

Regional variability of species-specific crown openness for aspen and spruce in western boreal Canada

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Abstract

In the Canadian boreal mixedwood region, there is currently increasing management desire to foster and release understory trees. Consequently, there is also an increased interest in modeling and predicting understory light levels.

In this study, species-specific crown openness is defined as the fraction of sky that can be seen through the crown of an individual tree of a given species. Species-specific crown openness is of general interest for understanding light transmission through forest canopies, and is an essential part of the light submodel in SORTIE. The main objective of this study was to investigate whether regional differences in mean species-specific crown openness exist for aspen (*Populus tremuloides* Michx) and white spruce (*Picea glauca* (Moench) Voss) in western boreal Canada. To ensure a robust comparison of regional mean species-specific crown openness, we initially investigated the underlying assumption that crown openness is unaffected by dbh and angle of view. In our data, both aspen and spruce crown openness was found to be independent of angle of view. Crown openness was also independent of dbh in aspen, while weak indications of a correlation between crown openness and dbh was found for white spruce. However, this relationship has little actual effect on crown openness and its effect on predicted understory light level is judged to be small.

We found significant regional differences in mean crown openness for both aspen and spruce. However, these regional differences are small and are likely to have relatively little effect on understory light levels predicted with SORTIE. The results from this study indicate that, although previous estimates of aspen and spruce crown openness in western boreal Canada varied greatly, this is more likely the result of different methodologies than actual differences in crown openness.

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1. Introduction

There is a large body of literature regarding the complex mechanisms of light transmission through forest canopies (e.g. Norman and Jarvis, 1975; Canham, 1988; Chazdon, 1988) and related methods to predict light transmission (reviewed in: Larsen and Kershaw, 1996; Brunner, 1998; Lieffers et al., 1999). Monsi and Saeki (1953) were the first to apply the Beer–Lambert law to light extinction in plant canopies. This law has since been the most frequently used method for predicting light levels under forest canopies. Application of the Beer–Lambert law in its original form produces an average light intensity, which is subject to several crude assumptions regarding canopy structure (Monsi and Saeki, 1953; Larsen and Kershaw, 1996).

As reviewed by Brunner (1998) and Lieffers et al. (1999), several complex models have dealt with some of the shortcomings of the original canopy structure assumptions by accounting for non-random foliage distribution, inclination angles, foliage clumping, and reflection and transmission from foliage. A problem with these complex models is that they require extensive input data regarding canopy structure and have often proven difficult and costly to calibrate (Brunner, 1998; Canham et al., 1999; Stadt and Lieffers, 2000). Thus from a management perspective there is a need for a light model which can be applied with readily available inventory data (Lieffers et al., 1999; Stadt and Lieffers, 2000).

SORTIE is a spatially explicit individual tree model where tree growth mainly is driven by light availability and neighborhood composition. The model was initially developed for modeling successional dynamics in northern hardwood forests by Pacala et al. (1993, 1996). Since then, the model has been further developed (SORTIE-BC and SORTIE-ND) and made more suitable for application to forest management issues

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in boreal Canada (Coates et al., 2004). Canham et al. (1994) parameterized and tested the light submodel in SORTIE and showed that spatial variability in understory light levels can be predicted with relatively simple input data. Additionally, the results indicated that understory light levels can be predicted with a simple model where light transmission is equally extinguished by each encountered crown of a given species independent of size and angle of view. This type of model was termed an absolute hits model and in this terminology each tree can be referred to as a hit. Additionally, it was shown that the majority of spatial heterogeneity in understory light levels can be explained from the position and crown allometry of neighborhood trees (Canham et al., 1994). Most light models are not absolute hits models (e.g. Brunner, 1998; Stadt and Lieffers, 2000) and light extinction is dependent on the path length through the individual crowns. Although an absolute hits model cannot predict the light environment within individual crowns, it can be advantageous in the prediction of understory light levels because of its simplicity (Canham et al., 1994). Canham et al. (1999) further developed the absolute hits version of SORTIE's light submodel and achieved good test results for subboreal sites in British Columbia.

In this paper, species-specific crown openness is defined as the fraction of sky that on average can be seen through the crown of an individual tree of a given species. The species-specific crown openness is assumed to be independent of tree size and angle of view. In the latest version of SORTIE's light submodel (Canham et al., 1999), species-specific crown openness is the only input factor that is not available from the literature or from reanalysis of permanent sample plots. The initial method used to determine species-specific crown openness was complex and included a three-dimensional reconstruction of a stand in conjunction with fisheye photos (Canham et al., 1994). This initial method was replaced by a simplified and direct method introduced by Canham et al. (1999). In this method, species-specific crown openness is determined directly from fisheye photos.

