

Measurement and Modeling of Spatially-explicit Variation in Light Transmission Through Interior  
Cedar-Hemlock Forests of British Columbia.

Charles D. Canham<sup>1</sup>

*Institute of Ecosystem Studies*

*Box AB, Millbrook, NY 12545 USA*

*phone (914) 677-5343*

*FAX (914) 677-5976*

*e-mail: ccanham@ecostudies.org*

K. Dave Coates and Paula Bartemucci

*British Columbia Forest Service, Research Section, Bag 5000,*

*Smithers, British Columbia V0J 2N0, Canada*

and

Stefan Quaglia

*Simon Fraser University*

*Burnaby, British Columbia V5A 1S6, Canada*

<sup>1</sup>Author to whom all correspondence should be addressed

## 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 to 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.

## 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 dy-

namics (Pacala et al. 1993, 1996). The light model in SORTIE predicts incident radiation at any given location within a forest as a function of (1) species-specific light transmission coefficients, (2) variation in crown geometry as a function of tree size, (3) the identities, sizes, and spacing of trees in the immediate neighborhood, and (4) 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, Canham et al. 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

1 model can really only be tested through application in a range of different systems. The original  
2 parameterization of the model in eastern deciduous forests led to a number of theoretical predic-  
3 tions on the nature of successional dynamics and species interactions in forests (Pacala et al.  
4 1996). The empirical studies used to parameterize the light model, for instance, confirmed  
5 Horn's early prediction (Horn 1971) that there should be a positive correlation between shade tol-  
6 erance and light interception. Our results in eastern forests (Canham et al. 1994) also revealed a  
7 correlation between shade tolerance and crown depth, and demonstrated that this was the princi-  
8 pal cause of interspecific variation in light interception (rather than differences in foliage density  
9 within the crown). In a very basic sense, the forest dynamics predicted by SORTIE are consis-  
10 tent with Horn's (1971) model and Connell and Slatyer's (1977) "tolerance" model that propose  
11 that secondary forest succession is driven by interspecific differences in resource uptake (light in-  
12 terception) by adults (Canham et al. 1994), and interspecific differences in tolerance by juveniles  
13 of resource depletion (shading) (Kobe et al. 1995).

14 Our research with SORTIE in British Columbia is also motivated by the need for a predic-  
15 tive model of forest dynamics that can be used to develop partial cutting strategies as an alterna-  
16 tive to clearcutting in western coniferous forests. The ability to predict spatial variation in un-  
17 derstory light levels under a wide range of partial cutting strategies (including both thinning and  
18 the formation of discrete gaps) will be critical to our ability to predict forest dynamics following  
19 harvests, and to develop silvicultural systems that produce the mix of light levels that will result in  
20 competitive growth rates by a wide range of species.

21 The specific objectives of the current study were to (1) characterize interspecific variation  
22 in light transmission and canopy geometry of the 9 dominant tree species of the interior cedar-  
23 hemlock (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 (2) to 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 mid-point 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 mid-point of a given sky region). In operational terms, the models 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  $\text{openness}_i$  is the species-specific openness (as a fraction) of the  $i^{\text{th}}$  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

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

where  $\text{incident}_j$  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.  $\text{incident}_j$ ) 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 vs. 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

1 contributed 50% of total, incident, photosynthetically active radiation (PAR) over the course of  
2 the growing season.

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

9 One of the strengths of this modeling approach is that it is directly analogous to the actual meth-  
10 ods used to estimate GLI from fisheye photography under field conditions (e.g. Canham et al.  
11 1994). In particular, the modeling approach is designed to predict the light levels experienced by  
12 individual seedlings and saplings at any point in the understory, in the same units that are used in  
13 the field to measure growth as a function of light level (e.g. Pacala et al. 1994, Wright et al.  
14 1998). Under field conditions, the entire 180 degree field of view of a fisheye photograph is ana-  
15 lyzed. This is obviously impossible in the model, since it would require mapping an infinitely  
16 large plane to determine all trees that could potentially intercept light at angles near the horizon.  
17 Thus, the model scans regions of the sky above a user-selected threshold (normally set at 45 de-  
18 grees, e.g. Pacala et al. 1996), and estimates GLI as a percent of the radiation that originates from  
19 that restricted portion of the sky (rather than as a percent of the radiation originating from the en-  
20 tire sky hemisphere). One of the goals of the test of the light model reported here was to deter-  
21 mine the congruence between the value of GLI predicted by scanning only a limited region of the  
22 sky (in the model) and the actual GLI values that would be calculated in the field by scanning over  
23 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 located near Hazelton, British Columbia, 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 9 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 (*P. sitchensis* [Bong.] Carr.) and occasionally Engelmann spruce (*P. 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 yrs+ 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 Interior Cedar-Hemlock (ICH) forests.

