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Crown Characteristics and Understory Light in Young Trembling Aspen Stands

By

Bradley Dean Pinno ©

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

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Abstract

The objective of this study was to predict crown characteristics and understory light levels in young trembling aspen stands. Understory light levels were measured in young aspen stands with a range of heights and densities. Crown size and individual tree leaf area could be effectively predicted using only stem diameter and crown class ($R^2 > 0.53$). Competition factors, such as relative density, affected stem diameter growth thereby affecting crown characteristics. Using this crown size and leaf area data, the light transmission model MIXLIGHT was able to predict well the average plot level understory light in similar validation stands. Other common stand characteristics, average stem diameter and density, were also able to predict understory light well. Stand level leaf area index, which is the major factor controlling light transmission to the understory, increased to a maximum of approximately 4 by age 9 in some stands and appeared to decrease after age 25. This information on understory light in young stands was then used to define aspen stand types with light regimes appropriate for underplanting of white spruce. MIXLIGHT was also used to analyze Alberta's free-to-grow standards from the perspective of available light for the coniferous crop trees in modeled aspen dominated mixedwood stands. It was found that distance from crop tree to the nearest competing tree is not important in determining the crop tree's light status but the size and density of competitors is.

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Chapter 1

Introduction

Light provides the necessary energy for all plants to develop and grow. However, light is especially important for understory plants since light is the resource which these plants are in most competition for. The amount of understory light is affected by the overstory density and composition and the time of year. In the boreal mixedwood forest, white spruce usually spend the first portion of their lives in the understory of trembling aspen stands. Silvicultural techniques, including clearcutting, shelterwoods and brushing, are used to manipulate light levels and benefit the desired species. Other techniques, such as underplanting of white spruce in aspen stands, can be used to take advantage of preexisting light conditions. There is a need to be able to predict understory light levels in order to choose the most appropriate silvicultural technique.

1.1 Boreal Mixedwoods

The mixedwood association of the boreal forest is the largest forest region in Western Canada and contains some of the most productive sites (Rowe 1972). The two major tree species are trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) which occur together in varying proportions. Other important tree species include balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*) and pines (*Pinus spp.*). After a disturbance, such as harvesting or fire, aspen is able to establish itself quickly on the site through suckering from roots of the previous stand. However, very little is known about how individual aspen trees develop at this stage in relation to their stem and crown size. Competition is thought to reduce crown size in young aspen trees (Puettmann and Reich 1995) but little is known on how competition affects crown radius, crown length and leaf area density of individual trees.

There is a reduction in available understory light in these young aspen stands during the first few years but light transmission is thought to increase once stands are past a young age (Lieffers and Stadt 1994; Constabel and Lieffers 1996), possibly due to increased intraspecific competition and subsequent natural thinning (Bates et al. 1989). Spruce establishes from seeds immediately after stand establishment or gradually over the next decades (Lieffers and Stadt 1994). The speed of establishment of the spruce depends upon available seed source and seedbeds (DeLong et al. 1997) but once seedlings have germinated successfully they are affected by the understory light levels. White spruce is a tolerant species that has slow growth when young but it is capable of growing in the understory (Burns and Honkala 1990). Eventually, the spruce will reach the canopy and dominate the stand since it is longer lived and can grow taller than aspen.

Benefits associated with boreal mixedwood stands, in comparison to single species stands, include suggested increases in biodiversity and productivity (Man and Lieffers 1999). Productivity benefits of mixed stands of aspen and spruce over single species stands may result from reduced crown competition for light between the understory spruce and overstory aspen as a result of the different shade tolerances of the two species (Cannell and Grace 1993). The overstory aspen is able to utilize most of the incoming light but still transmits enough to the understory for the spruce to grow, thereby increasing the total utilization of resources on the site. Increased nutrient cycling, reduced occurrences of pest attacks, and understory conditions which control competition may also contribute to the increased productivity of these stands (Longpré et al. 1994; Man and Lieffers 1999). Due to the benefits of mixedwoods and the desire for more natural ecosystems, there has been an increased interest in silvicultural techniques based on natural stand dynamics (Bergeron and Harvey 1997). This includes underplanting of white spruce in aspen stands in order to take advantage of the benefits of mixedwood stands, shelterwood and selection systems to promote the continual development of shade tolerant species, such as spruce and fir, on a site and clearcutting to promote the growth of shade intolerant species such as aspen and balsam poplar (Lieffers et al. 1996a).

1.2 Understory Environment

The understory is an important environment for many different species of plants, including shade tolerant white spruce, for the first part of their life. Light is one of the critical factors controlling the recruitment of these understory trees (Oliver and Larson 1990; Holbo et al. 1985). Once established, understory growth is directly related to the amount of light a seedling receives (Williams et al. 1999; Chen et al. 1996; Alexander et al. 1995; Emmingham and Waring 1973). Understory environments are characterized by lower light levels than open areas but understories have higher relative humidity, fewer damaging frosts and less diurnal temperature variation than open areas (Carlson and Groot 1997).

In general, the higher the canopy density, the less light is transmitted to the understory. Overstory composition is also important since different species of trees transmit different levels of light to the understory. For example, aspen canopies of maturing stands transmit between 18-40% light while canopies of mature spruce only transmit 5-11% (Lieffers and Stadt 1994). In general, shade tolerant species transmit less light and have larger crowns with which to intercept light than intolerant species (Canham et al. 1994).

The time of year is also important in estimating light transmission since deciduous trees have a distinct leaf off period during which light transmission to the understory is greatly increased (Constabel and Lieffers 1996; Ross et al. 1986; Hutchison and Matt 1977). For example, Constabel and Lieffers (1996) found that for 20 year old aspen stands, 60% of above canopy light was transmitted in the spring leaf off period compared to 19% transmission in the summer.

There is also spatial heterogeneity of understory light as a result of both small and large gaps in the overstory. Very small gaps between and within tree crowns result in sunflecks which are short periods of increased light quantity (Chazdon and Pearcy 1991). Sunflecks have been shown to contribute a large portion of daily radiation loads in the understory of shade intolerant species (Canham et al. 1994). Larger gaps in the canopy result in higher light levels reaching the understory for a prolonged period of time. Finally, leaf flutter in aspen also increases the amount of light reaching the understory (Roden and Pearcy 1993).

Trees have adapted to growing in understory conditions in a number of ways. Both understory Douglas-fir and white spruce were found to be more photosynthetically efficient at low light levels compared to open-grown seedlings (Chen and Klinka 1997; Man and Lieffers 1997a). Also, these species are able to utilize the periods of high light in the spring and fall as a result of the deciduous overstory losing its leaves.

Photosynthesis during these periods is thought to make up a large portion of the annual carbon balance for understory white spruce seedlings (Man and Lieffers 1997b). Understory white spruce actually have higher photosynthetic rates compared to open grown white spruce presumably because they are protected from adverse environmental conditions such as frost which can destroy photosystems when associated with high light (Lundmark and Hällgren 1987). Understory white spruce also exhibit lower photosynthetic compensation points than open grown seedlings. The photosynthetic compensation point for understory white spruce fluctuates depending on temperature and season but remains below a photosynthetic photon flux density of 50 $\mu m/m^2/s$ at all but extremely high temperatures (Man and Lieffers 1997a). However, to accurately measure light over an entire growing season would be very costly so instantaneous measurement of percentage overstory light transmission to the understory is often used instead.

For understory white spruce, height growth was equivalent to open grown trees at approximately 40% of above canopy light with height growth declining to 10% light (Lieffers et al. 1996b; Lieffers and Stadt 1994; Logan 1969). This is within the range of light conditions which are found under both juvenile and mature aspen stands. Since height growth is important in maintaining the competitive status of white spruce in relation to its competitors (Morris and MacDonald 1991), 10 and 40% light may be acceptable thresholds for making silvicultural decisions on underplanting spruce in aspen stands and in determining acceptable levels of competition for spruce which still ensure adequate growth.

1.3 Free-to-Grow Standards

Free-to-grow standards are a type of competition index and are intended to quantify the level of competition that a coniferous crop tree is experiencing. They are used to determine when conifer plantations have been successfully regenerated and are contributing to the overall forest production. They have been widely applied across Canada, including in Alberta where the standards are also applied to conifers within mixedwood blocks. Coniferous trees are generally considered free-to-grow when there is no competing brush surrounding the crop tree which is having a negative effect on conifer growth. This implies that a plantation is not restricted by interspecific competition and conifer tree growth is limited only by site resources (Brand and Weetman 1986). Free-to-grow standards are important in determining the annual allowable cut for a region (MacDonald and Weetman 1993) and were developed because basic regeneration surveys were not able to predict future yields (Brand and Weetman 1986). Free-to-grow standards are also supposed to predict competition levels into the future. If a tree is considered free-to-grow then it is expected to be free of competition well into the future. Since competition is mainly for light in young stands (Brand 1986), free-to-grow standards are all based on above-ground competition. The three main criteria used in determining free-to-grow status are that the crop tree is a suitable species for the site, it has reached acceptable size and it is not limited by interspecific competition (Brand and Weetman 1986). Although light is the important resource being competed for in these stands and what we hope to quantify by the free-to-grow standards, there has been little work dealing with the development of appropriate standards from the perspective of available light for the crop tree.

1.4 Modeling Understory Light

Due to the importance of light in the establishment and growth of understory trees, there has been great effort put into estimating and predicting understory light levels. Understory light can be continuously or instantaneously measured directly using light sensors but the cost, availability and time required limits their practical use by foresters (Lieffers et al. 1999). Since actually measuring understory light is not often possible, different methods of prediction have been developed. The most basic of these use common mensurational data such as basal area, relative density and canopy closure to predict understory light (Vales and Bunnell 1988). These methods provide adequate predictions only for homogeneous single species stands within a certain area so they are not widely applicable (Lieffers et al. 1999). However, since many young aspen stands have relatively homogeneous canopy structure, relationships may be developed based on these common data which are able to predict understory light levels reasonably well.

Light transmission models were developed because they could account for more of the variation in light transmission and were more widely applicable to a range of stand types and species compositions. Most light transmission models are based on the Beer-Lambert Law for light extinction through a plant canopy (Lieffers et al. 1999; Cannell and Grace 1993). Beer's Law can be applied to forest canopies in a simple equation:

$$I/I_o=e^{-k*c*p}$$

where I is the irradiance within a forest, I_o is the outside atmospheric radiation, k is a light extinction coefficient, c is a measure of the density of light absorbing objects and p is the path length through which light travels (Lieffers et al. 1999). In practice, c and p are often combined into a simpler term such as leaf area index or leaf area density. Some of the assumptions of Beer's Law are that the light absorbing objects are randomly distributed throughout the canopy and the light source is from only one direction (Cannell and Grace 1993). These conditions are not met in most forest stands as foliage is clumped into crowns and branches which produces different extinction rates for similar leaf areas (Korzhukin and Ter-Mikaelin 1995) and light comes from all parts of the sky in the form of diffuse radiation. These limitations can be overcome by changing extinction coefficients and dividing the sky into many small areas from which light originates and then estimating light transmission from each of these regions. The most important factor determining light transmission through a forest canopy is leaf area followed by clumping of the foliage (Sampson and Smith 1993; Oker-Blom 1986).

The most basic models which use Beer's Law often assume that the canopy is a single homogeneous layer, both vertically and horizontally (Larsen and Kershaw 1996) and only produce stand average light conditions. An example of this type of model would be that of Pierce and Running (1988) which accurately modeled stand level light in a coniferous forest. If leaf area index is available, then only an extinction coefficient for each stand type is needed in order to predict light. This type of model is best suited to pure, even-aged stands which are homogeneous in canopy structure.

To deal with the spatial heterogeneity of forest canopies and given the importance of microsite level light conditions for individual tree growth (Messier et al. 1999), spatially explicit light models were developed. These are still based on Beer's Law but instead of considering the canopy as one continuous layer, each individual crown is considered. Models which use this technique include Pukkala et al. (1993) for a *Pinus sylvestris* stand and Ter-Mikaelian and Wagner (1997) for forest plants in Ontario. These models are suited for stands that are not homogeneous in composition and when microsite level light predictions are required. However, they have not been widely applied since the determination of crown sizes and extinction coefficients is very time consuming.

MIXLIGHT, developed by Stadt and Lieffers (2000) in Alberta, is a light transmission model for mixed species stands that can be applied to a wide range of stand types and species mixtures to produce either stand average or microsite light conditions. MIXLIGHT can be applied to stands much more easily than other models since it uses common survey data along with foliage area density and foliage inclination. It can also be run with limited data sets, which may make it more applicable than other light transmission models. However, MIXLIGHT has only been applied to mature mixedwood stands so there is a need to validate it for use in young aspen stands.

1.5 Objectives

Although much work has been done on the understory light regime in boreal forests, there are still many questions to be answered. The understory light conditions in young aspen stands and modeling light in these stands has not been fully examined. Although there have been some studies dealing with light transmission with respect to competition in young stands (Comeau et al. 1993; Jobidon 1994) or a general characterization of the light regime in certain types of young stands (Constabel and Lieffers 1996; Brown and Parker 1994) there have been no studies which look at understory light in a wide range of young aspen stand types. It was thought that only extremely dense stands of young aspen could create light conditions that could harm tolerant conifers such as white spruce (Johansson 1989) but there has been no effort to distinguish the light regime among different types of young stands based on height or density of the stands. Also, there has been little work dealing with modeling light in a range of young stand types. Since light models depend upon accurate descriptions of canopy structure (Oker-Blom et al. 1991), this requires information on crown dimensions and leaf area of individual aspen crowns in young aspen stands of differing height and density in order to predict light transmission. Finally, no effort has been put into developing free-to-grow standards which are based on scientific data on the effects of competition on available light and crop tree growth. This information on individual aspen crown characteristics will allow us to model a variety of young aspen stands to simulate growth conditions for white spruce trees with differing free-to-grow status.

The objectives of this study are to validate the MIXLIGHT light transmission model for predicting understory light conditions in young aspen stands of a range of tree sizes and densities. The input data required for MIXLIGHT includes crown diameter, crown length, height and leaf area for individual trees. Once individual tree characteristic relationships are developed, MIXLIGHT will be validated for use in different young stands of the same range of tree sizes and densities. We will also try to predict light from common stand level data and examine leaf area development in young stands. We should then be able to describe young aspen stands appropriate for underplanting of white spruce. MIXLIGHT will also be used to analyze Alberta's free-to-grow standards from the basis of available light for the spruce crop trees in young mixedwood stands dominated by aspen.

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Chapter 2

Crown Characteristics and Understory Light in Young Trembling Aspen Stands

2.1 Introduction

The amount of light reaching a forest understory is a dominant characteristic of the understory environment. Understory light controls the recruitment, growth and survival of trees growing in the understory (Williams et al. 1999; Chen et al 1996; Oliver and Larson 1990). In boreal mixedwood forests, shade tolerant white spruce usually spend the early part of their life in the understory of trembling aspen stands. Suggested biodiversity and productivity benefits of mixedwood stands (Man and Lieffers 1999) has led to an increased emphasis on silvicultural techniques based on natural stand dynamics (Bergeron and Harvey 1997; Lieffers and Beck 1994). These techniques include underplanting of white spruce beneath aspen stands and partial cutting systems in the boreal mixedwood (Lieffers et al. 1996a).

Understory trees have developed many adaptations for living in this lower light environment. Understory spruce and Douglas-fir trees have been shown to be more photosynthetically efficient than open grown trees (Chen and Klinka 1997; Man and Lieffers 1997a). Understory trees are also able to utilize the high light levels in the spring and fall that results from deciduous canopies losing their leaves (Constabel and Lieffers 1996; Hutchison and Matt 1977). This is thought to make up a significant portion of understory spruce yearly carbon supply (Man and Lieffers 1997b). For white spruce saplings, the critical light level for maintaining height growth is 40% of above canopy light (Lieffers and Stadt 1994; Logan 1969) with death occurring below 10% light (Lieffers and Stadt 1994). Since height growth is a good measure of competitive status and 40% light is the level at which some shade intolerant competitors are suppressed (Lieffers et al. 1996b), 10 and 40% light may be good thresholds for making silvicultural decisions.

Leaf area index (LAI) is the total leaf area per unit of ground and is the main factor controlling light transmission to the understory (Sampson and Smith 1993). The strong relationship between LAI and available understory light will allow us to use LAI to estimate understory growth and make silvicultural decisions. Previous studies have determined LAI for young aspen stands (e.g. Pollard 1971) but they have generally not dealt with a wide range of young aspen stand types.

Given the importance of understory light levels for the growth of understory trees, great effort has been put into predicting understory light. Basic predictions use simple stand level characteristics such as basal area but these are only applicable to a narrow range of stand types (Vales and Bunnell 1988). Young aspen stands may be appropriate for using this type of light prediction due to their homogenous stand structure.

Light transmission models are applicable to a wider range of stand types. Most models are based on Beer's Law for light extinction through a plant canopy (Cannell and Grace 1993). Beer's Law can be applied to forest canopies in a simple equation:

$$I/I_o = e^{-k*c*p}$$

where I is the irradiance within a forest, I_o is the outside atmospheric radiation, k is a light extinction coefficient, c is a measure of the density of light absorbing objects and p is the path length through which light travels (Lieffers et al. 1999). Stand level (e.g.

Pierce and Running 1988) and microsite level models (e.g. Pukkala et al. 1993; Ter-Mikaelian et al. 1997) have been developed based on Beer's Law for a variety of forest stands. However, these models often require an extensive amount of calibration data and have not been validated in a range of stand types. MIXLIGHT, developed by Stadt and Lieffers (2000) in Alberta, is a spatially explicit light transmission model for mixed species stands which has fewer calibration requirements. However, it has only been applied to mature mixedwood stands so there is a need to validate it for use in young aspen stands.

Light transmission through a range of young aspen stand types has not been fully examined although some measurements have been done related to competition (Comeau et al. 1993) or a general characterization of light in young stands (Constabel and Lieffers 1996). In order to model understory light accurately, information is needed on how crown characteristics such as leaf area, crown radius and crown length vary with tree size and stand density. We hypothesize that individual tree leaf area density declines with tree size and relative density and that individual tree crown size decreases with increasing competition. The objectives of this study are to examine the development of individual tree characteristics as input data for the MIXLIGHT light transmission model and validate the model for use in young aspen stands. We will also determine if understory light in these stands can be predicted using basic stand level characteristics and examine the development of leaf area in these stands.

