Measuring and modelling the crown and light transmission characteristics of juvenile aspen

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Abstract: Crown dimensions, crown leaf areas, and leaf area densities were determined on individual trees in 96 juvenile Populus tremuloides Michx. stands in central Alberta, Canada. Crown radius, height, leaf area, and leaf area density were well explained by stem diameter at 30 cm (D30). Leaf area index, estimated using the LAI-2000, reached a maximum of 4 m²·m⁻² in some stands by age 9 and decreased after age 25. Leaf area indices for the same stands, estimated by allometric relationships, were greater than 7 m²·m⁻². Horizontal overlap between adjacent tree crowns declined from 68 to 38% of crown width with increasing average D30 from 1.5 to 15.0 cm. These data were used to calibrate MIXLIGHT, a spatially explicit light transmission model, to predict the range of light conditions in the understory of juvenile stands. Light predictions were validated in 18 additional plots in which light transmission was measured. Measured light transmission ranged from 4 to 68% of above canopy light among sites and from 16 to 53% within a mapped site. MIXLIGHT predicted transmission well for average stand light levels (R² = 0.80). For individual positions within the mapped stand there was a strong relationship between predicted and observed light (R² = 0.92), but there was underprediction at high light and over at low light.

Résumé : Les dimensions du buisson, la surface foliaire et la densité de surface foliaire ont été mesurées sur des arbres de 96 peuplements juvéniles de Populus tremuloides Michx. dans le centre de l’Alberta, au Canada. Le rayon du buisson, la hauteur, la surface foliaire et la densité de surface foliaire étaient correctement prédits à l’aide du diamètre de la tige à 30 cm (D30). L’indice de surface foliaire estimé au moyen du LAI-2000 atteignait un maximum de 4 m²·m⁻² pour quelques peuplements à l’âge de 9 ans et diminuait par la suite après 25 ans. Les indices de surface foliaire des mêmes peuplements estimés à l’aide de relations allométriques dépassaient 7 m²·m⁻². Le recouvrement horizontal des buissons voisins diminuait de 68 à 38% de la largeur du buisson lors de D30 moyen augmentait de 1.5 à 15.0 cm. Ces données ont été utilisées pour calibrer le modèle MIXLIGHT, un modèle de transmission de la lumière défini dans l’espace, de façon à prédire l’amplitude des conditions lumineuses dans le sous-bois des peuplements juvéniles. Les prédictions du niveau de lumière ont été validées dans 18 placettes additionnelles dans lesquelles la transmission de la lumière a été mesurée. Les mesures de transmission de la lumière variaient selon les sites de 4 à 68% de la lumière incidente et de 16 à 53% dans un peuplement cartographié. Le modèle MIXLIGHT prédit bien la transmission pour les niveaux lumineux moyens des peuplements (R² = 0.80). Pour les positions individuelles dans le peuplement cartographié, il y avait une forte relation entre les niveaux de lumière prédits et observés (R² = 0.92) mais avec une tendance à sous-estimer les intensités lumineuses élevées et à surestimer les intensités faibles.

[Traduit par la Rédaction]

Introduction

After disturbances such as fire or logging in boreal mixedwood forests, trembling aspen (Populus tremuloides Michx.) usually redevelops from root suckers to quickly dominate the new stand. Where seed supply and substrate are adequate, slower growing white spruce (Picea glauca (Moench) Voss) germinates and develops in the understory, spending the first half of its life below the aspen (Lieffers et al. 1996b). Spruce recruitment into these stands, however, is less assured than the establishment of the aspen (Navratil et al. 1991; Stewart et al. 1998). As the amount of light reaching a forest understory controls the recruitment, growth, and survival of trees growing in the understory (Williams et al. 1999; Chen et al. 1996; Oliver and Larson 1990), there is considerable interest in assessing the understory light environment of mixedwood stands. Prediction of light in juvenile stands is necessary to predict the competitive effects of aspen and the success of various mixedwood silvicultural systems (Lieffers et al. 1996; Bergeron and Harvey 1997).