### Canopy Tree Geometry

The light model requires a set of 3 functions that describe canopy geometry for each species: (1) height as a function of stem diameter (DBH); (2) crown depth as a fraction of tree height; and (3) 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 3 of the 4 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 3-dimensional crown onto 2 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 3 broadleaved species. Data on stem diameter, height, crown depth and crown radius of adult trees were collected for all 9 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 dataset on adult tree stem diameter and height from permanent sample plots maintained in this region by the BC Ministry of Forests. Our final dataset contained 3,522 observations for height-diameter relationships (with sample sizes ranging from 256 - 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 - 164 cm DBH and 1.2 - 47.7 m in height, but 96% of the stems were  $< 50$  cm DBH and 90% were less than 30 m in height.

We used non-linear regression to predict tree height as a function of DBH with an equation of the form:

$$HT = 1.35 + (MAXHT - 1.35) * (1 - e^{(-1.0 * b * DBH)})$$

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 4 of the species. Instead, for those 4 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 fisheye photography and computerized image analysis to document interspecific variation in the openness (and thus the transmission of gap light) for individual crowns of the 9 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 fisheye 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 8mm true fisheye 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 photo, 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 fisheye photograph is fundamentally fractal, at the resolution of the digitized image (1325 dpi), it was relatively straightforward to identify portions of the photo in which the canopy consisted of only a single crown of a previously identified tree. We limited analyses to photos in which the delineated area represented the majority of the crown of an individual tree. We ended up with a total of 146 photos, with sample sizes for individual species ranging from 10 - 23 photos (crowns). Photos for this purpose were taken from a very wide range of locations within the Date Creek study area. We used 1-way analysis of variance to test for variation in canopy openness among species.

We also took photos at 75 locations where 1 of 7 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 photos were used for a more thorough analysis of interspecific variation in light transmission, including variation in the angular distribution of canopy openness among the 7 species. We could not find sufficient numbers of pure stands of the remaining 2 species for this separate analysis. Photos 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 1-way analysis of variance to test for interspecific variation in the stand-level, gap light index (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 fisheye photographs distributed in 5 stands at Date Creek in which all trees  $\geq 15$  cm DBH had been previously mapped for a study of the dispersion of seedlings around parent trees (LePage et al., *submitted*). The 5 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 5 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 degrees from horizontal, and assumed that the sites were on level terrain.

## RESULTS AND DISCUSSION

### Canopy Tree Geometry

In contrast to species of eastern forests studied by Canham et al. (1994), there was no clear relationship between shade tolerance and crown depth among the 9 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 9 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 height-diameter relationships were fairly similar among all 9 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 - 30 cm DBH, western redcedar had the shortest height while lodgepole pine and the 3 broadleaved species had the greatest height at a given stem diameter.

### **Light Transmission by Individual Tree Crowns**

Canopy openness varied significantly among the 9 species ( $F = 8.41$ ,  $df = 8,137$ ,  $p < 0.0001$ ), and ranged from a low of 5.8% in paper birch to a high of 20.6% in trembling aspen (Fig. 1A). Among the 6 conifer species, the three least shade tolerant species (subalpine fir, hybrid spruce, and lodgepole pine) had the highest light transmission (Fig. 1A). In contrast to eastern broadleaved species (Canham et al. 1994), the three western broadleaved 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, broadleaved-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 ( $F = 10.03$ ,  $df = 6,68$ ,  $p < 0.001$ ) (Fig. 1B). While transmission of gap light through individual crowns of ICH species was extremely low relative to eastern species, gap light transmis-

sion 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 characteristics 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 - 70 %; however, very little radiation originates within 30 degrees 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 degrees 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 ( $r = 0.964$ , std. error 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 degree cone centered on the zenith) were also highly correlated with observed GLI values estimated from fisheye photographs that integrated over the entire sky hemisphere ( $r = 0.932$ , std. error 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 - 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 degrees 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

1 highest in the most open sites - ranging from 231 – 813 stems per ha in the partially cut study ar-  
2 eas (Coates et al. 1997) - and this could have resulted in observed values being somewhat lower  
3 than predicted values. Nonetheless, despite the limited field of view (90 degrees vs. 180 degrees)  
4 and the incorporation of only stems  $\geq 15$  cm DBH, GLI values predicted by the model provided  
5 relatively accurate estimates of light levels experienced by understory saplings, in units that match  
6 the methods used in our field studies of sapling response to light (e.g. Wright et al. 1998).