2.2 Methods

2.2.1 Overview

MIXLIGHT requires height, crown radius, height to live crown, leaf area density, leaf inclination angle and diameter for every tree in the plot which is to be analyzed. To calibrate the model, we measured individual tree and plot level characteristics and used these to develop equations to predict the tree characteristics required by MIXLIGHT. To validate the model, we measured light transmittance in separate plots. We then applied the equations developed to predict individual tree characteristics to each tree in these plots. MIXLIGHT was run in the modeled plots to predict average light per plot and the results compared to actual light measurements taken in these same plots. Other aspects of this study include predicting understory light using common stand characteristics and examining stand level leaf area development.

2.2.2 Site Selection

Young aspen stands, between 1 and 30 years old, were selected as possible sites within the boreal mixedwood forest near Drayton Valley, Slave Lake and Grande Prairie, Alberta (53°20' – 55°20' N, 113°10' – 118°50' W). Only stands on upland sites with less than 10% slope and with medium to rich nutrient status and mesic to sub-hygric ecological moisture regime were selected. Stands were selected from the boreal mixedwood BMd (low-bush cranberry) and BMe (dogwood) ecosites (Beckingham and Archibald 1996). Stands ranged from 1-12m tall and were of a wide range of densities. All stands had greater than 80% of total basal area as aspen, but also included other trees and shrubs such as balsam poplar, white birch, alder and willow in the overstory and occasionally white spruce and lodgepole pine in the understory. Both fire and harvest origin stands were selected. The sites contained no obvious linear patterns of tree distribution, which means that no stands that had disc trenching or ripper plowing as a site preparation treatment were selected. Within the stands a random plot centre location was found and the closest acceptable aspen tree to the plot centre was sampled. Acceptable trees had no obvious signs of damage or disease and had a symmetrical crown shape. No more than five plots were sampled within a single stand and most stands had three plots.

2.2.3 Plot Tree Measurements

Once the plot centre tree was identified in each of our 96 plots, it became the centre of a circular plot between 1 and 3 m in radius. Plot size depended on stand size and density with taller and sparser stands having larger plots. The following measurements were made on the plot tree: height, height to live crown, diameter at breast height (DBH), diameter at 30 cm height (D_{30}), crown class and crown diameter as an average of two perpendicular axes. Trees of two crown classes were treated as plot centres and were measured: 1) canopy trees (dominant and co-dominant) and 2) intermediate trees (intermediate and suppressed). The plot centre trees were cut and discs were taken at breast height (1.3 m) and at 30 cm in order to age the trees and determine sapwood area. Leaves were removed by hand and collected for leaf area determination. Actual leaf area of a subsample of leaves from each tree was determined using a leaf area meter and then oven dried. The rest of the sample was also oven dried and then using the relationship between actual leaf area and oven dry weight, total leaf area of each tree was determined.

The crown shape for all aspen trees was considered to be ellipsoidal based on visual examination.

2.2.4 Stand Measurements

Within the surrounding plot, the dominant understory vegetation was recorded by species and per cent cover along with any indicator species of nutrient and moisture regime which were present near the plot. DBH and species were recorded for all trees and large shrubs within the plot. If the trees were below 1.3 m tall then D_{30} was recorded. This information was used to determine total plot density and basal area of competing trees. In the four quadrants (NE, SE, SW, NW) surrounding the plot tree, the closest tree at least the height of the crown bottom of the subject tree was determined and D_{30}, DBH, height, species and distance to the plot centre tree were recorded.

The LAI-2000 plant canopy analyzer was used in each plot to estimate leaf area index and leaf inclination angle for the stand (LI-COR 1992). Two units were used in remote mode, one outside the stand to record outside sky conditions and one inside the stand to measure the leaf area. With the 90° view cap in place, 16 measurements were taken around the subject tree, going back a distance equal to the height of the tree. In subsequent analyses the bottom two rings of the sensor were eliminated.

The maximum horizontal crown overlap of canopy trees was needed in order to place restrictions on the random placement of canopy trees during the validation of MIXLIGHT. Totally random placement can result in two canopy trees occupying the exact same location. Since this is not realistic, an estimate of the acceptable amount of overlap was needed. Within eight selected stands, horizontal crown overlap of 60 pairs of canopy trees was determined. This was done by randomly locating pairs of canopy trees which were overlapping. Pairs of canopy trees which were not overlapping were not included in the sampling population because we were only concerned with the maximum possible overlap. On the pairs of canopy trees, the distance between the two stems (D) was measured along with the crown radius (CR) and DBH of each tree. Crown overlap was defined as 1-(D/CR1+CR2). Maximum horizontal crown overlap in relation to tree diameter was assumed to be the linear regression between crown overlap and DBH plus one standard deviation of the intercept (Fig. 2.1).

2.2.5 Crown Characteristics

MIXLIGHT requires the height, diameter, height to live crown, crown radius, leaf area density and leaf inclination angle of each tree in the plot. It also needs the slope, aspect, plot location and a stem map (Stadt and Lieffers 2000). All of this information was derived from the plot tree and plot level measurements.

For all subsequent relationships, D_{30} was used since not all of the trees measured were taller than 1.3 m where DBH is taken. However, only DBH was measured for most trees within the plot so these needed to be converted into D_{30}. A variety of linear and non-linear equations were assessed in order to determine the best relationship between DBH and D_{30}. D_{30} was estimated from DBH using non-linear regression based on DBH and D_{30} from all plot centre and the four quadrant trees in each plot (D_{30}=1.1843+0.6363(DBH)$^{1.194}$, R^2=0.980, n=324, figure not shown).

Height was estimated from D_{30} using the Chapman-Richards height-diameter equation. The parameters for this equation were developed using D_{30} and height from all plot centre trees and the four quadrant trees in each plot. For all trees, total tree height was predicted from the equation: $H=0.3 + 14.47(1-e^{-0.19D30})^{1.59}$ (Fig. 2.2).

Crown radius and crown length (used to derive height to live crown) were measured on each plot centre tree. Using SAS, a variety of linear, non-linear and multiple linear stepwise regression equations were developed to predict crown radius and crown length. A variety of predictor variables were tested including individual tree characteristics such as diameter and height and plot level data such as basal area, stem density, distance of nearest competitor to subject tree, size of nearest competitor, plot level leaf area index and relative density (Curtis 1982). Relative density combines basal area and average stem diameter so that density can be compared between stands of different height. Separate equations were developed for canopy and intermediate trees. The best relationship, based on R^2 and accuracy of prediction from examination of residual plots was then chosen for the model. R^2 for all equations, including non-linear equations, was calculated as 1 – (Error Sum of Squares / Corrected Total Sum of Squares) (Cornell and Berger 1987).

Leaf area per tree equations were developed in the same way as for crown radius. Possible equations included both linear and non-linear models and included individual tree and plot level data. For modeled trees, the crown volume and leaf area were calculated and from this leaf area density (i.e. the individual tree leaf area divided by its crown volume) was determined.

Leaf inclination angle was taken as the average of the mean tilt angle calculations from the LAI-2000 for each plot. The average mean tilt angle of all stands was 50° which is close enough to the random distribution of 60° that the random distribution value was used in the model. This random distribution is the average angle that would occur if the leaves were placed around the outside of a sphere. Chen et al. (1997) have also shown that aspen leaf inclination angle has a random distribution.

MIXLIGHT requires a stem map for plot level light predictions. Since the plots were not mapped trees needed to be placed in the model. Trees were positioned randomly within the plot but with restrictions placed on the distance between canopy trees using the relationship developed for maximum horizontal crown overlap. Based on the average diameter of all canopy trees in each plot, a maximum overlap value was determined (Fig. 2.1). This value was used to eliminate random points which would cause two canopy trees to have greater than the allowable horizontal crown overlap based on their crown radii and distance between stems. Intermediate and dead trees were placed randomly within the plot.

Aspen was the dominant species in all of the plots. For this reason, all trees and large shrubs were considered to be aspen in the model. Slope and aspect were not considered since all plots were relatively flat. The latitude and longitude were also determined for each test plot.

2.2.6 Light Measurements

In order to validate the MIXLIGHT forest light model for young aspen stands, understory light measurements were taken at a number of additional sites independent of the calibration plots. These validation plots were not tree centred but were randomly placed within a stand and were selected from the same range of both height and density as the tree centred plots. Light was measured on both sunny and uniformly cloudy days with sunny day measurements taken between 11:00 and 14:00 local time.

Light was measured in the understory and in the open to determine light transmission through the canopy using a linear radiometer with 80 sensors (Model SF-80, Decagon Devices Inc., Pullman, WA). A single circular sweep consisting of 15-20 light measurements was taken in the open followed by a sweep around the centre point beneath the overstory canopy and above the shrubs and finally another sweep was taken in the open. Measurement height ranged from 30-150 cm depending upon the site. On some sites the understory vegetation was trampled in order to get a measurement of just the overstory light transmission. Open and below canopy measurements were usually less than one minute apart and never more than two minutes. The average of all light measurements under the canopy and in the open were determined. Below canopy light values were divided by open light values in order to obtain per cent light transmission through the canopy.

Once the light measurements were taken, a 2-3 m radius plot was established surrounding the centre point. Within this plot the species and DBH of each tree and large shrub was recorded in order to determine basal area and density of the site. One of the larger trees within the plot was cut down and a stem disc taken at 30 cm was used for age determination. The per cent cover of the major understory vegetation species was also recorded.

2.2.7 Model Validation

Validation of MIXLIGHT for use in young aspen stands was done on 17 test plots in which light was measured. Individual tree height, crown size and leaf area was estimated for each tree in the modeled plots using the regression equations described. Since the size of each plot was small and we assumed that the surrounding stand was uniform, the plot was replicated around itself for a total of 25 plots. For each of these composite plots, MIXLIGHT estimated light within the central plot at 16 regularly spaced points at least 10 cm distance from the stem of any tree. MIXLIGHT was run five times for each plot with different tree locations and the results averaged in order to estimate the average light transmission through the aspen canopy. The light transmission values were then compared to the actual light measurements taken within the stand.

2.2.8 Light Prediction Using Stand Characteristics

Using the same 17 plots in which light transmission was measured, understory light conditions were regressed using of a variety of stand attributes as predictors. These predictors included average stem diameter, quadratic mean stem diameter, average height, total density and basal area of the stand. The combination of stand attributes which produced the best equation was chosen based on R^2 and examination of residuals. From this equation a table was produced which related light transmission in young aspen stands to stand size and density.

2.3 Results

2.3.1 Crown Characteristics

The best predictors of individual aspen tree crown radius (Fig. 2.3), crown length (Fig. 2.4) and leaf area (Fig. 2.5), were exponential functions of diameter at 30 cm height (D_{30}) for both the canopy and intermediate level trees. R^2 ranged from 0.69-0.78 for canopy trees and from 0.53-0.61 for intermediate trees. Analysis of the regression of the logarithm of D_{30} vs. logarithm of crown characteristics for canopy and intermediate trees showed that curves for crown radius vs. D_{30} ($p=0.255$) and crown length vs. D_{30} ($p=0.251$) were not significantly different between dominance class. Crown size did not level off as D_{30} increased indicating that crown size was still increasing over our entire range of tree sizes. For the leaf area vs. D_{30} curves, the relationships were significantly different between dominance classes ($p=0.0005$). This shows that canopy trees develop more leaf area than an intermediate tree of similar size (Fig 2.5). This occurred despite the fact that there was virtually no heartwood in any of the samples. Separate curves were developed for canopy and intermediate trees for all crown characteristics.

Including a measure of the degree of competition from neighbouring trees measured using basal area, density, relative density and size of or distance to the nearest competitor into multiple regression models did not improve the prediction of crown characteristics. For crown radius (Table 2.1), crown length (Table 2.2) and leaf area (Table 2.3), a variety of functions were assessed for goodness of fit. This information, along with analysis of residuals from the ideal relationship (Fig. 2.6) shows that non-linear functions of D_{30} are the best predictors of all individual tree characteristics.

Stand or adjacent tree competition did however, have an effect on individual tree crown characteristics. As competition increased, as shown by an increase in relative density or basal area, the slenderness coefficient (total height divided by diameter at 30 cm height) increased (Fig. 2.7). This shows that the diameter growth of trees responded negatively to increased competition thereby affecting the modeled crown parameters.

Leaf area density (total individual tree leaf area divided by crown volume) was also affected by changing tree size and competition. An increase in relative density caused a decrease in leaf area density showing that crown characteristics responded, along with diameter growth, to changing competition levels (Fig. 2.8a). Leaf area density was also related to individual tree size. As trees became larger, as shown by an increase in D_{30}, their leaf area density declined (Fig. 2.8b).

2.3.2 Model Validation

Validation of the MIXLIGHT model shows that it can predict understory light in young aspen stands for this entire range of light levels, from 4-66 % of above canopy light (Fig. 2.9). A basic t-test shows that the intercept of the predicted to actual % light relationship is not significantly different from 0 ($p=0.62$) and the slope is not different from 1 ($p=0.91$). This shows that MIXLIGHT does produce values close to the ideal 1:1 relationship between predicted and actual % light. Analysis of the residuals of MIXLIGHT predictions from the ideal 1:1 line show that MIXLIGHT tend to predict light transmission more accurately at lower light levels (less than 30%) compared to high light levels (Fig. 2.10).

2.3.3 Light Prediction Using Stand Characteristics

The best equations to predict understory light conditions included the average diameter, either arithmetic average diameter ($AvgD_{30}$) or the quadratic mean diameter (QMD_{30}), of all trees in the plot and stand density (stems per hectare). For the $AvgD_{30}$ and density equation, comparison of the predicted and actual light for the same 17 plots which were used for the validation of MIXLIGHT, shows that the equation can accurately predict light in this range of stand types (Fig. 2.11). The slope ($p=0.07$) and intercept ($p=0.23$) of the relationship between predicted and actual % light is not different from the ideal 1:1 relationship. Examination of the residuals of the predicted from actual light levels shows that the equation predicts light transmission more accurately at lower light levels (30% or less) compared to high light levels and that the equation predictions have even less variation than the MIXLIGHT predictions (Fig. 2.12).

For the QMD_{30} and density equation, the overall prediction is not as good. For the relationship between predicted and actual %light the slope is significantly different from the ideal 1:1 line ($p=0.02$) (Fig. 2.13). Both of these equations (Figs. 2.11 and 2.13) are biased at high light levels but they predict well at low light levels. From these equations, Tables 2.6 and 2.7 were produced which give estimates of stand average understory light conditions based on $AvgD_{30}$ or QMD_{30} and stems per hectare.

2.3.4 Stand leaf area

Stand level leaf area index (LAI) as measured by the LAI-2000 reached a maximum of approximately 4 by as early as age 9 in some stands and appeared to decrease at about age 25 (Fig. 2.15a). There was a great variation in LAI when stands were young but there tended to be less variation as stands aged. LAI was also related to stand basal area measured at 30 cm height ($BA_{(D30)}$) with LAI increasing rapidly until 20 m^2 where it levels off at a maximum of approximately 4 (Fig. 2.15b). There was a great deal of variation in LAI for a given $BA_{(D30)}$, particularly between 20-30 m^2. At higher and lower $BA_{(D30)}$ there is much less variation in LAI.

2.4 Discussion

In these juvenile aspen stands, the individual tree crown characteristics including crown length, crown radius and leaf area were best predicted using only diameter at 30 cm height (D_{30}); including a measure of competition such as relative density or basal area did not improve the prediction. However, D_{30} was affected by competition through a changing slenderness coefficient thus stand competition did have an effect on modeled crown characteristics. Also, increased competition negatively affected leaf area density (Fig. 2.8a) as has been shown previously with both stem diameter and juvenile aspen crown size responding to changing levels of competition (Puettmann and Reich 1995; Bella 1975). So, even though including competition did not improve our prediction of crown characteristics, the effects of competition reducing D_{30} compared to trees of similar height without competition, implicitly captured the effect of competition in our model.

Leaf area is the most important factor controlling light transmission to the understory (Sampson and Smith 1993). Destructively sampling each individual tree for leaf area allowed us to accurately measure leaf area. In our calibration, leaf area was determined for each tree based on crown class and diameter. Although time consuming, this method is feasible in young stands and is probably better than other studies which have used average leaf area density for a wide range of tree sizes. For example, Stadt and Lieffers (2000) derived average leaf area denstiy from light transmission through individual tree crowns while Brunner (1998) used stand level leaf area index to estimate individual tree leaf area density.

Leaf area has been shown to be correlated with sapwood area for aspen (Kaufmann and Troendle 1981) and other tree species (e.g. Long and Smith 1988). Since our young aspen trees had virtually no heartwood, D_{30} is a good estimate of sapwood area. However, the relationship between leaf area and D_{30} for canopy trees and intermediate trees is different (Fig. 2.5), thus a canopy tree of a given diameter is able to support more leaf area than an intermediate tree of similar size and presumably similar sapwood area. The same effect of crown class on the sapwood-leaf area relationship has been shown for other boreal forest tree species as well (Hungerford 1987). This means that sapwood of canopy trees is more effective in transporting water to the foliage in the crowns than the sapwood of intermediate trees.

At the stand level, LAI leveled off at a maximum of approximately 4 once $BA_{(D30)}$ reached 20 m^2. As $BA_{(D30)}$ continued to rise LAI stayed constant suggesting that the effective amount of sapwood is also remaining constant. Since there is virtually no heartwood in these trees, the effectiveness of the sapwood in transporting water to the transpiring leaves appears to decrease with increasing basal area. This relationship with sapwood conductivity declining with increasing competition has been shown to occur in other tree species as well (Long and Smith 1988, 1989). Also, there is a large range of

LAI values for stands with similar $BA_{(D30)}$. Therefore, using basal area alone may not be a good estimator of leaf area development in young aspen stands.

The leaf area density (leaf area / crown volume) declined with increasing crown size (Fig. 2.8b). The mechanism for this is not clear but may relate to relatively low amounts of leaves in the interior of large crowns relative to the outer shell of the crown.

