

Crown openness as influenced by tree and site characteristics for yellow birch, sugar maple, and eastern hemlock

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Abstract: Crown openness (CO) of mature trees influences light transmission within the forest canopy. However, in modeling, this variable is often considered constant within species, and its potential regional variability is ignored. The objective of this study was to evaluate if CO values of yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), and eastern hemlock (*Tsuga canadensis* (L.) Carrière) vary according to the following factors: (i) species, (ii) regional actual evapotranspiration (AET), (iii) tree size (i.e., diameter at breast height, DBH), and (iv) angle of transmission from zenith. To achieve this, CO was evaluated for 136 yellow birches, 109 sugar maples, and 68 hemlocks from different regions of western Quebec, southern Ontario, and northern Michigan. Results showed that all of the studied factors affected CO. While dominant trees can intercept light laterally as well as vertically, smaller trees are more efficient at intercepting light vertically. Increasing AET is associated with more open crowns. Given its importance in light transmission in the understory, a better understanding of how CO varies between individuals, species, and regions is needed.

Résumé : L'ouverture de la couronne (OC) des arbres influence la transmission de la lumière à travers la canopée forestière. Pourtant, en modélisation, l'OC est souvent considérée constante pour une espèce, et les variations régionales sont ignorées. L'objectif de cette étude est de déterminer si l'OC du bouleau jaune (*Betula alleghaniensis* Britt.), de l'érable à sucre (*Acer saccharum* Marsh.) et de la pruche du Canada (*Tsuga canadensis* (L.) Carrière) varie selon les facteurs suivants: (i) l'espèce, (ii) l'évapotranspiration actuelle (ETA) régionale, (iii) la taille des arbres (diamètre à hauteur de poitrine, DHP), (iv) l'angle de transmission de la lumière par rapport au zénith. Pour ce faire, l'OC a été évaluée pour 136 bouleaux jaunes, 109 érables à sucre et 68 pruches provenant de différentes régions de l'ouest du Québec, du sud de l'Ontario et du nord du Michigan. Les résultats indiquent que les facteurs étudiés ont tous un effet sur l'OC. Les arbres dominants semblent plus efficaces à intercepter la lumière (surtout latéralement) que les plus petits arbres. L'augmentation de l'ETA est associée à des couronnes plus ouvertes. Étant donné son importance dans la transmission de la lumière en sous-étage, il est nécessaire de mieux comprendre la variabilité interspécifique, intraspécifique et régionale de l'OC.

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Introduction

Understory light plays a crucial role in forest dynamics, because tree species regeneration largely depends on this resource to grow and reach the overstory. Light regimes are also important to consider in the context of forest management since, by manipulating the canopy, one can favour some species over others (Lieffers et al. 1999). Light availability in the understory is regulated by the climatic conditions (e.g., overcast vs. clear skies), the position of the sun in the sky, the characteristics of the canopy cover, and by the amount and distribution of between-tree gaps found at any time in a forest (Canham et al. 1990; Lieffers et al. 1999; Wirth et al. 2001). Of all of these factors, the characteristics of individual crowns forming the canopy are probably those that have been the least studied (Canham et al. 1994; Wirth et al. 2001).

Different approaches have been used to model and predict light transmission through forest canopies. Some models consider the canopy as homogeneous and monolayered (Norman and Jarvis 1975; Brown and Parker 1994; Larsen and Kershaw 1996). This representation of the canopy is appropriate for simulating light penetration in even-aged, monospecific stands that do not contain gaps in the canopy, but cannot account for the variability in the light regime created by heterogeneous canopies, as found in forests of the temperate deciduous biome. A spatially explicit modeling approach where the forest canopy is represented as being composed of individual crowns can better simulate light transmission in forests with discontinuous canopies (e.g., see SORTIE in Pacala et al. 1993; MIXLIGHT in Stadt and Lieffers 2000, 2005; and tRAYci in Brunner 1998).

Light transmission is usually modeled following the Beer law (Brown and Parker 1994; Larsen and Kershaw 1996;

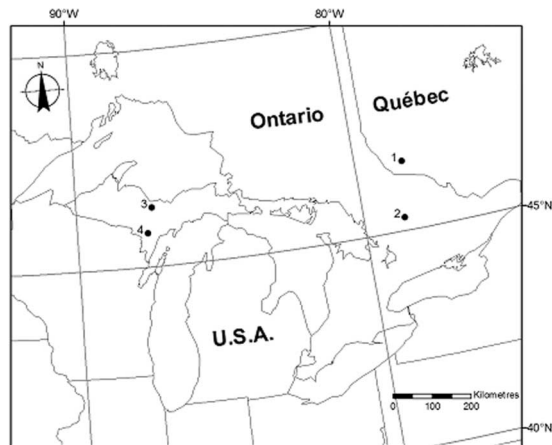
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Fig. 1. Map of study area with location of sampling sites in (1) Témiscamingue, (2) Ontario, (3) Marquette county, and (4) Menominee county.



