and

east core sapwood radii from diameter inside bark (DIB), averaging heartwood areas and subtracting from averaged basal areas inside bark. Before performing any calculations the ring widths were adjusted for radial shrinkage from the following factors; *A. balsamea* - 2.9%, *P. rubens* - 3.8% (Forest Products Laboratory 1999).

Leaf area measurement

SLA (cm^2/g) for each sample branch was calculated, after sorting and separating needles from any bark or branch tissue, by measuring (to the nearest 0.0001 cm^2) the projected needle area (PNA) with WinNeedle software. Needles were then dried for 48 h to determine needle dry weight (NDW) (measured to the nearest 0.001 gram). SLA was determined by dividing PNA by NDW. To estimate branch level leaf area, SLA values were multiplied by weight (grams) of all needles.

Branch and tree leaf area prediction

As part of a concurrent study (Meyer and Seymour, in prep.), branch and tree-level models were developed to predict branch leaf area (BRLA) and projected leaf area (PLA). A Weibull continuous distribution function (Maguire and Bennett 1996) was fitted for *A. balsamea* while *P. rubens* C, D and I trees were best modeled with a log-transformed peaking equation (Maguire et al. 1998). Overtopped trees were best modeled with a simplified version of the same model.

For *A. balsamea*:

$$[1] \quad \sqrt{\text{BRLA}} = 133.95 \text{ BRD}^{1.044} \text{ RDINC}^{(1.999-1)} \text{ EXP}[-(1.414 \text{ RDINC})^{1.999}], R^2 = 0.91$$

For *P. rubens* C, D and I trees:

$$[2] \quad \ln \text{BRLA} = 8.563 + 2.172 \ln \text{BRD} + 0.845 \ln \text{RDINC} - 2.946 \text{ RDINC}, R^2 = 0.86,$$

log bias ratio correction factor (Snowdon 1991) = 1.1421

For *P. rubens* O trees:

$$[3] \quad \ln\text{BRLA} = 2.92 + 3.226 \text{ BRD}, R^2 = 0.82, \text{ log bias ratio correction factor} = 1.1398$$

where BRLA is predicted branch leaf area (cm^2), BRD is branch basal diameter (mm),

RDINC is relative depth into the crown, measured from the leader (0.0) to LLB (1.0).

Tree-level equations (Meyer and Seymour, in prep.) for estimating PLA from SA and crown length were applied to all (*A. balsamea* – $n = 412$, *P. rubens* – $n = 373$) cored trees with sapwood measurements:

For *A. balsamea*:

$$[4] \quad \ln\text{PLA} = -1.802 + 0.797 \ln\text{SA} + 0.969 \ln\text{CL}, R^2 = 0.95, n = 43, \text{ log bias ratio correction factor} = 1.036$$

For *P. rubens*:

$$[5] \quad \ln\text{PLA} = -1.998 + 0.808 \ln\text{SA} + 0.836 \ln\text{CL}, R^2 = 0.87, n = 45, \text{ log bias ratio correction factor} = 0.9976$$

where PLA = predicted leaf area ($\text{m}^2 \text{ m}^{-2}$), SA = sapwood area (cm^2), CL = crown length (m). Residual analysis for each model was undertaken to ensure unbiased predictions across sites and to validate linear model assumptions.

Leaf area index estimation

SA equations ([4] and [5] above) were used to estimate PLA for all the plot measurement trees. From these results, site-specific (Gilmore and Seymour 2004) PLA models of the form $\ln\text{PLA} = b_0 + b_1 \ln\text{DBH} + \varepsilon$ were developed for the purpose of predicting PLA of non-cored trees (Table 1.7).

Table 1.7. Fit statistics \pm standard errors of tree-level projected leaf area (PLA)prediction models for *A. balsamea* and *P. rubens*.

Site	$b_0 \pm \text{s.e.}$	$b_1 \pm \text{s.e.}$	R^2	n	Bias ratio correction factor
For <i>Abies balsamea</i>					
AS	-1.917 ± 0.239	2.040 ± 0.090	0.90	54	1.0098
LM	-2.581 ± 0.395	2.155 ± 0.143	0.80	53	1.0454
LT	-1.638 ± 0.283	1.913 ± 0.106	0.87	44	1.0180
RC	-1.897 ± 0.322	1.991 ± 0.119	0.81	62	1.0240
RR	-6.086 ± 0.458	3.459 ± 0.199	0.84	54	1.0109
SA	-4.258 ± 0.298	2.832 ± 0.170	0.88	69	1.0710
WB	-3.445 ± 0.369	2.552 ± 0.142	0.83	63	1.0236
Pooled data	-2.752 ± 0.212	2.303 ± 0.079	0.95	43	1.0081
For <i>Picea rubens</i>					
GR	-5.137 ± 0.429	2.845 ± 0.168	0.84	51	1.0224
HR	-4.964 ± 0.489	2.733 ± 0.178	0.78	63	1.0212
RR	-3.871 ± 0.299	2.518 ± 0.119	0.90	48	1.0050
SC	-5.035 ± 0.498	2.720 ± 0.184	0.74	76	1.0681
SR	-3.816 ± 0.226	2.387 ± 0.092	0.86	105	1.0458
Pooled data	-3.949 ± 0.383	2.435 ± 0.139	0.87	44	1.0368

Note: log bias ratio correction factor defined by Snowdon (1991), R^2 as defined by

Kvålseth (1985), sites defined in Table 1.1.

For application where a site-specific model was not possible due to limited representatives of either species, an overall model was fit from the destructively sampled trees. All models were unbiased and normal with 74 – 95% of the variation accounted for.

All-sided leaf areas may be more appropriate than PLAs when physiological phenomenon such as direct measurement of light interception or respiration is needed since projected LAI does not take into account needle morphology, which differs slightly between *A. balsamea* and *P. rubens*. Because many plots include both species PLAs were converted to all-sided leaf areas (ALA), using published ratios of 2.3 for *A. balsamea* (Hunt et al. 1999) and 2.9 for *P. rubens* (Day 2000). These values fall within general limits suggested by Margolis et al. (1995). LAI was then calculated by summing tree-level ALAs on a per-plot basis and dividing by the plot area. Any plot with less than 80% *A. balsamea* – *P. rubens* species composition was eliminated from further analysis ($n = 6$). LAI values included *P. rubens* and *A. balsamea* trees only.

Analysis

Principal components analysis (PCA) was employed to reduce the post-treatment, plot data to a biologically justifiable and parsimonious structure. Linear relationships of the general form $Y = \beta_0 + \beta_1 X + \dots + \varepsilon$ were fitted with the general linear model (GLM) procedure in SYSTAT 10.2. All mean comparisons were done with analysis of variance (ANOVA). Various patterns were examined to assess the use of RD as an independent variable to predict LAI. The effect of age on observed levels of LAI was tested by using the mean of the tallest 100 TPHA (TOPHT) as a surrogate. The effect of species composition on LAI is graphically assessed. A common significance level of $\alpha = 0.05$

was used for all tests. Pearson's correlations coefficient (r^2), mean squared errors (MSE) and generalized coefficients of determination (R^2) defined in (Kvålseth 1985) are reported.

RESULTS

Two principal components accounting for 76% and 18% of the overall variation in the data structure were revealed by PCA ordination (Fig. 1.2). The 1st axis largely explains the differences in SI, species composition, age and RD between the PCT and NOPCT sites. Plot top height, age and RD had strong positive contributions to the 1st axis (see Fig. 2 axes labels), while species and SI contributed negatively (Table 1.8). Interestingly the 2nd axis had strong positive loadings for LAI and RD, the initial desired independent and dependent variables respectively, of this study. Gaussian ellipses (80% confidence interval) centered on treatment history means revealed distinct segregation of the PCT and NOPCT sites (Fig. 1.2) with the exception of site SA that overlaps both populations (hand-drawn ellipse, Fig. 1.2). Site SA is similar to the other NOPCT sites in spacing and RD only, SI (19.2 m at 50 years compared to ~ 14 m for NOPCT sites), age (mean dominant age of 33 years falls outside the 95% CI for NOPCT sites ($35 < 52 < 68$) and within that of PCT sites ($21 < 28 < 36$) and species composition (near homogenous *A. balsamea* Tables 5 and 6) were all similar to the PCT sites. These results put site SA in a unique position to bridge observed relationships of NOPCT and PCT spacing histories.

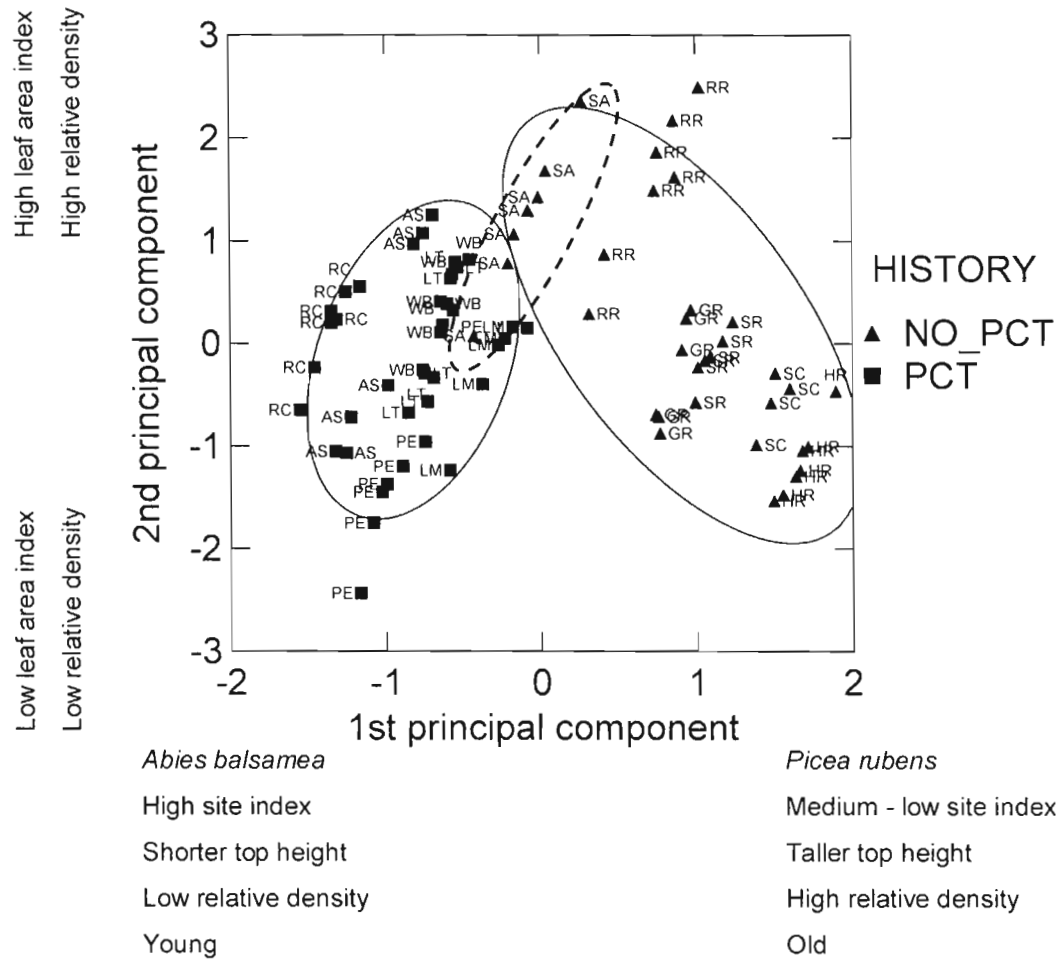


Fig. 1.2. Ordination plot of two principal components (PCs) with eigenvalues > 1.0

Gaussian confidence ellipses (80%) centered on history of precommercial thinning (PCT or NOPCT) means. A hand-drawn dotted ellipse around site SA suggests differences from both PCT histories. Positive or negative loadings are indicated by axes labels location. Points are labeled by site.

