Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec

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Abstract: This study was conducted in six different forest types in Abitibi, Que., (*i*) to identify the factors that most influence understory light transmission in the southern boreal forest and (*ii*) to develop light extinction coefficients (k), which could be used to simulate light transmission in the understory. Light availability and understory vegetation (cover, composition, vertical distribution, and leaf area index) were characterized within three strata (0.05–5 m) in a total of 180 quadrats. Calculated k values were based on measured light availability and leaf area index. These values varied among forest types, strata, understory vegetation types, and cover in the upper stratum. The highest k values were generally associated with a dense stratum of *Acer spicatum* Lam. We developed five sets of k values based on the factors that most affected light transmission. Measured transmission (T_m) was compared with transmission predicted (T_p) from each set of k values. Light transmission predicted using a single k value (mean k = 0.54) underestimated T_m. More accurate predictions were obtained when we used the other four sets of k values. Our results indicate that, in the southern boreal forest, the understory vegetation can be quite heterogeneous and patterns of light transmission cannot be accurately simulated using a unique k value. However, the various sets of k values developed in this study could be used in prediction models of forest dynamics to obtain relatively good predictions of understory light extinction in forest types similar to the ones studied here.

Résumé : Cette étude a été effectuée dans six différents types forestiers en Abitibi (Québec) afin (*i*) d'identifier les principaux facteurs influençant la transmission de la lumière en sous-bois dans la forêt boréale méridionale et (*ii*) de développer des coefficients d'extinction de la lumière (k) qui pourraient être utilisés pour simuler la transmission de la lumière en sous-bois. La disponibilité en lumière et la végétation en sous-bois (recouvrement, composition en espèces, distribution verticale et indice de surface foliaire) ont été caractérisées au sein de trois strates (0,05–5 m) dans un total de 180 quadrats. Des valeurs de k ont été calculées à partir des mesures de disponibilité en lumière et de l'indice de surface foliaire. Ces valeurs de k variaient en fonction du type forestier, de la strate de végétation, du type de végétation de sous-bois et du recouvrement dans la strate supérieure de végétation. Les valeurs de k les plus élevées étaient généralement associées à une strate dense d'*Acer spicatum* Lam. Nous avons développé cinq ensembles de valeurs de k en nous basant sur les facteurs qui influençaient le plus la transmission de la lumière. La transmission mesurée (T_m) a été comparée à la transmission prédite (T_p) à partir de chacun de ces cinq ensembles de k. La transmission prédite à partir d'une valeur unique de k (k moyen = 0,54) sous-estimait la T_m. Des prédictions plus justes ont été obtenues à partir des quatre autres ensembles de k. Nos résultats indiquent que dans la forêt boréale méridionale, la végétation de sous-bois peut être passablement hétérogène et que les patrons de transmission de la lumière ne peuvent être simulés de façon adéquate à partir d'une valeur unique de k. Toutefois, les différents ensembles de k que nous présentons pourraient être utilisés dans des modèles de simulation de la dynamique forestière afin d'obtenir des prédictions relativement justes de l'atténuation de la lumière en sous-étage dans des types forestiers similaires à ceux de cette étude.

Introduction

Understory light availability is important for forest dynamics in the boreal forest, since it influences several important plant regeneration processes, such as germination, early establishment, growth, and survival. The amount of light intercepted by forest stands is therefore one of the driving variables controlling forest succession, and most stand-level forest dynamics models explicitly simulate light attenuation through the canopy (e.g., ZELIG (Burton and Cumming 1991; Urban 1993); FORCYTE (Kimmins 1993); FORSKA (Leemans and Prentice 1989; Prentice and Leemans 1990); SORTIE (Pacala et al. 1993)). However, most of these models either do not consider the effect of understory vegetation on light attenuation or use a single light-extinction coefficient to simulate light attenuation through the understory vegetation.

In many forest ecosystems, including the boreal forest, light availability at or near the forest floor is not well correlated with the amount of light transmitted through the upper canopy because of dense, heterogeneous understory vegetation that strongly influences the amount of light reaching the

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Table 1. Characteristics of the six forest types studied.

	Aspen*	White birch*	Mixed*	Jack pine*	Closed conifer*	Open conifer
No. of plots	4	3	5	3	3	2
Stand age (years)†	50–70	70	108–230	70	230	230
Density (no./ha)‡	1464	1259	1358	1055	824	212
Basal area ($m^2 \cdot ha^{-1}$)§	37.62 (4)	20.63 (7)	29.59 (46)	31.21 (83)	40.05 (83)	27.85 (36)
Understory cover (%)	99.7±8.4*a*	72.4±5.0*b*	51.2±3.3*b*	103.1±5.0*a*	54.3±4.8*b*	126.1±3.9*a*
Height of understory (m)	3.4±0.2*a*	1.4±0.1*b*	1.4±0.1*b*	3.6±0.2*a*	1.3±0.1*b*	3.7±0.2*a*
Understory LAI ($m^2 \cdot m^{-2}$)‖	3.11±0.27*a*	2.52±0.16*b*	1.58±0.10*b*	3.22±0.16*a*	1.68±0.15*b*	3.95±0.13*a*

Note: Values for understory cover, height of understory, and understory LAI are mean ± SE. Forest types with the same letter for a variable were not significantly different at $P < 0.05$ (ANOVA and Scheffe's multiple comparison test).

*Same stands as in Messier et al. (1998).

†Time since last stand-destroying fire determined by Bergeron (1991) using dendrochronological techniques.

‡DBH > 5 cm.

§Percentage of conifer is given in parentheses.

‖Leaf area index of understory vegetation calculated from eq. 7.

forest floor (Ross et al. 1986; DeGrandpré et al. 1993; Constabel and Lieffers 1996; Messier et al. 1998). In fact, high light transmission through the upper canopy can lead to increased understory cover and to lower light availability at the ground level than in stands with a denser upper canopy but having only a sparse understory cover (Constabel and Lieffers 1996). Under such conditions, an accurate prediction of the understory light regime can only be obtained if the light attenuating effect of the understory vegetation is taken into account.