Stadt and Lieffers 2000), where a light extinction coefficient describes the ability of the foliage to intercept light within a stand canopy or an individual crown. The Beer law assumes that the light-absorbing elements (e.g., leaves) are randomly distributed within the canopy and that light is either transmitted or absorbed (i.e., no reflection). The extinction coefficient usually includes a measure of the density of the light-absorbing elements (e.g., leaf area density (LAD)) as well as a measure of the path length through the light-absorbing region (Brunner 1998; Stadt and Lieffers 2000, 2005). The extinction coefficient can also account for variation in the leaf angle distribution by incorporating a leaf angle coefficient, which, together with the LAD, determines the projected LAD. The leaf angle distribution can be modeled using various distribution functions (Campbell and Norman 1989). If the leaf angle distribution is uniform, light transmission (per unit of path length) should not vary with angle from zenith. Further refinements can be brought to the description of the light extinction properties of canopies, such as accounting for clumping of the light-absorbing elements.

Desirable characteristics of a light model include a satisfactory degree of precision and accuracy in the predictions under a wide range of conditions, combined with reasonable data requirements for model parameterization. The amount of input data required by the light model in SORTIE is remarkably small compared with most existing forest light models (Canham et al. 1999; Beaudet et al. 2002). In SORTIE, light transmission is modeled using a simplified representation of individual tree crowns based on species-specific crown allometry and crown openness (CO). Crown openness represents the total amount of empty space within the projection of a crown, and can be equated to a crown-level average transmittance. In SORTIE, the CO is a species-specific parameter. Crown openness, and more generally light extinction properties of tree crowns, do vary among species, for instance as a function of shade tolerance (Horn 1971; Canham et al. 1994; Kitajima et al. 2005). However, a number of other factors may affect the light interception capacity of a crown, including tree size (Kitajima et al. 2005), leaf angles (Barclay 2001; Falster and Westoby 2003), and crown shape (Horn 1971). Many light models explicitly account for variations in path length and angle to model light

transmission (e.g., MIXLIGHT in Stadt and Lieffers 2000, 2005; and tRAYci in Brunner 1998). However, in SORTIE, the CO is currently considered constant within a species, and independent of path length and angle of view (Canham et al. 1994; Astrup and Larson 2006).

Individual-tree, spatially explicit models are promising from a management perspective because they can simulate complex stands and enable an evaluation of the consequences of ecosystem-based silvicultural treatments (Lieffers et al. 1999; Messier et al. 2003). However, since such models often require a great deal of data for their parameterization, they have often been parameterized for only a few stands or regions, and in a limited range of environmental conditions (Lieffers et al. 1999; Beaudet et al. 2002; Sonohat et al. 2004). This is why variability in CO among regions with different biophysical conditions has received little attention to date (but see Astrup and Larson 2006 for a comparison of CO among regions for aspen and white spruce).

Regional variability in CO has been observed by Astrup and Larson (2006), but these authors could not identify the environmental factor causing such a variability (the study tested but failed to detect a significant effect of precipitation). Since actual evapotranspiration (AET) is the environmental variable most highly correlated with leaf area (Gholz 1982) along with precipitation (Waring et al. 1978; Grier and Running 1977), the species' ability to intercept light might also increase with water availability. This has been suggested by Messier et al. (1998), but could not be confirmed by Sonohat et al. (2004) for coniferous stands in the temperate biome, nor by Stadt et al. (2005) for species of the boreal forest. According to Zahner (1968) and Stadt et al. (2005), there is a lack of information on this relationship.

The objective of this study is to determine if and how CO varies with (i) species, (ii) regional actual evapotranspiration (AET), (iii) tree size (i.e., diameter at breast height, DBH), and (iv) angle of transmission from zenith for yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), and eastern hemlock (*Tsuga canadensis* (L.) Carrière) from various regions in northeast America.

Materials and methods

Study area

All field measurements were taken between 2 June and 12 September of 2004. The study sites were located in Témiscamingue (three sites) in western Québec, in the Haliburton forest (three sites) in southern Ontario, and in the Marquette (three sites) and Menominee (two sites) counties of the upper peninsula of Michigan (Fig. 1; Table 1). All of these forests were uneven aged and located on mesic sites. They were dominated by sugar maple and had been recently harvested by selection cut within the last 2 years. Sampling recently cut stands with thinned canopies enabled us to more easily assess the CO of individual tree crowns while ensuring that tree crowns would not have had time to respond to the opening of the canopy.

To characterize the forest along with the abiotic conditions at each site, we established three representative circular sampling plots of 400 m², at least 100 m apart. At the centre of these plots, position coordinates and altitude were determined with a Magellan SportTrack GPS. The altitude

Table 1. Summary of regional and site characteristics (average values of three plots).