Given the importance of light for the growth of understory trees, there has been considerable work in description and prediction of understory light in boreal forests (reviewed by Lieffers et al. 1999). In mature mixedwood stands, light transmission levels have been documented (Lieffers and Stadt 1994; Constabel and Lieffers 1996; Messier et al. 1998). Light transmission through the full range of young aspen stand densities and sizes, however, has not been fully examined, other than assessments of competition in small plots and a general characterization of light in 20-year-old stands (Constabel and Lieffers 1996). There have, however, been estimates of leaf mass (Bella and De Francheschi 1980;
DesRochers and Liefers (2001) area in juvenile stands. Predictions of light and competitive effects using simple stand level characteristics such as basal area have been useful for single species stands with similar canopy architecture (Vales and Bunnell 1988; MacDonald et al. 1990; Comeau 1996; Buckley et al. 1999). Light transmission models, however, may be more applicable over a wider range of tree sizes and stand compositions. These models operate on either the stand or the microsite level and account for the effect that the overlying leaf area has on the amount of light penetrating to the understory. The amount, orientation, and spatial distribution of this leaf area affects how much light is transmitted. Here, we use the MIXLIGHT model, which has been described and validated at the stand level for mature boreal mixedwood stands (Stadt and Liefers 2000). In spatial mode, this model represents trees as regular geometric shapes with spatial coordinates and uses a ray-tracing algorithm and Beer’s Law to calculate light transmission to points (microsites) within the canopy space. To make this model applicable to young aspen stands, basic information is required on how crown characteristics such as leaf area, crown radius, and depth, as well as the degree adjacent crowns overlap vary with tree size and stand density. Specifically, we hypothesize that individual tree leaf area density declines as tree size or relative density (RD) (Curtis 1982) increase and that individual tree crown size decreases with increasing RD. RD scales stem density of the stand in relation to the size of the trees; thus, densities of stands of different tree size can be compared.

The objectives of this study are to test the above hypotheses, examine the overall development of leaf area in juvenile aspen stands, and calibrate and test a light transmission model in young aspen stands.

Materials and methods

Overview

To predict light transmission to forest understory microsites, the MIXLIGHT model requires a tree list containing stem diameter, height, crown radius, height to live crown, leaf area density, leaf inclination angle, and position for each tree in the plot (Stadt and Liefers 2000). For the model to be useful in operational forestry or to support policy decisions, there may be too many variables to measure for each site. Typical inventory data contain the density and average height of the stand or a list of tree diameters (or heights) within a known plot area. To simplify the model, we measured individual tree and plot-level characteristics, then used these to develop equations based on simple measurements to predict the tree characteristics required by MIXLIGHT. To validate the model, we measured light transmission in separate validation plots. We then applied the equations developed to predict individual tree characteristics to each tree in these plots. MIXLIGHT was run on these tree lists, and the predicted mean light transmission for additional validation plots compared with actual light measurements both for plot averages and for exact points within a mapped stand.

Site selection

Twenty-six young aspen-dominated boreal mixedwood stands, between 1 and 30 years old, were selected near Drayton Valley, Slave Lake, and Grande Prairie, Alberta (53°20’–55°20’N, 113°10’–118°50’W). Stands were on upland sites with less than 10% slope, medium to rich nutrient status, and mesic to sub-hygic moisture regime were selected; these were from the boreal mixedwood BMd (low-bush cranberry) and BMd (dogwood) ecosites (Beckingham and Archibald 1996). Stands ranged from 1 to 12 m tall and were of a range of densities (2800 – 159 000 stems/ha). All stands had greater than 80% of total basal area as aspen but also included balsam poplar (Populus balsamifera L.), white birch (Betula papyrifera Marsh.), alder, and willow in the overstory. Most sites had small white spruce seedlings establishing in the understory. Both fire and harvest origin stands were selected. The sites contained no obvious linear patterns of tree distribution; thus, sites with disc trenching or ripper plowing were not selected. Within these stands, 96 random plot-centre locations were established and the closest acceptable aspen tree to the plot centre was sampled. Acceptable trees had no obvious signs of damage or disease. No more than five plots were sampled within a single stand; most stands had three plots.