7         A second set of predictions calculated using the empirically-derived functions for maxi-  
8 mum crown radius (Table 2) were still highly correlated with the observed openness ( $r = 0.924$ )  
9 and GLI ( $r = 0.865$ ). The predictions were unbiased (i.e. very close to a 1:1 relationship); how-  
10 ever, the predicted values were consistent underestimates of observed values (by roughly 0.2 for  
11 openness and 16 for GLI). Thus, the use of the maximum crown radius to characterize crown  
12 dimensions in the model would result in significant underestimates of GLI in these forests.

13         In contrast to the underlying simplicity of the light model, the parameter estimation meth-  
14 ods used in Canham et al. (1994) were extremely complex. That complexity was dictated in part  
15 by the nature of the canopies of the deciduous forests where the model was first developed. In  
16 contrast to western coniferous forests, it is very difficult to identify individual tree crowns in fish-  
17 eye photographs from the dense, closed canopies of eastern deciduous forests. The original  
18 method used in Canham et al. (1994) to estimate canopy openness was also dependent on pre-  
19 dicted crown geometry and the mapped distribution of trees around sample points. In effect, the  
20 method estimated canopy openness, given a set of crown geometry functions and the measured  
21 spatial distribution of neighboring trees. The current method of estimating canopy openness is not  
22 only far simpler, but also provides estimates that are independent of estimates of crown geometry  
23 and knowledge of the distribution and sizes of neighboring trees. In that sense, the current test of

1 the SORTIE light model is far more rigorous than the original test (Canham et al. 1994). Given  
2 the importance of crown geometry for accurate model predictions, it seems likely that the good-  
3 ness of fit of the model in these western coniferous forests is, in part, a function of the predictable  
4 canopy architecture of the coniferous tree species.

5       The assumption that tree crowns are cylinders with an effective radius equal to half of the  
6 average, maximum crown radius is obviously a very coarse approximation. It is not clear that in-  
7 corporating a more flexible range of idealized crown shapes (i.e. tapered cones or ellipsoids)  
8 would significantly increase the ability of the model to predict light levels near the ground, par-  
9 ticularly since most light that reaches the forest floor penetrates through regions of the sky near  
10 the zenith (Canham et al. 1990, Canham et al. 1994, present study). At incidence angles near the  
11 zenith, shading will be determined more by the horizontal, cross-sectional shape of the crown than  
12 the vertical cross-section. Our assumption of cylindrical crowns becomes more problematic for  
13 accurate predictions along vertical profiles up through the canopy. We did not measure vertical  
14 profiles of light in our stands, and thus have not truly validated the model for 3-dimensional pre-  
15 dictions. Since many of the conifers in our study sites have conical crowns, the assumption of  
16 cylindrical crowns would clearly overestimate shading of the foliage of canopy and subcanopy  
17 trees by taller neighbors (Herwitz et al. 1999). However, the goal of the light model in SORTIE  
18 is to be able to predict spatial variation in light levels experienced by juvenile trees in the forest  
19 understory. Sapling densities are relatively low in the understory in our study sites (Coates et al.  
20 1997). As a result, the light levels experienced by saplings are determined primarily by canopy  
21 trees rather than by adjacent saplings. Crown depths for all of the tree species in our study sites  
22 ranged from 20 – 46% of total height, with mature tree heights ranging from ~ 30 – 45 m (Tables  
23 1 and 3). Thus, there is relatively 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 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 (~ 1/3 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 southeast edge of the gap. The effects of a skid road into the gap from the northwest are also visible. Light levels within the gap range from ~ 30% to > 90% full sun, and as expected from solar geometry, the area of highest light levels inside the gap is displaced towards the north 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 interior cedar-hemlock forests of British Columbia generally had much lower canopy openness than did

1 species of transition oak - northern hardwood forests of New England (Canham et al. 1994).  
2 However, light transmission at the stand level was generally much higher in ICH forests. The  
3 higher overall light transmission of ICH forests was largely due to the frequent openings between  
4 the tall, conical crowns of the dominant conifer species. It thus seem likely that the basic differ-  
5 ences in the nature of light transmission in the two ecosystems are a direct consequence of that  
6 geometry. In particular, the frequent open spaces between individual tree crowns allow greater  
7 lateral lighting of individual crowns, and may thereby contribute to greater branch and needle  
8 formation within the crown.