Table 1.8. Factor loadings (percent) of plot variables after varimax rotation, eigenvalues (> 1.0) and percent of total variation explained

Site characteristic	1 st principal component	2 nd principal component
Species	-0.933	0.115
Plot top height	0.963	0.036
Leaf area index	-0.437	0.888
Relative density	0.804	0.537
Site index	-0.984	-0.059
Site age	0.975	-0.031
Eigenvalue	4.553	1.095
% of total variance explained	75.8	18.3

LAI predictions and site quality

Examination of residual plots from initial prediction equations of LAI over RD revealed bias with respect to SI, TOPHT and % *Abies balsamea* (percentage *A. balsamea* by basal area) for both spacing histories (Fig. 1.3), suggesting potential inclusion of these terms as additional predictors of LAI. The final model for PCT sites was:

$$[6] \quad \text{LAI} = -17.59 + 37.71 \text{ RD} + 0.788 \text{ SI}, R^2 = 0.89, n = 41$$

For NOPCT sites:

$$[7] \quad \text{LAI} = -5.231 + 6.885 \text{ RD} + 0.766 \text{ SI}, R^2 = 0.69, n = 37$$

where RD = relative density, SI = site index and TOPHT = mean height of tallest 100 TPHAs.

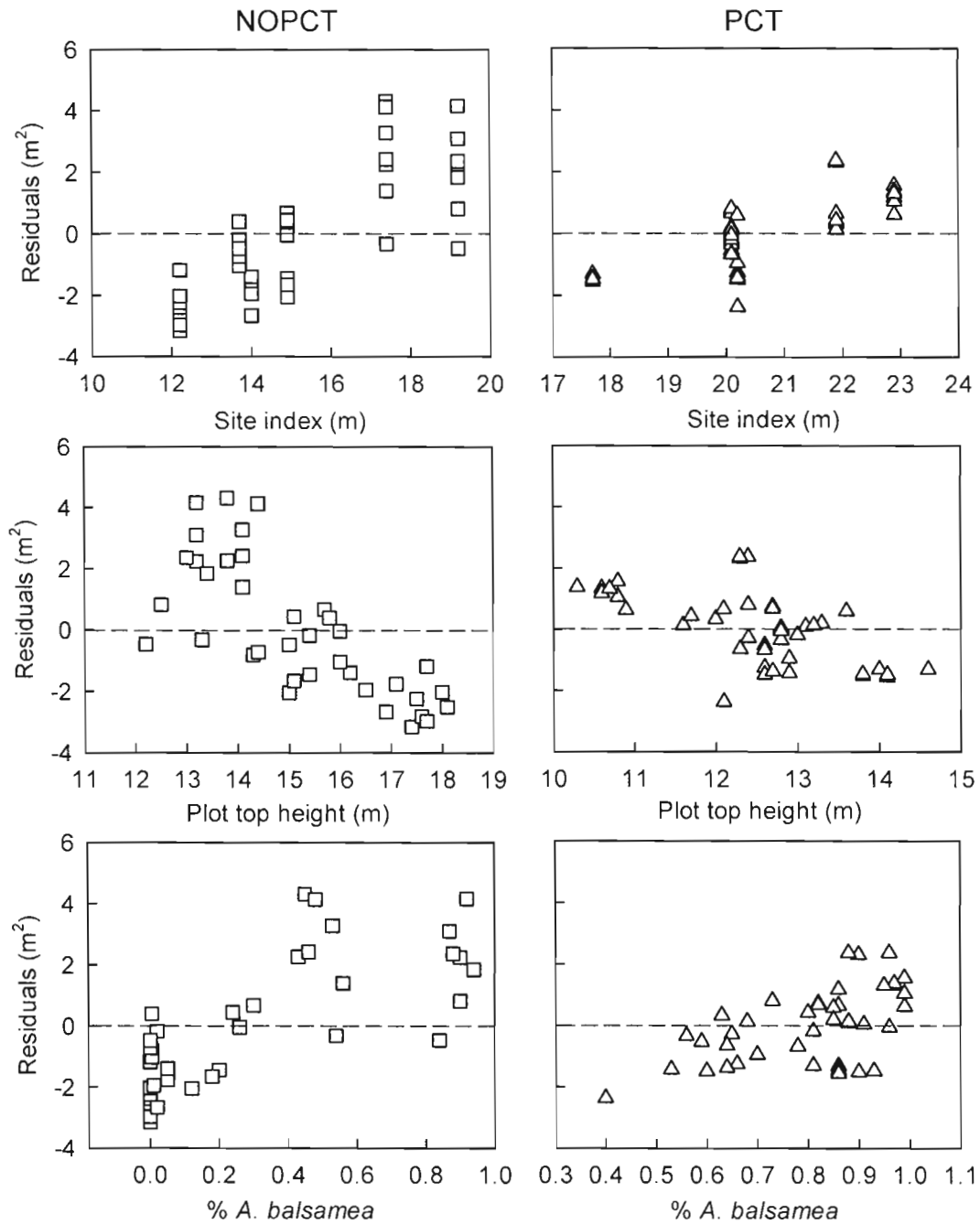


Fig. 1.3. Plots of residuals from the linear regression of LAI predicted from RD, by management history, showing potential bias with respect to site index (SI), plot top height (TOPHT) and % *Abies balsamea* composition

Note: Y-axes on similar scales, X-axes on different scales.

SI increased the variation accounted for from 46% to 89% in the PCT group. Collinearity between SI and TOPHT precluded its use in the model, however, SI served as a proxy for TOPHT since they were highly correlated ($r^2 = 0.90$). SI, while not solely related to LAI in PCT stands (Fig. 1.4), was highly significant ($P < 0.000$) in the overall model. TOPHT was not significant in predicting LAI of the older NOPCT sites. The term to describe the ratio of *A. balsamea* / *P. rubens* composition (% *Abies balsamea*) was not significant for PCT or NOPCT sites. Interestingly, RD was only significant ($P < 0.024$) in predicting LAI when SI ($P < 0.000$) was also included in the model, a consequence of the highly significant relationship between LAI and SI (Fig. 1.4). This suggests maximum LAI is strongly influenced by site quality.

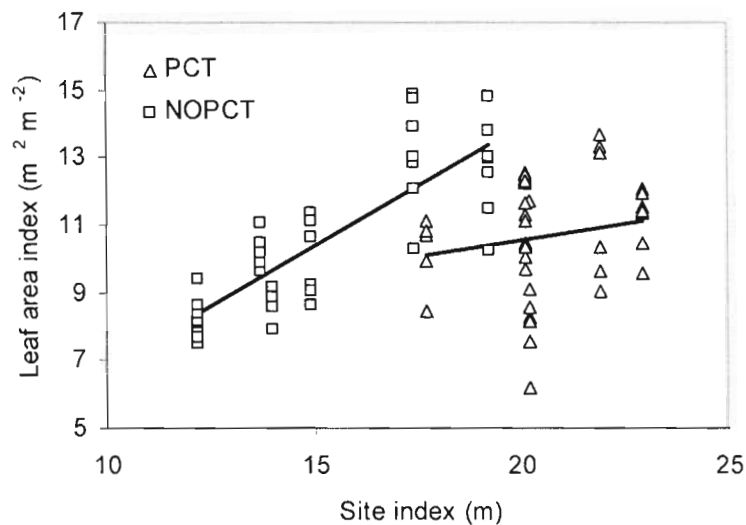


Fig. 1.4. Leaf area index (LAI) predicted from site index (SI) for each spacing history
NOPCT – LAI = $-0.283 + 0.710 \text{ SI}$, $R^2 = 0.65$, $P < 0.000$, PCT – LAI = $6.729 + 0.191 \text{ SI}$,
 $R^2 = 0.009$, $P = 0.246$. SIs are significantly different for each history, NOPCT = 15.4, $n=$
37, PCT = 20.6, $n=41$, $P < 0.000$.

LAI – RD patterns

Plotting best-fit prediction equations illustrate a positive trend of LAI over RD for both groups (Fig. 1.5). However, acceptance of hypothesized trend A cannot be made until effects of SI, age and species are reconciled. Differences in the LAI - RD relationship are evident for each group. The high site quality PCT sites, if viewed as a chronosequence, are clearly on an increasing trajectory and likely are still accumulating LAI because stands at such low RDs have not yet started to self-thin. NOPCT sites display a much wider spread of LAI perhaps as a result of larger variation in SIs and age. In contrast, most of the NOPCT stands have achieved RDs at which self-thinning is likely (i.e. RDs > 0.5). When LAI is standardized (SLAI) by the overall SI mean (18.1 m), to eliminate the apparent effects of site, the pattern over RD for both spacing histories can be viewed as a failure to reject hypothesized trend A (Fig. 1.6). Observations from Baskerville (1965) suggest what would have been observed had high density *A. balsamea* stands also been measured. The lack of data at the intersection of the two spacing histories, which occurs coincidentally at the apparent onset of self-thinning (Wilson et al 1999) makes it difficult to quantify the seemingly critical 'join point' of the two lines, if indeed they are one and the same population.