Few investigators have studied the effects of the herb and shrub layer on patterns of light attenuation in forest understories (Constabel and Lieffers 1996; Messier et al. 1998). Most studies of light attenuation by species other than trees have been done in agricultural crops (Tournebize and Sinoquet 1995), in cutovers (DeLong 1991; Comeau et al. 1993), or in grasslands (Hirose and Werger 1995).

Many investigators have used the Beer–Lambert law to describe the pattern of light transmission through diverse vegetation canopies (Monteith 1965; Pierce and Running 1988; Smith et al. 1991; Nel and Wessman 1993; Smith 1993; Brown and Parker 1994; Bergibier and Bonnefond 1995; Vose et al. 1995):

$$[1] \qquad T = I/I_0 = e^{-k\mathrm{LAI}}$$

where T is the light transmission through the canopy, I is the incident radiation at some point under a vegetation canopy, I_0 is the incident radiation at the top of the canopy, LAI is the leaf area index, and k is the light extinction coefficient (Smith et al. 1991). The light extinction coefficient (k) represents the light-interception capacity of the vegetation. The k coefficient can be used for comparing light attenuation through different types of canopies or to predict LAI when light transmission is known (Pierce and Running 1988; Smith and Clark 1990; Vose and Swank 1990; Smith et al. 1991; Nel and Wessman 1993; Smith 1993). A given amount of vegetation (i.e., LAI) can lead to different light transmission resulting from variations in k. Many studies have shown that a single k value cannot adequately predict light transmission through complex canopies, because k values are affected by different aspects of canopy structure, including foliage distribution, density and clumping, canopy height, and quantity of branches and stems (Russell et al. 1989; Smith et al. 1991; Nel and Wessman 1993; Smith 1993; Brown and Parker 1994; Chen and Cihlar 1995; Vose et al. 1995). However, determination of a k value specific to each type of canopy composition and structure in a complex vegetation community would be very time consuming.

The two main objectives of this study were (*i*) to relate understory vegetation characteristics (percent cover, species composition, LAI, and pattern of vertical distribution) to light transmission to the forest floor in six forest types representative of the southern boreal forest in Abitibi, Que., and (*ii*) to develop light extinction coefficients specific to understory vegetation using different methods of aggregating vegetation complexity to provide a simple and efficient way to simulate light attenuation through understory vegetation in the boreal forest.

Methods

Study site

The study area is located in the southern part of the boreal forest, at the Lake Duparquet Experimental Teaching and Research Forest, in the region of Abitibi, Que. (48°30′N, 79°27′W). Average annual temperature is 0.8°C, and annual precipitation averages 857 mm (Atmospheric Environment Service 1993). The region is part of the clay belt left by postglacial lakes (Vincent and Hardy 1977). All study plots were located on grey luvisols with moderate to good drainage (Agriculture Canada 1992).

Sampling

Sampling was conducted in six natural forest types typical of the region (Table 1): (*i*) pure aspen (*Populus tremuloides* Michx.); (*ii*) pure white birch (*Betula papyrifera* Marsh.); (*iii*) mixed deciduous–conifer (*Populus tremuloides*, *B. papyrifera*, *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill.); (*iv*) pure jack pine (*Pinus banksiana* Lamb.); (*v*) closed conifer (*Thuja occidentalis* L., *Picea glauca*, *B. papyrifera*, *Populus tremuloides*, *A. balsamea*); and (*vi*) conifer with an open canopy resulting from the last spruce budworm outbreak that occurred 15 years ago (*A. balsamea*, *T. occidentalis*, *B. papyrifera*). These six forest types were selected to cover a wide range of understory vegetation structure.

A total of 20 study plots (radius 17 m) were selected in the six forest types (Table 1). Nine 1-m^2 quadrats were established in each plot, for a total of 180 quadrats. Each quadrat was divided into three strata for light and vegetation sampling: (*i*) 5–50 cm, (*ii*) 51–100 cm, and (*iii*) 101 cm to above the understory vegetation (up to 5 m in height). A subsample of 22 quadrats was selected for more intensive measurements, as described below. These 22 quadrats were located in four different forest types: aspen (n = 7), mixed (n = 7), closed conifer (n = 4), and open conifer (n = 4) stands.

Light measurements

In July and August 1995, the percentage of above-canopy photosynthetic photon flux density (%PPFD) was measured at the centre of each quadrat at four heights: 5, 50, and 100 cm above the forest floor, and above the understory vegetation up to 5 m. All light measurements were made under completely overcast sky conditions following the method described in Parent and Messier (1996). These authors have shown that an instantaneous measurement of %PPFD made under overcast sky conditions (diffuse light only) provides a good estimate of the mean daily %PPFD under both overcast and clear sky conditions. Photosynthetic photon flux density (PPFD, 400–700 nm) was measured in the understory using a point quantum sensor (LI-190, LI-COR, Inc., Lincoln, Neb.). This is designated as location *i*. A second point quantum sensor was installed in an open area near the study sites and linked to a datalogger (LI-1000, LI-COR, Inc., Lincoln, Neb.) to record above-canopy PPFD (i.e., $\mathrm{PPFD_{open}}$). Percent PPFD at location *i* was calculated as

$$[2]\qquad \%\mathrm{PPFD}_i = (\mathrm{PPFD}_i / \mathrm{PPFD_{open}}) \times 100$$

where PPFD_i is the instantaneous measurement made at location *i* in the understory and $\mathrm{PPFD_{open}}$ is the above-canopy PPFD recorded in the open at the same time (±1 min).

In 1996, the light measurements obtained with the LI-190 point quantum sensor were compared with measurements obtained with a newly acquired line quantum sensor (Li-191, LI-COR, Inc., Lincoln, Neb.) in a subsample of 22 quadrats. Because measurements are integrated along an 80-cm sensor, we believe the LI-191 line quantum sensor provided better characterization of the light regime in heterogeneous vegetation canopies than the point quantum sensor (LI-COR, Inc. 1986). In the 22 quadrats, light measurements were taken at 5, 50, and 100 cm aboveground at the centre of the quadrats with both a LI-190 point quantum sensor and a LI-191 line quantum sensor. The regression line between light measurements obtained with these two types of sensor was highly significant (R^2 = 0.828, P < 0.001, n = 66), and the slope was not significantly different from 1 (P = 0.767). Therefore, one measurement made at the center of a 1-m^2 quadrat with a LI-190 point quantum sensor provided an adequate measure of light availability in the quadrat, and subsequently, only %PPFD obtained with the point quantum sensor was used in the analysis.

