

Measurement and modeling of spatially explicit variation in light transmission through interior cedar–hemlock forests of British Columbia¹

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Abstract: We have characterized canopy geometry and light transmission by the nine dominant conifer and broad-leaved tree species of the interior cedar–hemlock (ICH) forests of northern British Columbia. Our field data were used to parameterize a spatially explicit model of light transmission through mixed-species forests. That model, a component of the forest dynamics simulator SORTIE, was developed for eastern deciduous forests, and this paper presents a test of that model in a very different ecosystem. Our results show that individual crowns of the ICH forests intercepted much more light than species of eastern deciduous forests but that the canopy as a whole allowed greater light penetration, largely because of openings between the relatively narrow, conical crowns of the western conifers. Light transmission by individual crowns was correlated with shade tolerance among the conifers (as in eastern deciduous species), but crown depth was not (in contrast with eastern species). Despite the fundamental differences in the nature of light transmission in the two ecosystems, the SORTIE light model developed for eastern deciduous forests was effective at predicting spatial variation in understory light levels in these western coniferous forests. The goodness of fit of such a simple model suggests that the most important factors regulating spatial variation in understory light levels in these forests are simply the sizes and distribution of nearby trees, and the local sky brightness distribution. Discrete canopy gaps represent a special case in which a region of the canopy is not occupied by crowns.

Résumé : Nous avons caractérisé la géométrie de la canopée et la transmission de la lumière pour les neuf espèces forestières feuillues et résineuses qui dominent dans les forêts de cèdre et de pruche de l'intérieur dans le nord de la Colombie-Britannique. Nos données de terrain ont été utilisées pour définir les paramètres d'un modèle spatialement explicite de transmission de la lumière dans les forêts mélangées. Ce modèle, une composante du modèle de simulation de la dynamique forestière appelé SORTIE, a été développé pour les forêts feuillues de l'Est. Cet article présente un test réalisé avec ce modèle dans un écosystème très différent. Nos résultats montrent que les cimes individuelles des forêts de cèdre et de pruche interceptent beaucoup plus de lumière que les espèces des forêts feuillues de l'Est mais que la canopée dans son ensemble permet une meilleure pénétration de la lumière, surtout à cause des ouvertures entre les cimes coniques relativement étroites des conifères de l'Ouest. La transmission de la lumière par les cimes individuelles est corrélée avec la tolérance à l'ombre des conifères, comme c'est le cas chez les espèces feuillues de l'Est, mais la profondeur de la cime ne l'est pas, contrairement à ce qu'on observe chez les espèces de l'Est. Malgré les différences fondamentales dans la nature de la transmission de la lumière dans les deux écosystèmes, le modèle de transmission de la lumière SORTIE, qui a été développé pour les forêts feuillues de l'Est, est efficace pour prédire la variation spatiale du niveau de lumière en sous-étage dans ces forêts de conifères de l'Ouest. Le fait qu'un modèle aussi simple s'ajuste aussi bien suggère que les facteurs les plus importants qui influencent la variation spatiale du niveau de lumière en sous-étage dans ces forêts sont simplement la dimension et la distribution des arbres avoisinants ainsi que la distribution locale de la clarté du ciel. Les vrais trouées dans la canopée constituent un cas spécial où une partie de la canopée n'est pas occupée par des cimes.

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Introduction

Pacala et al. (1993, 1996) and Canham et al. (1994) have recently presented a simple model and a set of field methods for predicting spatial variation in light levels within mixed-species forests. The light model is a component of SORTIE, a simulation model of forest dynamics (Pacala et al. 1993, 1996). The light model in SORTIE predicts incident radiation at any given location within a forest as a function of (i) species-specific light transmission coefficients; (ii) variation in crown geometry as a function of tree size; (iii) the identities, sizes, and spacing of trees in the immediate neighborhood; and (iv) the local sky brightness distribution

(Pacala et al. 1993). The model was developed and originally calibrated for temperate deciduous forests of northeastern North America (Canham et al. 1994).

The SORTIE light model is an extraordinarily simple representation of the underlying complexity of light transmission through forest canopies and gaps (e.g., Bjorkman and Ludlow 1972; Hutchison and Matt 1976; Chazdon and Fetcher 1984; Messier and Bellefleur 1988; Canham et al. 1990, 1994). However, this simplicity is probably its greatest strength. While there are a number of much more mechanistic and detailed models of light transmission through forest canopies (e.g., Oker-Blom and Kellomaki 1982; Wang and Baldocchi 1989; Grace 1990; Pukkala et al. 1991; Brunner 1998), it has proven to be extremely difficult to parameterize them under field conditions and in mixed-species stands. In contrast, the parameters required by the SORTIE light model are operationally defined and can be readily estimated directly from field data (Canham et al. 1994). In particular, the modeling approach is designed to predict the light levels experienced by individual seedlings and saplings at any point in the understory, in the same units that are used in the field to measure growth as a function of light level (e.g., Pacala et al. 1994; Wright et al. 1998).