The difference in canopy and crown openness among species has received attention due to the effects of shading and shade tolerance on forest stand dynamics and succession (e.g. Horn, 1971; Oliver and Larson, 1996; Canham et al., 1994, 1999). Intraspecific variability between regions has received less attention but is interesting from several perspectives. From a modeling perspective, it is necessary to determine transferability of species-specific crown openness between regions in order to judge when light models should be re-parameterized. From a silvicultural standpoint, geographic variation in species-specific crown openness might influence understory light levels. In this case, the performance of understory trees and the success and transferability of various silvicultural systems are likely influenced. Several studies have shown that leaf area index varies with climate (e.g. Gholz et al., 1976; Grier and Running, 1977) and it is also likely that species-specific crown openness varies with climate.

The main objective of this study was to investigate the intraspecific variability of species-specific crown openness for both aspen (*Populus tremuloides* Michx) and spruce (*Picea glauca* (Moench) Voss) within western boreal Canada. This was

done by comparing mean species-specific crown openness estimates from five different regions in western boreal Canada. To ensure a robust comparison, we tested the assumptions that species-specific crown openness is independent of (1) tree size and (2) angle of view. The secondary objective of this study was to compare regional variation in species-specific crown openness to SORTIE's sensitivity to this parameter. This was done to evaluate possible regional differences in understory light environments caused by regional differences in species-specific crown openness.

2. Methods

2.1. Sampling and measurements

Five sampling regions located in northern British Columbia (BC), Alberta (AB) and Saskatchewan (SK) were selected. A sampling region was defined as an area 40 km in radius with relatively uniform climatic conditions. The sampling regions were selected to capture the range of climatic conditions in areas dominated by mixed stands of aspen and spruce throughout western boreal and subboreal Canada. The selected sampling regions were located in the vicinity of Smithers (BC), Fort Nelson (BC), Peace River (AB), Calling Lake (AB) and Porcupine Hills (SK). The geographic distribution of the sampling regions is illustrated in Fig. 1. In all five regions, both aspen and spruce were sampled. In the Smithers region, interior spruce (*P. glauca* × *engelmannii*) was sampled because it is the most common spruce on mesic sites (e.g. Banner et al., 1993). In the remaining regions white spruce was sampled. A short summary of climatic characteristics and sample site characteristics of each region is presented in Table 1.

Sampling was performed from late June till mid August 2003. Within a sampling region, between 10 and 12 stands located on zonal sites were sampled. In this paper, the term zonal is used for a site that best reflects the regional climate rather than edaphic or topographic factors.¹ An observed difference between sampling regions will thus be an effect of local climate rather than edaphic or topographic factors. In this project, focus will be on zonal sites classified to site series in BC and ecosite in AB and SK. The actual site types are given in Table 1. The sampled stands were mature (>30 years) aspen and spruce mixtures that ranged from aspen to spruce dominated. In each stand, between one and seven trees of each species were sampled. In stands where multiple trees were sampled, an effort was made to maximize the range of sampled tree sizes. For each sampled tree, the general methodology of Canham et al. (1999) was used to determine species-specific crown openness. For each sampled tree one fisheye photo was taken. For each photo, the camera was placed in a location where the crown of the selected tree could clearly be distinguished against the sky without any other trees blocking the view. Locating an appropriate camera position often

¹ This use of zonal site is equivalent to the use for classification in BC (Pojar et al., 1991) and equivalent to the term reference site used for classification in AB (Beckingham and Archibald, 1996) and SK (Beckingham et al., 1996).

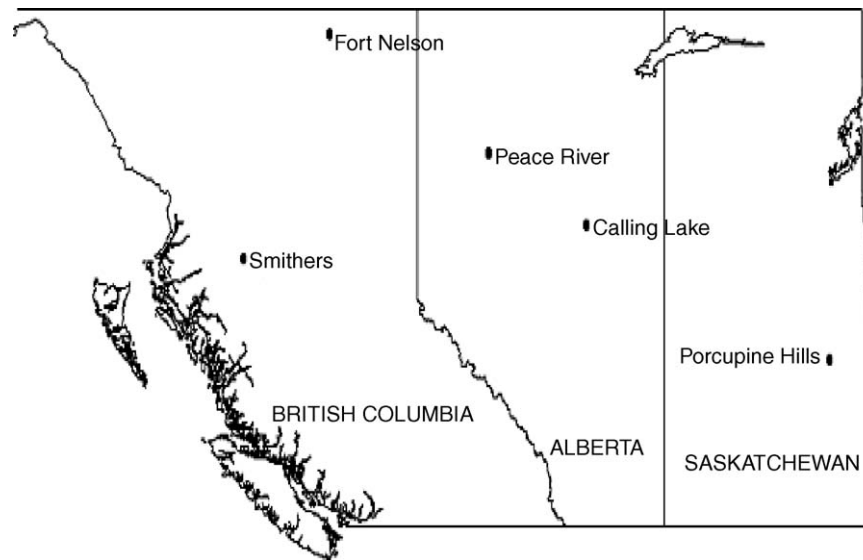


Fig. 1. Geographic distribution of sampling regions.

