Importance of needle age and shoot structure on canopy net photosynthesis of balsam fir (Abies balsamea): a spatially inexplicit modeling analysis

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Summary We have developed a spatially inexplicit model of canopy photosynthesis for balsam fir (Abies balsamea (L.) Mill.) that accounts for key processes of light–shoot interaction including irradiance interception by the shoot, spatial aggregation of shoots into branches and crowns, the differential propagation of diffuse and direct light within the canopy, and an ideal representation of penumbra. Also accounted for in the model are the effects of the average radiative climate and shoot age on needle retention, light interception, and photosynthetic capacity. We used reduced versions of this model to quantify the effects of simplifying canopy representation on modeled canopy net photosynthesis. Simplifications explored were the omission of direct beam transformation into penumbral light and the use of different constant shoot properties throughout the canopy. The model was parameterized for a relatively dense balsam fir stand (leaf area index of 5.8) north of Québec City, Canada, and run using hourly meteorological data obtained at the site. The overall performance of the complete model was satisfactory, with maximum values of canopy net photosynthesis of 23 µmol (m² ground)⁻¹ s⁻¹ (83 mmol m⁻² h⁻¹), and a near-saturation of the canopy at a photosynthetically active radiation photon flux density of about 750 µmol m⁻² s⁻¹ (2.7 mol m⁻² h⁻¹). The omission of penumbral effects through the use of unattenuated direct (beam) radiation at all layers of the canopy, as used for broad-leaved species, reduced canopy net photosynthesis by 3.7%. Analysis of the results show that the small impact of penumbra on canopy net photosynthesis stems from the high proportion of diffuse radiation (73%) estimated from our meteorological data set; single-hour results under clear sky conditions approach theoretical bias values of about 30%. Use of mean shoot photosynthetic, light capture and light transmission properties throughout the canopy biased canopy net photosynthesis by less than 3%. However, simulations carried out based on properties of 1-year-old shoots throughout the canopy overestimated canopy net photosynthesis by 9%. Use of the shoot as our smallest functional unit was a potential source of bias because the differential absorption of direct and diffuse radiation within the shoot could not be factored into the model. Other sources of potential bias are discussed.

Keywords: diffuse radiation, direct beam radiation, leaf mass per unit area, penumbra, STAR.

Introduction

Process-based modeling of forest productivity requires an unbiased modeling of canopy net photosynthesis. Recent advances in our understanding of the distribution of internal and external resources within the canopy have permitted the development of canopy photosynthesis models for broad-leaved hardwoods and conifers (Ellsworth and Reich 1993, Aber et al. 1995, Leuning et al. 1995). The key to these models is the representation of the interaction between light and the photosynthetic properties of foliage.

Spatial interactions between light and photosynthetic properties within a canopy can be represented at different resolutions, and choosing the proper resolution usually depends on the intended use. For application to a variety of sites, it is advantageous to develop a model with a functional description of canopy properties, in which the canopy properties are captured by the distribution function of selected leaf or shoot properties, not by the spatial distributions of their elements. Nitrogen (Leuning et al. 1995, De Pury and Farquhar 1997) and leaf mass per unit leaf area (Aber et al. 1995) have been used to achieve spatially inexplicit descriptions of canopies. Such functional representations can accurately describe the spatial distribution of the photosynthetic properties within the canopy. In broad-leaved species, this can be combined with a sun-shade, single-layer light environment to further simplify canopy representation (Leuning et al. 1995).

The development of a spatially inexplicit model for conifers faces difficulties linked to three specific characteristics of conifer foliage. First, the aggregation of conifer needles into shoots exerts substantial control over the light–leaf interaction
through the angular distribution of the needles and the self-shading within the shoots (Oker-Blom and Smolander 1988, Leverenz 1995). In turn, the spatial arrangement of this aggregation is often influenced by the light regime in which it developed (Carter and Smith 1985). Second, the small size of the needles, with respect to the solar disk, permits transmission of direct radiation deep within the canopy, but in an attenuated form known as penumbra (Stenberg 1995). The prevalence of penumbra enhances the efficiency of light capture by needles (Stenberg 1998). Third, the retention and aging of needles has the double effect of decoupling the needle and shoot properties from their ambient light environment, and of impairing the photosynthetic response of needles. Our measurements show needle retention of up to 12 years in balsam fir. A complete canopy model of evergreen conifers should account for all of these needle characteristics.

Mean shoot properties and total leaf area can be derived with relative ease at the plot level. Determining the distribution of properties such as age and shoot structure within the plot or stand requires additional intensive sampling that can be carried out only on a restricted number of sites. In order to facilitate application of the model to diverse sites, we must then strive to develop models that accurately represent the shoot-light interactions within coniferous canopies, but at the same time to simplify the canopy representation and thus the input requirements of the model. The objectives of this work were, therefore, to develop a spatially inexplicit model of balsam fir canopy photosynthesis, and to determine the bias incurred when age effects on physiological and morphological variables were omitted, and when shoot geometry was considered uniform throughout the canopy.

**Material and methods**

**Study site**

Field measurements were performed at a research site located within Université Laval’s Forêt Montmorency. Forêt Montmorency is located in the Laurentian highlands about 100 km north of Québec City, (71°06' 00"W, 47°19'00"N), and lies within the balsam fir–white birch domain, ecological region 8f of Thibault and Hotte (1985) with between 890 and 1000 degree-days above 5 °C annually. The site lies on a west-facing slope, at an altitude of 800 m, and is underlain by a well-drained, coarse glacial deposit with a moderate stone content. Slope varies between 15 and 25%. The stand is nearly pure and even-aged balsam fir, forming a dense, closed canopy with a sparse ground cover of mosses and small vascular plants. The stand originated from a clearcut in the 1930s. Mean tree height is 17 m. Composition by percent contribution to basal area is 91% balsam fir (Abies balsamea (L.) Mill.) and 9% white birch (Betula papyrifera Marsh.). Total basal area of the stand is 19.8 m² ha⁻¹.

In the spring of 1997, a 17-m canopy access tower was erected at the Forêt Montmorency site to permit the measurement of leaf gas exchange in canopies of three adjacent balsam fir trees. A meteorological tower was also built and instrumented with various sensors to monitor above- and below-canopy environmental variables. Incident shortwave radiation was measured above the canopy with Li-Cor silicon pyranometers (Model LI-200S, Li-Cor, Lincoln, NE). Other environmental sensors were mounted on or around the towers. All sensors were scanned every 5 min. The hourly mean of their readings was recorded with a data logger.