Region	Mean annual temperature (C°)	Annual actual evapotranspiration (mm)	Site coordinates	Mean CEC	pH	Soil texture	Humus type	Mean BA before harvest (m ² /ha)*	Mean BA after harvest (m ² /ha)	Mean density (trees/ha)*	Stand species composition†
Témiscamingue (Québec, Canada)	4.4	556.3	46°40'N, 78°30'E	2.00	4.43	Loam	Moder	29.9	24.8	525	SM, YB, EH
Haliburton (Ontario, Canada)	4.9	530.8	45°14'N, 78°37'E	3.30	4.93	Sandy loam	Mor-moder	26.0	22.2	550	SM, EH, AB, YB
			45°14'N, 78°37'E	3.71	5.04	Sandy loam	Moder	24.4	20.9	492	SM, YB, EH
			45°21'N, 78°32'E	2.24	4.26	Loam	Moder	22.6	20.9	608	SM, BF, YB, EH
Marquette (Michigan, USA)	3.9	537.6	46°20'N, 87°19'E	1.04	4.50	Sandy loam	Moder	32.5	26.5	525	SM, BC, YB, EH
			46°20'N, 87°20'E	0.66	4.26	Sandy loam	Moder	40.8	30.5	500	SM, YB
			46°20'N, 87°17'E	2.75	4.45	Sandy loam	Moder	38.5	28.2	617	SM, BC
Menominee (Michigan, USA)	5.5	559.8	45°45'N, 87°28'E	6.54	5.91	Clay loam	Mull	27.9	16.0	667	SM, EH
			45°45'N, 87°35'E	10.56	6.32	Clay loam	Mull	46.6	28.5	517	SM, YB, BF

Note: CEC, cationic exchange capability; BA, basal area.

*For trees over 9 cm in DBH and including stumps in harvested plots.

†Listed for each site in decreasing order of dominance: SM, sugar maple; YB, yellow birch; EH, eastern hemlock; AB, American beech; BF, balsam fir; BC, black cherry.

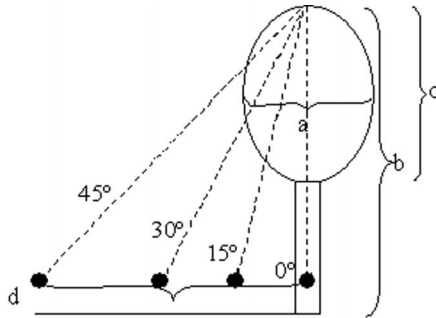
of the sites varied from 271 to 488 m above sea level. Drainage ranged from moderate–slow to moderate–good, and the slopes ranged from 0° to 15°. To calculate the plot preharvest basal area (BA), basal area was measured with a diameter tape for individuals over 9 cm in diameter at breast height (DBH), and when stumps were present, their diameter was measured at the base and their DBH was inferred using allometric relationships (Ministère des Ressources Naturelles Faunes et Parcs 2003). Humus type and soil texture were determined according to the Canadian system of soil classification (Agriculture and Agriculture–Food Canada 1998). A soil sample of the B horizon was taken in each plot at a depth of 20–25 cm (in the presence of two B horizons, both were sampled). Cationic exchange capability (CEC) was obtained with an atomic absorption spectrophotometer by using the barium chloride (BaCl₂) saturation technique. Acidity (pH) was measured in water with an electrode. Mean annual temperature and precipitation were obtained from monthly climate normals for the period between 1971 and 2000 for both countries (stations Chatham exp. farm 2 and Escanaba in Michigan: National Oceanic and Atmospheric Administration 2002; stations Algonquin park west and Barrage Témiscamingue: Environment Canada 2004). The AET was calculated using (i) the monthly climate normals (air temperature and precipitation), (ii) the water-holding capacity of the soil corresponding to a closed mature forest (Témiscamingue, fine sandy loam; other regions, silt loam), and (iii) conversion and computational tables, following the method of Thornthwaite et al. (1957).

Regions differed considerably from each other in their biophysical conditions, while the selected sites within a region were generally more similar (Table 1). Témiscamingue contains the northernmost sites (Fig. 1), but the regional AET was the second highest (Table 1). This can be attributable to its shallow sandy podzols (Brown 1981) with a lower water-holding capacity (which was taken into account in the AET calculation). Témiscamingue represents a transitional forest between the deciduous forests in the south and coniferous forests in the north. Sites sampled in Ontario (Haliburton forest) had the highest amount of precipitation and more fertile soils (higher CEC) of the brunisol order (Table 1). Sites in the Marquette County were located less than 100 km from the south shore of Lake Superior (Fig. 1). The sites, where *Prunus serotina* Ehrh. was common, seemed productive (high basal area) despite an abnormally low CEC (Table 1). The low CEC might be a consequence of heavy metal emission from the nearby coal plant in Marquette City, which causes the leaching of cations into the soil layer (Kimmins 1987). Sites in Menominee had the highest AET, very fertile soils with a good proportion of clay, a high CEC, and a less acidic pH (Table 1). This indicates older soils where glaciers retreated earlier during the last ice age. Measures in the Menominee County were interrupted because of an early fall, therefore only two sites were completed.