Table 1
Summary of site and climatic characteristics

Ecosystem classification	General location				
	Smithers (BC) SBSdk ^a 01a-Sxw- Spirea–Purple peavine	Fort Nelson (BC) BWBSmw2 ^b 01- SwAt-Step moss	Peace River (AB) Boreal mixedwood ^c BM-d low brush cranberry	Calling Lake (AB) Boreal Mixedwood ^c BM-d low brush cranberry	Porcupine Hills (SK) Mid-boreal highlands ^d D low brush cranberry
Latitude range of sampling region (N)	54°35'–54°39'	59°06'–59°18'	56°24'–56°48'	55°05'–55°31'	52°22'–52°30'
Longitude range of sampling region (W)	126°51'–127°01'	123°11'–123°28'	116°57'–117°14'	112°53'–113°27'	102°49'–103°08'
Elevation range of sampling region (m)	561–665	279–412	561–721	606–775	512–620
No. of sampling sites within sampling region	21	27	28	22	26
Mean annual precipitation (mm)	509.5	448.5	387.6	501.4	479.5
Mean May–September precipitation (mm)	164	259	208	295	224.6
Mean annual temperature (°C)	3.8	–1.1	0.7	1.8	0.6
Mean temperature of warmest month (°C)	14.9	16.7	15.9	16.3	17.3
Mean temperature of coldest month (°C)	–9	–22	–17.5	–15.6	–19.5
Growing degree days >5 °C	1164	1289	1276	1366	1472
Average wind (May–September) speed (km/h)	7.3	8.3	13.3	NA	NA
Soil characteristics of sampled sites	Fine textured soils. Mainly Gray Luvisols	Fine textured soils. Mainly Gray Luvisols	Fine textured soils. Mainly Gray Luvisols	Fine textured soils. Mainly Gray Luvisols	Fine textured soils. Mainly Gray Luvisols
Aspen site index	NA	NA	18.2	18.2	20
Spruce site index	17.8	15	16.8	16.8	19.7

The climatic data are environment Canada's 1990 climatic normals from the nearest weather station (Environment Canada, 2004). The following stations are used in the table: Smithers A (54°49'N, 127°11'W, altitude 523 m), Dease Lake (58°25'N, 130°00'W, altitude 816 m), Fort Nelson A (58°50'N, 122°35'W, altitude 382 m), Peace River A (56°14'N, 117°26'W, altitude 571 m), Athabasca 2 (54°49'N, 113°32'W, altitude 626), and Kuroki (52°00'N, 103°27'W, altitude 585). Alberta site indexes are from Beckingham and Archibald (1996). British Columbia site indexes are from (BC Ministry of Forests, 2003), Saskatchewan site indexes are from Beckingham et al. (1996). Not available (NA).

^a Banner et al. (1993).

^b DeLong et al. (1990).

^c Beckingham and Archibald (1996).

^d Beckingham et al. (1996).

required testing several camera positions until a satisfactory photo was obtained. Consequently, variable distance from the tree to the camera was necessary. Additionally, in each stand, a conscious effort was made to use variable distances between the camera and the sampled trees. For each sampled tree, distance from the camera and diameter at breast height (dbh) were measured. All photos were taken with a tripod-mounted digital Nikon Coolpix 950 with a Nikon true fisheye lens. Photos were taken under uniform sky conditions either early in the morning, late in the afternoon, or on uniform overcast days. The crown openness of an individual tree was determined through a three-step procedure with the computer program GLA version 2 software (Frazer et al., 1999, 2000). First, the crown outline was digitized. Second, the picture went through a manual thresholding procedure in which the tree components were distinguished from the background sky. Third, crown openness was calculated by dividing the number of pixels determined to be sky within the digitized crown by the total number of pixels within the same crown. The photos had a resolution of 2048×1536 pixels and the digitizing was performed at the same resolution.

2.2. Analysis

The analysis was performed with SAS Version 8.2 (SAS Institute Inc., Cary, NC) and all statistical tests were performed with $\alpha = 0.05$. Prior to analysis, the regionalized data were assessed for normality by means of descriptive statistics, histograms, normal probability plots, and boxplots. The sparse outlying data points were investigated, but only removed if they positively were caused by specific methodological errors.

In this paper, angle of view is considered to be the estimated angle from the camera to the top of the sampled tree. The angle of view was estimated in two steps. First, the height of the sampled tree was estimated with nonlinear dbh to height regression. This was done with the equation from Huang et al. (1992) for aspen and with the equation from Huang et al. (2000) for spruce. Secondly, the angle of view was estimated using the tangent trigonometric formula for a right triangle.