**Leaf gas exchange**

Light response curves were obtained on four 1-year-old shoots on July 6, 1998. Shoots were considered the elemental units for gas exchange measurements. The light response measurements were carried out on attached shoots with an open-mode, portable, gas-exchange measurement system (LCA4, Analytical Development Corporation, Hoddesdon, U.K.) using a cylindrical cuvette designed for use with conifers. Shoots were placed in the cuvette with their upper side facing the light source. Cuvette and needle temperatures were monitored with built-in sensors and energy balance corrections. The light source consisted of a white halogen bulb and reflector mounted on the cuvette. Air gaps and thermal filters prevented heating within the cuvette. Irradiance was controlled with a built-in voltage regulator, coupled with a diffuser and small neutral-density filters. Irradiance in the cuvette was measured before each measurement with a small detachable quantum meter. All irradiance measurements reported in this text are for photosynthetically active radiation (PAR) wavelengths. Five measurements were performed for each shoot at or near irradiances of physiological interest according to the recommendations of Hanson et al. (1987). Total darkness was obtained by wrapping aluminum foil around the cuvette.

The effect of light climate on photosynthetic properties was measured on nine 1-year-old shoots evenly distributed on three trees in reach of the access tower and selected to span the whole range of radiative environments, on May 8 and 27, 1998. On each occasion, maximum photosynthesis was measured on the attached shoots in artificial light at PAR irradiances greater than 1200 µmol m⁻² s⁻¹.

The effect of age on shoot morphology and photosynthetic properties was measured on four branches on two occasions: two branches of the upper canopy on June 12, 1998, and two branches of the middle and lower canopy on June 11, 1999. On each occasion, maximum photosynthesis was measured on the shoots of all age cohorts along the main axis of the branch, with the youngest shoot being that of the preceding year. Measurements were performed on detached shoots in artificial light in excess of 1300 µmol m⁻² s⁻¹. Terminal shoots were cut and immediately placed in the cuvette. The cut end of the shoot was covered with vacuum grease. Measurement of maximum photosynthesis was carried out within 2 to 3 min. We worked our way sequentially down the main axis of the branches until needles became sparse in the older age cohorts (foliage up to 9 years old). One possible confounding factor with leaf age is branch respiration because older cohorts are supported by branch segments of larger diameters. We therefore measured respiration
of leafless branch segments of different diameters. The segments were cut and placed in the cuvette after covering the cut ends with vacuum grease. Respiration rates of a total of 25 segments with diameters ranging from 3 to 15 mm were measured. The data were used to produce a simple model of respiration as a function of branch surface area, which was then used to correct the measured photosynthetic rates of the different age cohorts.

All gas exchange measurements are expressed on a needle hemisurface area basis. Measurement methods for obtaining total leaf area are detailed below.

**Light measurements**

We determined the mean irradiance for shoots on which gas exchange measurements were made using the technique of Parent and Messier (1996). Under completely overcast conditions, simultaneous horizontal measurements of PAR were made above the canopy and at the exact location of the shoots. Light response curves were made with detached shoots. Labels were placed in the tree to indicate the original location of the detached shoots. Shoots used in the age cohort measurements were made only on the 1999 branches before photosynthesis measurements on the different age cohorts were destructively sampled. Measurements were made with Li-Cor quantum sensors (Model LI-190SB) scanned and recorded every second with a data logger. The ratios of shoot-level to above-canopy PAR measurements were computed from 10-s means.

**Sampling the canopy**

Destructive sampling was performed to determine four canopy characteristics: total canopy leaf area, distribution of leaf area per class defined by needle mass per unit hemisurface area (NMA, g m⁻² needle), distribution of leaf area per classes of shoot age, and distribution of leaf area per classes defined by mean STAR (silhouette to total area ratio). The measurements were made within the stand, in two 400-m² satellite plots located about 100 m from the central plot containing the canopy access tower and the meteorological instruments. Within each satellite plot, we measured tree diameter at breast height and assigned trees to one of three social classes: dominant, codominant and intermediate or suppressed. One or two trees from each social class were selected and felled for destructive determination of needle mass and area. The crown was separated into two portions, above and below greatest crown width. The upper portion was further subdivided vertically into three equal parts. All the branch diameters at their insertion point were measured in each crown part. A branch of the median whorl was then selected at random by a process based on the cross-sectional area of the branch at its insertion point, which is considered proportional to needle area (Shinozaki et al. 1964), and by extension to total shoot area.

Randomized branch sampling (RBS, Gregoire et al. 1995) was applied once within each branch for shoot sampling. With RBS, each branch is considered as a network of segments and nodes. Starting at the base of the branch, each node of the segment to follow was selected at random after weighting the different segments at that node according to their basal area. Foliated segments on the path were divided into yearly growth units (shoots) and collected for further analysis.

To estimate the distribution of total shoot area per class of needle mass per unit hemisurface area (NMA), age or mean STAR, we first estimated the frequency at the stand level that each collected shoot would represent. The frequency, ν, represented by a single sampled shoot was calculated as:

\[
\nu_{\text{shptc}} = \frac{S_{\text{shptc}}G_s}{Q_{\text{shptc}}A_{\text{shptc}}G_cS_{\text{plot}}},
\]

where subscripts s, b, p, t and c represent a shoot (s) on a branch (b) selected in crown portion (p) of a tree (t) in social class (c). Superscript c indicates a collected sample. Variable \(S\) is shoot hemisurface area (m², includes needle and twig areas), \(Q\) is the expansion factor of shoot \(s\) on the branch (Gregoire et al. 1995), \(A\) is the sum of branch basal areas (cm²), \(G\) is basal area at the plot level (m² ha⁻¹) and \(S_{\text{plot}}\) is the plot shoot area. Distribution of properties within the canopy were computed from these frequencies, as in Raulier et al. (1999). Table 1 lists the main symbols used in the text.

In each satellite plot, measurements of irradiance below the canopy at a range of incident angles were obtained with a plant canopy analyzer (PCA, LAI-2000, Li-Cor) under an overcast sky and before the destructive sampling. Measurements were carried out at three points near the plot center. For each point, the measurements were repeated three times with the PCA. Another PCA was programmed to measure open-sky irradiance continuously in a nearby clearing.

**Shoot analysis**

After the measurements or samplings were completed, the shoots were detached and brought to the laboratory for further analysis. Shoot silhouette areas were measured with a 600 dpi video camera (Elmo CCD Model SE360, Plainview, NY) mounted above a light table. Projected areas of the shoots were measured at five different combinations of elevation (\(\phi\)) and rotation (\(\gamma\)) of the shoot main axis (sensu Stenberg 1996) (\(\phi, \gamma\) in degrees are: 0, 0; 0, 45; 0, 90; 45, 0; 45, 45). Area measurements of the scanned images were carried out with image analysis software (NIH Image v1.61, National Institutes of Health, Bethesda, MD).

