Introduction

Photosynthesis is the process that supplies the basic material for plant growth and ecosystem carbon cycling. Its spatial and temporal variations are determined primarily by the rate and total amount of absorbed photosynthetic photon flux density ($Q$; hereafter light and $Q$ are used interchangeably; see Table 1 for a summary of abbreviations). The interception of $Q$ is determined by canopy and crown architecture, including the spatial distribution of crowns in stands, the clumping of leaves in shoots, the dimensions of leaves, shoots and crowns, and the angle distribution of leaves (Ross 1981). In turn, the prevailing $Q$ at each location in the canopy affects leaf clumping and angles (Sprugel et al. 1996) as well as leaf photosynthetic characteristics, including mesophyll properties and leaf biochemistry (Sprugel 1989, Niinemets and Kull 1995, Terashima and Hikosaka 1995, Niinemets 1997, Stenberg et al. 2001) and leaf photosynthetic capacity (Oren 1996).
Table 1. Parameters and their definition in the model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_B$</td>
<td>Branch surface area</td>
<td>$m^2$ $m^{-2}$</td>
</tr>
<tr>
<td>$A_S$</td>
<td>Stem surface area</td>
<td>$m^2$ $m^{-2}$</td>
</tr>
<tr>
<td>$G(z,x,\theta)$</td>
<td>G-function</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$K(\theta)$</td>
<td>Extinction coefficient of total light in the canopy</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$K_b(z)$</td>
<td>Direct beam extinction coefficient</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$K_{b,branch}(z)$</td>
<td>Branch extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$K_{b,leaf}(z)$</td>
<td>Leaf extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$K_{b,stem}(z)$</td>
<td>Stem extinction coefficient in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$K_{b,total}(z)$</td>
<td>Average extinction coefficient to the zth layer weighted with leaf area in each layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$L$</td>
<td>Leaf area index</td>
<td>$m^2$ $m^{-2}$</td>
</tr>
<tr>
<td>$L(z)$</td>
<td>Cumulative leaf area density to the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$N$</td>
<td>Stand density</td>
<td>Trees $m^{-2}$</td>
</tr>
<tr>
<td>$Q$</td>
<td>Photosynthetic photon flux density</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{0}$</td>
<td>Photosynthetic photon flux density above the canopy</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{avg}$</td>
<td>Canopy average photosynthetic photon flux density</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_b$</td>
<td>Direct photosynthetic photon flux density</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{b}(z)$</td>
<td>direct photosynthetic photon flux density at the bottom of the zth layer</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{d}$</td>
<td>Diffuse photosynthetic photon flux density</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{d}(z)$</td>
<td>diffuse photosynthetic photon flux density at the bottom of the zth layer</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{ob}$</td>
<td>Direct photosynthetic photon flux density at the top of the canopy</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_{od}$</td>
<td>Diffuse photosynthetic photon flux density at the top of the canopy</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_s$</td>
<td>Scattered photosynthetic photon flux density</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$Q_r(z)$</td>
<td>Scattered photosynthetic photon flux density at the bottom of the zth layer</td>
<td>$\mu mol$ $m^{-2}$ $s^{-1}$</td>
</tr>
<tr>
<td>$S(z,\theta)$</td>
<td>Projected area of tree crown in zth layer at the zenith angle $\theta$</td>
<td>$m^2$</td>
</tr>
<tr>
<td>$a(\theta,z)$</td>
<td>The mean gap fraction of the zth layer in a single tree crown at the view angle $\theta$</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$x(z)$</td>
<td>Ratio of average projected areas of canopy leaves on horizontal and vertical surfaces in the zth layer</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$z$</td>
<td>Height from the ground</td>
<td>m</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Light absorptivity</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\tau_b$</td>
<td>Sunlit proportion</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\tau_{b}(z,\theta)$</td>
<td>Sunlit proportion in the zth layer at the zenith angle $\theta$</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\tau_{ob}(z,\theta)$</td>
<td>Total photosynthetic photon flux densities transmission coefficient in the zth layer at the zenith angle $\theta$</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\tau_{od}(z,\theta)$</td>
<td>Diffuse photosynthetic photon flux density transmission coefficient in the zth layer at the zenith angle $\theta$</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\Pi$</td>
<td>Shoot clumping factor</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\Theta$</td>
<td>Zenith angle of the sun</td>
<td>Radian</td>
</tr>
</tbody>
</table>

et al. 1986a, Palmroth and Hari 2001). Through the effect on photosynthesis, the distribution of $Q$ influences stand dynamics vis-à-vis regeneration, growth and mortality.

