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Understory Growth Dynamics and Mensuration Techniques in Uneven-Aged, Mixed-Species Northern Conifer Stands

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UNDERSTORY GROWTH DYNAMICS AND MENSURATION TECHNIQUES

IN UNEVEN-AGED, MIXED-SPECIES NORTHERN

CONIFER STANDS

By

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UNDERSTORY GROWTH DYNAMICS AND MENSURATION TECHNIQUES

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Thesis Advisor: Dr. Robert S. Seymour

Managing uneven-aged, mixed-species stands requires balancing the need for high

leaf area allocation in the overstory where it is most efficient versus the need to allow for

sufficient growth of younger cohorts in the understory. To help forest managers make

informed decisions to maintain this balance, the understory growth dynamics of northern

conifer species in stands managed under uneven-aged silvicultural systems were studied.

Sapling height growth of *Picea rubens* Sarg., *Abies balsamea* (L.) Mill, and *Tsuga*

canadensis (L.) Carr. were modeled as a function of overstory canopy openness (gap

fraction) using regression analysis. Research was conducted in four uneven-aged

northern conifer stands on the Penobscot Experimental Forest in eastern Maine; two

replicates each of selection cutting on five- and ten-year cycles. Gap fraction estimates

were obtained directly above 167 sample trees between 0.5-6.0 m in height, using a LI-

COR LAI-2000 plant canopy analyzer. These estimates were tested in several model

forms along with initial tree height to predict sapling height growth. The effect of

different vertical distributions of foliage on sapling height growth was also explored

using analysis of covariance. Using cluster analysis, plots were grouped into one of three

categories based on similar vertical leaf area structure. Species-specific height growth

was then compared between groups of similar vertical structure using initial tree height as

a covariate.

An innovative method employing vertical point sampling was used to obtain leaf

area estimates to quantify plot-level vertical leaf area structure. To validate the use of

vertical point sampling, plot-level leaf area index (LAI) and basal area (BA) estimates

based on vertical point sampling were compared with conventional horizontal point

sampling using a 2 m^2/ha basal area factor (BAF) prism. Tree-level LAI estimates were

replaced with species-specific constants based on projected leaf area (PLA)-height

squared and PLA-DBH^2 linear regression coefficients in an effort to develop a quick and

accurate method to estimate LAI in the field using both vertical point sampling and prism

sampling. Leaf area index measurements, BA, and tree tallies from vertical point

sampling were also related to gap fraction measurements to determine if an efficient

method for in-the-field gap fraction estimation could also be developed.

Regression modeling demonstrated that sapling height growth of all three species

followed a monotonically increasing pattern with respect to decreasing canopy closure.

Abies balsamea appeared to be the most aggressive competitor demonstrating the greatest

response to changes in gap fraction while *Tsuga canadensis* appeared to be the least

responsive to changes in gap fraction. Although total plot-level LAI was not significant in

predicting height growth in these complex stands, the vertical distribution of leaf area

was. While height growth of *Abies balsamea* and *Tsuga canadensis* were not significantly

different between vertical leaf area structures, height growth of *Picea rubens* was significantly higher in plots with well-developed understories with high LAI, regardless of overstory LAI.

Vertical point sampling showed strong promise in providing LAI estimates, and in particular facilitating in-the-field LAI estimation with the use of species-specific tree-level LAI constants that remove the need for individual tree measurements. More field-testing of this technique needs to be done. Simple vertical point sample measures were not successful in accurately predicting gap fraction.

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CHAPTER 1.

OVERSTORY INFLUENCE ON UNDERSTORY GROWTH DYNAMICS OF SHADE TOLERANT NORTHERN CONIFERS IN UNEVEN-AGED, MIXED-SPECIES STANDS

INTRODUCTION

There is an increased interest in maintaining complex mixed-species, uneven-aged stands in forestry today. These stands meet many non-timber objectives and maintain non-timber values by conserving important ecological characteristics of the forest. Maintaining these types of stands is especially applicable in Maine where the natural disturbance regime is dominated by small partial disturbances resulting in a naturally uneven-aged, mixed-species forest structure (Seymour et al. 2002). The growth dynamics of these stands are very complicated and poorly understood and thus present a challenge to foresters trying to manage complex stands through uneven-aged silviculture. This often results in mismanagement or conversion to simpler, better understood even-aged silvicultural systems.

While maintaining complex stands helps meet many non-timber objectives, maintaining high productivity is also key to meeting timber supply objectives. Stand-level stemwood volume increment is highly correlated to leaf area index (LAI), which is defined as leaf area per unit area of ground (Kenefic 2000; O'Hara et al. 2001). Maintaining high productivity requires maintaining high stand-level leaf area. Although

each stand has a maximum potential leaf area (Long and Smith 1984), additional

productivity can be achieved by maximizing the growth efficiency. Stemwood growth

efficiency (GE) is defined as stemwood volume increment per unit of foliage (Seymour

and Kenefic 2002).

Tree-level GE in complex northern conifer stands has been shown to exhibit a

peaking pattern with respect to tree-level projected leaf area (PLA) (Seymour and Kenefic

2002). Growth efficiency initially increases with increasing PLA as a tree rises through

the canopy and achieves improved light conditions. Maximum GE occurs once the tree

reaches the main canopy and experiences full light conditions. From that point, GE was

found to decline with continued crown expansion, holding age constant (Seymour and

Kenefic 2002). Maximum tree-level GE therefore occurs for small crowned trees in the

upper strata. At a stand level, O'Hara et al. (2001) found that overall stand-level volume

increment decreased in Picea abies (L.) Karst. (Norway spruce) and Pinus sylvestris L.

(Scots pine) stands as the portion of stand-level LAI occupied by the understory increased

relative to that in the overstory.

Age becomes a confounding factor in the GE-PLA relationship. While older trees

tend to have larger, less efficient crowns, reductions in growth efficiency are also the

result of advanced age, independent of crown size or canopy stratum (Seymour and

Kenefic 2002). Evidence of past suppression has also been shown to be correlated with

decreases in growth efficiency for Picea rubens Sarg. (red spruce) (Maguire et al. 1998).

This introduces a trade-off in managing complex northern conifer stands for maximum

GE. Maximizing current GE would require maintaining a large portion of the stand leaf

area in the upper stratum where trees are most efficient. By allocating too much leaf area to the upper stratum however, one may risk suppressing understory trees. The negative relationship between age, past suppression and GE suggests that potential GE may be compromised by suppressing the understory for extended periods of time. Timely advancement of seedlings and saplings through the understory and into higher strata is therefore necessary for maintaining productive and efficient multi-storied stands.

In order to balance a well-stocked upper stratum of growth efficient trees with adequate understory height growth, one must quantify the relationship between overstory density and understory height growth. Overstory density affects sapling height growth through a variety of mechanisms including air and soil temperature, relative humidity, soil moisture and nutrient availability (Norman and Campbell 1989; Bazzaz and Wayne 1994; Man and Lieffers 1997; Palik *et al.* 1997; Jennings *et al.* 1999). The effect that overstory competition has on understory light levels is of primary importance. Particularly in conditions of high overstory density, light is the limiting resource to sapling growth (Carter and Klinka 1992; Klinka *et al.* 1992; Parent and Messier 1995; Finzi and Canham 2000; Duchesneau *et al.* 2001).

The conifer species that dominate the stands in this study, *Abies balsamea* (L.) Mill.(balsam fir), *Picea rubens*, and *Tsuga canadensis* (L.) Carr. (eastern hemlock), are shade tolerant and capable of responding to release after prolonged periods of suppression in the understory (Blum 1990; Frank 1990; Godman and Lancaster 1990; Seymour 1992). Previous studies looking at seedling and sapling growth of these three species have found either a peaking trend in growth with respect to increasing light conditions (Logan 1969;

McConville 1998), or a monotonically increasing pattern of height growth with respect to increasing light (Parent and Messier 1995; Finzi and Canham 2000; Duchesneau *et al.* 2001).

Complex uneven-aged stands exhibit very irregular canopies with diverse vertical arrangements of leaf area (Seymour and Kenefic 1998). The quantity and quality of light reaching the understory is dependent on both the amount of overstory foliage, and its vertical distribution (Jarvis and Leverenz 1983; Sampson and Smith 1993; Baldocchi and Collineau 1994; Lieffers *et al.* 1999).

Light in canopies comes in the form of direct light from the solar disc and diffuse light from atmospheric scattering (which comes from all parts of the sky). Vertical leaf area distribution affects the proportion of direct to diffuse light in the understory, and thus influences the type of shade cast on vegetation (Baldocchi and Collineau 1994; Oliver and Larson 1996; Drever and Lertzman 2003). Conditions of high shade occur when there is large vertical distance from the shading foliage. This creates conditions of low-intensity uniform diffuse light conditions (Oliver and Larson 1996). These moderate shading conditions have been shown to promote greater seedling growth than lower light levels that are augmented periodically throughout the day by direct radiation in the form of sunflecks, even when the total amount of light is the same for the two conditions (Lieffers *et al.* 1999).

The purpose of this study was to explore the growth dynamics of understory trees in uneven-aged, mixed-species northern conifer stands dominated by *Abies balsamea, Picea rubens,* and *Tsuga canadensis.* The objectives were to 1) model sapling height

growth of these three species as a function of overstory density; 2) explore the influence

of heterogenous vertical canopy structure on understory growth; and 3) use these

relationships to determine maximum overstory densities and vertical distributions of

foliage that facilitate adequate understory height growth.

The hypotheses tested regarding sapling height growth with respect to overstory

density and canopy structure in mixed-species, uneven-aged northen conifer stands are as

follows:

(1)   (H_0): Sapling height growth is equivalent across overstory densities that exist in mixed-species, uneven-aged northen conifer stands.

(H_1): Sapling height growth increases in a linear pattern with respect to decreasing overstory density.

(H_2): Sapling height growth peaks under conditions of moderate overstory density and decreases as overstory density approaches high values or low values.

(H_3): Sapling height growth follows a monotonically increasing pattern with respect to decreasing overstory density.

(2)   (H_0): Sapling height growth is equivalent across varying canopy structures that exist in mixed-species, uneven-aged northen conifer stands.

(H_1): Sapling height growth responds differently to different arrangements of vertical foliage distribution.

METHODS

Study Site

Four mixed-species, uneven-aged stands located on the 1540-ha Penobscot

Experimental Forest (PEF) in Bradley, Maine were used in this study. This experimental

forest, owned by the University of Maine, is located at approximately 44°52' N and

68°38'W. It is the site of a long-term silvicultural research project established by the

USDA Forest Service in the 1950s and includes both even-aged and uneven-aged

silvicultural treatments (Seymour and Kenefic 1998).Two of the stands included in this

study, C9 and C16, are replicates of selection cutting on a five-year cycle, while the other

two, C12 and C20, are replicates of selection cutting on a ten-year cutting cycle. The

structural goal for these stands is defined by the BDq method (Guldin 1991). The two

replicates of the five-year selection cutting have a q-factor of 1.96 on 5-cm diameter

classes, a target residual basal area of 26 m^2/ha, and a maximum residual diameter goal of

48 cm. The two replicates of the ten-year selection cutting also have a q factor of 1.96, a

target residual basal area of 23 m^2/ha, and a maximum residual diameter goal of 46 cm

(Brissette and Kenefic 1999).

The PEF lies within the Acadian Forest Region, a transitional forest between the

broadleaf forest to the south and the boreal forest to the north. The natural disturbance

regime is dominated by sporadic partial disturbances such as insect epidemics and

windstorms. Species composition is mixed and highly variable due to differences in soil

drainage and stand structural condition. Dominant conifers on the PEF include *Picea*

rubens, Picea glauca (Moench) Voss (white spruce), *Abies balsamea, Thuja occidentalis*

L. (northern white cedar), *Pinus strobus* L. (eastern white pine), and *Tsuga canadensis.*

The more common hardwoods in this area are *Acer rubrum* L. (red maple), *Betula*

papyrifera Marsh. (paper birch), *Betula populifolia* Marsh. (gray birch), *Betula*

alleghaniensis Britt. (yellow birch), *Populus tremuloides* Michx.(quaking aspen), and

Populus grandidentata Michx. (bigtooth aspen). Glacial till is the principal soil parent

material with soil types ranging from well-drained loams and sandy loams on low-profile

ridges to poorly drained and very poorly drained loams and silt loams in flat areas

between the ridges (Brissette *et al.* 1999; Brissette and Kenefic 1999).

Sampling Scheme

A 25-m systematic grid was established on these stands in 1995 (Kenefic 2000),

with soil drainage class being recorded for each grid point. Only grid points with well

drained, moderately well drained, or somewhat poorly drained soils were considered for

this study. To ensure that the light environment in 2002 was representative of the light

environment during the five years prior to 2002, a grid point was excluded if there was

evidence of cutting within a 5.7 m radius of the grid point over the last five years. This

was determined by searching for recent stumps in conjunction with knowledge of

previous harvest dates. Grid points where there was a large hardwood influence in the

overstory (defined as having at least one hardwood tree greater than 10 cm DBH within a

5.7 m radius of the grid point) were also excluded. If the grid point was acceptable, then

all *Abies balsamea, Picea rubens,* and *Tsuga canadensis* saplings greater than 50 cm in

.

height were tallied within a 1/200-ha circular plot (4-m radius) centered at the grid point.

Saplings were divided into one of three height classes: 0.5-2 m, 2-4 m, and 4-6m. In July

2002, all grid points that were somewhat poorly drained of better were re-visited and their

light environment was characterized by measuring a gap fraction value (a measure of

canopy openness) 1.6 m directly above the grid point. Gap fraction was measured at 171

grid points over the four stands using a LI-COR LAI-2000 Plant Canopy Analyzer (LAI-

2000). This provided an overall gap fraction distribution for both the five-year selection

stands and the ten-year selection stands (Figure 1.1).

The target sample included 180 sample trees consisting of 20 trees per species per

height class distributed over the acceptable grid points. For each species and height class,

20 grid points were chosen as the site of a sample tree according to the following

priorities: 1) to evenly span the range of available light conditions so that open conditions

were represented on an equal basis to more closed conditions (as much as stand light

conditions permitted); and 2) to choose points where the species and height class in

question was most abundant. Each chosen grid point was revisited and a sapling of the

appropriate height class and species was randomly chosen within a 4-m radius of the grid

point. No more than one tree per species was sampled at each grid point.
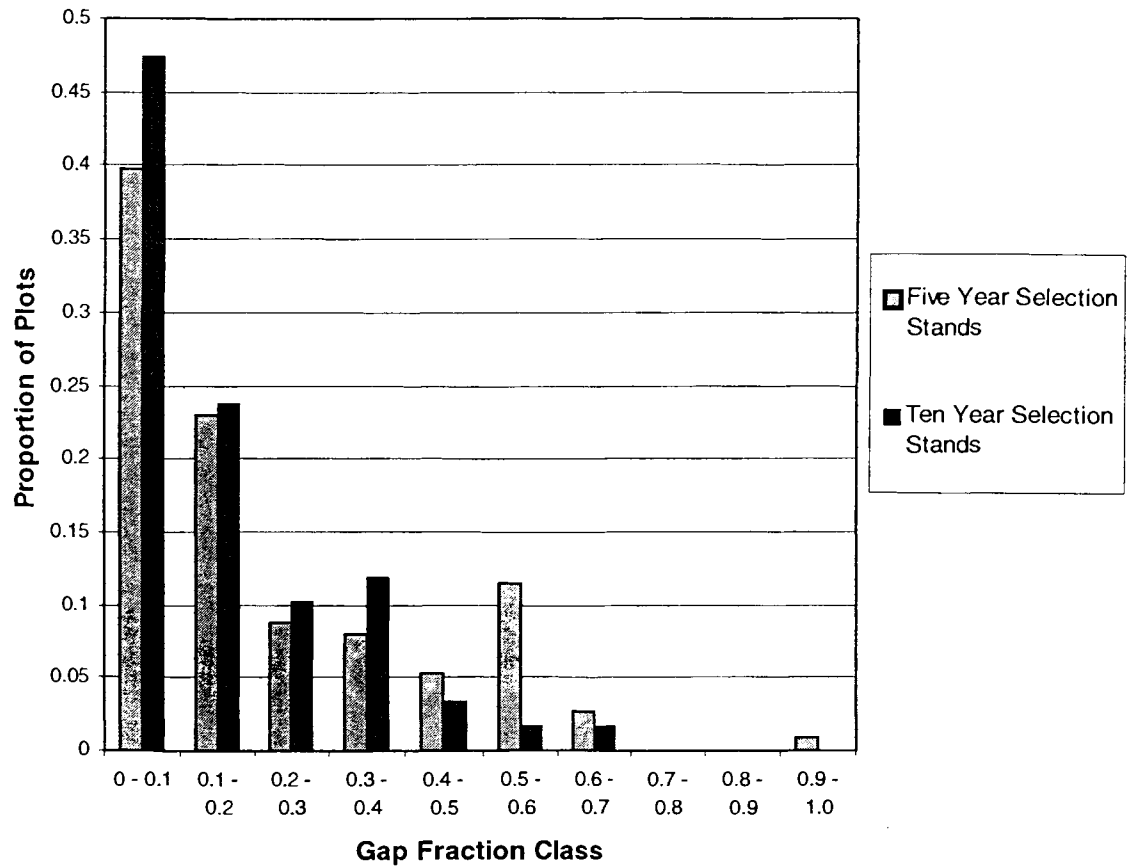
Figure 1.1 Gap fraction distribution of all grid points that were somewhat poorly drained or better on both the five-year selection and ten-year selection stands. The five-year selection stands contained 113 plots with an average gap fraction value of 0.21. The ten-year selection stands contained 59 plots with an average gap fraction value of 0.16.

Data Collection

Gap Fraction Measurements

Canopy closure, which is directly related to the understory light regime, was measured by taking gap fraction readings using the LAI 2000. Readings were taken from mid-August to mid-September in 2002. The LAI-2000, which measures diffuse non-intercepted light, is composed of two sensors, each connected to its own control unit to record measurements. One is set up in the open (the base sensor), while the other sensor takes readings below the canopy. Each sensor has a 150° field-of-view lens positioned above five concentric light detecting silicon rings that allow it to receive and measure light from five different zenith angles (0-13°, 16-28°, 32-43°, 47-58°, and 61-74°) simultaneously. Gap fraction or canopy transmittance represents the probability of unimpeded light penetration through the canopy. It is calculated by using the relationship between below-canopy intensity of diffuse non-intercepted light with a simultaneous measurement taken by a base sensor located above the canopy, usually at a nearby open site (Chanson *et al.* 1991; LI-COR 1992; Lieffers et al. 1999).

To avoid bias from direct beam sunlight, readings were taken within an hour of sunrise and sunset or on uniformly overcast days. The base sensor was set up on a tripod in the middle of an open field that was, depending on the stand, 1 km to 2.2 km from the sample sites. Distance between the base sensor and sample sites varied between approximately It was synchronized with the below-canopy sensor, and automatically logged readings every 15 seconds.

The below-canopy sensor was mounted to a PVC height pole, and raised to the leader of each sample tree, where four readings were taken. The pole was rotated 90° between readings. Depending on the height class of the tree, the below-canopy sensor was then raised directly above the sample tree to successive fixed heights. For trees between 0.5-2 m, the sensor was raised to 2.9 m, 5.5 m, 8.4 m, and 11.5 m. The readings at 2.9 m were skipped for trees in the 2-4 m height class, and both the 2.9 m readings and 5.5 m readings were skipped for trees in the 4-6 m height class. At each height, four readings were taken with the height pole being rotated 90° between readings. A carpenter's level was clamped to the base of the height pole, and the base of the height pole was leveled before each reading was taken. Due to the flexibility in the height pole however, it was impossible to level the sensor. Rotating the height pole between each reading at a particular height was an attempt to make sure the entire sky was sampled evenly. The four readings were averaged to give one gap fraction reading at each height. No lens cap was used for either sensor due to the inability to control the orientation of the below-canopy sensor higher in the canopy. Extreme care was taken to ensure that workers were not visible to the lens.

Gap fraction estimates were based on readings from the two innermost rings. This corresponds to a zenith angle of 28.6°. Extending the field of view of the LAI-2000 to the widest angles integrates canopy conditions over a larger area. This results in a homogenizing of conditions which decreases the range and variance of the estimates (Bunnell and Vales 1989). While the inner three rings (corresponding to a zenith angle of 47°) could have been used, we planned to estimate stand characteristics (including leaf

area index) using vertical point sampling and equate these to the gap fraction readings. Time limitations therefore forced us to use as few of the inner LAI-2000 rings as possible, thereby restricting the field of view and keeping the number of trees tallied in the vertical point sampling down to a manageable number. Other scientists (Biging and Dobbertin 1992; Puettmann and D'Amato 2002) have found that extending an angle of view beyond a zenith angle of 30° to select competitors does not improve height and diameter growth models.

Height Growth Measurements

Height growth measurements were taken between mid-August and late September in 2002. The distance from the base to the top of the tree, and the distance from the base to the first five nodes were measured for each sample tree using a PVC height pole or a measuring tape. Diameter at 5 cm above the trunk base of each tree was measured. For trees taller than 1.3 m, diameter at breast height was measured.

For some *Tsuga canadensis* trees, or *Picea rubens* and *Abies balsamea* trees which were severely suppressed, not all five nodes could be positively identified. In those cases, the height of each node was measured only down to the lowest positively identified node.

Vertical Point Sampling

In an effort to explore the effect of canopy structure on height growth, vertical point sampling was employed to develop detailed canopy architecture descriptions for a

subsample of the original saplings. This is a relatively unknown and unprecedented sampling method to detail canopy architecture. It was chosen over prism sampling and fixed radius plots for several reasons, including the uniqueness of the methodology. Projecting an inverted cone vertically through the canopy best simulates what the LAI-2000 is sensing, and vertical point sampling also has the advantage of quantifying vegetation of different strata into a single measure (Puettmann and D'Amato 2002).