Total needle area per shoot was obtained in a two-step process. First, total projected needle area was measured by scanning all detached needles with a Hewlett Packard 600 dpi scanner (Scanjet IIcx/T). Image analysis was performed with the WinNeedle software (Régent Instruments, Québec, Canada). Within shoots, we selected five needles at random, and obtained thin cross sections at their midpoint. The cross sections were scanned at 1850 dpi (ScanMaker 1850S, Microtek, Redondo Beach, CA) and measurements of their perimeter and width obtained with the NIH image analysis software and averaged for each shoot. Total needle area of each shoot was computed by multiplying the projected area by the mean cal-
Table 1. List of the main symbols used. Secondary symbols are explained in the text.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>$\Lambda_n$</td>
<td>Canopy net photosynthesis ($\mu$mol (m$^2$ ground)$^{-1}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$\Lambda_{\text{max}}$</td>
<td>Photosynthetic capacity ($\mu$mol (m$^2$ needle)$^{-1}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$\Lambda_s$</td>
<td>Shoot net photosynthesis ($\mu$mol (m$^2$ needle)$^{-1}$ s$^{-1}$), expressed on a hemisurface area basis</td>
</tr>
<tr>
<td>$a_s$</td>
<td>Shoot age</td>
</tr>
<tr>
<td>$I_b, I_{b0}, I_d, I_{d0}$</td>
<td>Mean direct (b) or diffuse (d) PAR irradiance on a horizontal surface ($\mu$mol (m$^2$ ground)$^{-1}$ s$^{-1}$), $I_{b0}$ and $I_{d0}$ are measured at the top of the canopy</td>
</tr>
<tr>
<td>$I_c$</td>
<td>PAR irradiance intercepted per unit of shoot hemisurface area at the compensation point ($\mu$mol (m$^2$ shoot)$^{-1}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$k_b, k_d$</td>
<td>Extinction coefficients for direct (b) and diffuse (d) irradiances</td>
</tr>
<tr>
<td>$\tilde{T}<em>{s,b}, \tilde{T}</em>{s,b0}, \tilde{T}<em>{s,d}, \tilde{T}</em>{s,d0}$</td>
<td>Mean direct (b) or diffuse (d) irradiance intercepted per unit of shoot hemisurface area ($\mu$mol (m$^2$ shoot)$^{-1}$ s$^{-1}$) either for a given shoot layer (s.b, s.d) or for its sunlit fraction (s.b0)</td>
</tr>
<tr>
<td>$m^*$</td>
<td>Needle mass per unit area (g m$^{-2}$), expressed on a shoot hemisurface area basis</td>
</tr>
<tr>
<td>$n^*$</td>
<td>Needle hemisurface area per unit of shoot hemisurface area</td>
</tr>
<tr>
<td>$R_d$</td>
<td>Needle dark respiration ($\mu$mol (m$^2$ needle)$^{-1}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$s_a^<em>, s_b^</em>, s_c^*$</td>
<td>Shoot STAR, shoot mean STAR and canopy mean STAR</td>
</tr>
<tr>
<td>$s'$</td>
<td>Shoot area index (m$^2$ shoot (m$^2$ ground)$^{-1}$), expressed on a hemisurface area basis</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Azimuth</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Rotation angle of the plane separating the upper and lower parts of a shoot</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Zenithal angle</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Elevation angle of shoot main axis</td>
</tr>
<tr>
<td>$\Omega$</td>
<td>Shoot clumping index</td>
</tr>
</tbody>
</table>

The mean canopy STAR was estimated for each satellite plot by summing the mean STAR of the sampled shoots weighted by their frequency at the plot level (Equation 1). Mean canopy STAR’s of both plots were then averaged to produce a mean canopy STAR for the stand.

**Model development**

The model developed below uses the shoot as the smallest functional unit, and considers all factors except light as non-limiting for photosynthesis. In that context, a multilayer model needs to detail three properties of the canopy: the transmission of irradiance through the canopy, the irradiance interception by the foliage and the sensitivity of photosynthesis to irradiance. Scattering of photosynthetically active radiation is not considered (Baldocchi 1993).

**Choice of covariables characterizing the shoot population**

Spatially inexplicit multilayer models can stratify the canopy into layers specified by a given shading leaf area index (LAI) between the open-sky and the considered layer (e.g., Reich et al. 1990, Leuning et al. 1995). In turn, this shading LAI serves to estimate the average light climate observed within the layer, which itself is well correlated to the photosynthetic properties of foliage. This is especially true with deciduous broad-leaved species (Reich et al. 1995, Raulier et al. 1999) but also holds for fir. Needles of fir are known to adapt morphologically and...
physiologically to their radiative environment (Clark 1961, Morgan et al. 1983, Brooks et al. 1996, Sprugel et al. 1996). In conifers, average light climate within the canopy is known to be correlated to shoot properties like needle density and STAR (Piene 1983, Carter and Smith 1985, Boyce 1993, Sprugel et al. 1996, Stenberg et al. 1998), as well as NMA (Morris 1951). In a preliminary analysis, we therefore focused on two of these variables, STAR and NMA, as possible covariables to represent the light climate distribution within the canopy. A preliminary analysis of the data revealed that NMA of needles less than 4 years old was better related to both mean, diffuse light environment and shoot, maximum photosynthetic rates than mean STAR (see Results section). The NMA was therefore chosen as the main covariable to describe the shoot population.

Shoot age also needs to be considered. The light environment at the time of shoot formation affects needle morphology and shoot STAR. On the other hand, the light environment of the needle changes during its life span, and needle photosynthetic properties are simultaneously affected by age and current light environment (Brooks et al. 1996). In addition, the NMA of needles may increase with age (Morris 1951, Gilmore et al. 1995). Age must therefore be taken into account in the relationship between the NMA and both the mean light climate (and shading LAI) and leaf photosynthetic properties.

For each satellite plot, we therefore computed the distribution frequency of the shoot population by classes of NMA and age by cumulating the shoot frequencies (Equation 1) in each class. The NMA and age classes were chosen to have 20 g m⁻² and 1-year amplitudes, respectively. A mean of plot frequency values was calculated for each class to scale at the stand level. The average radiative environment of each NMA and age class was estimated from a linear model adjusted to our field data that considered both simple effects and the interaction of NMA and age:

\[ T_d = \tau_1 + \tau_2 m^* + \tau_3 a_i + \tau_4 m^* a_i, \]  

where \( T_d \) is the observed canopy transmission of diffuse irradiance, \( m^* \) is NMA (g m⁻²), \( a_i \) is shoot age and \( \tau_1 \) to \( \tau_4 \) are parameters estimated by ordinary least squares (OLS) (Table 2).

**Light transmission through the canopy**

Irradiance needs to be separated into its diffuse and direct (beam) components because they differ in canopy penetration dynamics (Norman 1993). Because of the small size of the needles relative to canopy depth, penumbra also needs to be considered for modeling PAR distribution, as it reduces the fraction of foliage in full shade and even out direct sunlight deep into the canopy (Stenberg 1995). Explicit solutions for the correct representation of penumbral effects quickly become intractable, and approximations have been elaborated that separate between- and within-shoot shading (Stenberg 1995, 1998). Within-shoot shading is not explicitly modeled here because the effect of needle angle and sunlit/shaded fractions within the shoot are implicitly integrated in our measurements of shoot photosynthesis. Shoot-level measurements are made with the assumption that the radiation field inside the cuvette is similar to that under natural conditions.