Tree measurements

We sampled trees over 9 cm in DBH, with no sign of disease or senescence, that were not in proximity to roads or landings. On each site, data were collected ensuring that individuals were well distributed among DBH classes and

Fig. 2. Measures of variables for each tree include DBH and (a) crown width; (b) total tree height; (c) crown depth. Pictures were taken at 45°, 30°, 15°, and 0° from zenith (locations are represented by the black dots indicated on the (d) line).



from a wide range of DBH. In two regions (Témiscamingue and Marquette), eastern hemlock was not found in sufficient numbers on one of the sites, so more individuals were sampled on another site in the same region. A total of 136 yellow birches, 109 sugar maples, and 68 hemlocks were sampled. For all individuals, DBH was measured at 1.3 m height with a diameter tape. Total tree height was measured with a hypsometer Haglöf Vertex III.

Crown openness measurements

Pictures of the crowns were taken with a Nikon Coolpix 950 digital camera with a resolution of 2048 per 1536 pixels. Pictures of each crown were taken from four different angles (Fig. 2). The position of the camera was determined with a clinometer aimed at the top of the crown at 45°, 30°, 15°, and 0° from zenith. Only individuals that were not damaged by the previous harvest were selected. Their crown had to be clearly visible, with the sky as a background. Pictures were taken in various conditions (clear or overcast skies) but were not taken during rain or wind events, which could alter leaf or branch position, and never included the sun.

Crown openness values were obtained from the pictures as described in Beaudet et al. (2002). Pictures were analyzed in Photoshop (v. 7.0). All analyses were performed by the same person (first author) to avoid confounding a possible “operator” effect with the effects of the various factors investigated. The crown area was selected and consisted of a shape delimited within the crown, following the edge of the crown with a small buffer zone. After a threshold was determined for the whole picture, the images were transformed in black and white, where the crown elements, including branches, were in black and the sky was in white. When some foliage accidentally appeared in white because of light reflection, corrections were made manually to transform the area in black. The percentage of white pixels in the selected crown area was then calculated and provided an estimate of crown openness. The mean of the four angle-specific CO values (CO_{θ}) was calculated to have a mean CO value per individual (CO_{mean}).

Data analysis

Considering that our experimental units (or “subjects”) were the individual trees, and measurements of CO at the four angles (i.e., CO_{θ} values) were repeated measurements

Table 2. Results of the repeated measures analysis of variance, where crown openness measured at four different angles is the dependent variable, while species, actual evapotranspiration (AET), and DBH are between-subject factors, and angle is a within-subject factor.

Sources	SS	df	MS	F	P
Between-subject					
Species	5401.8	2	2700.9	28.656	<0.001
AET	3153.4	1	3153.4	33.457	<0.001
DBH	1427.5	1	1427.5	15.145	<0.001
Error	29029.4	308	94.3		
Within-subject					
Angle	104.6	3	34.9	2.278	0.078
Angle × species	340.6	6	56.8	3.709	0.001
Angle × AET	182.4	3	60.8	3.971	0.008
Angle × DBH	701.6	3	233.9	15.278	<0.001
Error	14142.9	924	15.3		

G–G epsilon: 0.8710

H–F epsilon: 0.8906

Note: SS, sum of squares; MS, mean square; G–G, Greenhouse–Geisser epsilon value; H–F, Huynh–Feldt epsilon value.

on each subject tree, we simultaneously tested the effect of species, AET, DBH, and angle on CO_{θ} using a generalized linear model (GLM) with repeated measures where the species, AET, and DBH were between-subject factors and the angle was a within-subject factor. The sample size to consider for the between-subject effects is therefore the one corresponding to the number of trees sampled, while in the case of the within-subject effects, the sample size corresponds to the number of photos taken (four per tree, hence four times the number of trees sampled). Note that when we refer to the CO_{mean} , it corresponds to the tree-level mean of the four angle-specific crown openness values (CO_{θ}). Note also that the results obtained regarding the between-subject effects correspond to those that would be obtained from a GLM with CO_{mean} as the dependent variable. All possible interactions were initially included in the GLM with a repeated measures model, but since none of the two- or three-way interactions (among the between-subject effects), or three- or four-way interactions (between the within-subject effect, angle, and the between-subject effects), were significant (at $\alpha = 0.05$), they were removed from the model, and only the simplified model is presented (see Table 2). However, since there were significant two-way interactions between the within-subject factor (angle) and the between-subject factors (species, DBH, and AET) — indicating that the effects of the between-subject factors varied depending on the angle of view — we performed separate analyses to test the effects of the between-subject factors for each angle of view (see Table 3). Post-hoc Tukey’s tests were used to determine which species differed from each other.