The original sample of *Picea rubens* trees was divided into gap fraction classes of 10%. Within each 10% gap fraction class, *Picea rubens* trees were sorted into the top quartile, the middle 50%, and the lowest quartile of height growth. One tree was selected from each of the three groups so that for each approximate light environment, a relatively fast growing tree, a average growing tree, and a slow growing tree were included in the subsample. In total, twenty three *Picea rubens* trees were chosen (not all gap fraction classes contained three trees). All *Abies balsamea*, and *Tsuga canadensis* trees located at the same grid point as a chosen *Picea rubens* tree were included in the subsample. A total of twenty four *Abies balsamea* and twenty two *Tsuga canadensis* trees were included in the subsample. Each subsample tree became its own plot center.

An inverted cone was projected from 1 m above the ground at each sample tree at a zenith angle of 28.6° using a clinometer. This angle was chosen to simulate the field of view of the first two rings of the LAI-2000. Each tree that intersected the inverted cone was marked, and its species, stratum, height, height to live crown (defined as lowest live branch for *Picea rubens, Tsuga canadensis,* and *Pinus strobus, Thuja occidentalis,* and defined as lowest live whorl for *Abies balsamea*), DBH, and horizontal distance to the

sample tree was recorded. Borderline trees whose inclusion in the vertical point sample
was questionable were tallied, and excluded later in the analysis if necessary by
calculating the limiting distance of inclusion for that tree (which was proportional to the
height of the tree).

Data Analysis

Height Growth Modeling

Average annual height increment (AAHINC) was calculated by summing the
internodal distances measured and dividing by the number of nodes. Several linear and
non-linear models (Table 1.1) were fit to predict AAHINC for each species using initial
height (IH) and gap fraction reading at the tree leader (DIFN1) as predictor variables. The
following alternative hypotheses of height growth response with respect to increases in
gap fraction were tested: 1) a linear increase, 2) a curvilinear monotonic increase, and 3) a
peaking pattern at intermediate gap fraction values. For 2nd order polynomial models, the
gap fraction reading was replaced with its deviation from the mean gap fraction reading
($difn1_i = DIFN1_i - DIFN1_{mean}$) to deal with the problem of multicollinearity (Neter *et al.*
1996).

The models were fit using SYSTAT v.10.2. Residual plots for both predictor
variables were examined to check for constancy of error variance, and Lilliefor's test was
conducted to ensure normal error variance. *Abies balsamea* and *Tsuga canadensis* height
growth models were weighted by $(IH)^{-1}$ and $(IH)^{-2}$ to correct for increasing error variance

with respect to increasing initial height, and natural log transformations were applied to

AAHINC for all *Picea rubens* models to address non-normal error distributions (Neter *et al.* 1996). Generalized R^2 values (Kvalseth 1985) were calculated for all weighted and transformed models. Furnival's index of fit (FI, Furnival 1961) was calculated for all weighted, transformed, and unweighted models. Furnival's index permits simultaneous comparison of root mean square error, normality, and homoskedasticity among model forms. The lower the FI value, the better the fit based on these criteria (Kenefic 2000). The best fitting model was then chosen by comparing the FI for each model within each species. If the difference in FI values for competing models was less than 10%, the R^2-value was used to determine the most appropriate model.

Additional predictor variables were created using gap fraction readings taken higher in the canopy to determine if differences in canopy structure explained additional variability in the height growth models. The new predictor variables defined were HS1 and HS2 where HS1 = (1-DIFN4)/(1-DIFN1) and HS2 = (1-DIFN5)/(1-DIFN1), where DIFN4 and DIFN5 were the gap fraction readings taken at 8.4 m and 11.5 m respectively. The two variables HS1 and HS2 were ratios of canopy closure at 8.4 m and 11.5 m to canopy closure at tree level and were an effort to quantify the proportion of high-shading foliage. Values close to one would indicate a large proportion of high-shading foliage while values close to zero would indicate a larger proportion of low-shading foliage. The ratios were created based on DIFN4 and DIFN5 since readings at these two heights were taken for all sample trees. These two predictor variables were added to the first-order linear models to test if these terms were significant. Adjusted R^2 values and mean square

Table 1.1   Linear and nonlinear regression models tested to predict *Abies balsamea,* *Picea rubens,* and *Tsuga canadensis* height growth from initial height and gap fraction. The height growth hypothesis that each model tested is described above and corresponds to the hypothesis number in the text.

Hypothesis	Model
1	$AAHINC = b_0 + b_1\,DIFN1 + b_2\,IH$
2	$AAHINC = b_0 * DIFN1^{b1} * (IH)^{b2}$
3	$AAHINC = b_0 + b_1 difn1 + b_2 difn1^2 + b_3\,IH$

AAHINC = average annual height increment (m); DIFN1 = gap fraction reading at tree height; difn1 = deviation of DIFN1 from mean DIFN1; IH = initial height of tree (tree height at beginning of measurement period).

error were compared between these first-order linear models and the original first-order linear models without these terms to determine if they improved the predictive capacity of the model.

LAI Calculations

One-sided projected leaf area index (LAI) was calculated for the subsample plot centered at each sample tree based on trees tallied in the vertical point sample. Estimates for one-sided tree-level projected leaf area (PLA) for *Abies balsamea, Picea rubens, Tsuga canadensis,* and *Pinus strobus* were determined using non-sapwood based equations based on the model proposed by Valentine *et al.* (1994) and used by Gilmore *et al.* (1996), Maguire *et al.* (1998), Kenefic and Seymour (1999), and Seymour (unpublished) (Table 1.2). For trees with modified live crown ratios greater than one, or trees whose DBH were outside the range in which Valentine's equations were fitted to,

Table 1.2 Projected leaf area equations used with coefficients and citations.

Species	PLA Model	Citation
Abies balsamea	$PLA = b_0(BA * mLCR)^{b1}$ $b_0 = 0.4763$ and $b_1 = 0.9021$	Seymour (unpublished), from Gilmore *et al.* (1996) data set.
Picea rubens	$PLA = b_0 BA^{b1} * mLCR^{b2}$ $b_0 = 0.5553$, $b_1 = 0.8532$, and $b_2 = 0.4925$	Kenefic (2000), from Maguire *et al.* data set.
Tsuga canadensis	$PLA = b_0 + b_1(BA * mLCR)$ $b_0 = 8.9221$ and $b_1 = 0.1789$	Kenefic and Seymour (1999)
Pinus strobus	$PLA = b_0(BA * mLCR)^{b1}$ $b_0 = 0.3050$ and $b_1 = 0.9470$	Seymour (unpublished)

PLA = projected leaf area (m^2); BA = basal area (cm^2); CL = crown length (m); mLCR = modified live crown ratio, (CL/tree height - 1.3) (Valentine *et al.* 1994).

biomass equations were used (Young *et al.* 1980). Specific leaf area (Table 1.3) values were used to convert leaf mass predicted by these equations to leaf area.

Young's *et al.* (1980) biomass equations were used to estimate PLA for most hardwood species and *Thuja occidentalis*. Leaf area was predicted for *Quercus rubra* L.(red oak) using biomass equations published by Tritton and Hornbeck (1982). Young's *et al.* (1980) biomass equation for *Acer rubrum* L. was used for leaf area estimation of both *Acer pensylvanicum* L. (stripped maple) and *Fraxinus americana* L. (white ash).

For species with no known published specific leaf area, specific leaf areas were calculated using leaf samples collected in September 2002 (Table1.3). The leaves were scanned using Winfolia ® software to calculate one sided leaf area. Each sample that was scanned was then put into an oven to dry for four days (until dry mass remained constant

Table 1.3 Specific leaf area (SLA) for all species tallied in the vertical point samples with citations.

Species	Specific Leaf Area (cm^2/g)	Citation
Tsuga canadensis	58.43	Kenefic and Seymour (1999)
Picea rubens	43.51	Maguire *et al.* (1998)
Abies balsamea	41.5	Gilmore *et al.* (1995)
Pinus strobus	67	Seymour (unpublished)
Thuja occidentalis	48.06	McConville (1998)
Acer rubrum	167	Leathers (1996)
Betula papyrifera	138	Moores (unpublished data)
Betula alleghaniensis	163	Moores (unpublished data)
Fraxinus americana	315	Moores (unpublished data)
Acer pensylvanicum	312	Moores (unpublished data)
Quercus rubra	155	Moores (unpublished data)

between daily measurements), at which point the dry mass of the sample was recorded.

Specific leaf area was then calculated by dividing the one-sided leaf area by the dry mass.

This was done for three samples of each tree species.

The contribution to stand-level LAI was calculated for each tree by dividing its

PLA by its respective plot size, $LAI = PLA / \pi R^2_{limiting}$, where $R_{limiting}$ was the limiting

radius for inclusion in the tally, defined by HT / tan 61.4°, HT being the height of the tree

(Husch *et al.* 1972). Plot-level LAI was estimated by summing up the LAI contribution of

each "in" tree.

LAI Stratification

To quantify canopy architecture, plot-level LAI was stratified into approximate 3-

m strata. The strata designations were: < 2.9 m, 2.9-5.5 m, 5.5-8.4 m, 8.4-11.5 m, 11.5-

14.5 m, 14.5-17.5 m, 17.5-20.5 m, and >20.5 m. The lower four LAI strata were chosen

to be equivalent to the heights at which gap fraction readings were taken. Cumulative leaf

distribution functions were used to distribute tree-level leaf area (LA) into these

respective strata. For conifers, cumulative leaf area distributions of the form $LA_i/TOTLA$

$= 1 - exp(-b_1 * RD_i^{b2})$, where LA_i is the leaf area above height I, TOTLA is the total leaf

area of the tree and RD_i is the relative depth into the crown at height I (defining 1 as the

base of the crown and 0 as the top of the crown) (Gilmore and Seymour 1997), were used.

Parameter estimates of $b_0 = 2.748$, and $b_1 = 3.027$ from Gilmore and Seymour (1997)

were used for *Abies balsamea*, and *Picea rubens*. The above cumulative leaf area

distribution function was fit to branch-level data provided by Kenefic (unpublished) for

Tsuga canadensis, giving parameter estimates of $b_0 = 2.933$, and $b_1 = 2.392$. These parameter estimates were also used for *Thuja occidentalis*. A rectangular leaf area distribution was assumed for all hardwood species, giving the following LA distribution function: $LA_i/TOTLA = RD_i$. Stratified tree-level leaf area was summed for all trees over the entire plot to form a plot-level leaf area profile.

The LA in each stratum was used to cluster the 69 subsample plots into groups of similar vertical leaf area distribution. Hierarchical clustering using Ward's minimum variance method was used to gauge the amount of the variation between plots, and choose an appropriate number of structures to define. K-means clustering was used to place each plot into an appropriate vertical leaf area structure using the LAI estimates of each 3-m stratum as the sorting variables.

Vertical Structural Analysis

To determine if AAHINC could be expressed as a function of tree species, vertical foliage structure, and initial height, analysis of covariance was performed on AAHINC using species and structure as factors and initial height as a covariate. Constancy of slopes was evaluated by calculating an F statistic based on the full and reduced analysis of covariance models. Lilliefor's test was conducted to verify normal error distribution, and a modified Levene test was used to ensure homogenous error variance. Pairwise Bonferroni comparisons were made between species and structure treatments at an alpha level of 0.05 and 0.10 to test for significant differences in height growth within species but between structures, and within structures but between species.

RESULTS

Annual Height Growth Models

Initial height (IH) alone as a predictor variable in a first-order linear regression model explained between 13 and 25% of the variation in height growth depending on species (Model A, Table 1.4). By adding canopy openness (DIFN1) to the first-order linear model as an additional predictor variable, 39%, 48%, and 66% of the variation was explained for *Picea rubens, Tsuga canadensis*, and *Abies balsamea* respectively (Model 1, Table 1.4).

Fitting height growth to 2nd order polynomial functions yielded an improvement for *Picea rubens*, but not *Abies balsamea*, or *Tsuga canadensis* (Table 1.4). Since the parameter estimate for difn1^2 was not significantly different from zero at $\alpha=0.05$ for Model 3 for *Abies balsamea*, and *Tsuga canadensis*, these models were excluded from further analysis for these two species.

Ratios of canopy closure at 8.4 m (HS1), and 11.5 m (HS2) to canopy closure at tree-level failed to improve the predictive capacity of first-order linear models that contained only DIFN1 and IH as predictor variables for all three species. This attempt to quantify the proportional amount of high-shading foliage had non-significant parameter estimates at a significance level of 0.05 (Model B, Table1.4).

Table 1.4 Adjusted R^2 values, Furnival's Index of Fit and p-values for parameter estimates by species for all linear height growth models tested. Natural log transformations were applied to height growth (AAHINC) for all *Picea rubens* models. *Abies balsamea* and *Tsuga canadensis* models are untransformed and unweighted. An asterisk (*) denotes significant predictor variables at $\alpha = 0.05$.

Ref. Number	Model	*Abies balsamea*	*Picea rubens*	*Tsuga canadensis*
A	AAHINC = f (IH)	$R^2 = 0.127$ FI = 0.0992 IH:　　p= 0.003*	$R^2 = 0.212$ FI = 0.0606 IH:　　p< 0.001*	$R^2 = 0.246$ FI = 0.0616 IH:　　p< 0.001*
1	AAHINC = f (IH, DIFN1)	$R^2 = 0.650$ FI = 0.0628 IH:　　p= 0.009* DIFN1:p< 0.001*	$R^2 = 0.322$ FI = 0.0472 IH:　　p< 0.001* DIFN1:p< 0.001*	$R^2 = 0.465$ FI = 0.0518 IH:　　p= 0.007* DIFN1:p< 0.001*
3	AAHINC = f (IH, difn1, $difn1^2$)	IH:　　p= 0.013* difn1: p< 0.001* $difn1^2$: p= 0.511	$R^2 = 0.518$ FI = 0.0447 IH:　　p< 0.001* difn1: p< 0.001* $difn1^2$: p= 0.017*	IH:　　p= 0.005* difn1: p< 0.001* $difn1^2$: p= 0.145
B	AAHINC = f (IH, DIFN1, HS1, HS2)	IH:　　p= 0.008* DIFN1:p< 0.001* HS1:　p= 0.465 HS2:　p= 0.953	IH:　　p< 0.001* DIFN1:p< 0.001* HS1:　p= 0.430 HS2:　p= 0.878	IH:　　p= 0.006* DIFN1:p< 0.001* HS1:　p= 0.431 HS2:　p= 0.327

AAHINC = average annual height increment (m); DIFN1 = gap fraction reading at tree height; difn1 = deviation of DIFN1 from mean DIFN1; IH = initial height of tree (tree height at beginning of measurement period, 1998); HS1 = ratio of canopy closure at 8.36 m to canopy closure at tree height, [(1-DIFN4)/(1-DIFN1)]; HS2 = ratio of canopy closure at 11.51 m to canopy closure at tree height, [(1-DIFN5)/(1-DIFN1)] .

Abies balsamea

The model yielding the best fit for *Abies balsamea* was a power function weighted by 1/(IH) (Model 2b, Table 1.5). This model provided the following estimate for AAHINC:

(Model 2b)   AAHINC = 0.270 * (DIFN1)$^{0.607}$ * (IH)$^{0.344}$

This model showed height increment following a monotonically increasing pattern with respect to increasing canopy openness. Height increment was also observed to be greater for saplings of greater height, independent of light availability (Figure 1.2).

Picea rubens

The model yielding the best fit for *Picea rubens* was a log transformed power function (Model 2d, Table 1.6). With a log bias correction factor of 1.289, this model provided the following estimate for AAHINC:

(Model 2d)   AAHINC = 1.289 * exp[-1.822 * (DIFN1)$^{-0.238}$ * (IH)$^{-0.173}$]

This model also showed height increment following a monotonically increasing pattern with respect to increasing canopy openness. Height increment was also observed to be greater for saplings of greater height, independent of light availability (Figure 1.3).

Tsuga canadensis

The model yielding the best fit for height growth of *Tsuga canadensis* was a power function weighted by 1/(IH) (Model 2f, Table 1.7). This model was chosen over Model 1f [a first-order linear model weighted by 1/(IH)] since the FI values for these two

Table 1.5 Corrected R^2 values and Furnival's Index of Fit for all weighted and unweighted models tested to predict *Abies balsamea* height growth.

Ref. Number	Model and Parameter Estimates	Weight	Furnival's Index of Fit	R^2
0.0417	AAHINC = b_0 + b_1 DIFN1 + b_2 IH $b_0 = 0.014$ $b_1 = 0.358$ $b_2 = 0.015$	none	0.0628	0.65
1b	AAHINC = b_0 + b_1 DIFN1 + b_2 IH $b_0 = 0.006$ $b_1 = 0.323$ $b_2 = 0.023$	1/(IH)	0.056	0.648
1c	AAHINC = b_0 + b_1 DIFN1 + b_2 IH $b_0 = 0.008$ $b_1 = 0.257$ $b_2 = 0.033$	1/(IH)^2	0.059	0.576
0.0833	AAHINC = b_0 * DIFN1^{b_1} * (IH)^{b_2} $b_0 = 0.294$ $b_1 = 0.626$ $b_2 = 0.258$	none	0.0604	0.687
2b	AAHINC = b_0 * DIFN1^{b_1} * (IH)^{b_2} $b_0 = 0.270$ $b_1 = 0.607$ $b_2 = 0.344$	1/(IH)	0.0535	0.681
2c	AAHINC = b_0 * DIFN1^{b_1} * (IH)^{b_2} $b_0 = 0.244$ $b_1 = 0.535$ $b_2 = 0.414$	1/(IH)^2	0.0564	0.657

AAHINC = average annual height increment (m); DIFN1 = gap fraction reading at tree height; IH = initial height of tree (tree height at beginning of measurement period).

Table 1.6   Corrected R^2 values and Furnival's Index of Fit for all transformed models tested to predict *Picea rubens* height growth.

Ref. Number	Model and Parameter Estimates	Furnival's Index of Fit	R^2
1d	log (AAHINC) = b_0 + b_1 DIFN1 + b_2 IH $b_0 = -4.138$ $b_1 = 2.480$ $b_2 = 0.362$	0.0472	0.322
2d	log (AAHINC) = b_0 * DIFN1^{b_1} * (IH)^{b_2} $b_0 = -1.822$ $b_1 = -0.238$ $b_2 = -0.173$	0.0441	0.702
3d	log (AAHINC) = b_0 + $b_1$difn1 + $b_2$difn1^2 + b_3 IH $b_0 = -3.139$ $b_1 = 3.690$ $b_2 = -3.602$ $b_3 = 0.345$	0.0447	0.518

AAHINC = average annual height increment (m); DIFN1 = gap fraction reading at tree height; difn1 = deviation of DIFN1 from mean DIFN1; IH = initial height of tree (tree height at beginning of measurement period).

models differed by less than one percent; however, the R^2 value for Model 2f was substantially higher than for Model 1f (0.502 versus 0.458 respectively). Model 2f provided the following estimate for AAHINC:

(Model 2f)   AAHINC = 0.174 * DIFN1$^{0.309}$ * (IH)$^{0.275}$

Compared to *Abies balsamea* and *Picea rubens*, there was a much smaller predicted height growth response for *Tsuga canadensis* with respect to changes in canopy openness (Figure 1.4); however, a monotonically increasing pattern was still observed.

Table 1.7 Corrected R^2 values and Furnival's Index of Fit for all weighted and unweighted models tested to predict *Tsuga canadensis* height growth.