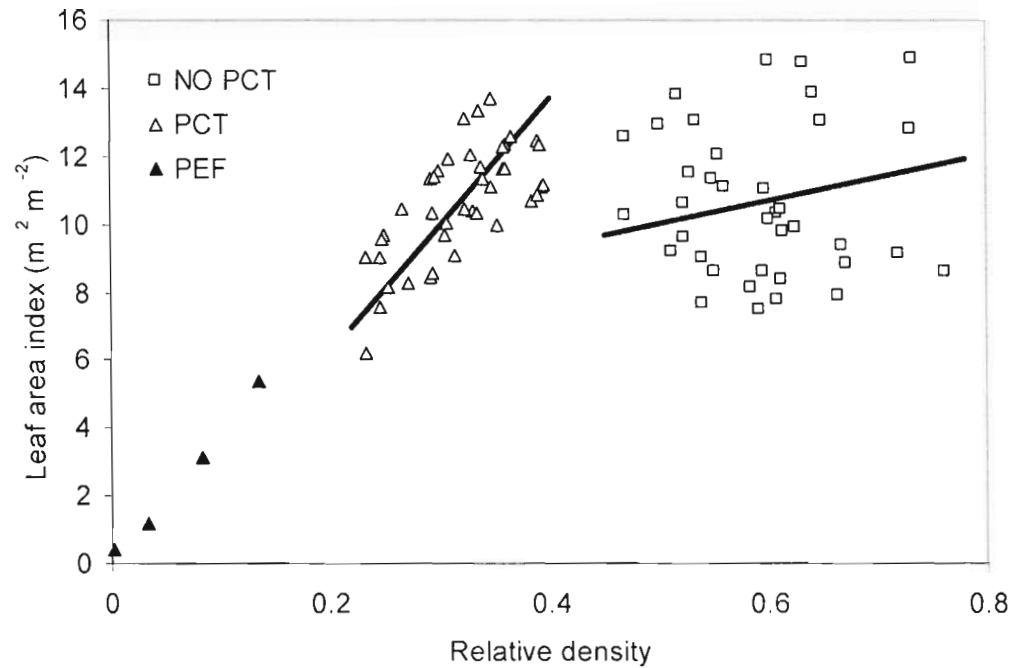


Fig. 1.5. Leaf area index (LAI) plotted over relative density (RD) for the CTRN plots
PCT - $\text{LAI} = -17.59 + 37.71 \text{ RD} + 0.788 \text{ SI}$, $R^2 = 0.89$, $n = 41$ and NOPCT - $\text{LAI} = -$
 $5.231 + 6.885 \text{ RD} + 0.766 \text{ SI}$, $R^2 = 0.69$, $n = 37$

Note: PEF = Penobscot Experimental Forest reference stands (▲) included to suggest an early trajectory of stand LAI – RD development, not used for fitted PCT line.

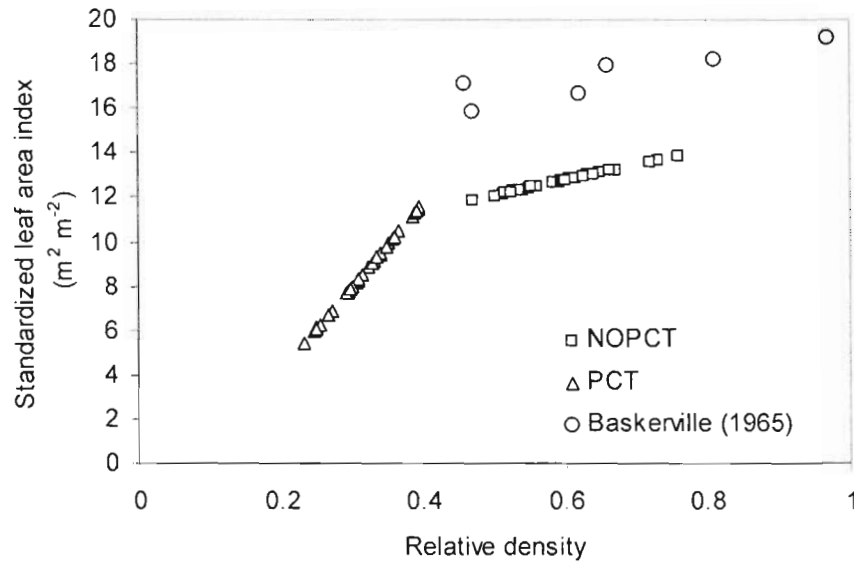


Fig. 1.6. Standardized leaf area index (SLAI $\text{m}^2 \text{m}^{-2}$) plotted over relative density (RD) for each spacing history.

Note: Data from Baskerville (1965) leaf area index (LAI) and RD converted from foliage biomass and volume respectively with data from this study.

Age

TOPHT is an appropriate surrogate for age in this study ($\text{TOPHT} = 9.176 + 0.118 \text{ AGE}$, $R^2 = 0.93$, $P < 0.000$). Only when SLAI is viewed over TOPHT (Fig. 1.7) can we suggest trends through time. It appears (Fig. 1.7) SLAI increases with TOPHT to $\sim 14 \text{ m}$ where it levels off while HT continues to increase. This suggests any LAI decline due to crown abrasion (suggesting trend C) was not detected. RD plotted over TOPHT as a surrogate for age reveals the distinct, SI independent, trajectories of each spacing history (Fig. 1.8). The void between point clouds likely indicates the start of self-thinning and the shift from significantly increasing RD (lower line) to non-significant increases at older ages (upper line).

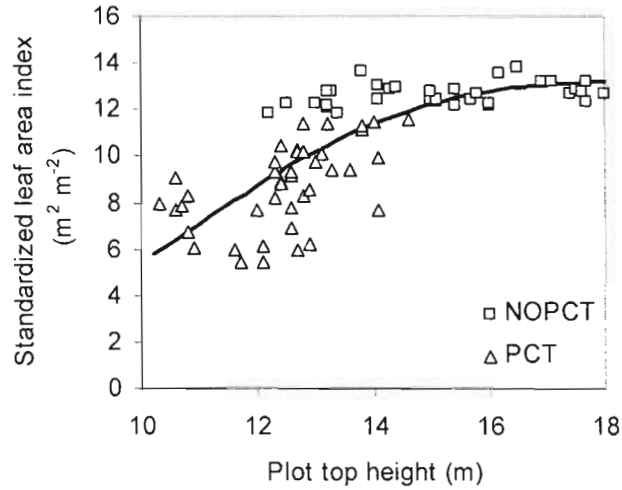


Fig. 1.7. Standardized leaf area index (SLAI) plotted over plot top height (TOPHT) as a surrogate for age, by treatment history

$$\text{SLAI} = 13.286 (1 - \text{EXP} [-(\text{TOPHT} / 11.784)^{3.911}]), R^2 = 0.58, \text{MSE} = 2.509, n = 78.$$

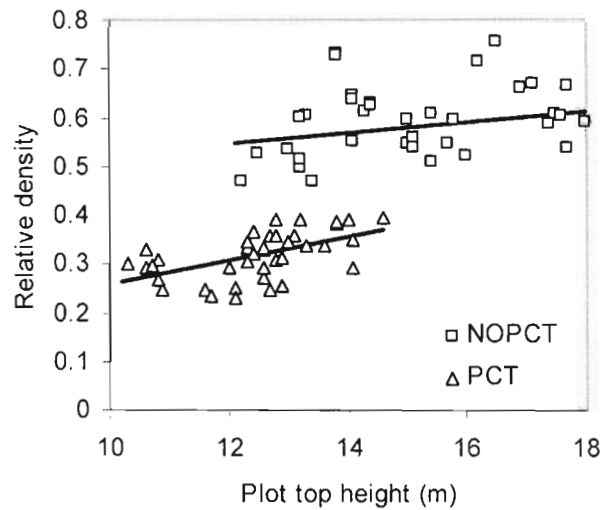


Fig. 1.8. Relative density (RD) plotted over plot top height (TOPHT) as a surrogate for age, by treatment history

$$\begin{aligned} \text{NOPCT} - \text{RD} &= 0.415 + 0.011 \text{ TOPHT}, R^2 = 0.05, P = 0.096, n = 37, \\ \text{PCT} - \text{RD} &= 0.0072 + 0.025 \text{ TOPHT}, R^2 = 0.28, P < 0.000, n = 41. \end{aligned}$$

Species composition

Regression of SLAI over species composition in the self-thinning stands (Fig. 1.9) suggests that sites with a higher percentage of *A. balsamea* have slightly less SLAI. The slope of the line is relatively flat indicating any differences due to species composition, after site quality has been taken into account, are small. The negative slope of the line is more likely due to young, *A. balsamea* stands having more SLAI than old, *P. rubens* stands. Sites of similar species composition and age are lacking in this study making a more formal test of LAI due to species composition unjustified.

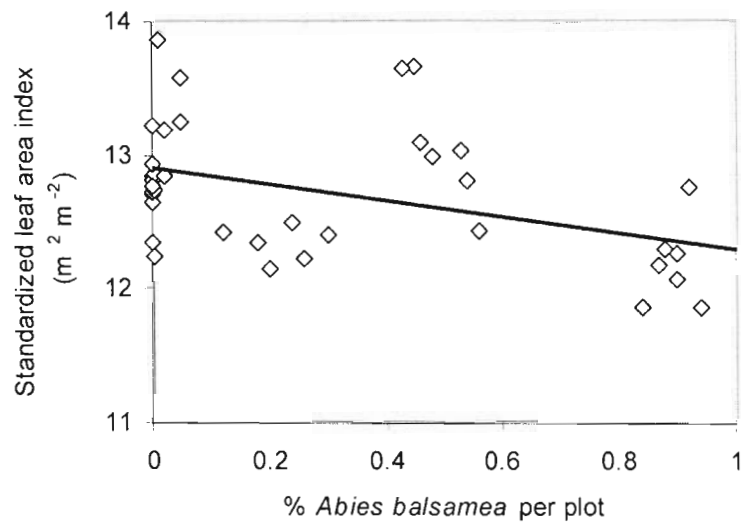


Fig. 1.9. Standardized leaf area index ($\text{m}^2 \text{m}^{-2}$) over % *Abies balsamea* per plot by basal area (BA)

$$\text{SLAI} = 12.9 - 0.589 \% \text{ Abies balsamea}, R^2 = 0.14, P < 0.013$$

DISCUSSION

Spacing histories

The ordination plot clearly showed the data in this study comprised two distinct spacing history groups, PCT and NOPCT. To elucidate why dividing the data analysis by spacing histories of the stands clarified the relationship between LAI and RD, we will consider the effects of PCT on these populations in more detail. PCT lets more sunlight into the lower canopy, increases branch retention allowing trees to maintain longer crowns. Since NOPCT plots reached crown closure earlier in stand development than PCT plots, the concomitant early crown recession, resultant shorter crowns and lower mean leaf areas per tree are expected (Table 4). This phenomenon is illustrated for mean-tree all-sided LA of each plot over density (Fig. 1.10). Additionally, the trade-off between individual tree and stand-level growth is a result of the distribution of the site maximum LAI, whether it is divided among a few large individuals or many smaller trees (Long and Smith 1984, Long 1985). While early PCT allows more LA per tree, it comes at the expense of early stand-level growth, causing maximum LAI to be reached later in age. If trees are similar in size, crown length is strongly related to density in self-thinning stands (Long 1985, Fig. 1.3). Initial density and early spacing will ultimately guide how wide the crowns become before inter-tree competition begins and crown abrasion occurs (Long and Smith 1992). Crown length and width will continue to be a function of height growth (Curtis and Reukema 1970, Mitchell 1975, Jack and Long 1991b) and crown position within even-aged stands.