Since the GLM analyses described above did not show any significant interactions among the species, AET, and DBH effects, it made it possible to predict the tree-level CO_{mean} and the CO_{θ} as linear combinations of those factors, with CO_{mean} or $CO_{\theta} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 \text{AET} + \beta_4 \text{DBH} + \varepsilon$, where θ is 0°, 15°, 30°, or 45°; X_1 and X_2 are

Table 3. Results of analyses of variance performed separately for crown openness measured at four different angles.

Dependent variable	Sources	SS	df	MS	<i>F</i>	<i>P</i>
CO ₀	Species	1819.4	2	909.7	41.532	<0.001
	AET	414.7	1	414.9	18.940	<0.001
	Error	6768.4	309	21.9		
CO ₁₅	Species	1897.0	2	948.5	29.347	<0.001
	AET	524.0	1	524.0	16.212	<0.001
	Error	9987.1	309	32.3		
CO ₃₀	Species	1315.2	2	657.6	15.561	<0.001
	AET	1028.7	1	1028.7	24.342	<0.001
	DBH	678.5	1	678.5	16.054	<0.001
	Error	13016.8	308	42.3		
CO ₄₅	Species	766.8	2	383.4	8.761	<0.001
	AET	1369.3	1	1369.3	31.290	<0.001
	DBH	1371.6	1	1371.6	31.342	<0.001
	Error	13478.8	308	43.8		

Note: Initially, all study factors (species, actual evapotranspiration (AET), and diameter (DBH)) and their interactions were included, but only the significant effects were kept and presented below. SS, sum of squares; MS, mean square.

dummy variables coding for species (with values of 0 and 0 for yellow birch, 1 and 0 for sugar maple, and 0 and 1 for hemlock); the AET is in mm/year; the DBH is in cm; ε is the unexplained error associated with each observation; and the β are the parameter values to be evaluated (β_0 being a constant). The parameter values of the multiple regression models are presented in Table 4, and the corresponding relationships are illustrated in Fig. 3.

To better illustrate one of the significant interactions that involved the angle of view, namely the angle \times DBH interaction, we calculated the CO _{θ} for each angle and species, holding the AET constant at an intermediate value of 545 mm/year. The variation in the predicted CO _{θ} as a function of DBH and angle is illustrated for each species in Fig. 4.

For all tests, homoscedasticity of the data was confirmed by plotting the residuals against the predicted values, while skewness and kurtosis of residuals were calculated to identify cases where a departure from normality would be present. Prior to the repeated measures analysis, residuals of CO values at 0°, 15°, 30°, and 45° were pooled to test normality, in addition to the previous test of normality, but the data did not need to be transformed. The assumption of sphericity of the covariance matrix associated with the repeated measures analysis was considered to be met when the Greenhouse–Geisser and Huynh–Feldt epsilon values were higher than 0.75 (Quinn and Keough 2003). All analyses were performed using SYSTAT (v. 10.0).

Results

Tree-level mean crown openness

Tree-level CO_{mean} ranged from 3.4% to 40.2% for yellow birch, from 3.1% to 26.1% for sugar maple, and from 3.5% to 25.0% for hemlock. The CO_{mean} differed among species ($P < 0.001$) (Table 2). Yellow birch had the highest species-specific CO_{mean} (15.1% \pm 6.1%, mean \pm SD), while sugar maple (10.5% \pm 4.4%) and eastern hemlock (11.0% \pm 4.4%) had similar values (post-hoc Tukey's test, not shown).

The actual evapotranspiration (AET) had a significant effect on CO_{mean} ($P < 0.001$) (Table 2). The CO_{mean} augmented with increasing AET (Fig. 3), and the effect did not differ among species (interaction species \times AET, $P > 0.05$, not shown).

The CO_{mean} was significantly affected by the tree DBH ($P < 0.001$) (Table 2). The overall effect of DBH on the CO_{mean} was negative (i.e., CO_{mean} decreased with increasing DBH) (Fig. 3), but it did not differ among species (interaction species \times DBH, $P > 0.05$, not shown).

Angle-specific crown openness

There were significant two-way interactions between angle and each of the between-subject factors (species, AET, and DBH) (Table 2), indicating that although all factors influenced the tree-level CO_{mean}, their effects in fact varied depending on the angle of view (i.e., if one considers the CO _{θ}). Analyses were therefore performed separately for each angle of view (see Table 3) to investigate further the nature of the interactions between angle and the other factors.