Characterization of understory vegetation

Percent vegetation cover

A visual estimate of total percent vegetation cover (between 0 and 100%) was made for each vegetation stratum, in each quadrat. Then, the proportion of the total percent cover for each of the five types of understory vegetation was evaluated. All estimates were done by the same observer to ensure consistency in the estimations. In each stratum, percent cover was estimated to the nearest 5%. While the percent cover of a stratum ranged from 0 to 100%, the total percent cover for a quadrat (calculated by adding percent cover of the three strata) could be >100%. A stratum was said to be dominated by a given type of vegetation if >60% of the total cover was composed of one particular type of vegetation. Five different vegetation types were considered: deciduous shrubs, coniferous shrubs, deciduous seedlings, coniferous seedlings, and herbaceous species. When none of the five vegetation types described above had a percent cover >60%, the stratum was considered a mixed cover type.

Leaf area index

The LAI of the 180 quadrats was estimated from measured percent vegetation cover using a predictive regression equation for LAI as a function of percent cover. This regression was obtained from direct measurements of LAI and percent cover made in the 22 intensively sampled quadrats. In each of the 22 quadrats, the LAI was evaluated from destructive harvesting of the vegetation; all plants were harvested in each stratum and separated by species. Only leaves were kept for analysis. A subsample of foliage for each species was used to calculate a species-specific area/mass ratio (Gartner 1991). Subsamples consisted of 20 leaf punches of known area; each punch was taken on a different leaf, except for conifer and fern species for which we sampled either a number of needles or a piece of frond. Dry mass was determined after oven-drying at 70°C for at least 48 h.

The leaf area of each species in each stratum of each quadrat was calculated as

$$[3]\qquad A_{i,s,q} = M_{i,s,q}(a_i / m_i)$$

where $A_{i,s,q}$ is the leaf area (m^2) of species *i* in stratum *s* and quadrat *q*; $M_{i,s,q}$ is the foliage dry mass (g) of species *i* in stratum *s* of quadrat *q*; and a_i/m_i is the leaf area to leaf dry mass ratio ($\mathrm{m^2 \cdot g^{-1}}$) of species *i* obtained from foliage subsample. The LAI was calculated for each stratum of each quadrat as

$$[4]\qquad \mathrm{LAI}_{s,q} = \frac{\sum_{i,s} A_{i,s,q}}{A_q}$$

where $\mathrm{LAI}_{s,q}$ ($\mathrm{m^2 \cdot m^{-2}}$) is the leaf area index in stratum *s* in quadrat *q*, A_q is the area (m^2) of the quadrat, and $A_{i,s,q}$ is as defined above. The LAI of each quadrat was calculated as

$$[5]\qquad \mathrm{LAI}_q = \sum_s \mathrm{LAI}_{s,q}$$

For the 22 quadrats in which LAI was obtained from destructive sampling, a good relationship was found between visual estimates of percent cover of a stratum and measured LAI values:

$$[6]\qquad \ln \mathrm{LAI}_{s,q} = (1.178 \ln \mathrm{cover}_{s,q}) - 4.066 \qquad (R^2 = 0.795,\ P < 0.001,\ n = 66)$$

where $\mathrm{LAI}_{s,q}$ is as defined above and $\mathrm{cover}_{s,q}$ is the visual estimate of percent cover in stratum *s* and quadrat *q*. Equation 6 was used to estimate LAI for each stratum of the 180 quadrats.

A good relationship also was obtained between total percent cover of a quadrat (cover_q) and measured LAI of the quadrat (LAI_q):

$$[7]\qquad \ln \mathrm{LAI}_q = (1.015 \ln \mathrm{cover}_q) - 3.536 \qquad (R^2 = 0.832,\ P < 0.001,\ n = 22)$$

Equation 7 was used to estimate LAI for the whole quadrat, for each of the 180 quadrats.

Light extinction coefficients

Calculated light extinction coefficients for each stratum and quadrat

Based on measured light availability and estimated LAI, a light extinction coefficient for each stratum of each quadrat was calculated using the following equation:

Table 2. Five different methods to obtain k values describing the light extinction properties of understory vegetation.

Equation for k	Description of variables	Method
[10] $k_{gen} = \frac{\sum_q k_q}{n}$	k_q, obtained from eq. 9 n, no. of quadrats with a total percent cover >10%*	(1) single k value
[11] $k_{ft} = \frac{\sum_q k_{q,ft}}{n_{ft}}$	$k_{q,ft}$, light extinction coefficient of quadrat q in forest type (ft) n_{ft}, no. of quadrats in forest type (ft) with a percent cover >10%*	(2) k value per forest type
[12] $k_s = \frac{\sum_q k_{s,q}}{n_s}$	$k_{s,q}$, light extinction coefficient of stratum s in quadrat q n_s, no. of quadrats with percent cover of stratum s >10%*	(3) k per stratum
[13] $k_{vt} = \frac{\sum_{s,q} k_{s,q,vt}}{n_{vt}}$	$k_{s,q,vt}$, light extinction coefficient of stratum s in quadrat q dominated by vegetation type (vt) n_{vt}, no. of strata dominated by vegetation type vt with a percent cover >10%*	(4) k per understory vegetation type
[14] $k_{cc} = \frac{\sum_q k_{q,cc}}{n_{cc}}$	$k_{q,cc}$, light extinction coefficient of quadrat q in cover class (cc) n_{cc}, no. of quadrats in cover class cc and having a total percent cover >10%*	(5) k based on cover in the upper stratum†

*Quadrats and (or) strata with percent cover <10% were excluded from the calculations of k values, because we felt that because of the sparse vegetation found in these quadrats and (or) strata, their k value would not be representative of the light extinction properties of the understory vegetation.