Ref. Number	Model and Parameter Estimates	Weight	Furnival's Index of Fit	R^2
1	AAHINC = b_0 + b_1 DIFN1 + b_2 IH $b_0 = 0.056$ $b_1 = 0.152$ $b_2 = 0.014$	none	0.0518	0.465
1f	AAHINC = b_0 + b_1 DIFN1 + b_2 IH $b_0 = 0.039$ $b_1 = 0.177$ $b_2 = 0.018$	1/(IH)	0.0461	0.458
1g	AAHINC = b_0 + b_1 DIFN1 + b_2 IH $b_0 = 0.032$ $b_1 = 0.184$ $b_2 = 0.022$	1/(IH)^2	0.0536	0.414
2	AAHINC = b_0 * DIFN-1^{b1} * (IH)^{b2} $b_0 = 0.172$ $b_1 = 0.269$ $b_2 = 0.226$	none	0.0503	0.514
2f	AAHINC = b_0 * DIFN1^{b1} * (IH)^{b2} $b_0 = 0.174$ $b_1 = 0.309$ $b_2 = 0.275$	1/(IH)	0.0465	0.502
2g	AAHINC = b_0 * DIFN1^{b1} * (IH)^{b2} $b_0 = 0.184$ $b_1 = 0.346$ $b_2 = 0.297$	1/(IH)^2	0.0557	0.464

AAHINC = average annual height increment (m); DIFN1 = gap fraction reading at tree height; IH = initial height of tree (tree height at beginning of measurement period).
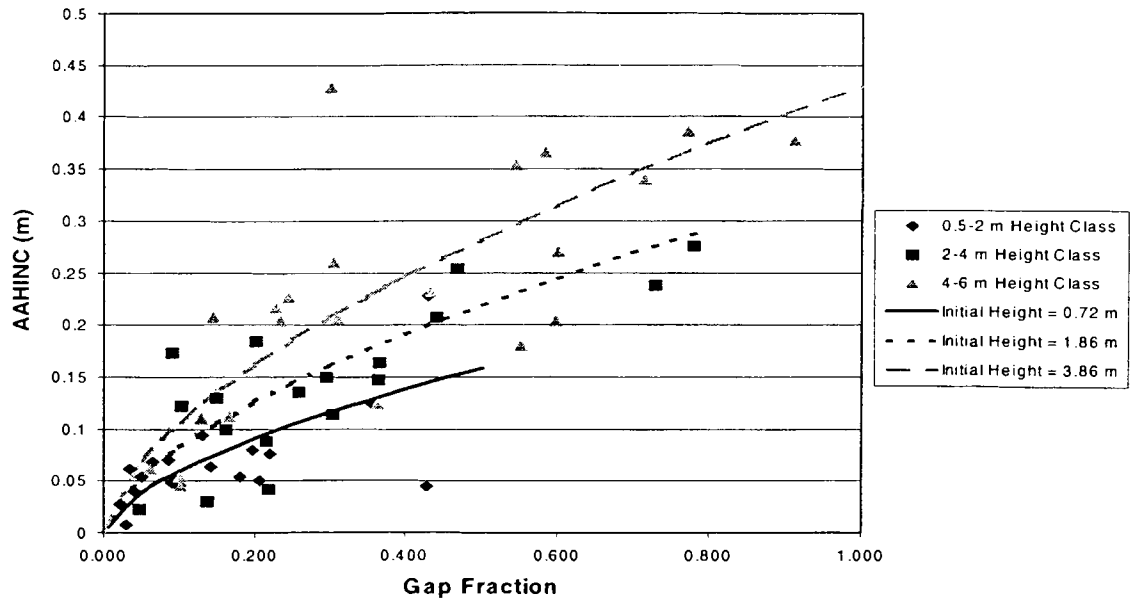
Figure 1.2   Scatter plot of *Abies balsamea* average annual height increment (AAHINC) and gap fraction, with best-fit model height curves for initial *Abies balsamea* heights of 0.72 m, 1.86 m, and 3.86 m.
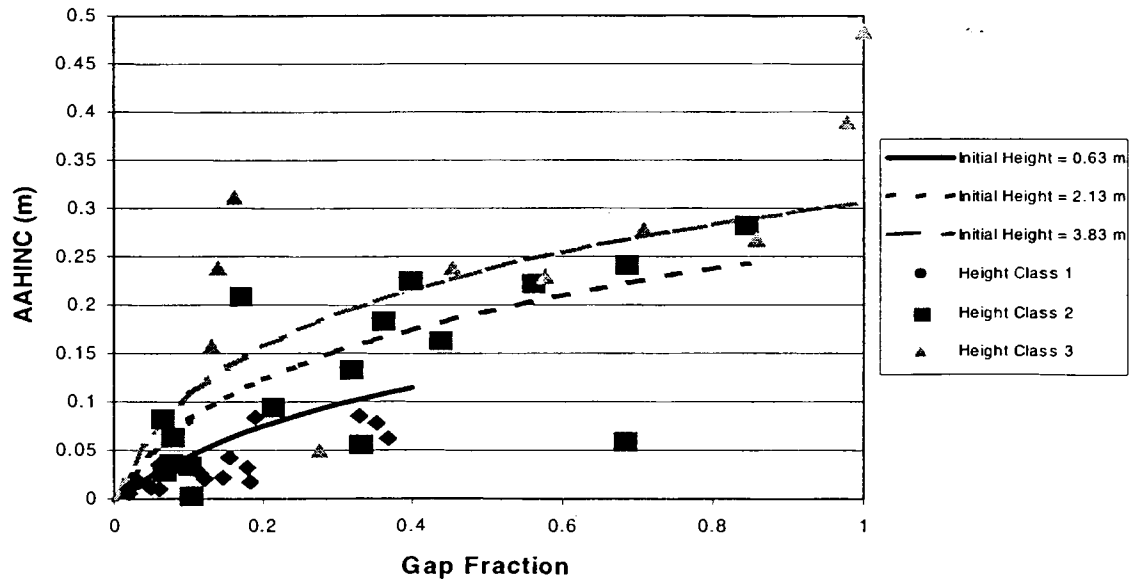
Figure 1.3   Scatter plot of *Picea rubens* average annual height increment (AAHINC) and gap fraction, with best-fit model height curves for initial *Picea rubens* heights of 0.63, 2.13 m, and 3.83 m.
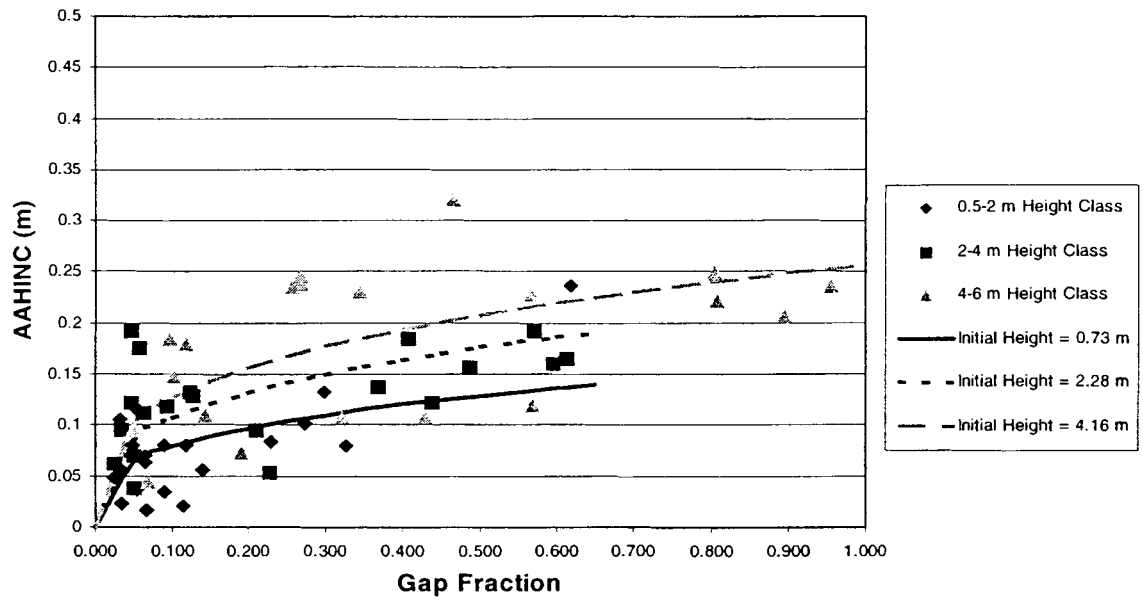
Figure 1.4   Scatter plot of *Tsuga canadensis* average annual height increment (AAHINC) and gap fraction, with best-fit model height curves for initial *Tsuga canadensis* heights of 0.73 m, 2.28 m, and 4.16 m.

Vertical Structural Analysis

Plot-level LAI

Height growth was predicted for subsample trees using the non linear power function, $AAHINC = b_0 * IH^{b1} * LAI^{b2}$ to test for the significance of plot-level LAI in predicting height growth. The parameter estimates for plot-level LAI were not significantly different from zero for all three species. This indicates that plot-level LAI is not significant in predicting sapling height growth in these complex, multi-cohort stands (Table 1.8). Compared to a power function model that contained only initial height as a predictor variable, adjusted R^2 values showed either no improvement or only minimal improvement, and mean square error showed no improvement by adding plot-level LAI to the model (Table 1.8).

Vertical Leaf Area Structure Cluster Analysis

Hierarchical clustering using Ward's minimum variance method suggested three to four distinct LA structures among the subsample (Figure 1.5). Three structures were chosen since the option of classifying plots into four structures would have produced one structure with only four plots, thereby complicating analysis due to the small sample size. Out of 69 plots, 30 were grouped into structure 1, 22 were grouped into structure 2, and 17 were grouped into structure 3 (Table 1.9). Structure 1 had the lowest mean LAI of 3.58, which was significantly lower than both structure 2 and structure 3 ($\alpha=0.05$). The average vertical LA profile of the plots grouped into this structure was unimodal, peaking

between 10-11 m in the canopy (Figure 1.6). Over half of the average total LAI of

structure 2 plots was concentrated in the understory, peaking at about 4 m (Table 1.9).

The amount of LAI below 8.36 m in structure 2 was significantly higher than in structure

1 or structure 3, (α = 0.05). Structure 3 has the highest mean LAI of 5.76. This is

significantly higher than structure 1 or 2 (α = 0.05). The majority of LAI in structure 3

plots was concentrated in the overstory, peaking between 12-13 m.. The vertical

distribution of LAI in structure 3 plots most closely resembled an even-aged structure

(Figure 1.6).

Analysis of Covariance

While total plot-level LAI was not significant in predicting height growth (Table

1.8), analysis of covariance showed that the vertical distribution of that foliage (plot-level

vertical leaf area structure) was highly significant in predicting AAHINC. Species was

not significant in determining height growth (α=0.05), nor were there any significant

interaction effects between species and structure. Fifty percent of the variation in height

growth was explained by the analysis of covariance (Table 1.10).

While mean annual height increment estimates, adjusted to a standard initial

height, varied between structures and species (Table 1.11), pairwise Bonferroni

comparisons showed significant differences in height growth between structures only for

Picea rubens (α=0.05) (Table 1.12). *Picea rubens* grew significantly better in structure 2

than both structure 1 or structure 3; however, height growth was not significantly

different between structure 1 and structure 3. There were no significant differences in

Table 1.8 Comparison of non linear power function models by species to predict height growth, with and without plot-level LAI as a predictor variable. P-values for parameter estimates (b_i) are provided. An asterisk (*) denotes significant predictor variables at $\alpha = 0.05$.

Species	AAHINC = b_0* IH^{b1}	AAHINC = b_0* IH^{b1}* LAI^{b2}
Abies balsamea	$R^2 = 0.393$ MSE = 0.009 IH: p = 0.006*	$R^2 = 0.417$ MSE = 0.009 IH: p = 0.010* LAI: p = 0.408
Picea rubens	$R^2 = 0.362$ MSE = 0.011 IH: p = 0.018*	$R^2 = 0.362$ MSE = 0.012 IH: p = 0.020* LAI: p = 0.966
Tsuga canadensis	$R^2 = 0.331$ MSE = 0.005 IH: p = 0.012*	$R^2 = 0.333$ MSE = 0.005 IH: p = 0.014* LAI: p = 0.834

Table 1.9 Number of plots and mean LAI characteristics for vertical LA structures.

Structure	Number of Plots	Mean LAI ± SE	Mean Understory (< 8.36 m) LAI± SE	Mean Overstory (> 8.36 m) LAI ± SE
1	30	3.58 ± 0.18	1.09 ± 0.11	2.32 ± 0.13
2	22	4.89 ± 0.21	2.74 ± 0.13	2.01 ± 0.15
3	17	5.76 ± 0.24	1.53 ± 0.14	4.02 ± 0.17

Cluster Tree
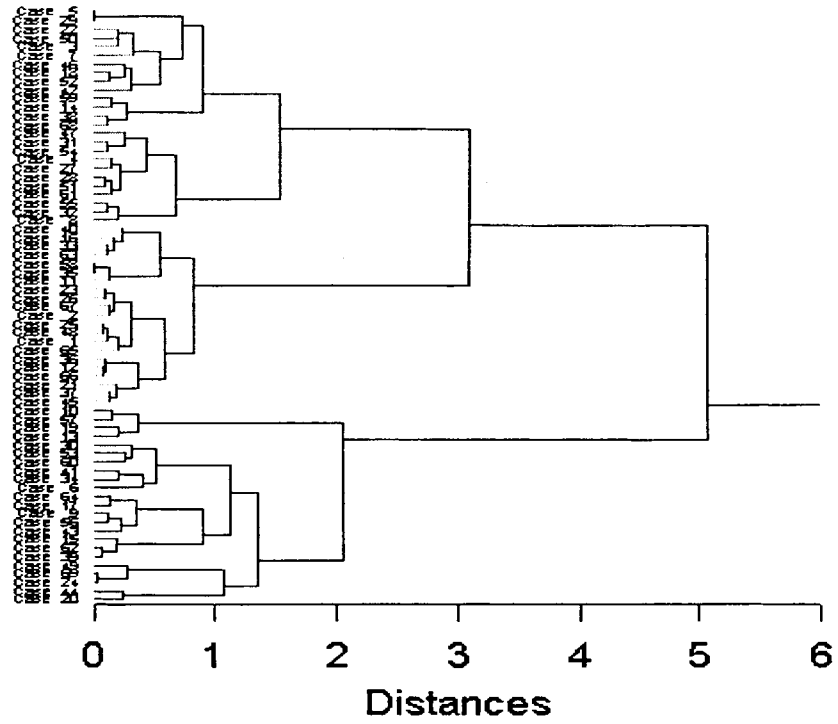
Figure 1.5 Hierarchical clustering diagram of subsample plots based on vertical leaf area distribution.
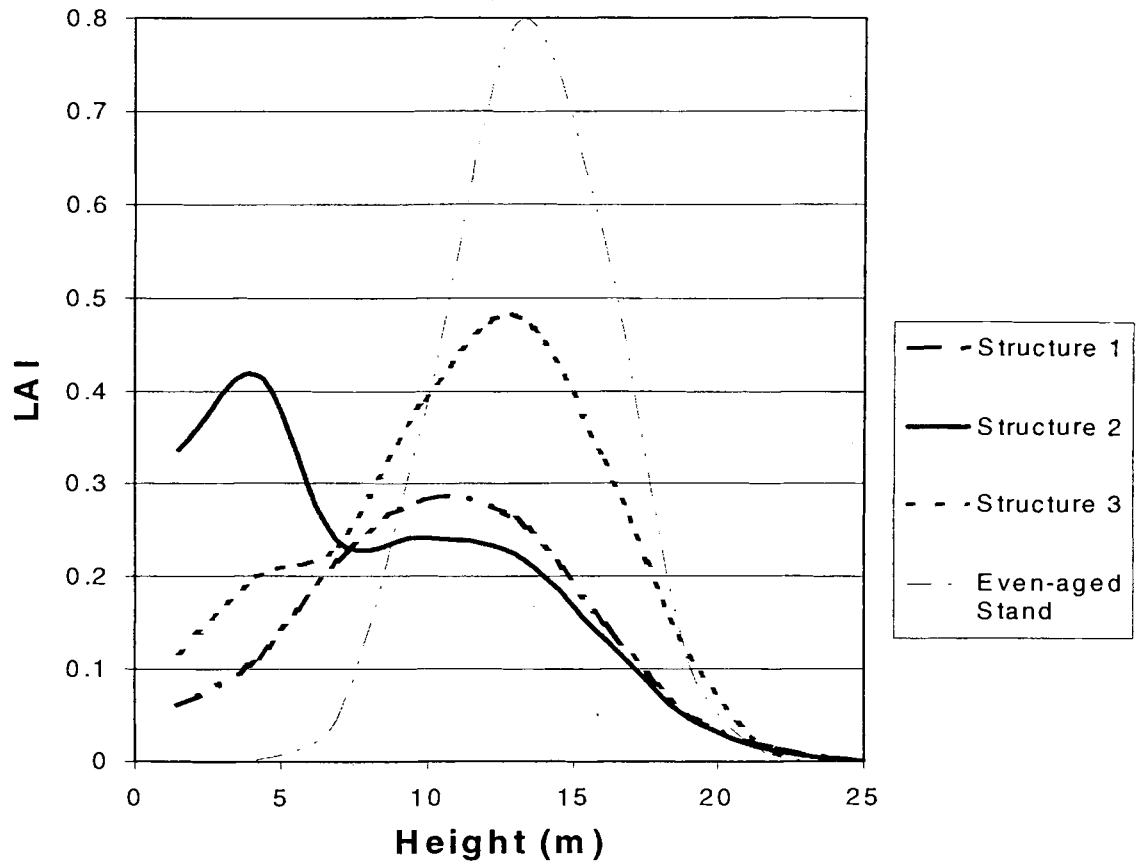
Figure 1.6 Average plot-level vertical LAI distributions for each structure. Curves are based on LAI estimates for discrete 3-m vertical strata but are smoothed for illustration purposes. Vertical LAI distribution for a fully stocked mature even-aged *Tsuga canadensis* stand is included for comparison purposes (Kenefic unpublished).

Table 1.10   Analysis of covariance table describing AAHINC as a function of species, vertical LA structure, and initial height of sample tree. An asterisk (*) denotes significant p-values at $\alpha = 0.05$.

Source	Sum-of-Squares	df	Mean Square	F-ratio	p-value
Species	0.025	2	0.013	1.78	0.178
Structure	0.104	2	0.052	7.348	0.001*
Species - Structure Interaction	0.045	4	0.011	1.592	0.188
Initial Height	0.214	1	0.214	30.153	< 0.001*
Error	0.418	59	0.007		

height growth between the different structures for *Abies balsamea* and *Tsuga canadensis* at significance levels of either 0.05 or 0.10 (Table 1.12).

Significant differences in height growth between species within each structure occurred only in structure 2 at an alpha level of 0.05. *Picea rubens* height growth was significantly higher in structure 2 than *Tsuga canadensis* height growth, while *Abies balsamea* height growth was not significantly different from *Tsuga canadensis* or *Picea rubens* height growth in structure 2 (Table 1.13). There were no significant differences in height growth between species in the other structures.

Table 1.11   Adjusted Least Squares Mean AAHINC (m) by species and structure.

Species	Structure	N	Adjusted Least Squares Mean AAHINC ± SE (m)
Abies balsamea	1	8	$\mu_{BF1} = 0.157 \pm 0.030$
	2	8	$\mu_{BF2} = 0.230 \pm 0.030$
	3	8	$\mu_{BF3} = 0.150 \pm 0.030$
Picea rubens	1	11	$\mu_{RS1} = 0.157 \pm 0.025$
	2	6	$\mu_{RS2} = 0.271 \pm 0.035$
	3	6	$\mu_{RS3} = 0.100 \pm 0.034$
Tsuga canadensis	1	11	$\mu_{EH1} = 0.164 \pm 0.026$
	2	8	$\mu_{EH2} = 0.152 \pm 0.030$
	3	3	$\mu_{EH3} = 0.077 \pm 0.049$

Table 1.12 Bonferroni pairwise comparisons between structures for each species with 95% and 90% family confidence intervals. An asterisk (*) denotes significant differences at $\alpha = 0.05$.

Species	Pairwise Comparison	95% Family Confidence Interval	90% Family Confidence Interval
Abies Balsamea	$\mu_{BF1} - \mu_{BF2} = 0.073$	(-0.177, 0.031)	(-0.165, 0.019)
	$\mu_{BF2} - \mu_{BF3} = 0.080$	(-0.024, 0.184)	(-0.012, 0.172)
	$\mu_{BF1} - \mu_{BF3} = 0.007$	(-0.097, 0.111)	(-0.085, 0.099)
Picea rubens	$\mu_{RS1} - \mu_{RS2} = -0.114$ *	(-0.219, -0.009)	(-0.207, -0.021)
	$\mu_{RS2} - \mu_{RS3} = 0.171$ *	(0.051, 0.291)	(0.065, 0.277)
	$\mu_{RS1} - \mu_{RS3} = 0.057$	(-0.048, 0.162)	(-0.036, 0.150)
Tsuga canadensis	$\mu_{EH1} - \mu_{EH2} = 0.012$	(-0.084, 0.109)	(-0.073, 0.097)
	$\mu_{EH2} - \mu_{EH3} = 0.075$	(-0.065, 0.215)	(-0.049, 0.199)
	$\mu_{EH1} - \mu_{EH3} = 0.087$	(-0.048, 0.221)	(-0.032, 0.206)

Table 1.13 Bonferroni pairwise comparisons between species within each structure with 95% family confidence intervals. An asterisk (*)denotes significant differences at α = 0.05.

Structure	Pairwise Comparison	95% Family Confidence Interval
1	$\mu_{BF1} - \mu_{RS1} = 0.000$	(-0.096, 0.096)
	$\mu_{RS1} - \mu_{EH1} = -0.007$	(-0.095, 0.081)
	$\mu_{BF1} - \mu_{EH1} = -0.007$	(-0.103, 0.089)
2	$\mu_{BF2} - \mu_{RS2} = -0.041$	(-0.153, 0.071)
	$\mu_{RS2} - \mu_{EH2} = 0.119 *$	(0.007, 0.231)
	$\mu_{BF2} - \mu_{EH2} = 0.078$	(-0.026, 0.182)
3	$\mu_{BF3} - \mu_{RS3} = 0.050$	(-0.062, 0.162)
	$\mu_{RS3} - \mu_{EH3} = 0.023$	(-0.123, 0.170)
	$\mu_{BF3} - \mu_{EH3} = 0.073$	(-0.067, 0.213)

DISCUSSION

Based on the best fitting regression models describing height growth, all three

species in this study showed a monotonically increasing trend. A positive response to

increasing diffuse light conditions was observed from full canopy closure to full canopy

openness but at a decreasing rate.

Abies balsamea

Height growth of *Abies balsamea* was best described with a power function

(Model 2b). Although all terms were significant in the first-order linear models (Models

1a, 1b, and 1c), they did not provide as good a fit as the power function. The squared gap

fraction term for the second-order polynomial regression model (Model 3) was non-

significant, thereby showing no evidence of a peaking pattern of height growth with

respect to gap fraction.

Previous studies looking at *Abies balsamea* sapling height growth have shown

different results. Studying height growth of *Abies balsamea* and *Picea rubens* in two-

storied stands with a pure *Pinus strobus* overstory, McConville (1998) suggested that

maximum height growth rates could be achieved for *Abies balsamea* at gap fraction

values of approximately 0.65 on fair sites, and 0.80 on poor sites, and found a negative

response to increases in gap fraction above these points. Logan (1969) grew seedlings of a

variety of species in the open and under lath and fiberglass shelters. He found that greater

Abies balsamea seedling height growth occurred in 45% full sunlight conditions

compared to 13% and 25% full sunlight, but that height growth was not significantly

different to seedlings growing in 100% full sunlight. Similar to our study, both Parent and

Messier (1995) and Duchesneau *et al.* (2001) found monotonically increasing height

growth patterns with respect to light for natural advance regeneration growing in

managed and unmanaged stands in the boreal forest. While height growth continued to

increase to the maximum light conditions measured in both of these studies (83% of

photosynthetic photon flux density), response was much less sensitive to increased light

conditions above 25% photosynthetic photon flux density (PPFD). While visual

inspection of height growth curves from our study showed a decrease in height growth

response at approximately 10% gap fraction (Figure 1.2), there was no evidence of the

curves reaching an asymptote. In contrast, height growth curves were much more

asymptotic for both Parent and Messier (1995) and Duchesneau *et al.* (2001).