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

18 Despite the fundamental differences in the details of canopy architecture and light trans-  
19 mission in the two ecosystems, a simple geometric model developed for eastern deciduous forests  
20 appears to work equally well (if not better) at predicting spatial variation in understory light levels  
21 in these western coniferous forests (Fig. 4). The ability of such a simple model to accurately pre-  
22 dict spatial variation in light levels within mixed-species stands suggests that the most important  
23 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, and this study). However, in ICH forests, the magnitude of the differences among the 6 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.

#### ACKNOWLEDGMENTS

This study was supported by grant SB96026-RE from Forest Renewal British Columbia, the silvicultural system program of the Ministry of Forests, Forest Practices Branch, Victoria, B.C., and the Mary Flagler Cary Charitable Trust. We thank Phil LePage for assistance with data on tree geometry, mapping of the stands used for model calibration, and comments on the manuscript. This study is a contribution to the program of the Institute of Ecosystem Studies.

#### LITERATURE CITED

- Banner, A., MacKenzie, W. Haeussler, S. Thompson, S., Pojar, J., and Trowbridge, R. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. B.C. Min. For. Land Manage. Handbk. 26.
- Bjorkman, O. and Ludlow, M. M. 1972. Characterization of the light climate on the floor of a Queensland rainforest. Carnegie Inst. Washington Yearbook 71:85-94.
- Brunner, A. 1998. A light model for spatially explicit forest stand models. For. Ecol. Manage. 107:19-46.

- 1 Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. *Ecology*  
2 69: 1634-1638.
- 3 Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., and White, P. S. 1990.  
4 Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests.  
5 *Can. J. For. Res.* 20:620-631.
- 6 Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences  
7 of resource heterogeneity in forests: Interspecific variation in light transmission by canopy  
8 trees. *Can. J. of For. Res.* 24:337-349.
- 9 Chazdon, R. L. and Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical  
10 rainforest in Costa Rica. *J. Ecol.* 72: 553-564.
- 11 Coates, K. D. , Banner, A., Steventon, J. D., LePage, P. and Bartemucci, P. 1997. The Date  
12 Creek silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern  
13 British Columbia: Overview and treatment summaries. B.C. Min. For. Land Manage.  
14 Handbk. 38.
- 15 Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and  
16 their role in community stability and organization. *Am. Nat.* 111:1119-1144.
- 17 Grace, J. C. 1990. Modeling the interception of solar radiant energy and net photosynthesis. pp  
18 142-158 in Dixon, R. K., R. S. Meldahl, G. A. Ruark, and W. G. Warren (eds.). *Process*  
19 *Modeling of Forest Growth Responses to Environmental Stress*. Timber Press, Portland,  
20 Oregon.
- 21 Herwitz, S. R., R. E. Slye, and S. M. Turton. 1999. Long-term survivorship and crown area  
22 dynamics of tropical rainforest canopy trees: effects of lateral shading. *Ecology*, *in press*.

- 1   Horn, H. S. 1971. The Adaptive Geometry of Trees. Monographs in Population Biology 3.  
2       Princeton University Press, Princeton, NJ. 144 pp.
- 3   Hutchison, B. A. And Matt, D. R. 1976. Beam enrichment of diffuse radiation in a deciduous  
4       forest. Agric. Meteorol. 17:93-110.
- 5   Kobe, R. K. and Coates, K. D. 1997. Models of sapling mortality as a function of growth to  
6       characterize interspecific variation in shade tolerance of eight tree species of northwestern  
7       British Columbia. Can. J. For. Res. 27:227-236.
- 8   Kobe, R. K., S. W. Pacala, J. A. Silander, Jr. and C. D. Canham. 1995. Juvenile tree survivor-  
9       ship as a component of shade tolerance. Ecol. Appl. 5:517-532.
- 10   LePage, P. 1995. The structure and development pattern of mixed-species forest stands in the  
11       Interior Cedar-Hemlock zone: Moist cold subzone of northwestern British Columbia.  
12       MSc thesis, Oregon State University, Corvallis Oregon. 91 pp.
- 13   LePage, P., Canham, C. D., Coates, K. D., and Bartemucci, P. Seed source versus substrate  
14       limitation of seedling recruitment in northern temperate forests of British Columbia. *Sub-*  
15       *mitted to* Can. J. For. Res.
- 16   Messier, C., and Bellefluer, P. 1988. Light quantity and quality on the forest floor of pioneer and  
17       climax stages in a birch - beech - sugar maple stand. Can. J. For. Res. 18:615-622.
- 18   Oker-Blom, P. and Kellomaki, S. 1982. Effect of angular distribution of foliage on light  
19       absorption and photosynthesis in the plant canopy: theoretical computations. Agric.  
20       Meteorol. 26:143-155.
- 21   Pacala, S. W., Canham, C. D., and Silander, J. A. 1993. Forest models defined by field  
22       measurements: I. The design of a northeastern forest simulator. Can. J. For. Res.  
23       23:1980-1988.