The initial analysis examined the assumption that species-specific crown openness is independent from both dbh and angle of view. This was done by assessing plots of openness versus dbh and angle of view. Additionally, the effect of distance between the camera and the tree (distance) was assessed. This was done because in a photo the number of pixels contained in a crown decreases with distance and can consequently influence the crown openness estimates. For each predictor variable (dbh, distance, and angle of view), two models were constructed:

$$\begin{aligned} \text{Full Model : } \text{Opn}_i &= \beta_0 + \beta_1 X_i + \beta_2 R_{i2} + \beta_3 R_{i3} + \beta_4 R_{i4} \\ &+ \beta_5 R_{i5} + \beta_6 X_i R_{i2} + \beta_7 X_i R_{i3} \\ &+ \beta_8 X_i R_{i4} + \beta_9 X_i R_{i5} + \varepsilon_i \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Regional Model : } \text{Opn}_i &= \beta_0 + \beta_1 R_{i2} + \beta_2 R_{i3} + \beta_3 R_{i4} \\ &+ \beta_4 R_{i5} + \varepsilon_i \end{aligned} \quad (2)$$

where Opn_i is the openness of tree i , β_0 the intercept, X_i the predictor variable of tree i (dbh, distance or angle of view), R_{i2} –

R_{i5} are indicator variables such that R_{ij} is 1 if tree i is from region j and 0 otherwise, and ε_i is the associated error term. These models will be referred to as: Full Model_{dbh} and Regional Model_{dbh} when $X_i = \text{dbh}_i$; Full Model_{dist} and Regional Model_{dist} when $X_i = \text{distance}_i$; and Full Model_{angle} and Regional Model_{angle} when $X_i = \text{angle of view}_i$.

Partial F -tests (Neter et al., 1996) were performed for each species between the Full Model_{dbh} and the Regional Model_{dbh} to test whether one or more parameters related to dbh were different from zero. The same procedure was repeated for distance and angle of view, using the appropriate Full Model and Regional Model. The partial F -test builds on the principle of extra sum of squares (ESS) where $\text{ESS} = [(\text{SSE}_R - \text{SSE}_F) / (df_R - df_F)] / (\text{SSE}_F / df_F)$, where SSE_F and df_F are the error sum of squares and the degrees of freedom for the Full Model, and SSE_R and df_R are the error sum of squares and the degrees of freedom for the Regional Model. ESS is distributed as an F -statistic with $(df_R - df_F, df_F)$ degrees of freedom (Neter et al., 1996). Following this analysis, under the assumption that species-specific crown openness is independent from dbh, distance, and angle of view, a one-way analysis of variance of species-specific crown openness was performed to test for regional differences, and Tukey's pairwise t -test was performed between the regional means.

3. Results

3.1. Assumptions of species-specific crown openness

The mean and the range of observations for dbh, distance, and angle of view are listed in Table 2. Scatter plots of species-specific crown openness versus distance, dbh and angle of view are illustrated in Fig. 2. Generally, no obvious trends emerge from these plots. The partial F -tests with distance and angle of view gave no significant results, indicating that the parameters related to distance or angle of view do not significantly differ from zero. For aspen, this was also true for the partial F -test with dbh. For spruce, the partial F -test with dbh indicated that one or more parameter related to dbh was significantly different from zero. Table 3 outlines the species-specific regionalized parameters from the Full Model_{dbh}. The majority of the slope parameters in Table 3 are negative but non-significant. The only significant slope parameters are found for spruce in the Fort Nelson and Porcupine Hills. These two parameters indicate that spruce crown openness decrease with dbh. Simultaneously, it should be noted that the remaining non-significant parameters only are slightly negative and some are even positive. In summary, there is weak indication in the dataset that spruce crown openness is slightly negatively correlated to dbh.

3.2. Regional differences in species-specific crown openness

The mean species-specific crown openness estimates for each region are shown in Table 2. A t -test indicated that aspen has a significantly ($P < 0.001$) higher mean species-specific

Table 2
Summary of species-specific crown openness

Region	<i>n</i>	Mean openness (Min–Max)	S.D.	95% CL for mean openness	Mean dbh (cm) (Min–Max)	Mean distance (m) (Min–Max)	Mean angle of view (degrees) (Min–Max)
Aspen							
CL	71	0.187 (0.12–0.27)	0.0341	0.179–0.195	28 (15–45)	3.9 (1.3–20.0)	80 (49–87)
FN	69	0.206 (0.10–0.33)	0.0429	0.195–0.216	35 (20–60)	3.7 (0.8–16.1)	82 (59–88)
PH	65	0.147 (0.08–0.24)	0.0375	0.138–0.157	30 (19–44)	4.3 (0.6–12.9)	79 (57–89)
PR	72	0.174 (0.09–0.28)	0.0351	0.166–0.183	30 (20–58)	3.8 (0.4–10.2)	81 (67–89)
Sm	50	0.207 (0.13–0.37)	0.0522	0.192–0.222	34 (24–53)	4.3 (1.7–11.8)	80 (66–86)
Pooled	327	0.183 (0.08–0.37)	0.0453	0.178–0.188	31 (15–60)	4.0 (0.4–20.0)	80 (49–89)
Spruce							
CL	68	0.123 (0.05–0.22)	0.0338	0.115–0.131	33 (20–52)	4.7 (0.3–15.1)	79 (62–89)
FN	71	0.137 (0.04–0.27)	0.0401	0.128–0.147	40 (22–66)	5.4 (0.2–17.0)	79 (61–89)
PH	66	0.098 (0.05–0.16)	0.0260	0.091–0.104	35 (16–55)	3.9 (0.3–10.6)	81 (64–89)
PR	67	0.142 (0.07–0.22)	0.0309	0.135–0.150	36 (20–55)	5.7 (2.2–12.0)	77 (67–84)
Sm	49	0.157 (0.08–0.26)	0.0390	0.146–0.168	37 (16–52)	5.5 (2.0–10.8)	78 (68–85)
Pooled	321	0.130 (0.04–0.27)	0.0392	0.126–0.134	36 (16–66)	5.0 (0.2–17.0)	79 (61–89)