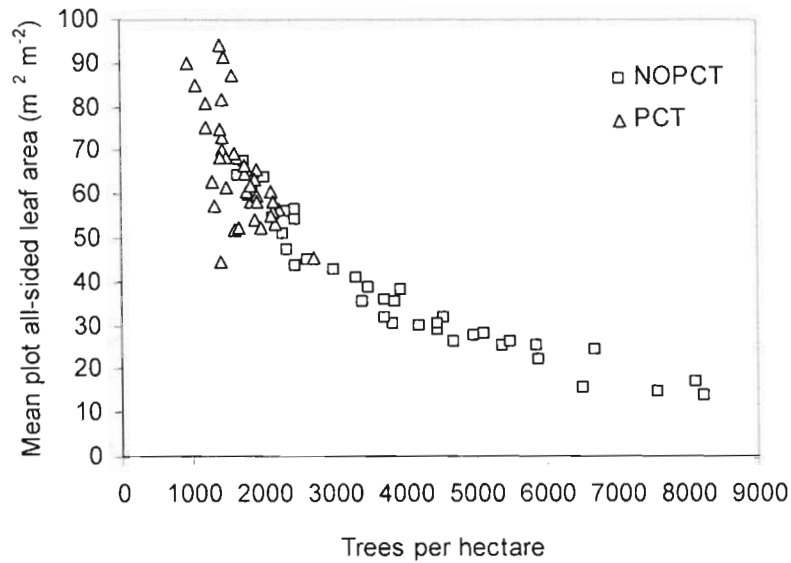


Fig. 1.10. Mean projected leaf area per plot over stems per hectare (TPHA) by spacing history

Predicting LAI

It appears (Fig. 1.3) the significant relationship between LAI and RD for PCT stands is a result of the young, *A. balsamea* stands having not yet reached maximum LAI. They also have RDs below the average self-thinning trajectory (Wilson et al. 1999). NOPCT sites (Fig. 1.3) however, have reached the “zone of imminent competition mortality” (Drew and Flewelling 1977) where self-thinning is underway and, in this study, LAI is weakly correlated to density (Fig. 1.5). The fact that LAI and RD are significantly correlated at high densities in this study provides evidence in support of trend A (Fig. 1.1) but also suggest RD as a sole predictor of LAI can be biased if site, age and *A. balsamea* – *P. rubens* composition are not also considered (Fig. 1.3).

The high SI, PCT, primarily *A. balsamea* stands provide a strong model with which one can predict stand-level LAI (eq. 6). The absence of data > 0.4 RD for PCT stands

(Fig. 1.5) makes LAI predictions in this range tenuous. This lack of data does not preclude predictive power of the model in stands with high SIs (14.8 – 22.9 m, base age 50) and RDs < 0.4. A model for NOPCT sites is also presented (eq. 7) for use in stands with RDs between 0.55 and 0.9 on medium quality sites (SIs 12.2 – 17.3 m, base age 50) with no spacing history. Interestingly, the term to describe species composition did not improve model fits for either spacing history despite showing potential bias in the residual analysis. Unfortunately with this limited range of data aspects of early stand dynamics are purely speculative, although the Penobscot Experimental Forest (PEF) long-term re-measurement data suggest a possible pattern (Fig. 1.5). The increasing nature of both relationships suggests conformance to trend A (Fig. 1.1).

Comparison with species from other geographic areas (Table 1.9) provides support that our vertically diverse stands of even-aged *P. rubens* and *A. balsamea* attain LAIs similar to those of other shade-tolerant conifers. Estimates of LAI for *A. balsamea* in Newfoundland nicely correspond to ours although no mention is made of site structural attributes or quality (Hunt et al. 1999). Smith and Long's (1989) *Abies lasiocarpa* one-sided LAI estimates, from a range of site quality would be much higher than our *A. balsamea* after conversion to all-sided leaf area. No published estimates of LAI for even-aged *P. rubens* exist however; half all-sided LAI estimates for *Picea abies* (Kußner and Mosandl 2000) span our data range and include much larger values.

Table 1.9. Leaf area index (LAI $\text{m}^2 \text{m}^{-2}$), location and reference of mid to very shade-tolerant species from a number of studies

Species	Location	LAI ($\text{m}^2 \text{m}^{-2}$)	Source
<i>Abies balsamea</i>	Maine	6.2 – 14.8	This study
<i>Abies balsamea</i>	Newfoundland	3.0 – 13.0	Hunt et al. (1999)
<i>Abies balsamea</i>	New Brunswick	15.9 – 19.2 ^a	Baskerville (1965)
<i>Abies lasiocarpa</i>	Utah	3.0 – 14.1 ^b	Smith and Long (1992)
<i>Picea abies</i>	Germany	6.2 – 25.5 ^c	Kußner and Mosandl (2000)
<i>Picea rubens</i>	Maine	7.5 – 14.9	This study
<i>Pinus strobus</i>	North Carolina	5.5 ^b	Vose and Swank (1990)
<i>Pseudotsuga menziesii</i>	Washington	8.6 ^b	Thomas and Winner (2000)
<i>P. menziesii</i> and <i>Tsuga heterophylla</i>	Oregon	8.3	Marshall and Waring (1986)

Note: ^a LAIs converted from SLAs used in this study, ^b indicates projected leaf area index ($\text{m}^2 \text{m}^{-2}$), ^c originally reported as half all-sided leaf area index ($\text{m}^2 \text{m}^{-2}$), doubled in table for comparison.

Site quality

Variations in site that are known to influence LAI (Grier and Running 1977, Waring et al. 1978, Gholz 1982) and productivity (Williams et al. 1991, Meng and Seymour 1992) are difficult to reconcile across such a broad geographic range, although selection for similarity of CTRN sites was rigorous. Further, although the stands in this study appear even-aged and are appropriately classified as such, they are the result of advance regeneration released by overstory removals, which make actual tree age more variable than plantation origin, even-aged stands. This range is much larger than typically defined (i.e. < 20% of rotation age) for even-aged stands (Appendix Tables A.1 and A.2). The fact that shade tolerant species develop complex vertical structures where I and O trees survive many meters below the main canopy (Roberts and Long 1992) and the

possibility, especially of *P. rubens*, to persist in the understory adds complexity to the observed relationships.

Although climate is thought to be an important factor determining maximum LAI (Waring et al. 1978), site quality (measured as SI) better explains the differences in LAI levels observed in this study. Since highly productive sites are commonly chosen to receive PCT, the high LAIs observed at early ages may arise partially as a result of inherently better site quality. Even site SA, which did not receive PCT, has a moderate SI when compared to other *A. balsamea* stands, reaching ~ 19 m in HT at 50 years when it takes the same amount of time for an average *P. rubens* site to attain ~14.5 m. The significant linear relation between LAI and SI found in NOPCT stands suggests SI influences LAI carrying capacity (Long and Smith 1990). That higher SIs yield higher LAIs at younger ages helps to explain the variation of LAIs observed in NOPCT stands. This relationship was not found in PCT stands where early spacing reduced LA, likely lengthening the time needed to reach maximum LAI when compared to similar, unspaced stands such as site SA.

In an attempt to reconcile the complicated interactions of SI by species and age consider the following comparisons; Site SA (SI = 19.2, age = 33, NOPCT) and site LM (SI = 17.7, age = 38, PCT) both relatively similar in age and different in SI, have large differences in mean LAIs, 12.7 at 0.52 RD and 10.4 at 0.37 RD respectively. Further, consider site WB (SI = 20.1, age = 28, PCT), which has a mean LAI of 11.1 at 0.36 RD, also similar in age but of higher SI than site SA. These sites, taken together, provide evidence that the LAI levels observed in this study are best explained by a combination of SI and RD.

LAI – RD patterns

This was not the first study to find a relationship between foliage and stand density; Baskerville (1965) found a weak positive trend between these metrics for *A. balsamea* in New Brunswick. Kenefic (2000) found a pattern similar to trend A in multi-aged, mixed species stands in central Maine. Similarly Jack and Long (1991a) found intolerant *P. contorta* and shade-tolerant *A. lasiocarpa* exhibited a pattern similar to trend A. Long and Smith (1984) found that foliar biomass in young stands of *Pseudotsuga menziesii* (Mirb.) Franco was correlated with density and that little relation exists after maximum foliage was reached. Given the marked silvical similarities of *A. balsamea* and *P. rubens*, specifically tolerance of shade and self-thinning relations (Wilson et al. 1999), the combination of *A. balsamea* - *P. rubens* data (Fig. 1.5) suggests a possible trend in LAI development with increasing RDs. Taken separately, the patterns observed for both species here support trend A (Figs. 1.1 and 1.6). The similarity within PCT sites in combination with foliage biomass values from Baskerville (1965) converted to LAI allows their use as a chronosequence (Fig. 1.6). When plotted over RD the trend in these points suggests the PCT sites will continue to increase in LAI. Since they are still relatively young, one could speculate a further increase in LAI, albeit at a much slower rate, based on published values (Table 1.9, Fig. 1.6).

Age

LAI was found to increase with time to about 14m in HT, after which LAI remained relatively constant (Fig. 1.7), a finding with relevance to the phenomenon of crown abrasion in older, even-aged stands. Crown abrasion, or ‘shyness’, has been attributed to the increasing sway of trees as they grow taller (Long and Smith 1992). Rudnicki et al.

(2003) found a negative relationship between crown cover, as a measure of leaf area, and stand height in *P. contorta*. In a chronosequence of *P. contorta* stands Long and Smith (1992) found LAI peaked at approximately 40 years of age and gradually decreased with increasing age (their Fig. 2). Given the range of NOPCT, *P. rubens* site ages in this study (39 - 76 yrs), it is possible they have experienced leaf area loss. This study, however, offers no evidence to support any reduction in LAI with increasing HT or age.

Species composition

The most difficult relationship to reconcile in this study was the effect of plot species composition on LAI. A plot of SLAI over % *A. balsamea* composition suggested that pure *P. rubens* stands had more LAI than those without. Unfortunately this result is inherently confounded with respect to TOPHT. If differences in LAI between species composition exist they are small. Previous work has shown similar ecological behavior between *P. rubens* and *A. balsamea* when they were combined to construct density management diagrams (Wilson et al. 1999). This particular management tool relies on the ecological rule of self-thinning (Jack and Long 1996), shown to be driven by LA (Westoby 1977), which suggests both species, when in the same growing conditions, have similar LA plasticity.

CONCLUSIONS

RD as a sole predictor for LAI in even-aged stands of *A. balsamea* and *P. rubens* ignores the inherent relationships of LAI to SI. After taking these variables into consideration, LAI prediction models were built for the ranges of data sampled (Fig. 1.5). Site index strongly influenced the observed levels of LAI for self-thinning stands. Differences in LAI as a result of species composition were small but no formal test was conducted.