Horizontal crown overlap of canopy trees decreases as trees become larger. The individual crowns begin to pull away from other trees due to suppressed trees beginning to die out between the canopy trees and possibly from mechanical abrasion between crowns. This separation of individual crowns may be important in allowing more light through the canopy to the understory as the overstory aspen trees become larger. As the crowns are more separated, small gaps are created between trees which will allow more light transmission through the canopy. This increase in gaps, combined with decreasing leaf area index as stands age, may allow recruitment and improved growth of white spruce in the understory. Crown shyness (Long and Smith 1992), with complete separation of individual crowns, will eventually occur but it is not clear when.

Our actual light transmission measurements cover a much wider range of young aspen stand types than previous studies. For example, Constabel and Lieffers (1996) only measured light in six similar young aspen stands while Messier et al. (1998) measured light in a number of similar mature aspen stands. Our lowest light transmission values of between 4-10 % are also lower than those previously reported for aspen stands in Western Canada. Light transmission measurements have ranged from 19 % in 20 year old aspen stands (Constabel and Lieffers 1996) to 26 and 32 % in mature aspen stands (Chen et al. 1997; Constabel and Lieffers 1996). Indeed, our lowest light transmission values of between 4-10 % are more similar to mature spruce stands (Lieffers and Stadt 1994) and are low enough to seriously reduce the growth and survival of understory white spruce since white spruce height growth decreases with decreasing light below 40 % light with death occurring below 8 % light (Lieffers and Stadt 1994; Logan 1969). These low light levels within some aspen stands may account for some of the variation in understory spruce recruitment into aspen stands with spruce not being able to survive in areas of very high aspen density. These low light levels also indicate that not all aspen stands are suitable for underplanting of white spruce.

MIXLIGHT was able to predict average plot light transmission well over a range of young aspen stand types of varying heights and densities. Other studies modeling light in young forest plant communities have not dealt with this wide range of stand types. For example, Ter-Mikaelian et al. (1997) modeled light in plots of varying density of 2 year old jack pine and other forest plants but only looked at this one size of plant while Brunner (1998) modeled light in a single 20 year old Douglas-fir stand. MIXLIGHT predictions were better at light levels below 30% of above canopy light than at higher light levels. Good prediction at low light levels, however, is much more important as this will allow accurate predictions of the critical points for plant survival and acceptable growth.

Possible sources of errors in predicting light transmission in these stands using MIXLIGHT include: 1) Not mapping the sites. Mapping of stem positions at each site may have accounted for more of the variation in light predictions, especially in sparse stands, but use of the maximum horizontal crown overlap (Fig 2.1) should have enabled us to produce reasonable stem maps for each site. Including crown overlap also makes

MIXLIGHT more flexible for use in young stands which would be difficult to map due to the high numbers of stems. 2) Moisture and nutrient status of the sites was not quantified although similar site types were chosen for all stands. Moisture is thought to be a limiting factor for the development of aspen leaf area (Messier et al. 1998) so slight differences in available moisture may have affected leaf area values and therefore light transmission. 3) Not including within crown wood branch area since this also intercepts light. However, 95% of all branch area is obscured from view by foliage (Kucharik et al. 1998) so this is not likely to significantly affect light transmission values.

Using basic stand attributes to estimate average understory light levels has been used in single species stands with relatively homogeneous canopy structure. Young aspen stands often meet these criteria and our study areas were chosen within homogeneous stands. Therefore, it was possible to predict understory light conditions using simple stand attributes, such as arithmetic average stem diameter ($AvgD_{30}$) or quadratic mean diameter (QMD_{30}) and number of stems per hectare in our study. The actual equations included $AvgD_{30}^2$ or QMD_{30}^2, along with density, which give an estimate of total stand level basal area or sapwood which should be related to leaf area. Although $AvgD_{30}^2$ should not produce as good of an estimate of sapwood area compared to QMD_{30}^2, $AvgD_{30}$ is easier to calculate. Also, the $AvgD_{30}$ equation is a better estimate of light transmission over the entire range of stand densities which make it a simple and useful light predictor. Both of these equations predict average stand light well, especially at low light levels, even better than the more complex MIXLIGHT model. It must be remembered however that MIXLIGHT is capable of spatially explicit microsite predictions, although these were not tested here. The equations (Figs. 2.11 and 2.13) and tables (Table 2.6 and 2.7) to predict understory light should provide guidance to forest managers to identify aspen stands which have appropriate understory light conditions for underplanting of white spruce.

In this study we have looked at two methods for predicting understory light conditions in young aspen stands: 1) the spatially explicit MIXLIGHT light transmission model and 2) the stand average light conditions from stand characteristics. Spatially explicit models such as MIXLIGHT have the benefit of being able to produce microsite light levels which is important for the growth of individual understory trees. They may also be used to evaluate spatially explicit regulations such as free-to-grow standards and thinning or brushing prescriptions from the standpoint of available light. However, this requires a detailed stem map. In young stands, individual tree light conditions may not be important to forest managers as there are possibly tens of thousands of trees per hectare. Stand average light levels, as predicted from average diameter and density, has the advantage of being easy to apply to any young aspen stand and producing appropriate light information for forest managers. However, these types of predictions can only be used in stands that have relatively homogeneous canopies which may limit their use in stands with large gaps and mixed-species stands.

Maximum stand level leaf area index of approximately 4 was reached by about age 9 in some stands and appeared to decline after age 25. This is similar to the maximum LAI of 3.9 measured in other juvenile aspen stands in Alberta (DesRochers 2000) but higher than other reported LAI values for young aspen stands: 2.4 in a 6 year old stand, and 2.9 in a 15 year old stand (Pollard 1970; Pollard 1971). This difference in LAI values may be a result of our study specifically sampling stands over the full range of stem sizes and densities, including very high density stands. Leaf area index in mature trembling aspen stands has be shown to be between 1.4 in a 55 year old stand (Poliard 1971) and 3.3 in a 70 year old stand (Kucharik et al. 1999). This shows that young aspen establishes leaf area on site very quickly and is capable of carrying at least as much or more leaf area than mature stands and therefore absorbing at least as much light.

The possible decline in LAI after age 25 was also seen by Lieffers and Stadt (1994) who showed an increase in light with age in aspen stands. This decline in LAI seems to correspond to the final period of major natural thinning in aspen stands between the ages of 21 and 25 (Peterson and Peterson 1992). Even though individual trees are continuing to increase their leaf area, the stand as a whole has a decreasing leaf area index. This could be a result of tree mortality and crown overlap decreasing as the trees becoming larger resulting in fewer leaf layers. The decrease in stand leaf area would allow more light to the understory enabling seedlings to become established and increasing growth rates of existing understory trees. If trees become established in the first few years after stand disturbance they may be able to survive in the dark understory and then increase their growth rate after overtopping leaf area begins to decrease as has been shown for understory spruce trees (Lieffers et al. 1996b). This information on leaf area development may be useful for managers making silvicultural decisions on underplanting of white spruce which may be delayed up to 25 years to correspond with decreasing overstory aspen leaf area.

In this study we looked at how young aspen trees and stands develop and the light regime in a variety of these young stands. At the individual tree level we examined crown size and leaf area in relation to tree size and competing density and found that crown size and leaf area are related to D_{30}. Including competition measures did not improve the prediction but they did have an effect on D_{30}. Stand level leaf area development was also examined in relation to stand age and basal area. It was found that LAI reached a maximum of 4 in some stands by age 9 and appeared to decrease after age 25. Basal area was not a good predictor of LAI as there was a great deal of variation in LAI for a given basal area. MIXLIGHT light transmission model was able to predict plot level average light well for the entire range of young stands. Using common stand characteristics such as density and average diameter, we were also able to predict light well in young aspen stands, particularly at low light levels. From this study we have been able to identify young aspen stand types which, on the basis on transmitted light, should be appropriate for underplanting of white spruce.

2.5 Figures

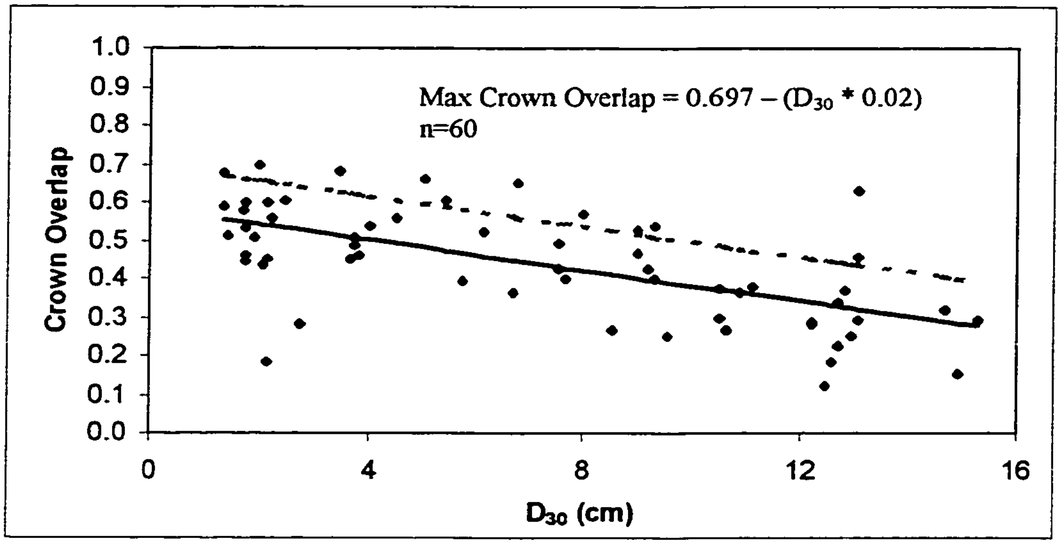

Figure 2.1: Maximum horizontal crown overlap of canopy trees in relation to their diameter at 30 cm height (D_{30}). Crown overlap is calculated as 1-(D/CR_1+CR_2) where D is the distance between the two canopy trees and CR is the crown radius of the individual trees. The solid line is the regression line and the dotted line is the regression line plus one standard deviation of the intecept which represents the maximum horizontal crown overlap.

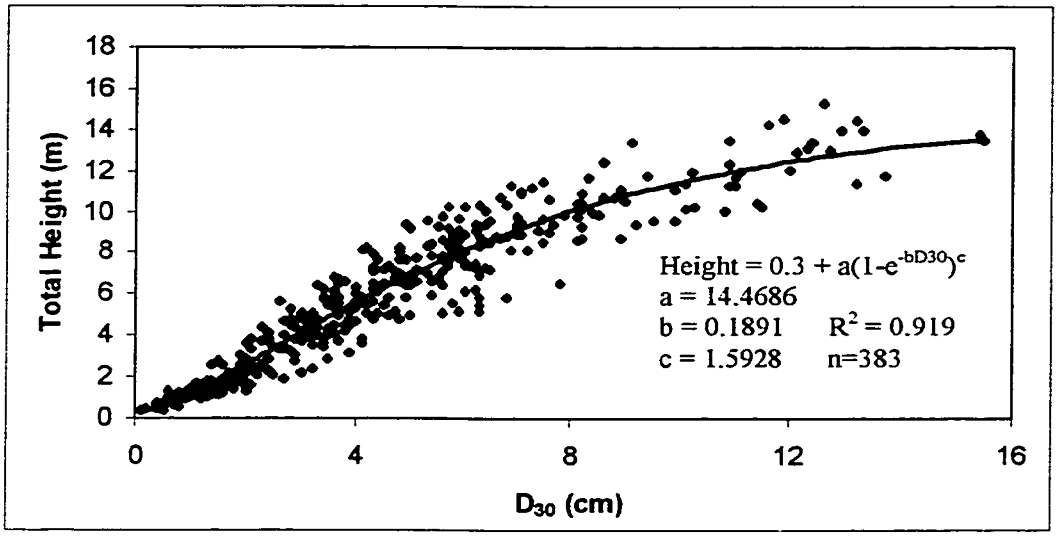

Figure 2.2: Total tree height of all trees in relation to their diameter at 30 cm height (D_{30}) using Chapman-Richards height-diameter equation.

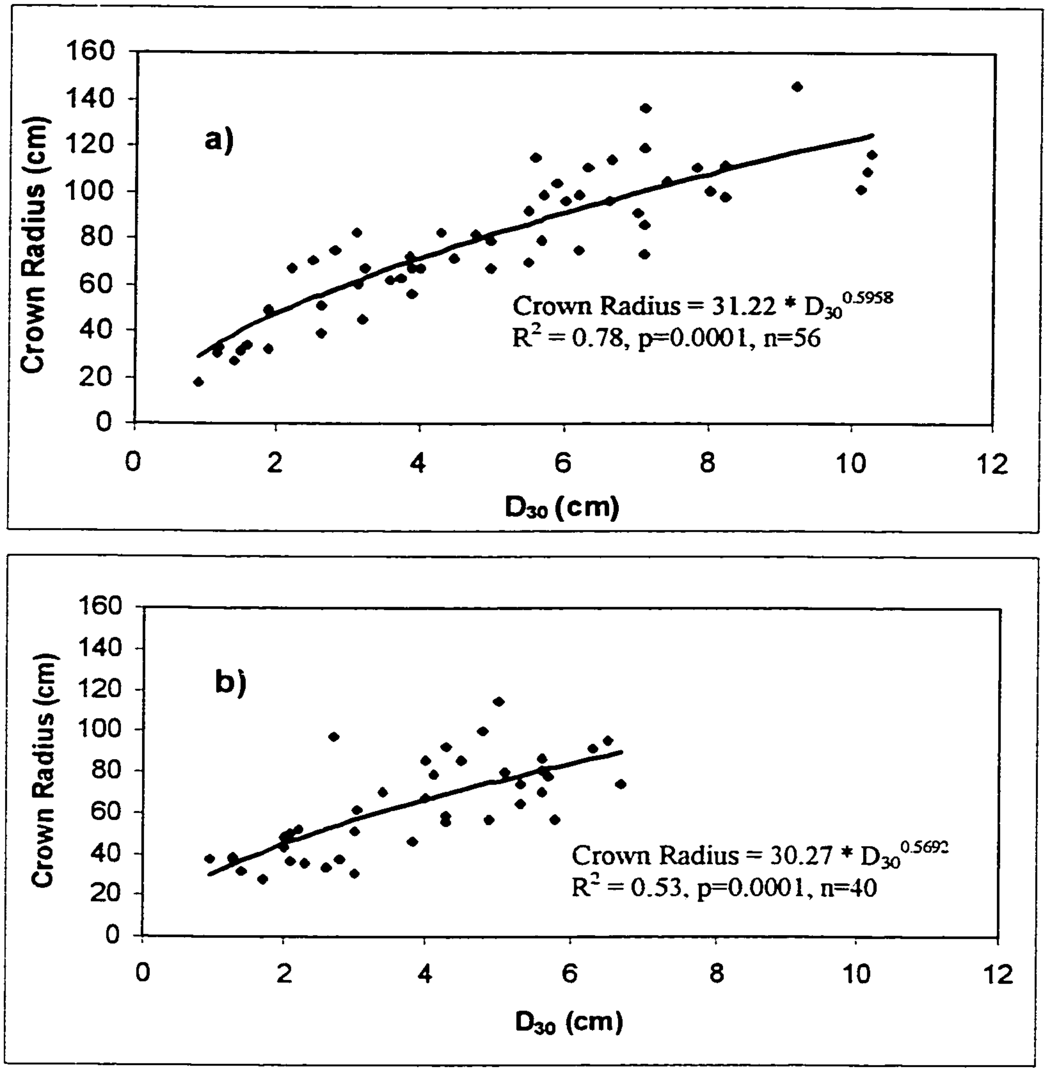

Figure 2.3: Crown radius of a) canopy trees and b) intermediate and suppressed trees in relation to their diameter at 30 cm height (D_{30}). The common equation for all trees is: Crown Radius = 29.67 * $D_{30}^{0.6125}$, R^2=0., p=0.0001, n=96.

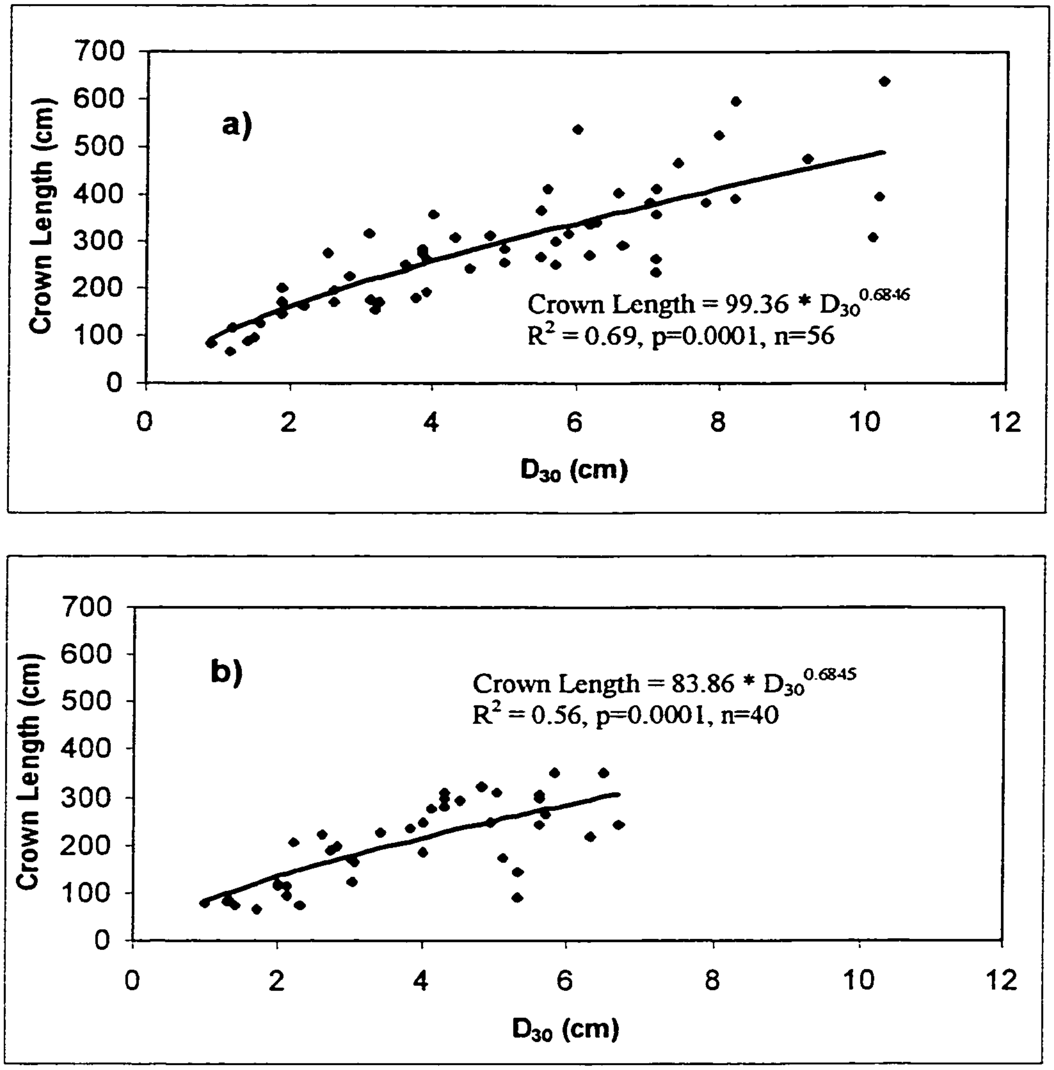

Figure 2.4: Crown length of a) canopy trees and b) intermediate and suppressed trees in relation to their diameter at 30 cm height (D_{30}). The common equation for all trees is: Crown Length = 84.89 * $D_{30}^{0.7461}$, R^2=0.67, p=0.0001, n=96.