n: number of samples, S.D.: standard deviation, Min: minimum observation, Max: maximum observation, CL: confidence limit. Region abbreviations are: Smithers (Sm), Fort Nelson (FN), Peace River (PR), Calling Lake (CL), and Porcupine Hills (PH).

crown openness than spruce in all regions. Both species have high variability in crown openness and the data points for the two species are overlapping within all regions and between all regions (Fig. 2). The results from the one-way analysis of variance indicate a significant ($P < 0.001$) difference in mean regional aspen crown openness. Tukey's pairwise *t*-test showed significant differences between most combinations of means. For aspen, all comparisons are significantly different except between Smithers–Fort Nelson and Calling Lake–Peace River. One-way analysis of variance of the spruce data indicated a significant ($P < 0.001$) difference in mean regional species-specific crown openness. The pairwise *t*-test illustrates that there are significant differences between all combinations of means except for between Smithers–Peace River, Fort Nelson–Peace River, and Fort Nelson–Calling Lake.

4. Discussion

4.1. Independence of angle of view and dbh

The initial method of Canham et al. (1994) for determining species-specific openness provided all the necessary data to test the independence of light extinction from calculated path length. The method used here does not directly give this possibility because each crown is treated as a two-dimensional entity with a specific openness. From casual observation of individual crowns, there appears to be areas of high openness and areas of low openness in an individual crown. It seems reasonable to assume that this variability in openness is caused by: (1) the path length through the crown and (2) the crown architecture including branch and leaf morphology (see review in Messier et al., 1999). Our tests for the influence of dbh and

Table 3
Summary of the regression estimates for the Full Model_{dbh}

Region	β_{0j}^a	Standard error (β_{0j})	β_{1j}^a	Standard error (β_{1j})	<i>P</i> -value for β_{1j}	r^{2b}
Spruce						
Smithers	0.147	0.024	0.00026	0.00066	0.6994	0.0032
Fort Nelson	0.188	0.0187	−0.00127	0.000455	0.0068	0.1015
Peace River	0.129	0.0147	0.000372	0.000395	0.3500	0.0134
Calling Lake	0.123	0.0180	−0.000015	0.000531	0.9978	0.0000
Porcupine Hills	0.130	0.0127	−0.000919	0.000358	0.0125	0.0936
Aspen						
Smithers	0.212	0.0354	−0.000148	0.00102	0.8856	0.0004
Fort Nelson	0.199	0.0228	0.000200	0.000636	0.7541	0.0015
Peace River	0.183	0.0174	−0.000289	0.000568	0.6045	0.0039
Calling Lake	0.197	0.0191	−0.000344	0.000660	0.6042	0.0039
Porcupine Hills	0.161	0.0247	−0.000479	0.000821	0.5622	0.005

^a The Full Model $Opn_i = \beta_0 + \beta_1 X_i + \beta_2 R_{i2} + \beta_3 R_{i3} + \beta_4 R_{i4} + \beta_5 R_{i5} + \beta_6 X_i R_{i2} + \beta_7 X_i R_{i3} + \beta_8 X_i R_{i4} + \beta_9 X_i R_{i5} + \epsilon_i$ can be rewritten for a particular region. For instance, for Region 2 the Full Model can be written as: $Opn_i = \beta_0 + \beta_1 X_i + \beta_2 + \beta_6 X_i + \epsilon_i$. This can be simplified to: $Opn_{i2} = \beta_{0,2} + \beta_{1,2} X_i + \epsilon_{i,2}$, where Opn_{i2} denotes the species-specific crown openness for tree *i* in region *j*, $\beta_{0,2} = \beta_0 + \beta_2$, $\beta_{1,2} = \beta_1 + \beta_6$, and $\epsilon_{i,2}$ is the associated error term. In general, $Opn_{ij} = \beta_{0j} + \beta_{1j} X_{ij} + \epsilon_{ij}$, for Region *j*.

^b r^2 was calculated separately for each region with the regional simple linear regression.