Picea rubens

The best fitting model used to describe *Picea rubens* height growth was a natural

log transformed power function (Model 2d). A natural log transformed quadratic

regression model (Model 3d) demonstrated a peak in height growth at gap fraction values

of approximately 0.80; however, this model did not provide as good a fit. A natural log

transformed linear model (Model 1d), which demonstrated an exponentially increasing

height growth response gave a very poor fit, with an R^2 value of only 0.322. Visual

inspection of the height growth model (Figure 1.3) showed a gradual leveling off of

height growth response; however, no sharp decline at any particular gap fraction value

was observed. Height-age curves based on this model (Figure 1.7) demonstrated that the

time required to grow from a height of 0.5 m to 6.0 m decreased substantially as gap

fraction values increased from 0.1 to 0.4; however, based on model predictions, a height

of 6.0 m was reached only seven years earlier for a sapling growing under canopy

openness levels of 0.7 compared to 0.4 (24 years versus 31 years), and a reduction in time

of only three years was achieved for a sapling growing in fully open conditions compared

to canopy openness levels of 0.7.

There are very few studies specifically looking at height growth of *Picea rubens*.

McConville (1998) found that *Picea rubens* grew best at gap fraction values of

approximately 0.65 on fair sites but on poor sites did best in more open conditions. He

also found that saplings growing in conditions of 30% canopy openness performed as

well as trees growing in open conditions. With the exception of McConville's results for

trees growing on poor sites, the model in our study predicts very different results,

showing no sign of a peak, and predicting a much higher growth rate for open grown trees

than for trees growing at gap fraction values of 30%.

Studies of *Picea glauca* and *Picea mariana* (Mill.) B.S.P. (black spruce) seedling

development have also produced dissimilar results. While Logan (1969) found that *Picea*

mariana, probably the least shade tolerant of the three *Picea spp.* (Viereck and Johnston

1990), grew best in full light intensity, with significant increases in height growth for

each increasing light intensity level (13%, 25%, 45%, and 100%), *Picea glauca* height

growth did not change significantly between light intensities of 45% full light and 100%

full light, suggesting asymptotic growth with respect to increasing light. Man and Lieffers
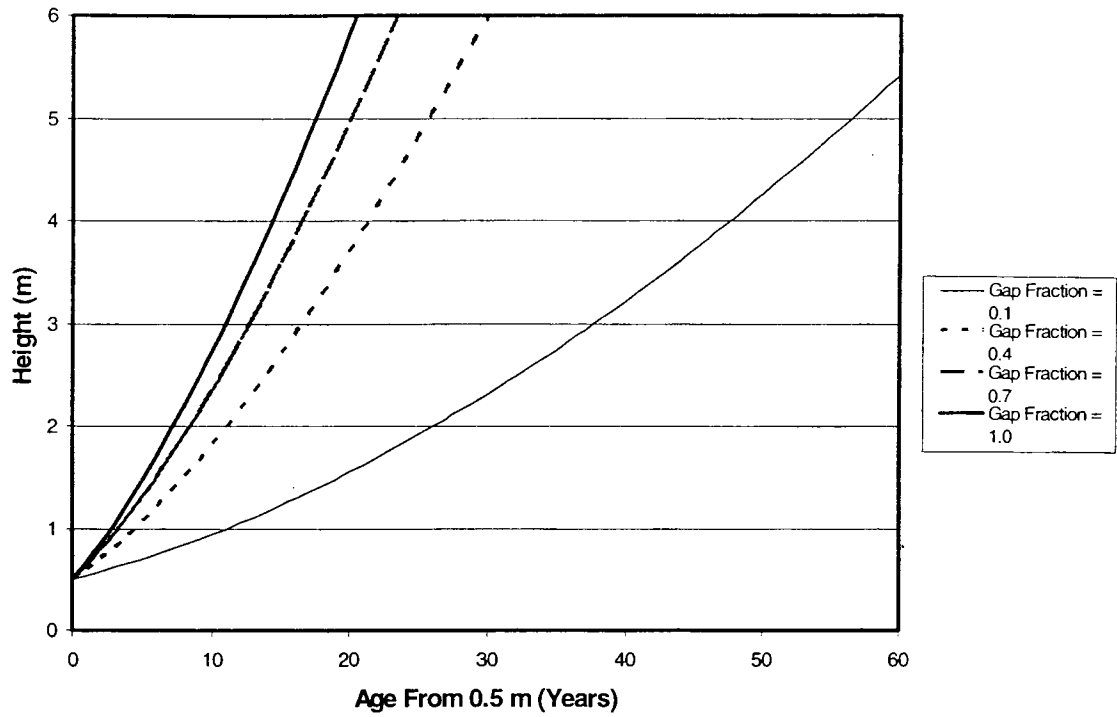
Figure 1.7   Understory height-age curves for *Picea rubens* saplings growing under gap fraction values of 0.10, 0.40, and 0.70, and 1.0.

(1997) found that *Picea glauca* height growth under an aspen overstory outpaced height growth in open conditions.

Tsuga canadensis

Tsuga canadensis followed a monotonically increasing pattern of height growth with respect to increasing canopy openness (Model 2f). This model provided better or equivalent FI values and better R^2 values than the linear models tested (Models 1e, 1f, and 1g). A second-order polynomial regression model (Model 3) contained a non-significant squared gap fraction term, thereby showing no evidence of a peaking pattern of height growth with respect to gap fraction.

Visual inspection of the height growth curves showed a sharp decrease in height growth response above gap fraction values of 0.05. While no peak in AAHINC was observed, the height growth response of *Tsuga canadensis* to increases in gap fraction was the weakest of the three species tested in this study except at extremely high levels of canopy closure (Figure 1.8). This is evidenced by the low R^2 value of the best fitting model, which only explained 50.2% of the variation in height growth. This finding is consistent with the extreme shade tolerance of *Tsuga canadensis,* and supports the idea that *Tsuga canadensis* is most shade tolerant of these three species (Baker 1949; Godman and Lancaster 1990).

While the low R^2 value for the *Tsuga canadensis* height growth model probably does indicate less responsiveness to changes in light, the different sapling crown morphology and the resulting methodology used to measure height growth for *Tsuga*

canadensis may also be reducing precision. Unlike *Picea rubens* and *Abies balsamea*, *Tsuga canadensis* has no well defined leader in low light conditions. All branches, including the future leader, grow laterally. This added uncertainty to the determination of the leader. Internodal distance down what was determined to be the terminal shoot was then a measure of stem growth as opposed to height growth since the terminal shoot was frequently growing out laterally resulting in no actual vertical difference between nodes. The resulting ambiguity over what was lateral and what was vertical growth could have resulted in higher AAHINC measurements for saplings in low light levels.

Two studies looking at *Tsuga canadensis* growth in different light environments showed differing results. Logan (1969) found that *Tsuga canadensis* height growth was highest in 45% full light conditions. Of all four treatments in his study (13%, 25%, 45%, and 100% full sunlight), height growth was actually lowest in the completely open conditions. Finzi and Canham (2000) looked at radial growth, which is more sensitive to intra-cohort competition (Smith *et al.* 1997), for *Tsuga canadensis* saplings growing both in understory and gap conditions in mixed conifer-hardwood forests in southern New England. Light intensities in their study ranged from 0.3% up to 42.9% of full intensity. Radial growth began to level off as the higher light intensities were reached; however, of the six species they measured, *Tsuga canadensis* had the highest asymptotic growth rate.

Compared to the other studies previously discussed, the saplings in this study spanned a larger range in size. The maximum sapling height for McConville (1998) was 3.91 m. Logan's (1969) seedlings originated as nursery stock and reached maximum heights of only 1.35 m, 1.60 m, and 0.66 m for *Abies balsamea, Picea glauca,* and *Tsuga*

canadensis respectively by the end of the measurement period. Parent and Messier (1995) studied 14 year-old *Abies balsamea* saplings that ranged in height from 0.15 to 2.69 m, while Duchesneau *et al.* (2001) studied saplings from 0.5 - 2 m in height. The largest *Tsuga canadensis* sapling in the study done by Finzi and Canham (2000) had a DBH of 4.0 cm. Saplings in our study ranged up to 6.0 m for all three species, with a maximum DBH of 10.7 cm for *Tsuga canadensis*. It was these larger saplings that formed the upper range of gap fraction values sampled (Figure 1.2, Figure 1.3, Figure 1.4). With the exception of one *Tsuga canadensis* sapling, all saplings under 2.0 m in height were growing in gap fraction conditions of less than 0.50. This most likely was due in part to the sampling scheme where grid points with evidence of cutting within the previous five years were avoided. Since open conditions sampled in this study had existed for more than five years, saplings would have had time to respond to the improved light conditions and would generally be taller.

The fact this study included larger, more advanced saplings, with the smaller trees sampled being restricted to the lower levels of canopy openness, could explain why no signs of a peak or plateau at high levels of canopy openness were observed. For *Picea rubens* it is known that while germination and establishment proceeds best under cover, full light conditions are needed for optimal growth once trees reach larger sapling and pole sizes (Blum 1990). Klinka *et al.* (1992) also noted the same trend in light requirements for shade tolerant *Abies amabilis* (Dougl. Ex Loud.) Forbes (Pacific silver fir) and *Abies lasiocarpa* (Hook.) Nutt.(subalpine fir). Since we were only sampling

larger trees at the higher levels of canopy openness, we would have missed a possible

peaking pattern with the smaller saplings.

Consistent with McConville (1998), initial height was found to be significant in

predicting conifer height growth and therefore was used as an additional predictor

variable. While most of the other studies mentioned above did not include initial height

(although Duchesneau *et al.* (2001) used relative height growth), it was an appropriate

predictor variable for this study since we were measuring saplings originating from

natural advance regeneration that not only spanned a large height gradient, but a large age

gradient encompassing differing past growing environments and histories. These factors

would have determined tree condition, vigor, and height in 1998 (the beginning of the

measurement period for the majority of the trees) which likely had a significant influence

on height growth during the time period measured. Including initial height was one way

to incorporate the effects of different past growth histories into these models.

Species Comparisons

Comparison of growth between the three species studied showed that *Tsuga*

canadensis grew best in low light levels (gap fraction values < 0.20) (Figure 1.8);

however, *Picea rubens* and *Abies balsamea* both surpassed *Tsuga canadensis* once gap

fraction values of 0.20 or greater were reached. Above gap fraction values of 0.20, the

models showed *Abies balsamea* to be the most aggressive competitor. Over all levels of

canopy openness, *Abies balsamea* outpaced *Picea rubens* in terms of height growth. The

larger slope of the *Abies balsamea* height growth model suggested that this species was

also the most responsive to increases in gap fraction. This is consistent with what we

know about the sapling growth dynamics of these species, and their responsiveness to gap

openings (Westveld 1931; Blum 1990; Godman and Lancaster 1990; Davis 1991;

Seymour 1992).

Based on the average gap fraction values measured in these stands for the three

different height classes (0.5-2 m, 2-4 m, 4-6 m), *Picea rubens* took 42 years to grow from

0.5 m to 6.0 m, while *Abies balsamea* took 37 years and *Tsuga canadensis* took 39 years

(Figure 1.9). While *Tsuga canadensis* may be the slowest growing species above gap

fraction values of 0.20, its predicted ability to grow faster as a small seedling in the low

light environments deep in the understories of these complex stands permitted it to reach

heights of 6.0 m in comparable time to the two other species.

Sources of Model Variability

Overall 68.1%, 65.5%, and 50.2% of the variation in *Abies balsamea, Picea*

rubens, and *Tsuga canadensis* height growth were explained by best fit models using

initial height and gap fraction as predictor variables. Some studies have been able to

achieve higher R^2 values (Parent and Messier 1995; Finzi and Canham 2000), while

others produced comparable or slightly less predictive models (based on R^2 values) (

McConville 1998; Duchesneau *et al.* 2001).

Sources of additional variability in these models could be due to site quality or

soil drainage class. While poorly and very poorly drained sites were not sampled, sampled

trees ranged between somewhat poorly drained, moderately drained and well drained
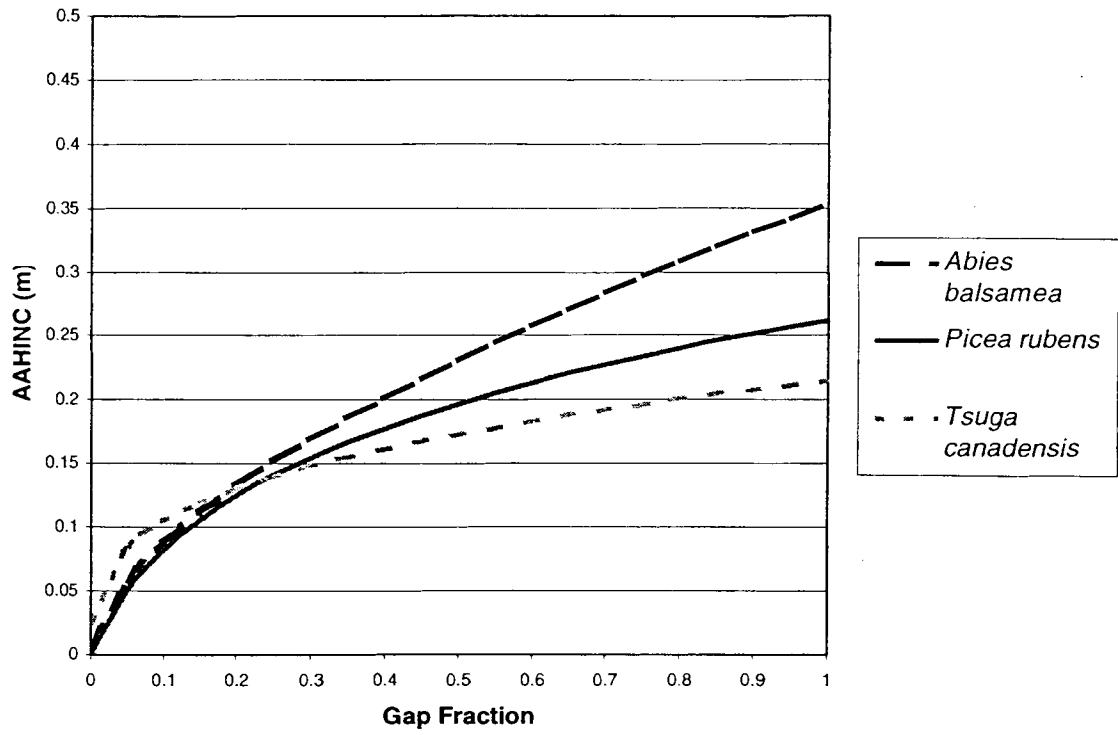
Figure 1.8   Height growth curves for *Abies balsamea, Picea rubens,* and *Tsuga canadensis* based on best fit models for each species, at an initial height of 2.18 m.
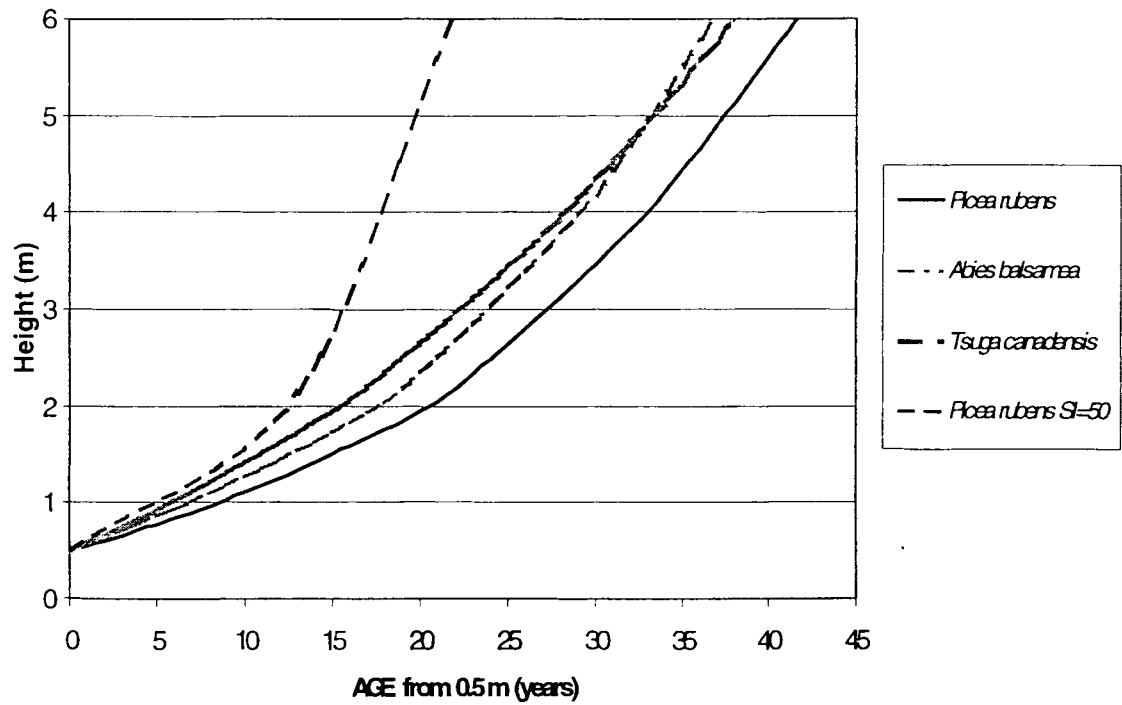
Figure 1.9 Understory height-age curves for *Abies balsamea, Picea rubens,* and *Tsuga canadensis* growing under average levels of canopy closure in the stands sampled. Even-aged *Picea rubens* height growth is included for comparison purposes.

sites. While growth of *Picea rubens* responds little to drainage class, growth of *Abies balsamea* is significantly greater on well drained soils than poorly drained soils (Meng and Seymour 1992). Site index, or site index interaction terms were significant in predicting sapling height growth for McConville (1998).

Height growth is relatively insensitive to moderate levels of intra-cohort competition (Mitchell 1975; Smith *et al.* 1997; Wagner *et al.* 1999). Baskerville (1965) found that average height of even-aged *Abies balsamea* stands differed only at extremely high densities (5000 stems/acre), and low densities (700 stems/acre), and Wampler (1993) found that understory tree density was not a significant parameter in predicting *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) height growth. Duchesneau (2001) found however, that while there was no significant relationship between intra-cohort competition and relative height growth in conditions below 25% of full sunlight, a significant negative relationship did exist for *Abies balsamea* trees in light conditions above 25% of full sunlight. While a competition index describing intra-cohort competition may have provided a slight improvement to these models, with the exception of a few saplings located in dense sapling thickets, it is unlikely that the level of intra-cohort competition experienced by most saplings in these stands would have been sufficient to reduce height growth.

Many studies of shade tolerant conifers have found that light is a limiting resource to sapling height growth below levels of 25-30% PPFD (Carter and Klinka 1992; Klinka *et al.* 1992; Parent and Messier 1995; Duchesneau *et al.* 2001). Above 25-30% full irradiance, other factors such as temperature, humidity, nutrient and water availability

become more limiting factors and growth-light relationships become more variable (Carter and Klinka 1992; Klinka *et al.* 1992; Parent and Messier 1995; Duchesneau *et al.* 2001). Gap fraction values were greater than 0.30 for 60 of the 167 trees in this study. These trees likely had increased variability in growth due to factors other than light. The variability added to the height growth models by omitting measures to include these limiting factors on growth would be minimized because all of these factors are influenced by the amount of canopy cover (Norman and Campbell 1989; Carter and Klinka 1992; Alexander *et al.* 1995; Man and Lieffers 1997), and are therefore implicit in the models.

While diffuse light measurements taken by the LAI-2000 are highly correlated with total growing season light transmission (Lieffers *et al.* 1999; Gendron *et al.* 1998), using gap fraction estimates based on instantaneous diffuse light measurements does have drawbacks that could add variability to the height growth-light relationships. The LAI-2000 filters out light above 490 nm, including beam enrichment. Beam enrichment is light transmitted through or scattered by the foliage, and can account for up to 40% of total light found beneath shade tolerant canopies (Gendron *et al.* 1998). The contribution of sunflecks is also missed by instantaneous measurements of the LAI-2000. While sunflecks are the main source of direct light beneath a canopy (Barnes *et al.* 1998; Drever and Lertzman 2003) and have been correlated with seedling growth rates (Klinka *et al.* 1992), they exhibit great temporal variation and are therefore missed with instantaneous measurements (Parent and Messier 1996).

Effects of Diffuse versus Direct Light

The failure of gap fraction readings taken higher in the canopy to improve the predictive capacity of the height growth models points to two conclusions. The first conclusion is simply that the total quantity of light reaching the tree is of primary importance in determining sapling height growth, and any variability in height growth response due to variations in relative proportions of direct to diffuse light from vertical heterogeneity in forest structure is muted when added to total quantity of light. Lieffers *et al.* (1999) reported that total light quantity is much more influential on understory tree growth than light quality. While Jarvis and Leverenz (1983) list vertical distribution of foliage as the second most important canopy structural property in determining light interception, Sampson and Smith (1993) found that vertical distribution of foliage ranked last among the structural properties they tested. In addition, the first gap fraction reading taken at tree leader partly accounts for the distance between the sapling and the shading foliage. The further away the shading foliage, the smaller the portion of the inverted cone it will occupy, therefore the less influence on gap fraction it will have. This is opposite for foliage closer to the tree leader. This may further minimize the significance of gap fraction readings taken higher in the canopy compared to the original gap fraction reading.

The second conclusion is that the method used in this study, determining the ratio of successive gap fraction readings at different vertical heights to the initial gap fraction reading at tree height, was unsuccessful at quantifying canopy structural differences as they relate height growth. Gower and Norman (1991) describe a method for quantifying

vertical LAI distribution using the LAI-2000 in which they took 10 different measurements at each height to characterize the vertical distribution of foliage. One instantaneous reading at each height may not be sufficient to quantify structural changes as they relate to a sapling located several meters below. The ratio of gap fraction readings at the different height intervals may not properly account for foliage overlap between the different heights at which gap fraction readings were taken. To make this more applicable a complex stands, more work exploring appropriate ratios to use between the vertically stratified readings may better quantify vertical LA distribution and produce more significant results relating it to understory height growth.