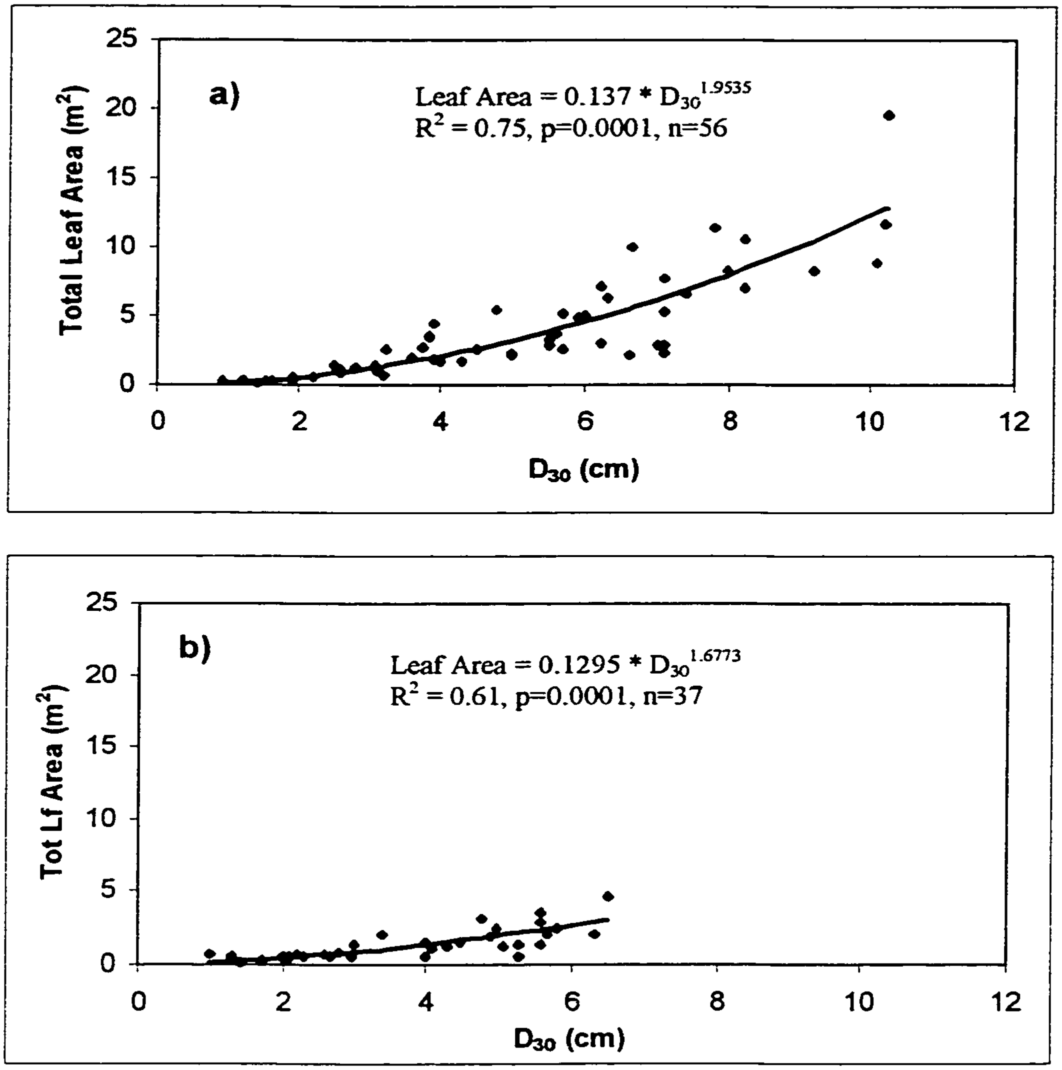

Figure 2.5: Total leaf area of a) canopy trees and b) intermediate and suppressed trees in relation to their diameter at 30 cm height (D_{30}). The relationships for canopy trees and intermediate trees are significantly different ($p=0.0005$).

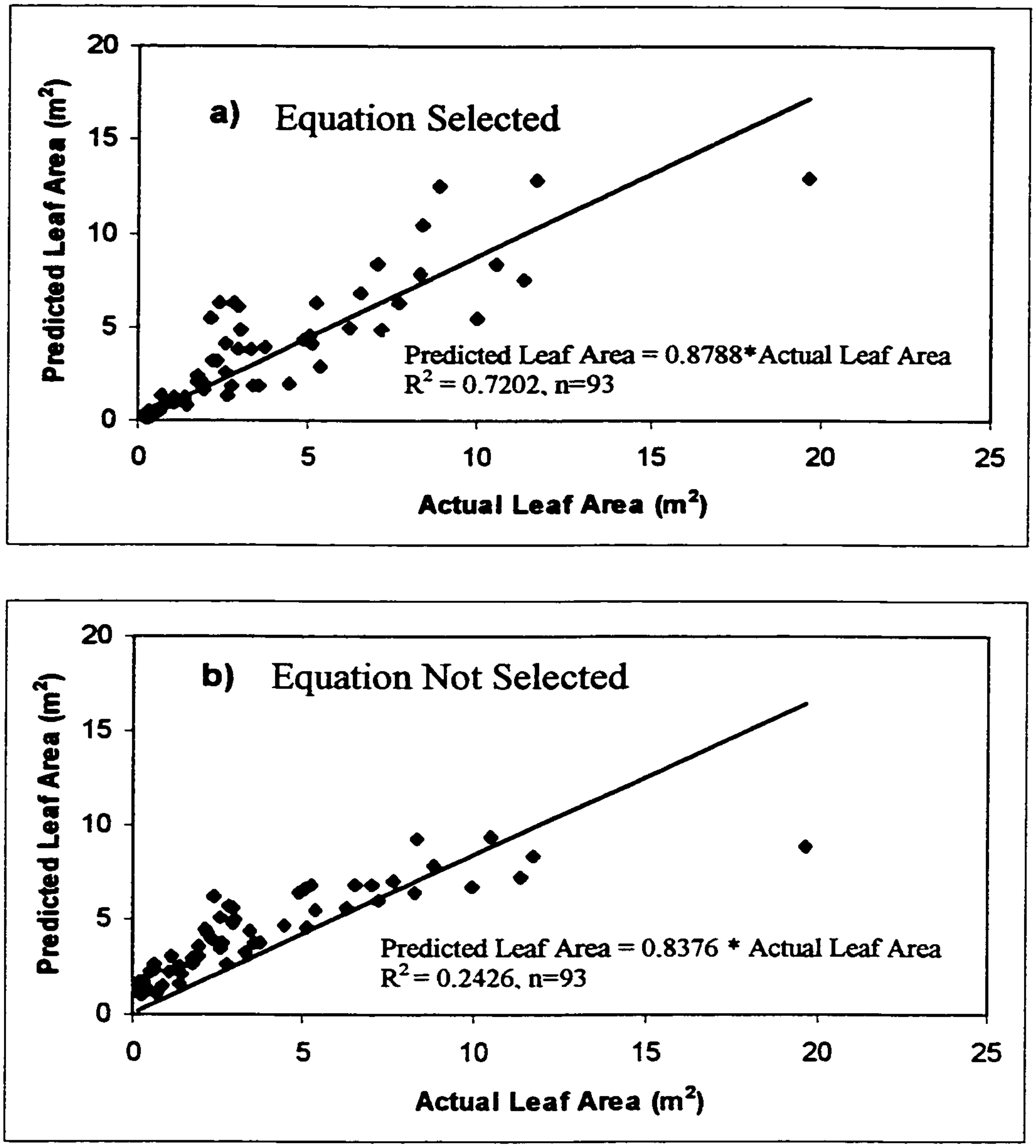

Figure 2.6: Predicted leaf area in relation to actual leaf area for canopy trees as predicted by a) the exponential function based on diameter at 30 cm height and used in the MIXLIGHT model, and b) multiple regression equation including basal area and diameter (Leaf Area = 1.2496*D_{30} – 0.1034*BA). The intercept was set at 0 to avoid negative leaf area values for small trees. This relationship was not used in the model.

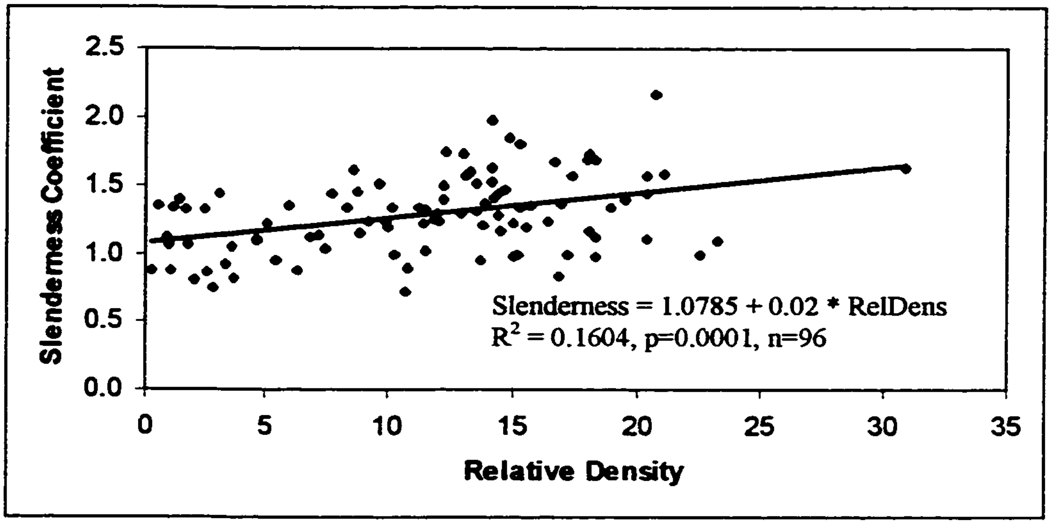

Figure 2.7: Slenderness coefficient of all trees in relation to relative density of the stand. Slenderness coefficient is the total height divided by diameter at 30 cm. Relative density combines stand basal area and average diameter to allow comparisons between stands of differing height and basal area (RelDens $= BA_{(D30)} / \text{Mean } D_{30}^{0.4}$).

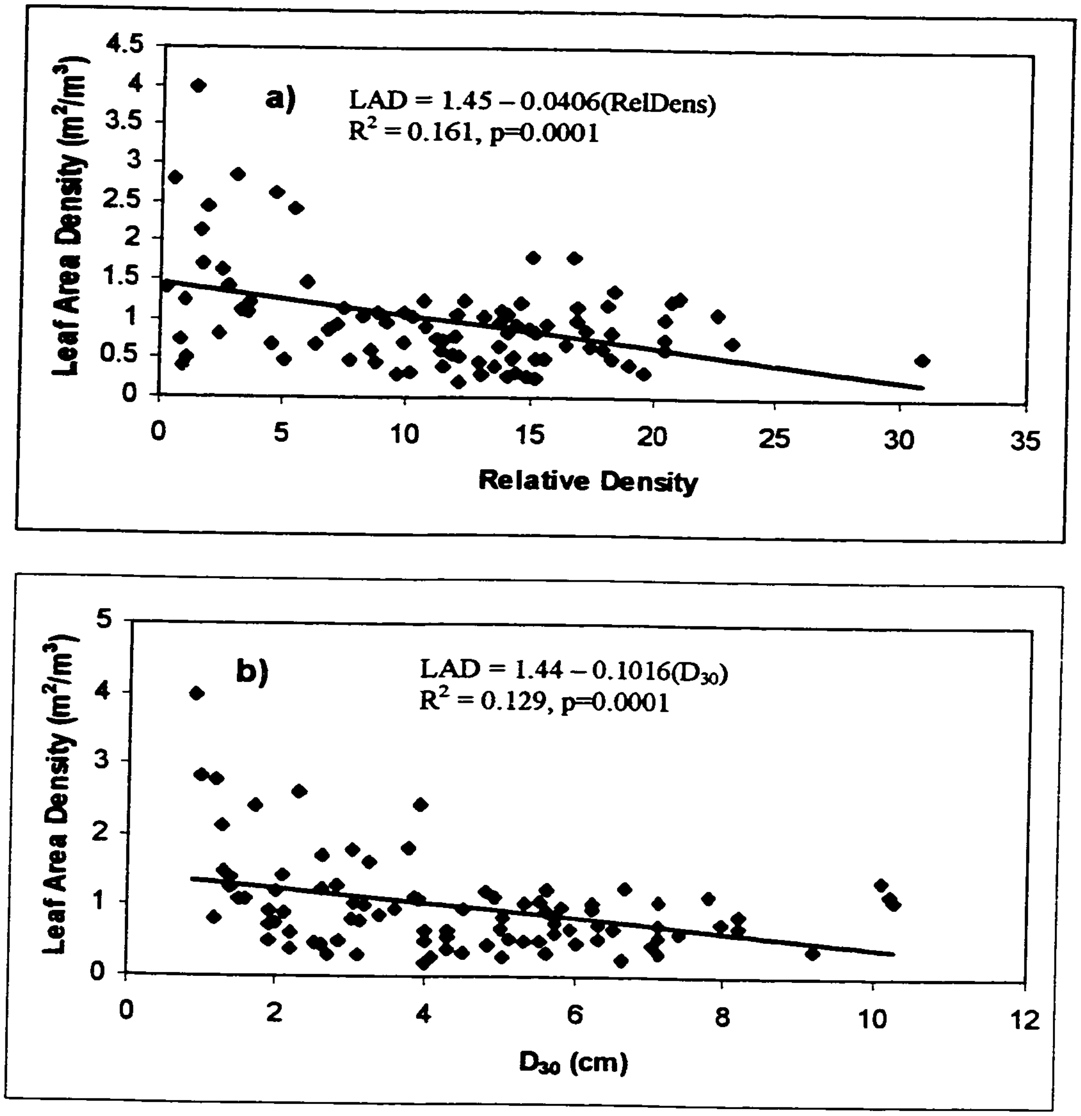

Figure 2.8: Leaf area density of all trees in relation to a) relative density of the stand and b) diameter at 30 cm height of the individual tree.

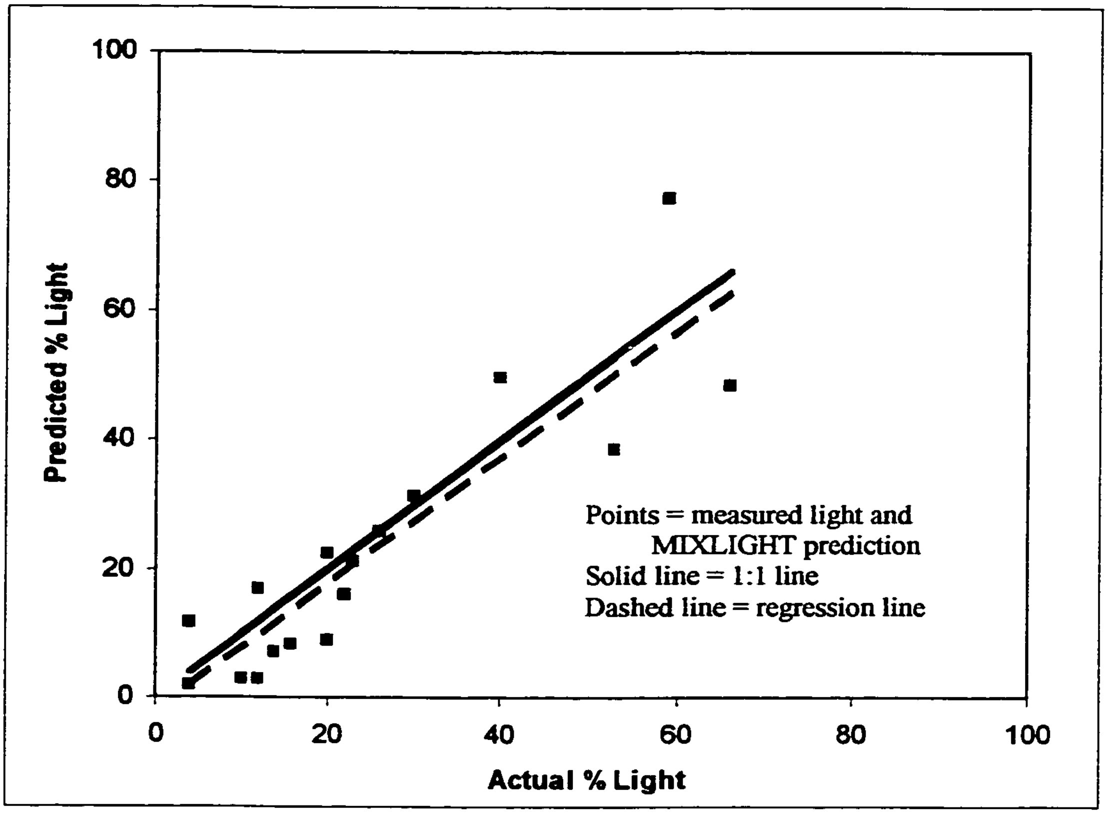

Figure 2.9: Predicted light transmission from MIXLIGHT in relation to actual light transmission. Solid line is the ideal 1:1 relationship and the dotted line is the regression line. The relationship between predicted and actual % light is not different from the ideal 1:1 relationship (slope=1, p=0.91; intercept=0, p=0.62). The equation for the regression line is: Predicted Light = -2.03 + (0.9859 * Actual Light)

$R^2 = 0.8005$, p=0.0001, n=17.