Greater simplification often results in larger errors or biases. In order to bound our errors, we used two mathematical representations that should underestimate or overestimate canopy photosynthesis. In the first model, penumbra is ignored and a shoot is assumed to be either in full (above-canopy) sunlight or in full shade (ML-1). Canopy photosynthesis will be underestimated with ML-1 because the effect of penumbra on irradiance variance is ignored (Stenberg 1995). In the second model, diffuse and direct irradiances are represented by their mean values (ML-2). Canopy photosynthesis will be overestimated in ML-2 because of the absence of stochastic variation in irradiance within each shoot class (Stenberg 1995). Thus, it represents an upper estimate of penumbral effects (Norman 1980).

The penetration of diffuse and direct irradiance is treated separately. Considering the clumping of needles in shoots, and neglecting the interception of irradiance by the non-foliated parts of the canopy, the profile of mean direct irradiance in a canopy can be approximated with the Beer–Lambert model (Nilson 1971, Chen et al. 1997):

\[ I_b = I_{b0} \exp(-k_b S^*), \]  

where \( I_b \) is the mean direct irradiance on a horizontal surface (\( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \)) observed under a shading shoot area index (SAI) of \( S^* \). \( I_{b0} \) is the direct irradiance above the canopy. As shoots, but not needles, are treated as the elemental functional units, the shoot area index, expressed on a hemisphere area basis, is considered instead of LAI. The shoot area is computed as the sum of total needle and twig surface areas. Assuming a spherical distribution of shoot angles with respect to the incoming radiation, the extinction coefficient for direct irradiance (\( k_b \)) is expressed as (Stenberg et al. 1994):

\[ k_b = \frac{2\Omega \tau^*}{\cos \theta_b}, \]  

where \( \Omega \) is a shoot clumping index for scales larger than the shoot, \( \tau^* \) is mean shoot STAR averaged over the canopy and \( \theta_b \) is solar zenith angle. A factor of two appears in Equation 6 as mean canopy STAR is expressed per unit of total shoot area, whereas SAI is expressed per unit of shoot hemisurface area. The shoot clumping index was obtained from the PCA measurements and the destructive SAI estimates were obtained in the satellite plots. Logarithms of transmittance values for each of the five PCA rings were averaged (Lang and Xiang 1986). Equations 5 and 6 were used to estimate \( \Omega \) for each ring of the PCA. Examination of the results showed a strong dependence of \( \Omega \) on the zenithal view angle. This dependence was explicitly taken into account with the following empirical function:

\[ \Omega_{ij} = \cos(\alpha_i(\theta_j - \alpha_j)) + \rho \varepsilon_{ij-1}, \]  

where $\Omega_{ij}$ is the shoot clumping index taken for ring $(j)$ of spot $(i)$; $\theta_j$ is the zenithal angle of the ring midpoint ($7^\circ$, $23^\circ$, $38^\circ$, $53^\circ$ and $68^\circ$); $\omega_1$, $\omega_2$ and $\rho$ are parameters to estimate with nonlinear OLS (Table 2); and $\varepsilon_{i(j-1)}$ is the residual of the preceding observation. The inclusion of a first-order autocorrelation process in the model with parameter $\rho$ causes the loss of one degree of freedom per PCA measurement. Ring measurements were thus ordered in ascending order of zenithal angle, causing the loss of the fifth ring. Equation 7 was fitted with the PROC NLIN module of the SAS software package (SAS Institute, Cary, NC).

Assuming an isotropic distribution of diffuse radiation in the sky, the irradiance per unit solid angle is $I_d/\pi$ (Thornley and Johnson 1990, their Equation 8.4d), $I_d$ being the diffuse irradiance incident on a horizontal surface ($\mu$mol (m$^{-2}$ ground)$^{-1}$ s$^{-1}$) below a given SAI. The profile of mean diffuse irradiance is then obtained with (Oker-Blom and Kellomäki 1982, their Equation 20):

$$ I = \int_0^{\pi/2} \int_0^\pi \frac{I_d}{\pi} \exp(-k_h S') \sin \theta_h \cos \theta_h \sin \alpha_h \cos \alpha_h \, d\alpha_h \, d\theta_h $$

$$ = \int_0^{\pi/2} 2 I_d \exp(-k_h S') \cos \theta_h \sin \theta_h \sin \theta_h \cos \theta_h \sin \alpha_h \cos \alpha_h \, d\alpha_h \, d\theta_h, $$

where $I_d$ is the mean diffuse radiation on a horizontal surface above the canopy, $\theta_h$ is zenithal angle, $\alpha_h$ is the azimuth of the view direction in the hemisphere and $k_h$ is the irradiance extinction coefficient in the view direction and defined by Equation 6. The term $\cos \theta_h$ is included because $I_d$ refers to irradiance on the horizontal, and $\sin \theta_h$ corresponds to the relative area of the hemisphere in the zenith angle band around $\theta_h$.

For both multilayer models, the transmission of diffuse irradiance measured for each class of NMA and shoot age (Equation 4) is needed to estimate the shading SAI lying between the considered class and the open sky. The shading SAI value can then be used to estimate the transmission of direct and diffuse irradiances reaching the class in question. For this purpose, a mean extinction coefficient for diffuse irradiance ($k_d$) was derived from Equation 8:

$$ k_d = -\frac{\ln(T_d)}{S'} $$

$$ = -\frac{1}{S'} \ln \left( \int_0^{\pi/2} 2 \exp(-k_h S') \sin \theta_h \cos \theta_h \sin \theta_h \cos \theta_h \sin \alpha_h \cos \alpha_h \, d\alpha_h \, d\theta_h \right). $$(9)

The right-hand term of Equation 9 was solved numerically by dividing the sky hemisphere into 10 zenithal angle classes. Because the value of $k_d$ depends on the SAI considered, it was estimated for values of shading SAI between 2 and 12 in steps of 2. Results were used to adjust the following function from which the $k_d$ was iteratively estimated with the shading SAI from the diffuse transmission estimated for each class of NMA and shoot age:

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Table 2. Model specification. Number of observations ($n$), mean square error (MSE), adjusted coefficient of determination ($r^2$adj), parameter estimates, standard error (SE) and correlation matrix.

<table>
<thead>
<tr>
<th>Equation</th>
<th>n</th>
<th>MSE</th>
<th>$r^2$adj</th>
<th>Parameters</th>
<th>Estimated value</th>
<th>SE</th>
<th>Correlation matrix</th>
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<td>76</td>
<td>0.0144</td>
<td>0.531</td>
<td>$\tau_1$</td>
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<td></td>
<td></td>
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<td>$\tau_2$</td>
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<td>$\tau_3$</td>
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<td>$\tau_4$</td>
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<td>24</td>
<td>0.0145</td>
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<td>$\omega_1$</td>
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TREE PHYSIOLOGY VOLUME 21, 2001

Downloaded from https://academic.oup.com/treephys/article-abstract/21/12-13/815/1626081/Importance-of-needle-age-and-shoot-structure-on by guest on 16 September 2017
\[ k_d = \kappa_1 + \kappa_2 \ln(S'), \]

where \( \kappa_1 \) and \( \kappa_2 \) are parameters estimated with OLS (Table 2). The shading SAI of any considered class of NMA and shoot age was estimated iteratively from Equation 8, together with \( k_d \) (Equation 10).

