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University of Alberta

Crown shyness and leaf area index in lodgepole pine stands of varying stand height, relative density and site index.

by

Heather Fish ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Master of Science*

in

Forest Biology and Management

Department of *Renewable Resources*

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Dedication

To my Netjan and Gordon Poisson, Justin and Erin. I love you all.
Go Banana

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Abstract

Crown shyness is the empty space between crowns in fully-stocked stands. I measured canopy closure (CC) (i.e., the inverse of crown shyness), effective leaf area index (LAIe), crown radius (CR) and length (CL), and green litterfall in stands of various height (HT) and relative density (RD); site factors including site index (SI) were also evaluated. LAIe and CC_H were measured using four hemispherical photographs; CC_L was also measured using line intercepts. CC_L and LAIe decreased with HT and increased with index SI and RD. Litterfall increased with HT and RD. CR and CL reached a plateau by 8-10 m height. Crown abrasion likely contributes to crown shyness, but the empty spaces between trees may also relate to the small upper limit of CR even in wide spacing. CL did not respond to changes in CC_L. Canopy closures estimated by hemispherical photography (CC_H) were nearly double that of CC_L.

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List of Abbreviations

AGE	Average stand age (years)
ASPECT	Stand aspect
ba	Tree basal area (cm^2)
BA	Average stand basal area (m^2/ha)
CC	Average stand canopy closure (%)
CC_H	Average stand canopy closure estimated from hemispherical photographs (%)
CC_L	Average stand canopy closure estimated from the line intercept method (%)
CDHT	Average height of codominant and dominant trees (m)
CL	Average crown length of trees (m)
cm	Centimeter
CR	Average crown radius of dominant trees (m)
DBH	Diameter at breast height (1.3 m) (cm)
DEN	Stand density (stems perhectare)
e	Natural logarithm
EV	Camera exposure value
g	Gram
$G(\theta)$	Gap fraction of angle θ (%)
GF_H	Gap fraction estimated from hemispherical photography (%)
ha	Hectare (10, 000 m^2)
ht	Tree height (m)
HT	Average stand height (m)
I_d	Morisita's Index of Dispersion
I_p	Standardized Morisita Index of Dispersion
k	Extinction coefficient for the calculation of gap fraction
k	Constant (0.0000785395) in the calculation of basal area
LA	Leaf area of green litter (cm^2/m^2)
LAI	Leaf area index (m^2/m^2)
LAIe	Effective leaf area index (m^2/m^2)
m	Meter

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M_c	Morisita Clumped index significance point
M_u	Morisita Uniform index significance point
mm	millimeter
n	Number of quadrats
POS	Hillslope position (crest, mid-slope, toe)
QMD	Quadratic mean diameter (cm)
RD	Stand relative density (Curtis')
SC	Average stand slenderness coefficient
SDI	Stand density index
SI	Stand site index
SLOPE	Slope gradient of stand (%)
sph	Stems per hectare
TOPHT	Stand top height (m)
x or x_i	Number of trees counted in quadrat
$\chi^2_{.975}$	Value of chi-square from table with n-1 degrees of freedom that has 97.5% area to the right
$\chi^2_{.025}$	Value of chi-square from table with n-1 degrees of freedom that has 2.5% area to the right
θ	Angle from zenith (°)

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Chapter 1: Introduction

Crown Shyness

It is generally believed that the competitive nature of plants encourages trees to fill a canopy with leaves and branches in order to out-compete their neighbors for resources that are often in limited supply (Sorrenson-Cothern et al., 1993). From an ecological perspective this is represented by the basic idea of a population carrying capacity; once the carrying capacity for resources has been reached, either growth must cease or mortality within the population must occur. In forest management, the self-thinning line is used to predict the carrying capacity of a stand. The self-thinning line (or –3/2 power rule) relates the maximum tree size for any given density before mortality will occur, as first discussed by Yoda (1963). As trees succumb to self-thinning, they leave gaps in the canopy for remaining trees to expand into (Long and Smith, 1992). Although this does occur to some degree in fully-stocked stands, not all gaps are filled following their creation, resulting in small gaps between trees known as crown shyness.

Crown shyness has been documented throughout the world, from the tropics to Canada's boreal forests, and is defined as the empty space between tree crowns of equal height (Putz et al., 1984). Generally stands suffering from crown shyness are composed of one species, however stands of mixed composition have been documented as suffering from crown shyness as well (Paijmans, 1973). Crown shyness has been documented in both deciduous and coniferous stands: the Eucalypts of Australia (Jacobs, 1955), *Pometia pinnata* and others in New Britain (Paijmans, 1973), *Dryobalanops aromatica* in Malaysia (Ng, 1977), *Avicennia germinans* in Costa Rica (Putz et al., 1984), *Piptadeniastrum africanum* in Africa (Offermans, 1986), and most recently *Pinus contorta* var. *latifolia* (Lodgepole pine) in Alberta, Canada (Rudnicki et al., 2004).

There are two theories proposing possible mechanisms responsible for crown shyness: Jacob (1955) suggested abrasion between crowns prevented the gaps from filling in, whereas Ng (1977) found no abrasion between tree crowns and suggested instead that mutual shading prevented the space between crowns from being used. Although crown expansion has been linked to photoreceptors within branches (see Aphalo et al., 1999), abrasion between crowns has also been documented (Putz et al.,

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1984; Long and Smith, 1992; Campbell, 1998; Rudnicki et al., 2003). The significance of abrasion in regulating crown shyness, however, is unknown.

Abrasion

Crown abrasion occurs as a result of tree sway. Trees sway in response to wind, dampening their sway with collisions involving neighboring crowns to release kinetic energy and reduce stress on their roots and boles to prevent stem failure (Putz and Sharitz, 1991; Cucchi and Bert, 2003). However, such collisions can result in foliage losses, which may have positive or negative effects on individual trees. Loss of foliage may reduce the ability of trees to capture resources through photosynthesis, but may have some adaptive advantages for trees in windy locations. For example, foliage lost to abrasion may even prevent stem failure during future wind events by streamlining tree crowns and reducing potential drag (horizontal force) on the crown (Hedden et al., 1995). This suggests that any stand characteristics that encourage sway dampening should also encourage abrasion.

Comparatively little research has focused on crown abrasion as opposed to many other aspects of crown development dynamics, however a potentially broad range of factors, including wind dynamics, and site and stand characteristics likely affect crown abrasion. Wind strength increases with height (Bergen, 1971) creating greater pressure on the tree to sway as height increases. Rooted in the ground with their tops free to sway, trees behave like levers under the pressure of wind; as levers, trees offer increasingly less resistance to bending and sway as they increase in height (Rudnicki et al., 2004). Bending and sway may be further exaggerated in taller, older stands because trees' resistance to wind may decline with the repeated wind exposure that accompanies age. Examples of this include decreased wood strength through the formation of compression wood following bending events (Nicholls, 1980; Cameron and Dunham, 1999), or reduced root stability following successive root movement during tree sway (Cremer, 1977; Watson, 2000).

Repeated wind exposure can result in increased bole diameter because trees that suffer from repeated wind exposure tend to allocate growth resources to their diameter rather than their height (Larson, 1963; Long and Smith, 1981; Valinger, 1992; Mitchell,

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2000). Increased girth provides a mechanism to resist wind and is expressed as greater tree taper or a low slenderness coefficient (SC; ht/diameter at 1.3 m). Trees having high SC suffer from increased tree sway (Cremer et al., 1982; Campbell, 1998; Rudnicki et al., 2003, 2004), likely because of their higher bole flexibility due to their smaller diameter. This creates the potential for greater damage during collisions because of higher sway speeds and sway distances in slender stands (Rudnicki et al., 2003). Crown size may counteract the effects of increased bole flexibility and wind speed in slender stands because slender boles tend to support smaller crowns (Jack and Long, 1991), creating less drag during wind events. This might limit both canopy closure and crown collisions depending on crown proximity, and crown proximity is dependent on tree density.

Relative density (RD provides an estimate of stand occupancy that is independent of tree size. The closer trees are to one another the more likely they are to have high canopy closure, however they might also be more likely to make contact with each other during wind events, resulting in greater abrasion. However, abrasion may be limited in high RD stands because wind loads are shared between more trees and wind gusts are thought to be more uniform (Curtis, 1943; Green et al., 1995; Peltola, 1996), such that trees are likely acclimate to the wind (Peltola et al., 1999) resulting in less damage than in low RD stands (Cremer et al., 1977). Wind uniformity is also related to canopy roughness (Cremer et al., 1977) such that stands lacking gaps, whether through high density or through more uniform tree arrangement should have less turbulence and as a result, less abrasion.

Site nutrition may also affect wind abrasion. Numerous studies indicate that foliage production is stimulated following fertilization (Vose and Allen, 1988; Weetman et al., 1988; Brockley and Sheran, 1994; Brockley, 1995; Yang, 1998), which would provide greater available surface area for crowns to capture wind and may increase the likelihood of collisions (Cucci and Bert, 2003). Both height and diameter growth increase with site quality (Muhairwe, 1994), and there is conflicting evidence as to the role of site index (SI) in SC. Muhairwe (1994) discovered no relationship between SC and SI, whereas both Wang et al. (1998) and Oliveira (1987) suggested that SC increases with SI perhaps because of greater allocation to height growth. Abrasion may also be influenced by genetics because tree growth and crown morphology, including tree leaf

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area and branching have been linked to genetics (St. Clair, 1994; McCrady and Jokela, 1996; Roberts et al. 2003).

Abrasion likely affects crowns lateral extension primarily; branch removal through abrasion between crowns would remove not only current foliage from a tree, but branch replacement following abrasion might be compromised through bud removal. Abrasion may also have an indirect effect on crown length (CL). Long and Smith (1992) suggested that crown length (CL) is longer in stands with lower CC. This may be a response to increased light penetration into the stand, or it may be a means for stands to recapture leaf area losses to abrasion (Beekhuis, 1965). Gillespie et al. (1994) have suggested that CL acts independent of changes to stand structure.

LAI-Productivity

The decline in stand productivity with stand age appears to be a widely accepted and yet poorly understood phenomenon (see review by Ryan et al., 1997). It has been suggested that the decline in productivity begins early in a stands' history, coinciding with the time of the decline in stand leaf area. Stand leaf area is generally expressed as leaf area index (LAI): a measure of half the surface area of leaves per area of ground (Lang et al., 1991; Chen and Black, 1992). Stand leaf area increases rapidly in juvenile stands and peaks at stand crown closure; following crown closure stand competition begins, including the onset of self-thinning. With every tree that succumbs to self-thinning, stand leaf area is temporarily reduced until remaining trees in the stand increase their crown size and replace lost leaf area, giving the impression that remaining trees will take advantage of all newly created space. However, Long and Smith (1984) have suggested that following self-thinning, remaining trees grow only enough to recapture the leaf area lost when the neighboring tree died. They attributed this limitation in leaf growth to a limitation in the sapwood area available to support it.

Sapwood efficiency (the unit of leaf area it can support per unit of sapwood area) declines with time (Mencuccini and Grace, 1996), which could support the link between sapwood area and leaf area. However, theories relating sapwood area to leaf area do not account for mechanical abrasion that occurs between crowns. It is likely that mechanical abrasion also contributes to the decline in leaf area over time; unless the foliage lost to

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abrasion is redistributed elsewhere within the crown (i.e. in crown length), crown abrasion may remove valuable leaf area from stands and contribute to the decline in stand productivity over time.

Leaf Area Measurement

Destructively measuring stand leaf area is not economically feasible in most research as destructive sampling is time consuming and labourious. Therefore, several optical measurements have been devised to estimate stand leaf area index (LAI), including hemispherical photography. Hemispherical photography was used to evaluate canopy light as early as 1959 when Evans and Coombe studied light penetration through forest canopy gaps. Prior to the invention of digital cameras and computers, photographs were often analyzed by hand or required scanning before they could be analyzed with a computer; the invention of the digital camera has made photograph capture and analysis more time efficient. Digital photographs may come at the expense of resolution compared to film-based photographs; however Hale and Edwards (2002) suggest that the lower resolution does not result in different estimates of gap fraction compared to film.

The analysis of hemispherical photography for canopy measurements has several important sources of error. Rich (1990) listed three potential types of error in using hemispherical photography: error related to image acquisition, image digitization and image analysis. During photograph acquisition, the camera may not be perfectly leveled, such that the photograph zenith will change with subsequent measurements. In stands of high gap fraction, tree boles increasingly contribute to the obstruction of light (Fournier et al., 1996); this is especially true when the camera is placed randomly nearer to a tree bole than to the centre of a gap.

Probably the most important factor influencing accurate canopy digitalization is the fact that hemispherical photography cannot account for clumping or overlap within the canopy. The gap fraction and LAI from hemispherical photographs is based on Beer's law:

$$G(\theta) = e^{-k(\theta)*LAI}$$

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where G is gap fraction, k(θ) is the extinction coefficient at angle θ (0.5), LAI is the leaf area index, and θ is zenith angle.

Beer's Law assumes random distribution of canopy elements, having random orientation (Chen et al., 1997). However, foliage in conifer canopies can be clumped at up to 4 levels: within shoot, within the branch, within the whorl and within the crown (Norman and Jarvis, 1974; Whitehead et al., 1990). Thus, hemispherical photography provides an estimate of effective LAI (LAIe), i.e. an estimate of LAI that does not account for clumping, such that effective leaf area index tends to underestimate actual LAI (Marshall and Waring, 1986; Gower and Norman, 1991; Chen et al., 1997).

Several researchers have developed clumping correction factors to estimate LAI from LAIe (i.e. Fassnacht et al., 1994; Stenberg, 1996; Chen et al., 1997; van Gardingen et al. 1999; Law et al., 2004). The theoretical basis for the correction factors tends to stem from two approaches. The first approach, the "finite-length averaging method", is based on the logarithm of gap fractions taken from small transects, with the length of the transect dependent on average leaf width of the stand being measured (Lang and Xiang, 1986). The second approach involves the characterization of gap size distribution as described by Chen and Cihlar (1995). Accurately characterizing clumping can be difficult, however, because clumping varies not only with species, but also with canopy structure and density (van Gardingen et al., 1999; Kucharik et al., 1999). Recently, Leblanc et al. (2005) have suggested that the most accurate clumping assessment is one that incorporates each of Chen and Cihlar's (1995) and Lang and Xiang's (1986) approaches.

Errors in LAIe estimates stemming from photograph analysis occur because the evaluation of photographs is dependent upon a single threshold value that is chosen to distinguish sky from not sky. Unfortunately blue light is easily scattered, and increased diffraction of light around the edges of foliage and branches causes an overestimation of gap size, especially at small zenith angles (Chen et al., 1997; van Gardingen et al., 1999; Frazer et al., 2000). Frazer et al. (2000) suggest that rather than a single threshold value being applied to the entire photograph, that threshold values should change with zenith in order to account for errors in gap estimation with changes to zenith. Since current software still relies on a single threshold value to distinguish between sky and non-sky,

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photographs must be taken when the contrast between the two is best, when light is diffuse: at dawn, dusk and on overcast days. White et al. (2000) discovered that there might even be differences in gap fraction estimates from photographs taken at dawn verses dusk.

Research Objectives

Chapter 2

The overall objective of Chapter 2 was to collect information on crown shyness that could be used by forest growth modelers, such that predictions of crown shyness could be included in forest models and the productivity of forests could be better estimated. The first objective was to examine the roles of the stand characteristics I believe regulate canopy closure (and therefore crown shyness) through abrasion: stand height, slenderness, relative density, site quality, aspect, slope position and tree arrangement. Rudnicki et al. (2004) conducted similar research on a smaller scale (plots of three trees) and discovered the controlling factor for crown shyness switched from relative density to slenderness once stands reached 15 m. I sought therefore, to examine the relationships at a scale that is more representative of entire stands. I hypothesized that my results would mimic those of Rudnicki et al. (2004), with relative density regulating canopy closure (CC) in short stands, and SC regulating CC in taller stands. I also hypothesized that the site factors I measured (site quality, aspect, slope position and tree arrangement) would influence canopy closure through their influence on wind dynamics.

The second objective of Chapter 2 was to quantify the amount of abrasion in a stand. I collected litter in the same plots I evaluated for canopy closure, and compared the same stand characteristics (height, density, slenderness, site quality, aspect, slope position and tree arrangement) to the number of litter pieces collected and to the length and leaf area of those pieces. I hypothesized that stands suffering from low canopy closure would suffer from higher litter production.

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Chapter 3

The first objective of my research, as outlined in Chapter 3, was to evaluate the relationship between canopy closure and leaf area index. Assuming that canopy closure varies with stand variables (as discovered in Chapter 2), I took hemispherical photographs of stands in order to evaluate leaf area index in stand of various height, slenderness, relative density, site quality, aspect, slope position and tree arrangement. I compared these values to those predicted by Smith and Long (1992).

The second objective of Chapter 3 was to evaluate canopy closure as measured using hemispherical photography with a direct measure of canopy closure using a vertical crown periscope (Rudnicki et al., 2001). In order to make the two measurements comparable, I removed the intra-crown gaps from the photographs before analysis. I hypothesized these measurements would yield the same results.

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Chapter 2: Crown shyness in lodgepole pine stands of varying stand height, density and site index in Upper Foothills, Alberta.

Introduction

Crown shyness, the gaps between tree crowns that are not the result of recent tree mortality (Putz et al., 1984), is believed to be the result of crown abrasion that occurs during windstorms. Rudnicki et al. (2003) demonstrated that there are many crown collisions per hour during moderate to strong windstorms, and the frequency and intensity of these collisions is at least partly related to the slenderness coefficient (SC, height/diameter at 1.3 m) of the trees in the stand. Many have speculated that abrasion between crowns removes branches (Jacobs, 1955; Putz et al., 1984; Maguire, 1994; Campbell, 1998; Cleugh et al., 1998; Rudnicki et al., 2003), and Long and Smith (1992) documented that artificial pickets were broken off during wind-induced crown collisions. It follows that litter production is likely higher in stands with greater abrasion; Campbell (1998) hypothesized that litter depth declined along transects into a stand because of declining wind strength, which increasingly limited abrasion. There is growing evidence that crown shyness in many coniferous forests may limit the leaf area of stands in the second half of their rotation (see review by Ryan et al., 1997). Indeed Long and Smith (1992) note that the decline in productivity in stands coincides with the onset of crown shyness. To date, information regarding litter production as the result of crown shyness is limited, and I know of no actual estimates of leaf area lost to abrasion from moderate wind events.

Rudnicki et al. (2004) tried to understand some of the stand characteristics controlling crown shyness by examining canopy closure (CC) in very small plots, i.e. within triangles formed by a group of three trees. This work suggested that CC was related to tree height (HT), in addition to relative density (RD) in shorter stands, and SC in taller stands. Higher rates of stocking (density) should result in increasing crown occupancy. This was true for short stands, however plots with high SC in tall stands had lower canopy closure, presumably because of increased tree sway related to slender stems abrading away the edges of crowns. To date, however, no one has examined crown shyness in larger plots that would be more representative of stand level responses.

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Furthermore, the influence of other stand level factors that might influence crown shyness including site quality, the spatial distribution of trees or the effects of landscape position have not been examined.

Crown shyness is expected to trim off the outer branches of a crown, thereby removing valuable tree leaf area and providing more favorable light conditions to lower branches. It is therefore possible that trees might compensate for this foliar loss by maintaining longer crowns. Both Beekhuis (1965) and Long and Smith (1992) suggested this, but to my knowledge a direct link between abrasion and crown length has not been investigated.

The objectives of this study were as follows: 1) to examine the stand height, relative density, slenderness coefficient, site quality and landscape position as predictors of crown shyness and 2) to examine the role of crown shyness on crown length. I hypothesize that crown shyness will increase where tree flexibility and proximity are highest, leading to higher frequency and intensity of collisions in stands with trees that are tall, slender, and high density. I also hypothesize that these stands will have higher litter production as the result of increased abrasion. Finally, stands suffering from greater abrasion should also have greater leaf area shed to the ground and longer crown lengths to compensate for foliar losses.