LAI Height Growth Predictions

The failure of LAI to be significant in predicting height growth of subsample trees does not necessarily indicate that LAI is not correlated with sapling height growth. More likely, the problem was with the sampling. For most trees, the inverted cone for the vertical point sample was projected from a lower height than the inverted cone projected by the LAI-2000. As a result, many trees were included in the vertical point sample that would not have been seen by the LAI-2000. Some of the foliage included in these LAI estimates was therefore distributed outside the zone of influence of the sapling in question. This would include foliage on surrounding saplings of similar or shorter height to the sample tree that were included in the vertical point sample, and much of the foliage distributed lower in the crowns of larger trees that were located on the periphery of the variable-sized plots. This does suggest however that total plot-level LAI, as measured in

this study (including all strata), is less predictive of height growth in stands with irregular and highly variable structures than it is in simpler two-storied stands.

Vertical Structural Analysis

The analysis of covariance defining height growth in terms of species and canopy architecture revealed that only *Picea rubens* responded to different vertical arrangements of foliage. While one would expect increased height growth of *Picea rubens* in structure 2 plots compared to structure 3 plots due to significantly less overstory leaf area in structure 2 plots, *Picea rubens* also grew significantly better in structure 2 plots compared to structure 1 plots, despite similar overstory leaf area between these two structures. The primary difference between structure 1 and 2 was that structure 2 plots had greater leaf area, and this greater leaf area was concentrated in the understory. How does greater understory leaf area promote *Picea rubens* height growth? The question that arises from this is whether leaf area distribution of these plots was influencing height growth, or whether a confounding factor was influencing both understory height growth and also determining leaf area distribution.

The understory was much more developed in structure 2 plots than structure 1 or 3 plots. The saplings in structure 2 plots therefore had much more intra-cohort competition than saplings in structure 1 or 3. While density does not promote height growth, isolated trees can become stunted (Smith *et al.* 1997). Many of the saplings that were classified into structure 1 plots in particular, were isolated within their cohort, with no near

neighbors. This isolation in the understory may be a cause for the reduced height growth of *Picea rubens* saplings in structure 1 plots.

It makes intuitive sense that the cause of greater *Picea rubens* vigor in structure 2 plots is also responsible for the more developed understory, in other words, the trees are growing better for a particular reason, therefore the understory is better developed. One would expect a more developed understory in structure 2 plots compared to structure 3 plots due to significantly less overstory leaf area. A possible explanation for the more developed understory in structure 2 compared to structure 1 could be a greater time lapse since the creation of canopy openings in structure 2 plots.

Compared to *Abies balsamea*, *Picea rubens* is not as aggressive at capturing vacant growing space and responding in height growth upon gap creation (Westveld 1931; Davis 1991). While *Picea rubens* saplings may have been just beginning to respond to decreased overstory competition in structure 1 plots, they had already had time to adapt to increased light conditions in structure 2 plots and respond in height, therefore were growing significantly better. The initial aggressive height growth response for *Abies balsamea* upon release from overhead competition and its less persistent ability to maintain that height growth compared to *Picea rubens* (Messier *et al.* 1999; Doucet and Blais 2000; Westveld 1931) could explain why there were no significant differences for *Abies balsamea* between structure 1 and 2, while *Tsuga canadensis* is just less responsive in general, therefore did not show significant differences between structures.

CONCLUSIONS AND SILVICULTURAL IMPLICATIONS

The findings of this research demonstrate that overstory canopy closure as defined as gap fraction significantly affects height growth of *Abies balsamea, Picea rubens,* and *Tsuga canadensis* saplings in uneven-aged, mixed-species northern conifer stands. For saplings up to 6.0 m, height growth continues to respond positively to decreases in overstory competition until conditions of full canopy openness are met. Average conditions of canopy closure in these stands significantly reduces the rate of height growth, and prolongs the time it takes for saplings to reach heights of 6.0 m compared to even-aged stands (Figure 1.9). Model predictions show that *Abies balsamea, Picea rubens,* and *Tsuga canadensis* can grow from heights of 0.5 m to 6.0 m in approximately 35-45 years under average understory conditions in these stands. This is a delay of about 15-20 years compared to a *Picea rubens* tree growing in an even-aged stand of site index 50 (Carmean *et al.* 1989).

While sapling height growth is reduced in these stands, they are still capable of advancing from seedlings and small saplings to larger saplings and pole-sized trees beneath well stocked, efficient overstories which are also simultaneously producing stemwood volume. This is an important benefit of uneven-aged management and this trade-off with reduced sapling height growth should be considered in any silvicultural decisions. Non-timber objectives are also important benefits of uneven-aged management that offset the reductions in sapling height growth.

The monotonically increasing nature of the best models for sapling height growth of all three species makes it difficult to suggest any particular goal for overstory density to balance the trade-off between efficient overstory leaf area allocation and sufficient sapling height growth. The monotonically increasing nature of the fits do show however that gains in the advancement of saplings through the understory are progressively reduced as higher and higher levels of canopy openness are obtained (Figure 1.7).

While this study did find significant effects of vertical leaf area distribution on *Picea rubens* height growth, it did not investigate a causal relationship. The question of whether vertical LA distribution was the cause for significant differences in *Picea rubens* height growth, or whether a separate reason was responsible for both the different vertical structural arrangements and the significant differences in *Picea rubens* height growth remains unanswered. Despite being unable to answer this question, *Picea rubens* appears to benefit more from reductions in overstory leaf area over the long term. *Picea rubens* was much more competitive in plots with less overstory leaf area (LAI > 8.4 m in height) and well developed understories than in plots with greater amounts of overstory leaf area, or plots with similar amounts of overstory leaf area but less developed understories. This suggests that *Picea rubens* benefits from gap creation which could be accomplished through group selection systems. The data also suggest that regardless of overstory conditions, *Picea rubens* is not initially competitive with *Abies balsamea* when small, but that as time progresses, it benefits more and more from gap creation as it grows in height. The effects of height and time since release appear to be less significant for *Abies balsamea* and *Tsuga canadensis*.

CHAPTER 2.

THE USE OF VERTICAL POINT SAMPLING AS A TOOL TO ESTIMATE LEAF AREA INDEX AND GAP FRACTION

INTRODUCTION

Canopy structure plays an important role in determining understory dynamics.

Canopy structure influences air temperature, leaf temperature, atmospheric moisture, soil

temperature, precipitation interception, leaf wetness duration, energy and nutrient cycling,

and in particular, the understory light environment (Norman and Campbell 1989;

Chanson *et al.* 1991; Baldocchi and Collineau 1994; Jennings *et al.* 1999; Radtke and

Bolstad 2001). Of canopy structural attributes that affect light interception, leaf area index

(LAI) is considered to be the most important (Jarvis and Leverenz 1983; Chanson *et al.*

1991; Sampson and Smith 1993). Since plant growth and survival are highly dependent

on their understory environment, in particular their light environment (Carter and Klinka

1992; Klinka *et al.* 1992; Parent and Messier 1995; Walters and Reich 1996; Finzi and

Canham 2000; Duchesneau *et al.* 2001), being able to quantify LAI is an important tool in

understanding how our manipulations of the forest affect understory plant growth and

survival.

Many different methods exist for estimating LAI. Direct methods include litterfall

trap collection (Marshall and Waring 1986; Pace 2002), the stratified clip method and the

dispersed individual plant method (Norman and Campbell 1989). These methods are very

labor intensive and time consuming and thus impractical to use. Indirect methods use radiation measurements to estimate light interception and then predict LAI based on Beer-Lambert's Law. Instruments to measure radiation include ceptometers (Pierce and Running 1988; Smith *et al.* 1991), and the LI-COR LAI-2000 plant canopy analyzer (LAI-2000) (Chason *et al.* 1991; Gower and Norman 1991; Strachan and McCaughey 1996; Pace 2002). These indirect methods are quicker; however, they involve expensive equipment, often require very specific environmental conditions, and require computers for data manipulation. Additionally, many studies have found that these indirect methods underestimate LAI (Chanson *et al.* 1991; Gower and Norman 1991; Smith *et al.* 1991).

A third method to estimate LAI is to use allometric equations to predict one-sided tree-level projected leaf area (PLA). Leaf area index is then estimated by expanding each tree in a subsample to a trees per hectare basis (TPH) and multiplying its PLA by TPH. Most studies that employ this method use fixed-radius plots to estimate tree density (Gower and Norman 1991; Sampson and Smith *et al.* 1991; Smith *et al.* 1991). Tree density can also be estimated using probability proportional to size (PPS) sampling, where the probability of sampling a tree is proportional to its size. The most common form of PPS sampling is horizontal point sampling, which is commonly used to determine basal area per hectare (BA/ha) (Husch *et al.* 2003). A lesser used form of PPS sampling is vertical point sampling where a vertical angle, ϕ, is projected from a point location. The probability of inclusion is proportional to the height squared (Ht^2) of the tree (Husch *et al.* 2003). Although there is little available literature on vertical point sampling, Weise and Glover (1993) found vertical line sampling, where a vertical angle,

φ, is projected perpendicular to a line instead of a point, to be accurate, efficient and objective in providing information on competing woody vegetation in *Pinus taeda* L. (loblolly pine) plantations.

Canopy closure is another measure that directly influences the understory light regime, and is linked to understory tree growth and survival (Wampler 1993; McConville 1998; Jennings *et al.* 1999). Canopy closure can be expressed as gap fraction, the percentage of sky that is not obscured by foliage. It is measured through hemispherical photography (Lieffers *et al.* 1999; Machado and Reich 1999; Drever and Lertzman 2000; Brandeis *et al.* 2001), visual estimation (Brandeis *et al.* 2001; Jennings *et al.* 1999), and photometrically (Gendron *et al.* 1998; McConville 1998; Machado and Reich 1999). The LAI-2000 provides a photometric method to estimate gap fraction by comparison of a below-canopy reading with an above- canopy reading of diffuse non-intercepted light (LI-COR Inc. 1992; Lieffers *et al.* 1999). While the LAI-2000 provides accurate measures of gap fraction, it suffers from a number of problems listed above that limit the practicality of its use for forest practitioners.

Knowledge of LAI and canopy closure would aid forest practitioners in making informed silvicultural decisions to promote desired species regeneration and growth. Developing easy and efficient ways to estimate these structural parameters in the field will help them achieve this goal.

The primary purpose of this study was to test the use of vertical point sampling as a tool to estimate stand-level LAI and gap fraction. The objectives were to: 1) validate the use of vertical point sampling as a method of sampling for LAI estimation; 2) to test the

efficacy of replacing tree-level LAI calculations with constants in both vertical point samples and horizontal point samples to further facilitate plot-level LAI estimation; and 3) to determine if a predictive model expressing gap fraction as a function of several different measures based on vertical point sampling could be developed.

METHODS

Study Site

Four mixed-species, uneven-aged stands located on the 1540-ha Penobscot Experimental Forest (PEF) in Bradley, Maine were used in this study. This experimental forest, owned by the University of Maine, is located at approximately 44°52' N and 68°38'W. It is the site of a long-term silvicultural research project established by the USDA Forest Service in the 1950s and includes both even-aged and uneven-aged silvicultural research (Seymour and Kenefic 1998).Two of the stands included in this study, C9 and C16, are replicates of selection cutting on a five-year cycle, while the other two, C12 and C20, are replicates of selection cutting on a ten-year cutting cycle. The structural goal for these stands is defined by the BDq method (Guldin 1991). The two replicates of the five-year selection cutting have a q-factor of 1.96 on 5-cm diameter classes, a target residual basal area of 26 m²/ha, and a maximum residual diameter goal of 48 cm. The two replicates of the ten-year selection cutting also have a q-factor of 1.96, a target residual basal area of 23 m²/ha, and a maximum residual diameter goal of 46 cm (Brissette and Kenefic 1999).

The PEF lies within the Acadian Forest Region, a transitional forest between the broadleaf forest to the south and the boreal forest to the north. The natural disturbance regime is dominated by sporadic partial disturbances such as insect epidemics and windstorms. Species composition is mixed and highly variable due to differences in soil drainage and stand structural condition. Dominate conifers on the PEF include *Picea rubens* Sarg. (red spruce), *Picea glauca* (Moench) Voss (white spruce), *Abies balsamea* (L.) Mill. (balsam fir), *Thuja occidentalis* L. (northern white cedar), *Pinus strobus* L. (eastern white pine), and *Tsuga canadensis* (L.) Carr. (eastern hemlock). The more common hardwoods in this area are *Acer rubrum* L. (red maple), *Betula papyrifera* Marsh. (paper birch), *Betula populifolia* Marsh. (gray birch), *Betula alleghaniensis* Britt. (yellow birch), *Populus tremuloides* Michx.(quaking aspen), and *Populus grandidentata* Michx. (bigtooth aspen). Glacial till is the principal soil parent material with soil types ranging from well-drained loams and sandy loams on low-profile ridges to poorly drained and very poorly drained loams and silt loams in flat areas between the ridges (Brissette *et al.* 1999; Brissette and Kenefic 1999).

Sampling Scheme

To test the efficacy of vertical point sampling in estimating stand structural attributes, a subsample of 69 trees was chosen from the 167 saplings between 0.5 and 6.0 m that were sampled to model height growth (Moores, Chapter 1). The original sample consisted of 60 *Abies balsamea* trees, 47 *Picea rubens* trees, and 60 *Tsuga canadensis* trees. The original sample of *Picea rubens* trees were divided into gap fraction classes of

10%. Within each 10% gap fraction class, *Picea rubens* trees were sorted into the top

quartile of height growth, the middle 50% of height growth, and the lowest quartile of

height growth. One tree was then selected from each of the three groups so that for each

approximate light environment, a relatively fast growing tree, a average growing tree, and

a slow growing tree were included in the subsample. In total twenty three *Picea rubens*

trees were chosen since not all gap fraction classes contained three trees. All *Abies*

balsamea and *Tsuga canadensis* trees located at the same site as a chosen *Picea rubens*

tree were also included in the subsample. A total of twenty four *Abies balsamea*, and

twenty two *Tsuga canadensis* trees were included in the subsample. Each subsample tree

then became plot center.

Data Collection

Gap Fraction Measurements

Canopy closure, which is directly related to the understory light regime was

measured by taking gap fraction readings using the LI-COR LAI 2000 Plant Canopy

Anaylzer (LAI-2000). Readings were taken from mid-August to mid-September, 2002.

The LAI-2000 measures diffuse non-intercepted light. The instrument is comprised of

two sensors, each connected to its own control unit to record measurements. One is set up

in the open (the base sensor), while the other sensor takes readings below the canopy.

Each sensor has a 150° field-of-view lens positioned above five concentric light detecting

silicon rings that allow it to receive and measure light from five different zenith angles (0-

13°, 16-28°, 32-43°, 47-58°, and 61-74°) simultaneously. Gap fraction or canopy transmittance represents the probability of unimpeded light penetration through the canopy. It is calculated by using the relationship between below-canopy intensity of diffuse non-intercepted light with a simultaneous measurement taken by a base sensor located above the canopy, usually at a nearby open site (Chanson *et al.* 1991; LI-COR 1992; Lieffers et al. 1999).

To avoid bias from direct beam sunlight, readings were taken within an hour of sunrise and sunset or on uniformly overcast days. The base sensor was set up on a tripod in the middle of an open field bordering the PEF. Distance between the base sensor and sample sites varied between approximately 1 km to 2.2 km. It was synchronized with the below-canopy sensor, and automatically logged readings every 15 seconds.

The below-canopy sensor was mounted to PVC height pole. It was then raised to the leader of each sample tree where four readings was taken. The height pole was rotated 90° between readings, and the four readings were averaged to give one gap fraction reading at the tree leader. No lens cap was used for either sensor due to the inability to control the orientation of the below-canopy sensor for some of the higher saplings.

Gap fraction estimates were based on readings from the two inner most rings. This corresponds to a zenith angle of 28.6°. Extending the field of view of the LAI-2000 to the widest angles means integrating canopy conditions over a larger area. This results in a homogenizing of conditions, and decreases the range and variance of the estimates (Bunnell and Vales 1989). While the inner three rings (corresponding to a zenith angle of 47°) could have been used, we planned to estimate stand characteristics (including LAI)

using vertical point sampling and equate these to the gap fraction readings. Time limitations therefore forced us to use as few of the inner LAI-2000 rings as possible in order to restrict the field of view and keep the number of trees tallied in the vertical point sampling to a manageable number. Other scientists (Biging and Dobbertin 1992; Puettmann and D'Amato 2002) have found that extending an angle of view beyond a zenith angle of 30° to select competitors does not improve height and diameter growth models.

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Vertical Point Sampling

An inverted cone was projected from each sample tree at a zenith angle of 28.6° using a clinometer. This angle was chosen to simulate the field of view of the first two rings of the LAI-2000. As mentioned earlier, this angle was chosen for time efficiency. The inverted cone was projected from 1 m above the ground. Each tree that intersected this inverted cone was sampled, and its species, stratum, height, height to live crown (defined as lowest live branch for *Picea rubens, Tsuga canadensis,* and *Pinus strobus, Thuja occidentalis,* and defined as lowest live whorl for *Abies balsamea*), DBH, and horizontal distance to the sample tree was recorded.

After the vertical point tally was completed, a prism tally was conducted using a prism with a basal area factor (BAF) of 2 m^2. Horizontal distance to the sample tree and DBH were recorded for any trees tallied by the prism but not included in the vertical point sample. A prism of BAF 2 m^2 was chosen because the plot size of such a prism tally was

shown to correspond most closely with a vertical point sample plot projected at a zenith

angle of 28.6° (Puettmann and D'Amato 2002).

Data Analysis

Basal Area Estimation

Basal area per hectare (BA) was calculated for each tree tallied in the vertical

point sample (VPS). Each tree was expanded to a TPH basis by the following formula

TPH = 10000 m^2 / πR$^2_{limiting}$, where R$_{limiting}$ is the limiting radius for inclusion in the tally

and is defined by tree height / tan 61.4°. Tree-level BA per hectare was obtained by

multiplying the BA of each tree by the TPH that it represented. Plot-level BA was

estimated by summing the BA/ha contribution of each individual tree over the entire plot.

Basal area per hectare was also measured at each plot by means of a 2 m^2 BAF prism. The

estimate based on the vertical point sample calculation was compared to the estimate

based on the prism sample by means of a paired T-test.

Stand LAI Calculations

One-sided projected tree-level LAI estimates were calculated based on one-sided

tree-level PLA estimates. For *Abies balsamea*, *Picea rubens*, *Tsuga canadensis*, and

Pinus strobus, PLA was determined by using non-sapwood based equations based on the

model proposed by Valentine *et al.* (1994) and used by Gilmore *et al.* (1996), Maguire *et*

al. (1998), Kenefic and Seymour (1999), and Seymour (unpublished) (Table 2.1). For

trees with modified live crown ratios greater than one, or trees whose DBH were outside the range in which Valentine's equations were fit, biomass equations were used (Young *et al.* 1980). Specific leaf area (Table 2.2) values were used to convert leaf mass, which is predicted by these equations, to leaf area.

Young's *et al.* (1980) biomass equations were also used to estimate PLA for most hardwood species and *Thuja occidentalis*. Leaf area was predicted for *Quercus rubra* L.(red oak) using biomass equations published by Tritton and Hornbeck (1982). Young's *et al.* (1980) biomass equation for *Acer rubrum* L. was used for leaf area estimation of both *Acer pensylvanicum* L. (stripped maple) and *Fraxinus americana* L. (white ash).

For species with no known published specific leaf area, specific leaf areas were calculated using leaf samples collected in September 2002 (Table1.3). The leaves were scanned into a computer to calculate one sided leaf area. Each sample that was scanned was then put into an oven to dry for four days (until dry mass remained constant between daily measurements), at which point the dry mass of the sample was recorded. Specific leaf area was then calculated by dividing the one-sided leaf area by the dry mass. This was done for three samples of each tree species.

Four different methods were used to calculate LAI for every subsample plot. Each method is described below.

Vertical Point Sample LAI Calculations

Leaf area index was calculated for each tree tallied in the vertical point sample by dividing its PLA by its respective plot size, $LAI = PLA / \pi R^2_{limiting}$, where $R_{limiting}$ is the

Table 2.1 PLA equations with coefficients and citations.

Species	PLA Model	Citation
Abies balsamea	PLA = b_0(BA * mLCR)^{b1} b_0 = 0.4763 and b_1 = 0.9021	Seymour (unpublished), from Gilmore *et al.* (1996) data set.
Picea rubens	PLA = b_0 BA^{b1} * mLCR^{b2} b_0 = 0.5553, b_1 = 0.8532, and b_2 = 0.4925	Kenefic (2000), from Maguire *et al.* dataset.
Tsuga canadensis	PLA = b_0 + b_1(BA * mLCR) b_0 = 8.9221 and b_1 = 0.1789	Kenefic and Seymour (1999)
Pinus strobus	PLA = b_0(BA * mLCR)^{b1} b_0 = 0.3050 and b_1 = 0.9470	Seymour (unpublished)

PLA = projected leaf area (m^2); BA = basal area (cm^2); CL = crown length (m); mLCR = modified live crown ratio, (CL/tree height - 1.3) (Valentine *et al.* 1994).

limiting radius for inclusion in the tally and is defined by HT / tan 61.4°, HT being the height of the tree (Husch *et al.* 1972). Plot-level LAI was estimated for each plot by then summing up the LAI contribution of each tree in the vertical point sample.

Prism Sample LAI Calculations

Leaf area index was calculated for each tree tallied in the prism sample by dividing its specific PLA by its respective plot size, LAI = PLA / $\pi R^2_{limiting}$, where $R^2_{limiting}$ is the limiting radius for inclusion in the prism tally and is defined by DBH / 100 k, where DBH is expressed in cm, and k is a constant unique to the BAF of the prism (k=0.0283 for a BAF prism of 2 m^2) (Husch *et al.* 1972). Plot-level LAI was estimated for each plot by summing up the LAI contribution of each tree in the prism tally.

Table 2.2 Specific leaf area (SLA) for all species included in vertical point sample tallies with citations.