SORTIE is currently being parameterized for western coniferous forests, specifically the interior cedar-hemlock (ICH) forests of northern British Columbia (Kobe and Coates 1997; Wright et al. 1998). That effort has both theoretical and applied motivations. One of the limitations of empirically based models is that the generality of the understanding derived from the model can really only be tested through application in a range of different systems. The original parameterization of the model in eastern deciduous forests led to a number of theoretical predictions on the nature of successional dynamics and species interactions in forests (Pacala et al. 1996). The empirical studies used to parameterize the light model, for instance, confirmed Horn's early prediction (Horn 1971) that there should be a positive correlation between shade tolerance and light interception. Our results in eastern forests (Canham et al. 1994) also revealed a correlation between shade tolerance and crown depth, and demonstrated that this was the principal cause of interspecific variation in light interception (rather than differences in foliage density within the crown). In a very basic sense, the forest dynamics predicted by SORTIE are consistent with Horn's (1971) model and Connell and Slatyer's (1977) "tolerance" model that propose that secondary forest succession is driven by interspecific differences in resource uptake (light interception) by adults (Canham et al. 1994) and interspecific differences in tolerance by juveniles of resource depletion (shading) (Kobe et al. 1995).

Our research with SORTIE in British Columbia is also motivated by the need for a predictive model of forest dynamics that can be used to develop partial cutting strategies as an alternative to clear-cutting in western coniferous forests. The ability to predict spatial variation in understory light levels under a wide range of partial-cutting strategies (including both thinning and the formation of discrete gaps) will be critical to our ability to predict forest dynamics following harvests and to develop silvicultural systems that produce the mix of light levels that will result in competitive growth rates by a wide range of species.

The specific objectives of the current study were to (i) characterize interspecific variation in light transmission and canopy geometry of the nine dominant tree species of the ICH forests of British Columbia and test the generality of the patterns of interspecific variation found in eastern deciduous forests by Canham et al. (1994) and (ii) conduct an explicit test of the ability of the basic light model in SORTIE to predict spatial variation in understory light levels in ICH forests. While the light model is a critical component of SORTIE, previous studies have not included any formal test of the ability of the model to accurately predict spatial variation in understory light.

Model structure

The basic design of the light model in SORTIE is extremely simple. The crowns of individual trees (from seedling to canopy tree size) are represented in the model as cylinders, with the radius of the crown (i.e., the cylinder) estimated as an empirical function of tree diameter at breast height (DBH). The top of the cylinder is specified by the height of the tree (again, predicted as an empirical function of DBH), and the base of the cylinder is set at the base of the live crown (using empirical, linear regressions between tree height and crown depth). Thus, all of the empirical functions needed to specify the dimensions of the crown can be estimated from readily available field data (e.g., Canham et al. 1994). Light interception by tree boles below the live crown is ignored. Crowns of each species are assumed to have a species-specific canopy openness (i.e., fraction of sky visible through the crown). Empirical results from the original calibration of the model indicated that, for species of temperate eastern forests, openness of the crown was independent of the angle of view through the crown, and independent of the path length through the crown (Canham et al. 1994).

Light levels at any point within the modeled stand are predicted by first dividing the canopy hemisphere above that point into a grid with equal-area cell sizes defined by divisions of azimuth (compass direction) and altitude (angle from horizontal). For each of these regions of the sky, the model then determines the numbers of cylindrical tree crowns of each species that have foliage at the midpoint of the region (by solving algebraically for the intersection between the cylindrical canopy and a line radiating from the point in the understory to the midpoint of a given sky region). In operational terms, the model checks all trees within a specified radius, with the radius calculated conservatively as a function of maximum potential tree height and diameter to ensure that all trees that could potentially have foliage in that portion of the sky hemisphere are checked. The fraction of incident gap light transmitted by the canopy (T_j) through that region (j) of the hemisphere is then estimated as

$$T_j = \prod_{i=1}^n \text{openness}_i$$

where openness_i is the species-specific openness (as a fraction) of the i th tree intercepted in that portion of the sky. The absolute amount of light transmitted through that portion of

the sky (L_j) (as a fraction of seasonal, total incident radiation) is then

$$L_j = T_j \times \text{incident}_j$$

where incident_j is the fraction of total potential incident radiation that originates from region j of the sky hemisphere (Canham et al. 1994). The sky brightness distribution (i.e., incident_j) is calculated by integrating both direct beam and diffuse radiation over the course of a predefined growing season and latitude. Zenith angle is used to cosine-correct both diffuse and direct radiation to provide estimates of light incident on a horizontal surface. Diffuse radiation (before cosine correction) is assumed to be isotropic (i.e., uniform over the sky hemisphere). The relative contribution of diffuse versus direct radiation at a site can be either estimated from field data or from empirical relationships with long-term average cloudiness (Canham et al. 1994). For our study sites in northern, interior British Columbia, we assumed that diffuse and direct radiation each contributed 50% of total, incident, photosynthetically active radiation (PAR) over the course of the growing season.

The light transmitted through each region of the sky is then summed to give the overall fraction of incident radiation that reaches a given point in the understory as a function of the spatial distribution and sizes of nearby trees. The fraction is converted to a percentage to convert it to a gap light index (GLI; Canham 1988), which specifies the percentage of combined diffuse and direct radiation that penetrates directly through openings in the canopy (of any size, ranging from large gaps to small openings between leaves or needles) over the course of the growing season.

One of the strengths of this modeling approach is that it is directly analogous to the actual methods used to estimate GLI from fish-eye photography under field conditions (e.g., Canham et al. 1994). In particular, the modeling approach is designed to predict the light levels experienced by individual seedlings and saplings at any point in the understory, in the same units that are used in the field to measure growth as a function of light level (e.g., Pacala et al. 1994; Wright et al. 1998). Under field conditions, the entire 180° field of view of a fish-eye photograph is analyzed. This is obviously impossible in the model, since it would require mapping an infinitely large plane to determine all trees that could potentially intercept light at angles near the horizon. Thus, the model scans regions of the sky above a user-selected threshold (normally set at 45°; e.g., Pacala et al. 1996) and estimates GLI as a percentage of the radiation that originates from that restricted portion of the sky (rather than as a percentage of the radiation originating from the entire sky hemisphere). One of the goals of the test of the light model reported here was to determine the congruence between the value of GLI predicted by scanning only a limited region of the sky (in the model) and the actual GLI values that would be calculated in the field by scanning over the entire sky hemisphere.