Methods

Stand Measurements

I selected 90 lodgepole pine stands within the Upper Foothills Ecoregion near Hinton, Alberta, having various combinations of heights and densities based on the stand density management diagrams (Farnden, 1996) (Table 2-1, Fig.2-1). Bole slenderness was visually assessed in the selected stands, to attempt to sample stands over a range of mean slenderness coefficient. A plot centre in each stand was selected based upon the following criteria: plots were located on windward slopes (east-facing slopes were avoided), were composed of at least 90% pine, were at least 2 tree lengths from stand edge and had not undergone silviculture treatments within at least 10 years. Plots also did not have mortality gaps within the plot or on their perimeter. Mortality gaps were defined using the crown closure line of the stand management diagram for unmanaged

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lodgepole pine stands (Farnden, 1996). For any average stand height, the density of trees on the crown closure line was determined. The space occupied by an individual tree was then used as the maximum-sized opening allowed in the plot.

Plot size varied with stand height. Plot radius was scaled by the average height of 2 dominant trees near plot centre and assuming the crown region of interest was 27° from zenith over plot centre. The slope, aspect, plant community type (Beckingham et al., 1996), elevation and slope position of each stand were also recorded.

In each plot, the diameter at 1.3 m (DBH) of all trees in the plot were recorded, and trees were divided into dominant, codominant, and intermediate crown class, from which 9 trees (3 per crown class) were measured for height and crown length using a laser hypsometer (Impulse 200LR). Suppressed trees (i.e. trees with their maximum height below the level of the main canopy) were not included in the analysis.

Crown length was measured at the lowest living full whorl of branches (Alberta Environmental Protection, 1997). Average crown radius of dominant trees was measured on each of the selected dominant trees. An extendable measuring pole was moved to the edge of the crown until the pole was judged to be at the edge of the crown and parallel with the bole, based upon a viewer at least 10 m away. Distance to the bole was measured with a tape measure. Four radii of the crown, 90° apart, were identified starting from the longest radius. The 2 radii that were neither shortest nor longest were measured. The age of the largest diameter tree in each stand was measured and site index calculated using the equations developed for lodgepole pine by Huang et al. (1994).

The dispersion of lodgepole pine stems in each plot was assessed by analysis of stem frequencies in nineteen –10 m^2 subplots. These subplots were positioned systematically in concentric rings in each plot. The Morisita Index of Dispersion (I_d) (Krebs, 1999) was calculated:

$$I_d = n\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \qquad \text{(EQ1.0)}$$

Where I_d is Morisita's index of dispersion, n is the number of subplots, and x is the number of trees counted in each subplot. The Standardized Morisita Index (I_p) was

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then calculated using I_d together with two significance points for the Morisita, as calculated from the following formulas:

$$\text{Uniform index} = M_u = \frac{\chi^2_{.975} - n + \sum x_i}{\left(\sum x_i - 1\right)} \tag{EQ1.1}$$

$$\text{Clumped index} = M_c = \frac{\chi^2_{.025} - n + \sum x_i}{\left(\sum x_i - 1\right)} \tag{EQ1.2}$$

Where $\chi^2_{.975}$ = Value of chi-square from table with n-1 degrees of freedom that has 97.5% area to the right

x_i = number of stems in quadrat

n = number of quadrats

$\chi^2_{.025}$ = Value of chi-square from table with n-1 degrees of freedom that has 2.5% area to the right

When $I_d \geq M_c > 1.0$:

$$I_p = 0.5 + 0.5\left(\frac{I_d - M_c}{n - M_c}\right) \tag{EQ1.3}$$

When $M_c \geq I_d \geq 1.0$:

$$I_p = -0.5\left(\frac{I_d - 1}{M_c - 1}\right) \tag{EQ1.4}$$

When $1.0 \geq I_d \geq M_u$:

$$I_p = -0.5\left(\frac{I_d - 1}{M_u - 1}\right) \tag{EQ1.5}$$

When $1.0 \geq M_u \geq I_d$:

$$I_p = -0.5 + 0.5\left(\frac{I_d - M_u}{M_u}\right) \tag{EQ1.6}$$

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Stands having standardized Morisita values (I_p) <0 were considered uniform, near 0 as random and >0 as clumped.

Canopy Closure

Canopy closure (CC) was estimated within each plot using a vertical periscope (Rudnicki et al., 2001). This instrument was designed to sight vertically using a monopod and level. Three north-south transects were established through the plot; one through the centre of the plot and one on either side of transect 1 at a distance from centre equal to 1/3 the diameter of the plot. On each transect the edge of crown and positions between crowns were carefully measured. Canopy closure was defined as the length of transect under crowns/total length of transect.

Green Litter

In early June 2004, branch litter with intact green needles was collected in 4 - 10 m^2 sub-plots within each plot. Subplots were systematically placed at plot centre and at 3 radii at a relative distance from the plot centre. In some plots there was evidence suggesting squirrel damage (i.e. litter branches with chewed needles); these plots were removed from the litter study. The "Munsell Color Charts for Plant Tissues" (Munsell, 1977) were used to identify 'green' litter for analysis. Litter with needle color of any chroma and value on Munsell Color Charts 5GY, 7.5GY and 2.5G, or 5/6, 5/7, 6/8, 6/10, 8/10 and 8/12 on 2.5GY were considered green, provided at least 75% of needles on the twig were green. The total number of green litter for the 4 sub-plots was counted and the length of each branch, from the tip of the terminal bud to the point of breakage, was measured with a ruler. Needles from the green litter were removed and litter leaf area per plot area (LA) (cm^2/m^2) was estimated using Sigma Scan (Version 5.0) by determining the specific leaf area (cm^2/g) of a random sample of needles and the total mass of the needles (g) from the 4 litter sub-plots per plot.

In order to get an approximate age of the 'green' litter, freshly-removed green twigs were dropped in stands of varying ages and then checked for their 'greenness' after periods of time. Results of the litter aging were similar in all sites (Table 2-2); samples dropped in mid June were no longer green by mid August, whereas samples dropped in

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mid August were green when they were last checked in mid October. This suggests that litter I collected in early June and classified as green had fallen after mid August of the previous year.

Data Analysis

I estimated the height of all non-suppressed trees in the plot using the relationship between diameter and height of the measured trees. From this I calculated the average height (HT) of all the trees in the stand and used Lorey height to estimate the average height of the codominant and dominant trees of the stand (CDHT):

$$CDHT = \frac{\Sigma(ba * ht)}{\Sigma ba} \qquad \text{(EQ2.0)}$$

where *ba* is tree basal area and *ht* is tree height. I also calculated the top height (TOPHT) of the stand assuming top height was the tallest 100 trees/ha. The individual tree heights were also used to calculate tree slenderness coefficients, and these values were averaged for each stand to provide stand slenderness coefficient (SC). Average crown length (CL) for all trees in the analysis was estimated from the relationship between DBH and crown length of the measured trees. The crown radii of the two dominant trees that I measured were averaged to estimate crown radius of dominant trees (CR). The average distance between trees was also estimated in each plot using plot density and area.

The relative density (RD) of each plot was calculated using Curtis' (1970) equation:

$$RD = \frac{BA}{QMD^{0.4}} \qquad \text{(EQ3.0)}$$

$$BA = \left(k * QMD^2 * DEN\right) \qquad \text{(EQ3.1)}$$

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$$QMD = \sqrt{\frac{\sum_{i=1}^{n} dbh_i^2}{x}} \qquad \text{(EQ3.2)}$$

Where BA is stand basal area, QMD is stand quadratic mean diameter, k is a constant (0.0000785395), DEN is the number of trees per hectare, dbh is diameter at 1.3 m height, and x is the number of trees measured.

Both simple and forward multiple regression analyses were completed on the data. Where data was tested within height classes, differences between the slopes and intercepts of the individual classes were tested with ANCOVA using linear contrasts. A correlation matrix was also completed to account for the co-variation of examined factors (Appendix 2-A).

Results

Canopy Closure

Canopy closure (CC) decreased linearly with mean tree height (HT) (Adj. R^2 = 0.482, p = <0.001, Fig. 2-2a). At the same time, the average distance between tree boles also increased with HT (Adj. R^2 = 0.642, p=<0.001, Fig. 2-2b), although the rate of distance change with HT slowed once stands reached 8-10 m. Canopy closure also increased with site index (SI) (Adj. R^2 = 0.166, p = <0.001, Fig. 2-3). Canopy closure was also positively correlated with relative density (RD) (Adj. R^2 = 0.079, p = 0.004, Fig. 2-4), and this was true across the three HT categories, although the tallest (>15 m) stands had lower CC (p = 0.005) across the range of RD than stands <15 m, as indicated with linear contrasts. There was no relationship between CC and slenderness coefficient (SC) (Adj. R^2 = 0, p = 0.660). The relationship between slenderness coefficient (SC) and RD for trees <15 m was positive and linear (Adj. R^2 = 0.460, p = <0.001, Fig. 2-5), whereas the relationship for stands >15 m had a different slope than stands < 15 m (p = 0.002), as indicated by linear contrasts. In stands >15 m there was no relationship between SC and RD.

Canopy closure was positively related to the standardized Morisita index (describing the dispersion of trees in the stands) (Adj. R^2 = 0.133, p = <0.001, Fig. 2-6) when all three height classes were regressed at the same time. It is noteworthy that in

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stands >15 m tall, the trees were more uniformly distributed ($p = <0.001$) than the trees in the shorter stands (<15 m).

The overall influence of all of the variables on the prediction of CC was explored using three multiple regression models, each with a different measurement of HT: 1) HT (average stand height), 2) CDHT (average height of codominant and dominant trees), and 3) TOPHT (stand top height). The following models were developed:

$$CC = -2.53HT + 1.88SI + 1.45RD \text{ (Adj. } R^2 = 0.603, p = <0.001) \quad \text{(EQ4.0)}$$

$$CC = -2.40CDHT + 1.96SI + 1.55RD \text{ (Adj. } R^2 = 0.605, p = <0.001) \quad \text{(EQ5.0)}$$

$$CC = -2.22TOPHT + 1.83SI + 1.66RD \text{ (Adj. } R^2 = 0.583, p = <0.001) \quad \text{(EQ6.0)}$$

The influence of height (all three expressions), stand relative density and site index were significant terms in prediction of CC in all three multiple regression models. All three models were highly significant and had similar correlation coefficients.

Crown Dimensions

Neither average crown length (CL) (Adj. $R^2 = 0.027$, $p = 0.066$, Fig. 2-7a) nor the crown radius of dominant trees (CR) (Adj. $R^2 = 0.004$, $p = 0.255$, Fig. 2-7b) were significantly related to CC. Crown length (CL) (Adj. $R^2 = 0.272$, $p = <0.001$, Fig. 2-8a) and crown radius (CR) (Adj. $R^2 = 0.234$, $p=<0.001$, Fig. 2-8b) were related to HT, however the relationships were not linear. Instead both CL and CR increase rapidly until approximately 8-10 m and thereafter increased only slightly with further increases in HT. The relationships for CL and CR with increasing SI were linear, with both CL (Adj. $R^2 = 0.062$, $p = 0.010$, Fig. 2-9a) and CR (Adj. $R^2 = 0.128$, $p = <0.001$, Fig. 2-9b) increasing with SI. Crown length decreased linearly with RD (Adj. $R^2 = 0.324$, $p = <0.001$, Fig. 2-10a), and the relationship between CR and RD was significant, but was not strong (Adj. $R^2 = 0.060$, $p = 0.012$, Fig. 2-10b). Finally, both CL (Adj. $R^2 = 0.378$, $p = <0.001$, Fig. 2-11a) and CR (Adj. $R^2 = 0.168$, $p = <0.001$, Fig. 2-11b) declined with SC.

From this information I developed the following models for CL and CR, using average stand height (HT):

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$$CL = 0.380HT - 0.020SC - 0.012\,HT^2 - 0.007RD + 0.043SI \text{ (Adj. } R^2 = 0.606, p = < 0.001) \qquad \text{(EQ7.0)}$$

$$CR = 0.038HT + 0.047SI - 0.004SC \text{ (Adj. } R^2 = 0.493, p = < 0.001) \qquad \text{(EQ8.0)}$$

Green Twig and Leaf Litter

Green litter collected from the forest floor in the spring increased with HT across the range of stands sampled, in terms of the number branches (Adj. $R^2 = 0.050$, $p = <0.001$, Fig. 2-12a), leaf area (LA) (cm^2/m^2) (Adj. $R^2 = 0.164$, $p = 0.023$, Fig. 2-12b) and total length (cm) (Adj. $R^2 = 0.177$, $p = <0.001$, Fig. 2-12c) of these branches. On average, leaf area losses for stands less than 10 m tall were 9.24 cm^2/m^2, for stands between 10 and 15 m tall, 16.9 cm^2/m^2, and for stands greater than 15 m tall, 77.4 cm^2/m^2 (Table 1).

The number of green litter branches increased with RD (Adj. $R^2 = 0.119$, $p = <0.001$, Fig. 2-13a). No relationship between leaf area of branches (Adj. $R^2 = 0.008$, $p = 0.198$, Fig. 2-13b) or total litter length (Adj. $R^2 = 0.011$, $p = 0.172$, Fig. 2-13c) with RD was observed.

Discussion

Canopy Closure

This study was correlative in nature, and many of the stand factors I examined in this study co-varied (Appendix 2-A), however trends in the data are still apparent. My results show that canopy closure (CC) decreased with increasing stand height (HT), but CC increased with increasing site index (SI) and relative density (RD) (EQs. 4.0 – 6.0). Increasing HT appeared to be the most important in limiting CC, and supports the hypothesis that collisions reduce the width of crowns in taller stands due to increased wind speed at the crown level (Bergen, 1971) and greater bole deflection (Rudnicki et al., 2001) that are characteristic of taller stands. The hypothesis of increased crown abrasion with increasing height was further supported by the data on green litter in these stands; taller stands had more litterfall, including total length of branches and more leaf area related to green litter on the forest floor, despite having greater distance between trees. Foliage distribution may have influenced branch litter loss, as Xu and Harrington (1998) noted that the loblolly pine in their study increasingly shifted foliage to the edge of the

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crown with age. Xu and Harrington (1998) suggested this might be a mechanism for shade-intolerant trees to maximize the area of the crown receiving light. In terms of abrasion, foliage held furthest from the tree is likely most susceptible to abrasion during collision events. Both the increased litter production and increased distance between tree boles appeared to be the reasons for the lower canopy closure in tall stands.

The increasing distance between boles as stands grew in height (Fig. 2-2b) likely became increasingly important to CC because crown radius (CR) peaked at approximately 8-10 m (Fig. 2-8b). This indicates that lateral branches do not successfully spread into adjacent spaces and do not take advantage of the higher light availability in stands of low CC. This could suggest that abrasion restricts CR as stands increase in HT, as suggested by Putz et al. (1984) thereby limiting CC, however the fact that CC increased with RD, despite some evidence of higher abrasion, i.e. more green litter in stands with high RD (Fig. 2-13a), suggests that factors other than abrasion also affected CC in older stands.

Site quality was expected to influence CC because of increased tree vigour in good sites. The fact that crown radius for trees of a given height was greater in good sites than in poor sites (Fig. 2-9b) suggests that these lodgepole pines fundamentally have more narrow crowns on poor sites than good sites. This notion is supported by numerous studies citing the fact that fertilization of lodgepole pine resulted in increased crown growth (Vose and Allen, 1988; Raison et al., 1992; Brockley and Sheran, 1994; Vose et al., 1994; Yang, 1998; Amponsah et al., 2004).

Over the range of data, I found that CC tended to increase with RD. This trend was similar to that observed for short stands by Rudnicki et al. (2004) and fits with accepted theory of increased utilization of crown space with increasing stocking (Assman, 1970; Curtis, 1982). Based upon Rudnicki et al. (2004), however, I expected to see little relationship between CC and RD in taller stands, but the trend for increasing CC with RD seemed to hold for tall stands as well (Fig. 2-4). This is surprising given that abrasion likely increased with RD, as supported by the data on green litter (Fig. 2-13a).

Reasons for the differences in findings between my study and that of Rudnicki et al. (2004) are not clear, but might relate to the following two factors. First, Rudnicki et

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al. (2004) used very small plots with relatively uniform sized trees within the plot. My study used stand average CC and had the full range of tree sizes, and random to clumped distributions expected for unmanaged stands. It is possible that the results of Rudnicki et al. (2004) are more representative of individual tree-level response to wind rather than stand-level response to wind. For example, Rudnicki et al. (2003) showed that crown movement in wind was greater in trees with high slenderness coefficient (SC), compared to trees with low slender coefficient. Rudnicki et al. (2004) found that in tall stands, canopy closure declined with increased slenderness coefficient of the trees. This is logical because slender trees should sway widely in wind and suffer more abrasion than stout trees. At the stand level, however, the association between SC and RD may reduce sway intensity because tree movement would become increasingly restricted with the higher density that accompanies slenderness (Harrington and Debell, 1996). Wind penetration into, and turbulence within the canopy decrease with density (Green et al., 1995), which may encourage more uniform movement of crowns, and thereby limit the number of crown collisions in dense stands compared to less dense stands. Second, the requirements for stands to be included in my data set were based upon the crown closure line of Farnden's (1996) stand density management diagrams. Given that after reaching 8-10 m in height that CR did not increase with further HT growth (Fig. 2-8b), I now question whether Farnden's definition of CC might be too inclusive of widely spaced stands. In my sample of stands some of the stands might have had unacceptably wide spacings and branches might never have been able to grow to the point of touching.

Crown Dimensions

Crown radius (CR) and crown length (CL) increased linearly with HT, but only until stands reached about 8-10 m after which their size changed very little (Fig. 2-8a and b). Previously CR has been directly linked to available space (Kellomaki, 1986; Sorrenson-Cothern et al., 1993), and although I found a positive relationship between CR and RD in my stands, the relationship was not strong. This is likely because the influence of neighboring trees on CR occurs at a smaller scale than at the stand level. Lateral competition for space, light and the effects of abrasion likely influence each tree differently depending on its dominance and proximity to neighbors. SI likely influences

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CR at the stand scale, however it is also likely that nutrient absorption and allocation differs between trees in a stand (Naidu et al., 1998) such that the contribution of SI to CR varies for individual trees as well.

CL appears to be more strongly related to stand conditions such as RD (Fig. 2-10a) than was CR. This suggests that there was increased survival of lower branches due to increased illumination of the lower crown, however increased illumination of the crown in stands of low CC did not result in longer CL (Fig. 2-7a). Gillespie et al. (1994) found similar effects; CL did not respond to changes to stand density or to fertilization, instead crown density increased. This may suggest that stand density and light availability during the formation of CL are more important than manipulations afterwards – that maximum CL is decided early in stand history and will decline if the conditions are less favorable. Regardless, this also suggests, in direct contrast to the suggestions of Beekhuis (1965), that CL did not respond to compensate for the reductions to CR resulting from abrasion in taller stands.

Finally, it appears SC plays a role in crown size; both CR and CL decreased with SC, despite the fact that there was no relationship between either green litter or CC with SC. This suggests the SC also affects trees at an individual, rather than a stand level, and it may do so through the regulation of crown size. The dependence of CR on DBH is well documented (Krajicek et al., 1964; Tabbush and White, 1988; Larocque and Marshall, 1994; Gill et al., 2000), currently under the assumption that crown size is related to sapwood area (Long and Smith, 1992; Mencuccini and Grace, 1996), such that trees cannot hydraulically support crowns past a certain size. This may become increasingly relevant with time because hydraulic conductivity declines as stands age (Yoder et al., 1994), which would increasingly limit the amount of foliage that crowns could retain. Crown shape (CR and CL) is also believed to have a genetic basis (St. Clair, 1994; McCrady and Jokela, 1996), such that some genotypes may be genetically predisposed to having larger crowns.