Plot tree measurements

The following measurements were made on the central tree:

- height, height to live crown, diameter at breast height (DBH), and
- DBH at 30 cm height (DBH30), crown class (canopy trees (dominant and codominant) and intermediate trees (intermediate and suppressed)), and
- crown radius (half the mean of two crown diameter measurements on perpendicular horizontal axes). Of the 96 tree-centred plots, 56 plots had a canopy tree as the plot-centre tree and 40 plots with an intermediate tree at the centre. The plot-centre trees were cut and discs were taken at breast height (1.3 m) and at 30 cm 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 (model LA3300M; LI-COR, Inc., Lincoln, Nebr.) and then oven-dried. The rest of the sample was also oven-dried and the relationship between actual leaf area and oven-dry mass used to obtain the total leaf area of each tree.

Stand measurements

Once the plot-centre tree was identified, it became the centre of a circular plot between 1, 2, or 3 m in radius; plot size depended upon stand height, using a 1-m radius for dense stands less than 2 m tall, a 2 m radius for stands 2-4 m tall, and a 3 m radius for stands greater than 4 m. Within the surrounding plot, the dominant understory vegetation was recorded by species and percent cover along with any indicator species of nutrient and moisture regime that were present near the plot. The DBH30 and species were recorded for all trees and large shrubs within the plot. If the trees were below 1.3 m tall, then DBH30 only was recorded. These data were used to determine plot density, basal area (BA = DBH302/plot area). 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 central tree was determined, and DBH30, DBH30, height, species, and distance to the plot-centre tree were recorded.

The plant canopy analyzer (model LAI-2000; LI-COR, Inc., Lincoln, Nebr.) was used in each plot to estimate stand leaf area index and leaf inclination angle for the stand (LI-COR, Inc. 1992). A second unit was used in remote mode outside the stand to record outside sky conditions. Using the top three rings, with the 90° restriction in place, 16 measurements were taken at 1.3 m height or less (below the canopy) in a plot two tree heights in width. The plot was slightly off centre relative to the central tree, but the LAI-2000 sensor was aimed in only one direction for all measurements, so that the canopy above the central tree was uniformly sampled. LAI-2000 measurements were also used to estimate leaf inclination angle.

A spatial light transmission model is ideally supported by a map of tree positions. Since positional data is rarely available, we developed a simple tree positioning algorithm that limits random placement of canopy trees to a maximum horizontal crown overlap. Totally random placement could result in two canopy tree crowns occupying the same location, which is not realistic. In 10 stands, selected to provide a wide range of tree diameters, horizontal
crown overlap of canopy trees was measured between random pairs of adjacent canopy trees. The distance between the two stems (d) at midcrown height was measured along with the crown radius (CR) and $D_{30}$ of each tree. Crown overlap was defined as $1 - d/(CR1 + CR2)$, which is zero if the crowns touch at their edges (no overlap) and one when the crowns are in the identical location (complete overlap). Trees with no overlap were not measured, so no negative overlap values were recorded. Maximum horizontal crown overlap in relation to tree diameter was assumed to be the linear regression between crown overlap and $D_{30}$ plus one standard deviation of the intercept of the regression line (Fig. 1). This placed an arbitrary upper cutoff for the relationship. This does not fully characterize the horizontal distribution of the aspen crowns, since the crowns could still be dispersed or clustered without overlapping, but this would occur only in stands of very low relative density, where light levels would be high. This overlap index is simple, easy to apply, and captures the critical component of nonrandomness in the stand structure.

**Model calibration**

As only $D_{30}$ was collected for most trees, $D_{30}$ for each tree was estimated from $D_{130}$ using nonlinear regression ($D_{30} = 1.1843 + 0.6363(D_{130})^{0.1941}$, $R^2 = 0.980$, $n = 324$, data not shown). Height was estimated from $D_{40}$ 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 of the calibration plots. For all trees, total tree height is predicted from the equation: $H = 0.3 + 14.47(1 - e^{-0.1908w})^{0.59}$, ($R^2 = 0.919$, $n = 383$, Figure not shown).

Using SAS (version 6.02; SAS Institute Inc., Cary, N.C.), a variety of linear, nonlinear, and multiple linear regression equations were developed to predict crown radius and crown depth from individual tree characteristics such as diameter and height, and plot data such as basal area, stem density, distance of nearest competitor to subject tree, size of nearest competitor, plot level leaf area index (estimated with the LAI-2000), and relative density (RD = BA/($D_{30}$)(/4)) (Curtis 1982). Bivariate plots were first examined. Separate equations were developed for canopy and intermediate trees using stepwise regression and log-transformed and untransformed data. The best relationships were based on $R^2$ or adjusted $R^2$ in the case of multiple regression and accuracy of prediction along the range of independent variables was examined using residual plots. The $R^2$ for all equations, including nonlinear equations, was calculated as $1 - (error sum of squares/corrected total sum of squares) (Cornell and Berger 1987)$.