High spatiotemporal variation in $Q$ in the canopy renders direct measurement impractical (Palmroth et al. 1999), particularly when stand-level information is needed over many years of stand development. This has led to a proliferation of models from simple one-layer turbid-medium models designed to estimate the total amount of absorbed $Q$ (QAI; e.g., Monsi and Saeki 2005) to highly detailed, three-dimensional (3-D) models that account for both vertical and horizontal heterogeneities in canopies and are often designed to estimate $Q$ distribution on leaf surfaces down the canopy (e.g., Norman and Wells 1983, Wang and Jarvis 1990, Canham et al. 1994, Cescatti 1997, Chen and Reynolds 1997, Brunner 1998, Mariscal et al. 2000, Martens et al. 2000, Stadt and Lieffers 2000, Sinoquet et al. 2001).

Simpler models are commonly employed as a component of more comprehensive models of stand growth or ecosystem (or larger scale) carbon dynamics (e.g., Running and Coughlan 1988, Mäkelä 1997). As 3-D models require much more detailed information to represent the canopy (Kubo et al. 2008), they are more commonly used to address specific scientific needs, e.g., testing hypotheses or validating simpler models (Sinoquet and Rivet 1997, Drouet 2003, Mariscal et al. 2004, Roupasard et al. 2008). Between the simple and complex extremes, a wide range of models simplify the non-random foliage area distribution and non-homogeneous stand structure of real forest stands, translating spatially explicit description of the canopy to more generic statistical distributions of properties of canopy layers or individual trees (e.g., Norman and Jarvis 1975, Oker-Blom and Kellomaki 1982, Wang and Baldocchi 1989, Stenberg 1998, Schäfer et al. 2003, Song and Band 2004, Duursma and Mäkelä 2007, Kim et al. 2008). Such multilayer models may describe the canopy with an idealized leaf angle distribution, typically spherical (Campbell 1986), average shoot clumping, typically used in confiners (Therezie et al. 2007) and tree clumping (Nilson 1999). Simplified canopy representation makes estimates of $Q_A$ or $Q$ distribution more practical.

The wide range of models presents opportunities for matching their complexities to specific needs. Indeed, even some models of intermediate complexity often require site-, species- and canopy depth-specific parameterizations. Knowing which stand conditions allow simplifying without compromising the accuracy of $Q$ estimates would potentially decrease the need for information that is difficult to obtain. Although the interception or distribution of light has been assessed in a number of studies (e.g., Stadt and Lieffers 2000, Bernier et al. 2001, Beaudet et al. 2002, Song and Band 2004, Duursma and Mäkelä 2007, Roupasard et al. 2008), the effect of simplifying each structural attribute is rarely investigated over the natural range of each of the other attributes. The purpose of this study was to quantify the effect of simplifying important structural properties of canopy...
...elements (leaf angle distribution, and clumping at the shoot and tree level) on both the total $Q_A$ and its vertical distribution based on a multilayer (1-D) framework, the approach most commonly used in models of canopy photosynthesis.

The canopy $Q$ interception and attenuation with depth in a horizontally homogeneous canopy is commonly modeled based on the Beer–Lambert law, used for estimating total $Q_A$, although it is designed for estimating absorption of direct beam $Q$. Thus, a simple representation of Beer–Lambert for estimating horizontally averaged $Q$ at levels through the canopy is commonly expressed as

$$Q = Q_0(-e^{-K(\theta)i}),$$

(1)

where $Q_0$ is the incident $Q$ above the canopy, $K(\theta)$ is the mean leaf horizontal projection per unit leaf area, i.e., the canopy extinction coefficient of $Q$, and $L$ is the leaf area index. $K(\theta)$ depends on the solar zenith angle $\theta$ and the distribution of leaf inclination angles (Campbell 1986). This Beer–Lambert formulation assumes a random distribution of leaves in the canopy volume. Such canopy representation intercepts $Q$ more efficiently than real canopies, where leaves are sometimes clumped at the shoot scale and always at the tree scale. Therefore, the interception of light in real canopies is often less efficient.