### Irradiance interception by the shoots

When scattering is ignored, the irradiance is either transmitted through the canopy or intercepted by it. The intercepted irradiance \((-dI)\) divided by the intercepting area \((dS')\) of a canopy layer gives the mean irradiance on the shoot area for that layer. The shoot population within a given layer needs to be further subdivided into angular subclasses as irradiance interception by a shoot depends on the elevation and rotation angle of the shoot (Equation 3). Finally, the interception of diffuse and direct irradiances is to be treated separately.

For the first multilayer model (ML-1), the direct irradiance intercepted by a given SAI layer is equal to (demonstrated in Appendix 1):

\[ -\frac{dI_b}{dS'} = \sum_0^\infty \sum_0^\pi \nu_b \nu_{b,\alpha} \tilde{I}_{b,\alpha}, \]

where:

\[ \nu_b = \Omega \exp(-k_b S'), \]

\[ \nu_{b,\alpha} = \sin \theta \Delta \theta \sin \alpha \Delta \alpha \frac{2}{\pi}, \]

and

\[ \tilde{I}_{b,\alpha} = \frac{2s^2}{\cos \theta} I_{b,\alpha}, \]

if the shoots within a considered layer are subdivided into zenithal and azimuthal classes. Because shoots are assumed to be spherically oriented, the frequency of a considered angular class is equal to the product of the probability density functions of the zenith angle \((f(\theta_\alpha) = \sin \theta d\theta_\alpha, 0 \leq \theta_\alpha \leq \pi/2)\) and of the azimuthal angle \((f(\alpha) = d\alpha / 2\pi)\). The frequency \( \nu_b \) corresponds to the shoot proportion that is sunlit within the considered layer and \( \tilde{I}_{b,\alpha} \) is the mean direct irradiance intercepted per unit of sunlit shoot hemisurface area (\(\mu\text{mol} \ (m^2 \text{ shoot})^{-1} \text{ s}^{-1}\)) within a given angular subclass. Note that \( s \) is defined by Equation 2 that depends on the shoot elevation and rotation angles \((\phi, \gamma)\). Given the sun zenith and azimuth angles \((\phi_\gamma, \gamma_\gamma)\), the correspondence between both reference systems is (Stenberg 1996, her Equations 1 and 2):

\[ \phi = \sin^{-1}\left[ \sin \theta_\gamma \sin \theta_\gamma \cos(\alpha_\gamma - \alpha_\gamma) + \cos \theta_\gamma \cos \theta_\gamma \right]. \]
\[ s'(\phi, \gamma) = a + b \cos \phi - c \gamma \cos \phi, \quad (22) \]

\[
\begin{align*}
  s'(0,0) &= \sigma_1 + \frac{\sigma_2}{m} + \sigma_3 a,
  b &= \sigma_4 + \sigma_5 s'(0,0), \\
  a &= s'(0,0) - b, \\
  c &= \sigma_6 b
\end{align*}
\]

and where \( \sigma_1 \) to \( \sigma_6 \) are parameters estimated with nonlinear OLS (Table 2).

**Light response curves**

The photosynthetic response to light was represented by the non-rectangular hyperbola of Hanson et al. (1987), modified to account for the arrangement of the needle surface in a shoot. We followed the fitting procedure described in Raulier et al. (1999) to relate the parameters of Hanson’s model to NMA and needle age. We first fitted Hanson’s model with PROC NLIN using our light response measurements. In a second step, using the results from the fitted functions, we related the estimated parameters of Hanson’s model to values of NMA and age. In a third step, the parameters were replaced with their respective parameterized equations, and the full model estimated once more with nonlinear OLS (West et al. 1984):

\[
A_n = A_{\text{max}} \left[ 1 - \left( 1 - \frac{R_n}{A_{\text{max}}} \right)^{1/\gamma} \right] , \quad (23)
\]

where

\[
\begin{align*}
  A_{\text{max}} &= (\beta_1 + \beta_2 a_\text{m}) m^s, \\
  R_n &= \beta_3 A_{\text{max}} \gamma \\
  I_\gamma &= \beta_4 I_\text{d}
\end{align*}
\]

in which \( A_n \) is shoot net photosynthesis (\( \mu \text{mol} (\text{m}^2 \text{ half needle})^{-1} \text{s}^{-1} \)), \( \bar{I}_\gamma \) is the mean intercepted irradiance per unit of shoot hemisurface area (\( \mu \text{mol} (\text{m}^2 \text{ half shoot})^{-1} \text{s}^{-1} \)) in the photosynthetically active wavebands (PAR = 400–700 nm), and \( A_{\text{max}} \), \( R_n \) and \( I_\gamma \) are intermediate parameters that depend on the parameters \( \beta_1 \) to \( \beta_4 \) estimated with nonlinear OLS (Table 2). Parameter \( A_{\text{max}} \) corresponds to the photosynthetic capacity (\( \mu \text{mol} (\text{m}^2 \text{ half needle})^{-1} \text{s}^{-1} \)), i.e., to \( A_n \) at \( \bar{I}_\gamma \) above saturation. Parameter \( R_n \) corresponds to the respiration rate at \( \bar{I}_\gamma = 0 \) (\( \mu \text{mol} (\text{m}^2 \text{ half needle})^{-1} \text{s}^{-1} \)). Parameter \( I_\gamma \) is the irradiance at the compensation point (\( \mu \text{mol} (\text{m}^2 \text{ half shoot})^{-1} \text{s}^{-1} \)). For the calibration of Equation 23, values of \( \bar{I}_\gamma \) were obtained by multiplying the irradiance value measured with the quantum meter by twice the horizontal STAR value \( s'(0,0) \), Equation 14). In the last step, all our photosynthetic measurements were combined to estimate the parameters. Also, the contribution of a quadratic effect of shoot age in explaining photosynthetic capacity was tested with a likelihood ratio (Bates and Watts 1988).

Shoot photosynthesis is expressed per unit of needle hemisurface area to allow comparisons with standard measurements. However, for our canopy photosynthesis calculations, shoot photosynthesis needs to be converted into units of shoot hemisurface area. The needle area per unit of shoot area \( (n') \) can be expected to vary primarily with shoot age and average radiative environment. We used all shoots for which we measured the average radiative environment and a preliminary examination of \( n' \) showed a concave function of shoot age. To express the relationship, we chose a variant of the reciprocal function (Ratkowsky 1990) and replaced its parameters with simple functions of NMA, because the average radiative environment of the shoot is already modeled in Equation 4 as a function of NMA and shoot age:

\[
n' = \frac{\eta_1}{1 + \eta_2 a_s} , \quad (24)
\]

where \( \eta_1 \), \( \eta_2 \) and \( \eta_3 \) are shoot age and \( \eta_1 \), \( \eta_2 \) and \( \eta_3 \) are parameters estimated with nonlinear OLS (Table 2).