For the plot-centre trees, the possible linear and nonlinear regression models between individual tree leaf area and tree and stand variables were developed as above for crown radius and length. Leaf area density of the plot-centre trees was determined by dividing tree leaf area by its crown volume.

**Validation**

To validate the light predictions, an additional 17 plots were established in seven different young aspen stands to calibrate the crown size and leaf area equations, with the same range of both height and density as the tree-centred plots. These validation plots were 2–3 m in radius (plots with taller trees or low density had a 3–m radius) and were not tree centred. Light was measured on uniformly cloudy days or sunny days (within 3 h of solar noon). Light was measured in the understory and in the open using a linear radiometer with 80 sensors (ceptometer, model SF-80; Decagon Devices Inc., Pullman, Wash.). A single circular sweep consisting of 15–20 light measurements was taken in the open followed by a similar sweep around the centre point beneath the overstory canopy but above the shrubs and understory spruce, followed by another sweep in the open. Above- and below-canopy measurements were never more than 2 min apart. Measurement height ranged from 30 to 150 cm depending upon the site. The mean of all light measurements under the canopy and in the open were determined. Below-canopy light values were divided by open light values to obtain percent light transmission through the canopy.

Within the validation plot, the species and $D_{130}$ of each tree and large shrubs was recorded. One of the larger trees within the plot was cut down, and a stem disc taken at 30 cm was used for age determination. Individual tree height, crown size, and leaf area were estimated for each tree in these plots using the regression equations described above.

Since the validation plots were not mapped, the trees needed to be placed in x–y coordinates to run MIXLIGHT. Canopy trees were positioned randomly within the plot but with a minimum distance between trees using the relationship developed for maximum horizontal crown overlap (Fig. 1), based on the mean diameter of all canopy trees in each plot and the crown radius of the adjacent trees. A new random point was chosen if the crown of a tree overlapped too much with its neighbours. Intermediate and dead trees were placed randomly within the plot. Since the size of each validation plot was small but these plots were representative of the surrounding stand, the plot tree list was scaled to a square plot of equal area. The data from this plot was replicated 24 times around itself (a total of 25 plots) so that tree information from a larger area

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could be used in the simulation. 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. For the simulation, all trees and large shrubs were considered to be aspen. The $D_{30}$ of the trees and its relationship to crown width, depth, and leaf area were the major plot input parameters. MIXLIGHT was run five times for each plot with different tree locations, and the results were averaged to estimate the average light transmission through the aspen canopy. The light transmission values were then compared with the actual light measurements from the stand.

For validation of light predictions to specific positions, an additional pure aspen stand, 6 m tall and 9 years old was selected. A 16 x 16 m plot was established, and the $D_{130}$ and the position of each tree was determined using a tape measure and transit. In the center of this plot, 16 points were established on a ~2 m grid leaving a ~4 m buffer to minimize edge effects (Fig. 2). Transmitted light to each of these points was estimated near midday in uniformly cloudy conditions, from two spectrometer readings, taken at 90° directions, at 1 m height (above the shrub layer), at the 16 positions. Above canopy light was measured simultaneously using a light sensor (model LI800, LI-COR, Inc., Lincoln, Nebr.) in a nearby clearing.

For simulations under cloudy conditions, the radiance distribution across the sky dome was adjusted to reflect the approximately threefold increase in light transmission from sky positions near vertical compared with the horizon (Moon and Spencer 1942). This was verified by our own measurement of skylight distribution under uniformly cloudy conditions, aiming a light sensor, placed in a tube to receive radiation from a cone with a half-angle of 7.5°, at various elevations and directions.