Changing the specification of leaf angle distribution has been shown, in some studies, to carry little influence on the vertical trend of $Q_A$ (Goudriaan 1988, Oker-Blom and Kellomaki 1982, Chen et al. 1997). Thus, another widely used simplification in models is to assume a spherical leaf angle distribution in the canopy volume (Campbell and Norman 1998), often combined with a further simplification of Equation (1), assuming a constant ‘effective’ extinction coefficient (Landsberg and Waring 1997, Duursma and Mäkelä 2007). An unintended joint outcome of these simplifications (i.e., assuming random distribution, spherical orientation of leaf elements and constant effective extinction coefficient $K$ typically set equal to 0.5; e.g., BIOME-BGC, tRayci) is that in some situations it compensates for neglecting leaf and tree clumping, resulting in light penetrating deeper into the canopy (Kim et al. 2008). Nevertheless, in some cases, the assumption of spherical leaf angle distribution caused an underestimation of vertically transmitted light (Stadt and Lieffers 2000). Leaf angle distribution in crowns of many tree species was found not to be spherical (i.e., the average distribution $x \neq 1.0$, $x$ is the average ratio of projected areas of canopy elements on horizontal and vertical surfaces for ellipsoidal leaf angle distribution), some having more vertically oriented leaves ($x < 1.0$) and others more horizontally oriented leaves ($x > 1.0$) (Thomas and Winner 2000, Barclay 2001, Wirth et al. 2001). It is possible that assuming spherical leaf angle distribution caused variable impact in studies of total $Q_A$ and vertical $Q$ distribution depending on the actual $x$ in the canopy, naturally with the effect higher where actual $x$ departs greatly from spherical distribution. In this study, we aim to determine the canopy conditions under which each architectural variable affects $Q_A$, thereby informing on conditions for which a simple representation suffices and conditions requiring more complex canopy structure and optical representation.

Although some canopy $Q$ absorption models account for the effects of shoot- or tree-level clumping, most tend to ignore the vertical variation in shoot characteristics, i.e., the changes in the interception efficiency of shoots along the $Q$ gradient (Sprugel et al. 1996, Stenberg et al. 1999, Palmroth et al. 2002). By assuming a constant value for each characteristic, these models avoid the added complexity and data required for vertically specified architectural properties (e.g., Bernier et al. 2001, Alton and North 2007). This simplification may have relatively small effect on total $Q_A$ over longer integration periods, but can affect the distribution of intercepted $Q$ among canopy layers. In addition, canopy photosynthesis is highly sensitive not only to $Q_A$, but also to $Q$ distribution within canopies. Thus, we also investigated the effect on $Q_A$ of representing the canopy with variable versus constant $x$ and shoot clumping, accounting for tree-level clumping in each layer by incorporating changes in stand density and crown shape in the 1-D framework (Nilson and Kuusk 2004, Song 2007, Kim et al. 2008).

Materials and methods

Model description

The light model we present estimates light absorption and vertical distribution combining essential elements of three models: (i) Campbell and Norman (1998), (ii) Nilson (1999) and (iii) Stenberg (1998). In our configuration, the model can handle tree clumping (i.e., the effect of having foliage clumped in crowns) in a 1-D structure, estimating canopy openness and light in each canopy layer, which can be composed of crowns of a variety of shapes (e.g., representing different species).

To calculate $Q$ absorption by different layers in the canopy, above-canopy incident $Q$ ($Q_0$) was partitioned into direct ($Q_{a,d}$) and diffuse ($Q_{a,d}$) components (Spitters et al. 1986), using measured and modeled clear day radiation (Campbell and Norman 1998). Scattered light ($Q_s$) was assumed to be zero above the canopy. The interception of direct beam ($Q_d$), diffuse ($Q_d$) and scattered ($Q_s$) radiation was estimated separately in sequential 1-m deep layers downward through the canopy. Our 1-D approach to calculating $Q$ at the bottom of a layer was based on the value at the top of the canopy and average properties from the top of the canopy to the bottom of the layer. This was done to force crowns to be continuous across layers in the estimation of tree clumping, thus integrating the effect of all higher layers when the effect of tree clumping on $Q_s$ (and thus $Q_d$) is modeled, and because this is the only approach to estimating $Q_s$ due to the non-linearity in the governing relationships.
In every layer, $Q_b$ on the sunlit horizontal surface is the same as at the top of the canopy:

$$Q_b(z) = Q_{ab}$$  \hspace{1cm} (2)