Implications

My data clearly shows that there is a loss in canopy closure with increasing height; indeed in the tallest stands, 60% of the view of the sky was not covered by

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crowns, despite the fact that my sampling eliminated those stands with obvious tree-fall gaps. Previous studies and the fact that there was increased green litterfall in taller stands suggest that crown abrasion is important in developing crown shyness in these taller stands. My study, however, also shows that CR and CL reach their maximum size early in stand development; the fact that there was not an increase in CL to take advantage of the open spaces between crowns in these taller stands suggest that other factors besides crown abrasion play a role in these Upper Foothills stands. My data shows that CR and CL at a given height are greater in stands with high SI. It is likely that other issues such as genetics and hydraulic limitations to tree growth also influence the crown development of these stands.

The basis for my study was my suspicion of a link between stand productivity and foliage loss to abrasion. I was able to detect up to 0.0392 m^2/m^2 of foliage loss in one stand taller than 15 m, where foliage loss was greatest, with an average of 0.00774 m^2/m^2 of foliage loss in these stands. Unfortunately I have no estimates of stand LAI to compare my litter estimates to, however these leaf areas seem very small. This could suggest that leaf area loss to abrasion may not be as significant to stand productivity as originally thought, however such a conclusion will require further research to verify.

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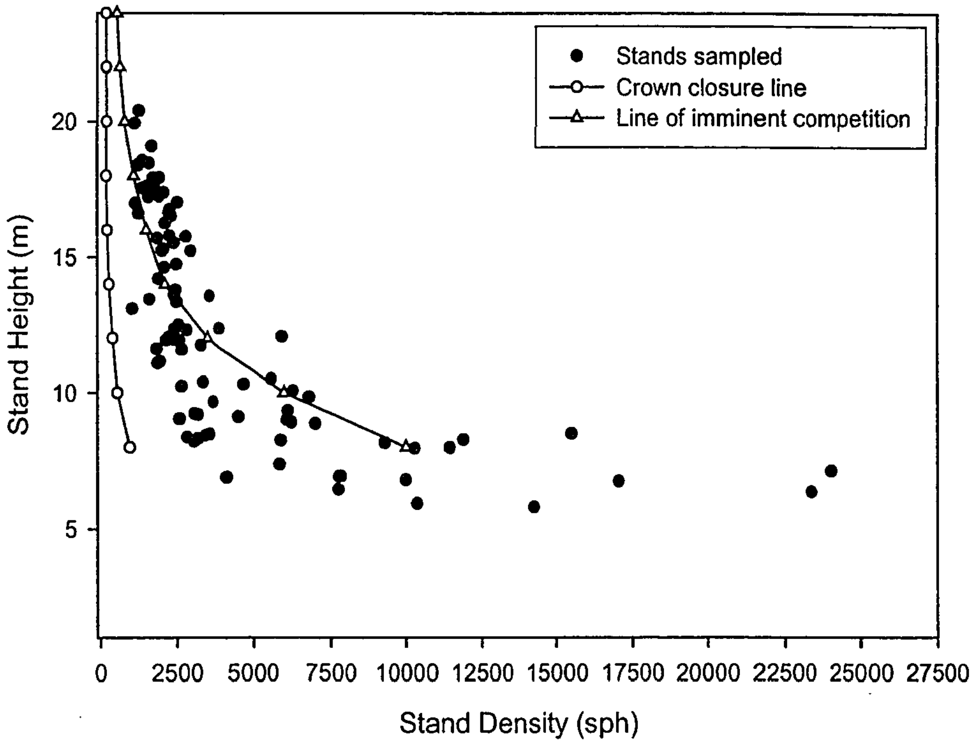

Figure 2-1: Stand height in relation to stand density for sample plots. The lines depict the crown closure line and the line of imminent competition from a stand density management diagram for natural lodgepole pine stands (Farnden, 1996).

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Table 2-1: Mean, standard deviation, minimum and maximum of measured stand characteristics in the lodgepole pine plots (n = 90).

Site Characteristic		Mean	Standard Deviation	Minimum	Maximum
Average stand canopy closure (%)		62.1	16.5	26.6	96.2
Average stand height (m)		12.5	4.02	5.8	20.4
Average slenderness		108.2	14.40	71.50	158.1
Relative density		12.7	2.88	7.90	21.6
Average stand crown length (m)		3.30	0.79	1.60	4.70
Average crown radius of dominants (m)		1.00	0.30	0.30	1.90
Stand density (sph)		4322	4424	1046	24028
Stand age		54	29.7	16	113
Site index		15.4	2.69	9.50	21.5
Average distance between boles (m)		1.88	0.62	0.65	3.50
Average number of green litter pieces	All stands	5.33	8.92	0	50
	< 10 m	3.69	8.49	0	44
	10 – 15 m	3.59	9.60	0	50
	>15 m	8.81	7.91	0	27
Average green litter leaf area (cm^2/m^2)	All Stands	33.9	69.1	0	391.9
	< 10 m	9.24	23.2	0	122.3
	10 – 15 m	16.9	33.9	0	158.6
	>15 m	77.4	102.0	0	391.9
Average length green litter pieces (cm)	All stands	6.83	9.58	0	69.7
	< 10 m	3.79	3.69	0	12.2
	10 – 15 m	6.29	14.21	0	69.7
	>15 m	10.62	7.00	0	24.8

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Table 2-2: Assessment of the retention of green color of foliage after dropping green branches in the understory of closed-canopy lodgepole pine sites at two different times. Green color was assessed using the "Munsell Color Charts for Plant Tissues" (Munsell, 1977) (see Methods).

	Drop Date: June 15, 2004 Collection Assessment Date: August 16, 2004		Drop Date: August 16, 2004 Collection Assessment Date: October 15, 2004	
Location	Brown	Green	Brown	Green
MC48-2	5	0	0	5
R16.5	4	1	0	5
J35-2	5	0	0	5
J35-2B	5	0	0	5

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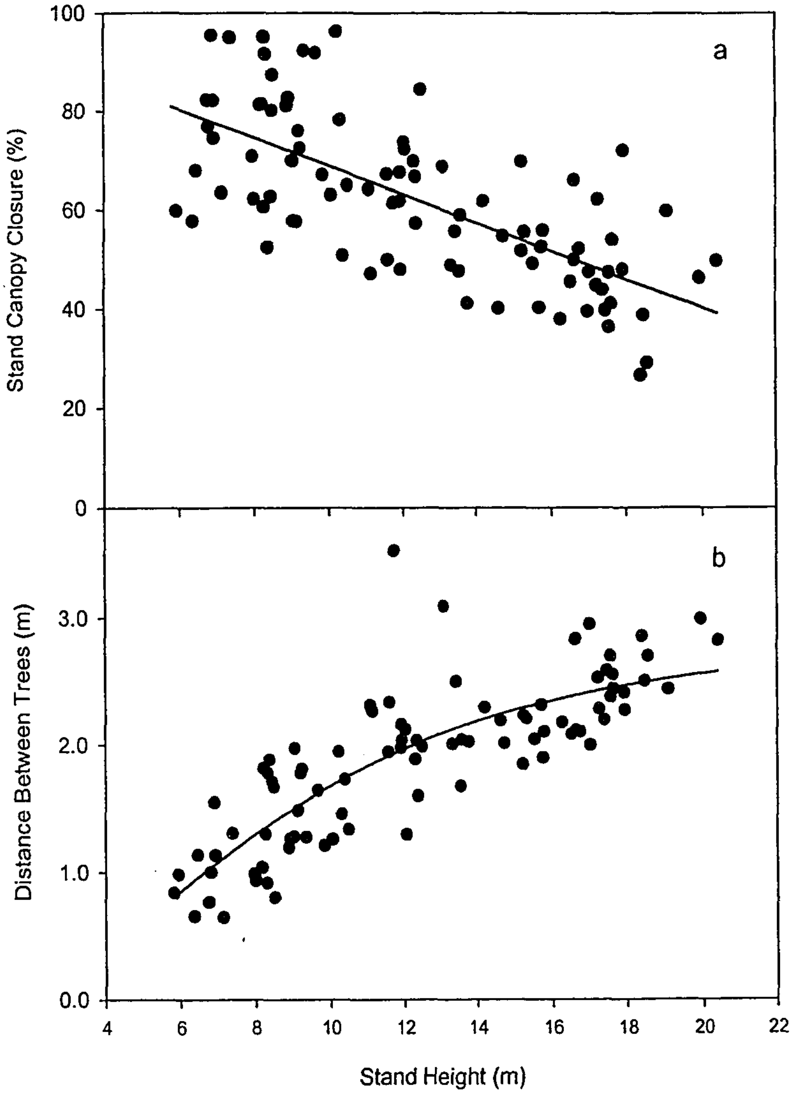

Figure 2-2a: Average stand canopy closure and b: average distance between trees in relation to average stand height. For a: Adj. $R^2 = 0.482$, $p = <0.001$, $y = -2.86x + 97.6$, $n = 90$ and for b: Adj. $R^2 = 0.642$, $p = <0.001$, $y = (4.18x^{1.39})/c^{1.39} + x^{1.39}$, $n = 90$.

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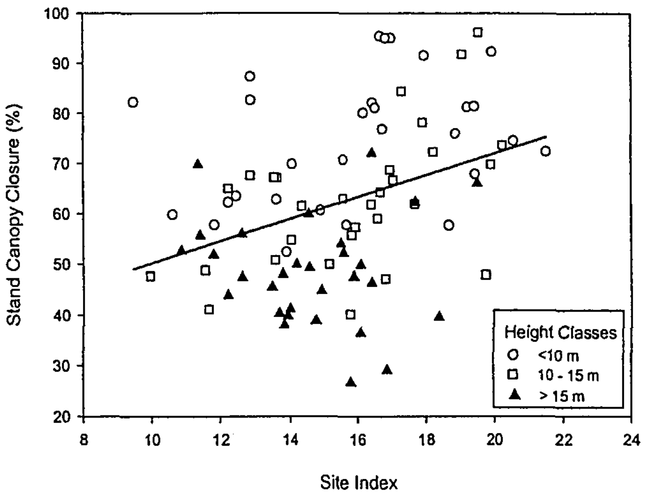

Figure 2-3: Stand canopy closure in relation to site index. Note the symbols for the three stand height classes. Adj. $R^2 = 0.166$, $p = <0.001$, $y = 2.18x + 28.5$, $n = 90$. There were no significant differences among height classes as tested using linear contrasts.

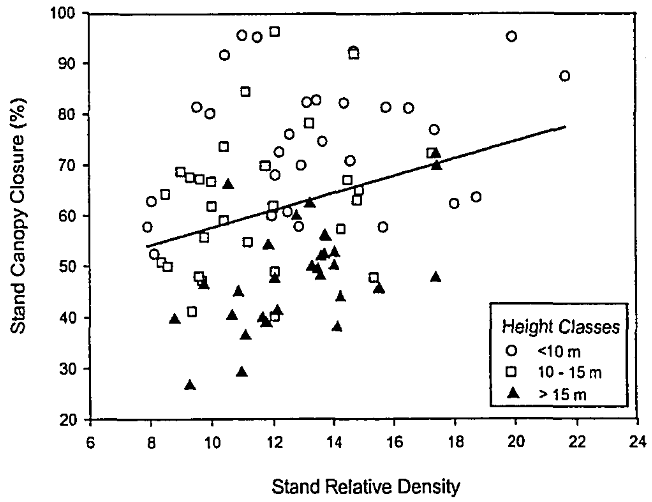

Figure 2-4: Average canopy closure in relation to stand relative density. Note the symbols for the three height classes. Adj. $R^2 = 0.079$, $p = 0.004$, $y = 1.71x + 40.5$, $n = 90$. When the stand height classes were analyzed independently using linear contrasts, stands >15 m had significantly lower canopy closure ($p = 0.005$) across the range of relative densities than stands <15 m.

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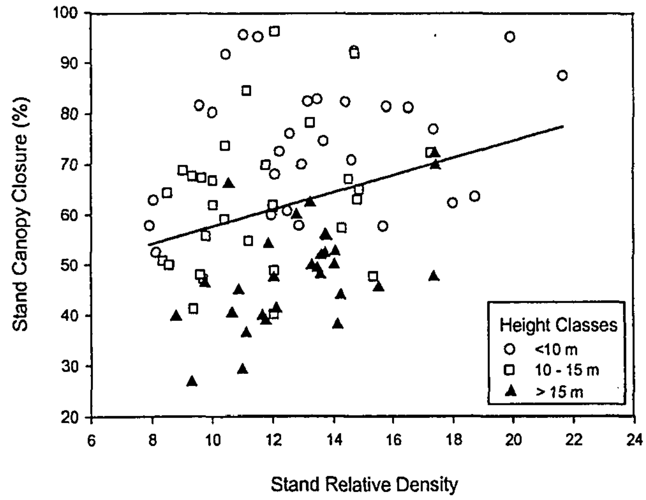

Figure 2-5: Average stand slenderness (HT/DBH) in relation to stand relative density. Note the symbols for the three stand height classes. Adj. R^2 for stands <15 m = 0.460, p = <0.001, y = 3.69x + 63.3, n = 90. When analyzed independently, stands > 15 m had a different slope than stands < 15 m (p = 0.002), as established using linear contrasts; stands >15 m had no relationship between slenderness coefficient and relative density.

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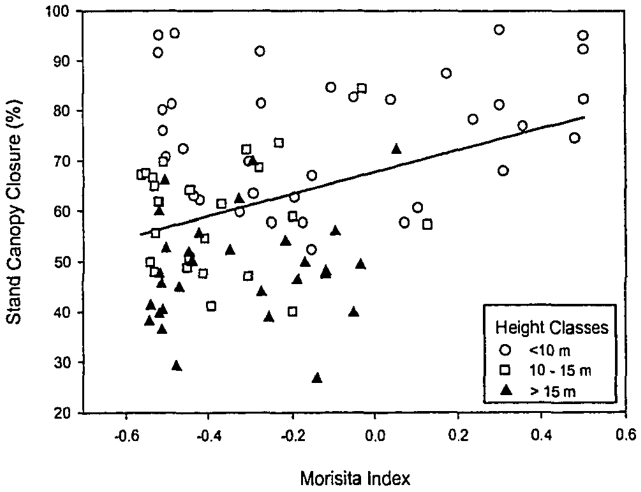

Figure 2-6: Average canopy closure in relation to the standardized Morisita index for distribution of lodgepole pine stems (<0 = uniform, 0 = random and >0 = clumped). Note the symbols for the three stand height classes. Adj. $R^2 = 0.133$, p = <0.001, $y = 21.7x + 67.7$, n = 90. When the stand height classes were analyzed independently using linear contrasts, stands <15 m had significantly lower standardized Morisita Index values than stands >15 m (p = <0.001).

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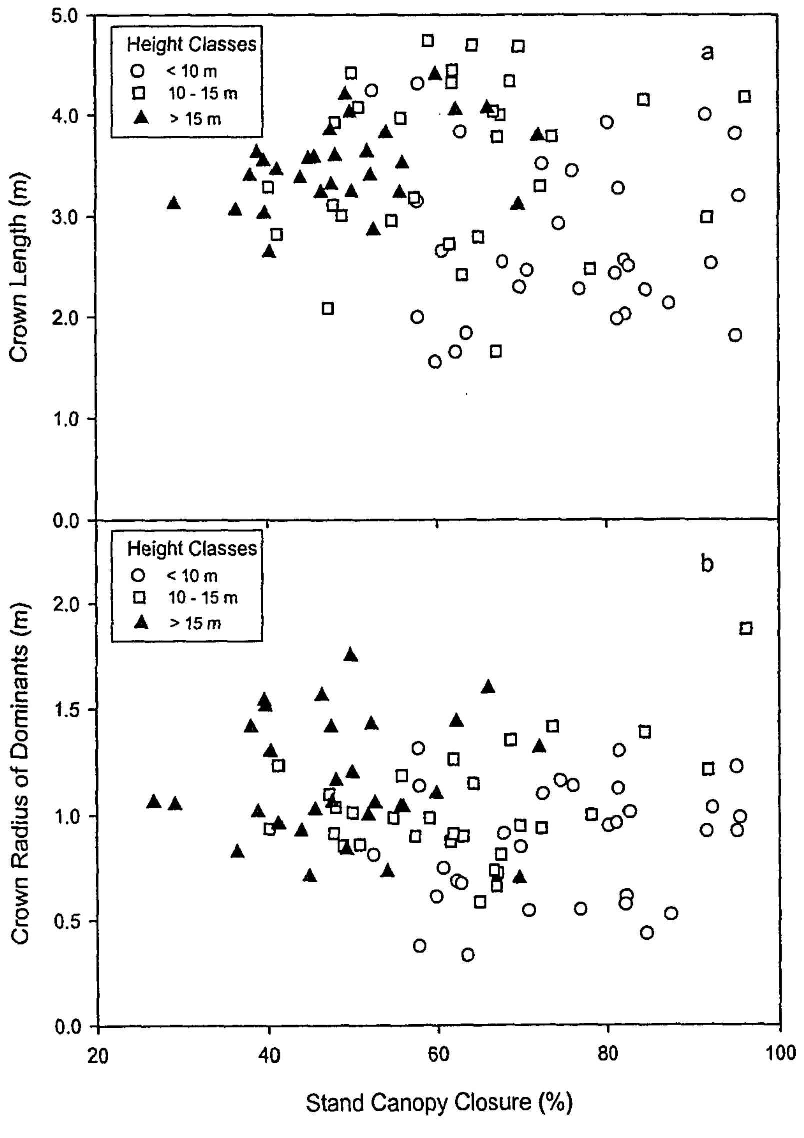

Figure 2-7a: Average stand crown length and b: crown radius of dominants in relation to average stand canopy closure. Note the different height classes. For a: Adj. $R^2 = 0.027$, $p = 0.066$, $y = 3.87 - 0.010x$, $n = 90$ and b) Adj. $R^2 = 0.004$, $p = 0.255$, $y = -1.15 - 0.002x$, $n = 90$. There were no differences in slope or intercept among the three height classes as tested using linear contrasts.

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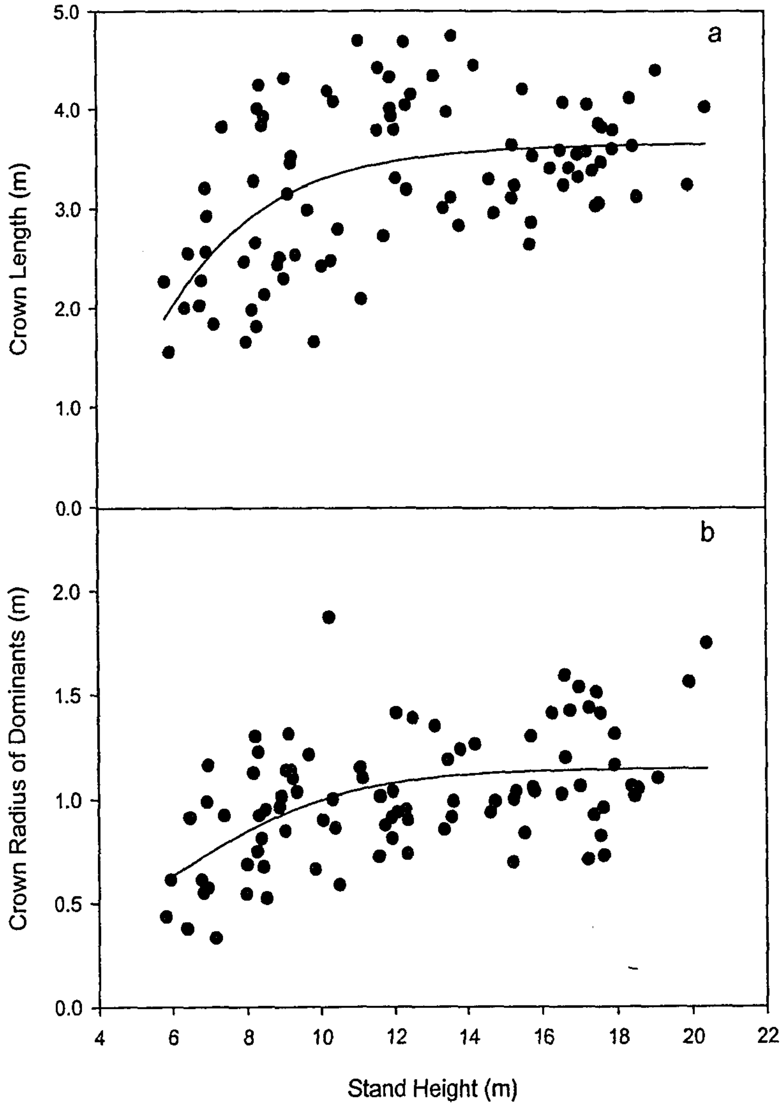

Figure 2-8a: Average crown length and b: average crown radius of dominants in relation to average stand height. For a: Adj. $R^2 = 0.272$, $p = <0.001$, $y = 3.68x^{3.80}/759.14 + x^{3.80}$, $n = 90$ and for b: Adj. $R^2 = 0.234$, $p = < 0.001$, $y = 1.19x^{3.00}/206.26 + x^{3.00}$, $n = 90$.