Field methods

Study area and species

The research was conducted as part of the Date Creek Silvicultural Systems Study (Coates et al. 1997), at sites lo-

cated near Hazelton, B.C., Canada (55°22'N, 127°50'W; 370–665 m elevation). The study area lies within the Moist Cold subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmc) (Pojar et al. 1987). Our research focused on the nine common tree species within the region. Mature forests at Date Creek (130–140 years since fire) are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) but are intimately mixed with western redcedar (*Thuja plicata* Donn ex D. Don in Lamb.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), hybrid spruce (the complex of white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and occasionally Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray). Subalpine fir is commonly replaced by amabilis fir (*Abies amabilis* Dougl. ex Forbes) at higher elevations. Old-growth stands (≥ 350 years since fire) are dominated by western hemlock with minor components of western redcedar, subalpine fir, and amabilis fir. See Banner et al. (1993) for a detailed description of ICH forests.

Canopy tree geometry

The light model requires a set of three functions that describe canopy geometry for each species: (i) height as a function of DBH; (ii) crown depth as a fraction of tree height; and (iii) crown radius as a function of DBH. Crown depth is defined as the distance from the top of the tree to the base of the live crown. We defined the base of the live crown as the point where foliage occupied at least three of the four quadrants around the stem. Crown radius was measured by projecting the outermost margin of the crown on the ground, and taking the average of the two longest perpendicular radii. By projecting the three-dimensional crown onto two dimensions, this is essentially a measurement of the maximum radius of the crown for a given DBH. For most of the conifer species, which have conical crowns, the maximum crown radius occurs at or near the bottom of the crown, while the maximum crown radius often occurred much closer to the top of the crowns for the three broad-leaved species. Data on stem diameter, height, crown depth, and crown radius of adult trees were collected for all nine species from sites within the ICH zone. We also used data from saplings collected for a related study of sapling response to variation in light (Wright et al. 1998) and a stand reconstruction study (LePage 1995) at the Date Creek study area. We supplemented this with a large data set on adult tree stem diameter and height from permanent sample plots maintained in this region by the B.C. Ministry of Forests. Our final data set contained 3522 observations for height–diameter relationships (with sample sizes ranging from 256 to 1051 for individual species), 778 observations of crown depth ($n = 48$ –221 per species), and 736 observations of crown radius ($n = 48$ –196 per species). Tree sizes ranged from 0 to 164 cm DBH and from 1.2 to 47.7 m in height, but 96% of the stems were <50 cm DBH, and 90% were <30 m in height.

We used nonlinear regression to predict tree height as a function of DBH with an equation of the form

$$HT = 1.35 + (\text{MAXHT} - 1.35) \times (1 - e^{(-1.0 \times B \times \text{DBH})})$$

The equation is offset to predict a tree height of 1.35 m at 0 cm DBH and produces a curve with an exponential approach to an asymptotic maximum height (MAXHT), with the steepness of the curve controlled by the exponential decay parameter B . We did not have enough data on very large trees to accurately estimate MAXHT for four of the species. Instead, for those four species we set MAXHT based on visual inspection of the data and estimated the single parameter B (see Results). Crown depth was predicted as a linear function of height and crown radius was predicted as a linear function of DBH (using least-squares regression). The intercepts of the linear regression were generally not significantly different than zero. Thus, to simplify the number of parameters in the model, the final regressions for crown depth and radius were done without intercepts.

Estimating light transmission using canopy photography and image analysis

As in Canham et al. (1994), we used fish-eye photography and computerized image analysis to document interspecific variation in the openness (and thus the transmission of gap light) for individual crowns of the nine species. The much more open canopies of ICH forests allowed us to identify individual tree crowns within specific photographs, and thereby allowed us to use a much simpler and more direct method of estimating species-specific canopy openness than in Canham et al. (1994). Our general method consisted of taking fish-eye photos in locations where either a significant portion or the entire crown of an identified, individual tree could be clearly delineated in the photograph. All photographs were taken with a tripod-mounted Nikon camera equipped with a Nikkor 8-mm true fish-eye lens and Fujichrome Sensia 400 ASA color slide film. The camera was leveled at a height of 1–1.5 m, and was equipped with colored LEDs mounted within the frame of the circular image to orient the image on an east–west axis. The processed slides were scanned in color with a Polaroid Sprintscan 35 slide scanner. The digitized images were then analyzed using GLI/C software developed by the first author. The software allows the user to manually trace the outline of an object, and then calculate the openness of that object (i.e., percent of sky visible through the crown). We traced the actual outline of the crown visible in the photograph, rather than attempt to define the outline that would be generated by our assumption that crowns were cylindrical. While the outline of a tree crown projected on a fish-eye photograph is fundamentally fractal, at the resolution of the digitized image (1325 dpi), it was relatively straightforward to identify portions of the photograph in which the canopy consisted of only a single crown of a previously identified tree. We limited analyses to photographs in which the delineated area represented the majority of the crown of an individual tree. We ended up with a total of 146 photographs, with sample sizes for individual species ranging from 10 to 23 photographs (crowns). Photographs for this purpose were taken from a very wide range of locations within the Date Creek study area. We used one-way analysis of variance to test for variation in canopy openness among species.