**Prediction of canopy net photosynthesis**

All the elements are gathered to allow a formal definition of the canopy photosynthesis models. Shoot population is thus distributed into observed classes of NMA and shoot age, themselves subdivided into classes of shoot zenith and azimuth. In turn, the elements necessary to characterize the average radiative environment, the irradiance interception and the photosynthetic sensitivity to irradiance are derived from NMA and shoot age with empirical functions based on field data. These elements are: shoot average radiative environment, shading SAI, proportion of needle area included in shoot area, shoot STAR and needle photosynthetic capacity. To bound our canopy photosynthesis predictions, we used two simple but biased models of light transmission within the canopy that either ignore penumbra (ML-1) or incorporate an ideal representation of penumbras in a fully diffusive canopy (ML-2). For comparative purposes, we consider ML-2 as our closest match to true canopy photosynthesis.

With model ML-1, canopy net photosynthesis is estimated as:

\[
A_c = S \sum_i n_i \sum_j \sum_k \left[ v_{b,n} A_c(\bar{I}_{s,10} + \bar{I}_{s,d}) \right] , \quad (25)
\]

where \( A_c \) is canopy net photosynthesis (mol (m\(^2\) ground\(^{-1}\) s\(^{-1}\)), \( A_c(\bar{I}_{s,d}) \) is shoot net photosynthesis (Equation 23) for a mean intercepted irradiance (Equations 14 and 21), \( v \) is the distribution frequency of shoot hemisurface area within a class \( i \) of NMA and age (Equation 1), \( V_{sa} \) is the distribution frequency of shoot area within an angular class (Equation 13) and \( v_s \) corresponds to the fraction of sunlit shoot area in a given NMA and age class (Equation 12). Term \( n' \) is estimated with Equation 24. Sixty shoot angular classes were considered (five for...
the zenith and 12 for the azimuth). With model ML-2, canopy net photosynthesis is calculated with:

\[
A_c = S' \sum_{i=1}^{n} \nu_i n_i \sum_{\alpha} \nu_{0,\alpha} A_\alpha (\bar{I}_{i,\alpha} + \bar{I}_{b,\alpha}) \tag{26}
\]

This time, direct irradiance interception \((\bar{I}_{b,\alpha})\) is estimated with Equation 18. Otherwise, all other terms are similar to those of Equation 25.

**Simulations with multilayer models**

The consideration of shoot age in a multilayer, conifer photosynthesis model demands a much greater quantity of field data than in a model of deciduous trees. We have found in the literature at least three approaches for dealing with the photosynthetic properties of non-deciduous foliage. The first is to measure photosynthesis in all age classes and to model the effect of age on photosynthetic capacity (Wang and Jarvis 1990, Zhang et al. 1994). The second is to consider only the youngest age classes (McMurtrie et al. 1992, Bonan 1993). The last is to estimate the photosynthetic capacity of the shoot of mean age or even to consider the invariance of average shoot properties through the canopy (Aber et al. 1995, Frolking et al. 1996). The impact of these different approaches in dealing with shoot age were investigated by modifying the ML-2 model.

In both ML-1 and ML-2, all shoot properties are defined as empirical functions of NMA and age. Model ML-2 was thus altered to consider either a fixed shoot age of 1 year but letting NMA vary (ML-2a), a fixed mean shoot age with a variable NMA (ML-2b) or a fixed mean shoot age and NMA (ML-2c). All three options therefore constrained both STAR and photosynthetic properties, from varying with light availability and shoot age (ML-2). Rather, they were made to conform throughout the canopy to the properties of either 1-year-old shoots (ML-2a) or mean-aged shoots (ML-2c). All five models (ML-1, ML2 and their variants a, b and c) were used to estimate hourly canopy photosynthesis from May 15 to October 1, 1997. All environmental variables, except irradiance, were considered to be optimal. The incident shortwave radiation measured above the canopy drove the simulations. The relative importance of diffuse and direct radiation was estimated with the relationship between hourly and daily amounts of diffuse radiation of Liu and Jordan (1960). This fairly accurate algorithm (Collares-Pereira and Rabl 1979, Gates 1980) requires the hour angle of sunset and solar time considered, derived from the Astronomical Almanac (Michalsky 1988), and the daily amount of diffuse radiation, estimated from the measured daily total shortwave radiation and a daily clearness index (Raulier et al. 2000). Similarly, the solar elevation required by Equation 6 was obtained from the Astronomical Almanac.

**Results and discussion**

**Characterization of shoot population**

Mean LAI of the two sites selected for destructive sampling within the stand was 5.76 and mean SAI was 6.55. Shoot area distribution among age cohorts conformed to a regular exponential decay-type model (Kleinschmidt et al. 1980) (Figure 1). The strong departure from this distribution in our data for the 1998 foliage was caused by an above average flowering year. Shoots supporting the clusters of male flowers were short, and their needles smaller than those of the previous year’s shoots. Morris (1951) reports a reduction of up to 45% in needle production during years of heavy flowering in balsam fir stands in northern New Brunswick. Needle shedding in our samples was also quite gradual. Using Equation 24, and field-derived parameter estimates shown in Table 2, the contribution of needle surface to total shoot surface area went from 91% at Age 0 to 70% at Age 10, with an area-weighted mean of 87%. Absolute decrease in needle surface with age was even less, because the increase in twig size by itself tends to cause a decrease in needle surface to total shoot surface. The area-weighted mean shoot age was 3 years.

Results of the stand-level sampling of mean STAR and of NMA are shown in Figures 2a and 2b. The canopy mean STAR was 0.145 (SD = 0.033). Canopy mean NMA was 179 g m\(^{-2}\) (SD = 30). The frequency distributions of both variables are slightly skewed toward the left and cannot be assimilated to normal distributions (for mean STAR: \(\chi^2_{\text{obs}} = 65.8, \chi^2_{0.05,6} = 12.6\) and for NMA: \(\chi^2_{\text{obs}} = 14.9, \chi^2_{0.05,4} = 9.5\)).