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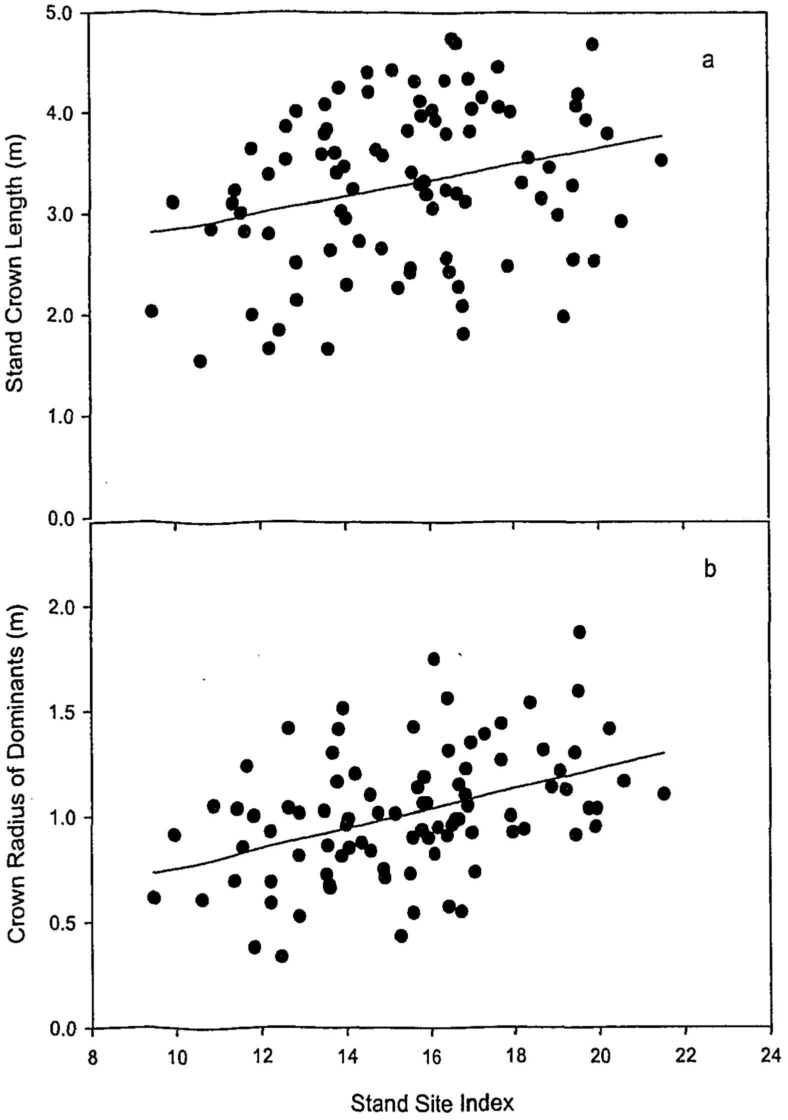

Figure 2-9a: Average crown length and b: average crown radius of dominants in relation to stand site index. For a: Adj. $R^2 = 0.062$, $p = 0.010$, $y = 2.054 - 0.080x$, $n = 90$ and for b) Adj. $R^2 = 0.128$, $p = < 0.001$, $y = 139.5 - 1.99x$, $n = 90$.

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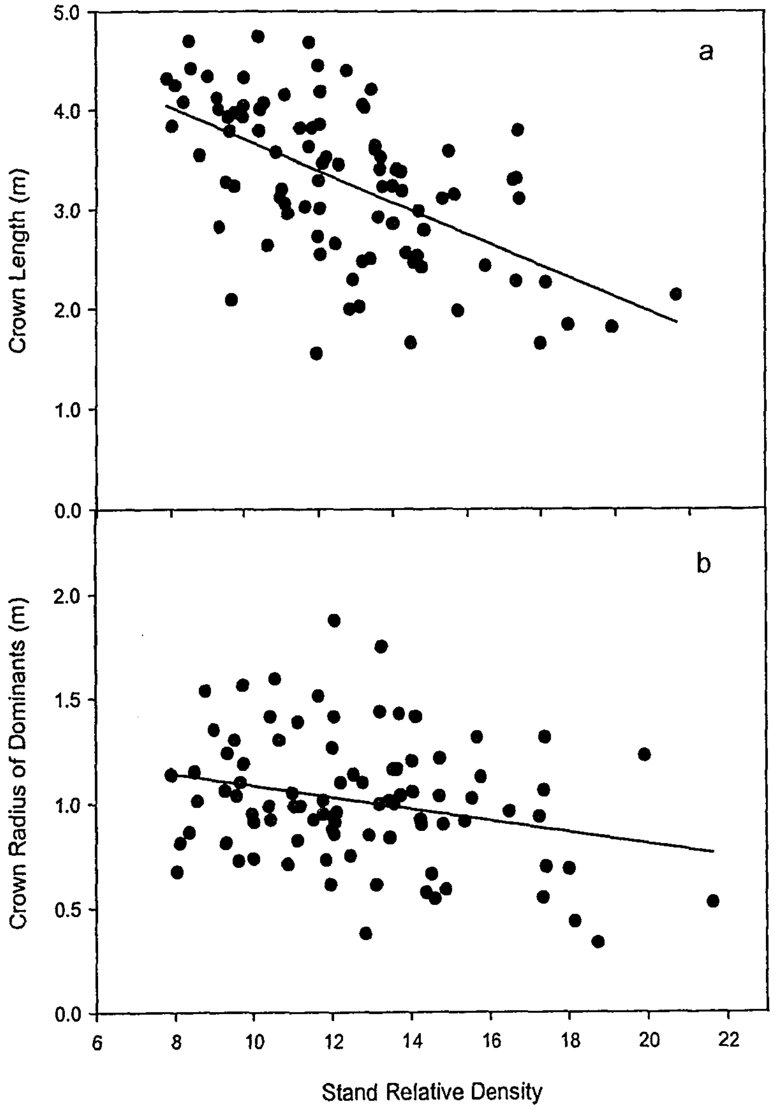

Figure 2-10a: Average crown length and b: average crown radius of dominants in relation to stand relative density. For a: Adj. $R^2 = 0.324$, $p = < 0.001$, $y = 5.30 - 0.159x$, $n = 90$ and for b) Adj. $R^2 = 0.060$, $p = 0.012$, $y = 1.36 - 0.028x$, $n = 90$.

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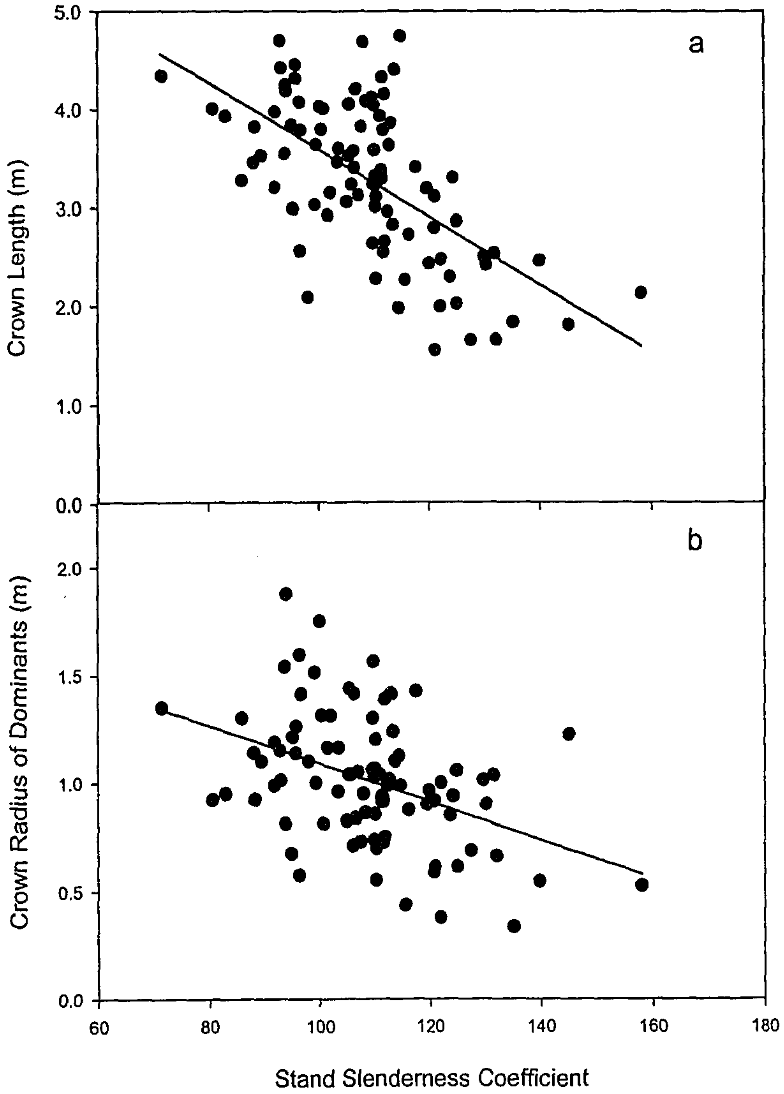

Figure 2-11a: Average crown length and b: average crown radius of dominants in relation to average stand slenderness coefficient (average height/diameter at 1.3 m). For a: Adj. $R^2 = 0.378$, $p = < 0.001$, $y = 7.00 - 0.034x$, $n = 90$ and for b: Adj. $R^2 = 0.168$, $p = <0.001$, $y = 1.97 - 0.009x$, $n = 90$.

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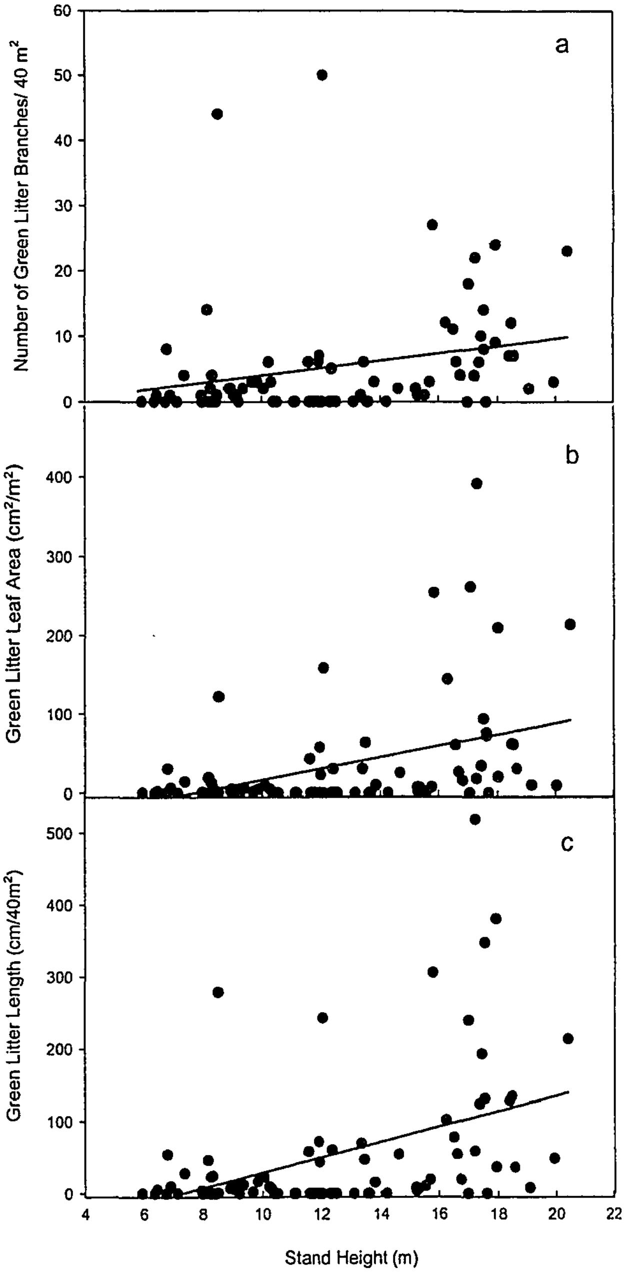

Figure 2-12: Green litterfall a: number of branches b: leaf area and c: total length in relation to stand height. For a: Adj. $R^2 = 0.050$, $p = 0.023$, $y = 0.558x - 1.55$, $n = 82$, for b: Adj. $R^2 = 0.164$, $p = <0.001$, $y = 7.23x - 55.6$, $n = 82$, and for c: Adj. $R^2 = 0.177$, $p = <0.001$, $y = 10.67x - 77.34$, $n = 82$.

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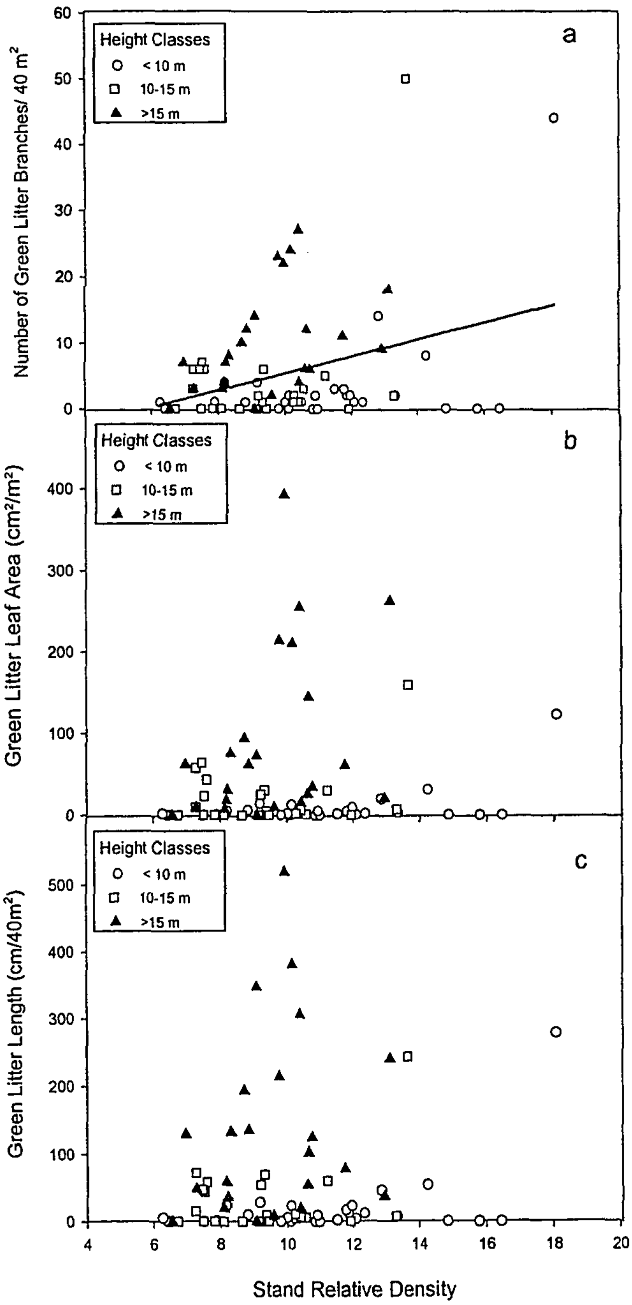

Figure 2-13: Green litterfall a: number of branches b: leaf area and c: total length in relation to relative density each separated into three stand height classes; only the number of branches was significantly related to RD. For a: Adj. $R^2 = 0.119$, $p = < 0.001$, $y = 1.28x - 7.39$, $n = 82$, and b: Adj. $R^2 = 0.008$, $p = 0.198$, $y = 3.92x - 5.11$, $n = 82$, and for c: Adj. $R^2 = 0.011$, $p = 0.172$, $y = 5.92x - 4.61$, $n = 82$. There were no significant differences in slope or intercept among height classes as tested with linear contrasts.

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Chapter 3: Leaf area index and canopy closure measurements in lodgepole pine.

Introduction

Stands rely on their leaves for photosynthesis, thus stand leaf area index (LAI), half of the total leaf area per unit ground area (Lang et al., 1991; Chen and Black 1992), is an important stand attribute regulating stand productivity and provides the foundation for many forest growth and succession models. Stand LAI peaks relatively early in stand development and then declines, reaching a plateau late in the stand's development sequence (Long and Smith, 1992). Long and Smith (1992) also noted that the decline in LAI also coincides with the decline in stand productivity; thus, understanding the mechanisms responsible for the decline in stand LAI may be very important to understanding the regulation of stand productivity.

Stand leaf area is thought to remain constant following density changes; following the natural self-thinning of a stand (the mortality of trees in a canopy that have been out-competed for resources) foliage is thought to be redistributed among remaining stand members (Long and Smith, 1992). This supports the general belief that tree crowns expand into all available space as a mechanism of competition (Sorrenson-Cothern et al., 1993), yet in many fully-stocked stands space between crowns remains unoccupied. This space is termed crown shyness, and it is believed to be the result of abrasion between neighboring crowns (Putz et al., 1984). Furthermore, crown shyness is believed to be related to the decline in stand LAI over time (Ryan et al., 1997). Abrasion occurs as the result of tree sway; trees sway to release energy captured during wind events (Cucchi and Bert, 2003), and, in doing so, often collide with their neighbors resulting in the abrasion of branches.

Because direct estimates of LAI are labourious and time consuming, several optical methods have been developed to estimate canopy closure and LAI. Hemispherical photography is one such method and provides an estimate of both gap fraction and LAI based on Beer's law:

$$G(\theta) = e^{-k(\theta)*\mathrm{LAI}} \qquad \text{(EQ1.0)}$$

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where G is gap fraction, k(θ) is the extinction coefficient at angle θ, LAI is the leaf area index, and θ is zenith angle.

Beer's Law is based on the assumptions that a canopy has random distribution of elements, whereas conifer canopies are well documented as being clumped at 4 levels: within shoot, within the branch, within the whorl and within the crown (Norman and Jarvis, 1974). Thus, hemispherical photography provides an estimate of effective LAI (LAIe), i.e. an estimate of LAI that does not account for clumping, such that effective leaf area index tends to underestimate actual LAI (Marshall and Waring, 1986; Gower and Norman, 1991; Chen et al., 1997). Several researchers have attempted to account for clumping within forest canopies and thereby increase the accuracy of LAI estimates (Fassnacht et al., 1994; Stenberg, 1996; Chen et al., 1997; van Gardingen et al. 1999; Law et al., 2004). Accurately characterizing clumping can be difficult, however, because clumping varies with canopy structure and density (van Gardingen et al., 1999; Kucharik et al., 1999). Leblanc et al., 2005 suggest a combination of gap size frequency estimates (see Chen and Cihlar, 1995) and the logarithm of average gap size estimates from small transects (see Lang and Xiang, 1986) to estimate clumping in forest stands.

Another important limitation to the precision of canopy estimates using hemispherical photographs is that the removal of non-foliage elements blocking the skyview (i.e. branches and boles) is not possible, thus these materials are also included in LAIe and gap fraction estimates. For this reason, it has been suggested that hemispherical photography should not be used for canopy measurement in stands differing in woody biomass content (Chason et al., 1991; Martens et al., 1993; Deblonde et al., 1994), which would limit the use of hemispherical photography in a study such as this that includes stands of varying height. Gill et al. (2000) and Bunnell and Vales (1990) have suggested restricting the region of the photograph analyzed to the target being measured. By restricting photography analysis to the centremost region of the photograph, it may be possible to reduce the amount of woody biomass included in the estimates, such that trends between canopy measurements and stand factors will still be apparent.