We also took photographs at 75 locations where one of seven of the species (i.e., all of the species except *amabilis* fir and cottonwood) was the overwhelming dominant (i.e., >75% of basal area in the immediate neighborhood). These

photographs were used for a more thorough analysis of interspecific variation in light transmission, including variation in the angular distribution of canopy openness among the seven species. We could not find sufficient numbers of pure stands of the remaining two species for this separate analysis. Photographs were taken, processed, and digitized using the same basic methods described above. Patterns of light transmission through the entire canopy were then analyzed using the GLI/C software. We used one-way analysis of variance to test for interspecific variation in the stand-level GLI that specifies the percent transmission of incident radiation over the course of the growing season (which was assumed to run from April 15 to September 15).

Model validation and tests

For a test of the light model, we took an additional 67 fish-eye photographs distributed in five stands at Date Creek in which all trees ≥ 15 cm DBH had been previously mapped for a study of the dispersion of seedlings around parent trees (LePage et al. 2000). The five sites ranged from undisturbed, mature stands to stands that had had various levels of partial cutting and included gaps ranging up to 0.5 ha in size. The five validation sites were physically separate from the sites where calibration photos were taken. All of the sites were on relatively level terrain. GLI was estimated from the digitized photographs using our standard methods (described above). The X , Y coordinates and stem diameters of the mapped trees were then entered into SORTIE/BC, along with the empirically estimated crown geometry relationships and the empirically estimated light transmission coefficients, to generate GLI and overall canopy openness values predicted by the model for each location.

Because of the conical to oval shapes of the crowns of most of the ICH species (particularly the conifer species), the “effective” crown radius for model calculations was assumed to be 50% of the maximum crown radius measured in the field. This rescaling factor was selected to produce a cylinder with a vertical cross-sectional surface area equal to a cone, with the predicted maximum radius assumed to occur at either the base or the top of the crown. An additional set of predictions were generated assuming that there was no taper or variation in crown width with height (i.e., that the cylinder of the crown had a radius equal to the maximum predicted radius for a stem with that DBH). All model calculations were restricted to regions of the sky above 45° from horizontal and assumed that the sites were on level terrain.

Results and discussion

Canopy tree geometry

In contrast with species of eastern forests studied by Canham et al. (1994), there was no clear relationship between shade tolerance and crown depth among the nine ICH species (Table 1). Crown depth ranged from a low of 20% of tree height in lodgepole pine to a high of 46% of tree height in *amabilis* fir (Table 1). Maximum crown radius was a linear function of stem diameter for all nine species (Table 2). The two most shade-tolerant conifers (western hemlock and western redcedar) had distinctively broader crowns than all of the other conifers, which are characterized at these high latitudes by extremely narrow crowns (Table 2). While the

Table 1. Shade tolerance and crown depth (as a percentage of total tree height) for the major tree species of ICH forests.

Species	Shade tolerance (% survival)	Crown depth (%)		R^2 (%)
		Estimate	SE	
Western hemlock	86.7	38.9	0.74	92.6
Western redcedar	84.2	36.8	1.03	91.3
Amabilis fir	51.4	46.4	1.55	94.7
Subalpine fir	47.0	45.4	1.97	90.0
Hybrid spruce	30.8	40.5	1.08	93.4
Lodgepole pine	4.2	20.1	1.36	82.3
Trembling aspen	15.5	30.1	1.36	91.3
Cottonwood	9.1	42.0	1.83	90.4
Paper birch	4.7	31.5	1.76	82.2

Note: Shade tolerance was quantified as the percent survival of saplings over a 5-year period at 10% full sun, using empirical relationships from Kobe and Coates (1997) and Wright et al. (1998). Also reported are the standard error of the crown depth estimate (SE) and the R^2 of the regression used to estimate crown depth. Species are listed in descending order of shade tolerance for the six conifer and three broad-leaved species separately.

height–diameter relationships were fairly similar among all nine species (Table 3), there was a slight trend for the least shade-tolerant species to have the fastest approach to asymptotic height (i.e., the largest B parameters; Table 3). As a result, within the range from 0 to 30 cm DBH, western redcedar had the shortest height while lodgepole pine and the three broad-leaved species had the greatest height at a given stem diameter.

Light transmission by individual tree crowns

Canopy openness varied significantly among the nine species ($F_{[8,137]} = 8.41$, $p < 0.0001$) and ranged from a low of 5.8% in paper birch to a high of 20.6% in trembling aspen (Fig. 1A). Among the six conifer species, the three least shade-tolerant species (subalpine fir, hybrid spruce, and lodgepole pine) had the highest light transmission (Fig. 1A). In contrast with eastern broad-leaved species (Canham et al. 1994), the three western broad-leaved species studied here (aspen, birch, and cottonwood) showed an inverse relationship between canopy openness and shade intolerance (Fig. 1A). In general, the species of high-latitude, temperate coniferous forests reported here had much less open crowns than species of lower latitude, broadleaf-dominated forests in eastern North America (which ranged from 7.4% for eastern hemlock to 56.5% for northern red oak; Canham et al. 1994).

Stand-level variation in light transmission

There were significant differences in understory GLI in stands dominated by different tree species ($F_{[6,68]} = 10.03$, $p < 0.001$) (Fig. 1B). While transmission of gap light through individual crowns of ICH species was extremely low relative to eastern species, gap light transmission at the stand level was relatively high, with GLI values in undisturbed stands ranging from 8.1% of incident radiation in stands dominated by western redcedar to 29.2% of incident radiation in stands dominated by lodgepole pine. In general, understory light levels mirrored the light transmission char-

Table 2. Regression coefficients for maximum crown radius (m) as a linear function of DBH (cm).