†Three different cover classes (cc) were defined: percent cover of the upper stratum ≤25%; 26%–74%; and ≥75%.

$$[8] \qquad k_{s,q} = \frac{-\ln(\mathrm{PPFD}_{\mathrm{below}}/\mathrm{PPFD}_{\mathrm{above}})}{\mathrm{LAI}_{s,q}}$$

where $k_{s,q}$ is the light extinction coefficient of stratum s in quadrat q; $\mathrm{PPFD}_{\mathrm{below}}$ is PPFD measured below stratum s; $\mathrm{PPFD}_{\mathrm{above}}$ is PPFD measured above stratum s; and $\mathrm{LAI}_{s,q}$ is as calculated in eq. 6.

A light extinction coefficient also was calculated for each quadrat as

$$[9] \qquad k_q = \frac{-\ln(\mathrm{PPFD}_{\mathrm{below}}/\mathrm{PPFD}_{\mathrm{above}})}{\mathrm{LAI}_q}$$

where k_q is the light extinction coefficient of quadrat q; $\mathrm{PPFD}_{\mathrm{below}}$ is PPFD measured at the lower limit of the lowest stratum of quadrat q; $\mathrm{PPFD}_{\mathrm{above}}$ is PPFD measured at the upper limit of the highest stratum of quadrat q; and LAI_q is the LAI of quadrat q derived from percent cover (eq. 7).

Five methods to obtain simplified estimates of light extinction coefficients

To determine the most efficient way to estimate light attenuation by understory vegetation, we calculated different sets of k values according to five different methods (Table 2): (*i*) a general k value equal to the mean light extinction coefficient of all quadrats (eq. 10); (*ii*) k values for the understory vegetation of each of the six studied forest types (eq. 11); (*iii*) k values for the three vegetation strata (eq. 12); (*iv*) k values for the six understory vegetation types (eq. 13); and (*v*) k values dependent on the percent cover of the upper stratum only (eq. 14).

Assessment of the predictive power of the different sets of light extinction coefficients

To compare the predictive power of these different sets of k values, the measured light transmission (T_m) was compared with light transmission predicted (T_p) from each of the five different sets of k values. T_m was calculated for each quadrat as

$$[15] \qquad T_{mq} = \mathrm{PPFD}_{\mathrm{below},q} / \mathrm{PPFD}_{\mathrm{above},q}$$

where $\mathrm{PPFD}_{\mathrm{below},q}$ is PPFD measured below the lowest stratum (i.e., at 5 cm) in quadrat q, and $\mathrm{PPFD}_{\mathrm{above},q}$ is PPFD measured above the understory vegetation in quadrat q.

T_p was calculated for each quadrat from eq. 1 using the LAI value estimated for each quadrat and one of the five types of light extinction coefficient described above (Table 3). Relationships between T_m (from eq. 15) and the different sets of T_p (Table 3, eqs. 16–20) were evaluated using regression analysis in order to determine which type of simplified light extinction coefficient would provide the most precise and accurate prediction of light transmission.

Data analysis

Understory vegetation characteristics (height, percent cover, and LAI) were compared among forest types using analysis of variance (ANOVA). Differences in light extinction coefficients among forest types, strata, dominant vegetation type, and cover class of the upper stratum were tested for statistical significance by ANOVA. When some variables failed normality tests even after natural log transformation and when a multiple comparison procedure was required, ANOVA and Scheffe's test were performed on rank-transformed data (Potvin and Roff 1993). Spearman correlation was used to assess correlation between understory vegetation and light characteristics. Linear regression analysis was used to evaluate relationships between measured (T_m) and predicted light transmission (T_p), after natural log transformation of the transmission values. The coefficient of determination (R^2) was used to determine the precision of these relationships. The slopes of the regression lines were compared with a theoretical slope of 1 (H_0: slope = 1) to identify potential bias in the estimation of T_m by T_p. P values <0.05 were considered significant, unless otherwise stated. All statistical analyses were performed using SYSTAT (version 7.0).

Table 3. Predicted light transmission for a quadrat using five different methods for obtaining the k value.

Equation for predicted light transmission		Description of variables	Method
[16]	$T_p = e^{-k_{gen}LAI_q}$	k_{gen}, from eq. 10 LAI_q, LAI of quadrat q (eq. 7)	(1) single k value
[17]	$T_p = e^{-k_{ft}LAI_q}$	k_{ft}, light extinction coefficient for forest type (ft) LAI_q, LAI of quadrat q (eq. 7)	(2) k value per forest type
[18]	$T_p = e^{-\sum_s k_s LAI_{s,q}}$	k_s, light extinction coefficient of stratum s (eq. 12) $LAI_{s,q}$, LAI of stratum s in quadrat q (eq. 6)	(3) k per stratum
[19]	$T_p = e^{-\sum_s k_{s,vt} LAI_{s,q}}$	$k_{s,vt}$, light extinction coefficient of vegetation type (vt) in stratum s (eq. 13) $LAI_{s,q}$, LAI of stratum s in quadrat q (eq. 6)	(4) k per understory vegetation type
[20]	$T_p = e^{-k_{cc}LAI_q}$	k_{cc}, light extinction coefficient of quadrats with cover class (cc) (eq. 14) LAI_q, LAI of quadrat q (eq. 7)	(5) k based on cover in the upper stratum

Results

Understory vegetation characteristics and patterns of light transmission

The maximum height of the understory vegetation ranged from 50 cm in closed and dense coniferous stands (mixed stand type) to more than 5 m in aspen and open conifer stands (data not shown). Mean understory vegetation height was significantly higher in aspen, jack pine, and open coniferous stands (ca. 3.5 m), compared with white birch, mixed, and closed coniferous stands (ca. 1.3 m; Table 1). Total percent cover of understory vegetation was positively correlated with understory vegetation height (Spearman r = 0.751): stand types with taller understory vegetation also had significantly higher percent cover (Table 1).

Leaf area index (LAI_q), as derived from percent vegetation cover (eq. 7), ranged from 0.06 to 5.51 $m^2 \cdot m^{-2}$. Mean LAI_q differed significantly among forest types (Table 1) with aspen, jack pine, and open conifer stands having the highest understory LAI_q (>3); mixed and closed conifer stands having the lowest (<2); and birch having an intermediate LAI_q (2–3).