Precision is further difficult with hemispherical photography because the technique requires photographs be taken when the canopy is evenly lit in order to

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properly classify pixels in the images because classification is based on a single subjective threshold value to separate leaves and background sky. Classification is especially difficult at gaps closer to zenith, which tend to be overestimated (Fournier et al., 1996; Chen et al., 1997; Frazer et al., 2000), because of the scattering of blue wavelengths of light.

I used hemispherical photography to estimate effective leaf area index (LAIe) in stands of varying height, relative density, slenderness coefficient (height/diameter at 1.3 m), site quality and tree dispersion, in order to assess the relationship between crown shyness and stand LAIe. I hypothesized that stands having less crown shyness (short, high relative density stands) would have higher LAIe than stands with more crown shyness, such that LAIe would increase with canopy cover. I also compared the canopy cover estimated from hemispherical photographs with the direct measurement of canopy closure provided by a vertical periscope. I expected the measurements provided by these two methods would be the same.

Methods

Stand Measurements

I selected 90 lodgepole pine stands within the Upper Foothills Ecoregion near Hinton, Alberta, having various combinations of heights and densities based on the stand density management diagrams (Farnden, 1996) (Table 3-1). Bole slenderness was visually assessed in the selected stands to attempt to sample stands over a range of mean slenderness coefficient. A plot centre in each stand was selected based upon the following criteria: plots were located on windward slopes (east-facing slopes were avoided), were composed of at least 90% pine, were at least 2 tree lengths from stand edge and had not undergone silviculture treatments within at least 10 years. Plots also did not have mortality gaps within the plot or on their perimeter. Mortality gaps were defined using the expected space available for such trees at the crown closure line of the stand management diagram for unmanaged lodgepole pine stands (Farnden, 1996). For any average stand height, the density of trees on the crown closure line was determined. The space occupied by an individual tree was then used as the maximum-sized opening allowed in the plot.

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Plot size varied with stand height. Plot radius was scaled by the average height of 2 dominant trees near plot centre and assuming the crown region of interest was 27° from zenith over plot centre. The slope, aspect, plant community type (Beckingham et al., 1996), elevation and slope position of each stand were also recorded.

In each plot, the diameter at 1.3 m (DBH) of all trees in the plot were recorded, and trees were divided into dominant, codominant, and intermediate crown class, from which 9 trees (3 per crown class) were measured for height and crown length using a laser hypsometer (Impulse 200LR). Suppressed trees (i.e. trees with crowns below the level of the main canopy) were not included in the analysis.

Crown length was measured at the lowest living full whorl of branches (Alberta Environmental Protection, 1997). Average crown radius of dominant trees was measured on each of the selected dominant trees. An extendable measuring pole was moved to the edge the crown until the pole was judged to be at the edge of the crown and parallel with the bole, based upon a viewer at least 10 m away. Distance to the bole was measured with a tape measure. Four radii of the crown, 90° apart, were identified starting from the longest radius. The 2 radii that were neither shortest nor longest were measured. The age of the largest tree in each stand was measured and site index calculated using the equations developed for lodgepole pine by Huang et al. (1994).

The dispersion of lodgepole pine stems in each plot was assessed by analysis of stem frequencies in nineteen 10 m^2 subplots. These subplots were positioned systematically in concentric rings in each plot. The standardized Morisita index of dispersion (I_d) (Krebs, 1999) was calculated:

$$I_d = n \frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \qquad \text{(EQ2.0)}$$

Where I_d is Morisita's index of dispersion, n is the number of subplots, and x is the number of trees counted in each subplot. The Standardized Morisita Index (I_p) was then calculated using I_d together with two significance points for the Morisita, as calculated from the following formulas:

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$$\text{Uniform index} = M_u = \frac{\chi^2_{.975} - n + \sum x_i}{\left(\sum x_i - 1\right)} \qquad \text{(EQ2.1)}$$

$$\text{Clumped index} = M_c = \frac{\chi^2_{.025} - n + \sum x_i}{\left(\sum x_i - 1\right)} \qquad \text{(EQ2.2)}$$

Where $\chi^2_{.975}$ = Value of chi-square from table with n-1 degrees of freedom that has

97.5% area to the right

x_i = number of stems in quadrat

n = number of quadrats

$\chi^2_{.025}$ = Value of chi-square from table with n-1 degrees of freedom that

has 2.5% area to the right

When $I_d \geq M_c > 1.0$:

$$I_p = 0.5 + 0.5\left(\frac{I_d - M_c}{n - M_c}\right) \qquad \text{(EQ2.3)}$$

When $M_c \geq I_d \geq 1.0$:

$$I_p = -0.5\left(\frac{I_d - 1}{M_c - 1}\right) \qquad \text{(EQ2.4)}$$

When $1.0 \geq I_d \geq M_u$:

$$I_p = -0.5\left(\frac{I_d - 1}{M_u - 1}\right) \qquad \text{(EQ2.5)}$$

When $1.0 \geq M_u \geq I_d$:

$$I_p = -0.5 + 0.5\left(\frac{I_d - M_u}{M_u}\right) \qquad \text{(EQ2.6)}$$

Stands having standardized Morisita values (I_p)<0 were considered uniform, near 0 as random and >0 as clumped.

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Hemispherical Photography

Four hemispherical photographs were taken in each plot using a Nikon Coolpix 995 digital camera (Table 3-2), with a Nikon EC-F8 fisheye converter lens. Photographs were taken in late summer/early fall when leaf area had most likely reached its seasonal maximum. Photographs were black and white and were taken when light conditions were most even (dawn/dusk and overcast days) at four photo-points in each plot: one at plot centre, another at 0° and then at 120° and 240° from centre, at a distance from the centre where the 9° regions of the photographs would not overlap but would be inside the original 27° plot boundary. A simple ratio of tan9°/tan27° yielded the photopoint distance of 0.62*plot radius that would meet these requirements. All pictures were taken using a tripod set to the same height (1.15 m off the ground), leveled using a bubble level on the top of the camera. All non-target vegetation (i.e. shrubs, snags) was removed from the field of view before the photograph was taken. It is well documented that hemispherical photography tends to underestimate foliage closest to zenith (van Gardingen et al., 1999; Chen et al., 1997; Frazer et al., 2000), and to compensate for this four pictures were taken at each photo-point: a photograph with its exposure value (EV) determined by the camera's light meter, and then at +0.3, +0.7 and +1 EV over the original value. My intention was then to evaluate each set of photographs and choose the picture most representative of the canopy for analysis. It was apparent even on the small digital camera monitor, however, that the pictures increasingly lost their accuracy with increased EV values, such that only photographs with 0 EV were selected for analysis. Hale and Edwards (2002) found a similar trend and generally used photographs taken at 0 EV for their analysis.

Photograph analysis was performed using Hemiview Version 2.1 SR1 software, which separated each photograph into 40 units of measurement (based on 5 concentric rings and 8 radii). Because, the targets of my analysis were the tree crowns closest to zenith in the photograph, I restricted my Hemiview analysis to the two centermost rings within the 5 concentric rings of analysis, which corresponded to the region 27° from zenith.

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Leaf Area Index

Using Hemiview, the effective leaf area index (LAIe) from first 2 rings (representing 27° from zenith) were averaged to estimate LAIe per photograph. The stand average LAI was calculated by averaging the LAIe from each of the 4 photographs per plot. One observer chose all threshold values for the analysis of the photographs and practiced before and throughout the analysis of the photographs to ensure consistency.

LAI was also estimated using the equation provided by Long and Smith (1992):

$$LAI = -42.6 * \left(-0.69 * Age^{-0.69}\right) * e^{\left(-\left(\frac{\left({}^{Age}\!/\!_{145}\right)^{-0.69}}{0.032}\right)\right)} * SDI^{0.46} \quad \text{(EQ3.0)}$$

Where SDI is the stand density index, calculated as:

$$SDI = DEN * \left(\frac{QMD}{25.4}\right)^{1.605} \quad \text{(EQ3.1)}$$

with DEN being density in stems per hectare and QMD being quadratic mean diameter.

Canopy Closure

The canopy closure based on analysis of hemispherical photography (CC_H) was evaluated on each of the 4 photographs per plot. Individual tree crowns within the 27° region were identified and a 6-sided shape was drawn and filled over them using Sigmascan Version 5.0. This was done to mask the crown so the image would contain only inter- tree canopy (not intra-tree canopy) gaps. Generally, the furthest tips of the longest branches down each side of a crown decided the corners of the 6-sided shape. The boles were also colored so they would be included in the CC_H analysis. Once the photographs were masked, the inter-canopy gap fraction of each photograph was measured with Hemiview. The gap fractions from centre 2 rings (representing 27° from zenith) were averaged, and the averages from the 4 photographs from each plot were averaged to provide average stand canopy closure.

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Canopy closure was also measured using the line intercept method via a vertical periscope (CC_L) (Rudnicki et al., 2001). CC_L was evaluated along three north-south transects through the plot; one through the centre of the plot and one on either side of transect 1 at a distance from centre equal to 1/3 the diameter of the plot. On each transect the edge of crown and positions between crowns were carefully measured. Canopy closure was defined as the length of transect under crowns/total length of transect.

Both simple and forward stepping multiple regression analyses were completed on the data. Comparisons of slope and intercept of CC_H and CC_L were completed with ANCOVA using linear contrasts.

Results

Leaf Area Index

Effective leaf area index (LAIe) increased linearly with canopy closure (CC_L) ($R^2 = 0.211$, $p = <0.001$, Fig. 3-1). In contrast, LAIe changed relatively little with increasing stand height (HT) until stands reached approximately 8-10 m, at which point LAIe began to decline ($R^2 = 0.087$, $p = 0.005$, Fig. 3-2). This relationship was weak, however, and there was great variability in LAIe at every stand HT.

Effective leaf area index increased linearly with RD, ($R^2 = 0.010$, $p = 0.001$, Fig. 3-3) and increased slightly with site index (SI) ($R^2 = 0.036$, $p = 0.046$, Fig. 3-4), however there was strong variability in relationships among LAIe with RD and SI.

My estimates of LAIe showed a decline with stand age (Fig. 3-5a), though the relationship of LAIe with age differed (particularly for the two height extremes) from that predicted by the equations of Long and Smith (1992) (EQ3.0, Fig. 3-5b) on the same sites. There was also strong variability in my estimates of LAIe at any given height such that the relationship between my estimates of LAIe and age was not strong ($R^2 = 0.088$, $p = 0.003$, Fig. 3-5a).

Canopy Closure

The relationship between canopy closure estimated using the hemispherical photographs (CC_H) and the vertical periscope (CC_L) had a positive correlation ($R^2 = 0.665$, $p = <0.001$, Fig. 3-6) but at the lower values of canopy closure (i.e. those in taller

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stands) the CC_H gave higher estimates than CC_L. The bias appeared to be dependent on tree height (HT) because the slope of the relationship between CC_H and HT was different from CC_L and HT ($p = <0.001$, Fig. 3-7) as indicated by linear contrasts. This is further illustrated by examining photographs taken in a tall stand (19.9 m, Fig. 3-8a-c), where the CC_L appears to provide a more reasonable estimate of canopy closure based on ocular assessment of the photographs compared to a shorter stand (5.6 m, Fig. 3-8d-f). Ocular assessment also suggests that the difference between CC_L and CC_H may relate to the way that photographs were masked for the CC_H estimate.

Discussion

Leaf Area Index

My estimates of effective leaf area index (LAIe) were highly variable from stand to stand, and only weak trends in the data were apparent. The relationship between canopy closure (CC_L) and LAIe has not been well established, and although the relationship is weak ($R^2 = 0.211$, Fig. 3-1), my results suggest that effective leaf area increases with canopy closure. This lends support to crown shyness as a mechanism limiting stand leaf area over time as suggested by Ryan et al., (1997). This notion is further supported by the curvilinear decline in LAIe with HT following 8-10 m, and also supports the trend of declining LAI with age as predicted by Long and Smith (1992). This relationship is also weak however ($R^2 = 0.08$, Fig. 3-2), and the high variability in my LAIe-age relationship (Fig. 5a) (in contrast to the variation predicted by Long and Smith (1992) (Fig. 3-5b)) suggests that my estimates may not be accurate representations of LAIe. This conclusion is also supported by the weak relationship between LAIe and RD ($R^2 = 0.097$, Fig. 3-3); Long and Smith (1992) suggest that LAIe is dependent on RD reflected by their inclusion of stand density index (a variation of relative density) in their LAIe model (see EQ4.0).

The accuracy of LAIe estimates is dependent on the amount of foliage captured in the photographs; unfortunately non-foliar elements (i.e. branches and boles) cannot be removed from the images during their analysis. Despite restriction of the region of analysis to 27°, increasing woody biomass with stand height (HT) and relative (RD) likely led to overestimates of LAIe in tall and dense stands. Canopy capture might also

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have been affected by lighting effects; hemispherical photography can underestimate foliage because the distinction between foliage tips and sky becomes blurred due to scattering of blue light (Chen et al., 1997). Another important factor in foliage capture is tree arrangement in the photograph; because the horizontal overlap of trees appears to increase with HT and RD, there is the possibility that LAIe is overestimated in tall and high RD stands. I suspect these sources of error resulted in my LAIe estimates reflecting all non-sky in the photograph (i.e. the CC_L). This is further evidenced by the strong resemblance in the shape of the relationships between LAIe and both RD and SI compared to the relationships between CC_L and both RD and SI (see Chapter 2). This suggests that accurate comparisons of LAIe between stands so variable in woody biomass and crown overlap (i.e. variable in HT and RD) might not be possible with hemispherical photography. The net result appears to be that error in the LAIe estimates likely masked the probable effects of leaf area losses from branches lost to crown shyness.

Canopy Closure

The difference between canopy closure estimated using the hemispherical photographs (CC_H) versus the direct measurement using the vertical periscope (CC_L) was surprising. Both methods measure canopy closure from below in order to assess the fraction of sky over ground and were expected to produce similar estimates of CC. However, my results suggest a strong bias in the CC_H estimate. The difference in slope in the regressions between CC_H and CC_L with HT indicates that the bias increases with HT. There is inherent error involved in the use of hemispherical photography to measure canopy closure, as proper lighting conditions are required to properly capture foliage; blurring of foliage edges results in overestimation of gaps (Chen et al., 1997). Also, woody biomass increases with HT and RD but cannot be excluded from CC_H and this may have also contributed to the biased CC_H in taller stands. I may have also inadvertently added bias to my CC_H analysis because it appears my assignment of 6-sided shapes to the crowns may have differed with HT (see Fig. 3-8 a-f). Because the hemispherical lens distorts the photograph it can be difficult to distinguish branches between crowns, especially when foliage is captured further from the camera lens (i.e. in taller stands); it is possible I outlined overly large crowns during the masking process,

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especially on the taller trees. Gaps in taller stands were smaller and more numerous, such that constant overestimation of crown outline would contribute more to CC_H overestimate with increasing HT.

Error in the direct measurement of canopy closure with the crown scope was likely less important and limited to sighting, leveling and positioning. Before entering the field the crown scope was first tested on fixed vertical points inside tall buildings and was considered to give accurate sighting within 10 cm over 25 m. During field measurements, I moved down the transect in one direction, viewing each crown edge in the same direction using the same technique. This should have balanced out any systematic bias in estimation of crown edge because of the use of the instrument. The scope is also composed of levels and high-quality mirrors with a very large aperture to reduce sighting errors. Because the locations of transects were dependent on distance from plot centre, there was no systematic bias in terms of positioning the scope in either crown-rich or crown-poor areas.

The bias in the CC_H estimates raises important questions on the suitability of hemispherical photography for analysis of canopy closure using manual masking to remove intra-crown gaps. Although some trends in the data were still apparent, restricting the region of analysis did not appear to remove all the effects of increasing woody biomass with increasing stand height and relative density from estimates of LAIe. It is also possible my estimation of CC_H and LAIe had errors related to the small sample size of four photographs per plot; more photographs might have better captured within-stand variations. However there is no reason to believe that low sample size would induce the systematic bias present in the CC_H measurement.

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Table 3-1: Mean, standard deviation, minimum and maximum of measured stand characteristics and estimated leaf area index (LAI) using the equation of Smith and Long (1992) (EQ3.0 – 3.1) in the lodgepole pine plots (n = 90).

Site Characteristic	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**
Average stand canopy closure measured using the line intercept method (%)	62.1	16.48	26.6	96.2
Average stand canopy closure measured with hemispherical photography (%)	81.4	6.48	67.3	97.6
Average stand leaf area index (m^2/m^2)	2.53	0.498	1.48	3.67
Average stand leaf area index using the equations of Smith and Long (1992) (m^2/m^2)	3.05	0.572	1.96	4.64
Average stand height (m)	12.5	4.02	5.8	20.4
Average slenderness	108.2	14.40	71.5	158.1
Relative density	12.7	2.88	7.9	21.6
Average stand crown length (m)	3.3	0.79	1.6	4.7
Average crown radius of dominants (m)	1.0	0.30	0.3	1.9
Stand density (sph)	4322	4424	1046	24028
Stand age	54	29.70	16	113
Site index	15.4	2.69	9.5	21.5
Average distance between boles (m)	1.88	0.62	0.65	3.5

Table 3-2: Digital camera settings used in the hemispherical photograph analysis.

Type of Setting	Setting
Lens	Fisheye 1
Light metering	Centre-weighted
Shutter speed	Auto
Aperture	Auto
Shooting sensitivity	Auto
Image Quality	Fine (1/4 compression)
Size	Full (2048 * 1536)
Focus	Infinity mode
Image adjustment	Normal
Image sharpening	Off
Bracketing	Off
Noise reduction	Off
Best shot selector	Off

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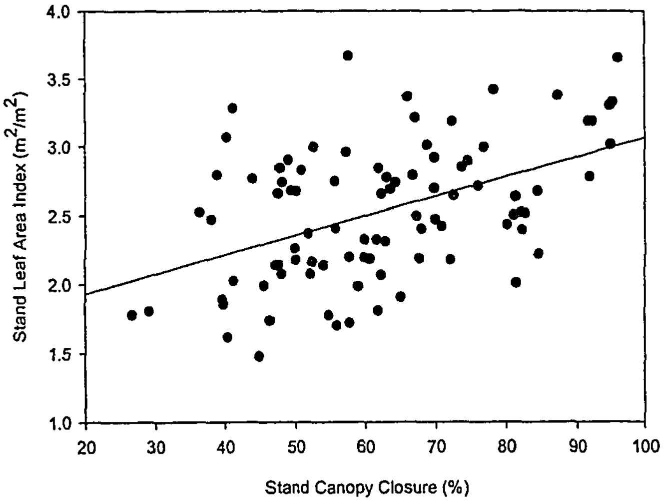

Figure 3-1: Stand effective leaf area index (LAIe) versus stand canopy closure (CC_L) as measured via crown scope. Adj. $R^2 = 0.211$, $p = <0.001$, $y = 1.65 + 0.014x$, $n = 90$.

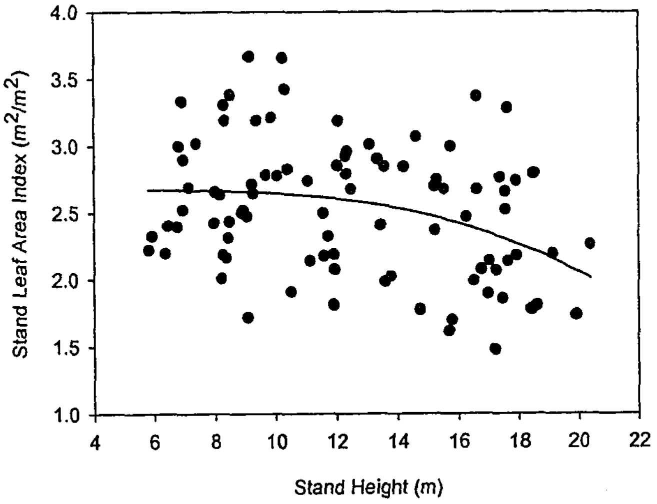

Figure 3-2: Stand effective leaf area index (LAIe) versus average stand height. Adj. $R^2 = 0.087$, $p = 0.005$, $y = 2.67x^{-4.77}/25.74^{-4.77} + x^{-4.77}$, n=90.