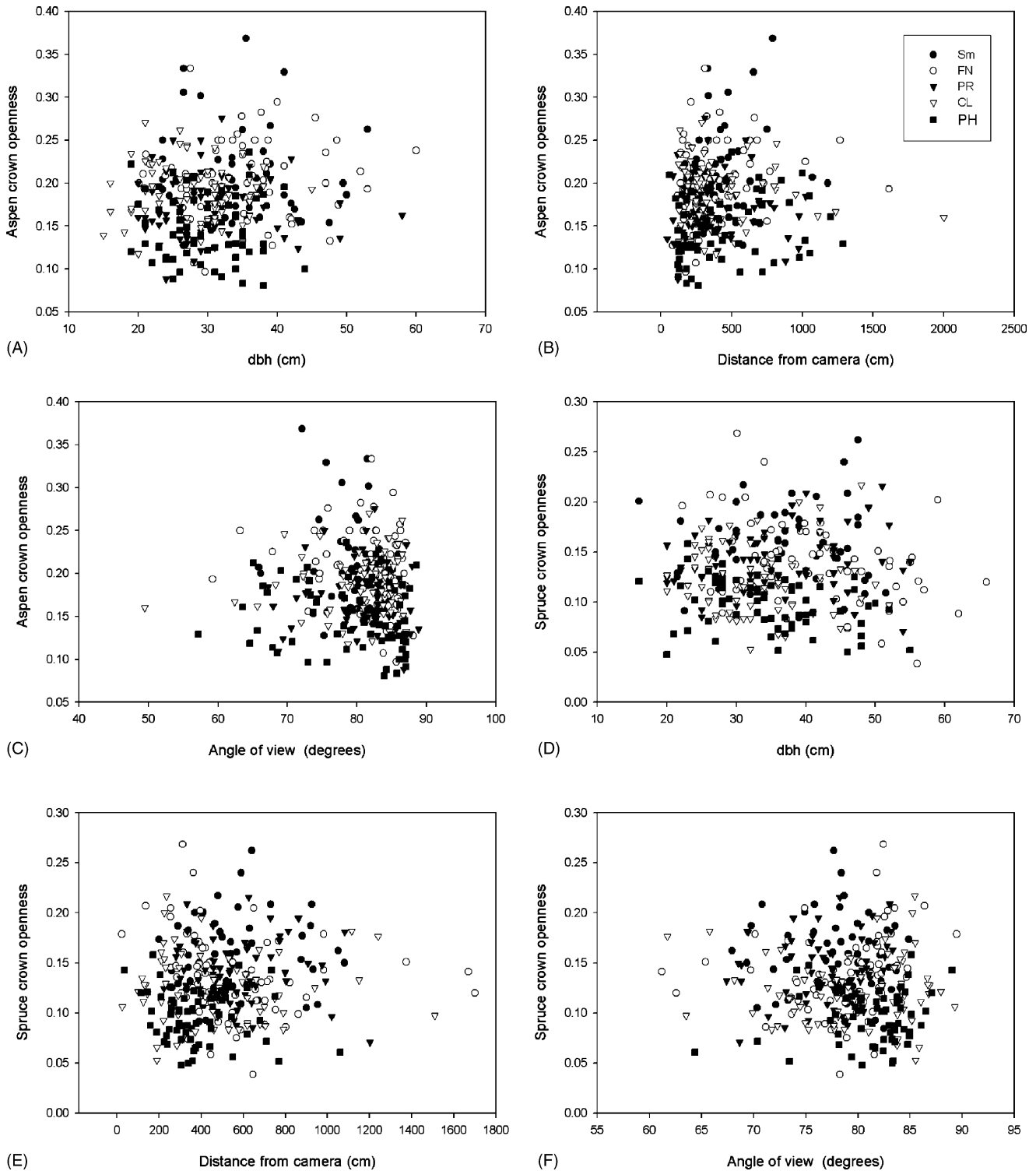


Fig. 2. Scatter plots of crown openness vs. dbh, angle of view, and distance from camera. Region abbreviations: Smithers (Sm), Fort Nelson (FN), Peace River (PR), Calling Lake (CL), and Porcupine Hills (PH).

angle of view on crown openness relate to whether the proportion of the crown with high openness changes with dbh or angle of view. It has been shown that light extinction is correlated with a calculated path length through an individual crown (e.g. Stadt and Lieffers, 2000). This is not inconsistent with the assumptions of species-specific crown openness

because the central part of a crown can be less open than the outer part of the crown. The main assumption for use of species-specific crown openness is that the proportion of high and low openness areas (a function of path length and foliage distribution) within a crown is independent of dbh and angle of view. The performed tests showed no significant effect of

dbh, distance or angle of view on openness for aspen. This indicates that use of a species-specific value for aspen meets the necessary assumptions. For spruce, a small but significant effect of dbh on openness was found in two out of five regions. Thus, use of species-specific crown openness might cause a biased estimate in stands with low or high average dbh. It must be noted that the inclusion of dbh only explains a small portion of the overall variation (r^2 -values < 0.14 in Table 3) and only has a significant effect in two out of five regions. Accordingly, within the range of data collected in this study, species-specific crown openness appears to be a relatively robust measure.