Individually, the data are poorly suited to fully distinguish which trend of LAI over RD (Fig. 1.1) stands of these species follow. When standardized by site index *A. balsamea* – *P. rubens* stands exhibit trend A. No evidence of either trend B or C was found.

**CHAPTER TWO: VOLUME INCREMENT AND GROWTH
EFFICIENCY IN EVEN-AGED *ABIES BALSAMEA* – *PICEA RUBENS*
STANDS**

ABSTRACT

Volume increment (VINC) and growth efficiency (GE) were studied in even-aged *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg. stands in Maine. Dominant and codominant trees from 12 sites across the state of Maine were used to test for differences in GE by site quality. Young *A. balsamea* trees ($n = 205$) were pre-commercially thinned (PCT) 15 – 20 years ago while the older *P. rubens* trees ($n = 173$) were not. A model incorporating individual tree all-sided leaf area (ALA) and site index (SI) best predicted VINC. A monotonic decreasing pattern of GE over ALA was found for both species; GEs were higher overall for *P. rubens*. GE was used with previously reported LAIs from the same sites to calculate mean annual increments, periodic annual increments (PAI), and stand-level GE. These metrics showed all sites in this study have yet to achieve culmination of mean annual increment. Stand-level GEs were similar for both species, although *P. rubens* occurred on lower-quality sites. *P. rubens* were more productive when viewed in terms of PAI per unit of SI.

INTRODUCTION

Projected leaf area (PLA m^2) and its relationship to stemwood volume increment (VINC dm^3), growth efficiency (GE), defined as VINC / PLA has been extensively used in the literature to assess stand vigor (Blanche et al. 1985, Kaufmann and Ryan 1986), production (O'Hara 1988 Long and Smith 1990, Roberts and Long 1992), and response to cultural treatments (Binkley and Reid 1984, Velazquez-Martinez et al. 1992). While differences in GE have been found between structural characteristics (Long and Smith 1990, Roberts and Long 1992, Gilmore and Seymour 1996), shade tolerance (Roberts and Long 1993) and ages (Seymour and Kenefic 2002), GE behavior with varying site quality has received relatively little study, particularly when the variation in site is a natural environmental gradient and not induced by fertilization.

By definition GE is the combination of tree-level attributes (VINC and PLA). The implied trends of GE over PLA have been shown to behave in three distinct patterns: monotonic increasing, sigmoid and monotonic decreasing (Seymour and Kenefic 2002). The PLA – VINC relationships associated with these patterns are of particular interest, specifically the monotonic decreasing found for conifers in Maine (Gilmore and Seymour 1996, Maguire et al. 1998) and elsewhere for other species (Assmann 1970, Oren et al. 1987, Long and Smith 1990, Roberts et al. 1993). This constantly decreasing trend reflects less VINC per unit PLA as crown size increases, which equates to lower GE for large-crowned trees.

Increasing the amount of light or nutrients trees receive through cultural treatments obviously increases productivity, but is this the result of increases in leaf area index (LAI), GE or both? Fertilization has been shown to affect both stand-level LAI and GE

(Brix 1983, Binkely and Reid 1984, Stoneman and Whitford 1995,) in specific cases. In a study of Eucalypts in Hawaii Binkley et al. (2004) found similar evidence for stands which had different combinations of fertilization and irrigation. Velasquez-Martinez et al. (1992) found GE increases in response to thinning, but only when fertilizer was also applied. Vose and Allen (1988) found LAI increased significantly in response to thinning but GE was not affected in two of three stands. Although these studies all controlled resource availability to assess potential treatment effects as a result of cultural intervention on GE, they fall short of assessing differences in natural site variability.

Fertilization obviously affects PLA – VINC relationships and, if representative of limitations in natural stands, suggests GE differs with site quality. Better understood relationships known to exist between GE and crown size can help to elucidate the effect of site on GE. In this study *Abies balsamea* (L.) Mill and *Picea rubens* Sarg. data, collected statewide over a range of site qualities, were used to assess relationships between GE, leaf area and site index (SI). The specific purpose of this research was to ascertain whether differences in GE were related to SI.

METHODS

Study sites

The Cooperative Forestry Research Unit (CFRU) Commercial Thinning Research Network (CTRN) sites were used for this study and are described in detail elsewhere (chapter one). These sites were selected for treatment, measurement and assessment of a number of forest management activities including intensive silviculture, harvest practice effects, forest growth and economic return. During site selection care was taken to ensure similarity between sites for each installment (R. Seymour, R. Wagner pers. comm.). Sites

are dominated by either *Picea rubens* Sarg. or *Abies balsamea* (L.) Mill. but also include *Picea glauca* (Moench) Voss., *Tsuga Canadensis* (L.) Carr. and *Pinus strobus* L. All CTRN sites fall within the Acadian Forest Region (Table 1.1) with the Northern Hardwood Forests to the south and the Boreal Forest to the north (Rowe 1972). Sites were naturally regenerated by even-aged silvicultural methods. Six sites have a history of precommercial thinning (PCT) in the early 1980s and are dominated by *A. balsamea* (Table 1.6) while the other six sites have no history of precommercial thinning (NOPCT) and are dominated by *P. rubens* and *A. balsamea* (Table 1.5).

Plot measurements

Sites were measured for this study the summer after plot treatment, prior to any detectable response (Table 2.1).

Table 2.1. Sample tree and site attributes

<i>Abies balsamea</i>	Mean \pm s.e.	Minimum	Maximum	<i>n</i>
Age	27 \pm 1	15	14	205
Height (HT m)	12.7 \pm 0.11	7.8	17.1	205
All-sided leaf area (ALA m ² m ⁻²)	99.4 \pm 3.2	6.7	247.8	205
Stemwood volume increment (VINC dm ³ yr ⁻¹)	8.3 \pm 0.26	1.827	26.56	205
Growth efficiency (GE dm ³ m ⁻²)	0.086 \pm 0.001	0.044	0.174	205
Site index (SI m)	20.6 \pm 0.13	17.7	22.9	5
Relative density	0.33 \pm 0.05	0.23	0.39	19
<i>Picea rubens</i>				
Age	55 \pm 1	31	81	173
Height (HT m)	14.5 \pm 0.16	7.5	19.8	173
All-sided leaf area (ALA m ² m ⁻²)	58.6 \pm 3.3	21.8	262.1	173
Stemwood volume increment (VINC dm ³ yr ⁻¹)	5.3 \pm 0.26	1.138	22.15	173
Growth efficiency (GE dm ³ m ⁻²)	0.098 \pm 0.002	0.039	0.182	173
Site index (m)	14.3 \pm 0.13	12.2	17.4	5
Relative density	0.61 \pm 0.07	0.51	0.76	20

Five plots per site were chosen from the NOPCT stands, the dominant and low thinning 33% and 50% reduction plots to maximize potential treatment contrasts, and the control. Four plots per site were chosen from the PCT stands: the two treated stands (33% and 50% reduction) and the two remaining untreated stands with the highest RD. A total of 49 plots were measured. To accurately represent the range of variability in each site, the 2002 post-thinning plot measurements were stratified into 5.1 cm DBH (1.0 in = 2.54 cm) classes by three live crown ratio (LCR, crown length / tree HT) classes and grouped according to quartiles, class 1 = 0-25%, class 2 = 25-75%, class 3 = 75-100%. This division was selected to represent the entire range in LCR. The LCR classes were calculated relative to the range of LCR for the untreated control at each site. The remaining plot trees were assigned a LCR class based on this range. One in ten trees was randomly selected from each cell in the DBH - LCR array. Individual tree measurements taken on each plot include: DBH, measured with a metal D-tape to the nearest 0.1 cm at 1.3 m above the ground; bark thickness, measured to the nearest mm with a bark gauge at breast height on the north and east sides of the tree; and height (HT) and HT to lowest live branch (LLB) were measured to the nearest 0.1 m with a Haglof© Vertex II hypsometer. Crown class (CC) designations were given to each tree as follows (Smith 1997 p.30, Nyland 2002 p.387), dominant (D), co-dominant (C), intermediate (I) or overtopped (O). Care was taken to instruct field workers of appropriate characteristics to take into account when defining crown class (Nicholas et al. 1991). Two increment cores for each tree were taken 90° apart at breast height using a cordless power drill and increment borer. Sapwood was determined immediately in the field by holding the core to light and marking the boundary between the translucent sapwood and opaque heartwood.

They were then placed into grooved boards where both bark and sapwood were marked with an indelible pencil to help with the identification of bark and sapwood boundaries in subsequent lab analysis.

Stem analysis

Seven or eight trees from each site covering a range of DBH and CCs were chosen from the plot buffers, directly outside the measurement plots but within the treatment plots. *A. balsamea* trees were sampled on PCT sites and site SA, *P. rubens* trees were sampled on NOPCT sites. In total, 94 trees were measured for height and marked on the bole at 1.3 m. The trees were then felled with care to damage as few branches as possible. True tree height was measured and one meter increments marked along the bole. Random sample branches at three positions within the crown, one from the upper half and one each from the two lower quartiles. The crown was divided as such to compensate for the biologic necessity of lower larger branch foliage to recede as it nears mortality (Maguire and Bennett 1996) and to account for known differences in specific leaf area (SLA) with crown depth (Keane and Weetman 1987). Branch basal diameters (BRD) were measured to the nearest 0.1 cm using digital calipers and their associated height was measured from a tape stretched along the bole. Approximately 100 needles were taken from across the range of needle ages for each branch. Needles were immediately placed in plastic bags and put in a cooler. Upon return from the field the needle samples were stored in a freezer until analysis. Sample branches were placed in large paper bags and moved to a drying room.

Sapwood area measurement

The core boards collected during plot sampling were scanned and analyzed using WinDendro 2003a. Prior to scanning core boards were sanded to aid in the distinction between early and latewood cells. North core ring widths from the pith outward were measured for age and sapwood widths (to the nearest 0.001 mm.). East core ring widths were measured from the sapwood mark outward. Any cores with missing pieces, indistinguishable rings or of an obviously older age class were eliminated from the analysis. Sapwood areas (SA) for each tree were determined by subtracting the north and east core sapwood radii from diameter inside bark (DIB), averaging heartwood areas and subtracting from averaged basal areas inside bark. Before performing any calculations the ring widths were adjusted for radial shrinkage from the following factors; *A. balsamea* - 2.9%, *P. rubens* – 3.8% (Forest Products Laboratory 1999).

Leaf area measurement

SLA (cm^2 / g) for each sample branch was calculated, after sorting and separating needles from any bark or branch tissue, by measuring (to the nearest 0.0001 cm^2) the projected needle area (PNA) with WinNeedle software. Needles were then dried for 48 h to determine needle dry weight (NDW) (measured to the nearest 0.001 gram). SLA was determined by dividing PNA by NDW. To estimate branch level leaf area, SLA values were multiplied by weight (grams) of all needles.