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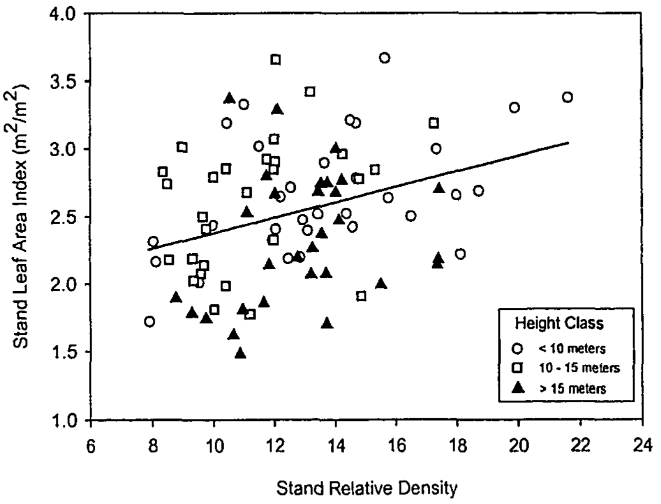

Figure 3-3: Stand effective leaf area index (LAIe) versus stand relative density. Adj. R^2 = 0.010, p = 0.001, y = 1.80 + 0.057x, n=90, separated into three height classes, there were no significant differences in slope or intercept among height classes as tested using linear contrasts.

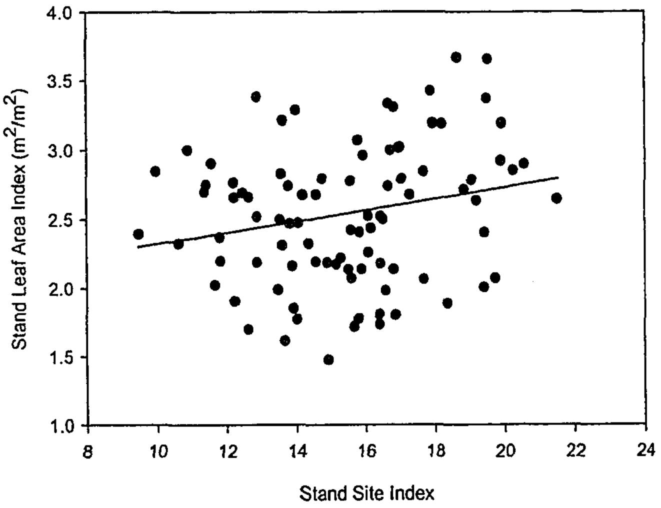

Figure 3-4: Stand effective leaf area index versus stand site index. Adj. R^2 = 0.036, p = 0.046, y = 1.92 + 0.039x, n=90.

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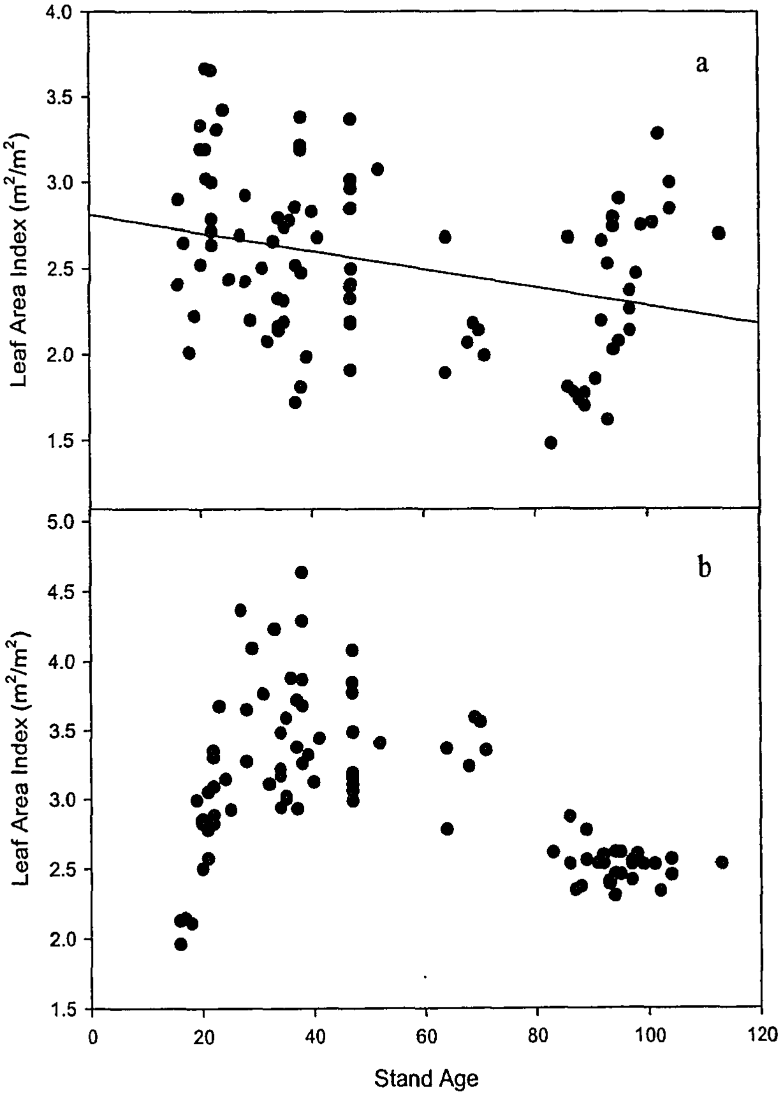

Figure 3-5a: Stand effective leaf area index versus stand age as estimated using hemispherical photographs ($R^2 = 0.088$, $p = 0.003$, $y = 2.81 - 0.005x$, $n=90$) and b: estimated for my stands using the equations of Long and Smith (1992) (EQ3.0 – 3.1).

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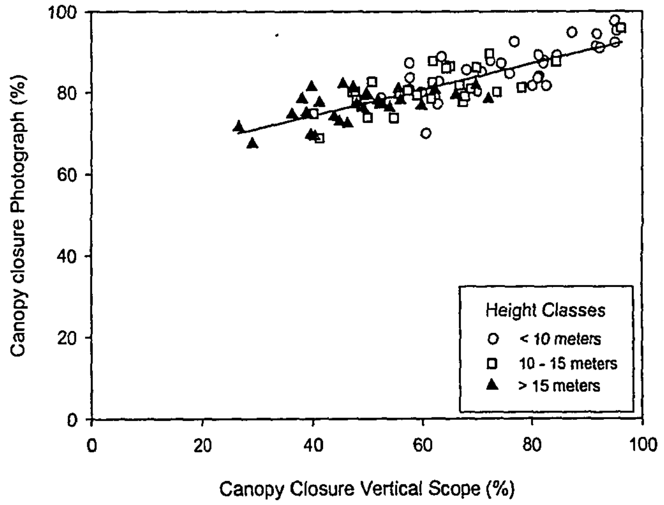

Figure 3-6: Canopy closure measured using hemispherical photographs versus canopy closure measured using the line intercept method, separated into three height classes. For the overall relationship, the adjusted $R^2 = 0.665$, $p = <0.001$, $y = 61.4 + 0.322x$, $n=90$.

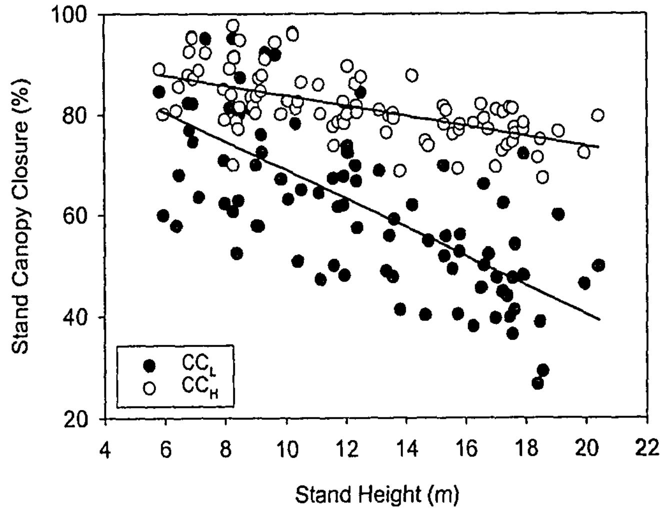

Figure 3-7: Stand canopy closure as measured by hemispherical photography (CC_H) and the line intercept method (CC_L) versus stand height. For CC_L Adj. $R^2 = 0.480$, $p = <0.001$, $y = 97.5 - 2.86x$, $n=90$ and for CC_H Adj. $R^2 = 0.381$, $p = <0.001$, $y = 93.7 - 1.00x$, $n=90$. The slopes of the two regressions are significantly different ($p = <0.001$) as indicated by linear contrasts.

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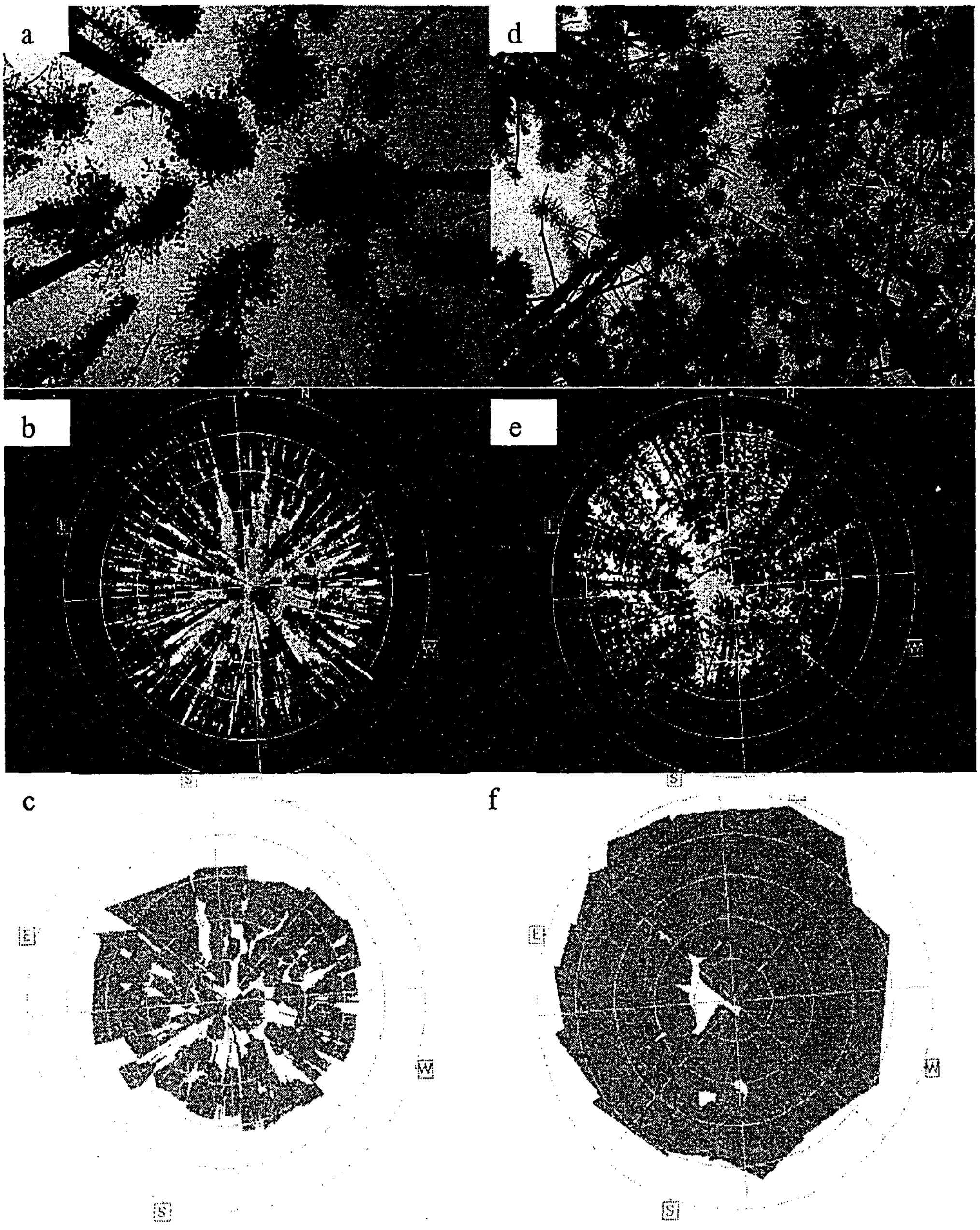

Figure 3-8: Canopy photographs from two stands, a tall stand (19.9 m): a) photographed with standard 55 mm lens, b) photographed with hemispherical lens and c) masked image of b, and a short stand (5.8 m): d) photographed with a standard 55 mm lens, e) photographed with hemispherical lens and f) masked image of e. Photographs taken with the standard lens were taken at random locations within the stands. On the hemispherical photographs and masked images, only the 2 innermost rings were used for leaf area index and canopy closure analysis.

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Chapter 4: Synthesis

Crown Shyness

The first objective of this study was to examine the roles of stand characteristics and site factors on the development of crown shyness, with the intention that my results be incorporated into forest growth models to accurately account for growth losses from crown shyness. In order to do this, I examined canopy closure in stands of varying height, density, slenderness, site quality, and having various site factors. I also collected samples of the green litter that was likely created as the result of abrasion in these stands, and examined the relationships between the quantity, size and leaf area of the litter in the different stands.

The results of my study support the ideas of Putz et al. (1984) that abrasion in forest stands may influence crown shyness. Stand height (HT) appeared to be the most important factor regulating canopy closure (CC), with CC declining with HT. The increased number, length and leaf area of green litter pieces found in tall stands suggests that abrasion increases with HT. Canopy closure is not a function of abrasion alone, however, because CC increased with RD, despite the fact that abrasion was likely higher in these stands too, as indicated by the higher number of litter pieces. Average crown radius of dominant trees (CR) also peaked following stands attaining heights of 8-10 m, despite increasing space between trees with increasing stand age. This likely also contributed to crown shyness. Crown shyness was partially countered by the increased crown size and CC in stands of higher site index (SI).

It was surprising that neither of slope nor aspect significantly influenced crown shyness or abrasion. I suspected that trees located on steeper slopes would have shallower root systems and this might allow greater tree sway during wind events. Tree slenderness coefficients (SC) are known to increase with increased exposure to wind (Larson, 1963; Long and Smith, 1981;Valinger, 1992; Mitchell, 2000). It is possible such an acclimation resulted in reduced tree sway, as well the increased SC might have allowed trees to maintain larger crowns (Jack and Long, 1991), thereby masking the effects of abrasion in stands located on steeper slopes. The same logic may hold for stand aspect, as I expected that stands facing the dominant wind direction would experience greater sway than those with aspects running perpendicular to the dominant

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wind directions. It is possible that stands facing the dominant wind direction, too, became acclimatized to stronger wind conditions such that the effects of crown shyness were not apparent.

It is noteworthy that young stands were more likely to be of clumped dispersion than older stands according to the standardized Morisita index, with older stands tending to be uniformly arranged. This finding is likely related to the accumulated losses of trees to self-thinning.

Crown Shape

I expected average crown length (CL) would increase with increasing available light that accompanies stands of higher crown shyness (lower canopy closure), however canopy closure did not appear to influence CL. Instead HT appeared to more important in regulating CL, with CL becoming static at stand heights of 8-10 m despite increased spacing as stands grew taller. This could suggest that changes to available space/light do not regulate crown shape, however CL also declined with increased relative density (RD). This finding may not reflect responses to available light however, as CL also declined with increasing slenderness coefficient (SC), supporting the idea that crown size may be partially regulated by available sapwood area. Finally, the increased nutrient availability afforded by stands of higher site index (SI) appeared to allow trees to maintain longer crowns. This could suggest that nutrient amendments might encourage trees to maintain longer crowns.

Crown radius (CR) and CC were also not correlated. This is likely related to the fact that although CC declined with HT, CR stayed relatively constant after reaching a plateau at approximately 8-10 m, despite increased spacing between boles. The relationship between CR and RD was relatively weak ($R^2 = 0.060$), as was the relationship between CR and SC ($R^2 = 0.168$). These relationships suggest that CR may be an inherent feature of trees rather than being dependent on outside stimuli; this is further supported by the research indicating that crown dimensions, including branch length are a heritable trait (St. Clair, 1994; McCrady and Jokela, 1996; Roberts et al., 2003).

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Effective Leaf Area Index (LAIe)

In order to link crown shyness more directly to leaf area, I also estimated effective leaf area index (LAIe) using hemispherical photography. My measures of effective leaf area index (LAIe) declining with stand age support the findings of Long and Smith (1992). My results also suggest that LAIe increases with canopy closure (CC_L). The noisiness of the data and weak relationships between LAIe and the site characteristics (range $R^2 = 0.036 - 0.211$) makes it hard to conclude whether the decline in LAIe with age is related to abrasion or instead is simply representative of the amount of non-sky captured in the photographs (i.e. canopy closure). With the litter results suggesting that abrasion likely increases with both stand height (HT) and relative density (RD), I expected LAIe estimates to show negative relationships with HT and RD. Instead LAIe declined curvilinearly with HT, and increased slightly with both RD and site index (SI). All relationships were weak, however, and suggest that hemispherical photography did not capture the effects of abrasion on LAIe loss resulting from crown shyness.

Reasons for the weak relationships between LAIe and the stand variables I measured might be related to abrasion losses being replaced by increasing leaf area density within crowns (Mainwairing and Maguire, 2004). However, the shapes of the relationships between my LAIe estimates and the stand variables I examined suggest that my estimates of LAIe simply reflect my canopy closure (CC) estimates. This is likely because the increase in woody tissue captured in the photographs likely increased with both HT and RD, but could not be removed from the LAIe analysis. Similarly, the amount of crown overlap would have increased with RD and in shorter stands, such that woody biomass likely led to LAIe overestimates and leaf area missed from analysis likely led to underestimates, ultimately resulting in unreliable LAIe estimates. Limiting the region of analysis to the same zenith angle for all tree heights likely also influenced my findings. By restricting the region of analysis to 27°, shorter stands may have had some leaf area missed from evaluation, whereas taller stands had comparably more bole included in the analysis than did shorter stands. My results support other research (i.e. Chason et al., 1991; Martens et al., 1993; Deblonde et al., 1994) that hemispherical photography should not used to compare stands of differing heights and densities.

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Hemispherical Photography Versus the Line Intercept method

I compared the use of hemispherical photography to estimate canopy closure (CC_H) with canopy closure estimated using the line intercept method and a vertical crown scope (CC_L). Canopy closure measured with hemispherical photography was biased compared to CC_L. This bias increased with stand height (HT) and could have been the result of increasing woody biomass captured in the photographs as stand height increased. Similar to my LAIe estimates, restricting my analysis to the region of the photograph 27° from zenith may have also influenced the results, with some crown area lost from measurement in shorter stands and more bole captured in taller stands compared to shorter ones. I believe the bulk of the bias in my CC_H estimates however, lies within the crown outlines used to remove intracrown gaps. It appears I may have made the crown outlines larger than they should have been, and because the gaps between trees were smaller and more numerous in taller stands, the larger crown outlines affected canopy closure estimates more in tall stands than shorter ones. Because the bulk of the error in my canopy closure estimates from hemispherical photography came from my methodology, I cannot discount the use of hemispherical photography for the measurement of canopy closure. However the line intercept method was more time efficient (it did not require early mornings and late nights for measurement, nor countless hours at a computer for analysis) and I am confident that it gave very accurate estimates of canopy closure.