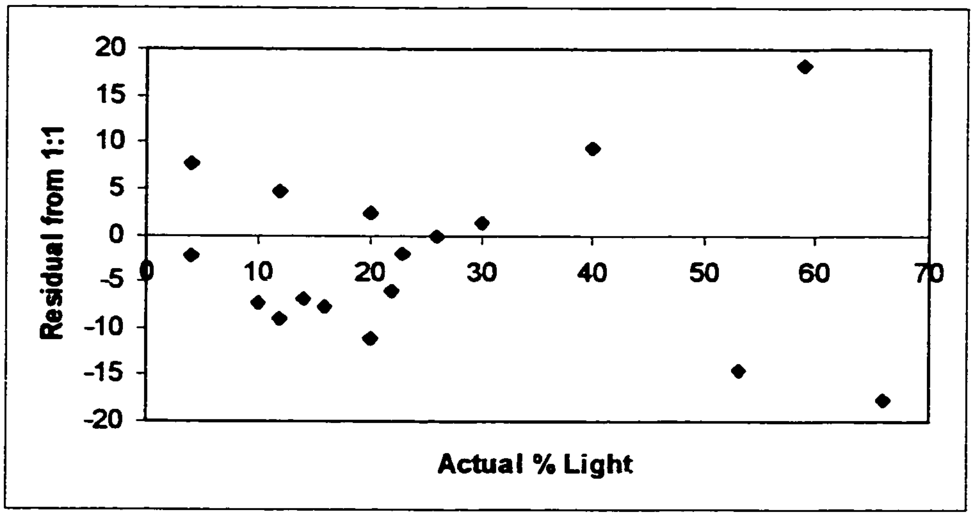

Figure 2.10: Residual of MIXLIGHT predicted % light from the ideal 1:1 relationship.

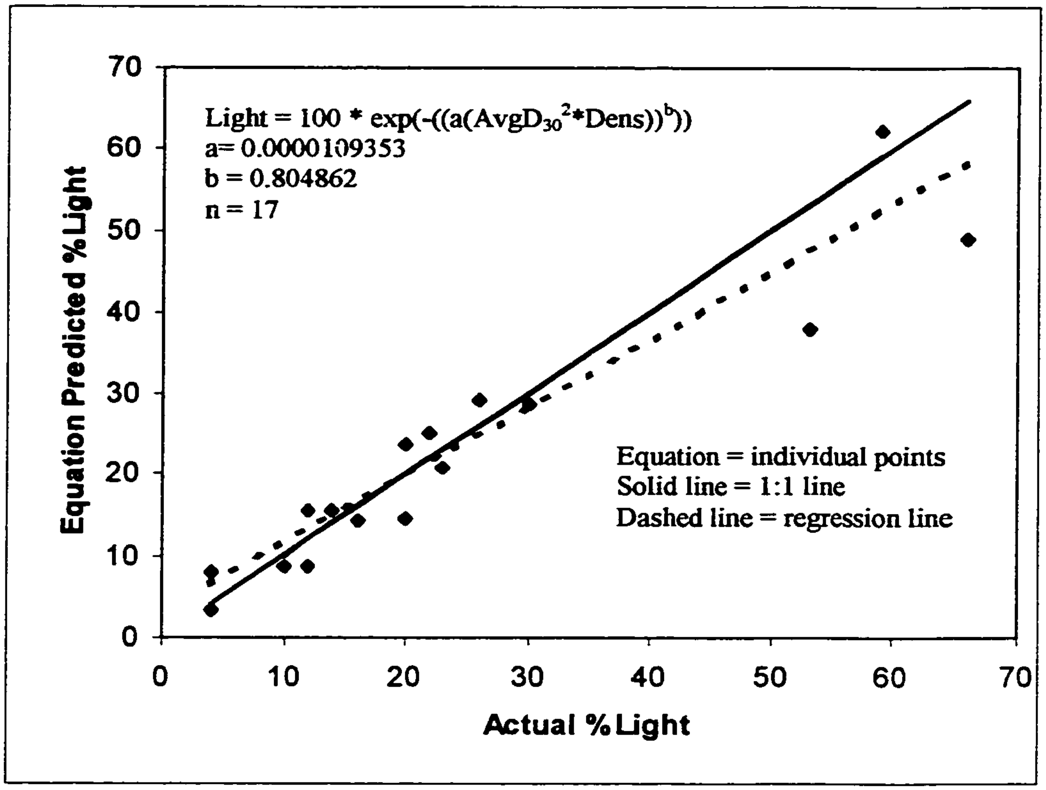

Figure 2.11: Predicted light transmission in relation to actual light transmission. Light transmission is predicted from an equation which uses the arithmetic average stand diameter at 30 cm ($AvgD_{30}$) and stand density (stems per hectare). The solid line is the ideal 1:1 relationship and the dashed line is the regression line between predicted and actual light transmission. The equation for the regression line is:

Predicted Light = 3.2581 + (0.8365 * Actual Light)

$R^2 = 0.869$, p=0.0001

This relationship is not different from the ideal 1:1 relationship (slope=1, p=0.07; intercept=0, p=0.23).

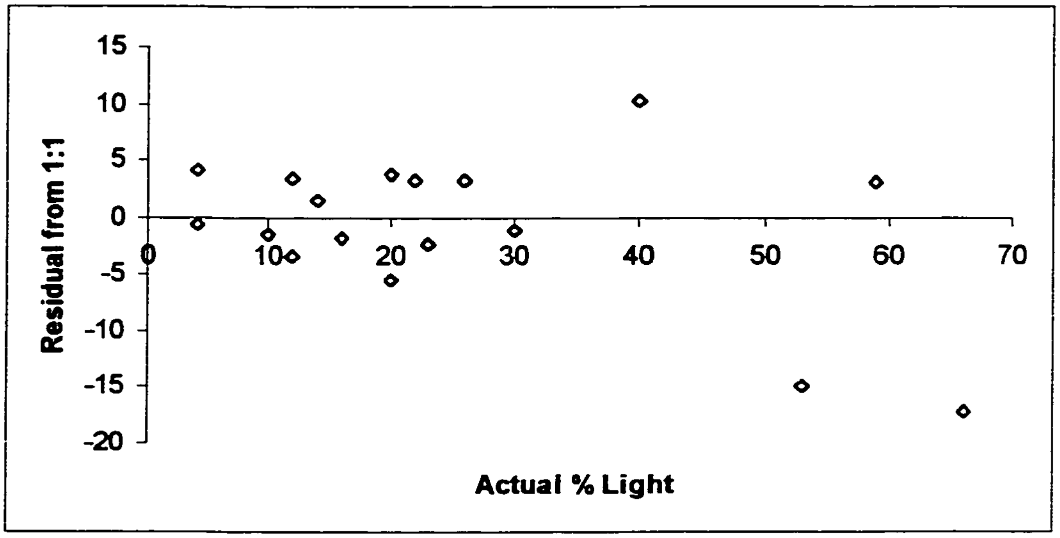

Figure 2.12: Residuals from the equation prediction of light transmission to the ideal 1:1 relationship between predicted and actual light transmission. Light prediction equation contains $\mathrm{AvgD}_{30}{}^2$ and Density.

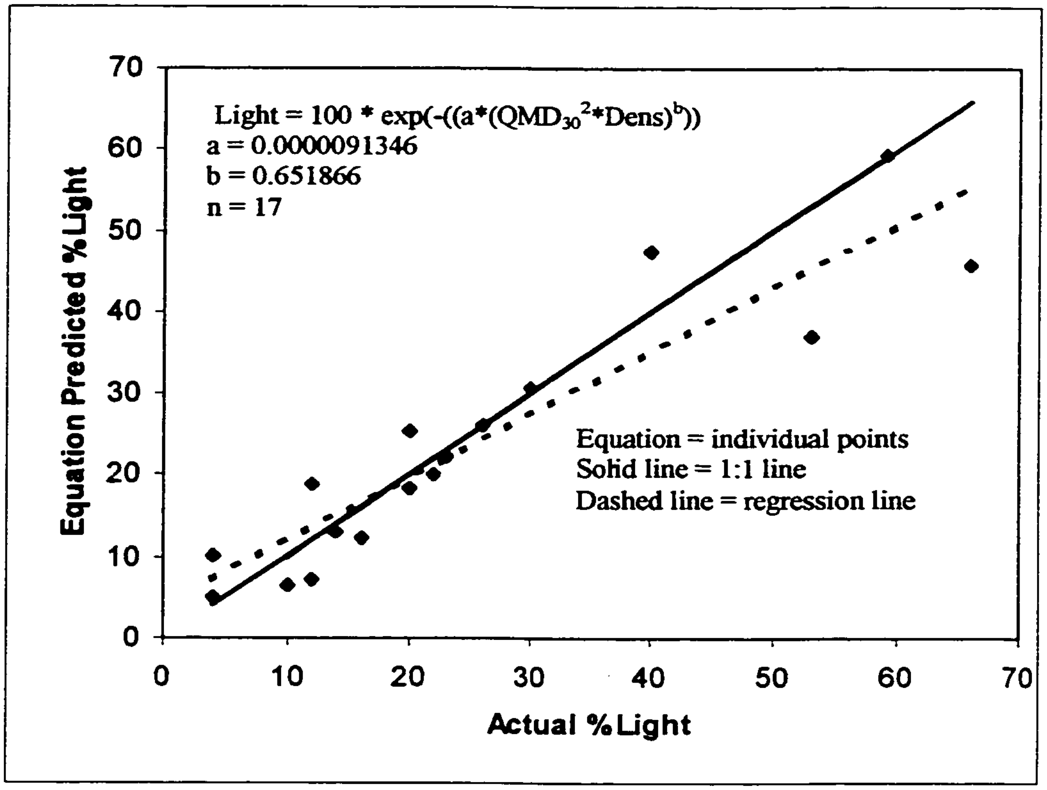

Figure 2.13: Predicted light transmission in relation to actual light transmission. Light transmission is predicted from an equation which uses the quadratic mean diameter at 30 cm of the stand (QMD_{30}) and stand density (stems per hectare). The solid line is the ideal 1:1 relationship and the dotted line is the regression line between predicted and actual light transmission. The equation for the regression line is:

Predicted Light = 4.1942 + (0.7778 * Actual Light)
$R^2 = 0.852$, p=0.0001

The slope of this relationship is significantly different from the ideal slope of 1 (p=0.02) but the intercept is not significantly different from the ideal intercept of 0 (p=0.23).

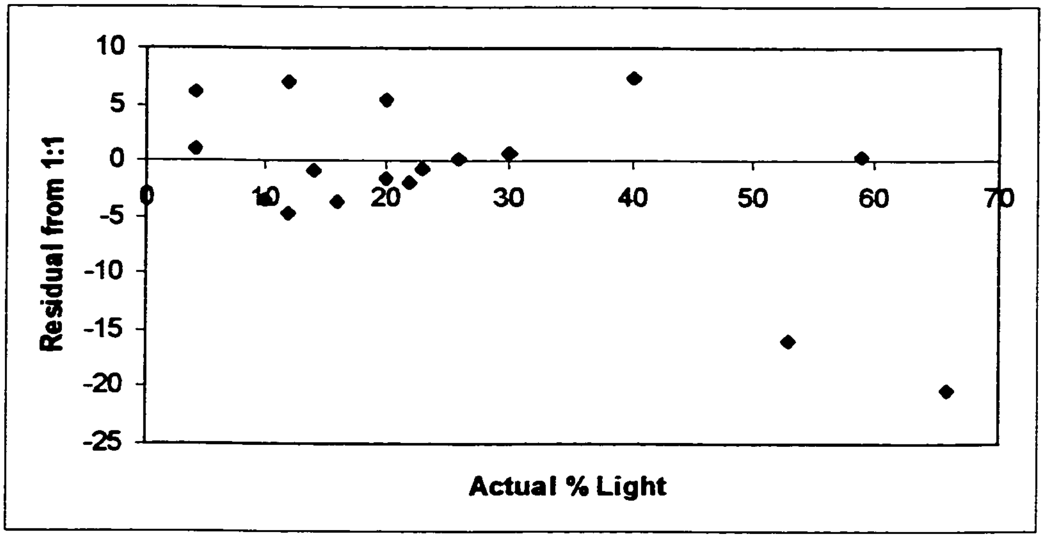

Figure 2.14: Residuals from the equation prediction of light transmission to the ideal 1:1 relationship between predicted and actual light transmission. Light prediction equation contains QMD_{30}^2 and Density.

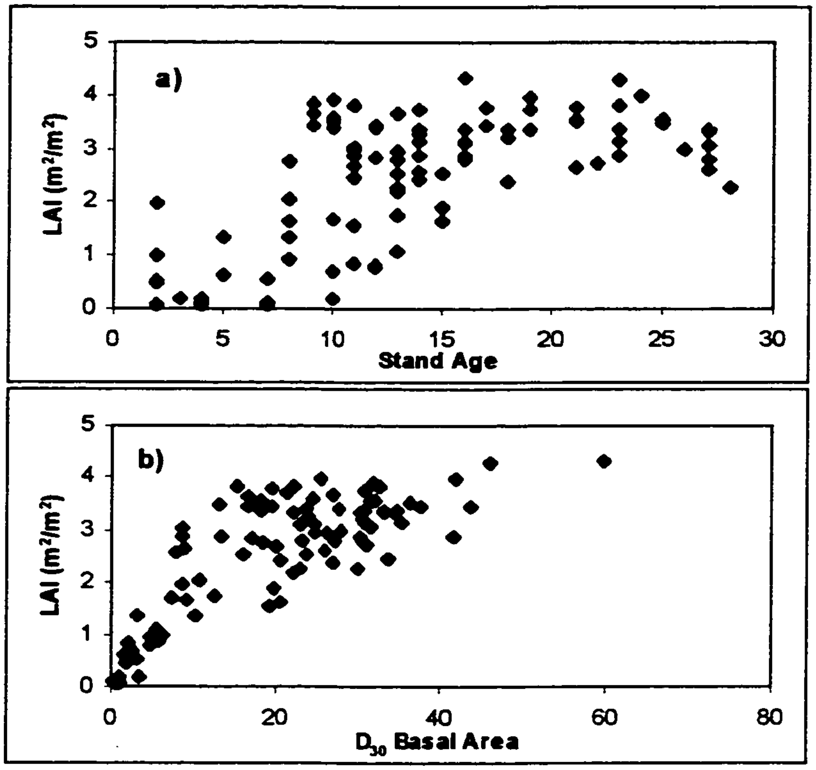

Figure 2.15: Stand level leaf area index in relation to a) stand age and b) stand level basal area at 30 cm height.

2.6 Tables

Table 2.1: Summary of regression equations for crown radius. The non-linear equations containing D_{30} were used in the model.

Canopy Tree Crown Radius

Dependent Variable	Independent Variables	R^2	Equation	Regression Type
CrRad	D_{30}	0.780	$51.22 * D_{30}^{0.5958}$	Non-linear
ln(CrRad)	$\ln(D_{30})$	0.837	$1.43 + (0.67 * \ln(D_{30}))$	Log-log
CrRad	D_{30}	0.748	$28.02 + (10.11 * D_{30})$	Linear
CrRad	$BA_{(D30)}$	0.349	$52.72 + (1.46 * BA_{(D30)})$	Linear
CrRad	D_{30}, CompD_{30}	0.763	$27.92 + (9.96*D30) + (0.23*CompD30)$	Multiple Linear

Intermediate Trees Crown Radius

Dependent Variable	Independent Variables	R^2	Equation	Regression Type
CrRad	D_{30}	0.530	$30.27 * D_{30}^{0.5692}$	Non-Linear
ln(CrRad)	$\ln(D_{30})$	0.563	$1.47 + (0.57 * \ln(D_{30}))$	Log-log
CrRad	D_{30}	0.505	$24.66 + (10.11 * D_{30})$	Linear
CrRad	D_{30}, Dens	0.535	$39.51 + (8.08 * D_{30}) - (0.0005 * Dens)$	Multiple Linear

Key:
CrRad – crown radius of individual tree
ln(CrRad) – natural logarithm of CrRad
D_{30} – stem diameter at 30 cm height
$\ln(D_{30})$ – natural logarithm of D_{30}
$BA_{(D30)}$ – stand basal area measured at 30 cm height
CompD_{30} – average D_{30} of closest competing tree in each of four quadrants surrounding the subject tree
Dens – stand density in stems/ha

Note: p-val of all relationships was 0.0001 or less. Other multiple regressions, including either $\ln(D_{30})$ or D_{30}, were tried but none significantly improved the prediction.

Table 2.2: Summary of regression equations for crown length. The non-linear equations containing D_{30} were used in the model.