Results

Model calibration

The best equations for predicting individual aspen tree crown radius (Fig. 3a), crown depth (Fig. 3b), and leaf area (Fig. 4) were power functions of $D_{30}$. The regressions for canopy and intermediate trees were compared using log of $D_{30}$ versus log crown characteristic; the slope and intercept for these regressions were compared using a t test. Crown radius versus $D_{30}$ and crown depth versus $D_{30}$ were not significantly different between the dominance classes. For the leaf area versus $D_{30}$ curves, the relationships were significantly different between canopy versus intermediate trees ($p = 0.001$). For the plot-centre tree, including a measure of the degree of competition from neighboring trees, using basal area, density, relative density, and size of or distance to the nearest competitor in multiple regression models did not improve the prediction of crown radius, crown depth, or leaf area of centre trees. The slenderness coefficient (SC) of plot-centre trees (total height divided by diameter), however, was positively correlated to RD (SC = $1.08 + 0.02$RD, $R^2 = 0.16$, $p = 0.0001$, n = 96). This suggests that the diameter growth of trees responded negatively to increased competition, thereby reducing their crown dimensions. Leaf area density of individual trees was negatively correlated with the RD of the plot (Fig. 5a). Leaf area density was also negatively correlated with tree size ($D_{30}$) (Fig. 5b).

Model validation

Measured light in the 17 validation plots indicated light transmission from 4 to 66% of above-canopy light. The MIXLIGHT model predicted measured light well ($R^2 = 0.80$; Fig. 6). The intercept of the predicted to measured light relationship is not significantly different from 0 ($p = 0.62$), nor is the slope different from 1 ($p = 0.91$). Analysis of the residuals of this relationship showed that MIXLIGHT predicted light transmission more accurately (on an absolute deviation from predicted) at lower light levels (less than 30% transmission) than high light levels.

For the validation of prediction at individual points within the mapped stand, there was a strong correlation between the measured and predicted light transmission. The slope of this relationship deviated significantly from the 1:1 line (Fig. 7). However, since leaf area is the most important variable for light transmission and there is considerable uncertainty in predicting leaf area from tree diameters (Fig. 4), we ran MIXLIGHT twice more using the leaf area densities calculated using the upper and lower 95% confidence limits of the leaf area versus diameter relationship. The range of transmission values predicted for these runs overlapped the 1:1 line for most microsites (Fig. 7).

Stand leaf area

Stand level leaf area index (LAI) estimated using 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. 8a). Variation in LAI was greatest in young stands but stands became less variable with age. When LAI was determined by the allometric relationships used in MIXLIGHT values ranged over 6 and peaked at 8.1. LAI was also related to stand basal area (BA30), increasing rapidly with BA30 until 20 m$^2$.ha$^{-1}$ (Fig. 8b) and leveled off in the LAI-2000 estimates but continued to rise with the allometric estimates.

The average leaf inclination angle taken from the LAI-2000 readings for each plot was approximately 50°. This is
Fig. 3. Crown radius (a) and crown depth (b) of all trees in relation to stem diameter at 30 cm height ($D_{30}$) (Fig. 3a: RMSE = 14.63; Fig. 3b: RMSE = 68.78).

Fig. 4. Individual leaf area of (a) canopy trees and (b) intermediate and suppressed trees in relation to their diameter at 30 cm height ($D_{30}$). The slopes of these relationships are significantly different ($p = 0.0005$) (Fig. 4a: RMSE = 1.8899; Fig. 4b: RMSE = 0.6457).

slightly more horizontal than the mean inclination angle for a random (spherical) leaf angle distribution (57°) found by Chen et al. (1997).

**Discussion**

In these juvenile stands, the crown dimensions of single aspen trees were best predicted by their $D_{30}$ (Fig. 3). There was no improvement in prediction when stand stem density or relative density were added to the regression model. Leaf area per tree was also well predicted by $D_{30}$ (Fig. 4), and there also was no improvement in prediction when density or RD was also included in the model. Thus, our hypothesis that RD affects crown size or leaf area per tree is not supported by these results. However, the slenderness coefficient (stem diameter to tree height) increased with RD; therefore, trees of a given height at higher RD tended to have a lower $D_{30}$. Likewise there was a modest reduction of crown size with increasing density or RD, when $D_{30}$ was not considered. Thus, the reduction in diameter caused by density captured all the effect of competition in our model. Any change in density appears to be rapidly reflected in tree diameter growth, as might be expected given the high rate of self-thinning in juvenile stands (Oliver and Larsen 1990). In other studies of thinned aspen that considered both diameter and height of juvenile aspen, crown size have been shown to decrease with increasing competition (Pueettmann and Reich 1995; Bella 1975), but these values were not corrected for differences in stem diameter.