Future Directions

The ultimate goal of this study was to quantify crown shyness in terms of foliage area so these losses can be incorporated into growth and yield models. Currently these models do not account for foliage losses to abrasion, and thus might be overestimating stand productivity as a result. I believe more work is required before these results can be incorporated into these models. First, a quantified relationship between abrasion and productivity must be established. My results suggest that leaf area losses to abrasion may be relatively small, but I do not have estimates of total crown leaf areas, so cannot draw any conclusions. Measurement of abrasion induced litterfall should also remove the possibility non-abrasion events contributing to the green litter (i.e. animal damage). The

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ideal collection will also represent wind events for more than one year; my collection also only represents wind events from the year of 2004, and only branches; there is no measurement of individual needles removed as the result of abrasion. Average values for selected measurements are included in Appendix 4-A to aid further study.

I was very surprised that slenderness coefficient (SC – height/diameter at 1.3 m) did not relate to green litterfall or canopy closure. This was especially puzzling because crown width and length appeared to be so heavily influenced by SC. Rudnicki et al. (2003) linked tree slenderness to increased sway, suggesting these stands should also suffer more crown collisions, but the role of SC on crown shyness at the stand level remains unknown. A future direction might include exploring the role of slenderness coefficient at the stand level; my results suggest that slenderness coefficients averaged across trees of varying crown classes did not accurately indicate the slenderness of a stand.

Previous studies have examined the role of forest gaps in forest ecosystems (i.e. Van Pelt and Franklin, 2000); since crown shyness gaps tend to be small compared to tree fall gaps, future research might be undertaken to assess the effect of crown shyness gaps on understory light availability and biodiversity. The creation of space for light to breach the canopy coupled with the addition of acidic litterfall to the forest floor might each contribute to understory composition.

Finally, my research calls into question the validity of Farnden's (1996) Stand Density Management Diagrams, especially the locations on the diagram of the crown closure line and crown cover isolines for lodgepole pine. In the 95 stands I sampled, and a hundred more that I assessed for potential plot locations, I could not find even one stand that was below his crown closure line. In fact, one stand I decided not to include in my study (15.5 m tall with 500 stems per hectare) had on average 5 meters between tree boles, and this stand was above the crown closure line on Farden's diagram. Similarly, his crown cover isolines suggest that stands greater than 18 m should have at least 90% cover at approximately 800 stems per hectare. In the stands I sampled that were 18 m tall and greater, every stand had stem densities over 1000 stems per hectare, and yet the largest CC measured was near 60%, with the average CC much lower. My finding that crown radius does not increase over time, despite increased spacing, suggests that a CC

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of 90% in older stands would be impossible. A future direction of my work may be to re-evaluate Farden's crown closure and canopy closure isolines for natural stand canopies and to redraw these diagrams to better represent actual stand conditions.

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Appendix 2-A: Correlation matrix of factors

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                                        gap fraction          14:29 Monday, April 25, 2005  61

                                      The CORR Procedure

  20  Variables:      CCH    CCL      HT        COHT      TOPHT      SC        RD        CL       CR
                      DEN     AGE        SI        LAIe     GFH       IP        SLOPE     ASPECT    POS
                      DBH     SPACE


                                      Simple Statistics

 Variable               N          Mean       Std Dev           Sum       Minimum       Maximum

 CCH                   90      81.35745       6.47711          7322      67.29995      97.64102
 CCL                   90      62.13481      16.47546          5592      26.64000      96.20000
 HT                    90      12.38964       4.02224          1115       5.81924      20.39981
 COHT                  90      12.67946       4.19116          1141       4.95525      20.96829
 TOPHT                 90      14.89293       4.45684          1340       6.87898      22.93717
 SC                    90     108.85878      14.40036          9797      71.52299     158.08475
 RD                    90      12.68743       2.87704          1142       7.90792      21.63915
 CL                    90       3.28328       0.79317     295.49556       1.55366       4.74209
 CR                    90       1.01183       0.30049      91.06500       0.33250       1.87500
 DEN                   90          4426          4424        398320          1046         24028
 AGE                   90      53.61111      29.69534          4825      16.00000     113.00000
 SI                    90      15.46717       2.69241          1392       9.46940      21.51650
 LAIe                  90       2.52815       0.49770     227.53352       1.47618       3.66595
 GFH                   90       0.42679       0.06448      38.41154       0.26824       0.55859
 IP                    90      -0.25831       0.28678     -23.24764      -0.56408       0.50136
 SLOPE                 90      13.45556      10.86295          1211       1.00000      52.00000
 ASPECT                90       3.75556       0.98655     338.00000       1.00000       5.00000
 POS                   90       2.88889       0.90497     260.00000       1.00000       4.00000
 DBH                   90      13.22666       4.20744          1190       5.93284      21.84468
 SPACE                 90       1.88444       0.61671     169.59942       0.64513       3.53048
```

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Pearson Correlation Coefficients, N = 90
Prob > |r| under H0: Rho=0

	CC_H	CC_L	HT	COHT	TOPHT	SC	RD
CC_H	1.00000	0.81779 <.0001	-0.62306 <.0001	-0.61020 <.0001	-0.62624 <.0001	0.09135 0.3918	0.42619 <.0001
CC_L	0.81779 <.0001	1.00000	-0.69806 <.0001	-0.68314 <.0001	-0.67468 <.0001	0.04699 0.6601	0.29843 0.0043
HT	-0.62306 <.0001	-0.69806 <.0001	1.00000	0.99506 <.0001	0.98115 <.0001	-0.13453 0.2062	-0.14616 0.1693
COHT	-0.61020 <.0001	-0.68314 <.0001	0.99506 <.0001	1.00000	0.98103 <.0001	-0.11534 0.2790	-0.12282 0.2488
TOPHT	-0.62624 <.0001	-0.67468 <.0001	0.98115 <.0001	0.98103 <.0001	1.00000	-0.06158 0.5642	-0.08767 0.4113
SC	0.09135 0.3918	0.04699 0.6601	-0.13453 0.2062	-0.11534 0.2790	-0.06158 0.5642	1.00000	0.61199 <.0001
RD	0.42619 <.0001	0.29843 0.0043	-0.14616 0.1693	-0.12282 0.2488	-0.08767 0.4113	0.61199 <.0001	1.00000
CL	-0.17332 0.1023	-0.19469 0.0659	0.44538 <.0001	0.43791 <.0001	0.38563 0.0002	-0.62055 <.0001	-0.57580 <.0001
CR	-0.09274 0.3847	-0.12134 0.2546	0.48402 <.0001	0.48745 <.0001	0.44736 <.0001	-0.42113 <.0001	-0.26497 0.0116
DEN	0.44779 <.0001	0.40097 <.0001	-0.65140 <.0001	-0.67010 <.0001	-0.60551 <.0001	0.55765 <.0001	0.53623 <.0001
AGE	-0.64375 <.0001	-0.71501 <.0001	0.85903 <.0001	0.84992 <.0001	0.87435 <.0001	0.02487 0.8160	-0.02637 0.8051
SI	0.33532 0.0012	0.35576 0.0006	-0.14119 0.1844	-0.12584 0.2373	-0.16733 0.1149	-0.37073 0.0003	-0.14939 0.1599
LAI_e	0.55611 <.0001	0.46946 <.0001	-0.29404 0.0049	-0.27102 0.0098	-0.27174 0.0096	0.10365 0.3309	0.33140 0.0014
GF_H	-0.73784 <.0001	-0.62173 <.0001	0.30442 0.0035	0.28655 0.0062	0.30149 0.0039	-0.02884 0.7873	-0.48609 <.0001
I_P	0.34640 0.0008	0.37757 0.0002	-0.31387 0.0026	-0.29947 0.0041	-0.30344 0.0036	0.29999 0.0041	0.36244 0.0004
SLOPE	-0.02357 0.8255	0.01060 0.9210	-0.13386 0.2084	-0.12648 0.2349	-0.12916 0.2250	-0.05424 0.6117	-0.14290 0.1791
ASPECT	0.12112 0.2555	0.00224 0.9833	0.09038 0.3969	0.08319 0.4357	0.06260 0.5578	-0.13229 0.2139	-0.11626 0.2752
POS	-0.08870 0.4058	-0.04448 0.6772	0.14277 0.1795	0.14535 0.1717	0.14209 0.1816	-0.09487 0.3738	-0.16071 0.1302
DBH	-0.56138 <.0001	-0.62631 <.0001	0.93500 <.0001	0.92488 <.0001	0.89769 <.0001	-0.41640 <.0001	-0.28692 0.0061
SPACE	-0.57950 <.0001	-0.58670 <.0001	0.80316 <.0001	0.80240 <.0001	0.75107 <.0001	-0.50373 <.0001	-0.54118 <.0001

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                              The CORR Procedure

                   Pearson Correlation Coefficients, N = 90
                          Prob > |r| under H0: Rho=0

              CL         CR        DEN        AGE         SI       LAI_e       GF_H

CC_H     -0.17332   -0.09274    0.44779   -0.64375    0.33532    0.55611   -0.73784
           0.1023     0.3847     <.0001     <.0001     0.0012     <.0001     <.0001

CC_L     -0.19469   -0.12134    0.40097   -0.71501    0.35576    0.46946   -0.62173
           0.0659     0.2546     <.0001     <.0001     0.0006     <.0001     <.0001

HT        0.44538    0.48402   -0.65140    0.85903   -0.14119   -0.29404    0.30442
           <.0001     <.0001     <.0001     <.0001     0.1844     0.0049     0.0035

COHT      0.43791    0.48745   -0.67010    0.84992   -0.12584   -0.27102    0.28655
           <.0001     <.0001     <.0001     <.0001     0.2373     0.0098     0.0062

TOPHT     0.38563    0.44736   -0.60551    0.87435   -0.16733   -0.27174    0.30149
           0.0002     <.0001     <.0001     <.0001     0.1149     0.0096     0.0039

SC       -0.62055   -0.42113    0.55765    0.02487   -0.37073    0.10365   -0.02884
           <.0001     <.0001     <.0001     0.8160     0.0003     0.3309     0.7873

RD       -0.57580   -0.26497    0.53623   -0.02637   -0.14939    0.33140   -0.48609
           <.0001     0.0116     <.0001     0.8051     0.1599     0.0014     <.0001

CL        1.00000    0.42451   -0.68179    0.18337    0.26990   -0.11224    0.10645
                      <.0001     <.0001     0.0836     0.0101     0.2922     0.3180

CR        0.42451    1.00000   -0.58955    0.23378    0.42083    0.00950   -0.11901
           <.0001                <.0001     0.0266     <.0001     0.9292     0.2639

DEN      -0.68179   -0.58955    1.00000   -0.45155   -0.20345    0.16543   -0.18033
           <.0001     <.0001                <.0001     0.0544     0.1192     0.0890

AGE       0.18337    0.23378   -0.45155    1.00000   -0.53147   -0.31384    0.39947
           0.0836     0.0266     <.0001                <.0001     0.0026     <.0001

SI        0.26990    0.42083   -0.20345   -0.53147    1.00000    0.21121   -0.35185
           0.0101     <.0001     0.0544     <.0001                0.0457     0.0007

LAI_e    -0.11224    0.00950    0.16543   -0.31384    0.21121    1.00000   -0.59395
           0.2922     0.9292     0.1192     0.0026     0.0457                <.0001

GF_H      0.10645   -0.11901   -0.18033    0.39947   -0.35185   -0.59395    1.00000
           0.3180     0.2639     0.0890     <.0001     0.0007     <.0001

I_P      -0.34541   -0.00631    0.37440   -0.28424    0.13357    0.25870   -0.21360
           0.0009     0.9529     0.0003     0.0066     0.2095     0.0138     0.0432

SLOPE     0.09505   -0.26815   -0.00366    0.02981   -0.23534    0.07063    0.11065
           0.3729     0.0106     0.9727     0.7803     0.0256     0.5083     0.2992

ASPECT    0.20968    0.06824   -0.11588    0.00477    0.11333    0.08287   -0.07425
           0.0473     0.5228     0.2767     0.9644     0.2875     0.4374     0.4868

POS       0.15582    0.11666   -0.16055    0.13509    0.03814    0.09508   -0.00925
           0.1425     0.2735     0.1306     0.2043     0.7211     0.3727     0.9311

DBH       0.54176    0.60316   -0.73124    0.77362   -0.01171   -0.28123    0.25667
           <.0001     <.0001     <.0001     <.0001     0.9128     0.0072     0.0146

SPACE     0.62807    0.56831   -0.79902    0.58834    0.07664   -0.29803    0.33701
           <.0001     <.0001     <.0001     <.0001     0.4728     0.0043     0.0012
```

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	I_P	SLOPE	ASPECT	POS	DBH	SPACE
CC_H	0.34640 0.0008	-0.02357 0.8255	0.12112 0.2555	-0.08870 0.4058	-0.56138 <.0001	-0.57950 <.0001
CC_L	0.37757 0.0002	0.01060 0.9210	0.00224 0.9833	-0.04448 0.6772	-0.62631 <.0001	-0.58670 <.0001
HT	-0.31387 0.0026	-0.13386 0.2084	0.09038 0.3969	0.14277 0.1795	0.93500 <.0001	0.80316 <.0001
COHT	-0.29947 0.0041	-0.12648 0.2349	0.08319 0.4357	0.14535 0.1717	0.92488 <.0001	0.80240 <.0001
TOPHT	-0.30344 0.0036	-0.12916 0.2250	0.06260 0.5578	0.14209 0.1816	0.89769 <.0001	0.75107 <.0001
SC	0.29999 0.0041	-0.05424 0.6117	-0.13229 0.2139	-0.09487 0.3738	-0.41640 <.0001	-0.50373 <.0001
RD	0.36244 0.0004	-0.14290 0.1791	-0.11626 0.2752	-0.16071 0.1302	-0.28692 0.0061	-0.54118 <.0001
CL	-0.34541 0.0009	0.09505 0.3729	0.20968 0.0473	0.15582 0.1425	0.54176 <.0001	0.62807 <.0001
CR	-0.00631 0.9529	-0.26815 0.0106	0.06824 0.5228	0.11666 0.2735	0.60316 <.0001	0.56831 <.0001
DEN	0.37440 0.0003	-0.00366 0.9727	-0.11588 0.2767	-0.16055 0.1306	-0.73124 <.0001	-0.79902 <.0001
AGE	-0.28424 0.0066	0.02981 0.7803	0.00477 0.9644	0.13509 0.2043	0.77362 <.0001	0.58834 <.0001
SI	0.13357 0.2095	-0.23534 0.0256	0.11333 0.2875	0.03814 0.7211	-0.01171 0.9128	0.07664 0.4728
LAI_e	0.25870 0.0138	0.07063 0.5083	0.08287 0.4374	0.09508 0.3727	-0.28123 0.0072	-0.29803 0.0043
GF_H	-0.21360 0.0432	0.11065 0.2992	-0.07425 0.4868	-0.00925 0.9311	0.25667 0.0146	0.33701 0.0012
I_P	1.00000	-0.16723 0.1152	-0.14270 0.1797	-0.11626 0.2752	-0.33147 0.0014	-0.40306 <.0001
SLOPE	-0.16723 0.1152	1.00000	0.05454 0.6096	0.43381 <.0001	-0.13762 0.1958	-0.04964 0.6422
ASPECT	-0.14270 0.1797	0.05454 0.6096	1.00000	-0.06852 0.5211	0.13930 0.1904	0.18775 0.0764
POS	-0.11626 0.2752	0.43381 <.0001	-0.06852 0.5211	1.00000	0.19190 0.0700	0.19497 0.0655
DBH	-0.33147 0.0014	-0.13762 0.1958	0.13930 0.1904	0.19190 0.0700	1.00000	0.86650 <.0001
SPACE	-0.40306 <.0001	-0.04964 0.6422	0.18775 0.0764	0.19497 0.0655	0.86650 <.0001	1.00000

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Appendix 4-A: Average values for selected measurements for all stands evaluated.