4.2. Regional variability in species-specific crown openness

The results indicate that there are differences in species-specific crown openness between regions. Table 4 outlines openness results from other regions and studies. A comparison between Tables 2 and 4 reveals several interesting points. The Alberta openness estimates from Table 4 (Stadt and Lieffers, 2000) are from the same geographic area as the Calling Lake region in this study. The estimates from the Calling Lake area of this study and the estimates from Table 4 are not within the same range. There are several possible explanations for this disagreement. The sample size of Stadt and Lieffers (2000) is small and some of the difference might be sampling related. Stadt and Lieffers (2000) used a very different methodology, in which the actual light level in the shadow of an individual tree was measured. Their method indirectly included beam enrichment, which is not included in the fisheye photo method used in this study. Beam enrichment might explain some of the higher openness found by Stadt and Lieffers (2000) but should not result in a two-fold difference. The method used to determine crown openness in this study has three potential associated errors that might explain some of the difference. Firstly, there is the issue of lack of objectivity and problems in the manual thresholding procedure. These issues are discussed in detail by Wagner (1998, 2001). It is possible that the thresholding method has led to some bias in the estimates presented here, but it is unlikely that the bias amounts to a value close to 100%. Secondly, some concerns about the use of

digital cameras for fisheye photos of forest canopy have been raised (Frazer et al., 2001). In very dense canopies, canopy openness estimates obtained from digital fisheye photos have been shown to overestimate the openness compared to estimates obtained with a traditional film camera (Frazer et al., 2001). This error is less important in more open canopies, and this error biases towards higher openness estimates. Consequently, this error should result in overestimation of openness with our methodology, which is the opposite of the observed difference. Thirdly, analyses for openness using fisheye photos are not very accurate at low openness levels. Machado and Reich (1999) found problems with estimation of light transmission of less than 6% above canopy photosynthetic photon flux density. Consequently, it is likely that the low crown openness estimates of spruce have slightly higher uncertainty than the higher aspen crown openness estimates. The reported mean crown openness estimates from this study are all above 12% and this problem should consequently not be large. The large difference in openness estimates between this study and that of Stadt and Lieffers (2000) is likely caused by unidentified methodological differences and possibly the small sample size in the study of Stadt and Lieffers (2000).

Regional variability of species-specific crown openness can be caused by both variations in crown architecture, including branch and leaf morphology, or path length. The results of this study do not give any possibility for teasing apart these effects. The observed geographic variability can therefore be attributed to one or both of those factors. Fig. 3A illustrates a plot of

Table 4
Species-specific crown openness estimates from related studies

Region	Openness	95% Confidence limits	Sample size
Aspen			
Hazelton (BC)	0.21	0.167–24.5	20
Calling Lake (AB)	0.36	NA	11
Quebec	0.16	0.015–0.18	38
Spruce			
Hazelton (BC)	0.11	0.08–0.147	20
Calling Lake (AB)	0.19	NA	5
Quebec	0.11	0.094–0.12	37

British Columbia (BC) data from Canham et al. (1999); Alberta (AB) data from Stadt and Lieffers (2000); Quebec data from Coates (unpublished) personnel communication. Not available (NA).

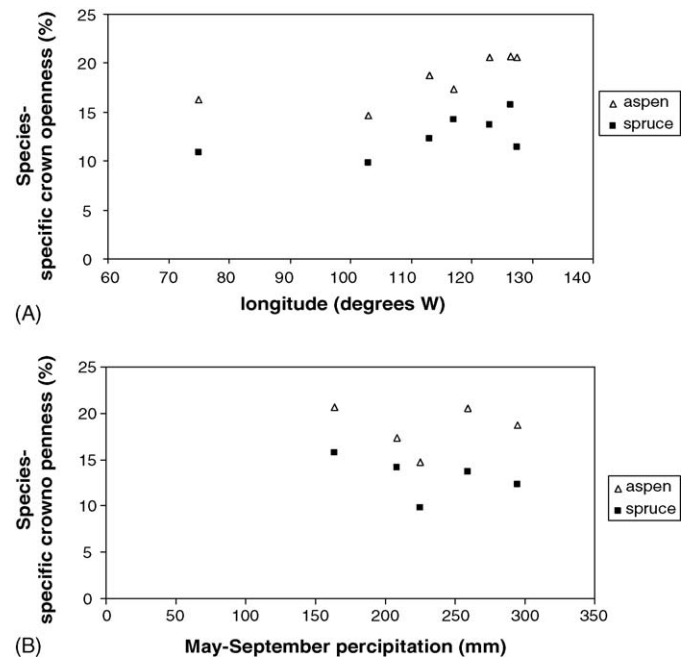


Fig. 3. Species-specific crown openness vs. longitude and precipitation. (A) From east the data points are: Quebec, Porcupine Hills, Calling Lake, Peace River, Fort Nelson, Smithers, and Hazelton. Quebec data from Coates (unpublished, personnel communications) and Hazelton data from Canham et al. (1999). (B) Data from this study only, see Table 1 for sources of precipitation data and additional climatic information.