Branch and tree leaf area prediction

As part of a concurrent study (Meyer and Seymour, in prep.), branch and tree-level models were developed to predict branch leaf area (BRLA) and projected leaf area (PLA). A Weibull continuous distribution function (Maguire and Bennett 1996) was

fitted for *A. balsamea* while *P. rubens* C, D and I trees were best modeled with a log-transformed peaking equation (Maguire et al. 1998). Overtopped trees were best modeled with a simplified version of the same model.

For *A. balsamea*:

$$[1] \quad \text{sqrt(BRLA)} = 133.95 \text{ BRD}^{1.044} \text{ RDINC}^{(1.999-1)} \text{ EXP}[-(1.414 \text{ RDINC})^{1.999}], R^2 =$$

0.91, For *P. rubens* C, D and I trees:

$$[2] \quad \ln \text{BRLA} = 8.563 + 2.172 \ln \text{BRD} + 0.845 \ln \text{RDINC} - 2.946 \text{ RDINC}, R^2 = 0.86,$$

log bias ratio correction factor (Snowdon 1991) = 1.1421

For *P. rubens* O trees:

$$[3] \quad \ln \text{BRLA} = 2.92 + 3.226 \text{ BRD}, R^2 = 0.82, \text{ log bias ratio correction factor} = 1.1398$$

where BRLA is predicted branch leaf area (cm²), BRD is branch basal diameter (mm), RDINC is relative depth into the crown, measured from the leader (0.0) to LLB (1.0).

Tree-level equations (Meyer and Seymour, in prep.) for estimating PLA from SA and crown length were applied to all (*A. balsamea* – $n = 412$, *P. rubens* – $n = 373$) cored trees with sapwood measurements:

For *A. balsamea*:

$$[4] \quad \ln \text{PLA} = -1.802 + 0.797 \ln \text{SA} + 0.969 \ln \text{CL}, R^2 = 0.95, n = 43, \text{ log bias ratio correction factor} = 1.036$$

For *P. rubens*:

$$[5] \quad \ln \text{PLA} = -1.998 + 0.808 \ln \text{SA} + 0.836 \ln \text{CL}, R^2 = 0.87, n = 45, \text{ log bias ratio correction factor} = 0.9976$$

where PLA = predicted leaf area (m² m⁻²), SA = sapwood area (cm²), CL = crown length (m). Residual analysis for each model was undertaken to ensure unbiased predictions

across sites and to validate linear model assumptions. To account for needle morphology, which differs slightly between *A. balsamea* and *P. rubens* PLAs were converted to individual tree all-sided leaf areas (ALA), using published ratios of 2.3 for *A. balsamea* (Hunt et al. 1999) and 2.9 for *P. rubens* (Day 2000). These values fall within general limits suggested by Margolis et al. (1995).

Volume estimation

Actual tree volumes inside bark were calculated for the stem-analyzed trees using Smalian's formula (Husch et al. 1993) except for the stump (0.3 - 1.3 m) and top sections where formulae for a neiloid frustum and cone, respectively, were used. These volumes were then compared (Fig. 2.1) to those calculated by Honer's (1967) volume equations which use tree DBH and HT to determine cubic foot volume, using a conversion of $1.0 \text{ ft}^3 = 0.028317 \text{ m}^3$. Bias found to exist between the two methods (Fig. 2.1) prompted the development of species-specific regression models for volume prediction.

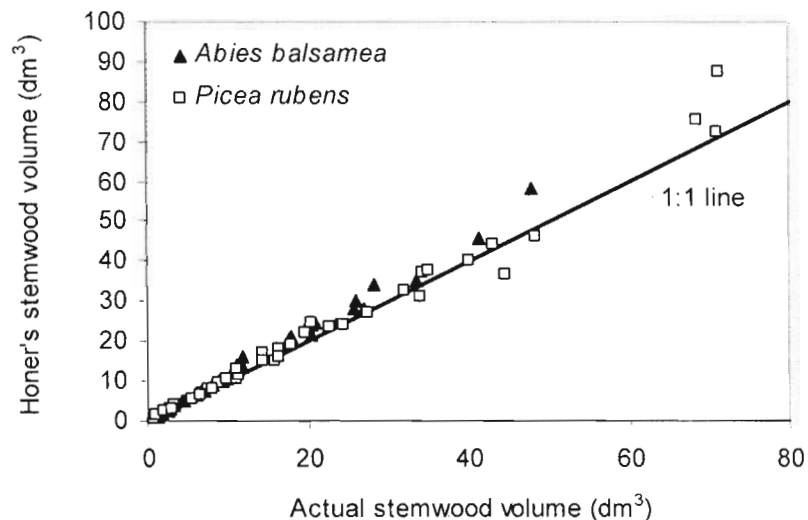


Fig. 2.1. Comparison of actual stemwood volume outside bark (dm^3) and volume predicted from Honer's (1967) volume equations for *A. balsamea* and *P. rubens*

Data from the stem analyzed trees were used to fit the equations;

[1] $\text{Vol} = 0.041 \text{ BA}^{0.873} \text{ HT}^{1.263}$, Generalized $R^2 = 0.996$ for *A. balsamea* and,

[2] $\text{Vol} = 0.049 \text{ BA}^{0.876} \text{ HT}^{1.245}$, Generalized $R^2 = 0.988$ for *P. rubens*

where Vol = tree volume inside bark (dm^3), BA = basal area (cm^2) at 1.3 m, HT = tree height (m), Generalized R^2 (Kvålseth 1985). Predictions were screened to ensure estimates were unbiased across CCs and site for both species besides meeting the assumptions of normality and constancy of error variance.

To determine annual volume increment (VINC) five year radial growth was used in combination with the past five year HT growth predicted from SI curves (Wilson et al. 1999). Five year radial increment was determined from five year radial growth, including the current year growth, from each core, which were then averaged and multiplied by two and a shrinkage factor before subtracting from current DBH. This method assumed constant bark thickness in the last five years. Predicted volume five years ago was subtracted from estimated volume now and divided by five.

Analysis

The general linear model (GLM) and non-linear model procedures (SYSTAT 10.2) were used to assess the relationships between VINC / ALA. Models were evaluated based on residual analysis and generalized coefficients of determination (R^2) as defined by Kvålseth (1985). All tests were performed at $\alpha = 0.05$. Analysis of covariance (ANCOVA) was used to test GE differences between species. A log-transformed model was necessary to meet linear model assumptions. Concomitant variables ALA and SI were used as they were found to vary with GE and should be reconciled before comparison between species. Upper crown level (C and D) trees were used in all analyses

in order to avoid potentially inaccurate GEs resulting from missing rings and rapidly shrinking crowns in the lower CCs. Since destructively sampled *P. rubens* on site SA did not represent the majority species composition (Table 1.6) it was not included in the analysis.

RESULTS

Volume increment

Preliminary linear models suggested SI in combination with ALA was significant in the prediction of VINC. The non-linear model $VINC = b_1 ALA^{b_2} SI^{b_3}$, chosen to assess patterns of VINC over ALA for both species converged quickly and easily (less than 12 iterations, Table 2.2, Fig. 2.2). We rejected a test for linearity ($b_2 = 1.0$) for both species (95% confidence interval (CI) for *A. balsamea* $0.75 < b_2 < 0.89$ and *P. rubens* $0.81 < b_2 < 0.89$). Wald 95% CIs indicated significant parameter estimates (Table 2.2). The larger site term exponent for *A. balsamea* suggested VINC is more responsive to increasing SI than *P. rubens*. This equation revealed slight curvature at smaller ALAs for both species that was not apparent in preliminary linear models. In these even-aged stands a monotonic increasing pattern of VINC over ALA was found for both species. ALA increased with VINC, but at a decreasing rate.

Growth efficiency

When GE, calculated as $VINC / ALA$, is plotted over ALA a pattern emerges that clearly shows the effect of SI on GE (Fig. 2.3). The GE difference with SI is much larger for *A. balsamea* than *P. rubens*. While the range of SIs for each species was similar (5.2 m, Table 2.1) the absolute values (~ 5 m in SI) are much higher for *A. balsamea*. The early

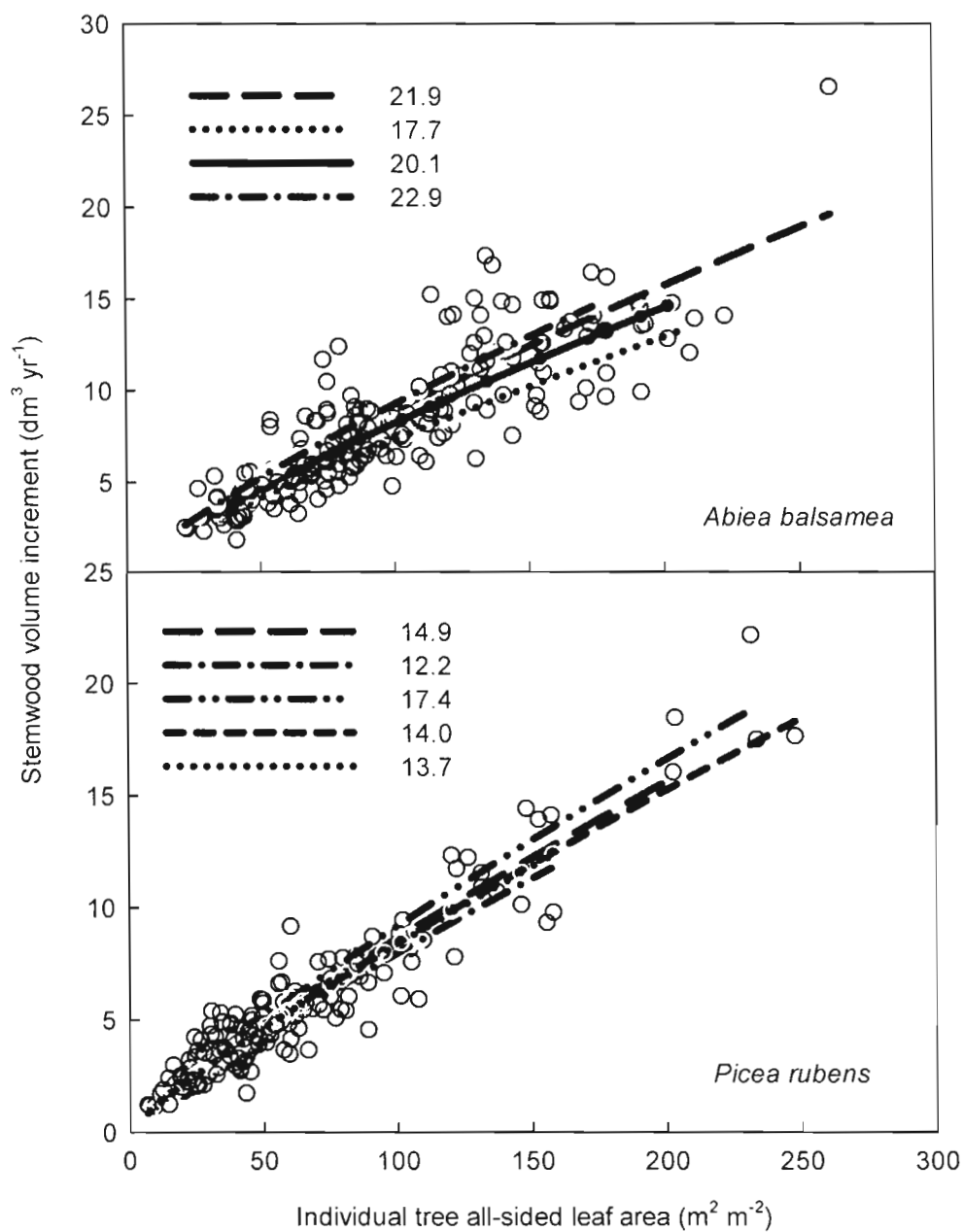


Fig. 2.2. Observed values of stemwood volume increment (VINC dm³ yr⁻¹) over individual tree all-sided leaf area (ALA m² m⁻²) with predicted trends by site index (SI) *A. balsamea* - VINC = 0.0117 ALA^{0.8229} SI^{0.9185}, $R^2 = 0.76$, MSE = 3.321 and *P. rubens* - VINC = 0.0575 ALA^{0.8555} SI^{0.3971}, $R^2 = 0.89$, MSE 1.259.