- 1 Pacala, S. W., Canham C. D., Silander Jr, J. A. and Kobe, R. K.. 1994. Sapling growth as a  
2 function of resources in a north temperate forest. *Can. J. For. Res.* 24:2172-2183.
- 3 Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996.  
4 Forest models defined by field measurements: II. Estimation, error analysis and dynamics.  
5 *Ecol. Monogr.* 66:1-43.
- 6 Pojar, J., Klinka, K., and Meidinger, D. V. 1987. Biogeoclimatic ecosystem classification in  
7 British Columbia. *For. Ecol. Manage.* 22:119-154.
- 8 Pukkala, T., Becker, P., Kuuluvainen, T., and Oker-Blom, P. 1991. Predicting spatial  
9 distribution of direct radiation below forest canopies. *Agric. For. Meteorol.* 55:295-307.
- 10 Wang, H. and Baldocchi, D. D. 1989. A numerical model for simulating the radiation regime  
11 within a deciduous forest canopy. *Agric. For. Meteorol.* 46: 313-337.
- 12 Wright, E. F., K. D. Coates, C. D. Canham, and P. Bartemucci. Species variability in growth  
13 response to light across climatic regions in northwestern British Columbia. *Can. J. For.*  
14 *Res.* 28:871-886.

Table 1. Shade tolerance and crown depth (as a % of total tree height) for the major tree species of Interior Cedar-Hemlock forests. Shade tolerance was quantified as the % 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 (S.E. ) and the  $R^2$  of the regression used to estimate crown depth. Species are listed in descending order of shade tolerance for the 6 conifer and 3 broadleaved species separately.

| SPECIES          | SHADE     | CROWN DEPTH | S.E. | $R^2$ |
|------------------|-----------|-------------|------|-------|
|                  | TOLERANCE | (%)         |      | (%)   |
| 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  |

Table 2. Regression coefficients for maximum crown radius (cm) as a linear function of DBH (cm). Models were fitted without intercepts. Also reported are the standard error of the coefficient (S.E.), the predicted maximum crown radius (m) for a 50 cm DBH tree, and the  $R^2$  of the regression relationship.

| SPECIES          | REGRESSION<br>COEFFICIENT | S.E. | MAX. CROWN<br>RADIUS (m) <sup>1</sup> | R <sup>2</sup><br>(%) |
|------------------|---------------------------|------|---------------------------------------|-----------------------|
| 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                  |

<sup>1</sup> For a 50 cm DBH tree



Table 3. Height-diameter relationships for the major tree species of Interior Cedar-Hemlock forests.  $HT = 1.35 + (MAXHT - 1.35) * (1 - \exp(-1.0*B*DBH))$ , where HT is height (m), MAXHT is asymptotic tree height (m), DBH is in cm, and B is the slope of the exponential approach to asymptotic height. 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 (S.E.) of the parameter estimates, and predicted tree height at 50 cm DBH.

| SPECIES          | B      | S.E.   | MAXHT           | S.E.  | R2<br>(%) | HT at 50 cm<br>DBH |
|------------------|--------|--------|-----------------|-------|-----------|--------------------|
| 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 <sup>1</sup> | --    | 97.2      | 29.64              |
| subalpine fir    | 0.0264 | 0.0006 | 40 <sup>1</sup> | --    | 94.5      | 29.67              |
| hybrid spruce    | 0.0264 | 0.0004 | 45 <sup>1</sup> | --    | 97.2      | 33.36              |
| lodgepole pine   | 0.0333 | 0.0008 | 40 <sup>1</sup> | --    | 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              |

<sup>1</sup>MAXHT was fixed at 40 m for 3 of the species and at 45 m for hybrid spruce (see text for details).

### Figure Legends

Figure 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.

Figure 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.

Figure 3. The fraction of incident beam, diffuse, and global (beam + diffuse) radiation, and the fraction of the sky hemisphere, contributed by 5 degree bands of the sky hemisphere at the latitude of our study sites ( $55^{\circ} 22' \text{ N}$ ).

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

Figure 5. (A) Map of the distribution of canopy trees (stems  $\geq 15 \text{ cm DBH}$ ) in a band around an  $\sim 1/3 \text{ ha}$  gap. (B) GLI values predicted by the SORTIE light model as a function of shading by the trees shown in panel A. The area outside the band of trees is assumed to be unoccupied.