Species	Regression coefficient	SE	Maximum crown radius*	R^2 (%)
Western hemlock	10.98	0.41	5.49	78.3
Western redcedar	12.28	0.66	6.14	76.6
Amabilis fir	4.84	0.22	2.42	90.6
Subalpine fir	5.01	0.24	2.51	88.4
Hybrid spruce	4.78	0.22	2.39	82.6
Lodgepole pine	6.05	0.29	3.03	90.3
Trembling aspen	6.55	0.32	3.28	90.1
Cottonwood	4.93	0.33	2.47	79.7
Paper birch	9.68	0.51	4.84	83.5

Note: Models were fitted without intercepts. Also reported are the standard error of the coefficient (SE), the predicted maximum crown radius (m) for a 50 cm DBH tree, and the R^2 of the regression relationship.

*For a 50 cm DBH tree.

acteristics of the dominant species, with the lowest light levels in stands dominated by the most shade-tolerant conifers (Fig. 1). Canopy openness was an approximately linear function of angle from the horizon for all of the stands, with the slope of the relationship varying as a function of the dominant species (Fig. 2A). Canopy openness directly overhead was relatively high, ranging from 20 to 70%; however, very little radiation originates within 30° of the zenith at the high latitudes of our study sites (Fig. 3). Thus, the bulk of understory radiation penetrated through canopies at incidence angles of 35–60° from horizontal (Fig. 2B).

Test of the SORTIE light model

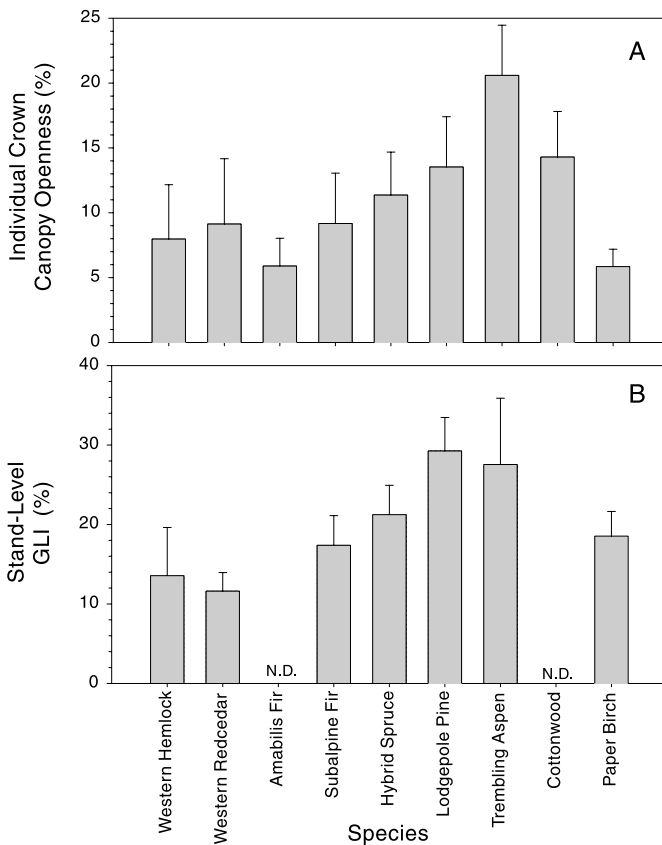
The light model, using cylindrical crowns with radii set at 50% of maximum crown radius, produced excellent fits to the test data set (Fig. 4). Predicted canopy openness was very highly correlated with observed canopy openness ($r = 0.964$, SE of estimate = 0.072), although the model slightly underestimated canopy openness when observed openness exceeded 50% (Fig. 4A). GLI values predicted by the model (integrated over a 90° cone centered on the zenith) were also highly correlated with observed GLI values estimated from fish-eye photographs that integrated over the entire sky hemisphere ($r = 0.932$, SE of estimate = 8.37) (Fig. 4B). As was the case with canopy openness, the fit of the model was best at GLI values from 0 to 50% of full sun (Fig. 4B). There is an inherent tendency for the model to overestimate GLI slightly under very open conditions because the model focuses only on portions of the sky above 45° from horizontal. Additionally, small trees (<15 cm DBH) were not recorded in the stem mapped area used by the model to predict GLI. The densities of these stems were generally highest in the most open sites, ranging from 231 to 813 stems/ha in the partially cut study areas (Coates et al. 1997), and this could have resulted in observed values being somewhat lower than predicted values. Nonetheless, despite the limited field of view (90° vs. 180°) and the incorporation of only stems ≥ 15 cm DBH, GLI values predicted by the model provided relatively accurate estimates of light levels experienced by understory saplings, in units that match the methods used in

Table 3. Height–diameter relationships for the major tree species of ICH forests: $HT = 1.35 + (MAXHT - 1.35) \times (1 - e^{-1.0 \times B \times DBH})$, where HT is height (m), MAXHT is asymptotic tree height (m), DBH is in centimetres, and B is the slope of the exponential approach to asymptotic height.