Canopy Tree Crown Length

Dependent Variable	Independent Variables	R^2	Equation	Regression Type
CrLen	D_{30}	0.690	$99.36 * D_{30}^{0.6846}$	Non-linear
ln(CrLen)	$\ln(D_{30})$	0.786	$1.95 + (0.72 * \ln(D_{30}))$	Log-linear
CrLen	D_{30}	0.671	$79.33 + (42.12 * D_{30})$	Linear
CrLen	$BA_{(D30)}$	0.298	$184.36 + (5.95 * BA(D_{30}))$	Linear
CrLen	D_{30}, $BA_{(D30)}$	0.678	$77.69 + (49.00 * D_{30}) - (1.87 * BA_{(D30)})$	Multiple Linear
CrLen	D_{30}, $CompD_{30}$	0.697	$79.26 + (42.02 * D_{30}) + (0.15 * CompD_{30})$	Multiple Linear

Intermediate Tree Crown Length

Dependent Variable	Independent Variables	R^2	Equation	Regression Type
CrLen	D_{30}	0.560	$83.86 * D_{30}^{0.6845}$	Non-Linear
ln(CrLen)	$\ln(D_{30})$	0.614	$1.84 + (0.79 * \ln(D_{30}))$	Log-linear
CrLen	D_{30}	0.531	$52.98 + (39.7 * D_{30})$	Linear
CrLen	D_{30}, $BA_{(D30)}$	0.575	$33.08 + (33.6 * D_{30}) + (1.78 * BA_{(D30)})$	Multiple Linear
ln(CrLen)	$\ln(D_{30})$, $BA_{(D30)}$	0.653	$1.81 + (0.65 * \ln(D_{30})) + (0.004 * BA_{(D30)})$	Multiple Linear
ln(CrLen)	$\ln(D_{30})$, $\ln(BA_{(D30)})$	0.651	$1.74 + (0.60 * \ln(D_{30})) + (0.15 * \ln(BA_{(D30)}))$	Multiple Linear

Key:

CrLen – crown length of individual trees

ln(CrLen) – natural logarithm of CrLen

D_{30} – diameter at 30 cm height

$\ln(D_{30})$ – natural logarithm of D_{30}

$BA_{(D30)}$ – stand basal area measured at 30 cm height

$\ln(BA_{(D30)})$ – natural logarithm of $BA_{(D30)}$

$CompD_{30}$ – average D_{30} of closest competing tree in each of four quadrants surrounding the subject tree.

Note: p-val of all relationships was 0.0001 or less. Other multiple regressions, including either $\ln(D_{30})$ or D_{30}, were tried but none significantly improved the prediction.

Table 2.3: Summary of regression equations for individual tree leaf area. The non-linear equations containing D_{30} were used in the model.

Canopy Tree Leaf Area

Dependent Variable	Independent Variables	R^2	Equation	Regression Type
Leaf Area	D_{30}	0.750	$0.137 * D_{30}^{1.6773}$	Non-linear
ln(Leaf Area)	$\ln(D_{30})$	0.870	$-1.75 + (1.79 * \ln(D_{30}))$	Log-linear
Leaf Area	D_{30}	0.695	$-2.37 + (1.27 * D_{30})$	Linear
Leaf Area	D_{30}, $BA_{(D30)}$	0.742	$-2.47 + (1.68 * D_{30}) - (0.11 * BA_{(D30)})$	Multiple Linear
Leaf Area	D_{30}, $CompD_{30}$	0.750	$-2.12 + (1.65 * D_{30}) - (0.56 * CompD_{30})$	Multiple Linear

Intermediate Tree Leaf Area

Dependent Variable	Independent Variables	R^2	Equation	Regression Type
Leaf Area	D_{30}	0.610	$0.1295 * D_{30}^{1.6773}$	Non-linear
ln(Leaf Area)	$\ln(D_{30})$	0.626	$-1.42 + (1.19 * \ln(D_{30}))$	Log-linear
Leaf Area	D_{30}	0.567	$-0.47 + (0.48 * D_{30})$	Linear
Leaf Area	D_{30}, $BA_{(D30)}$	0.624	$-0.23 + (0.56 * D_{30}) - (0.11 * BA_{(D30)})$	Multiple Linear
Leaf Area	D_{30}, $CompD_{30}$	0.677	$-0.46 + (0.63 * D_{30}) - (0.12 * CompD_{30})$	Multiple Linear

Key:
D_{30} – diameter at 30 cm height
$\ln(D_{30})$ – natural logarithm of D_{30}
$BA_{(D30)}$ – stand basal area measured at 30 cm height
$\ln(BA_{(D30)})$ – natural logarithm of $BA_{(D30)}$
$AvgD_{30}$ – average D_{30} of closest competing tree in each of four quadrants surrounding the subject tree.

Note: p-val of all relationships was 0.0001 or less. Other multiple regressions, including either $\ln(D_{30})$ or D_{30}, were tried but none significantly improved the prediction.

Table 2.4: Correlation matrix for canopy tree characteristics.

r	D_{30}	ln(D_{30})	Leaf Area	ln(LfArea)	CrRad	ln(CrRad)	
D_{30}	1	0.95	0.836	0.892	0.868	0.840	
ln(D_{30})	0.95	1	0.742	0.934	0.888	0.917	
Leaf Area	0.84	0.742	1	0.838	0.745	0.683	
ln(LfArea)	0.89	0.934	0.838	1	0.890	0.910	
CrRad	0.87	0.888	0.745	0.890	1	0.966	
ln(CrRad)	0.84	0.917	0.686	0.910	0.966	1	
CrLen	0.82	0.819	0.768	0.819	0.831	0.813	
ln(CrLen)	0.83	0.889	0.695	0.872	0.871	0.902	
BA	0.77	0.750	0.496	0.584	0.600	0.613	
RelDens	0.64	0.660	0.444	0.523	0.524	0.553	
Dens	-0.42	-0.448	-0.296	-0.480	-0.432	-0.457	
Slender	-0.09	-0.103	-0.322	-0.242	-0.070	-0.073	
Comp D_{30}	0.80	0.739	0.521	0.598	0.604	0.595	

r	CrLen	ln(CrLen)	BA	RelDens	Dens	Slender	Comp D_{30}
D_{30}	0.822	0.826	0.766	0.636	-0.419	-0.085	0.80
ln(D_{30})	0.819	0.889	0.750	0.660	-0.448	-0.103	0.74
Leaf Area	0.768	0.695	0.496	0.444	-0.296	-0.322	0.52
ln(LfArea)	0.819	0.872	0.584	0.523	0.480	-0.242	0.60
CrRad	0.831	0.871	0.600	0.524	-0.432	-0.070	0.60
ln(CrRad)	0.813	0.902	0.613	0.553	-0.457	-0.073	0.59
CrLen	1	0.952	0.558	0.519	-0.376	0.028	0.55
ln(CrLen)	0.952	1	0.606	0.567	-0.401	0.023	0.58
BA	0.558	0.606	1	0.927	-0.179	0.252	0.80
RelDens	0.519	0.567	0.927	1	0.027	0.174	0.59
Dens	-0.376	-0.401	-0.179	0.027	1	-0.009	-0.40
Slender	0.028	0.023	0.252	0.174	-0.01	1	0.15
Comp D_{30}	0.552	0.578	0.804	0.592	-0.40	0.150	1

Key:
D_{30} – diameter at 30 cm height
ln(D_{30}) – natural logarithm of D30
Leaf Area – leaf area of individual canopy trees
ln(LfArea) – natural logarithm of Leaf Area
CrRad - crown radius of individual canopy trees
ln(CrRad) – natural logarithm of CrRad
CrLen – crown length of individual canopy trees
ln(CrLen) – natural logarithm of CrLen
BA – stand basal area measured at 30 cm height
RelDens – relative density of the stand
Dens – density of the stand
Slender – slenderness coefficient of the individual canopy tree
CompD30 –average D_{30} of closest competing trees

Table 2.5: Correlation matrix for intermediate tree characteristics.

r	D_{30}	ln(D_{30})	Leaf Area	ln(LfArea)	CrRad	ln(CrRad)	
D_{30}	1	0.975	0.761	0.827	0.742	0.769	
ln(D_{30})	0.975	1	0.700	0.798	0.735	0.768	
Leaf Area	0.761	0.700	1	0.929	0.660	0.654	
ln(LfArea)	0.827	0.798	0.929	1	0.705	0.732	
CrRad	0.742	0.735	0.660	0.705	1	0.985	
ln(CrRad)	0.769	0.768	0.654	0.732	0.985	1	
CrLen	0.751	0.768	0.757	0.841	0.644	0.659	
ln(CrLen)	0.749	0.791	0.712	0.835	0.659	0.686	
BA	0.439	0.536	0.104	0.319	0.260	0.324	
RelDens	0.238	0.361	-0.001	0.203	0.101	0.171	
Dens	-0.731	-0.655	-0.487	-0.500	-0.638	-0.623	
Slender	0.175	0.236	-0.140	0.078	0.210	0.224	
Comp D_{30}	0.815	0.812	0.432	0.580	0.638	0.681	
r	CrLen	ln(CrLen)	BA	RelDens	Dens	Slender	Comp D_{30}
D_{30}	0.751	0.749	0.439	0.238	-0.731	0.175	0.815
ln(D_{30})	0.768	0.791	0.536	0.361	-0.655	0.236	0.812
Leaf Area	0.757	0.712	0.104	-0.001	-0.487	-0.140	0.432
ln(LfArea)	0.841	0.835	0.319	0.203	-0.500	0.078	0.580
CrRad	0.644	0.659	0.260	0.101	-0.638	0.210	0.638
ln(CrRad)	0.659	0.686	0.324	0.171	-0.623	0.224	0.681
CrLen	1	0.979	0.524	0.421	-0.443	0.312	0.575
ln(CrLen)	0.979	1	0.599	0.591	-0.405	0.370	0.605
BA	0.524	0.599	1	0.953	-0.056	0.580	0.561
RelDens	0.421	0.591	0.953	1	-0.227	0.546	0.348
Dens	-0.443	-0.405	-0.056	-0.227	1	-0.112	-0.697
Slender	0.312	0.370	0.580	0.546	-0.112	1	0.333
Comp D_{30}	0.575	0.605	0.561	0.348	-0.697	0.33270	1

Key:
D_{30} – diameter at 30 cm height
ln(D_{30}) – natural logarithm of D30
Leaf Area – leaf area of individual intermediate trees
ln(LfArea) – natural logarithm of Leaf Area
CrRad - crown radius of individual intermediate trees
ln(CrRad) – natural logarithm of CrRad
CrLen – crown length of individual intermediate trees
ln(CrLen) – natural logarithm of CrLen
BA – stand basal area measured at 30 cm height
RelDens – relative density of the stand
Dens – density of the stand
Slender – slenderness coefficient of the individual intermediate tree
CompD30 –average D_{30} of closest competing trees

Table 2.6: Predicted understory light conditions based on average stand D_{30} (AvgD_{30}) and density.

Density\AvgD$_{30}$	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9	9.5	10	10.5	11
500	100	99	97	95	94	92	89	87	84	82	79	76	74	71	68	65	62	60	57	54	51	49
1000	99	97	95	92	89	86	82	78	74	70	66	62	58	55	51	47	44	**40**	**37**	**34**	**31**	**29**
1500	99	96	93	89	85	81	76	71	66	61	57	52	48	43	**39**	**35**	**32**	**28**	**25**	**23**	**20**	**18**
2000	99	95	92	87	82	76	71	65	60	54	49	44	**39**	**35**	**31**	**27**	**24**	**21**	**18**	**15**	**13**	**11**
2500	98	95	90	84	79	72	66	60	54	48	42	**37**	**33**	**28**	**24**	**21**	**18**	**15**	**13**	**11**	9	7
3000	98	94	88	82	76	69	62	55	49	43	**37**	**32**	**27**	**23**	**19**	**16**	**13**	**11**	9	7	6	5
3500	98	93	87	80	73	65	58	51	44	**38**	**32**	**27**	**23**	**19**	**16**	**13**	**10**	8	7	5	4	3
4000	97	92	86	78	70	62	55	47	**40**	**34**	**29**	**24**	**19**	**16**	**13**	**10**	8	6	5	4	3	2
4500	97	92	84	76	68	60	51	44	**37**	**31**	**25**	**21**	**16**	**13**	**10**	8	6	5	4	3	2	
5000	97	91	83	75	66	57	48	41	**34**	**28**	**22**	**18**	**14**	**11**	8	6	5	4	3	2		
5500	97	90	82	73	63	54	46	**38**	**31**	**25**	**20**	**16**	**12**	9	7	5	4	3	2			
6000	96	89	81	71	61	52	43	**35**	**28**	**23**	**18**	**14**	**10**	8	6	4	3	2	2			
6500	96	89	80	70	59	50	41	**33**	**26**	**20**	**16**	**12**	9	7	5	3	2	2				
7000	96	88	78	68	58	48	**39**	**31**	**24**	**19**	**14**	**10**	8	6	4	3	2					
7500	96	87	77	67	56	46	**37**	**29**	**22**	**17**	**13**	9	7	5	3	2	2					
8000	95	87	76	65	54	44	**35**	**27**	**21**	**15**	**11**	8	6	4	3	2						
8500	95	86	75	64	52	42	**33**	**25**	**19**	**14**	**10**	7	5	3	2							
9000	95	86	74	62	51	**40**	**31**	**24**	**18**	**13**	9	6	4	3	2							
9500	95	85	73	61	49	**39**	**30**	**22**	**16**	**12**	8	6	4	2	2							
10000	95	84	72	60	48	**37**	**28**	**21**	**15**	**11**	7	5	3	2								
10500	94	84	71	59	47	**36**	**27**	**20**	**14**	**10**	7	4	3	2								
11000	94	83	71	57	45	**34**	**26**	**18**	**13**	9	6	4	2	2								
11500	94	83	70	56	44	**33**	**24**	**17**	**12**	8	5	3	2									
12000	94	82	69	55	43	**32**	**23**	**16**	**11**	7	5	3	2									
12500	94	82	68	54	41	**31**	**22**	**15**	**10**	7	4	3	2									
13000	93	81	67	53	**40**	**30**	**21**	**14**	**10**	6	4	2										
13500	93	81	66	52	**39**	**28**	**20**	**14**	9	6	4	2										
14000	93	80	65	51	**38**	**27**	**19**	**13**	8	5	3	2										
14500	93	80	65	50	**37**	**26**	**18**	**12**	8	5	3	2										
15000	93	79	64	49	**36**	**25**	**17**	**11**	7	4	3	2										
16000	92	78	62	47	**34**	**24**	**16**	**10**	6	4	2											
17000	92	77	61	45	**32**	**22**	**14**	9	5	3	2											
18000	92	76	60	44	**31**	**21**	**13**	8	5	3												
19000	91	75	58	42	**29**	**19**	**12**	7	4	2												
20000	91	75	57	41	**28**	**18**	**11**	6	4	2												
21000	90	74	56	**39**	**26**	**17**	**10**	6	3	2												
22000	90	73	54	**38**	**25**	**16**	9	5	3													
23000	90	72	53	**37**	**24**	**15**	8	5	2													
24000	89	71	52	**35**	**23**	**14**	8	4	2													
25000	89	70	51	**34**	**21**	**13**	7	4	2													
26000	89	70	50	**33**	**20**	**12**	7	3	2													
27000	88	69	49	**32**	**19**	**11**	6	3														
28000	88	68	48	**31**	**19**	**10**	6	3														
29000	88	67	47	**30**	**18**	**10**	5	2														
30000	87	67	46	**29**	**17**	9	5	2														
31000	87	66	45	**28**	**16**	9	4	2														
32000	87	65	44	**27**	**15**	8	4	2														
33000	87	64	43	**26**	**15**	8	4	2														
34000	86	64	42	**25**	**14**	7	3															
35000	86	63	41	**24**	**13**	7	3															
36000	86	62	**40**	**24**	**13**	6	3															
37000	85	62	**40**	**23**	**12**	6	3															
38000	85	61	**39**	**22**	**12**	6	2															
39000	85	60	**38**	**22**	**11**	5	2															
40000	84	60	**37**	**21**	**11**	5	2															
45000	83	57	**34**	**18**	8	4																
50000	82	54	**31**	**15**	7	3																
55000	80	51	**28**	**13**	5	2																
60000	79	49	**25**	**11**	4	2																
65000	78	47	**23**	**10**	4																	
70000	77	45	**21**	9	3																	
75000	76	43	**19**	7	2																	

Light = 100 * exp(-((a*(AvgD$_{30}^2$*Density))^b))

a = 0.0000109353

b = 0.804862

$R^2 = 0.869$

Values in bold are between 10-40% light, conditions which are appropriate for the underplanting of white spruce.

Table 2.7: Predicted understory light conditions based on quadratic mean D_{30} (QMD_{30}) and density.