Shoot geometry and needle morphology of fir are both influenced by the light environment during development (Clark 1961, Carter and Smith 1985). Measurements on shoots between 1 and 3 years old revealed a relatively good relationship between either NMA, mean STAR or horizontal STAR and mean radiative environment of the shoots (irradiance transmission under conditions of diffuse radiation) (Figures 3a–c). However, no relationship appeared between either mean or horizontal STAR and photosynthetic capacity (expressed on the basis of needle hemisurface area) (Figures 3d–e). We chose NMA as our scaling variable for balsam fir because it is
more closely related than STAR to both light environment and photosynthetic capacity, although its relationship with photosynthetic capacity was weak (Figure 3d). The photosynthetic capacity of shoots less than 4 years old varied from 2.8 to 6.1 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), and this variability was unrelated to the mean radiative environment of the shoots (Figure 4). These results contrast with those obtained on sugar maple (Raulier et al. 1999), in which the photosynthetic capacity varies nearly fourfold (from 3.5 to 12 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)), and is strongly related to leaf mass per unit area and average radiative environment. However, our current observation on the narrow range of shoot photosynthetic capacity in balsam fir agrees well with those of Carter and Smith (1985) and Leverenz (1995). Shoot photosynthetic capacity also dropped with increasing shoot age (Figure 5a). This linear decrease in photosynthetic capacity was slow, going from a mean of 4.3 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in 1-year-old foliage to 2.6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in 7-year-old shoots (Figure 5a). Similar observations have been made on *Abies amabilis* (Dougl.) Forbes (Teskey et al. 1984) and *Picea mariana* (Mill.) BSP (Hom and Oechel 1983). Shoot age was weakly correlated with NMA (Figure 5b) but the much larger shoot sample of the satellite plots (258 versus 41) was needed to obtain a significant relationship. When all other factors were confounded, mean NMA shifts from 173 to 206 g m\(^{-2}\) between 0 and 7 years. This increase in NMA with age was probably caused by secondary growth (Ewers 1982, Gilmore et al. 1995). The increase in NMA with age also coincided with a decrease in light environment, a non-causal relationship that countered the positive relationship between NMA and either radiative environment (Figure 3a) or photosynthetic capacity (Figure 3d) observed in young cohorts.

The measured value of \( \Omega \) (Table 2, Equation 7) depends on the zenithal view angle (Figure 6) in a manner similar to that described by Chen and Black (1991) for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), by Cascetti (1997) for Norway spruce (*Picea abies* Karst.), and by Chen (1996) for boreal conifers for zenithal angles up to 60°. The clumping of the shoots in branches, which are typically horizontal for balsam fir (Gilmore and Seymour 1997), strongly increased the gap fraction at large zenith angles and the clumping of the branches within crowns had the same effect for low zenith angles. At a zenith angle of approximately 34° (phasing parameter \( \phi \), Table 2, Equation 7), \( \Omega \) tended toward unity (which is implicitly assumed in Equation 7) and, for some plots, exceeded one. A likelihood ratio test showed that the amplitude of Equation 7 is not different from unity (\( F_{\text{obs}} = 0.28, F_{0.05;1,20} = 4.35 \)). One note of caution, however, is that our indirect computational method makes the values of \( \Omega \) strongly dependent on the assumption related to crown and shoot geometry, and particularly the assumption of spherical shoot angular distribution.

**Canopy photosynthesis**

Results of hourly and daily simulations over the course of the growing season are shown in Figure 7, as modeled by ML-1 (Equation 23), a model without penumbra, and ML-2 (Equation 24), a model that simulates the effect of an ideal penumbra on the propagation of direct light between shoots. For model ML-2 (the reference model), the absolute maximum value of 23 \( \mu \text{mol (m}^2 \text{ground})^{-1} \text{s}^{-1} \) (83 \( \text{mmol m}^{-2} \text{h}^{-1} \)) for net photosynthesis (27.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for gross photosynthesis) is as expected for a coniferous canopy (Jarvis et al. 1976, Fan et al. 1995, Ruimy et al. 1995, Goulden et al. 1997, Jarvis et al. 1997). Light saturation of the canopy (irradiance required to reach 95% of the canopy photosynthetic capacity) occurs at PAR values of about 750 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (2.7 mol m\(^{-2}\) h\(^{-1}\)). This result agrees with measurements on boreal conifers (Jarvis et al. 1997, Goulden et al. 1997), and contrasts with modeled values of up to 1500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (2.7 mol m\(^{-2}\) h\(^{-1}\)) for sugar maple (Raulier et al. 1999). Although the canopy appears light-saturated in Figure 7, not all the shoots of the canopy are at their photosynthetic capacity because of shading. If all shoots were at their photosynthetic capacity, canopy net photosynthesis would reach 27 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (97 \( \text{mmol m}^{-2} \text{h}^{-1} \)).

The model without penumbra produced estimates of canopy photosynthesis that were within 3.7% of those predicted by simulating an ideal penumbra. This result is in apparent contradiction to results predicted by the theoretical analysis of Stenberg (1998), in which the omission of penumbra at high LAI decreases canopy net photosynthesis by up to 30%. What is apparent from this comparison is that the impact of penumbra on canopy net photosynthesis is greatly reduced when the
The proportion of diffuse radiation increases, because diffuse radiation produces a more uniform radiation field within the canopy. For her simulation, Stenberg (1998) used a clear sky condition with a proportion of diffuse radiation of 13% at the sun’s zenith. In contrast, for the present simulations, we used meteorological data from the Forêt Montmorency, a high precipitation area (1500 mm per year), with a predicted mean diffuse radiation component of 73% of incoming photosynthetically active radiation. Figure 8 shows the relative difference between ML-1 (without penumbra) and ML-2 (with penumbra). The results are expressed as a function of the ratio of diffuse to total radiation obtained using the Forêt Montmorency data. Uner clear skies, when this proportion dips below 0.2, the omission of penumbra reduces canopy net photosynthesis by 20–25%, a value comparable with that of Stenberg (1998). This result is encouraging given the differences in detail between the studies. Stenberg (1998) built her theoretical analysis from the needle level, and included within-shoot processes of needle shading and differences in needle areas receiving direct and diffuse irradiance.

The proportion of diffuse radiation at the Forêt Montmorency is high at 73%. The Jean Brébeuf weather station, near Montreal (annual precipitation of about 1000 mm), shows long-term monthly ratios of diffuse to total radiation of 44% for the months of May to August (Anonymous 1982a, 1982b). Data from the Old Aspen site of BOREAS (Sellers et al. 1997)
north of Prince Albert, Saskatchewan, in 1995 shows a diffuse component of 43% of total incident shortwave radiation. It is to be expected that simulations performed for drier areas with less diffuse radiation will reveal greater bias when omitting penumbra, close to the 15% estimated by Norman and Jarvis (1975).

Shoot age and NMA are used to define the mean STAR, the proportion of needle to total shoot area and the photosynthetic properties ($A_{\text{max}}$, $R_d$ and $I_c$) of shoots through empirical rela-

Figure 5. Observed relationships between age and photosynthetic capacity (a), NMA (b) and the proportion of needle hemisurface area in the shoot hemisurface area (c). Linear regressions are indicative only of the strength of the relationships and were not used in the canopy photosynthesis models.

Figure 6. Variation of the shoot clumping index (Equation 7) with the zenithal view angle.

Figure 7. Predicted canopy net photosynthesis at the scale of hours (a) and days (b) (○: multilayer model ML-1, +: multilayer model ML-2).

Figure 8. Relationship between the hourly proportion of diffuse irradiance and the relative difference between multilayer models ML-1 and ML-2.
Sources of bias

Aside from their compatibility with published measurements of CO₂ uptake rates, a striking feature of the hourly estimates was the strong regularity of the curve. The modeled canopy appears responsive only to the amount of light, and is not strongly sensitive to the hourly variability in the direct/diffuse mix and in the angle of direct beam incidence. This is contrary to expectations. For example, measurements on black spruce (Picea mariana) in Manitoba indicated greater absorption efficiency of diffuse light in conifers (Goulden et al. 1997, their Figure 8). Closer analysis of the model reveals several necessary assumptions and simplifications that could alter the model’s response.