The angle-specific crown openness (CO _{θ}) differed among species whatever the angle of view (Table 3), but the presence and magnitude of differences among species varied with the angle of view. Post-hoc Tukey's tests (not shown) indicated that at 0°, 15°, and 30° yellow birch had a significantly ($P < 0.05$) higher crown openness than both sugar maple and hemlock (which did not differ from each other, $P > 0.1$), while at 45° the crown openness of hemlock was intermediate between, and not significantly different ($P > 0.1$) from those of yellow birch and maple, while the latter two species remained significantly different from each other ($P < 0.001$). Variations among angles in the magnitude of the interspecific differences are observable on Figs. 3B–3E.

The presence of a significant interaction between angle and AET (Table 2) was due to variations, among angles, in the magnitude of the AET effect (Fig. 4). The crown openness increased with increasing AET at all four angles, but the effect was more pronounced at higher angles (e.g., at

Table 4. Parameter values of the multiple linear regression models that best described how crown openness (either the tree-level CO_{mean} , or the angle-specific CO_{θ} values) varied as a function of species, actual evapotranspiration (AET, mm/year), and DBH (cm).

Dependent variable	β_0	β_1	β_2	β_3	β_4	P	R^2	n
CO_{mean}	-58.398	-4.523	-3.526	+0.139	-0.074	<0.001	0.270	313
CO_0	-42.993	-4.711	-5.114	+0.101	ns	<0.001	0.259	313
CO_{15}	-47.919	-5.001	-4.936	+0.113	ns	<0.001	0.205	313
CO_{30}	-66.999	-4.650	-2.696	+0.159	-0.102	<0.001	0.197	313
CO_{45}	-77.595	-3.582	-1.743	+0.183	-0.144	<0.001	0.212	313

Note: The models are of the form $CO = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 AET + \beta_4 DBH + \varepsilon$, where β_0 is a constant, and where the variables X_1 and X_2 are dummies coding for species and taking values of 0 and 0, 1 and 0, and 0 and 1 for yellow birch, sugar maple, and hemlock, respectively. For CO_0 and CO_{15} , the DBH effect was not significant (see Table 3), and therefore not included in the final model. Each model is illustrated in Fig. 3.

45° vs. 0°) (Fig. 4, and see Table 4 for the values of the β_3 parameter, the partial regression coefficient associated with AET).

Finally, the significant interaction between angle and DBH (Table 2) was due to variations among angles in the presence, and magnitude, of a DBH effect (Table 3; Fig. 4). The crown openness measured at low angles, that is at 0° and 15°, was not significantly affected by variations in DBH ($P > 0.05$) (Table 3). The DBH term was therefore not included in the models for CO_0 and CO_{15} (Table 4; Fig. 3). The DBH, however, had a significant effect on the crown openness measured at higher angles (i.e., 30° and 45°) (Table 3), and the magnitude of this effect tended to be greater at 45° than at 30° (Fig. 4, and see Table 4 for the values of the β_4 parameter, the partial regression coefficient associated with DBH). The significant interaction between angle and DBH (Table 2) also indicates that differences in crown openness (CO_{θ}) among angles were greater for trees with smaller DBH than for larger trees (Fig. 4).

Discussion

Interspecific differences in crown openness

Crown openness values obtained in this study are comparable to values reported in other studies using a similar method (Canham et al. 1999; Beaudet et al. 2002; Astrup and Larson 2006). Species-specific mean CO generally range between 10% and 20% for various tree species. Our observation that yellow birch generally had higher CO values than the other two, more shade-tolerant species is also in agreement with previous reports of less shade-tolerant species having higher CO values than more shade-tolerant species (Messier and Bellefleur 1988; Canham et al. 1999; Beaudet et al. 2002). If compared solely with other results for the same species, our results agree with Horn (1971), but differ slightly from those of Canham et al. (1994), who found that eastern hemlock casts more shade than sugar maple. In this study, we did not detect any significant difference between these two species. This discrepancy could be attributed to differences in methodology. In Canham et al. (1994), CO was derived from hemispherical photographs of the whole forest canopy, and therefore included stand-level canopy features (e.g., spacing between crowns) in addition to individual tree crown characteristics. The openness of the forest canopy in eastern hemlock stands (or patches) might

therefore be lower than for sugar maple, while the two species might not differ in terms of crown-level openness.