A total of 58 plant species were recorded in the sampled quadrats. The lower stratum was mainly composed of herbs such as *Aster macrophyllus* L., *Clintonia borealis* (Ait.) Raf., and *Aralia nudicaulis* L., and a low coniferous shrub (*Taxus canadensis* Marsh.) in older stands. This stratum was the most diverse in terms of number of species. A large component of the upper stratum consisted of deciduous shrubs such as *Acer spicatum* Lam. and *Corylus cornuta* Marsh. Coniferous seedlings were found in most forest types, while deciduous seedlings were rare.

The vertical distribution of vegetation cover differed markedly among the six forest types (Fig. 1). However, the vertical patterns could be grouped in three types according to the vertical structure. Aspen and jack pine forest types had both a very dense and tall shrub cover above 100 cm (mainly *A. spicatum*) and a well-developed herbaceous cover below 50 cm. Birch, mixed, and closed shade-tolerant conifer forest types had a high percent vegetation cover below 50 cm (composed of herbs, coniferous seedlings, and coniferous shrubs) but very little vegetation above 100 cm. Finally, the open conifer stand had a dense, tall deciduous shrub cover (mainly *A. spicatum*) and poorly developed vegetation cover below 50 cm. Little vegetation cover was present in the 50- to 100-cm stratum in all six forest types.

Figure 1 also shows the vertical distribution of light availability within the understory vegetation in the six forest types. Light transmission was negatively correlated with percent vegetation cover (Spearman r = –0.739) but was not correlated with light availability above the understory vegetation (Spearman r = 0.06). For instance, open conifer stands where %PPFD above the understory vegetation was high (38.7% of above-canopy PPFD) received less light at the forest floor (0.8% PPFD) than any of the other stands (1.7–6.6% PPFD) (Fig. 1).

Factors affecting the light extinction coefficient of understory vegetation

The mean light extinction coefficient of all quadrats was 0.54 ± 0.03 (mean ± SE; Table 4). Light extinction coefficients varied among forest types (P < 0.001), mixed stands having the lowest k values (0.40 ± 0.05) and open conifer having the highest (0.98 ± 0.05) (Table 4). Extinction coefficients varied among strata (P < 0.001) with the highest stratum having a significantly higher k value than the other two strata (Table 4). Extinction coefficients also varied according to types of understory vegetation (P < 0.001). The mixed vegetation type and the deciduous shrubs had the highest light extinction coefficients, while the herbaceous type had the lowest (Table 4). Light extinction coefficients varied with percent vegetation cover in the upper stratum. Quadrats with ≥75% cover in the upper stratum had a significantly higher light extinction coefficient than quadrats from the other two cover classes (≤25%, 26–74%) (Table 4). Light extinction coefficients did not vary with height of the understory vegetation (Spearman r = –0.02).

Prediction of light transmission using different k values

Linear regression between T_m and T_p were calculated to assess the predictive power of the five different sets of light extinction coefficients (Table 5, Fig. 2). For method 1, in which light transmission was predicted for all quadrats using

Fig. 1. Vertical distribution of vegetation cover and light transmission through the understory vegetation in each of six forest types: aspen, jack pine, white birch, mixed deciduous–conifer, closed conifer, and open conifer. Percent cover of understory vegetation is shown by the wide horizontal bars (one per vegetation stratum), which are subdivided by type of vegetation. The light transmission through the understory vegetation, which is the percentage of above understory light level, is indicated by the open squares and the solid lines. The numbers in parentheses indicate the actual measured percent of above-canopy light (%PPFD) above the understory vegetation and at the forest floor.