Species	B	SE	MAXHT	SE	R ² (%)	HT when DBH = 50 cm
Western hemlock	0.0299	0.0009	39.48	0.596	95.1	30.91
Western redcedar	0.0241	0.0008	39.54	0.719	95.6	28.08
Amabilis fir	0.0263	0.0006	40*	—	97.2	29.64
Subalpine fir	0.0264	0.0006	40*	—	94.5	29.67
Hybrid spruce	0.0264	0.0004	45*	—	97.2	33.36
Lodgepole pine	0.0333	0.0008	40*	—	92.6	32.72
Trembling aspen	0.0352	0.0015	39.14	0.988	95.4	32.63
Cottonwood	0.0347	0.0011	39.47	0.601	95.9	32.75
Paper birch	0.0454	0.0028	33.18	1.187	92.2	29.90

Note: The equation is adjusted to predict a tree height of 1.35 m at 0 cm DBH. Equations were fit using nonlinear regression. Also reported are the asymptotic standard errors (SE) of the parameter estimates and predicted tree height at 50 cm DBH. *MAXHT was fixed at 40 m for three of the species and at 45 m for hybrid spruce (see text for details).

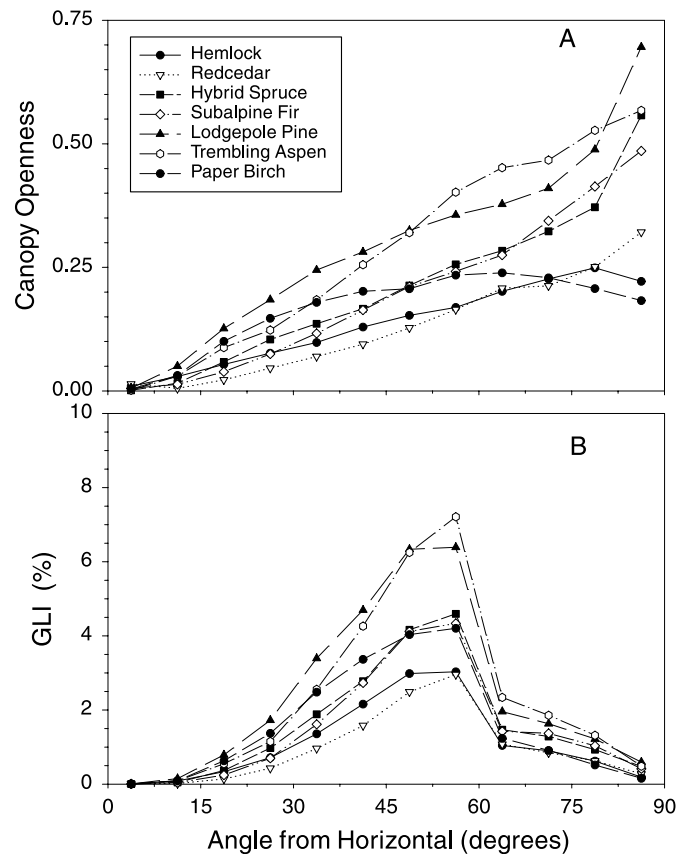
Fig. 1. Means and 95% confidence intervals for (A) individual crown canopy openness (%) and (B) understory GLI (% of full sun) in stands dominated by the designated species. No data were available for stand-level GLI for amabilis fir and cottonwood.



our field studies of sapling response to light (e.g., Wright et al. 1998).

A second set of predictions calculated using the empirically derived functions for maximum crown radius (Table 2) were still highly correlated with the observed openness ($r = 0.924$) and GLI ($r = 0.865$). The predictions were unbiased

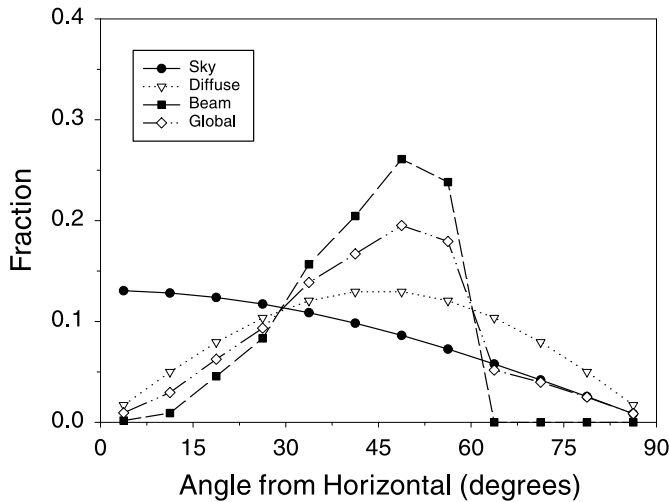
Fig. 2. (A) Stand-level canopy openness (fraction of sky visible) and (B) GLI (% of incident radiation) as a function of angle from horizontal in stands dominated by the designated species.



(i.e., very close to a 1:1 relationship); however, the predicted values were consistent underestimates of observed values (by roughly 0.2 for openness and 16 for GLI). Thus, the use of the maximum crown radius to characterize crown dimensions in the model would result in significant underestimates of GLI in these forests.