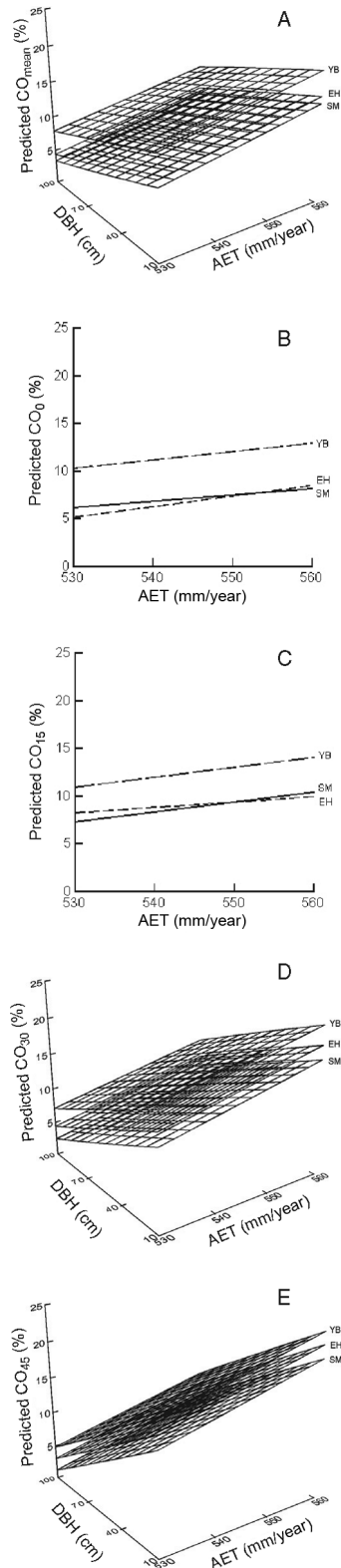
Effect of actual evapotranspiration on crown openness

Our results on the effect of regional AET on CO are in agreement with the general assumption that the quantity of foliage decreases with decreasing water availability (Zahner 1968; Jose and Gillespie 1996). While the effect of precipitation could not be identified as a significant determinant of the regional variability of CO in Astrup and Larson (2006), our results suggest that regional AET contributes to changes in CO, among other environmental factors. This has been hypothesized before by Messier et al. (1998) to explain the lower light transmission in stands of *Populus tremuloides* Michx. in wetter regions of eastern Canada compared with stands in dry western Canada.

Effect of angle of transmission and DBH on crown openness

Although some models assume that a crown's light transmission properties do not vary with the direction of the incoming light, our results show that there is an increase in CO with the angle from zenith, at least among smaller trees. There are many possible explanations for this interaction between the angle of transmission and tree size. First, the larger the tree and its crown, the higher the probability that leaves would intercept light no matter the angle of measurements. Second, if smaller trees are suppressed, they receive less lateral light (Horn 1971) and may invest in a more horizontal display of leaves compared with the dominant trees. This "horizontal efficiency" as expressed by Falster and Westoby (2003) is typically employed by smaller or suppressed trees in the understory (Horn 1971; Givnish 1988; Niinemets et al. 2005) to maximize their light interception and cast shade on competitors. Our results showed that as tree size decreases, CO augments with higher angles (30° and 45°). This suggests that the dominant trees are much more efficient at intercepting light coming from all directions than the smaller and possibly suppressed trees. It also shows that CO is not a constant parameter within a tree species, but can vary either through ontogeny or because of shading. As individuals increase in size, they experience an increase in light availability from many directions (Aiba and Kohyama 1997; Osada et al. 2004; Sterck and Bongers 2005). As a result, during ontogeny, leaf and branch display is subject to change, and this can ultimately translate to the

Fig. 3. Predicted crown openness (A, tree-level CO_{mean} ; and B–E, each of the angle-specific CO_{θ} (degrees)) for yellow birch (YB), sugar maple (SM), and eastern hemlock (EH) as a function of actual evapotranspiration (AET) and, when significant, diameter at breast height (DBH). See Table 4 for more details about the predictive models.



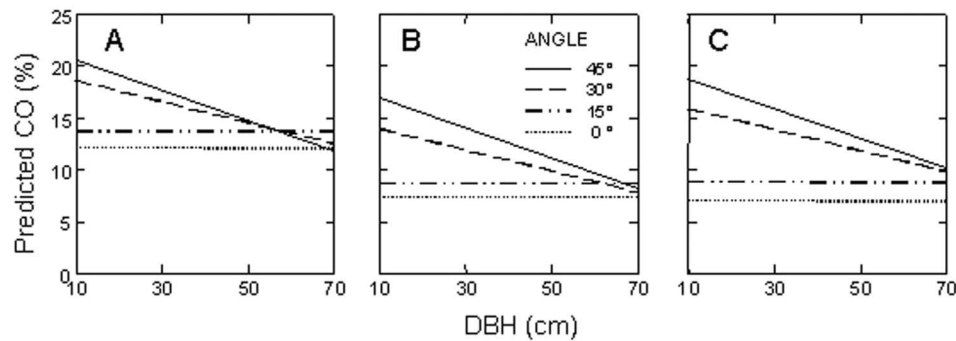
development of orthotropic branches (Horn 1971; King 1991; King and Maindonald 1999), where leaves with a steeper angle can maximize light interception at low angles while minimizing respiration cost and avoiding photoinhibition (Givnish 1988; Falster and Westoby 2003). It has been reported that a random leaf angle distribution allows for optimal light interception efficiency when the light source is multidirectional (Barclay 2001; Sinoquet et al. 2005). The higher CO we observe among smaller trees when their crowns were viewed from the side rather than from below, as well as the possible absence of an angle effect among larger trees, suggest that the leaf angle distribution might be preferentially horizontal among smaller trees and might become increasingly random with increasing tree size. Our results also suggest that with an increase in light from the side, trees might be able to modify their leaf angle distribution, enabling them to fully exploit this resource (Aiba and Kohyama 1997; Sterck et al. 2001). Note however that other factors such as foliage clumping, variations in leaf area density (LAD), and penumbra effect might also play a role in the observed trends.