The leaf area versus stem size relationship (Fig. 4) for intermediate trees had a lower slope than for the dominants. This is interesting for two reasons. First, it suggests that trees suppressed by neighbours did not have as high a leaf area as similar-sized dominant trees. Thus, competition from neighbours does appear to impact leaf area development. Secondly, 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). As virtually all of the stem cross-sectional area was sapwood, the leaf area versus sapwood area relationship had a lower slope in intermediate trees. Thus, a given cross-sectional sapwood area of canopy trees supports more leaf area than intermediate trees. This higher leaf area to sapwood area relationship for the canopy trees has been shown for other forest tree species (Hungerford 1987; Long and Smith 1988, 1989). On a stand level basis, LAI (estimated by LAI-2000) appeared to peak at 4 m²·m⁻² when $BA_{30}$ of these young stands reached 20 m²·ha⁻¹ (Fig. 8b). This is likely the point where the LAI-2000 is unable to detect more leaf area, while the allometric relationship continued to rise steadily with in-
crease in basal area. The underestimate of LAI by the LAI-2000 in conditions of high leaf area or clumped leaf distribution has been reported previously (Smolander and Stenberg 1996; Eschenbach and Kappen 1996; Smith et al. 1993).

Individual tree leaf area density (leaf area/crown volume) declined with increasing tree size (Fig. 5b) and, presumably, crown size. 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, as Canham et al. (1994) suggested for shade-intolerant species.

The measured light transmission in these stands, ranging down to 4% of above-canopy light, was considerably lower than that reported for other aspen stands in Western Canada. Constabel and Lieffers (1996) reported a mean of 19% transmission for 20-year-old stands, while mature stands had 26 (Chen et al. 1997) and 32% transmission (Constabel and Lieffers 1996). In Quebec, Messier et al. (1998) reported 8–13% transmission in mature aspen stands. The suggested trend for a decrease in LAI, which is associated with an increase in light transmission with stands older than about 25 years (Fig. 8a), is supported by a report of increased transmission with aspen stands greater than 35 years old in westcentral Alberta (Lieffers and Stadt 1994). In our juvenile stands, the low light transmission values of 4–10% are more similar to values reported for mature spruce stands (Lieffers and Stadt 1994) and are low enough to seriously inhibit growth and survival of understory white spruce. Height growth of white spruce saplings decreases with light transmission below 40%, with death occurring below 10% light (Lieffers and Stadt 1994; Logan 1969). These low light levels also indicate that not all aspen stands are suitable for survival of white spruce seedlings.

The very low light transmission in our young stands is also associated with LAIs ranging up to 4 m²·m⁻² (measured by the LAI-2000) and 6 m²·m⁻² or more (estimated by allometric relationships) by about age 9. These values are greater than the maximum leaf area of 3.9 m²·m⁻² collected from 3 × 3 m plots in juvenile aspen stands in Alberta (DesRochers and Lieffers 2001), 2.4 m²·m⁻² for a 6-year-old stand (Pollard 1970), and 2.9 m²·m⁻² for a 15-year-old stand (Pollard 1971). LAI in our juvenile stands is also higher than reported values for mature aspen stands: 3 m²·m⁻² for 43- to 73-year-old aspen stands (DeLong et al. 1997), 1.4 m²·m⁻² in a 55-year-old stand (Pollard 1970), and 3.3 m²·m⁻² in a 70-year-old stand (Kucharik et al. 1999). The high leaf area in young stands appears to be related to two factors. First, while the leaf area borne by an individual tree increased, there was a decline in leaf area density with tree age (Fig. 8a) and presumably size. Secondly, there was substan-
Fig. 6. Predicted mean plot light transmission from MIXLIGHT in relation to actual light transmission measured in 17 separate plots ($R^2 = 0.801$). The equation is as follows: predicted light = 0.9859(actual light) – 2.0299. The straight line is the ideal 1:1 relationship. The relationship between predicted and actual percent light transmission is not different from the ideal 1:1 relationship (slope = 1, $p = 0.91$; intercept = 0, $p = 0.62$).