In contrast with the underlying simplicity of the light model, the parameter estimation methods used in Canham

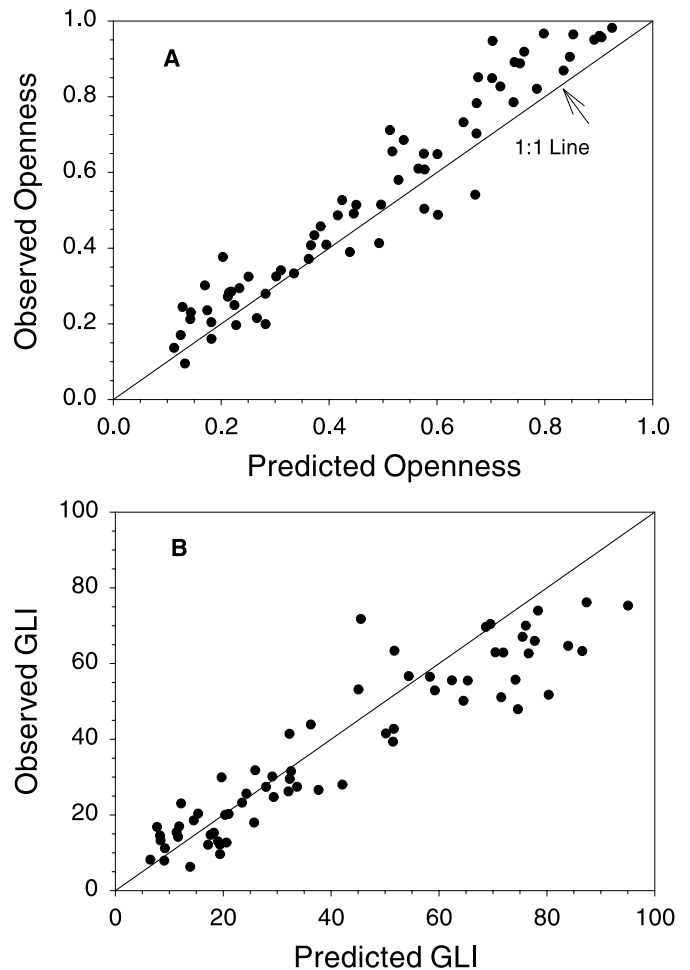
Fig. 3. The fraction of incident beam, diffuse, and global (beam + diffuse) radiation, and the fraction of the sky hemisphere, contributed by 5° bands of the sky hemisphere at the latitude of our study sites (55°22'N).



et al. (1994) were extremely complex. That complexity was dictated in part by the nature of the canopies of the deciduous forests where the model was first developed. In contrast with western coniferous forests, it is very difficult to identify individual tree crowns in fish-eye photographs from the dense, closed canopies of eastern deciduous forests. The original method used in Canham et al. (1994) to estimate canopy openness was also dependent on predicted crown geometry and the mapped distribution of trees around sample points. In effect, the method estimated canopy openness, given a set of crown geometry functions and the measured spatial distribution of neighboring trees. The current method of estimating canopy openness is not only far simpler but also provides estimates that are independent of estimates of crown geometry and knowledge of the distribution and sizes of neighboring trees. In that sense, the current test of the SORTIE light model is far more rigorous than the original test (Canham et al. 1994). Given the importance of crown geometry for accurate model predictions, it seems likely that the goodness of fit of the model in these western coniferous forests is, in part, a function of the predictable canopy architecture of the coniferous tree species.

The assumption that tree crowns are cylinders with an effective radius equal to half of the average, maximum crown radius is obviously a very coarse approximation. It is not clear that incorporating a more flexible range of idealized crown shapes (i.e., tapered cones or ellipsoids) would significantly increase the ability of the model to predict light levels near the ground, particularly since most light that reaches the forest floor penetrates through regions of the sky near the zenith (Canham et al. 1990, 1994; present study). At incidence angles near the zenith, shading will be determined more by the horizontal, cross-sectional shape of the crown than by the vertical cross section. Our assumption of cylindrical crowns becomes more problematic for accurate predictions along vertical profiles up through the canopy. We did not measure vertical profiles of light in our stands and, thus, have not truly validated the model for three-

Fig. 4. Relationships between observed and predicted (A) canopy openness and (B) GLI. A 1:1 line is plotted in each panel.