Another potential factor affecting crown openness is crown shape. Horn (1971) schematized how a cylinder-shaped crown would intercept more light than a cone-shaped crown of the same height. The distance completed by the sunrays would be greater in a crown with a high convexity, increasing the path length of the light beam. It is believed that CO varies depending on the path length of the light beam through the canopy, as hypothesized by Astrup and Larson (2006). In this study, we failed to detect the effect of the path length (results not shown). Such results can be explained by the fact that mature hardwood trees usually have a hollow at the centre of their crowns, the effect being greater for shade-intolerant trees (Horn 1971; Canham et al. 1994; Sterck et al. 2001). In a modeling experiment, Canham et al. (1994) also pointed out that accounting for this type of leaf distribution in modeling light transmission increased the accuracy of the predictions, as opposed to considering the crown volume homogenous (as in a path length model).

The uneven distribution of foliage within the canopy strata could also explain the decrease of CO with tree size (Figs. 3 and 4). Trees that typically occupy the understory or the subcanopy could have a reduced amount of LAD, since most of the foliage in a forest canopy is usually concentrated on the top layer of the canopy (Brown and Parker 1994; Vose et al. 1995; Kitajima et al. 2005), and this sparse display of foliage would lead to a higher CO. The same mechanism operates within the crown, with a higher concentration of foliage at the top of the crown, which gradually becomes discontinuous at lower heights (Aber et al. 1982). This would also explain the dependence of CO on angle.

Our results regarding the variation of CO as a function of angle of transmission and DBH (Tables 2 and 3; Fig. 3) do not agree with those of Astrup and Larson (2006) for white spruce and aspen. In the latter study, CO did not vary with angle. However, the range of angles of transmission in Astrup and Larson (2006) was slightly more limited (mostly between 0° and 15° from zenith) than in this study (0° – 45° from zenith). Also, while in this study the angle effect could be isolated as a within-subject effect from repeated measure-

Fig. 4. Angle-specific crown openness as a function of DBH, predicted using the models presented in Table 4, holding the actual evapotranspiration (AET) constant at an intermediate value of 545 mm/year, for (A) yellow birch, (B) sugar maple, and (C) eastern hemlock.



ments of CO from different angles for each individual tree, in Astrup and Larson (2006) measurements of CO from different angles were obtained from different trees, which may have increased the amount of unexplained variability and decreased their ability to detect an angle effect, if present in their study species. As for DBH, Astrup and Larson (2006) did not find any effect on CO for aspen, and only a weak negative effect for white spruce, while a significant negative effect was found in this study, independent of species. Considering the greater DBH effect observed at higher angles from zenith in this study, we suggest that the absence of a DBH effect on CO (or presence of a weak one) in Astrup and Larson (2006) might in part be due to the fact that their photos were generally taken at low angles from zenith.

Conclusion

Reasonable data requirements for model parameterization are obviously a desirable characteristic for a light model. The precision and accuracy in the predictions under a wide range of conditions also have to meet a satisfactory degree. In SORTIE, the light transmission is modeled using a simplified representation of individual trees where the light extinction properties of the crowns are represented by a single species-specific parameter, the CO, which is relatively simply obtained compared with the data requirements of other models. This study showed interspecific differences in CO, with higher CO in the less tolerant species compared with the more shade-tolerant ones, in agreement with previous reports (Canham et al. 1994, 1999; Beaudet et al. 2002). The relative differences in CO among species appeared to hold in all conditions found on distant sites from western Quebec, southern Ontario, and northern Michigan. However, despite the consistent ranking of the species, the absolute CO values varied according to the biophysical conditions (i.e., AET), and the size (DBH) of trees. If one uses CO values only based upon species differentiation, the possible variability between site conditions and tree size should be acknowledged.

The overall ecological significance of the results presented in this study are still unknown (e.g., if the higher CO attributed to suppressed trees is contributing much to the overall dynamic of light transmission in forests). Furthermore, Beaudet et al. (2002) have shown that changes in CO have relatively less impact on light transmission than changes in crown geometry variables. The same phenomenon was observed with the tRAYci model when changes

in LAD did not affect light predictions significantly (Gersonde et al. 2004; Piboule et al. 2005). Further research is needed to better assess the potential ecological impacts of variations of CO.

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