Density\QMD$_3$	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9	9.5	10	10.5	11
500	99	97	95	93	91	88	86	83	81	78	76	73	71	69	66	64	62	59	57	55	53	51
1000	98	95	92	89	86	82	79	75	72	68	65	62	58	55	52	49	47	44	41	**39**	**37**	**34**
1500	98	94	90	86	82	77	73	69	65	61	57	53	50	46	43	**40**	**37**	**34**	**32**	**29**	**27**	**25**
2000	97	93	88	83	78	73	69	64	59	55	51	47	43	**39**	**36**	**33**	**30**	**27**	**25**	**23**	**21**	**19**
2500	97	92	87	81	75	70	65	60	55	50	46	41	**38**	**34**	**31**	**28**	**25**	**22**	**20**	**18**	**16**	**14**
3000	96	91	85	79	73	67	61	56	51	46	41	**37**	**33**	**30**	**27**	**24**	**21**	**19**	**16**	**15**	**13**	**11**
3500	96	90	84	77	70	64	58	52	47	42	**38**	**33**	**30**	**26**	**23**	**20**	**18**	**16**	**14**	**12**	**10**	9
4000	95	89	82	75	68	62	55	49	44	**39**	**34**	**30**	**27**	**23**	**20**	**18**	**15**	**13**	**11**	**10**	8	7
4500	95	88	81	73	66	59	53	47	41	**36**	**32**	**27**	**24**	**21**	**18**	**15**	**13**	**11**	**10**	8	7	6
5000	95	87	80	72	64	57	50	44	**39**	**34**	**29**	**25**	**22**	**18**	**16**	**13**	**11**	**10**	8	7	6	5
5500	94	87	79	70	63	55	48	42	**36**	**31**	**27**	**23**	**20**	**17**	**14**	**12**	**10**	8	7	6	5	4
6000	94	86	77	69	61	53	46	**40**	**34**	**29**	**25**	**21**	**18**	**15**	**12**	**10**	9	7	6	5	4	3
6500	94	85	76	68	59	51	44	**38**	**32**	**27**	**23**	**19**	**16**	**13**	**11**	9	8	6	5	4	3	3
7000	93	85	75	66	58	50	43	**36**	**31**	**26**	**21**	**18**	**15**	**12**	**10**	8	7	5	4	4	3	2
7500	93	84	74	65	56	48	41	**35**	**29**	**24**	**20**	**17**	**14**	**11**	9	7	6	5	4	3	2	2
8000	93	83	73	64	55	47	**39**	**33**	**27**	**23**	**19**	**15**	**12**	**10**	8	6	5	4	3	3	2	2
8500	93	83	73	63	54	45	**38**	**32**	**26**	**21**	**17**	**14**	**11**	9	7	6	5	4	3	2	2	
9000	92	82	72	62	52	44	**37**	**30**	**25**	**20**	**16**	**13**	**11**	8	7	5	4	3	2	2		
9500	92	82	71	61	51	43	**35**	**29**	**24**	**19**	**15**	**12**	**10**	8	6	5	4	3	2	2		
10000	92	81	70	60	50	41	**34**	**28**	**22**	**18**	**14**	**11**	9	7	5	4	3	3	2			
10500	92	80	69	59	49	**40**	**33**	**27**	**21**	**17**	**14**	**11**	8	6	5	4	3	2	2			
11000	91	80	68	58	48	**39**	**32**	**26**	**20**	**16**	**13**	**10**	8	6	5	3	3	2				
11500	91	79	68	57	47	**38**	**31**	**25**	**19**	**15**	**12**	9	7	5	4	3	2	2				
12000	91	79	67	56	46	**37**	**30**	**24**	**19**	**15**	**11**	9	7	5	4	3	2	2				
12500	91	78	66	55	45	**36**	**29**	**23**	**18**	**14**	**11**	8	6	5	3	3	2					
13000	90	78	66	54	44	**35**	**28**	**22**	**17**	**13**	**10**	8	6	4	3	2	2					
13500	90	77	65	53	43	**34**	**27**	**21**	**16**	**12**	9	7	5	4	3	2	2					
14000	90	77	64	52	42	**33**	**26**	**20**	**16**	**12**	9	7	5	4	3	2						
14500	90	77	63	52	41	**33**	**25**	**20**	**15**	**11**	8	6	5	3	2	2						
15000	90	76	63	51	41	**32**	**25**	**19**	**14**	**11**	8	6	4	3	2	2						
16000	89	75	62	49	**39**	**30**	**23**	**18**	**13**	**10**	7	5	4	3	2							
17000	89	74	60	48	**38**	**28**	**22**	**16**	**12**	9	6	5	3	2	2							
18000	88	73	59	47	**36**	**27**	**21**	**15**	**11**	8	6	4	3	2								
19000	88	73	58	45	**35**	**26**	**19**	**14**	**10**	7	5	4	3	2								
20000	87	72	57	44	**34**	**25**	**18**	**13**	**10**	7	5	3	2	2								
21000	87	71	56	43	**32**	**24**	**17**	**13**	9	6	4	3	2									
22000	87	70	55	42	**31**	**23**	**17**	**12**	8	6	4	3	2									
23000	86	70	54	41	**30**	**22**	**16**	**11**	8	5	4	2	2									
24000	86	69	53	**40**	**29**	**21**	**15**	**10**	7	5	3	2										
25000	86	68	52	**39**	**28**	**20**	**14**	**10**	7	4	3	2										
26000	85	68	51	**38**	**27**	**19**	**13**	9	6	4	3	2										
27000	85	67	51	**37**	**27**	**19**	**13**	9	6	4	2	2										
28000	85	66	50	**36**	**26**	**18**	**12**	8	5	4	2											
29000	84	66	49	**35**	**25**	**17**	**12**	8	5	3	2											
30000	84	65	48	**35**	**24**	**17**	**11**	7	5	3	2											
31000	84	64	47	**34**	**23**	**16**	**11**	7	4	3	2											
32000	83	64	47	**33**	**23**	**15**	**10**	6	4	3	2											
33000	83	63	46	**32**	**22**	**15**	**10**	6	4	2												
34000	83	63	45	**32**	**21**	**14**	9	6	4	2												
35000	82	62	45	**31**	**21**	**14**	9	6	3	2												
36000	82	62	44	**30**	**20**	**13**	8	5	3	2												
37000	82	61	43	**30**	**20**	**13**	8	5	3	2												
38000	82	61	43	**29**	**19**	**12**	8	5	3	2												
39000	81	60	42	**28**	**19**	**12**	7	4	3	2												
40000	81	60	41	**28**	**18**	**11**	7	4	3													
45000	80	57	**39**	**25**	**16**	**10**	6	3	2													
50000	78	55	**36**	**23**	**14**	8	5	3														
55000	77	53	**34**	**21**	**12**	7	4	2														
60000	76	51	**32**	**19**	**11**	6	3	2														
65000	75	49	**30**	**17**	**10**	5	3															
70000	74	47	**28**	**16**	8	4	2															
75000	73	46	**27**	**15**	8	4	2															

Light = 100 * exp(-((a*(QMD_{30}^2*Density))^b))

a = 0.0000091346

b = 0.651866

$R^2 = 0.852$

Values in bold are between 10-40% light, conditions which are appropriate for the underplanting of white spruce.

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Chapter 3

Analysis of Alberta's Free-to-Grow Standards Using MIXLIGHT

3.1 Introduction

Free-to-grow (FTG) standards were developed to determine when conifer plantations have been successfully regenerated and are contributing to the overall forest production. They have been widely applied across Canada, including Alberta where the standards are also applied to conifer trees within mixedwood stands. Coniferous trees are considered FTG when adjacent hardwood or shrub species are sufficiently far away from the conifer crop tree that they are considered to have minimal competitive effects. This implies that conifer tree growth in a FTG plantation is limited only by site resources (Brand and Weetman 1986). FTG standards and the assumptions about tree growth of stands meeting FTG standards are important in sustaining the annual allowable cut for a region (MacDonald and Weetman 1993). They were developed because basic regeneration surveys were not able to predict future yields (Brand and Weetman 1986). The FTG standards are also intended to predict competition levels into the future and ensure that the conifer trees remain free from competition. Since competition is mainly for light in young stands (Brand 1986), FTG standards are all based on above-ground competition. The three main criteria used in determining FTG status are that the crop tree is a suitable species for the site, it has reached acceptable size and it is not limited by interspecific competition (Brand and Weetman 1986).

FTG standards are a type of competition index and are intended to quantify the level of competition that a coniferous crop tree is experiencing. Competition can be for light, water and nutrients but light is generally the resource in most demand in young stands (Brand 1986). Severe overtopping competition can result in reduced crop tree growth and mortality in young conifer plantations (Eis 1981). In the boreal mixedwood forest, a major source of competition for juvenile white spruce is from trembling aspen.

In Alberta, performance surveys, which determine the FTG status of a plantation, are carried out 8-14 years after harvesting. Mixedwood standards require that spruce trees be at least 1 m tall and be free of competing vegetation greater than 2/3 the height of the spruce tree within a 270° arc within a 1.5 m radius (Alberta Environment 2000). The previous requirements were that there be no competing brush greater than 2/3 the height of the spruce tree within a 1 m radius (Alberta Forest Service 1992). However, there has been little empirical or modeling research to justify the standards.

Spruce height growth, which is a good indicator of vigour and competitive status, is reduced at light levels below 40% of overstory light (Lieffers and Stadt 1994; Logan 1969). Therefore, 40% transmitted light may be an acceptable threshold for FTG standards. However, no research has been done on light levels associated with different FTG standards. It should be possible to use the MIXLIGHT light transmission model (Stadt and Lieffers 2000) to evaluate the FTG standards in Alberta from the perspective of available light for a spruce tree in mixedwood stands with competing aspen trees.

The objectives of this study are to model available light at various positions under the canopy of aspen stands of different size and spatial configuration. This can then be used to test and project the impact of meeting the FTG standard on available light. Some specific research questions include: 1) Is the distance to competitors an important predictor of available light for the crop tree? 2) What is the effect of average hardwood tree size and density on light transmission? 3) Are the standards able to predict competition levels into the future or just at a single time?

3.2 Methods

In order to examine Alberta's FTG standards, 14 x 14 m modeled stands of young aspen trees were developed for a variety of height and density classes. Using the relationships previously developed between crown characteristics and diameter (see Chapter 2), all of the trees within the plots were modeled based on their diameter at 30 cm height (D_{30}) and crown class. The modeled characteristics include height, crown radius, crown length and leaf area. Three stands with different spatial arrangements were used and each was modeled several times with increasing sizes of trees intended to simulate growth of the stand. Stand 1 had varying densities of aspen trees within it as well as different sized trees of both canopy and intermediate crown class (Fig. 3.1). Three separate stands with different sizes of trees were modeled using this spatial arrangement which had average D_{30} of 2.5, 4.5 and 6.5 cm. The tree positions were chosen in order to produce a variety of possible FTG combinations. The stand was grown by adding 2 cm to the D_{30} of each tree. For the largest tree size the growth of some of the canopy trees was reduced in areas of high density in order to maintain the appropriate crown overlap (Fig. 2.1). Tree positions were never changed and there was no mortality. The other stands, Stand 2 (Fig 3.2) and Stand 3 (Fig. 3.3), had 2 and 3 m regular spacing of aspen trees with all trees being the same size and in the canopy crown class. Five size classes were examined for each spacing regime with D_{30} of 1.5, 3, 4.5, 6 and 8cm which corresponded to heights of approximately 2, 4, 6, 8 and 10 m tall.

Growth of these stands was modeled in the same way by increasing the D_{30} of all the trees. These regular spacing scenarios were intended to represent possible brushing programs to meet FTG standards. The 2 m spacing was chosen because with this density there could have been trees which were FTG under the old standard. The 3 m spacing was chosen since all conifer trees would be considered FTG with this spacing under the new FTG standards.

Within these modeled stands, points were chosen which represented a variety of possible FTG combinations. Points at 1 m height, which is the minimum height for white spruce in Alberta's performance survey, were intended to represent white spruce crop trees for which FTG surveys would be conducted. Estimated points included positions that were categorized as FTG, positions that were not FTG, various distances to competing trees, different spatial arrangements of competing trees and varying densities and sizes of competing trees. Using MIXLIGHT (Stadt and Lieffers 2000), understory light was modeled for completely overcast conditions which means that light originates equally from all parts of the sky. This was done because instantaneous light measurements of uniform canopies during diffuse light conditions are thought to well represent the seasonal light transmission to that point (Messier and Puttonen 1995). These modeled light values were then compared to FTG status and the required light levels for acceptable spruce growth.

3.3 Results

The distance from the crop tree to the nearest competing aspen stem did not appear to greatly affect the amount of available light. For example, in Stand 3 with D_{30} of 4.5, point 4 was 0.41 m from the nearest competitor while point 11 was 1.41 m from the nearest competitor but the light transmission values were 79.7 and 77.9 % respectively. This shows that the distance between the crop tree and the nearest single competing tree did not have a great effect on available light if spacing and density are relatively uniform throughout the stand. This trend appeared in all modeled stands regardless of density and average tree size.

The size of the competing aspen trees had a much greater impact on available light. For example, in Stand 2 the available light at point 8 decreased from 97.0 to 21.4 % as the aspen D_{30} increased from 1.5 to 8 cm. The distance from the point to the surrounding stems and the total stem density remain unchanged but light decreased dramatically as competing stem size increased even though this point would have always been considered FTG. This also shows that meeting a FTG standard does not ensure high light availability into the future.

The density of competing stems also had an important effect on available light. Comparisons between Stands 2 and 3 show that for each size class the light transmission values were much lower in Stand 2 with a 2 m regular spacing than in Stand 3 with a 3 m regular spacing. For example, with a D_{30} of 6, Stand 2 had approximately 41 % light transmission while Stand 3 had approximately 65 % light transmission. When the stands are not evenly spaced the effect of localized density was important in determining the amount of available light. For example, Stand 1 had fairly low overall density but point 1 occurred in a localized area of very high density so the available light was much lower than nearby locations. It appears that for very low light conditions which are harmful to white spruce growth, many aspen trees with overlapping crowns are required.

The regular spacing arrangements simulate possible thinning regimes done to ensure the FTG status of the conifer trees. Stand 2, with a density of 2500 stems per hectare and 2 m spacing, was projected to have the tree crowns touching each other at 8 cm D_{30}. At this point light transmission through the overstory was reduced to approximately 23 % (Table 3.2). This light level is low enough to reduce the height growth of spruce but not low enough to cause death of spruce seedlings. For Stand 3, with a density of approximately 1100 stems per hectare and 3 m spacing, crowns were still not touching at 8 cm D_{30}. Here light transmission was approximately 49%, light levels which would allow for maximum spruce height growth.

It appears that with both the old and the new FTG standards that FTG status is not always related to available light. There were points which would be considered FTG which had less light than points not FTG. For example, in Stand 2 with a D_{30} of 6, point 9 would be considered FTG under the new standards with 39.1 % light while point 1 would not be considered FTG even though it has 50.5 % light. With the old standard the lack of relationship which can occur between FTG status and light is even more noticeable. For example, in Stand 1 with average D_{30} of 6.5 cm, point 12 would have been considered FTG as there were no competing stems within 1 m even though available light was only 21.1 %. There are many points within this stand which are not FTG but which have a much higher light level. The FTG standards seem to take into account the distance to competitors in the form of the plot radius but do not deal with size or density of competing aspen trees which appears to be a more important factor determining available light.

3.4 Discussion

Based upon the above analysis, the Alberta FTG standards appear to be an arbitrary concept. The distance from the crop tree to the nearest competing tree does not seem to have much effect on available light for the crop tree. This calls into question the FTG plot radius of 1.5 m in the new mixedwood standard and 1 m in the old standard. It appears that the main reason for these plot sizes is ease of operation, they allow the surveys to be carried out quickly, efficiently and reproducibly. However there is very little justification for their plot size as is the case with most competition indices such as Comeau et al. (1993), Brand (1986) and DeLong (1991). Determining an appropriate plot size which takes into account most competing vegetation which affects light transmission to the crop tree would be beneficial but this plot size would have to change as the competing trees became larger and taller (Burton 1993). Taller trees can affect the light regime of the crop tree from farther away and FTG standards should incorporate this in the form of larger plot sizes.

The size of the competing trees is also important in determining the amount of light reaching the crop tree. As aspen trees become larger they carry much more leaf area than smaller trees and therefore absorb more light. This means that one large tree may have more effect on the light regime of the crop tree than two smaller trees. However, under the new standards one large competing tree could be acceptable but two smaller trees positioned nearby in different quadrants of the plot would not. Therefore, size of competing stems should be taken into account within the FTG standards but this is not currently done other than as a single threshold point at 2/3 of the conifer height. Also, as the same stand grows and the aspen trees become larger, light is greatly reduced even if the FTG status of the crop trees remains the same. This inability to deal with changing conditions is common to most competition indices (Burton 1993).

Density is another major factor affecting light transmission to the crop tree. This includes both overall stand density outside of the FTG plot and localized density within the plot. At the stand level, if aspen density is reduced to an acceptable level there should be enough light for the spruce trees to grow well. This density can be determined from the previously developed light table (Table 2.6) based on the size of the aspen trees and the desired light level. Density also affects crown overlap in the modeled stands. In Stand 3, branches of different trees never touched each other and there was always plenty of light for spruce growth. Even if this stand was grown further, there would probably never be any crown overlap since overlap decreases as the size of canopy trees increases (see Chapter 2). Thus light levels would probably never reach harmful levels for spruce growth. This density of approximately 1100 stems per hectare may be an appropriate level of aspen in mixedwood stands to allow spruce growth. Even if the crop tree were considered FTG with no competing trees within the plot, light levels may still be reduced if the surrounding stem density is high and the competing trees are tall. It appears that stand level characteristics are more important predictors of light transmission and the potential future growth of the crop tree than simple rules about the distance to the nearest competitor.

Localized density around the crop tree is also important. For light levels to be seriously reduced under aspen trees there needs to be very high density with overlapping crowns. This overlapping of crowns greatly increases the local leaf area and could produce very low light levels. The exact number of trees needed to produce undesirable light levels depends on the size of competing stems and could be estimated from the light table (Table 2.6). Aspen stem density needs to be at an acceptable level in the vicinity around the conifer tree and this should be incorporated into the standards along with stand level density.

A good FTG standard for boreal mixedwood forests should be based on light levels which incorporate acceptable spruce growth while still allowing for the maintenance of the aspen component. It is not necessary or desirable to remove all of the aspen trees as there are many benefits associated with mixed-species stands including increased biodiversity and productivity (Man and Lieffers 1999). For this to be done acceptable overall stand density of the aspen needs to be established. The old FTG standard in Alberta did not allow any competing tree within 1 m of the coniferous crop tree. This was a very strict standard. The new FTG regulations for spruce in mixedwood stands allow competition within a 90° arc surrounding the tree, the other 270° arc must be free of competition within a 1.5 m radius thereby increasing the chance of having some aspen trees remain on the site. In short stands a 1 m plot radius may be sufficient to capture all of the competing vegetation but in tall stands, as they can be at 14 years old, a larger plot is needed to get an accurate picture of the stand level density. When trees are large, perhaps moving to a 50 m^2 plot with a plot radius of 3.99 m or even larger would be necessary. However, high localized density is also important since this is the only way of creating harmfully low light levels for spruce growth so a smaller plot may be needed within the larger plot. Finally, there should be less reliance on the distance to nearest competitor since this is less important in determining average available light. If local areas had very high densities they should not be FTG regardless of the distance to nearest competitor or the spatial arrangement of the competitors. These recommendations could help to create better FTG standards which are more effective in predicting the actual growing conditions of the spruce crop trees and better at predicting future competition.