Species	Specific Leaf Area (cm²/g)	Citation
Tsuga canadensis	58.43	Kenefic and Seymour (1999)
Picea rubens	43.51	Maguire *et al.* (1998)
Abies balsamea	41.5	Gilmore *et al.* (1995)
Pinus strobus	67	Seymour (unpublished)
Thuja occidentalis	48.06	McConville (1998)
Acer rubrum	167	Leathers (1996)
Betula papyrifera	138	Moores (unpublished data)
Betula alleghaniensis	163	Moores (unpublished data)
Fraxinus americana	315	Moores (unpublished data)
Acer pensylvanicum	312	Moores (unpublished data)
Quercus rubra	155	Moores (unpublished data)

LAI Estimates Based on Height Squared Regression Coefficients

Linear regression was used to predict tree-level PLA from Ht^2 in an effort to test the efficiency and accuracy of using vertical point sampling as method for quickly obtaining LAI estimates in the field. The LAI of each tree included in the vertical point sample is defined as: $LAI = PLA / \pi R^2_{limiting}$. Substituting $Ht/\tan 61.4°$ for $R_{limiting}$, this equation can be simplified to $LAI = k * PLA / Ht^2$, where $k = (\tan 61.4°)^2/\pi$.

Trees were categorized by species and height class, with height classes of 0-7 m, 7-15 m, and >15 m. Projected leaf area was regressed as a linear function of Ht^2 for each species and height class with the intercept forced through the origin (see Appendix for data). Tree-level LAI estimates were made for each species and height class by multiplying the regression coefficients by k (k=1.07). The LAI estimates of every "in" tree based on these regression coefficients were summed over the entire plot to estimate plot-level LAI.

LAI Estimates Based on DBH Squared Regression Coefficients

Linear regression was used to predict tree-level PLA from DBH^2 in an effort to test the efficiency and accuracy of using prism sampling as method for obtaining LAI estimates quickly in the field. The LAI of each tree included in a prism sample is defined as: $LAI = PLA / \pi R^2_{limiting}$. The limiting radius here is defined as $R_{limiting} = DBH/2.83$ (for a prism of BAF 2 m^2). This equation can then be simplified to $LAI = k * PLA / DBH^2$, where $k = 2.83^2/\pi$.

Projected leaf area was regressed as a linear function of DBH^2 for each species, forcing the intercept through the origin (see Appendix for data). Tree-level LAI estimates were made for each species by multiplying the regression coefficients by k (k=2.55). The LAI estimates of every tree in the prism sample, based on the DBH^2 regression coefficients, were summed over the entire plot to obtain a fourth estimate of plot-level LAI.

Comparison of LAI Estimates

Four comparisons were made between the different LAI estimates. The two estimates based on vertical point sampling were compared to each other. The two estimates based on prism sampling were compared to each other. The two estimates based on tree-specific LAI calculations were compared to each other (one method using vertical point sampling, the other method using prism sampling). Finally the two estimates based on PLA regression coefficients were compared to each other (one method using Ht^2 regression coefficients, the other method using DBH^2 regression coefficients). Each comparison involved calculating the coefficient of correlation between the two estimates and conducting a paired T-test to determine if the means of the estimates differed significantly.

Gap Fraction Predictions Based on Vertical Point Sampling

Several measures based on vertical point sampling were tested in their efficacy at predicting gap fraction readings directly above a sample sapling. Gap fraction was

predicted as a linear model of the height at which the reading was taken (sample tree height in the summer of 2002). Height was retained as a predictor variable and seven different vertical point sampling measures described below were added individually as additional predictor variables to the first-order linear model. The predictive capacity of each measure was judged by testing for significance of the parameter value, and by comparing adjusted R^2 values and mean square error (MSE) among the gap fraction models.

The first measure tested as a predictor variable of gap fraction was the number of trees tallied in the vertical point sample (VPS tree count). The second gap fraction prediction model divided this tree count into three categories: understory trees (0-7 m), midstory trees (7-15 m), and overstory trees (> 15 m). These three tree counts were simultaneously used with height to predict gap fraction. Basal area per hectare based on the prism sample, total plot-level LAI based on the vertical point sample, in-tree LAI (ITLAI) and in-cone LAI (INLAI), which are both described below, were also used as gap fraction predictor variables.

Non-height dependent measures (total tree count, BA/ha, total plot-level LAI) were re-tested using the general linear model option of SYSTAT v.10.2. The vertical leaf area structure of the plot (Moores, Chapter 1) was added as a qualitative variable to aid in gap fraction prediction. Finally, inspection of a scatter-plot of gap fraction versus in-cone LAI revealed a possible negative exponential relationship. The three different LAI measures were therefore re-tested using the non-linear model $GF = b_0*\exp(-b_1*X + b_2*HT)$, where X represents the LAI estimate being used.

In-tree LAI

An inverted cone was mathematically projected from the top of each sample tree at a zenith angle of 28.6° to more closely simulate the gap fraction readings taken by the LAI-2000 at each tree leader. Trees intersecting this cone were determined by the following formula: $R_{limiting} = (Ht - Ht_{sample}) / \tan 61.4°$, where $R_{limiting}$ is the limiting radius of inclusion, Ht is the height of the competing tree in question and Ht_{sample} is the height of the sample tree. This produced a smaller limiting radius for each tree compared to the vertical point sample done at ground level. In-tree LAI estimates were then formed by summing tree-level LAI for all trees that intercepted this elevated inverted cone.

In-cone LAI

In-cone LAI differed from in-tree LAI in that only the leaf area above the intersection point of the elevated inverted cone and the subject tree were included in calculating in-cone LAI (whereas the entire leaf area of all "in" trees was summed to estimate in-tree LAI). The height at which the elevated inverted cone intersected the subject tree is given by $Ht_{intersecting} = d_{horz} * \tan 61.4° + Ht_{sample}$, where d_{horz} is the horizontal distance between the sample tree and the subject tree. Relative depth into the crown was determined for the intersection point, and the proportion of leaf area above that intersection point ($LA_i/TOTLA$) was calculated using cumulative leaf area distribution functions (Moores, Chapter 1). The total LAI of the tree was multiplied by the proportion of LAI above the intersection point to estimate tree-level in-cone LAI. Plot-level in-cone

LAI was determined by summing tree-level in-cone LAI for all trees that intercepted the elevated inverted cone.

RESULTS

Basal Area Estimation

Calculations based on vertical point sampling provided a stand-level BA estimate of 25.1 m²/ha with a standard error of 0.828 m²/ha. Mean stand-level BA based on prism sampling was 28.1 m²/ha with a standard error of 0.966 m²/ha. Overall, prism sampling provided a higher BA estimate than vertical point sampling, as can be seen by the scatter of the two estimates around the one to one line (Figure 2.1). A paired T-test between the two estimates gave a mean difference of 2.91 m²/ha, ranging from 1.33 m²/ha to 4.49 m²/ha within a 95% confidence interval (CI). This indicates that the two estimates are significantly different with a p-value of less than 0.001.

LAI Estimation

Average plot-level LAI estimates based on the four methods described above varied between 5.18 and 4.53 (Table 2.3).
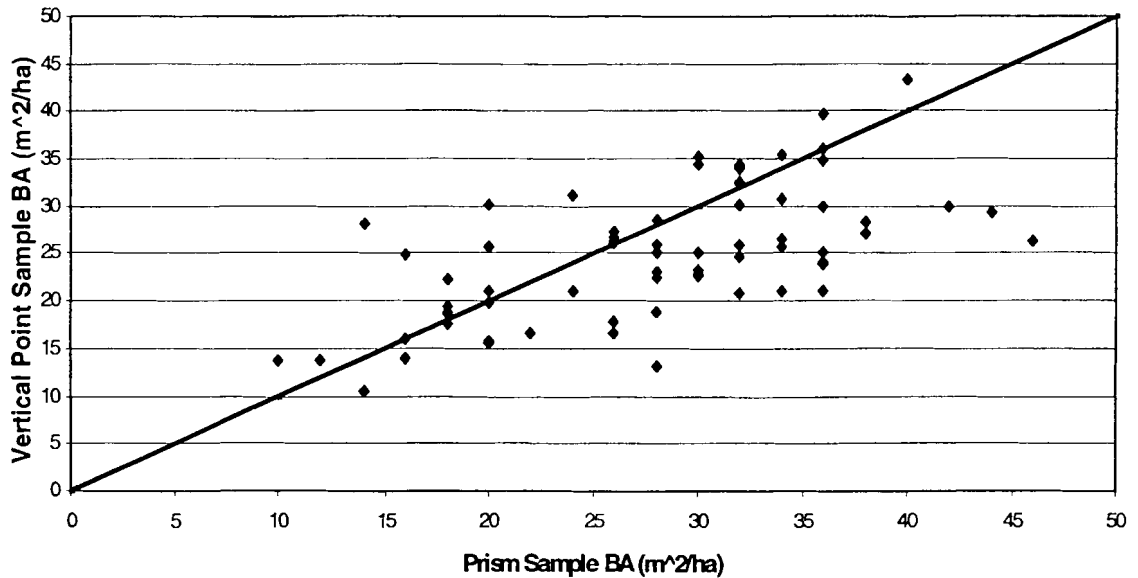
Figure 2.1   Scatter plot of plot-level basal area estimates (BA) using vertical point sampling and prism sampling with a one-one line for comparison.

Projected Leaf Area Versus Height Squared Regression Estimates

First-order linear regression between tree-level PLA and height squared varied by species and height class. Tree-level LAI estimates varied between 0.124 for sapling hardwoods to 0.540 for the tallest *Pinus strobus* trees (Table 2.4).

Projected Leaf Area Versus DBH Squared Regression Estimates

Tree-level LAI estimates based on first-order linear regression coefficients between tree-level PLA and DBH^2 ranges between 0.194 for *Thuja occidentalis* to 0.619 for hardwoods (Table 2.5).

Vertical Point Sampling Versus Prism Sampling

The mean difference between average plot-level LAI estimates based on vertical point sampling (VPS) and prism sampling was 0.648, ranging from 0.339 to 0.958 within a 95% CI. The paired t-test showed that the two estimates were significantly different with a p-value of less than 0.001. The correlation coefficient between the two estimates was 0.712. The prism sample generally provided a higher estimate of LAI than the vertical point sample (Figure 2.2).

Vertical Point Sampling - Height Squared Regression Comparison

The two plot-level LAI estimates based on VPS, where one LAI estimate was calculated by approximating each tree with an LAI constant (Table 2.4) provided fairly close estimates. Although there was some scatter about the 1-1 line, the scatter was equally distributed about this line (Figure 2.3). The mean difference between the two estimates was 0.056, ranging from 0.228 to -0.115 within a 95% CI. These means were not significantly different, with a p-value for the paired t-test of 0.514. The two estimates were also fairly highly correlated with a correlation coefficient of 0.900.

Prism Sampling - DBH Squared Regression Comparison

The two plot-level LAI estimates based on prism sampling, where one LAI estimate was calculated by approximating each tree with an LAI constant (Table 2.5), differed significantly. The mean difference between the two estimates was 0.627, ranging from 0.472 to 0.782 within a 95% CI. The p-value for the paired t-test was less than

Table 2.3 Mean plot-level LAI estimates based on the four different estimation methods.

LAI Estimation Method	Mean Plot-level LAI Estimate ± SE
Vertical Point Sampling	4.53 ± 0.159
Prism Sampling	5.18 ± 0.221
Height Squared Regression Estimates (VPS)	4.59 ± 0.194
DBH Squared Regression Estimates (prism sampling)	4.56 ± 0.188

0.001. Despite this, the two estimates were highly correlated with a correlation coefficient between the two estimates of 0.941. Approximating the LAI of each tree by a constant consistently provided a lower plot-level LAI estimate for 54 out of the 69 plots (Figure 2.4).

Height Squared Regression Estimates Versus DBH Squared Regression Estimates

The two plot-level estimates based on tree-level LAI constants provided very similar estimates despite different sampling techniques (VPS versus prism sampling). The mean difference between the two estimates was 0.035, ranging from -0.206 to 0.275 within a 95% CI. The p-value for the paired t-test was 0.774, indicating these means were not significantly different. Despite the close averages, there was still scatter between the two plot-level estimations about the 1-1 line, with a coefficient of correlation of 0.801 between the two estimates (Figure 2.5).

Table 2.4   Tree-level LAI constants based on PLA-Ht^2 regression coefficients.

Species	Height Class	LAI/tree [a]
Abies balsamea	0 - 7 m	0.252
	7 - 15 m	0.249
	> 15 m	0.157
Picea rubens	0 - 7 m	0.229
	7 - 15 m	0.28
	> 15 m	0.378
Tsuga canadensis	0 - 7 m	0.311
	7 - 15 m	0.383
	> 15 m	0.473
Pinus strobus	0 - 7 m	0.321
	7 - 15 m	0.439
	> 15 m	0.54
Thuja occidentalis	7 - 15 m	0.322
	> 15 m	0.278
Hardwoods	0 - 7 m	0.124
	7 - 15 m	0.361
	> 15 m	0.506

[a] LAI estimates are based on vertical point sampling at an angle of 61.4° from the horizontal.

Table 2.5   Tree-level LAI constants based on PLA-DBH^2 regression coefficients.

Species	LAI/tree [a]
Abies balsamea	0.359
Picea rubens	0.306
Tsuga canadensis	0.306
Pinus strobus	0.267
Thuja occidentalis	0.194
Hardwoods	0.619

[a] LAI estimates are based on horizontal point sampling with a 2 m^2 BAF prism.

Gap Fraction Predictions Based on Vertical Point Sampling

Height alone explained 37% of the variation in LAI-2000 gap fraction readings (Model 1, Table 2.6). Addition of all predictor variables improved the R^2 values, and all were significant α=0.05 except for the number of "in" trees in the understory (US) (Model 3), while the number of trees in the midstory and overstory were significant in the Model 3. Adding plot-level LAI as a predictor variable provided the least amount of improvement (Model 5), and was actually less predictive than using the VPS tree count (Model 2), or the prism-based BA estimate (Model 4) as predictor variables. Vertical LA structure of the plot was highly significant in predicting gap fraction when added as a qualitative variable to all three height independent measures, BA (Model 9), LAI (Model 10) and VPS tree count (Model 8).
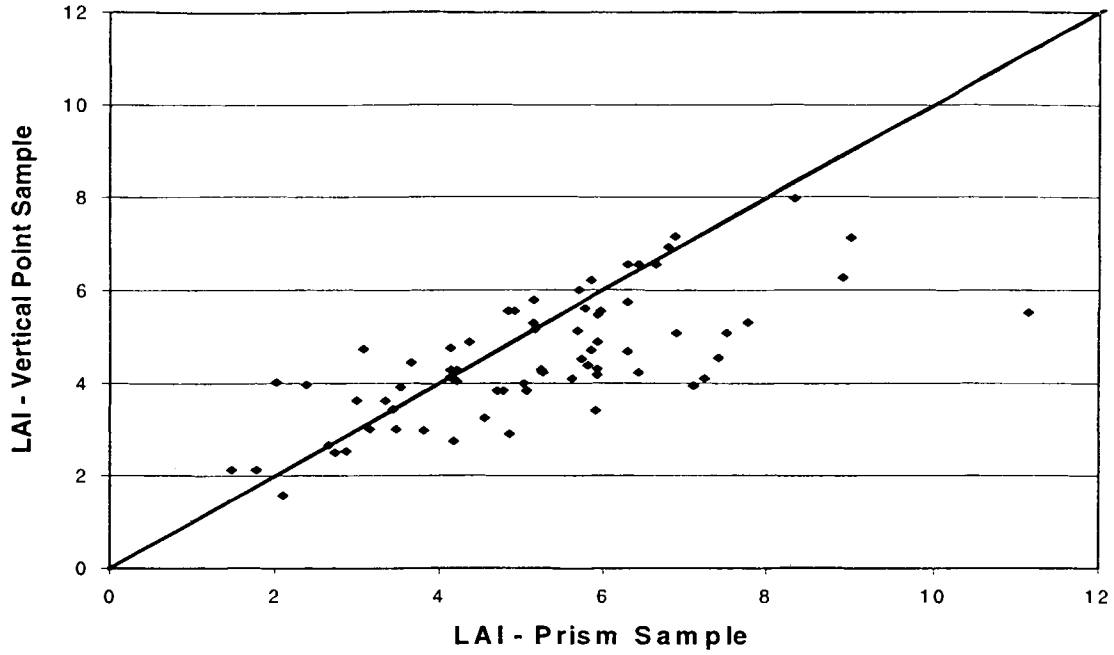
Figure 2.2   Scatter plot of plot-level LAI estimates using vertical point sampling and prism sampling with a one-one line for comparison.
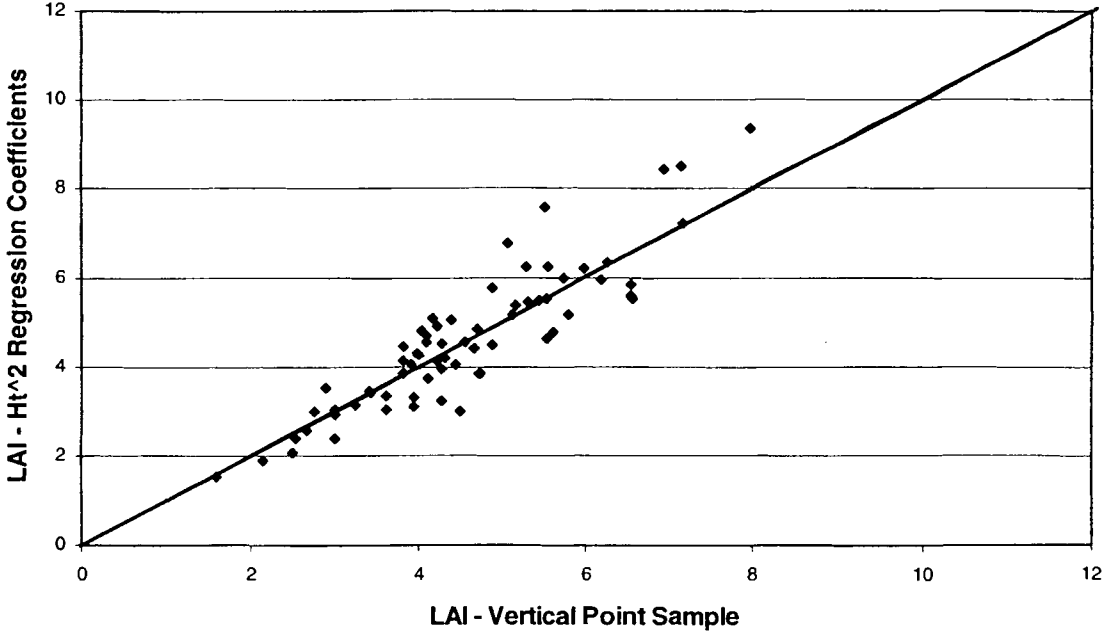

Figure 2.3   Scatter plot of vertical point sample plot-level LAI estimates based tree-level LAI calculations and regression coefficient based tree-level LAI estimates with a one-one line for comparison.
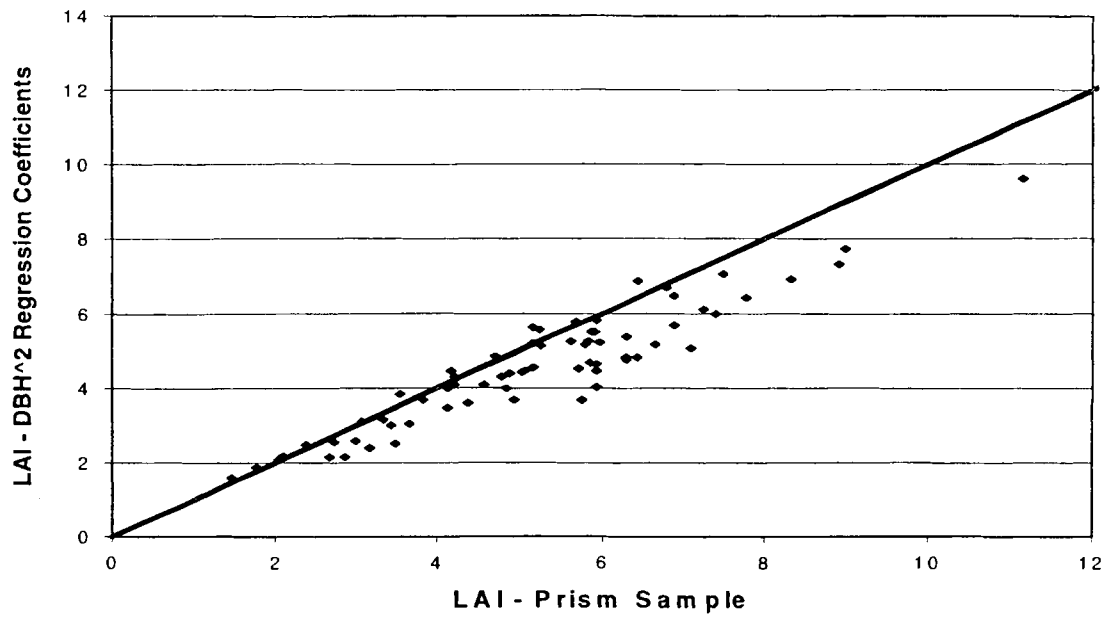
Figure 2.4   Scatter plot of prism sample plot-level LAI estimates based on tree-level LAI calculations and regression coefficient based tree-level LAI estimates with a one-one line for comparison.
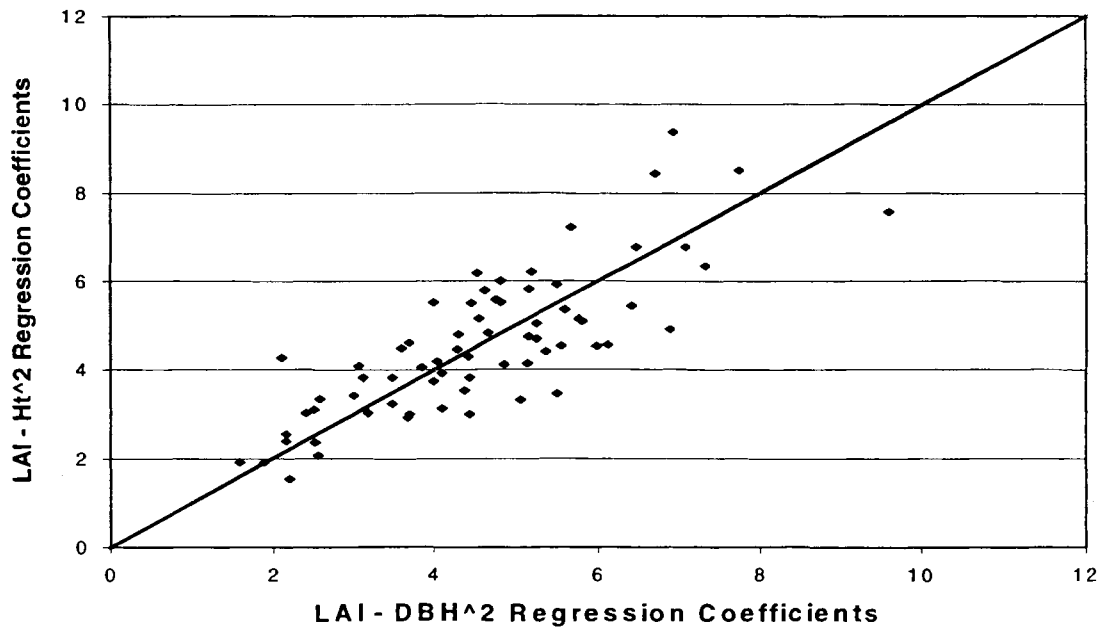

Figure 2.5   Scatter plot of vertical point sample plot-level LAI estimates based on Ht^2 regression coefficients for tree-level LAI and prism sample plot-level LAI estimates based on DBH^2 regression coefficients for tree-level LAI estimates with a one-one line for comparison.