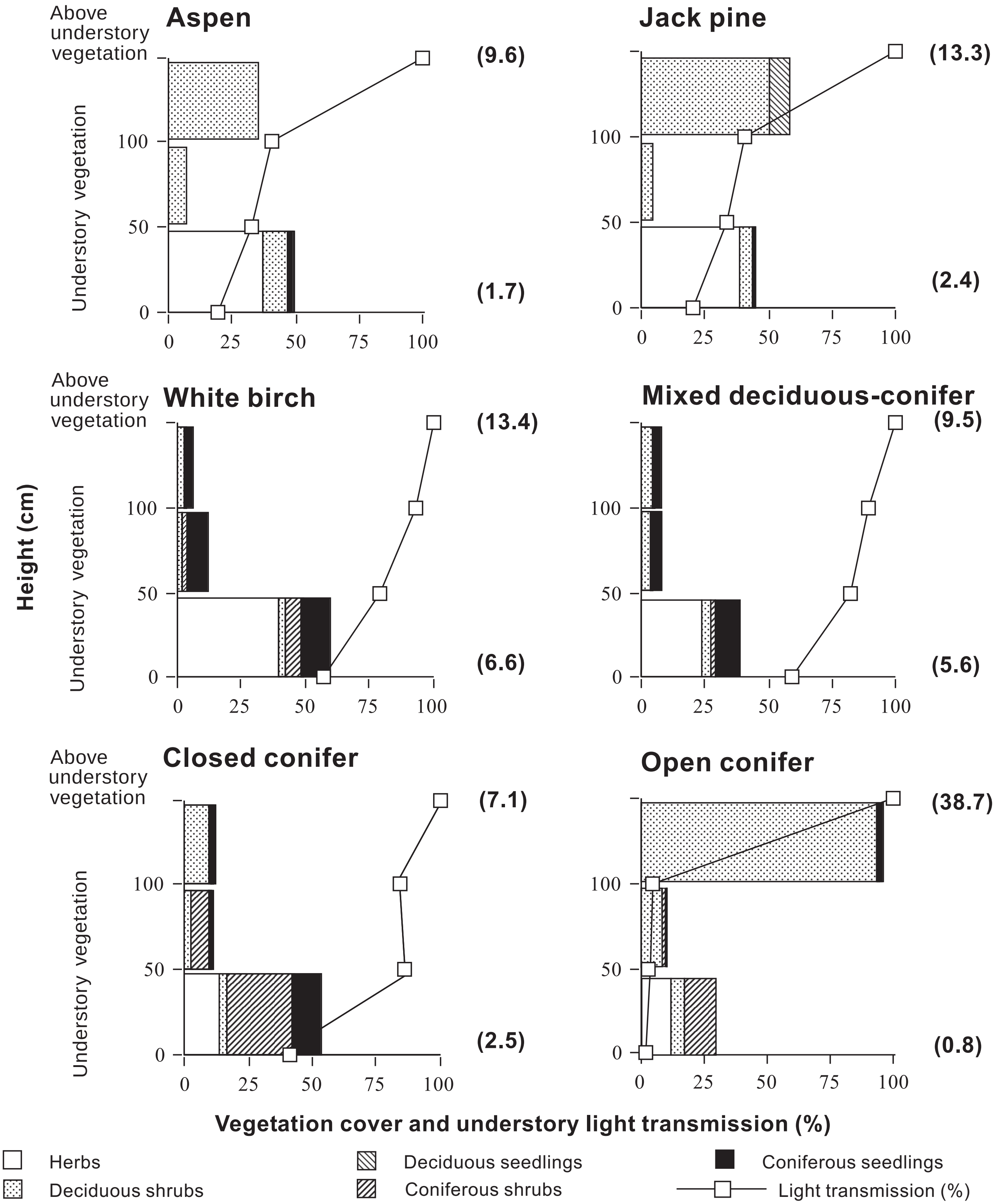


Table 4. Light extinction coefficients calculated using five different methods (mean ± SE).

Method		k	n_q	n_s
(1) General		0.54±0.03	170	—
(2) Forest type	Birch	0.44±0.06*ab*	26	—
	Aspen	0.64±0.04*bc*	22	—
	Mixed	0.40±0.05*a*	44	—
	Jack pine	0.57±0.05*ab*	22	—
	Closed conifer	0.52±0.06*ab*	40	—
	Open conifer	0.98±0.05*c*	16	—
(3) Strata	Lower (5–50 cm)	0.43±0.03*a*	—	164
	Middle (51–100 cm)	0.63±0.11*a*	—	34
	Upper (100–500 cm)	0.77±0.06*b*	—	76
(4) Vegetation type	Deciduous shrubs	0.69±0.06*bc*	—	73
	Taxus canadensis	0.54±0.08*abc*	—	29
	Deciduous seedlings	0.49±0.09*abc*	—	5
	Coniferous seedlings	0.45±0.07*ab*	—	37
	Herbaceous	0.37±0.03*a*	—	97
	Mixed	0.77±0.08*c*	—	59
(5) Percent cover in upper stratum	≥75%	0.78±0.06*a*	24	—
	26–74%	0.53±0.04*b*	32	—
	≤25%	0.50±0.03*b*	114	—

Note: For a given method, k values with the same letter were not significantly different (P > 0.05) from each other (Sheffe's multiple comparison test). Values of n indicate the number of quadrats (n_q) or vegetation strata (n_s) from which the different k values were calculated.

Table 5. Regression coefficients for the linear regression between measured light transmission (T_m) and predicted light transmission (T_p) using five different methods for the determination of the light extinction coefficients of the understory vegetation.

Method	a	b	R^2	P_1	P_2
(1) General	1.296	0.313	0.544	<0.001	0.001
(2) Forest types	0.930	–0.045	0.733	<0.001	0.096
(3) Strata	0.904	–0.025	0.604	<0.001	0.082
(4) Vegetation type	0.907	–0.046	0.627	<0.001	0.072
(5) Cover in upper stratum	0.984	–0.002	0.597	<0.001	0.789

Note: Regression form is $\ln T_m = (a \ln T_p) + b$. P_1 values <0.05 indicate that the regression model $\ln T_m = (a \ln T_p) + b$ is significant, while P_2 values <0.05 indicate that the slope coefficient (a) is significantly different from 1.

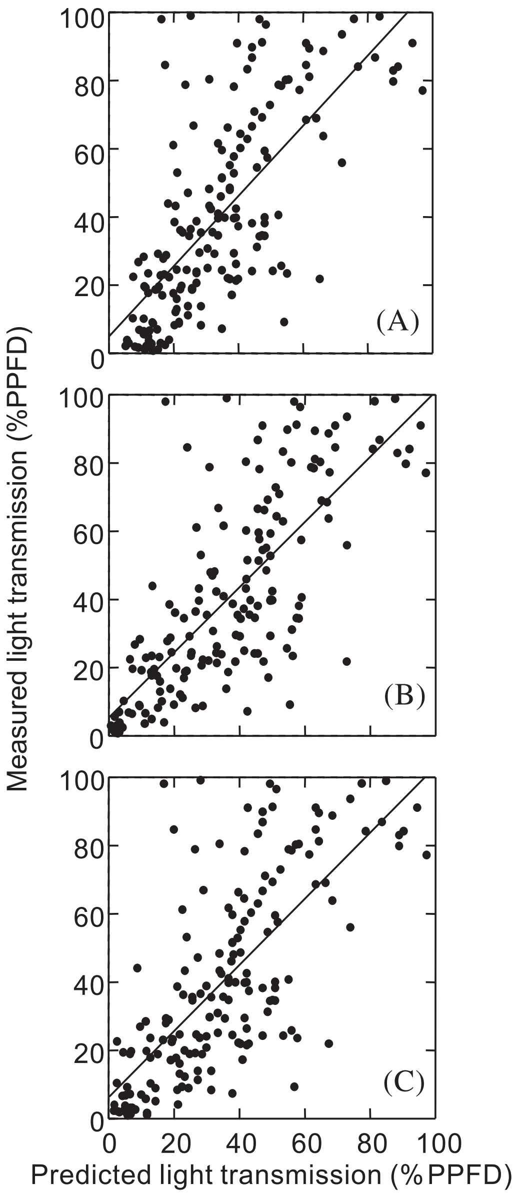
a single light extinction coefficient of 0.54, T_p was significantly correlated with T_m (R^2 = 0.544; Table 5), but the slope was significantly different from 1 (P = 0.001), and T_p tended to underestimate T_m (Table 5, Fig. 2A). For the methods based on k values determined by forest type, by strata, and by vegetation type, we obtained fairly good relationships between T_m and T_p (R^2 from 0.627 to 0.733). However, the relationship between T_p and T_m tended to depart from 1 (tests of H_0: slope = 1 were marginally significant with P values ranging from 0.072 to 0.096), indicating that T_p tended to overestimate T_m (Table 5, Fig. 2B). The method by class cover in the upper stratum gave an accurate prediction of T_m as the slope clearly did not significantly differ from 1 (P = 0.789) and the R^2 was fairly good (0.597) (Fig. 2C).