One key simplification of this work is the use of shoots as functional units. This choice was conditioned by the desire to obtain in situ measurements of net photosynthesis and of light response curves, and by acceptance of this unit of organization as the basic foliage element of conifers (Gower and Norman 1991). As a consequence, within-shoot processes, outside those broadly captured by the shoot-level measurements, are not explicitly represented in the model, with unknown consequence to the simulation results. One such process is the change with canopy development in the proportion of needle area subjected to direct and diffuse radiation. In ML-2 and its variants, both components of intercepted radiation are applied to the needle hemisurface within the shoot. This is compatible with the expression of the light response curves obtained in the field. However, these curves were obtained under predominantly direct light conditions, and thus cannot accurately represent the additional shoot response to diffuse light. Because we assume that both light fractions are applied uniformly to the needle hemisurface, we likely overestimate the actual net photosynthesis in a mixed light regime.

A second assumption linked to the use of shoots as functional units is that, under varying illumination angle, shoot photosynthesis is determined only by how much light the shoot intercepts (Equations 14 and 18), following a relationship obtained in the field with the shoots placed perpendicular to the light beam. In reality, however, the needles have preferential angular distributions that may affect the shape of the photosynthetic response curve when the angle of incidence of radiation changes. For Scots pine (Pinus sylvestris L.), Smolander et al. (1987) concluded that the effect of differences in needle angular distribution with respect to solar angle had a minor impact on shoot photosynthesis. In balsam fir, needles have preferential angular distributions, with a strongly horizontal arrangement of needles for shade shoots, and a strongly vertical one for sun shoots (see Figure 1 of Carter and Smith 1985). It is difficult to assess the bias introduced by this assumption, because it will vary with the importance of the diffuse component in the incoming solar radiation. More diffuse radiation will tend to reduce the importance of needle angular distribution.

Another implicit assumption in our models is reflected in the absence of stochastic variability in the radiative environment. By including an ideal penumbra, ML-2 produces a representation of light distribution within the canopy that is likely closer to reality than the simple use of unattenuated direct and diffuse radiation. However, by treating penumbra-attenuated direct light as a constant within each NMA layer, the model fails to represent the gap-and-shade distribution still present in a particular layer. Because of the nonlinearity of the light response curve, using only the average irradiance without accounting for its distribution should result in an overestimation of canopy photosynthesis (Stenberg 1995). Again, however, the large proportion of diffuse radiation should homogenize the within-canopy radiative environment and thus reduce the bias induced by the assumed homogeneity in the radiative environment.

One last assumption is the spherical distribution of shoots...
within the crowns. This assumption has driven the integration of net photosynthesis over the various representations of STAR(φ, γ) in Equations 3 and 13, as well as the computation of Ω. But this assumption is only partially valid because shoot angular distribution within a canopy with respect to the solar beam is constrained within limits smaller than 0, π/2. Use of an elliptical shoot angle distribution is realistic (Cescatti 1997), and the values of the two axes should be a function of shading SAI or NMA to account for the variability observed in the field. If we assume that the natural orientation of shoots within the canopy optimizes light capture and net photosynthesis at the needle level, then it is likely that the spherical assumption causes a decrease in modeled direct radiation penetration in the canopy and a resulting underestimation of canopy net photosynthesis.

Conclusion

The objective of the present study was to determine the bias incurred in the estimation of canopy net photosynthesis when age effects on physiological and morphological variables are omitted, and when shoot geometry is considered uniform throughout the canopy. Results for balsam fir showed that the use of mean shoot properties induces a bias of less than 3%. The weakness of the bias can be explained by the weak relationships between shoot photosynthetic properties and shoot age or mean radiative environment. Sampling methods, however, should be designed to allow the estimation of the mean canopy shoot properties. For example, the use of an age of 1 year for all shoots overestimates canopy net photosynthesis by 9%. The results highlight the importance of diffuse radiation within the canopy both because of the great efficacy with which it is absorbed by the shoots, and because its presence tends to reduce differences linked to the geometry of shoot (or needle)–light interactions.

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References


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Appendix: Irradiance interception

The following shows that for both ML-1 and ML-2, incoming photosynthetically active radiant energy is conserved within the system, (i.e., it is either absorbed or transmitted through the canopy). Scattering of PAR has not been considered.

Direct (beam) irradiance

When scattering is ignored, the direct irradiance intercepted by the canopy can be expressed as:

\[ I_{b0} - I_b = (1 - T_b) I_{b0}, \]  
(A1)

where \( T_b \) is the canopy transmisssion of direct irradiance (see Equation 5). The first derivative of Equation A1 with respect to SAI gives the amount of irradiance intercepted by a shoot layer \( dS' \):

\[ -\frac{dI_b}{dS'} = I_{b0} \exp(-k_b S') \frac{d(k_b S')}{dS'} \]
\( = I_{b0} \exp(-k_b S') \left[ 2\Omega / \cos \theta_b \frac{d(\bar{x}' S')} {dS'} \right] \]  
(A2)

Then (by definition):

\[ \bar{x}' S' = \int_0^{\bar{x}'} dS' \]  
(A3)

thus:

\[ 2\Omega / \cos \theta_b \frac{d(\bar{x}' S')} {dS'} = 2\bar{x}' \Omega / \cos \theta_b. \]  
(A4)

Note that \( \bar{x}' \) is evaluated under a shading SAI of \( S' \) and is thus a property of the layer \( dS' \) for which Equation A2 is calculated. When Equation A4 is introduced into Equation A2 and the definition of mean STAR is expanded (Equation 3), Equation A2 becomes:

\[ -\frac{dI_b}{dS'} = \int_0^{\pi/2} \int_0^{\pi/2} 2\bar{x}' \Omega \exp(-k_b S') I_{b0} \sin \theta_b d\theta_b d\alpha_b. \]  
(A5)

Equation A5 can be evaluated numerically by either Equation 11 or 17, depending on the multilayer model (ML-1 or ML-2).

Diffuse irradiance

By following the same procedure developed for direct irradiance, the first derivative of diffuse irradiance (Equation 6) with respect to SAI is equal to:

\[ -\frac{dI_d}{dS'} = \int_0^{\pi/2} \int_0^{\pi/2} 2\bar{x}' \Omega \exp(-k_b S') I_{b0} \frac{\sin \theta_b d\theta_b d\alpha_b}{\pi}. \]  
(A6)

By expanding the definition of mean STAR (Equation 3) in Equation A6 and by rearranging the terms, we have:

\[ -\frac{dI_d}{dS'} = \int_0^{\pi/2} \int_0^{\pi/2} \int_0^{\pi/2} 2\bar{x}' \Omega \exp(-k_b S') I_{b0} \frac{\sin \theta_b d\theta_b d\alpha_b}{\pi} \]
\( \times \sin \theta_b d\theta_b d\alpha_b. \]  
(A7)

As for Equation A5, Equation A7 can be numerically solved with Equation 20.