As expected, the more that LAI calculations were restricted to what was actually in the LAI-2000 field of view, the better the gap fraction prediction. By limiting the LAI calculation to only what was above the intersection point of the "in" tree and the inverted cone projected from tree leader (INLAI), the significance of height vanished (Model 7), indicating that INLAI was successful in taking into account the various heights at which the gap fraction readings were taken. Nonlinear exponential models varied in terms of their effectiveness when compared to the corresponding linear model. There was no improvement by switching to an exponential model when using plot-level LAI (Figure 2.6). The exponential model was an improvement over the linear model when using in-tree LAI, and there was a substantial improvement when using in-cone LAI, suggesting that the relationship between LAI seen by the LAI-2000 and gap fraction is a negative exponential relationship (Figure 2.7). This model performed the best with an R^2 value of 0.756 and gave the following equation for predicting gap fraction:

(Model 13)   DIFN = 1.189 * exp(-1.272 INLAI - 0.059 Ht)

where DIFN is gap fraction reading provided by the LAI-2000, INLAI is in-cone LAI, and Ht is height of the reading (which was tree height).

Table 2.6 Adjusted R^2 values, mean square error (MSE), and p-values of parameter estimates for all predictive models of gap fraction that were tested. An asterisk (*)denotes significant predictor variables at $\alpha = 0.05$.

Ref. Number	Model	Adjusted R^2	MSE	Parameter Estimate p-value	
1	DIFN = b_0 + b_1 Ht	0.37	0.051	Ht:	p < 0.001*
2	DIFN = b_0 + b_1 Ht + b_2 TC	0.437	0.046	Ht: TC:	p < 0.000* p = 0.004*
3	DIFN = b_0 + b_1 Ht + b_2 OS + b_3 MS + b_4 US	0.498	0.041	Ht: OS: MS: US:	p < 0.001* p < 0.001* p = 0.033* p = 0.909
4	DIFN = b_0 + b_1 Ht + b_2 BA_{Prism}	0.477	0.043	Ht: BA_{Prism}:	p < 0.001* p< 0.001*
5	DIFN = b_0 + b_1 Ht + b_2 LAI	0.413	0.048	Ht: LAI:	p < 0.001* p = 0.018*
6	DIFN = b_0 + b_1 Ht + b_2 ITLAI	0.567	0.035	Ht: ITLAI:	p = 0.036* p < 0.001*
7	DIFN = b_0 + b_1 Ht + b_2 INLAI	0.607	0.032	Ht: INLAI:	p = 0.428 p < 0.001*
8	DIFN = b_0 + b_1 Ht + b_2 TC + b_3 St	0.548	0.039	Ht: TC: St:	p < 0.001* p = 0.002* p = 0.002*
9	DIFN = b_0 + b_1 Ht + b_2 BA_{Prism} + b_3 St	0.556	0.038	Ht: BA: St:	p < 0.001* p = 0.001* p = 0.013*
10	DIFN = b_0 + b_1 Ht + b_2 LAI + b_3 St	0.515	0.042	Ht: LAI: St:	p < 0.001* p = 0.025* p = 0.006*
11	DIFN = b_0 * exp(-b_1 LAI + b_2 Ht)	0.407	0.05		
12	DIFN = b_0 * exp(-b_1 ITLAI + b_2 Ht)	0.637	0.03		
13	DIFN = b_0 * exp(-b_1 INLAI + b_2 Ht)	0.756	0.02		

DIFN = gap fraction reading; Ht = height of gap fraction reading; TC = vertical point sample tree count; OS = overstory tree count (tree height > 15 m); MS = mid-story tree count (7 m < tree height < 15 m); US = understory tree count (tree height < 7 m); BA_{Prism} = basal area estimate by prism tally; LAI = plot-level LAI; ITLAI = in-tree LAI; ITLAI = in-cone LAI; St = vertical leaf area structure of plot (1, 2, or 3) (Moores Chapter 1).
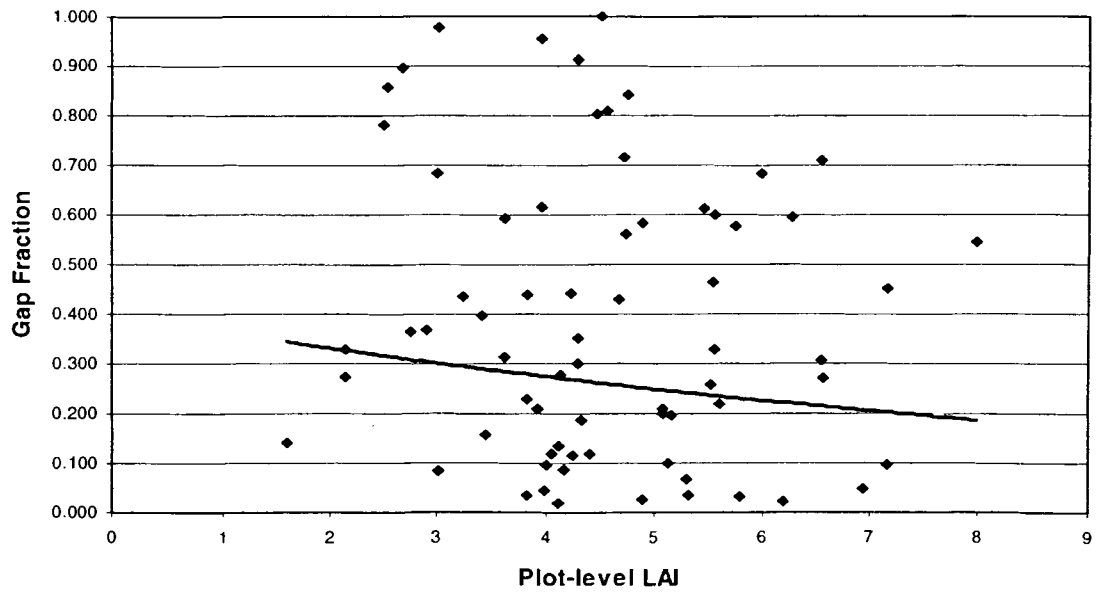
Figure 2.6   Scatter plot of plot-level LAI taken 1 m above ground and gap fraction fit with a negative exponential curve demonstrating the lack of a relationship between the two measures.
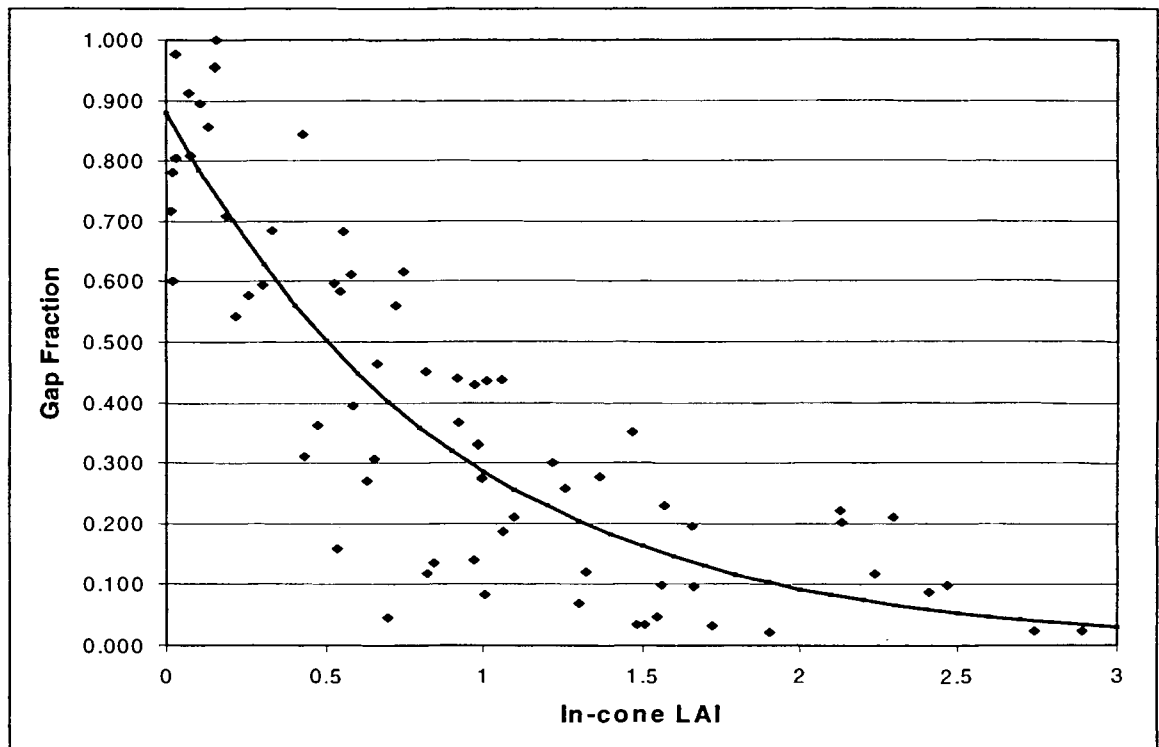

Figure 2.7   Scatter plot of in-cone LAI above sample tree and gap fraction fit with a negative exponential curve demonstrating the relationship between the two measures.

DISCUSSION

Prism sampling provided significantly higher stand-level BA and LAI estimates than vertical point sampling. It is not uncommon for horizontal point sampling to provide higher basal area estimates than fixed radius plot sampling (Oderwald and Gregoire 1995). Oderwald and Gregoire (1995) attributed this to "pushing the point", meaning not holding the prism directly over plot center. While the prism was used to judge whether trees were in or not in our study, no tree was included in the prism tally without a distance from plot center and DBH measurement taken for that tree. Distance from plot center was measured, using an electronic distance measuring device (DME) that involved placing a transponder on the subject tree. While care was taken to hold the DME over plot center, the transponder was placed on the front of the subject tree. This could have mimicked the effect of slightly "pushing the point" as described by Oderwald and Gregoire (1995) and inflated our BA and LAI estimates.

Since there is no absolute standard LAI to compare the various estimates to, it is difficult to make judgements about the accuracy of LAI estimates based on prism sampling or vertical point sampling. Kenefic (2000) measured plot-level BA and LAI on the two stands being operated on five-year cutting cycles using fixed-radius plots. She reported a mean BA estimate of 21.78 m^2/ha, and LAI estimates ranging between 1.52 and 5.96 with a mean LAI estimate of 4.05. This is in closer agreement with estimates provided by the vertical point sample. It is also noteworthy that the mean LAI estimate based on prism sampling using DBH^2 regression coefficients was significantly different

from the original LAI estimate based on prism sampling, but it was not significantly different from the two LAI estimates based on vertical point sampling. This makes it difficult to judge the accuracy of LAI constants based on PLA-DBH^2 regression coefficients. It also suggests that overestimation of LAI from prism sampling is occurring due to tree-level LAI calculations and not due to oversampling.

Since the two estimates based on prism sampling included were formed from the same tally of trees, plots where these two LAI estimates differed substantially were examined. Of the trees in the prism sample whose LAI calculation was greater than its respective DBH^2 regression estimate by more than 0.1, 50.6% of them were *Abies balsamea* trees. Most of these *Abies balsamea* trees were less than 10 cm in DBH. This suggests that the PLA equation used for *Abies balsamea* (Seymour (unpublished), from Gilmore *et al.* (1996) data set) could be overestimating small diameter trees and this small difference became magnified due to the large number of TPH these small diameter trees represented. The same PLA equation was used for *Abies balsamea* trees tallied in the vertical point sample; however, these trees on the whole were weighted less heavily in the vertical point sample than they were in the prism sample. Trees for which the two prism estimates differed by more than 0.1 represented on average 854 TPH in the prism sample, while these same trees represented on average only 463 TPH when tallied in the vertical point sample.

This provides preliminary evidence that vertical point sampling is a legitimate method to estimate plot-level or stand-level LAI. Despite closer agreement to LAI data of Kenefic (2000) than prism sampling, the mean LAI estimate based on vertical point

sampling was still 12% higher than that of Kenefic (2000). Although there are very few studies of vertical point sampling as a sampling method to measure stand structural characteristics, Biging and Dobbertin (1992) estimated crown volume and crown surface area of potential competitors using a similar method with a height angle gauge. Competition indices based on using the height angle gauge were superior in predicting height and diameter growth of several western conifer species to competition indices based on using a DBH angle gauge. Brown and Mugasha (1988) used vertical point sampling to generate a preliminary sample, which was then subsampled using a computational procedure to arrive at a horizontal point sample. This intermediate step could easily be eliminated and the vertical point sample used directly; however, further validation of vertical point sampling is needed. Direct comparisons between LAI estimation based on vertical point sampling and LAI estimation based on conventional fixed-radius plots are needed to validate vertical point sampling as a tool for LAI estimation.

Substituting tree-level LAI calculations with estimates based on Ht^2 regression coefficients also shows strong potential as a quick, efficient and accurate way to estimate stand-level LAI using vertical point sampling. No statistical difference in the stand-level LAI estimate resulted from substituting the actual LAI calculations with constants based on the PLA-Ht^2 regression coefficients. Through personal experience, it was found that tree boles at breast height were often obscured by understory vegetation making prism sampling challenging in these complex stands. While tree crowns were also often obscured, they were generally more visible and easier to sight to than tree boles at breast

height. A vertical point sample could easily be done in such a complex stand in 5-10 minutes. A simple tally of each "in" tree by species and approximate height could then provide an LAI estimate without having to measure any structural attributes. This would need to be conducted over enough sample points to ensure statistically similar mean estimates. As mentioned earlier, further validation of vertical point sampling is needed before this quick technique of LAI estimation can be employed.

The second objective of this study was to predict gap fraction readings based on stand structural attributes easily measured in the field. Despite significant parameter estimates for all but one of the variables tested, results were not very successful in achieving this objective. It is encouraging that 75.6% of the variation in gap fraction was explained by estimating the amount of leaf area inside the inverted cone projected by the first two rings of the LAI-2000. This provides further confirmation that VPS accurately tallies trees within a saplings "zone of influence." This is not however a simple measure that would be practical for a practitioner to measure in the field. Calculation of INLAI involved intensive field data collection and elaborate data manipulation using spreadsheets. The second most predictive structural attribute, ITLAI, is also very impractical to calculate. While the whole LAI of each "in" tree was summed to predict plot-level ITLAI (which could therefore eliminate tree measurements by simply using LAI constants), it also involved intensive data collection and manipulation to determine if particular trees were still "in" once the inverted cone was shifted upward to the tree leader from ground-level. This does suggest that this measure may be more applicable if an

estimate of gap fraction was needed at eye-level height where no shifting would be needed.

Other measures including LAI, BA, and number of "in" trees were much more predictive if plot leaf area structure was included in the models, but these models still explained less than 60% of the variation in gap fraction. The inclusion of trees in these estimates that were in the same stratum as the trees being measured decreased the predictive strength of LAI, BA, and VPS tree count. Trees in the same stratum would not have been providing overhead competition, and likely were not seen by the LAI-2000 at a zenith angle of 28.6°, yet they were included in the estimates of LAI, BA, and VPS tree count.

McConville (1998) was much more successful in predicting gap fraction readings from stand structural attributes. He achieved R^2 values of 0.85-0.90 using BA, crown projection area, and projected leaf area as predictor variables. One of the probable reasons this study was not able to produce similar R^2 values was due to the complexity and spatial heterogeneity (both vertical and horizontal) of these stands. The stands that McConville (1998) studied were fairly homogeneous in structure and species composition with only one overstory cohort of a single species, to which he restricted his structural measurements. There was no clear boundary between overstory, midstory, and understory in the multi-cohort stands used in the present study. Similar to McConville (1998) however, the relationship between gap fraction and leaf area was best described as a negative exponential relationship. This is also consistent with several other studies that have reported negative exponential relationships between LAI and gap fraction or light

interception measures (Lang and Yueqin 1986; Gower and Norman 1991; Sampson and Smith 1993).

CONCLUSIONS AND SILVICULTURAL IMPLICATIONS

The use of vertical point sampling as a method of sampling for LAI estimates shows strong promise. The success of replacing tree-level LAI estimates with constants based on PLA-Ht^2 regression coefficients suggests that vertical point sampling could provide foresters with a quick and accurate way to estimate plot or stand-level LAI in the field. Further development and validation of these LAI estimation methods should be undertaken.

This study was unsuccessful at relating canopy openness to more easily measurable in-the-field measurements such as LAI, vertical point sample tree counts, or basal area. Providing forest managers with no easy way to estimate gap fraction values reduces the applicability of this study. Future research could examine how gap fraction varies with different sized gap openings, or how gap fraction varies with respect to the number of trees felled in group selection during a harvest entry. This could aid foresters in determining how many trees to take out in a group to produce desired height growth response.

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APPENDIX.

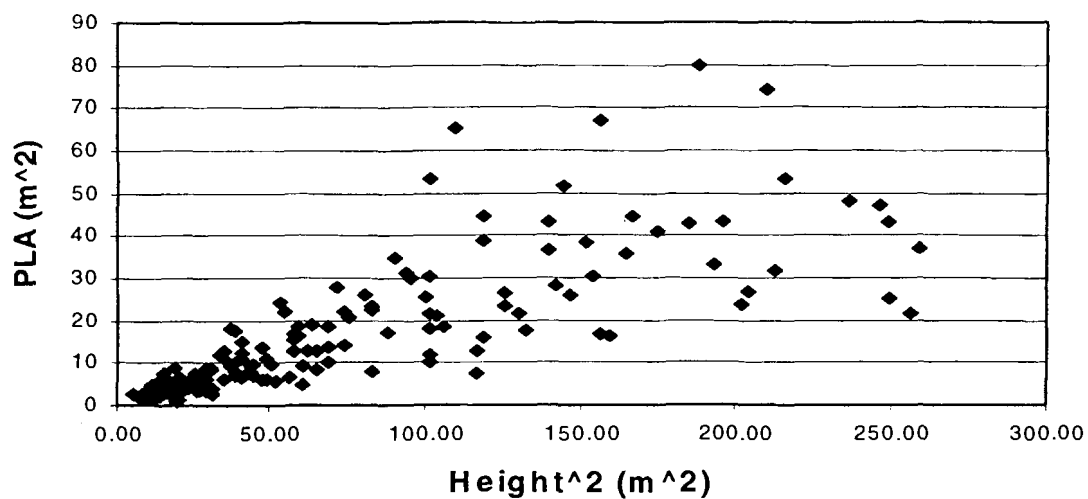## PROJECTED LEAF AREA VERSUS HEIGHT SQUARED AND DBH SQUARED SCATTER PLOTS BY SPECIES