Table 2.2. Parameter estimates and Wald 95% confidence intervals for the volume increment model $VINC = b_1 ALA^{b_2} SI^{b_3}$

Parameter estimate	Estimated value \pm s.e.	Wald 95% Confidence Intervals	
		Lower	Upper
<i>Abies balsamea</i>			
b_1	0.0117 ± 0.0062	-0.0005	0.0241
b_2	0.8229 ± 0.0357	0.7525	0.8933
b_3	0.9185 ± 0.1675	0.5882	1.249
<i>Picea rubens</i>			
b_1	0.0575 ± 0.0160	0.0256	0.0893
b_2	0.8555 ± 0.0222	0.8116	0.8993
b_3	0.3971 ± 0.1086	0.1827	0.6115

PCT is evident from the lack of small-crowned *A. balsamea* trees $< 50 \text{ m}^2$ ALA (Fig. 2.3); In contrast, small-crowned C and D *P. rubens* trees, a result of self-thinning, are quite numerous.

Species differences

ANCOVA results suggest *P. rubens* is more growth efficient than *A. balsamea* (Table 2.3). Both the factor and covariates were highly significant in the model (all $P < 0.000$). The negative coefficient for *A. balsamea* suggests it has lower mean GEs than *P. rubens*. Similarly, the negative ALA coefficient suggests that GE decreases with an increase in crown size. The positive coefficient for SI provides further evidence that GE increases with increasing site index.

Table 2.3. Coefficients for log-transformed analysis of covariance between species with covariates leaf area (ALA) and site index (SI)

	Coefficient	<i>P</i> - value
Constant	-2.977	-
<i>Abies balsamea</i>	-0.091	0.000 107
lnALA	-0.197	0.000 000
lnSI	0.487	0.000 006

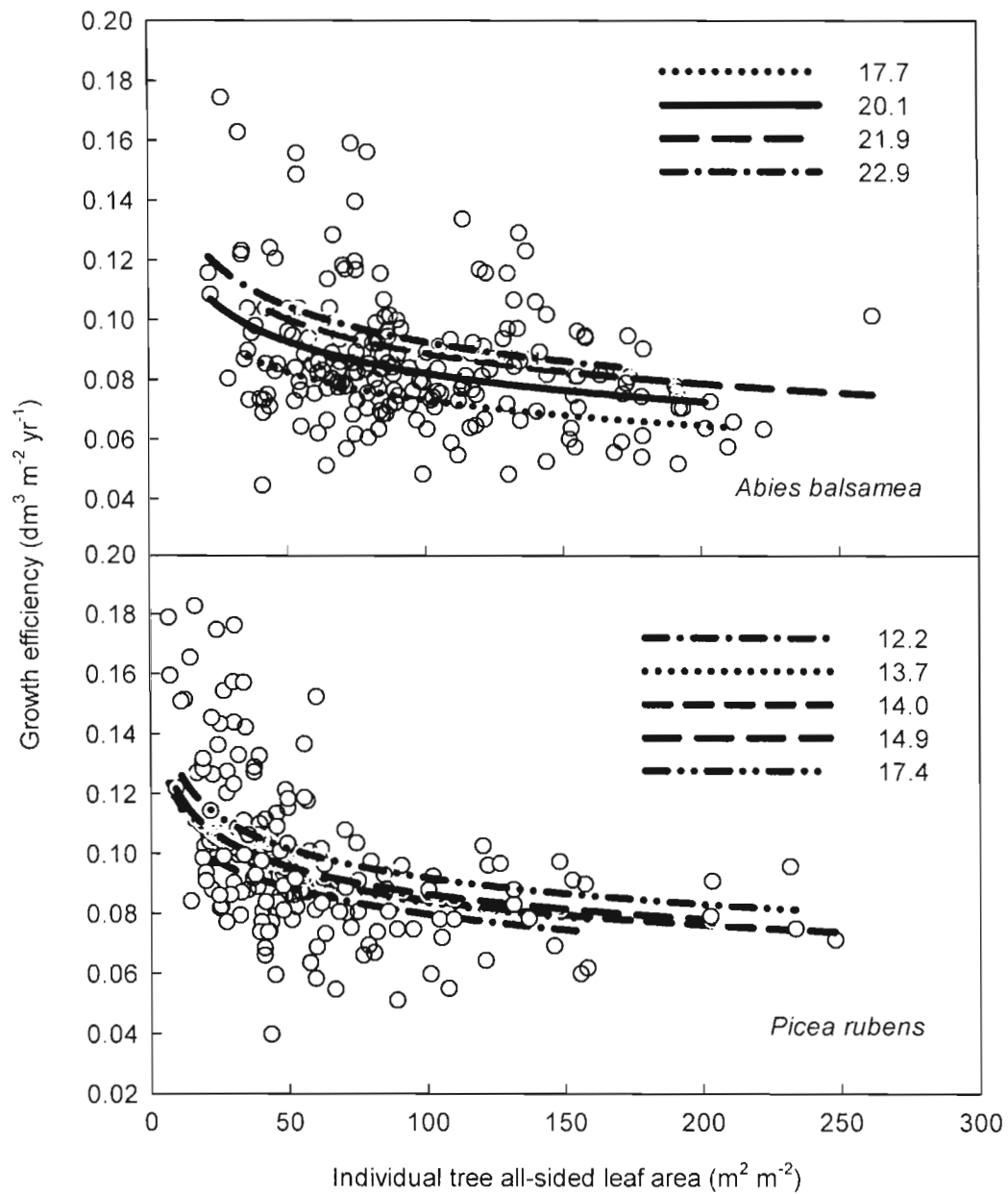


Fig. 2.3. Observed values of growth efficiency ($\text{GE dm}^3 \text{ m}^{-2}$) plotted over all-sided leaf area (ALA m^2) with implied patterns by site index for *A. balsamea* and *P. rubens*

DISCUSSION

Volume increment

When SI was included in the model the predicted VINCs display unique, site-specific trends (Fig. 2.2). The non-linear nature of the model (Fig. 2.2) shows larger crowned trees produce somewhat less VINC than would be predicted by a strict linear relationship. The mathematical result of this pattern is the apparent decrease in GE with increasing ALA. All-sided leaf area (PLA in most other studies) has been found to be a strong predictor in numerous other studies (Roberts and Long 1992, O'Hara 1996, Gilmore and Seymour 1996, Maguire et al. 1998, Seymour and Kenefic 2002), thus the emphasis on its biologic importance in influencing VINC.

Growth efficiency

The commonly observed pattern (Gilmore and Seymour 1996, Maguire et al. 1998, Seymour and Kenefic 2002) of decreasing GE with increasing crown size (Fig. 2.3) has been attributed to the ratio of photosynthesizing to respiring tissue in tree crowns (Roberts and Long 1992) and canopy depth (Smith and Long 1989). In uneven-aged stands of *P. rubens*, Maguire et al. (1998) found that a decline in GE with increasing PLA could be attributed to relative stand position, LA or past suppression. In similar stands Seymour and Kenefic (2002) found that variation in ALA produced a peaking pattern in GE for *P. rubens*, but only when age was included in the model. This was likely influenced by the large range of ages (~5 - 150 years) measured, nearly twice that of those reported here (Table 2.1). Long and Smith (1990) found this pattern for *Pinus contorta* var. *latifolia* Engelm. trees in Utah and Wyoming. Although a large range of site

qualities were represented in their sample, differences in GE between them were not tested in their study.

The relative contribution of LA and GE to overall stand production has long been the subject of debate. Arguably the best experiment designed to partition these effects was performed by Brix (1983), in which *Pseudotsuga menziesii* (Mirb.) Franco stands were thinned and fertilized to quantify relative contribution of PLA and GE to production. Codominant trees in the thinning and fertilization treatments showed marked response over the controls, but the majority (63-80%) of production was related to increases in PLA, not its efficiency. While our study did not assess fertilization or thinning response such treatments can be thought of as surrogates for differences in resource availability in natural stands.

That VINC, and subsequently GE, varies by site is evident (Table 2.2); however, the large coefficient for *A. balsamea* suggests it is more responsive. Meng and Seymour (1992) found *P. rubens* were unresponsive to increased site quality, measured as drainage, while *A. balsamea* showed marked increases in production. We found, for a tree of average crown size, *A. balsamea* responded better in gross periodic annual increment (PAI) to a 1.0 m increase in SI than *P. rubens*, 0.37 compared to 0.27 m³ yr⁻¹ ha⁻¹. Williams et al. (1990) found essentially similar biomass production between poorly drained (low site quality) and well-drained (higher site quality) *A. balsamea* – *P. rubens* sites, although their methodology might tend to underestimate high site production losses due to mortality and differences in stand stocking. Kaufmann and Ryan (1986) found GE was predicted best with site variables (azimuth, elevation) for *P. contorta* in the Rocky Mountains. Whether either of these site quality metrics have a significant impact on tree

growth for *A. balsamea* or *P. rubens* is unknown, although Briggs and Lemin (1992) suggest elevation and precipitation in Maine are roughly correlated.