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Plot	Location	11U Easting	Northing	CC_H (%)	CC_L (%)	HT (m)	SC	RD	CL (m)	CR (m)	Density (sph)	Age	SI	LAIe (m^2/m^2)
1	PR43/3-1	486038	5895095	97.64	95.05	8.29	145.14	19.92	1.81	1.23	11881	23	16.84	3.31
2	PR43/3-2	486023	5895084	90.94	92.30	9.35	131.67	14.70	2.53	1.04	6119	20	19.94	3.19
3	PR43/3-3	486054	5895144	81.16	78.21	10.32	122.05	13.22	2.48	1.00	4694	24	17.90	3.42
4	PR43/1.5	487452	5894344	79.30	66.03	16.62	96.37	10.56	4.07	1.60	1246	47	19.51	3.37
5	PR48-1	491139	5891254	74.78	40.16	14.62	111.39	12.02	3.29	0.94	2083	52	15.79	3.07
6	PR48-2	491300	5891278	76.06	49.27	15.54	106.61	13.46	4.20	0.84	2391	64	14.58	2.68
7	MC48-1	493523	5892465	79.16	49.99	16.63	110.26	14.02	3.24	1.20	2241	86	14.19	2.68
8	MC48-2	493552	5892419	77.02	48.01	17.93	103.43	13.55	3.60	1.16	1713	94	13.78	2.74
9	MC48-3	493573	5892546	81.22	47.44	17.56	113.00	12.04	3.85	1.41	1765	92	12.63	2.66
10	Pow-1	493875	5888562	76.61	59.86	19.09	113.69	12.78	4.40	1.10	1677	92	14.56	2.19
11	Pow-2	493896	5888688	79.64	49.78	20.40	100.00	13.27	4.03	1.75	1252	97	16.09	2.26
12	Pow-3	494000	5888532	78.28	38.01	16.26	106.30	14.12	3.40	1.41	2111	98	13.82	2.47
13	J35-1	474572	5898986	85.89	64.26	11.08	92.76	8.50	4.70	1.15	1865	35	16.68	2.74
14	J35-2	474660	5898971	87.53	84.42	12.49	111.91	11.13	4.15	1.39	2535	41	17.30	2.68
15	J40-1	476560	5897597	83.65	57.78	9.05	95.63	7.91	4.31	1.14	2566	37	15.69	1.72
16	J40-2	476464	5897578	79.23	59.03	13.60	114.78	10.41	4.74	0.99	2399	39	16.59	1.98
17	R16.5	471781	5909017	80.84	55.64	15.31	105.76	13.75	3.23	1.04	2049	99	11.41	2.75
18	H47	510334	5882364	78.05	51.80	15.24	99.33	13.57	3.64	1.00	2009	97	11.81	2.37
19	K-1	515057	5871998	82.04	45.54	16.52	109.99	15.52	3.58	1.03	2301	71	13.48	1.99
20	K-2	515016	5871950	78.30	72.04	17.94	100.39	17.41	3.79	1.31	1928	69	16.44	2.18
21	K-3	515027	5879901	80.91	47.55	17.02	110.14	17.37	3.32	1.06	2503	70	15.90	2.14
22	PR40-1	486845	5898899	95.84	96.20	10.23	93.96	12.07	4.18	1.88	2639	22	19.55	3.65
23	PR40-2	486765	5898849	94.33	91.83	9.67	95.15	14.72	2.99	1.21	3711	22	19.07	2.78
24	PR40-3	486806	5898849	87.22	57.69	9.13	102.00	15.66	3.15	1.31	4528	21	18.67	3.67
25	PR51.5-1	492591	5888848	73.94	43.89	17.39	111.27	14.24	3.38	0.93	2068	101	12.22	2.76
27	JTHIN2-2	475495	5898525	80.90	68.74	13.10	71.52	9.02	4.34	1.35	1046	47	16.96	3.01
28	JTHIN2-3	475536	5898497	80.46	57.35	12.36	119.46	14.26	3.19	0.90	3913	47	15.94	2.96
29	JTHIN2-4	475504	5898484	87.72	61.90	14.20	95.68	12.01	4.45	1.26	1894	47	17.68	2.84
31	J41OIL-1	476539	5894298	69.96	60.64	8.27	111.85	12.47	2.66	0.75	5895	35	14.89	2.19
32	J41OIL-2	476580	5894310	83.48	81.09	8.88	119.87	16.50	2.43	0.96	7004	31	16.52	2.50
33	J41OIL-3	476590	5894351	81.66	82.68	8.92	129.79	13.43	2.51	1.01	6241	37	12.87	2.52
34	J41OIL-4	476609	5894351	80.07	67.06	9.84	132.17	14.51	1.66	0.66	6801	38	13.61	3.21
35	J41OIL-5	476530	5894165	78.94	62.23	8.00	127.57	18.00	1.65	0.69	11433	33	12.22	2.66
36	J41OIL-6	476517	5894126	80.08	59.85	5.94	120.99	11.96	1.55	0.61	10361	34	10.61	2.32
37	J41OIL-7	476663	5894298	80.24	69.89	9.03	123.75	12.94	2.30	0.85	6090	38	14.06	2.47
38	J41OIL-8	476683	5894354	82.69	63.04	10.06	130.29	14.81	2.42	0.90	6293	36	15.58	2.78
39	JTHIN3-1	476369	5897682	78.44	61.52	11.74	116.26	12.00	2.73	0.88	3276	47	14.36	2.32
42	JTHIN3-4	476315	5897727	79.73	55.74	13.45	91.80	9.77	3.97	1.19	1598	47	15.84	2.41
43	JTHIN3-5	476301	5897752	77.64	67.23	11.57	111.65	9.65	3.78	0.73	2642	47	13.54	2.50
44	JTHIN3-6	476320	5897775	79.02	67.59	11.92	100.72	9.33	4.00	0.81	2139	47	12.87	2.19
45	J39-1	476412	5897674	78.16	47.97	11.95	111.01	9.59	3.93	1.04	2407	32	19.75	2.07
46	J39-2	476444	5897672	82.49	61.83	11.92	111.41	10.02	4.32	0.91	2558	38	16.41	1.81
54	OTHIN-2	475751	5899861	86.47	64.98	10.51	120.81	14.87	2.79	0.59	5578	47	12.22	1.91
55	OTHIN-3	475735	5899887	73.79	49.98	11.60	92.99	8.56	4.42	1.01	1831	47	15.16	2.18
57	OTHINBND	475719	5899931	87.85	82.27	6.76	125.06	13.13	2.02	0.61	17043	47	9.47	2.39
59	J35-1A	475031	5898739	80.09	47.19	11.14	97.98	9.69	2.09	1.10	1943	34	16.82	2.14
60	J35-2B	474966	5898782	80.03	73.67	12.04	96.60	10.44	3.79	1.41	2225	37	20.25	2.85
61	STOP4-1	475040	5899435	78.65	52.42	8.38	93.75	8.13	4.25	0.81	2815	34	13.89	2.16
62	STOP4-2	475067	5899452	77.15	62.79	8.44	94.89	8.05	3.83	0.68	3427	35	13.60	2.31
63	STOP4-3	475100	5899473	81.56	80.12	8.48	82.94	9.99	3.93	0.95	3592	25	16.17	2.43
64	STOP5-1	475120	5899320	81.78	66.70	12.34	109.96	10.01	4.04	0.74	2411	34	17.05	2.79
65	STOP5-2	475139	5899345	86.10	69.81	12.30	107.99	11.77	4.68	0.95	2808	28	19.91	2.92
66	STOP5-3	475159	5899376	82.59	50.82	10.39	108.41	8.36	4.08	0.86	3350	40	13.56	2.83
67	D36E-1	471461	5946288	83.95	81.42	8.22	85.87	9.54	3.28	1.30	3039	18	19.42	2.01
68	D36E-2	471465	5946346	87.76	72.46	9.24	89.37	12.22	3.52	1.10	3056	17	21.52	2.64
69	D36E-3	471521	5946389	84.64	75.98	9.20	88.05	12.56	3.45	1.14	3166	22	18.86	2.71
70	D36W	471306	5946225	89.14	81.29	8.17	114.47	15.76	1.98	1.13	9279	22	19.21	2.64
71	P30	455257	5940551	71.41	26.64	18.39	109.65	9.29	4.12	1.06	1223	87	15.82	1.78
72	B80/3-1	516767	5962318	94.80	87.38	8.51	158.08	21.64	2.13	0.53	15501	38	12.88	3.38
73	B80/3-2	510728	5962324	89.56	72.29	12.06	124.21	17.26	3.30	0.94	5936	38	18.21	3.19
74	YelTow1	498432	5893021	77.06	52.18	16.76	117.53	13.70	3.41	1.43	2258	95	15.60	2.07
75	YelTow2	498354	5892966	72.85	44.84	17.22	106.12	10.87	3.57	0.71	1560	83	14.92	1.48
76	YelTow3	498434	5893068	76.18	54.03	17.64	107.63	11.84	3.82	0.73	1675	97	15.52	2.14

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Plot	Location	11U Easting	Northing	CC_H (%)	CC_L (%)	HT (m)	SC	RD	CL (m)	CR (m)	Density (sph)	Age	SI	LAIe (m^2/m^2)
77	T5kmH-1	466550	5902383	81.66	69.73	15.23	110.36	17.43	3.11	0.70	2933	113	11.36	2.70
78	T6kmH-1	466967	5902196	77.37	41.17	17.62	103.31	12.12	3.46	0.96	1529	102	13.99	3.28
79	T6kmH-2	466964	5902212	76.93	52.61	15.76	124.91	14.04	2.86	1.06	2776	104	10.87	3.00
80	T6kmH-3	466899	5902216	80.22	47.74	13.56	120.91	15.35	3.11	0.92	3570	104	9.96	2.85
81	T6kmH-4	466857	5902246	76.42	48.89	13.35	110.18	12.04	3.01	0.86	2481	95	11.56	2.90
82	J38Oil-1	474434	5896456	91.28	91.58	8.32	80.63	10.46	4.00	0.92	3159	21	17.95	3.19
83	J38Oil-2	474268	5896508	95.17	95.43	6.91	91.71	11.03	3.20	0.99	4166	20	16.68	3.33
84	J38Oil-3	474232	5896492	92.26	95.06	7.38	88.28	11.52	3.82	0.92	5853	21	17.00	3.02
85	G39Oil-1	471255	5897838	88.78	63.49	7.14	135.21	18.74	1.84	0.33	24028	27	12.46	2.69
86	G39Oil-2	471225	5897844	85.06	70.78	7.97	139.84	14.60	2.46	0.55	10280	28	15.59	2.42
87	G39Oil-3	471229	5897823	80.76	57.76	6.37	121.98	12.86	2.00	0.38	23366	29	11.83	2.20
88	Gwest-1	461972	5898855	89.08	84.58	5.82	115.64	18.15	2.27	0.44	14245	19	15.29	2.22
89	Gwest-2	461885	5898945	87.16	82.16	6.93	96.37	14.38	2.56	0.58	7764	20	16.45	2.52
90	Gwest-3	461897	5898895	92.52	76.85	6.81	110.35	17.36	2.28	0.55	9985	22	16.73	3.00
91	PR51.5-2	492629	5888791	75.00	38.82	18.47	112.68	11.76	3.63	1.02	1591	94	14.75	2.79
92	PR51.5-3	492581	5888811	74.50	36.38	17.56	104.93	11.12	3.06	0.83	1370	93	16.09	2.52
93	W40-1	461679	5950163	72.26	46.32	19.93	109.80	9.75	3.24	1.56	1117	88	16.42	1.74
94	W40-2	461306	5950849	67.30	29.13	18.57	107.06	10.98	3.12	1.05	1370	86	16.88	1.80
95	Q47-1	446858	5944070	81.38	39.76	17.46	99.12	11.65	3.03	1.51	1494	91	13.92	1.85
96	Q47-2	446804	5944040	78.05	55.94	15.79	105.33	13.71	3.53	1.04	2256	89	12.62	1.70
97	Q47-3	446728	5944048	69.51	39.57	16.99	93.64	8.79	3.55	1.54	1148	64	18.37	1.89
98	Q47-4	446738	5944103	80.53	62.26	17.25	105.40	13.22	4.05	1.44	1918	68	17.69	2.07
99	Q60-1	450002	5959837	73.75	54.76	14.73	112.38	11.19	2.96	0.99	2470	89	14.03	1.77
100	Q60-2	449988	5959793	68.70	41.21	13.79	113.35	9.36	2.82	1.24	2439	94	11.66	2.02
101	Q60-3	449919	5959814	69.18	40.32	15.71	109.69	10.66	2.64	1.30	1861	93	13.67	1.62
104	I2km-3	495001	5957162	87.10	74.53	6.95	101.47	13.65	2.92	1.16	7822	16	20.58	2.90
105	I2km-4	495062	5957229	85.54	67.91	6.46	111.59	12.07	2.55	0.91	7747	16	19.44	2.40

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Plot	GF_H (%)	I_p	Slope (%)	Aspect	Position	DBH (cm)	Distance btw trees (m)	# litter branches	Litter Sum Length (cm)	Av Branch Length (cm)	Av # tips	Total Tips (#)	Litter Dry Wt (g)	BR LA/m2
1	0.33	0.50	3	W	toe	8.35	0.92	0	0	0	0	0	0	0
2	0.36	0.50	5	N	crest	9.29	1.28	2	11.9	6.0	1	2	1.1	6.2
3	0.46	0.24	1	N	upper	10.51	1.46	3	5.7	1.9	1	3	0.4	1.5
4	0.39	-0.51	3	W	crest	18.26	2.83	NA	NA	NA	NA	NA	NA	NA
5	0.45	-0.20	22	SW	crest	16.42	2.19	2	54.4	27.2	1.0	2	6.2	25.2
6	0.40	-0.04	3	SW	toe	15.78	2.05	1	10.3	10.3	1.0	1	0.4	1.5
7	0.41	-0.44	3	SW	upper	17.79	2.11	6	54.2	9.0	1.1	8	8.4	26.0
8	0.40	-0.12	3	SW	upper	18.98	2.42	24	380.8	15.9	1.9	45	62.3	209.8
9	0.41	-0.12	3	SW	upper	17.75	2.38	14	347.3	24.8	1.1	16	25	72.4
10	0.41	-0.52	8	N	upper	19.38	2.44	2	7.9	4.0	1.0	2	2	9.9
11	0.40	-0.17	8	SW	crest	21.84	2.83	23	213.7	9.3	1.3	30	77.1	213.6
12	0.37	-0.54	5	N	upper	17.53	2.18	12	102.0	8.5	1.2	14	53.4	144.3
13	0.43	-0.44	26	SW	upper	12.84	2.32	0	0.0	0.0	0.0	0	0	0
14	0.35	-0.03	15	SW	upper	12.98	1.99	0	0.0	0.0	0.0	0	0	0
15	0.46	-0.25	17	SW	upper	10.43	1.97	1	5.2	5.2	1.0	1	0.6	2.0
16	0.45	-0.20	18	SW	upper	12.65	2.04	0	0.0	0.0	0.0	0	0	0
17	0.43	-0.42	11	SW	crest	19.74	2.21	1	6.5	6.5	1.0	1	1.4	6.6
18	0.47	-0.45	7	SW	toe	16.14	2.23	2	3.9	2.0	1.0	2	0.6	2.0
19	0.35	-0.51	20	W	upper	16.59	2.08	11	77.8	7.1	1.1	12	15.8	60.5
20	0.35	0.05	10	N	crest	19.33	2.28	9	36.7	4.1	1.0	9	5.2	20.3
21	0.37	-0.52	1	N	toe	16.82	2.00	18	239.9	13.3	4.1	74	83.5	261.9
22	0.29	0.30	25	W	upper	12.61	1.95	6	9.4	1.6	0.7	4	0.5	4.8
23	0.33	-0.28	5	S	crest	11.63	1.64	3	2.2	0.7	1.0	3	0.4	1.6
24	0.33	0.07	8	N	upper	11.00	1.49	1	12.2	12.2	2.0	2	0.7	2.1
25	0.50	-0.27	13	SW	upper	16.80	2.20	6	123.9	20.7	3.2	19	10.6	34.2
27	0.41	-0.28	12	SW	upper	18.58	3.09	0	0.0	0.0	0.0	0	0	0
28	0.38	0.13	10	SW	upper	10.81	1.60	5	60.1	12.0	1.2	6	9.1	30.2
29	0.37	-0.52	10	SW	upper	15.43	2.30	0	0.0	0.0	0.0	0	0	0
31	0.50	0.10	25	S	upper	8.28	1.30	2	22.9	11.5	1.0	2	2.8	12.4
32	0.39	0.30	25	S	upper	8.60	1.19	2	6.8	3.4	1.0	2	0.9	3.1
33	0.42	-0.05	25	N	upper	8.05	1.27	2	9.2	4.6	1.0	2	0.6	5.0
34	0.37	-0.15	3	SW	toe	7.88	1.21	3	16.6	5.5	1.0	3	1	4.8
35	0.45	-0.42	2	N	toe	7.42	0.94	0	0.0	0.0	0.0	0	0	0
36	0.48	-0.33	9	N	toe	5.94	0.98	0	0.0	0.0	0.0	0	0	0
37	0.41	-0.30	9	S	upper	8.45	1.28	1	6.4	6.4	1.0	1	0.6	2.3
38	0.41	-0.43	14	SW	upper	8.45	1.26	2	23.1	11.6	1.0	2	2.2	9.4
39	0.45	-0.37	14	SW	upper	11.19	3.53	0	0.0	0.0	0.0	0	0	0
42	0.47	-0.53	14	SW	upper	15.11	2.50	6	47.3	7.9	1.3	8	17.7	63.9
43	0.46	-0.56	13	SW	upper	11.10	1.95	6	58.1	9.7	1.0	6	13.5	42.9
44	0.46	-0.55	30	W	crest	12.53	2.16	6	71.9	12.0	1.8	11	22.2	57.6
45	0.48	-0.53	23	SW	upper	12.16	2.04	7	43.9	6.3	1.0	7	6.6	23.2
46	0.42	-0.52	25	SW	upper	11.96	1.98	0	0.0	0.0	0.0	0	0	0
54	0.43	-0.53	3	SW	toe	9.72	1.34	0	0.0	0.0	0.0	0	0	0
55	0.49	-0.54	3	SW	toe	13.11	2.34	0	0.0	0.0	0.0	0	0	0
57	0.44	0.50	3	SW	toe	6.57	0.77	0	0.0	0.0	0.0	0	0	0
59	0.42	-0.31	25	W	crest	13.90	2.27	0	0.0	0.0	0.0	0	0	0
60	0.42	-0.23	20	W	crest	15.60	2.12	0	0.0	0.0	0.0	0	0	0
61	0.55	-0.15	26	SW	upper	11.07	1.88	0	0.0	0.0	0.0	0	0	0
62	0.53	-0.19	23	SW	crest	10.47	1.71	0	0.0	0.0	0.0	0	0	0
63	0.50	-0.51	30	SW	upper	10.56	1.67	1	0.9	0.9	1.0	1	0.2	0.4
64	0.51	-0.54	10	W	upper	11.94	2.04	0	0.0	0.0	0.0	0	0	0
65	0.40	-0.51	21	SW	upper	12.42	1.89	0	0.0	0.0	0.0	0	0	0
66	0.49	-0.45	27	SW	upper	11.31	1.73	0	0.0	0.0	0.0	0	0	0
67	0.43	-0.27	1	W	mid	11.99	1.81	0	0.0	0.0	0.0	0	0	0
68	0.38	-0.46	2	W	mid	12.20	1.81	NA	NA	NA	NA	NA	NA	NA
69	0.39	-0.51	2	W	upper	12.76	1.78	0	0	0	0	0	0	0
70	0.33	-0.49	1	W	mid	8.50	1.04	14	46.1	3.3	0.8	11	4.6	19.5
71	0.49	-0.14	4	W	upper	19.26	2.86	7	128.6	18.4	1.9	15	16.9	61.8
72	0.32	0.17	2	W	upper	5.93	0.80	44	278.6	6.3	1.0	44	39.2	122.3
73	0.32	-0.31	2	W	upper	10.32	1.30	50	242.8	4.9	2.7	44	41.9	158.6
74	0.49	-0.35	16	SW	upper	16.63	2.10	4	19.4	4.9	1.0	4	4.4	15.6
75	0.50	-0.47	14	W	upper	17.65	2.53	4	58.8	14.7	2.3	9	4.9	18.1
76	0.47	-0.22	12	W	upper	17.99	2.44	NA	NA	NA	NA	NA	NA	NA

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Plot	GF_H (%)	I_p	Slope (%)	Aspect	Position	DBH (cm)	Distance btw trees (m)	# litter branches	Litter Sum Length (cm)	Av Branch Length (cm)	Av # tips	Total Tips (#)	Litter Dry Wt (g)	BR LA/m2
77	0.42	-0.30	39	SW	upper	14.97	1.85	2	7.9	4.0	1	2	1.1	6.9
78	0.44	-0.54	31	W	upper	18.61	2.56	0	0	0	0	0	0	0
79	0.45	-0.50	46	SW	crest	13.96	1.90	NA	NA	NA	NA	NA	NA	NA
80	0.44	-0.41	25	SW	crest	13.28	1.67	0	0	0	0	0	0	0
81	0.45	-0.45	52	W	crest	13.76	2.01	1	69.7	69.7	4.0	4.0	6	30.5
82	0.31	-0.52	19	SW	upper	11.51	1.78	4	24.3	6.1	1.3	5.0	0.9	5.5
83	0.27	-0.48	18	SW	crest	10.47	1.55	1	10.0	10.0	1.0	1.0	0.8	6.3
84	0.34	-0.52	13	SW	upper	10.30	1.31	4	28.1	7.0	1.0	3.0	3.4	14.3
85	0.43	-0.29	16	N	upper	6.46	0.65	0	0.0	0.0	0.0	0.0	0	0
86	0.43	-0.50	25	SW	upper	7.95	0.99	1	4.1	4.1	1.0	1.0	0.2	0.9
87	0.51	-0.18	25	N	crest	6.02	0.65	0	0.0	0.0	0.0	0.0	0	0
88	0.37	-0.11	32	SW	crest	7.56	0.84	12	55.7	4.6	1.0	12.0	6.8	26.6
89	0.34	0.04	19	SW	toe	9.54	1.13	NA	NA	NA	NA	NA	NA	NA
90	0.32	0.36	12	SW	crest	8.37	1.00	8	54.2	6.8	1.0	8.0	8.6	30.8
91	0.50	-0.26	8	N	upper	18.42	2.51	12	134.6	11.2	1.9	23.0	18.5	61.2
92	0.50	-0.51	24	N	upper	17.58	2.70	8	131.5	16.4	1.4	11.0	25.6	75.7
93	0.55	-0.19	2	N	upper	19.89	2.99	3	48.5	16.2	1.0	3.0	2	9.1
94	0.56	-0.48	3	N	upper	19.12	2.70	7	36.4	5.2	1.0	7.0	8.3	30.6
95	0.51	-0.05	7	SW	mid	20.16	2.59	10	192.9	19.3	1.5	15.0	29.3	93.9
96	0.55	-0.10	6	SW	mid	17.60	2.11	27	305.8	11.3	1.5	40.0	74.1	254.3
97	0.44	-0.52	4	SW	mid	18.76	2.95	0	0	0	0	0	0	0
98	0.45	-0.33	3	SW	mid	18.63	2.28	22	519	23.6	2.4	50	136.9	391.9
99	0.52	-0.41	7	N	crest	15.24	2.01	NA	NA	NA	NA	NA	NA	NA
100	0.45	-0.39	6	N	crest	15.75	2.02	3	15.3	5.1	1	3	2.7	9.7
101	0.50	-0.51	6	N	crest	17.46	2.32	3	19.3	6.4	1.3	4	1.6	7.2
104	0.43	0.48	5	N	mid	8.84	1.13	NA	NA	NA	NA	NA	NA	NA
105	0.45	0.31	5	N	mid	6.91	1.14	1	5.4	5.4	1	1	0.6	1.9

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