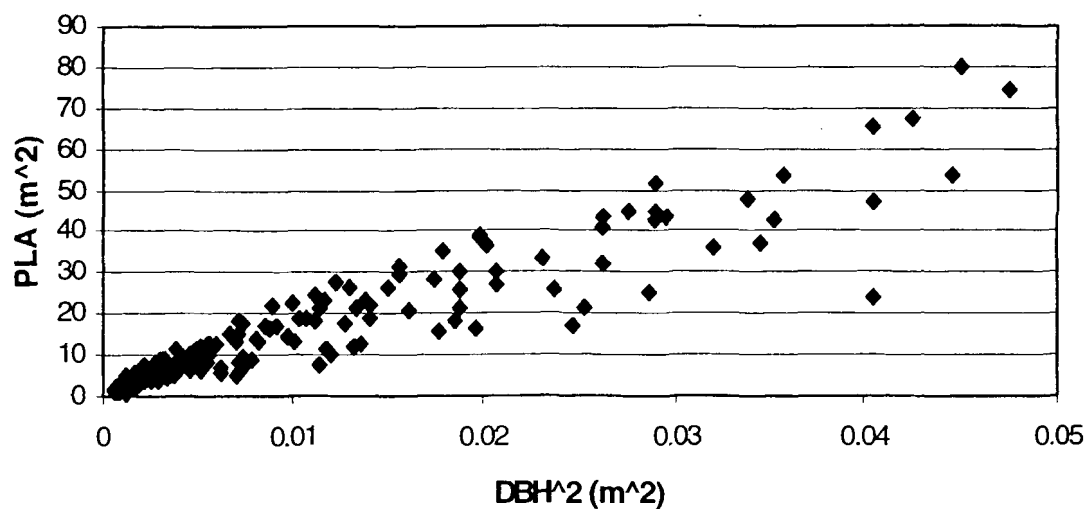Figure A.1 Scatter plot of individual tree projected leaf area (PLA) versus height squared for *Abies balsamea*.
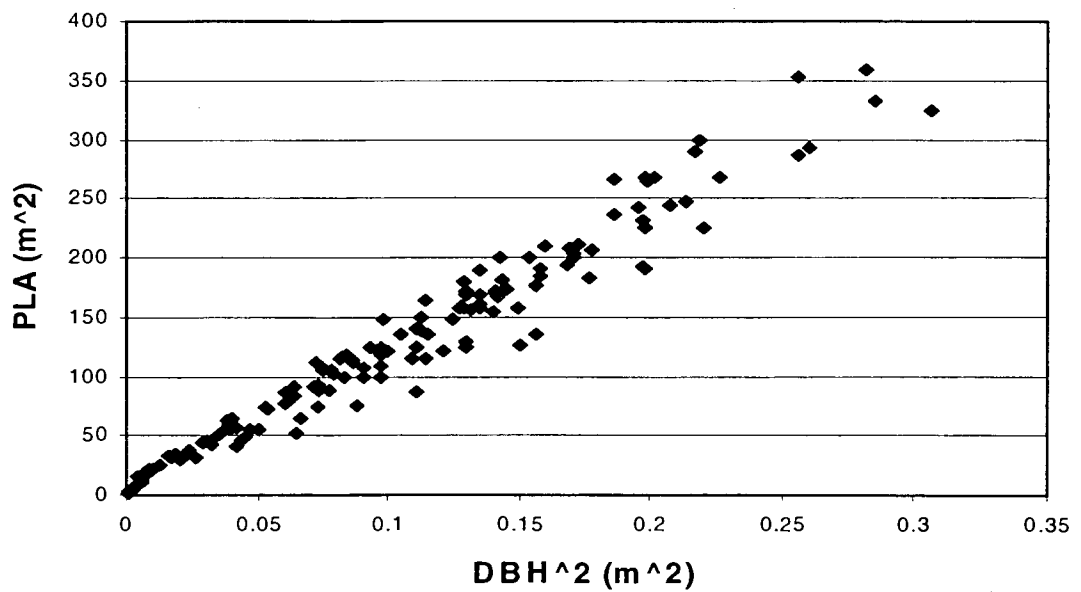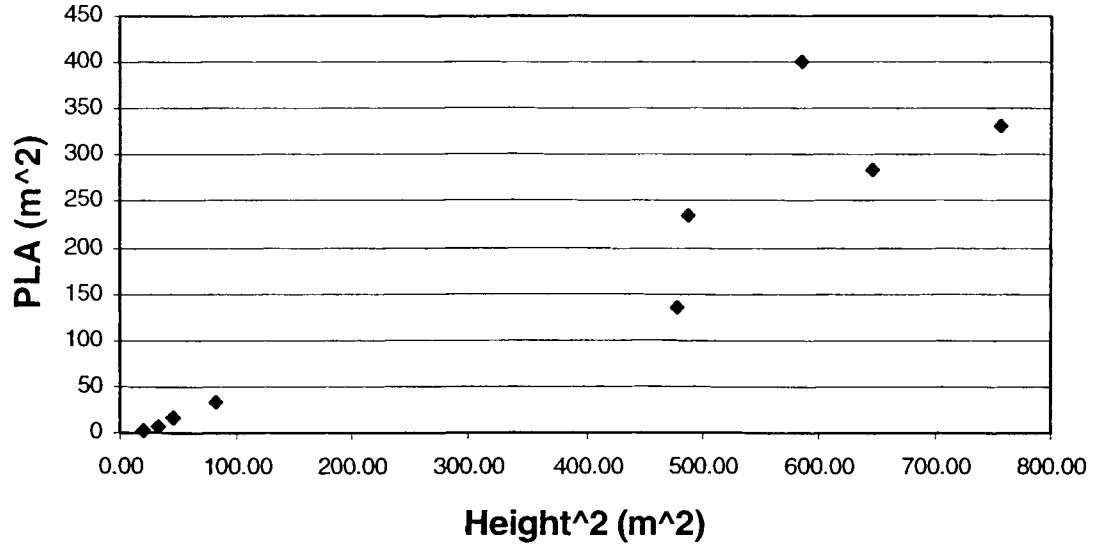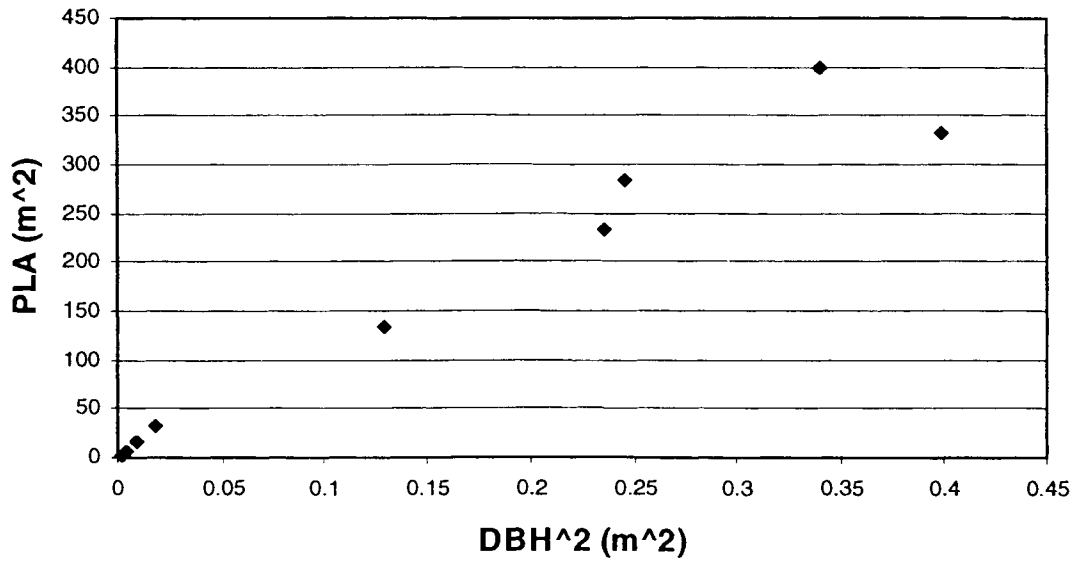

Figure A.2 Scatter plot of individual tree projected leaf area (PLA) versus DBH squared for *Abies balsamea*.
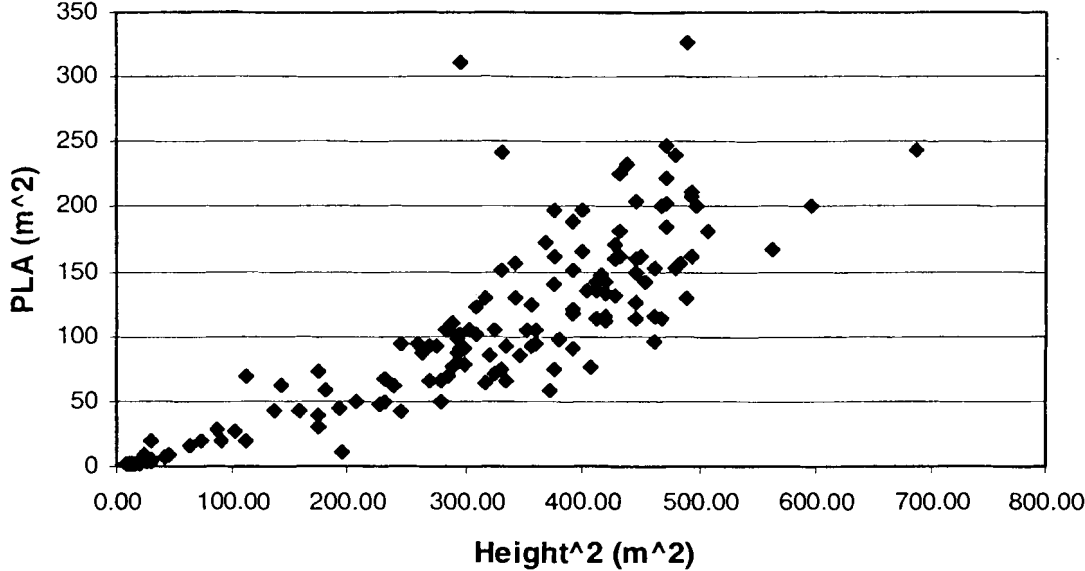
Figure A.3   Scatter plot of individual tree projected leaf area (PLA) versus height squared for *Picea rubens*.
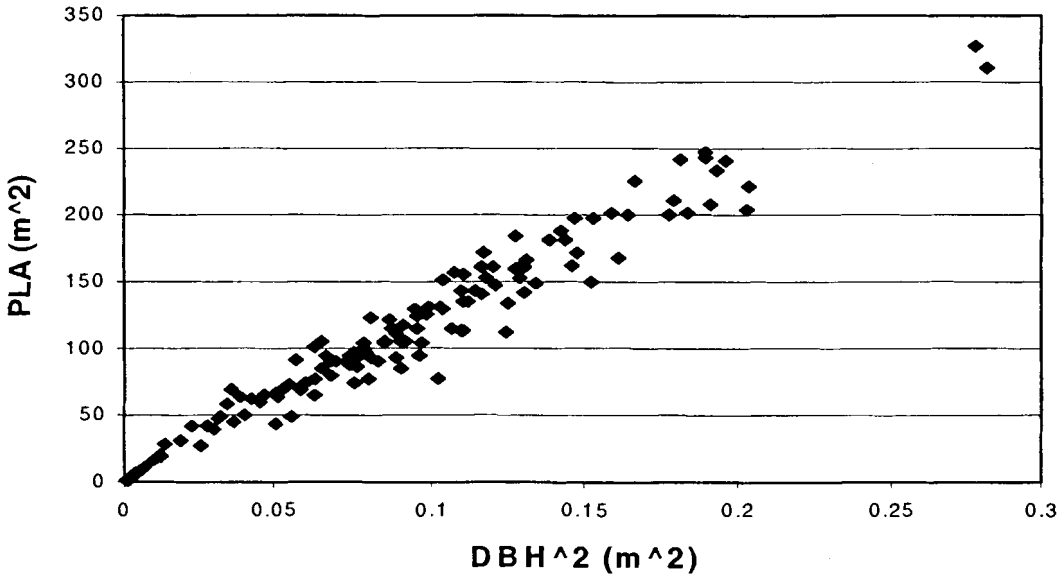
Figure A.4   Scatter plot of individual tree projected leaf area (PLA) versus DBH squared for *Picea rubens*.
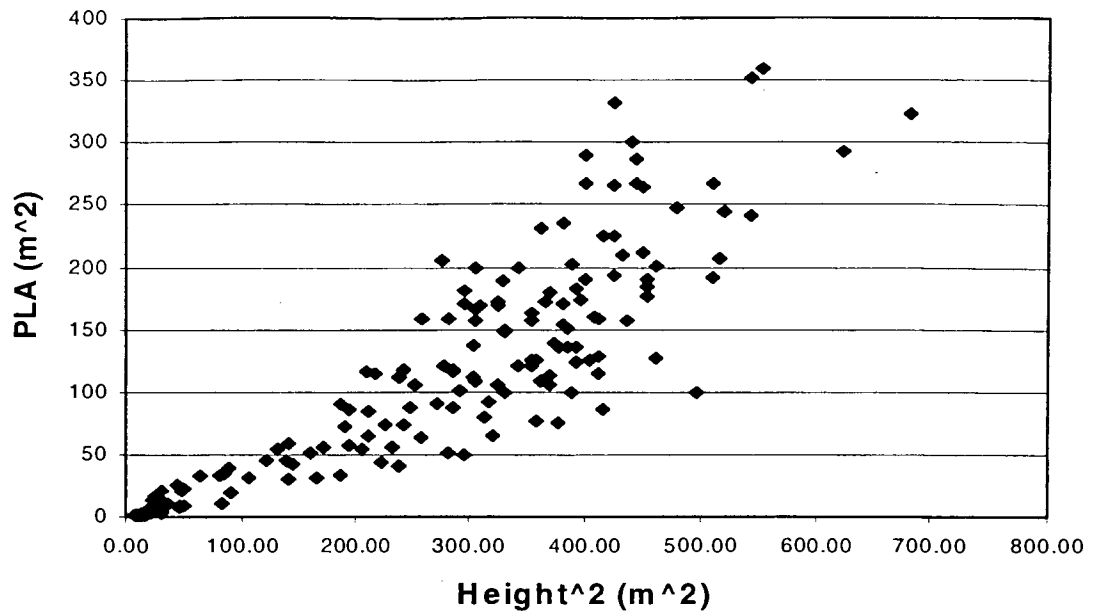
Figure A.5 Scatter plot of individual tree projected leaf area (PLA) versus height squared for *Tsuga canadensis*.

Figure A.6 Scatter plot of individual tree projected leaf area (PLA) versus DBH squared for *Tsuga canadensis*.

Figure A.7   Scatter plot of individual tree projected leaf area (PLA) versus height squared for *Pinus strobus*.

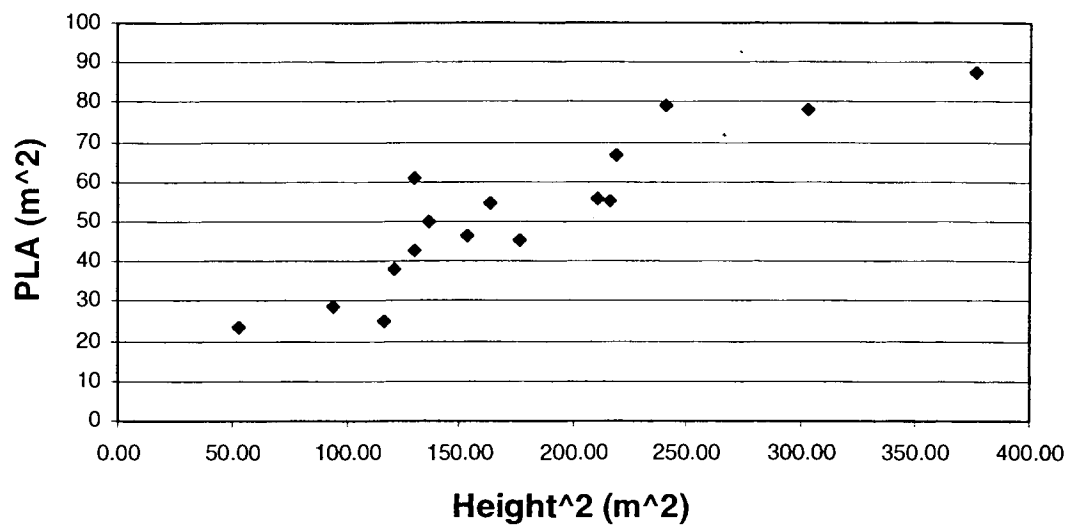Figure A.8   Scatter plot of individual tree projected leaf area (PLA) versus DBH squared for *Pinus strobus*.

Figure A.9   Scatter plot of individual tree projected leaf area (PLA) versus height squared for *Thuja occidentalis*.
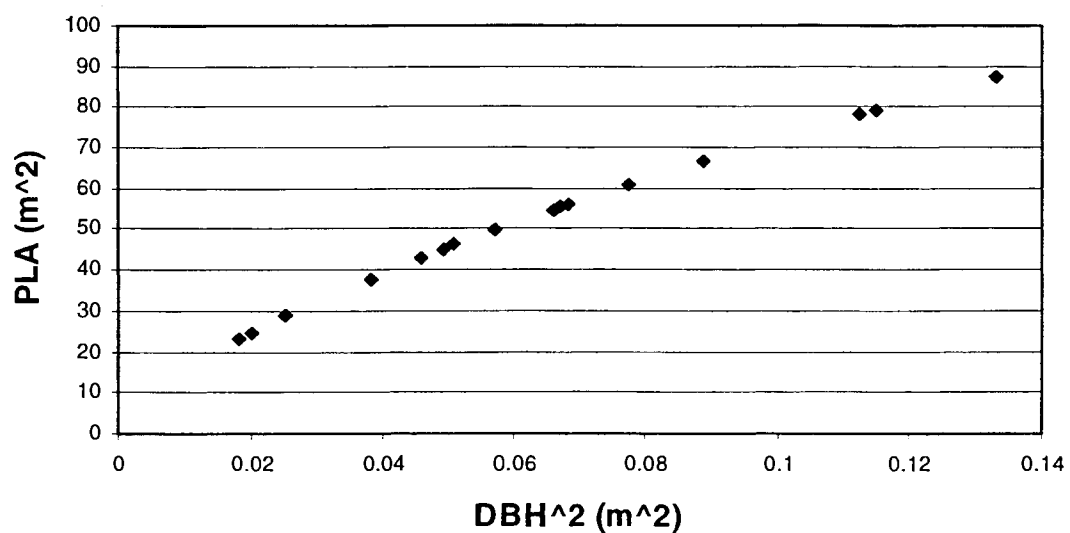

Figure A.10   Scatter plot of individual tree projected leaf area (PLA) versus DBH squared for *Thuja occidentalis*.
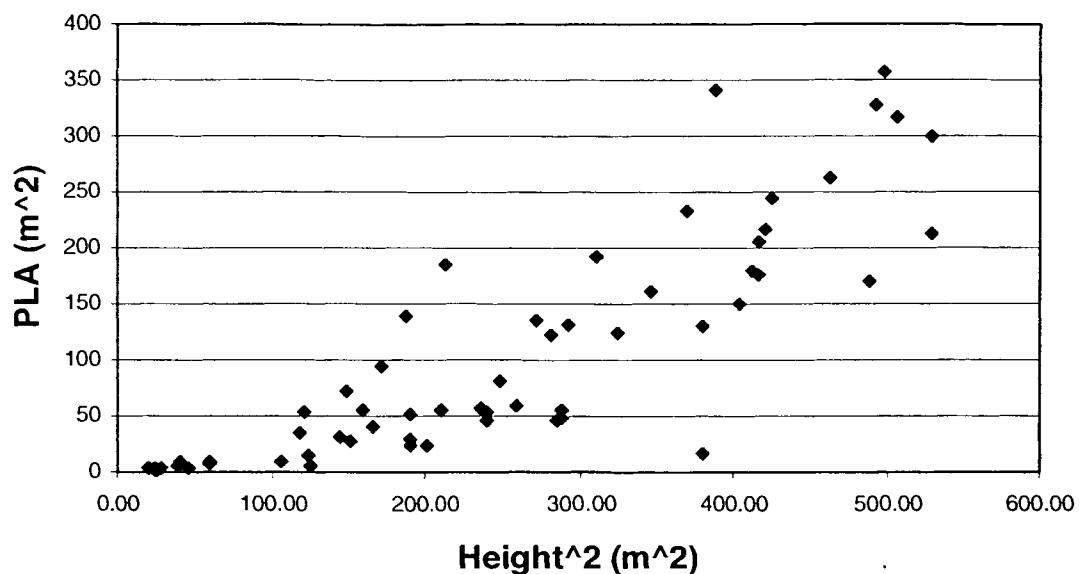
Figure A.11   Scatter plot of individual tree projected leaf area (PLA) versus height squared for all hardwood species.
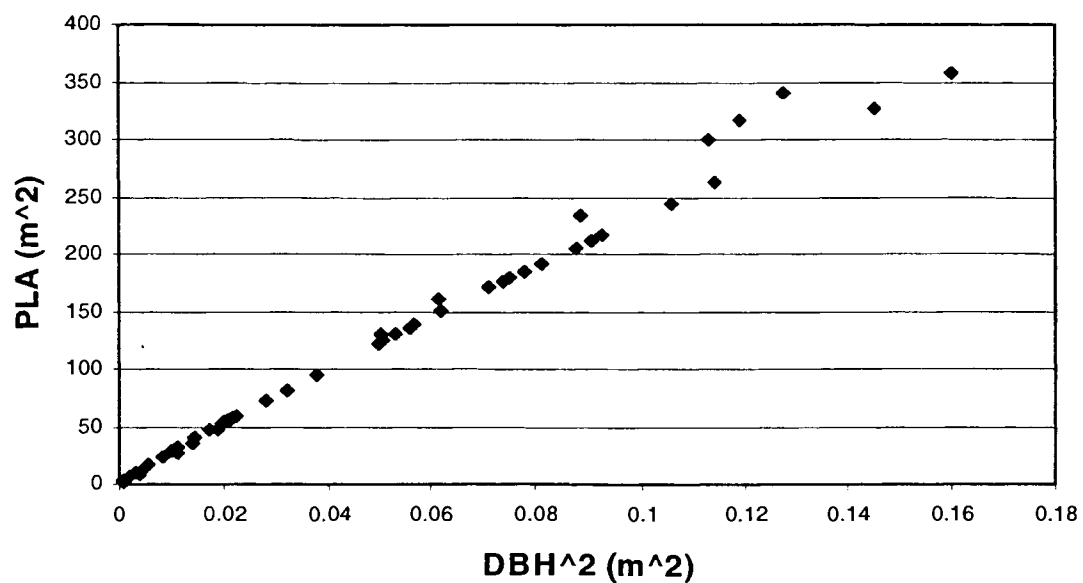

Figure A.12   Scatter plot of individual tree projected leaf area (PLA) versus DBH squared for all hardwood species.

BIOGRAPHY OF THE AUTHOR

Andrew Moores was born in Yarmouth, Nova Scotia on September 23, 1975. He was raised in Port Maitland, Nova Scotia and graduated from Yarmouth Memorial High School in 1993. He attended Acadia University in Wolfville, Nova Scotia, and graduated with a Bachelor's degree in Physics in 1997. After graduating from his undergraduate degree, Andrew had a variety of jobs including leading trail construction crews for the Appalachian Trail Conference in Virginia and Tennessee, and working at Windhorse Farms, an ecoforestry business in Lunenburg County, Nova Scotia. Andrew's love for the forest and the outdoors fostered an interest in ecologically based forestry. This interest brought him back to school to work with Dr. Robert Seymour at the University of Maine where he has been fortunate to study uneven-aged silviculture. Andrew is currently a student and a national member of the Society of American Foresters. Andrew is a candidate for the Master of Science degree in Forestry from The University of Maine in August, 2003.