Species differences and silvicultural implications

P. rubens trees, which occurred on a lower range of site qualities, were slightly more growth efficient overall than *A. balsamea* in this study (Table 2.3). Two potential explanations are offered: inherent species differences in production efficiency, and architectural dissimilarities as a result of early PCT in the *A. balsamea* stands. Implied patterns of efficiency for each species suggest implications for silvicultural intervention. The declining trend of GE with increasing ALA in both species corroborates previous work citing small-crowned codominants as the most growth-efficient trees in even-aged stands (Assmann 1970, Jack and Long 1992). These trees are a result of initial stand density, made evident by the larger number of growth-efficient *P. rubens* trees which occur in higher density stands than the PCT *A. balsamea* trees. A stand of *P. rubens* may be more efficient at overall biomass production, but this would come at the expense of individual tree growth. Chapter one shows the *A. balsamea* trees under study have significantly higher mean tree ALAs and thus larger stemwood growth (Table 2.1), albeit with lower GE. As a result of early PCT *A. balsamea* are exhibiting maximum tree growth potential at the expense of overall stand growth (Long and Smith 1984). Despite the fact that PCT was done 15 – 20 years earlier, the canopy of these *A. balsamea* stands remains open, and RDs are well below those that would indicate self-thinning (Wilson et al. 1999).

PAI, mean GEs multiplied by LAI (from chapter one), when compared with mean annual increment (MAI) from plot establishment data shows (Table 2.4) all stands have

yet to achieve culmination of MAI (CMAI). Stand-level GE (estimated LAI / PAI) suggested *A. balsamea* is the most efficient species. The *A. balsamea* stands received fairly wide spacing during PCT (2.4 m by 2.4 m), or 1,680 TPHA, yielding large-crowned (slightly less growth-efficient) trees. If a narrower spacing were used, an arrangement of more growth-efficient trees would result. For example, if we assume average stand LAI of 10 (chapter one), and SI = 20 then, had 2.1 m spacing been used (2,195 TPHA), mean tree ALA would be 45.5 m² versus 59.5 m² for 2.4 m spacing. Using the VINC eq. 3 for *A. balsamea* we calculate GEs of 0.088 and 0.093 dm³ m⁻² respectively, which suggests PAI would have increases from 8.8 to 9.3 m³ yr⁻¹ ha⁻¹. *P. rubens*, at much lower SIs, have stand-level GEs similar to *A. balsamea* indicating its productive potential. Indeed, when PAIs are displayed per unit of SI (Fig. 2.4) it is apparent low quality *P. rubens* stands are more productive.

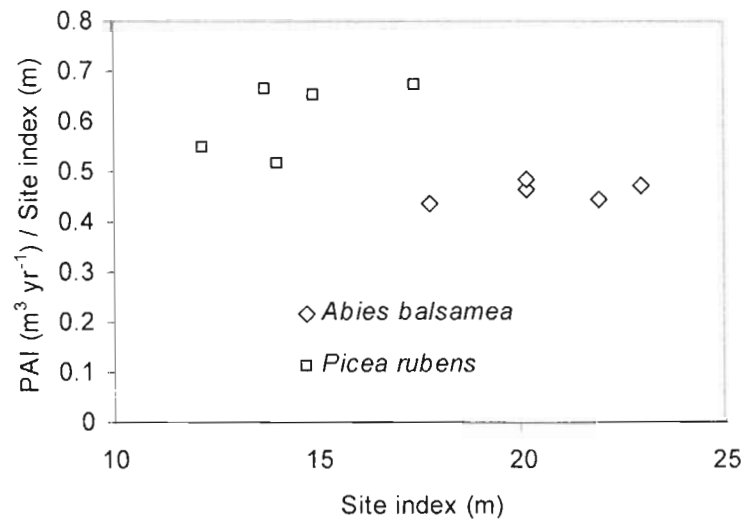


Fig. 2.4. Gross periodic annual increment (PAI) divided by site index (SI) plotted over SI for *A. balsamea* and *P. rubens* stands

The values of MAI (Table 2.4) for *P. rubens* stands can be interpreted as the potential for the site, whereas *A. balsamea*, as a result of having not yet reached maximum LAI yet, cannot. For both species the obvious message is that these stands are still growing well, even the older *P. rubens* stands, and CMAI appears to be decades in the future.

Table 2.4. Mean plot mean annual increment (MAI $\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$), gross periodic annual increment (PAI $\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$, 5 year average) and corresponding GEs for study plots of both species derived from leaf area indices (LAIs, chapter one)

	Site				
	AS	LM	LT	RC	WB
<i>Abies balsamea</i>					
PAI ($\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$)	9.7	7.7	9.3	10.8	9.7
MAI ($\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$)	5.4	4.7	5.6	6.3	5.9
Stand-level GE ($\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$)	1.19	1.37	1.21	1.08	1.22
<i>Picea rubens</i>	GR	HR	RR	SC	SR
PAI ($\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$)	9.7	6.7	11.7	7.2	9.1
MAI ($\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$)	4.5	3.9	6.6	4.8	5.1
Stand-level GE ($\text{m}^3 \text{yr}^{-1} \text{ha}^{-1}$)	1.09	1.19	1.07	1.14	1.09

Note: AS – site Alder Stream, LM – site Lake Macwahoc, LT – site Lazy Tom, RC – site Ronco Cove, WB – site Weeks Brook, GR – site Golden Road, HR – site Harlow Road, RR – site Rump Road, SC – site Schoolbus Road, SR – site Sarah’s Road.

Favoring *A. balsamea*, the preferred host for the spruce budworm (*Choristoneura fumiferana* Clem.), across wide geographic areas could have important implications for forest management (Seymour 1992). The high vulnerability of stands with a large percentage of *A. balsamea* (MacLean 1980, Osawa 1989) argues in support of favoring *P. rubens*. Even-aged stands of *A. balsamea* – *P. rubens*, while potentially extremely productive, involve increased risk for forest managers. The literature (reviewed by

Seymour 1992) suggests the pre-settlement state of these forests was *P. rubens* dominate and uneven- or two-aged.

CONCLUSIONS

VINC prediction models provided evidence of site quality effects on GE for *A. balsamea* and *P. rubens* in Maine. Implied patterns of GE over ALA showed the commonly found pattern of decreasing GE with increasing crown size. *P. rubens* trees are probably more growth-efficient given their similar GEs at much lower SIs, but at the stand level *A. balsamea* appears to be more growth efficient than *P. rubens*. Mean plot PAIs > MAIs for all study sites suggest CMAI has yet to be reached. When viewed as PAI / SI, *P. rubens* appears to be more productive in this study. VINC and ALA could be incorporated into biologically meaningful forest management.

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**APPENDIX: SITES, PLOTS, TREATMENTS, AGES AND VOLUMES FOR
COMMERCIAL THINNING NETWORK PLOTS**

Table A.1. Sites that received no precommercial thinning (NOPCT) plot, treatment and breast height age information

Site	Plot	Treatment	NOPCT			
			Mean age \pm SD	Minimum	Maximum	Vol. (m ³ /ha)
GR	2	DOM50	47 \pm 10	31	66	815
GR	4	Control	49 \pm 5	36	56	8707
GR	6	LOW50	53 \pm 3	47	58	1284
GR	7	DOM33	51 \pm 3	44	56	1445
HR	1	LOW33	71 \pm 6	56	81	3001
HR	2	Control	67 \pm 8	43	76	6138
HR	5	LOW50	70 \pm 3	66	74	1173
HR	6	DOM33	66 \pm 6	51	77	3199
HR	7	DOM50	65 \pm 6	55	74	1247
RR	1	DOM50	36 \pm 4	27	43	1927
RR	2	DOM33	36 \pm 3	30	40	1927
RR	3	Control	34 \pm 5	19	41	3273
RR	4	LOW33	35 \pm 3	28	40	3680
RR	5	LOW50	35 \pm 7	18	42	2198
SA	1	Control	29 \pm 4	119	35	6224
SA	3	LOW33	28 \pm 6	16	33	889
SA	5	LOW50	31 \pm 2	27	35	679
SA	6	DOM33	29 \pm 3	21	33	3199
SA	7	DOM50	30 \pm 4	24	34	2013
SC	1	Control	54 \pm 7	33	64	10436
SC	2	DOM33	60 \pm 6	52	70	1840
SC	3	LOW50	61 \pm 3	57	65	2013
SC	5	DOM50	57 \pm 5	46	64	1396
SC	7	LOW33	65 \pm 7	42	69	3260
SR	1	Control	44 \pm 7	27	56	14215
SR	2	DOM50	49 \pm 12	26	72	1396
SR	3	DOM33	41 \pm 7	25	50	3693
SR	5	LOW50	55 \pm 3	51	59	2137
SR	6	LOW33	51 \pm 7	36	72	3989

Note: Definitions found in Table 1.5.

Table A.2. Sites that received precommercial thinning (PCT) plot, treatment and breast height age information

Site	Plot	Treatment	PCT			
			Mean age \pm SD	Minimum	Maximum	Vol. (m ³ /ha)
AS	1	5a	23 \pm 5	16	30	3631
AS	2	Control	22 \pm 4	16	28	3680
AS	4	55%	23 \pm 4	15	29	716
AS	6	33%	24 \pm 5	13	29	1803
LM	2	Control	36 \pm 5	23	42	3433
LM	4	33%	36 \pm 5	22	41	1371
LM	5	10a	37 \pm 4	29	42	3903
LM	7	55%	37 \pm 2	35	40	580
LT	1	55%	28 \pm 4	22	34	815
LT	4	10a	26 \pm 3	19	32	4397
LT	6	33%	25 \pm 4	16	31	1840
LT	7	Control	24 \pm 4	15	30	3088
RC	1	55%	18 \pm 2	15	23	741
RC	3	33%	23 \pm 2	19	26	1470
RC	5	5b	23 \pm 3	15	25	3717
RC	7	Control	19 \pm 2	15	23	3470
WB	3	55%	28 \pm 3	23	32	7225
WB	4	Control	25 \pm 4	13	32	3594
WB	6	5b	24 \pm 4	18	31	4323
WB	7	33%	25 \pm 3	17	29	1457

Note: Definitions found in Table 1.6.

BIOGRAPHY OF THE AUTHOR

Justin DeRose was born December 7th, 1976 in Salt Lake City, Utah. He was raised in the suburbs just south of Salt Lake where he graduated from Brighton High School in 1995. He attended Salt Lake Community College in Taylorsville, Utah where he received his Associate of Science. Justin then attended Utah State University in Logan, Utah where he graduated Cum Laude with a Bachelor of Science in Forestry in 2002. Justin is currently a member of the Society of American Foresters, Phi Kappa Phi and Xi Sigma Pi. During his undergraduate education Justin had the opportunity to work for the Forest Service in central Oregon. He also worked part time for Ph.D. candidate John Shaw at Utah State University on a large array of research related topics. Upon receiving his Bachelor's degree Justin moved to Rottenberg, Deutschland to spend a summer studying German forestry at the Hochschule für Forstwirtschaft and traveling through Europe. He came to Maine to study silviculture and stand dynamics under the advisement of Dr. Robert S. Seymour. Justin is a candidate for the Master of Science degree in Forestry from The University of Maine, in December 2004.