Discussion

Understory vegetation characteristics and patterns of light transmission

This study underlined how differences in understory vegetation cover, composition, and structure can affect light transmission in the mixed boreal forest of southwestern Quebec. Our results generally support the idea that understory vegetation cover is inversely related to overstory vegetation cover (Cannell and Grace 1993; Constabel and Lieffers 1996). However, we found that understory light transmission patterns were not only affected by the overall quantity of the vegetation (i.e., cover and LAI) but also by the composition and vertical distribution of the vegetation through their effects on the extension coefficient, i.e., k value. Using different methods, we found that k values vary from a low of 0.37 for a low herbaceous vegetation type to a high of 0.98 for the understory vegetation found in the open conifer forest type. Some of the differences in k values reported in Table 4 were clearly related to interspecific differences. For example, *Taxus canadensis* has a higher k (0.54) than a lower stratum composed of herbaceous vegetation (0.37). However, most of the significant variations in k values reported in Table 4 were related to the vegetation cover in the upper stratum, suggesting that a tall shrub subcanopy such as *A. spicatum* can have a high light interception efficiency. Although this study did not clearly separate the

Fig. 2. Relationships between measured light transmission (T_m) and predicted light transmission (T_p) using (A) the general single *k* method, (B) the forest type method, and (C) the percent cover in upper stratum method. We did not show the relationships for the strata and vegetation type methods, because they were very similar to the forest type method. Statistics and equations are given in Table 5.



effects of different species, the *k* value associated with the upper stratum (0.77) can be considered representative of the light extinction coefficient of *A. spicatum*, since most of the deciduous vegetation of the upper stratum was composed of this species.

Brown and Parker (1994) have suggested that the spatial arrangement of stems and leaves could have a greater effect on understory light regime than the quantity of foliage itself. Oker-Blom (1986) found that variation in leaf orientation can lead to variation in light extinction properties of vegetation canopies. A horizontal leaf orientation is generally associated with higher light extinction coefficient values than other orientations. Also, canopies with clumped and heterogeneous foliage generally have lower *k* values than canopies with homogenous foliage arrangement. We observed that an *A. spicatum* canopy generally is homogenous with a horizontal orientation. Furthermore, *A. spicatum* foliage generally was located in the upper stratum. We suggest that this foliage arrangement explains, in part, the high light extinction properties observed for the upper stratum.

Evaluation of different sets of *k* values for prediction of understory light transmission

Our calculated mean light extinction coefficient of 0.54 is in agreement with values reported in the literature for conifer canopies (0.4–0.65 in Jarvis and Leverenz 1983) and values obtained by Law and Waring (1994) for two shrubs species (bitterbush: 0.52 and manzanita: 0.46). Our results indicated that the use of this single general *k* value for prediction of light transmission through the understory vegetation led to an underestimation and a fairly good prediction (i.e., R^2 = 0.544) of light transmission. In some forest ecosystems, the homogeneity of the tree canopy and a sparse and low understory vegetation allow the use a single *k* value. For instance, Pierce and Running (1988) found that a *k* value of 0.52 was appropriate for prediction of light transmission in seven conifer stands. However, in many forest types the complexity of the vegetation structure does not allow the use of a single *k* value (Smith 1993; Brown and Parker 1994; Vose et al. 1995; this study). Some authors have therefore suggested the use of species-specific light extinction coefficients (Smith et al. 1991). However, the understory vegetation of the southern boreal forests has so many species and such a complex vertical structure that it would be difficult to obtain a *k* value for each species and structure. Our results showed that significant improvements in accuracy (i.e., slope closer to 1) and precision (i.e., greater R^2) of the prediction can be obtained by using a few different *k* values that incorporate the effect of either or both the diversity of understory vegetation species and vertical structure. The best prediction in terms of R^2 was actually obtained by using different *k* values for each of the six forest types. Such *k* values actually incorporate both differences in species and structure among these six forest types.

Most stand-level forest simulation models either do not consider the understory vegetation or use a single light extinction coefficient to simulate light attenuation by understory vegetation (e.g., FORSKA and SORTIE). FORSKA, for instance, is a forest dynamics model that was first developed in Sweden for managed monospecific stands with sparse understory vegetation (Leemans and Prentice 1989). The model uses a single light extinction coefficient of 0.4 for both the understory and the upper canopy (D. Clark, personal communication). Our results suggest that, even if such an approach might be appropriate for closed stands with a low herbaceous cover, it is inappropriate for boreal forests that have a well-developed understory vegetation of tall understory shrubs such as found in early successional stands and in large gaps in late-successional stands. We present, in this study, different sets of *k* values that could be used to predict light attenuation in boreal forest understory based on the vertical structure and overall composition of the understory vegetation. The choice of the appropriate *k* values for a model will ultimately depend on the type of information that is already available to the modeler or that could be easily obtained. Obviously, different understory species or vegetation types could have significantly different *k* values, and changes in understory species composition in relation to canopy opening, overstory tree species, or succession should be considered in the models. Species composition in the lower stratum was found to vary from mainly herbaceous species in the early successional stands to mainly *Taxus canadensis* in the late-successional stands (Fig. 1). Also, the cover of *A. spicatum* in the upper stratum was found to decrease with succession and to be very abundant in spruce budworm gaps in late-successional stands. Some feedback also is required between the overstory and understory cover to appropriately predict not only the abundance of the understory vegetation but also its vertical structure. We believe that such considerations could improve simulation of the understory light environment. Although different sets of *k* values than those reported in this study might have to be used for completely different forests and understory vegetation types, similar improvements in prediction could be gained by using a few *k* values instead of a single general one.