Clumping of canopy elements can be incorporated into radiation transfer models using an average quantity that integrates shoot- and tree-level clumping (Niinemets et al. 2004). However, as stand density increases, so does the gradient of light and within-canopy shading, causing more variation in shoot characteristics; for example, shoot clumping decreases with increasing shade, facilitating a greater light absorption per unit leaf area deeper in the canopy (Therezien et al. 2007). Thus, using an average clumping representation neither permits evaluation of the effect of each factor independently nor allows delineation of the stand density at which accounting for shoot-level density is required. Thus, we calculated the proportion of sunlit area on horizontal surface at each sun angle, i.e., the transmission of a direct beam of $Q(t_s(z, \theta))$, based on the tree-level clumping calculation accounting for cumulative crown shape down to the layer and stand density ($N$) assuming trees are Poisson distributed in the stand, as is the case in many mixed-species and uneven-aged stands. According to Nilson (1999)

$$\tau_b(z, \theta) = e^{-\sum_{j=1}^{m} (-a_j(z, \theta)(1-a_j(z, \theta)))}$$  \hspace{1cm} (3)

where

$$a_j(z, \theta) = e^{-\sum_{i=0}^{j-1} K_{j,b}(z) S_j(z, \theta) \Pi(z) K_{j,stem}(z) + K_{j,leaf}(z) a_j(z, \theta) / \Pi(z) A_j(z) N_j S_j(z, \theta)}$$  \hspace{1cm} (4)

and $N_j$ is the stand density of the $j$th species, $S_j(z, \theta)$ is the projected area of crown for the $j$th species and $a_j(z, \theta)$ is the mean gap fraction in a single tree crown at the zenith angle $\theta$ (Nilson 1999). The parameters with $z$ indicate the cumulative (for crown-shape-related parameters) or leaf area weighted average (for other parameters) quantity down to the layer. The extinction coefficients of direct beam ($K_b(z)$) of stem and branch area of all species and leaf area of broadleaved species was calculated according to Campbell and Norman (1998) for ellipsoidal distribution as

$$K_b(z, \theta) = \frac{\sqrt{x(z) + tan^2 \theta}}{x(z) + 1.774(x(z) + 1.182)^{-0.733}}$$  \hspace{1cm} (5a)

The extinction coefficient of a conifer leaf (needle) was calculated as

$$K_{b,leaf}(z, \theta) = \frac{G(z, x(z), \theta)}{cos(\theta)}$$  \hspace{1cm} (5b)

The G-function, or the projection of unit foliage hemi-surface (or half total surface) area on the plane perpendicular to the view direction $\theta$, was calculated according to Stenberg (2006).

In equations (5a) and (b), $x(z)$ is the average ratio of canopy elements on horizontal and vertical surfaces (Campbell 1986). Stenberg (2006) used needle inclination angle and sun angle to calculate the G-function, and needle inclination angle is trigonometrically convertible to $x(z)$. We assume that the branch angle distribution is the same as the leaf angle, and $x(z)$ of both reflects the observation that needles and branches tend to orient more vertically at the top of the canopy and more horizontally at the bottom. Because stems are nearly vertical in orientation, $x(z)$ was set to 0.01 for $K_{b, stem}$.

$L_j(z, A_{b,j}(z)$ and $A_{s,j}(z)$ are defined as leaf, branch and stem hemi-surface area down to depth $z$ (in m, hereafter referred to as the $z$th layer) for $j$th species, respectively. Shoot clumping ($\Pi(z)$) is defined as the average ratio of shoot silhouette area to the projection area of all leaves with their natural orientation, but spread out, so they do not shade each other (Stenberg 1998).

Scattered radiation ($Q_s$) was also derived from layer-specific information according to Campbell and Norman (1998)

$$Q_s(z) = (\tau_d(z, \theta) - \tau_t(z, \theta))Q_t(z)$$  \hspace{1cm} (6)

The attenuation of diffuse radiation ($Q_d$) was calculated as

$$Q_d(z) = \tau_d(z)Q_d$$  \hspace{1cm} (7)

The transmission of diffuse $Q (\tau_t(z))$ and the sum of total transmitted $Q$ (direct, diffuse and down-scattered radiation; $\tau_r(z, \theta)$) were calculated according to Campbell and Norman (1998) as

$$\tau_d(z) = 2 \int_0^{\pi/2} \tau_t(z, \theta) sin \theta \cos \theta d\theta$$  \hspace{1cm} (8)

and

$$\tau_{\omega}(z, \theta)e^{-\sum_{j=1}^{m} (-a_j(z, \theta) N_j S_j(z, \theta))}$$  \hspace{1cm} (9)

where $\alpha$ is the canopy absorptivity, the ratio of absorbed-to-intercepted radiation of the whole canopy is set at 0.83 (Lai et al. 2000) after finding that using different values for the absorptance of leaves (0.80; Long et al., 1994) and bark (0.9; Henrion and Tributsch 2009) did not have a noticeable effect on the transmission coefficient ($\tau$).