species-specific crown openness versus longitude. Visual inspection of this plot indicates that species-specific crown openness estimates seem to decrease directionally from west to east. This is consistent with stand level understory light observations by Messier et al. (1998) who compared their own results from Quebec with results from northern Alberta (Lieffers and Stadt, 1994; Constabel and Lieffers, 1996). This comparison indicated that understory light levels were lower in Quebec than in Alberta for similar deciduous and mixed stands. It is likely that this systematic variation is caused by the systematic variation of several climatic factors. The challenge is to determine which combination of factors influences species-specific crown openness because no individual factor seems to exhibit the observed pattern. Messier et al. (1998) speculated that the difference in understory light levels in Quebec and Alberta might be caused by higher precipitation in Quebec. Fig. 3B illustrates a plot of species-specific crown openness versus May–September precipitation. For spruce Fig. 3B seems to indicate a slight drop in species-specific crown openness as the May–September precipitation increases. For aspen, this relationship is not apparent. A simple linear regression in which species-specific crown openness was predicted as a function of May–September precipitation gave non-significant results for both species (spruce: $P = 0.41$; aspen: $P = 0.92$). These non-significant results are probably due to the many factors influencing species-specific crown openness and the small sample size.

Crown transparency (also referred to as crown density) is an alternative measure of the amount of sky visible through an individual crown that is often used for forest health assessment (e.g. Innes, 1993; USDA Forest Service, 2002; Redfern and Boswell, 2004). Crown transparency is normally visually estimated by comparison to a reference illustration (e.g. Innes, 1990; USDA Forest Service, 2002). The reference used for estimation often varies between countries or regions and this results in different measurement scales. Regional variations in crown transparency should fundamentally be consistent with regional variations in species-specific crown openness. Unfortunately, regional comparisons of crown transparency are problematic due to biases created by the estimation methods (e.g. Innes, 1993; De Vries et al., 2000). Still, several studies have shown regional variation in crown transparency (e.g. Innes and Boswell, 1988; Innes, 1993; Klap et al., 2000). This variation is very similar to the geographic variation of species-specific crown openness shown in this paper. As for species-specific crown openness, it is generally difficult to determine which factors are responsible for regional variation in crown transparency as the determinants are plentiful and often correlated (Innes and Boswell, 1988).

4.3. SORTIE's sensitivity to species-specific crown openness

This study shows that mean species-specific crown openness does vary between regions. Furthermore, it was also found that dbh might influence the crown openness of spruce and thus

potentially bias understory light predictions. The impact of the geographic intraspecific variability of species-specific crown openness and the possible effect of dbh on light predictions can only be assessed through a modeling test and sensitivity analysis. Beaudet et al. (2002) performed a validation and sensitivity analysis of the light submodel of SORTIE for the northern hardwoods in eastern Canada. This sensitivity analysis showed that the understory light predictions were relatively insensitive to changes in species-specific crown openness while being more sensitive to changes in crown dimensions. Despite this relative insensitivity, the range of species-specific crown openness estimates found in the literature from western boreal Canada would still be sufficient to cause significant differences in understory light levels.

SORTIE predicts understory light levels with the Gap Light Index (GLI) which is 100% in full light and 0% in full shade. Beaudet et al. (2002) investigated the effect on GLI from doubling the estimate of species-specific crown openness from 0.2 to 0.4. Under a closed canopy this was found to change the predicted GLI from approximately 6 to 9%. South of a 400 m² gap the change was larger and the predicted GLI changed from 19 to 27%. North of a 400 m² gap the predicted GLI changed from 50 to 57%.

The literature indicated regional variations in species-specific crown openness close to 100% in western boreal Canada (Table 4). If this regional variability is true, regional variation of understory light levels would be suspected to vary in a similarly magnitude to the predictions from the sensitivity analysis of Beaudet et al. (2002). This study indicated that the actual regional variability of species-specific crown openness in the investigated part of western boreal Canada is less than indicated by the literature for the same area (Table 4). Dbh was found to cause species-specific crown openness estimate to change by less than 30% while regional differences cause the species-specific crown openness estimate to vary by less than 50%. The variation of understory light levels caused by regional variations in species-specific crown openness can thus be expected to be approximately half of the outlined numbers from the sensitivity analysis.

The importance of such regional variations of understory light levels is dependent on the process in question. In terms of quantifying annual growth of understory trees (e.g. Wright et al., 1998) the differences in predicted growth from such variations in light levels are small. The differences are more likely to be important for processes with a threshold value or a very steep response related to understory light level. Thus, the observed regional variability could potentially have a larger impact on a process such as understory tree mortality.

In relation to most management issues the above outlined variations in understory light levels caused by the regional variability of species-specific crown openness are small. Thus, for most management purposes the light model is portable between regions without remeasurement of local species-specific crown openness. It should be noted that the climatic variation investigated in this study is relatively narrow compared to the climatic ranges of the two species. Thus, it is unknown if similar conclusion hold under more extreme

climatic conditions. Species-specific crown openness is the only parameter in SORTIE's light model that cannot be obtained from published equations, or reanalysis of permanent sample plots. Accordingly, the results presented here must be seen as an asset for the model, because they facilitate the model's application without large associated cost of reparameterization.

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