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References

Agriculture Canada. 1992. Le système canadien de classification des sols. 2nd ed. Agric. Can. Publ. No. 1646.

Atmospheric Environmental Service. 1993. Canadian climate normals 1961–1990. Canadian climate program, Environment Canada, Atmospheric Environmental Service, Downsview, Ont.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regime. Ecology, **72**: 1980–1992.

Bergibier, P., and Bonnefond, J.M. 1995. Measurement and modelling of radiation transmission within a stand of maritime pine (*Pinus pinaster* Ait.). Ann. Sci. For. **52**: 23–42.

Brown, M.J., and Parker, G.G. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. Can. J. For. Res. **24**: 1694–1703.

Burton, P.J., and Cumming, S.G. 1991. ZELIG BC: user's guide to the prototype of a forest succession simulator for the evaluation of partial cutting options in British Columbia. University of British Columbia, Vancouver.

Cannell, M.G.R., and Grace, J. 1993. Competition for light: detection, measurement, and quantification. Can. J. For. Res. **23**: 1969–1979.

Chen, J.M., and Cihlar, J. 1995. Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. IEEE Trans. Geosci. Remote Sens. **33**: 777–787.

Comeau, P.G., Braumandl, T.F., and Xie, C.-Y. 1993. Effects of overtopping vegetation on light availability and growth of Engelmann spruce (*Picea engelmannii*) seedlings. Can. J. For. Res. **23**: 2044–2048.

Constabel, A.J., and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. **26**: 1008–1014.

DeGranpré, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. **4**: 803–810.

DeLong, S.C. 1991. The light interception index: a potential tool for assisting in vegetation management decisions. Can. J. For. Res. **21**: 1037–1042.

Gartner, B.L. 1991. Structural stability and architecture of vines vs. shrubs of poison oak, *Toxicodendron diversilobum*. Ecology, **72**: 2005–2015.

Hirose, T., and Werger, M.J.A. 1995. Canopy structure and photon flux partitioning among species in a herbaceous plant community. Ecology, **76**: 466–474.

Jarvis, P.G., and Leverenz, J.W. 1983. Production of temperate, deciduous and evergreen forests. *In* Plant physiological ecology. IV. Vol. 12D. Ecosystem processes: mineral cycling, production and man's influence. *Edited by* O.L. Lange, P.S. Noble, and H. Ziegler. Springer-Verlag, New York.

Kimmins, J.P. 1993. Scientific foundations for the simulation of ecosystem function and management in FORCYTE-11. For. Can. North. For. Cent. Inf. Rep. No. NOR-X-328.

Law, B.E., and Waring, R.H. 1994. Remote sensing of leaf area index and radiation intercepted by understory vegetation. Ecol. Appl. **4**: 272–279.

Leemans, R., and Prenctice, I.C. 1989. FORSKA, a general forest succession model. Medd. Väst-biol. Inst. Uppsala No. 89/2.

LI-COR, Inc. 1986. LI-COR radiation sensors, type SA. Instruction manual. LI-COR, Inc, Lincoln, Neb.

Messier, C., Parent, S., and Bergeron, Y. 1998. Characterization of understory light environment in closed mixed broadleaf–conifer boreal forests: effects of overstory and understory vegetation. J. Veg. Sci. **9**: 511–520.

Monteith, J.L. 1965. Light distribution and photosynthesis in field crops. Ann. Bot. (London), **29**: 17–37.

Nel, E.M., and Wessman, C.A. 1993. Canopy transmittance models for estimating forest leaf area index. Can. J. For. Res. **23**: 2579–2586.

Oker-Blom, P. 1986. Photosynthetic radiation regime and canopy structure in modeled forest stands. Acta For. Fenn. **197**(1).

Pacala, S.W., Canham, C.D., and Silander, J.A., Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Can. J. For. Res. **23**: 1980–1988.

Parent, S., and Messier, C. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. Can. J. For. Res. **26**: 151–154.

Pierce, L.L., and Running, S.W. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. Ecology, **69**: 1762–1767.

Potvin, C., and Roff, D.A. 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics. Ecology, **74**: 1617–1628.

Prentice, I.C., and Leemans, R. 1990. Pattern and process and the dynamics of forest structure: a simulation appraoch. J. Ecol. **78**: 340–355.

Ross, M.S., Flanagan, L.B., and La Roi, G.H. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Can. J. Bot. **64**: 2792–2799.

Russell, G., Jarvis, P.G., and Monteith, J.L. 1989. Absorption of radiation by canopies and stand growth. Ch. 2 *In* Plant canopies: their growth, form and function. *Edited by* G. Russell, B. Marshall, and P.G. Jarvis. Cambridge University Press, Cambridge, U.K. pp. 21–39.

Smith, F.W., Sampson, D.A., and Long, J.N. 1991. Comparison of leaf area index estimates from tree allometrics and measured light incerception. For. Sci. **37**: 1682–1688.

Smith, N.J. 1993. Estimating leaf area index and light extinction coefficients in stands of Douglas-fir (*Pseudotsuga menziesii*). Can. J. For. Res. **23**: 317–321.

Smith, N.J., and Clark, D.R. 1990. Estimating salal leaf area index and leaf biomass from diffuse light attenuation. Can. J. For. Res. **20**: 1265–1270.

Tournebize, R., and Sinoquet, H. 1995. Light interception and partitioning in a shrub–grass mixture. Agric. For. Meteorol. **72**: 277–294.

Urban, D.L. 1993. A user's guide to ZELIG version 2 with notes on upgrades from version 1. Department of Forest Sciences, Colorado State University, Fort Collins.

Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway et territoire québécois. Géogr. Phys. Quat. **31**: 357–372.

Vose, J.M., and Swank, T.W. 1990. Assessing seasonal leaf area dynamics and vertical leaf area distribution in eastern white pine (*Pinus strobus* L.) with a portable light meter. Tree Physiol. **7**: 125–134.

Vose, J.M., Sullivan, N.H., Clinton, B.D., and Bolstad, P.V. 1995. Vertical leaf area distribution, light transmittance, and application of the Beer–Lambert Law in four mature hardwood stands in the southern Appalachians. Can. J. For. Res. **25**: 1036–1043.