Possible shortcomings of this study include: 1) Only looking at light transmission in modeled aspen stands, not including other competing species such as alder, hazel or willow. These species can seriously reduce the available light and further research needs to be done on their light attenuation in regards to FTG standards. However, in the boreal mixedwood forest competition is often between the two major tree species, aspen and white spruce, so this study should be useful for a great number of stands. 2) There has been no attempt to deal with below ground competition for nutrients and water. Although this may be important on some dry or nutrient poor sites, in the majority of young stands competition is mainly for light (Brand 1986). When below ground competition has been added to other competition indices it has generally been based on above ground attributes (Holmes and Reed 1991) and since leaf area is correlated with root biomass in young aspen stands above ground attributes may be a good predictor of below ground competition (DesRochers 2000). 3) Light was only modeled for completely overcast coniditions. On sunny days overtopping trees and trees to the south of the crop tree would have a greater effect on available light. However, the FTG standards have no aspect considerations for competing trees. Also, overcast conditions should give accurate estimates of the average yearly light conditions in uniform canopies (Messier and Puttonen 1995). 4) MIXLIGHT has not been properly validated to predict microsite light conditions in young aspen stands. It has only been validated to predict plot average light conditions (see Chapter 2). This is work which needs to be completed in the future. 5) This study only dealt with aspen and spruce mixedwoods. In stands that are intended to be single species coniferous stands and in stands which contain shade-intolerant conifer crop trees such as jack pine, different recommendations would be necessary.

The new Alberta FTG standards are an improvement over the previous standards but there has still been little work done to quantify and analyze the standards from the perspective of available light for the spruce crop trees. This work indicates that the distance between the crop tree and competing tree is not very important in determining available light. The more important factors are competing tree size and competing density, both within and outside of the plot, and these should be incorporated into the FTG standards.

3.5 Figures

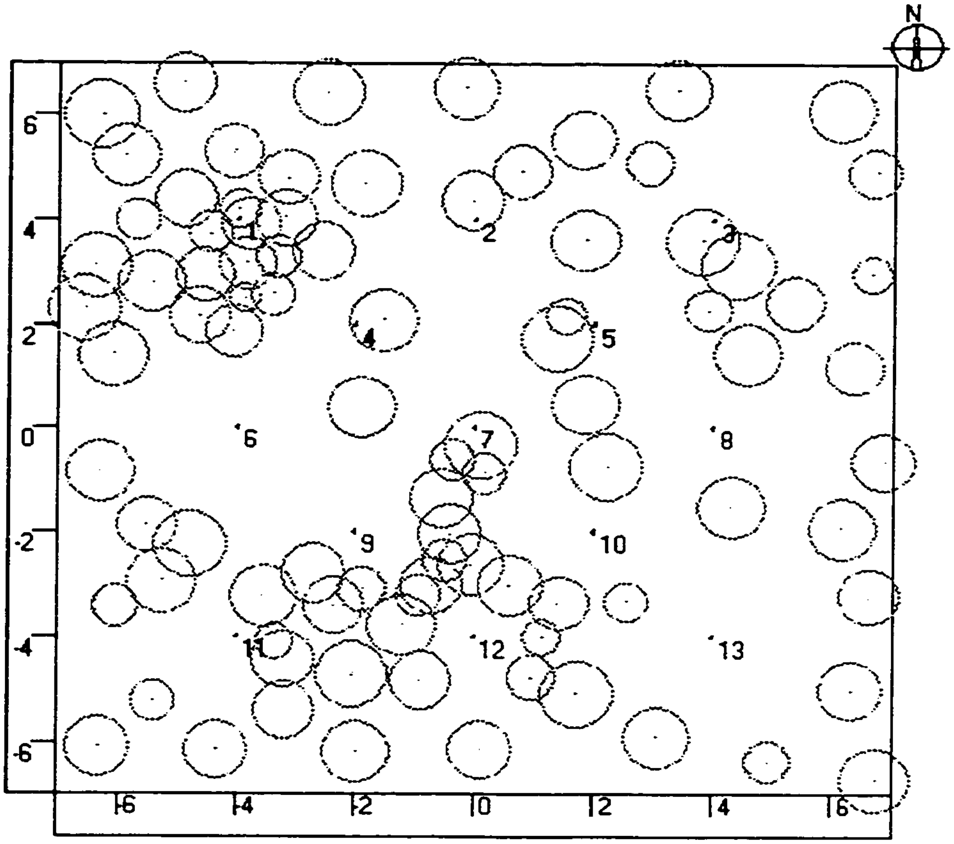

Figure 3.1: Stand 1 with average D_{30} of 2.5 cm. Density is approximately 4600 stems / ha. The numbered points are where light was predicted.

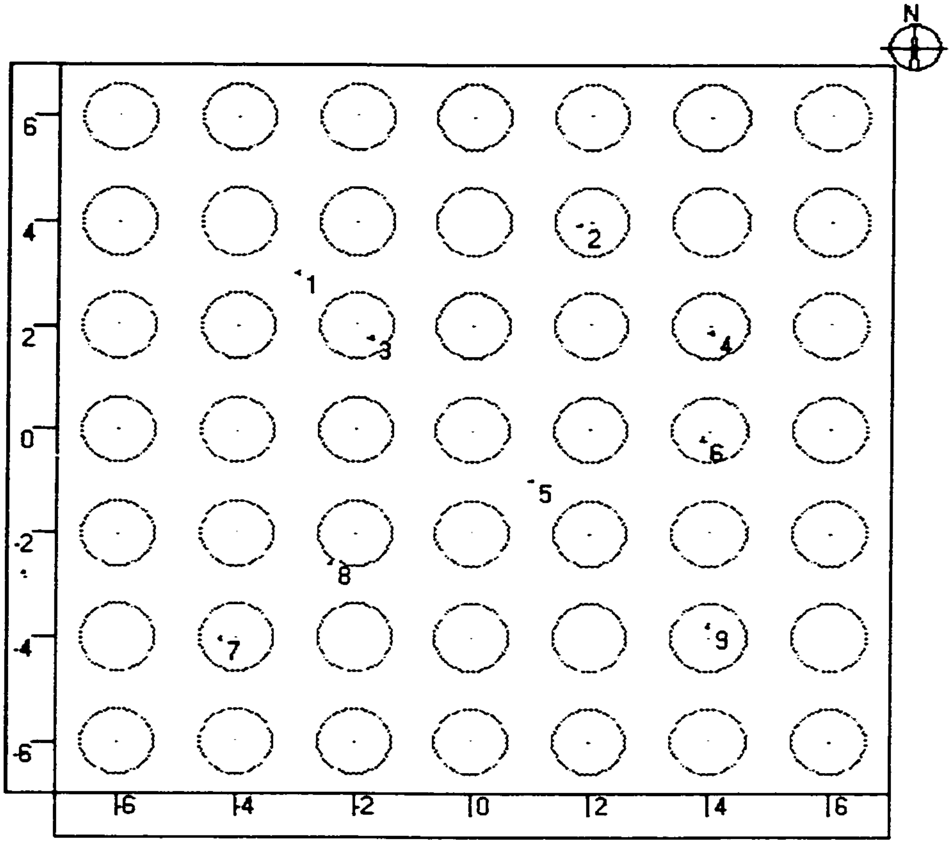

Figure 3.2: Stand 2 with regular spacing of 2 m and tree D_{30} of 3 cm. Density is 2500 stems / ha. The numbered points are where light was predicted.

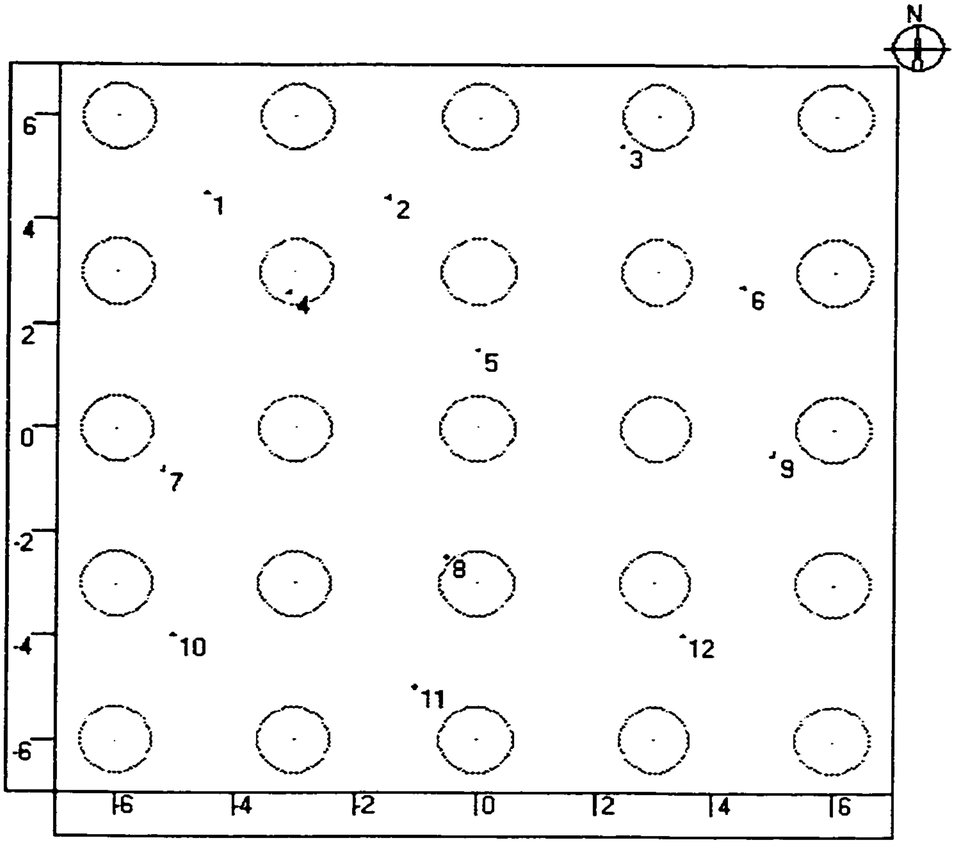

Figure 3.3: Stand 3 with regular spacing of 3 m and tree D_{30} of 3 cm. Density is approximately 1100 stems / ha. The numbered points are where light was predicted.

3.6 Tables

Table 3.1: Summary of free-to-grow status and light conditions for various points below Stand 1 for three different tree sizes (see Fig. 3.1).

			AvgD$_{30}$ = 2.5 cm	= 4.5 cm	= 6.5 cm
Point	New FTG	Old FTG	% Light	% Light	% Light
1	No	No	55.4	36.8	19.4
2	Yes	No	80.4	50.5	26.7
3	Yes	No	82.4	50.9	28.0
4	Yes	No	81.7	50.1	26.1
5	Yes	No	81.1	52.4	30.2
6	Yes	Yes	85.9	51.0	26.7
7	Yes	No	80.0	50.5	28.6
8	Yes	Yes	84.8	54.4	29.1
9	No	Yes	78	45.9	24.9
10	No	Yes	83.5	49.8	28.0
11	No	No	76.8	46.5	24.8
12	No	Yes	75.6	41.3	21.1
13	Yes	Yes	88.2	55.2	29.3

D_{30} - aspen stem diameter at 30 cm height

New FTG - this represents whether the point would be considered free-to-grow under the new standards.

Old FTG – this represents whether the point would be considered free-to-grow under the old standards.

Table 3.2: Summary of free-to-grow status and light condition for various points below Stand 2 for five different tree sizes (see Fig. 3.2).

			Height = 1.9 m	= 4.1 m	= 6.3 m	=8.1 m	=10.0 m
			D_{30} =1.5 cm	= 3 cm	=4.5 cm	=6 cm	=8 cm
Point	New FTG	Old FTG	% Light	% Light	% Light	% Light	% Light
1	No	Yes	97.9	80.9	63.4	50.5	25.5
2	Yes	No	90.9	80.4	59.3	39.6	22.1
3	Yes	No	87.1	79.0	61.5	41.8	22.9
4	Yes	No	87.8	78.4	59.1	39.4	21.2
5	No	Yes	97.8	81.2	62.4	50.7	25.5
6	Yes	No	88.8	80.1	61.4	41.7	22.0
7	Yes	No	94.3	79.8	60.5	41.5	21.8
8	Yes	No	97.0	79.6	60.6	40.3	21.4
9	Yes	No	87.3	77.9	59.5	39.1	21.8

Height - aspen tree height
D_{30} - aspen stem diameter at 30 cm height
New FTG - this represents whether the point would be considered free-to-grow under the new standards.
Old FTG – this represents whether the point would be considered free-to-grow under the old standards

Table 3.3: Summary of free-to-grow status and light conditions for various points below Stand 3 for five different tree sizes (see Fig. 3.3).

			Height = 1.9 m	= 4.1 m	= 6.3 m	= 8.1 m	=10.0 m
			D_{30} =1.5 cm	= 3 cm	=4.5 cm	= 6 cm	= 8 cm
Point	New FTG	Old FTG	% Light	% Light	% Light	% Light	% Light
1	Yes	Yes	99.5	89.5	77.7	66.4	52.0
2	Yes	Yes	99.5	89.3	77.7	67.3	53.5
3	Yes	No	98.6	90.0	77.6	64.5	47.2
4	Yes	No	92.1	89.8	79.7	66.9	45.6
5	Yes	Yes	99.3	88.9	75.1	61.8	47.4
6	Yes	Yes	99.3	90.1	77.4	63.9	48.5
7	Yes	Yes	99.0	90.0	78.4	65.3	46.8
8	Yes	No	97.6	89.7	78.5	65.6	47.8
9	Yes	Yes	99.0	89.5	77.9	65.1	49.1
10	Yes	Yes	99.4	89.9	77.7	64.9	49.2
11	Yes	Yes	99.4	89.8	77.9	65.7	50.9
12	Yes	Yes	98.9	90.3	78.9	65.7	49.3

Height - aspen tree height

D_{30} - aspen stem diameter at 30 cm height

New FTG - this represents whether the point would be considered free-to-grow under the new standards.

Old FTG – this represents whether the point would be considered free-to-grow under the old standards

3.7 References

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Chapter 4

Summary and Future Work

4.1 Summary

Recently there has been increased interest in more natural silvicultural techniques. In the boreal mixedwood forest this means maintaining both spruce and aspen in mixedwood stands and not converting them to either single species hardwood or softwood stands. There are both biodiversity and productivity benefits to maintaining mixedwood stands but the silvicultural techniques required to achieve these benefits have not been fully developed. These techniques include underplanting of white spruce in aspen stands to create the desired mixedwood stands where they have not developed naturally. However, it is still not clear what types of aspen stands are suitable for underplanting. Maintaining mixedwood stands may also require changing our reforestation policies, in particular the free-to-grow standards. These standards should reflect acceptable growing conditions for spruce trees while maintaining aspen on the site. Since light is the resource in most demand in young forest stands, understory light prediction models can help us develop better silvicultural techniques and standards.

The objective of Chapter 2 was to predict light in a variety of young aspen stands using different light prediction methods. Examination of individual tree characteristic development for input into the MIXLIGHT forest light transmission model shows that crown characteristics of young aspen trees, including crown size and leaf area, are best predicted from stem diameter and crown class. Including a measure of competition such as stand basal area or relative density did not improve the prediction; however, competition did affect diameter growth of the trees thereby affecting crown characteristics. Leaf area was also affected by crown class with canopy trees carrying much more leaf area than intermediate trees of similar size. As there was virtually no heartwood in these trees this indicates a difference in the hydraulic conductivity of the sapwood between crown classes. Validation of MIXLIGHT showed that it was able to predict average plot level light conditions well for a wide variety of young aspen stand types. Average diameter and density, also predicted stand level light well in these same young aspen stands. Finally, stand level leaf area index, which is a major factor controlling understory light conditions, reached a maximum of approximately 4 by age 9 in some stands and appeared to decrease past age 25. From all of this information on light conditions in young aspen stands it was possible to make recommendations as to which types of aspen stands have appropriate light levels for the underplanting of white spruce.

The objective of Chapter 3 was to analyze Alberta's free-to-grow (FTG) standards from the perspective of available light and recommend possible improvements. A variety of young aspen stands of differing densities and heights were developed which included a variety of different FTG combinations and then MIXLIGHT was used to predict light at certain points within the stands. Although Alberta's current FTG standards rely heavily on the distance from the crop tree to the competing trees, it was found that this was not a good predictor of available light. Based on model predictions about available understory light, it appears that the overall stand density and size of competitors is more important in determining the FTG status of a conifer tree.

4.2 Future Work

Given the importance of mixedwood management there is still a great deal of work that can be done to improve our understanding of these systems and improve our management techniques. These studies only dealt with the development of individual aspen trees and relatively pure aspen stands. In reality our mixedwood forests are composed of many different species so this same individual tree information is needed for these other species in both pure and mixed juvenile stands. This information includes crown shape and size, leaf area development and the effects of individual tree size and competing density on species such as balsam poplar, white birch, willow and alder. At the stand level, more information is needed on the development of total stand leaf area in both pure and mixed species stands.

With this information it should be possible to recommend certain types of hardwood stands for underplanting of white spruce. Although light is one of the major factors controlling understory tree growth and development, other factors such as nutrient and moisture regime are also important. The interactions of all of these factors needs to be determined in order to make better recommendations for the underplanting of white spruce. The impact of these understory spruce trees on the overstory aspen also needs to be examined.

MIXLIGHT has been validated for plot average light conditions. However, it still needs to be validated for spatially explicit microsite light prediction. This would allow us to be more comfortable with the free-to-grow recommendations which were made from the spatially explicit microsite light predictions. It would also help with the prediction of individual understory tree light conditions which could be incorporated into growth and yield models.

Finally, Alberta's free-to-grow standards for mixedwood stands are inadequate with respect to the stand characteristics which most greatly affect the available light for the crop tree, that is stand density and size of competitors. The field surveys to assess which stands meet the standards must be relatively easy to conduct and the information should tell us about the future competition for that stand. For this to occur, the free-to-grow standards need to be validated so that they can accurately predict whether or not a spruce tree has enough light for acceptable growth now and in the future. These free-to-grow standards will then be better linked to growth and yield models which are so important in the management of our forests. This may involve predicting the average light conditions for all spruce trees in a stand based on the size and density of competing aspen trees. This light level could then be used to predict understory spruce growth.

These studies have presented data on the understory light conditions in a variety of young trembling aspen stands and related this information on understory light to the potential growth of white spruce seedlings. This type of information is crucial for the development of better silvicultural techniques and policies in the boreal mixedwood forest.