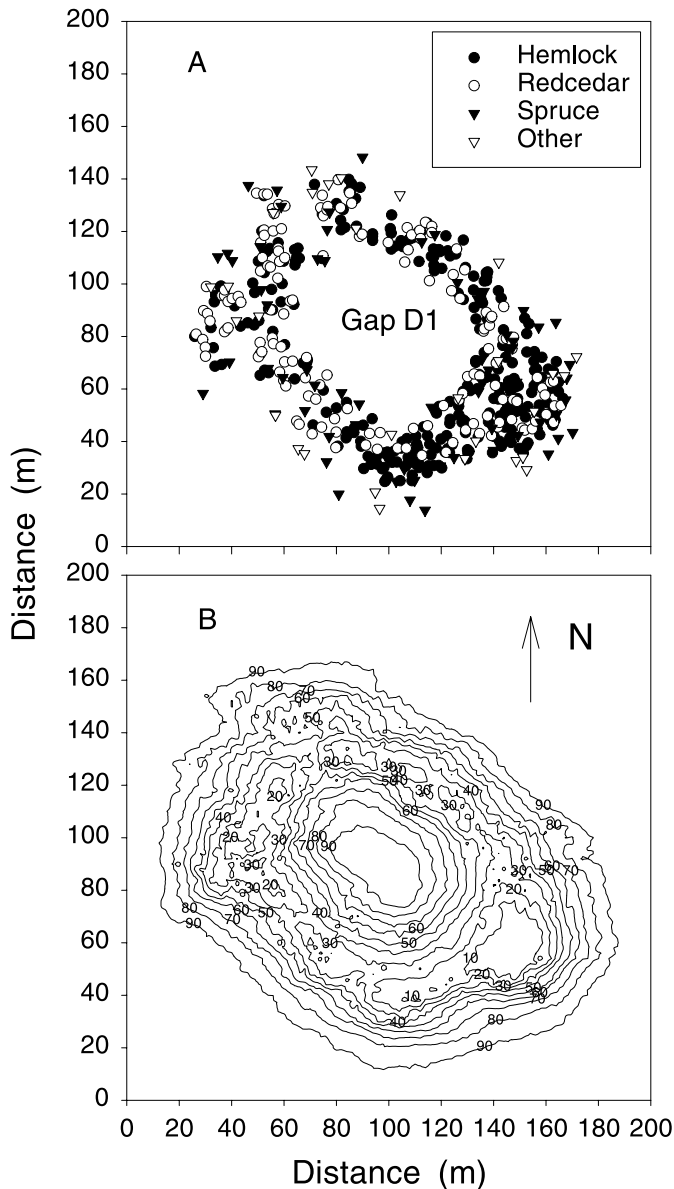


dimensional predictions. Since many of the conifers in our study sites have conical crowns, the assumption of cylindrical crowns would clearly overestimate shading of the foliage of canopy and subcanopy trees by taller neighbors (Herwitz et al. 2000). However, the goal of the light model in SORTIE is to be able to predict spatial variation in light levels experienced by juvenile trees in the forest understory. Sapling densities are relatively low in the understory in our study sites (Coates et al. 1997). As a result, the light levels experienced by saplings are determined primarily by canopy trees rather than by adjacent saplings. Crown depths for all of the tree species in our study sites ranged from 20 to 46% of total height, with mature tree heights ranging from ~30 to 45 m (Tables 1 and 3). Thus, there is relatively little change in the foliage height profile within 15 m of the ground, and the assumption of cylindrical crown shapes should have little effect on the accuracy of model estimates below that height.

Application of the light model

The power of the SORTIE light model is largely a function of the simplicity of the input required for accurate predictions of spatial variation in understory light levels. Given the species-specific light transmission coefficients and crown geometry relationships described above, the only other input required by the model consists of a map of the

Fig. 5. (A) Map of the distribution of canopy trees (stems ≥ 15 cm DBH) in a band around a ~ 0.33 -ha gap. (B) GLI values predicted by the SORTIE light model as a function of shading by the trees shown in Fig. 5A. The area outside the band of trees is assumed to be unoccupied.



spatial distribution, sizes and identities of trees within a stand. As an example, Fig. 5 shows the predicted spatial variation in understory light levels (GLI, at 1 m above the forest floor) in the vicinity of a large (~ 0.33 ha) gap in a mature ICH forest. Canopy trees (>15 cm DBH) were only mapped within a band around the gap, and the predictions in Fig. 5 assume that the remainder of the area (both inside and outside the band of trees) was unoccupied by trees. The three dominant species at this site (hemlock, redcedar, and spruce) do not differ widely in light transmission. Thus, the patterns illustrated in Fig. 5 are largely a function of the spacing and sizes of the trees. The model predicts an area of deep shade (GLI $<10\%$ full sun) beneath a dense cluster of hemlock and redcedar trees on the southeastern edge of the

gap. The effects of a skid road into the gap from the north-west are also visible. Light levels within the gap range from $\sim 30\%$ to $>90\%$ full sun, and as expected from solar geometry, the area of highest light levels inside the gap is displaced towards the northern edge of the gap (Canham et al. 1990).

Summary and conclusions

These western coniferous forests differed significantly from eastern deciduous forests in the nature of light transmission through the canopy. Individual crowns of species of the ICH forests of British Columbia generally had much lower canopy openness than did species of transition oak – northern hardwood forests of New England (Canham et al. 1994). However, light transmission at the stand level was generally much higher in ICH forests. The higher overall light transmission of ICH forests was largely due to the frequent openings between the tall, conical crowns of the dominant conifer species. It thus seems likely that the basic differences in the nature of light transmission in the two ecosystems are a direct consequence of that geometry. In particular, the frequent open spaces between individual tree crowns allow greater lateral lighting of individual crowns, and may thereby contribute to greater branch and needle formation within the crown.

Effects of latitude on the angular distribution of sky brightness in northern British Columbia ($\sim 55^\circ\text{N}$) versus southern New England ($\sim 40^\circ\text{N}$) may also contribute to differences in canopy architecture and light transmission in the two regions. Crown depth (as a percentage of total tree height) was generally lower in ICH species than in lower latitude, northern hardwood species (Canham et al. 1994), and the western species did not show a clear correlation between crown depth and shade tolerance as in eastern species. We suggest that, despite the frequent openings between individual crowns in ICH forests, the very low incidence angle for beam radiation at such high latitudes (Fig. 3) limits the effectiveness of those openings in allowing lateral lighting deep into the canopy.

Despite the fundamental differences in the details of canopy architecture and light transmission in the two ecosystems, a simple geometric model developed for eastern deciduous forests appears to work equally well (if not better) at predicting spatial variation in understory light levels in these western coniferous forests (Fig. 4). The ability of such a simple model to accurately predict spatial variation in light levels within mixed-species stands suggests that the most important factors regulating spatial variation in understory light levels are the basic geometry of tree crowns, combined with information on the sizes and distribution of nearby trees, and the local sky brightness distribution. Discrete canopy gaps simply represent a special case in which a region of the canopy is not occupied by crowns. There were significant differences in light transmission through individual crowns of both eastern and western species (Canham et al. 1994; this study). However, in ICH forests, the magnitude of the differences among the six dominant conifer species were relatively slight (Fig. 1A), suggesting that interspecific variation in openness of individual crowns was of secondary

importance to the size and spacing of tree crowns, regardless of species.

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