Fig. 7. MIXLIGHT predictions for microsite light transmission in relation to measured light transmission at 16 points within the same stand. Triangles show the light transmission predicted for the microsite using the mean leaf area – diameter relationship to generate individual tree leaf areas. The broken lines show the upper and lower light predictions for the same microsite that were generated when the lower and upper 95% confidence limits of the leaf area – diameter relationship are used in prediction. The 1:1 line is shown for comparison.

Potential overlap in crowns in smaller trees, thus stacking more leaves in the same volume. Horizontal crown overlap of canopy trees decreased as trees became larger and older (Fig. 1). The mechanism for this separation is not clear but may relate to mortality of suppressed trees between the canopy trees and to mechanical abrasion between crowns of taller trees (Long and Smith 1992). Our data indicate that aspen establishes leaf area on a site very quickly, and young stands are capable of carrying more leaf area than mature stands.

Destructively sampling each individual tree for leaf area allowed us to accurately measure leaf area. Although time consuming, this method allowed an accurate estimate of leaf area density and was feasible in young stands. Others have also used allometric relationships between stem diameter or sapwood area to provide leaf area estimates for light modelling with mixed success (Bartelink 1998; Oker-Blom et al. 1991). Alternatively, Bartelink (1998) and Stadt and Lieffers (2000) derived mean leaf area density for mature trees from light transmission through individual tree crowns. Canham et al. (1999) used a similar approach to estimate crown openness, the projected leaf area density of the entire crown. This method may be difficult to apply in young, dense stands, however, as it requires unobstructed projections of the crowns against the sun or sky. Canham et al. (1994) and Brunner (1998) obtained openness or leaf area density estimates by iterating their models until predicted light transmission levels for individual microsites corresponded to the measured light values. This may be quite effective but is computationally intensive and requires independent validation. The method of estimating leaf area should suit the situation.

MIXLIGHT was able to predict mean plot light transmission well over a range of young aspen stand types of varying heights and densities. MIXLIGHT stand-average predictions were particularly good at light levels below 30% which is in the critical range for prediction of spruce survival and acceptable height growth (Lieffers and Stadt 1994; Logan 1969). From microsite to microsite within a stand, MIXLIGHT predictions correspond well with measured light, with some tendency to predict lower than measured light transmission in gaps and higher than measured transmission under dense canopy.

Few studies modelling light in young forest plant communities have dealt with this wide range of stand ages and sizes. Ter-Mikaelian et al. (1997) modeled light in plots of varying densities of 2-year-old jack pine and competing vegetation but only looked at plots of this one age. Brunner (1998) modeled light in a single 20-year-old Douglas-fir stand and Bartelink (1998) tested his model in a 25-year-old Douglas-fir stand as well as three much older stands. Validation is difficult because of the time required to map sites large enough that edge effects are minimized, both for measurement and simulation of the light transmission. We reduced this difficulty by carefully mapping one larger site to show the ability of MIXLIGHT to simulate within-stand variation then measured light, density, and tree diameters in a large number of small plots where tree positions were generated with a simple restriction on crown overlap. Additional sources of errors in predicting light transmission include site quality and wood area. 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. Bole area is included in the MIXLIGHT model (Stadt and
Fig. 8. Stand level leaf area index as measure by the LAI-2000 and by allometric relationships in relation to (a) stand age and (b) stand level basal area at 30 cm height.

Lieffers 2000); however, branch area was not measured and included in this study. As 95% of all branch area is obscured from view by foliage (Kucharik et al. 1998), this is not likely to significantly affect light transmission values in summer.

This study shows that it is quite feasible to model light in young aspen stands. It is clear that very dense young stands may support sufficient leaf area that would kill understory spruce. Small aspen of low stem density, however, are unlikely to suppress spruce height development. This study also suggests that stands less than 20 years old may support substantially more leaf area than older stands because of the decline in stem density and tree leaf area density with stand age and because of the decline in the overlap of crowns. Thus, it may be advantageous to delay the planting of white spruce under aspen canopies until after this time.

Acknowledgements

We thank Ben Seaman and Jim Cuthbertson for field assistance and Weldwood of Canada Ltd., Weyerhaeuser Canada Ltd., and the Natural Sciences and Engineering Research Council for funding. We also thank two referees and the Associate Editor for constructive comments.
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