The average of total $Q$ on a horizontal surface ($Q_{avg}(z)$) was calculated by summing direct, diffuse and scattered radiation according to Campbell and Norman (1998):

$$Q_{avg}(z) = \tau_t(z)(Q_t(z) + Q_s(z) + Q_d(z))$$  \hspace{1cm} (10)

$$+ (1 - \tau_t(z))(Q_d(z) + Q_s(z))$$

Tree Physiology Online at http://www.treephys.oxfordjournals.org
Q_{0}, of the layer was calculated by subtracting Q_{avg}(z) from Q_{avg}(z - 1), and canopy total Q_{0} (Q_{0,t}) was calculated by subtracting Q_{avg}(z) at the bottom of canopy from Q_{0}.

**Model evaluation**

The distribution of Q measured both within and below the canopy is highly variable and contains errors associated with difficulties of maintaining the sensors perfectly horizontal. Thus, Q measurements may not constitute a very good benchmark for model testing. Canopy openness, the fraction of open sky above the layer, integrates over a large portion of the canopy for model testing. Canopy openness profiles and the same data averaging treatments of (Q_{dn}, LAI-2000 User Manual). The quantum sensor provided one spot measurement, whereas the canopy tetrax provided the average measurement of 80 quantum sensors located on an 80-cm-long bar. Three different types of measurement were done in March 2004 and October 2005, corresponding to values of L (here expressed as projected leaf area) ranging from 1.5 to 6 m² m⁻². Although all model calculations used hemi-surface L for the pine, we present projected L for ease of comparison with most published literature. For conifers, hemi-surface L is 1.57 times greater than the projected L according to Cauchy’s theorem (Lang 1991). In March 2004, ≥40 Q measurements were performed in each plot below the canopy at the six FACE plots (Plot 1 was measured twice); the measurements in each plot were averaged, producing n = 7 (with Plot 1 contributing two values). In October 2005, below-canopy measurements were made over 2 days at Plot 4, a plot with leaf area index close to the average of all the plots at the site. Measurements were made at 5-min intervals and averaged every 30 min to synchronize with the measurements of Q_{dn}, providing 41 daytime measurements. In addition, eight measurement profiles from the central towers of Plots 1 and 2 having the lowest and highest proportion of broadleaved species leaf area index were made in October. Eight profiles were obtained from mid-morning to late afternoon at an ~45-min cycle, each profile following an identical protocol to that for obtaining canopy openness profiles and the same data averaging treatments (Table 1).

For model validation, we evaluated seven models with different complexities (v1–v7, Table 2). Model v1 was a simple Beer–Lambert model using L estimates for hardwood and conifers corresponding to our simulation dates from McCarthy et al. (2007) and unpublished data (e.g., Figure 1a). We assumed no shoot clumping (l = 1) and a spherical leaf angle distribution (x_{1,0}) for both conifer and hardwood species. We calculated the vertical leaf area distribution of the stand by summing the vertical leaf area for individual trees assuming a normal distribution.

Figure 1. A sample of the vertical distribution of the surface areas of (a) leaves, (b) branches and (c) stems used in all models, with broad-leaved species represented by dashed lines. In (a), a continuous thin line represents the foliage profile in the non-growing season. Vertical distributions of (d), shoot clumping (lI) and (e) the parameter describing leaf angle distribution (x_{1}) used in the most detailed model (v7, see text), and the extremes of crown dimensions and shape used in all models except v1 and v2, which did not include tree clumping. (f) Crown shape, length and width from stand density equals 100 and 3000 trees per hectare.
of leaf area within the live crown (Vose et al. 1994). This vertical leaf area distribution was similar to the shape observed in our stand based on LAI-2000 measurements made over several years (McCarthy et al. 2007).

We added a constant value for shoot clumping in model v2, with \( \Pi = 0.65 \), representing the average for pine of our stand, close to the 0.6 of pine species (Therezien et al. 2007) and 0.95 for broadleaved species according to Kim et al. (2008) (Figure 1d).

In model v3, we replaced shoot clumping with tree-level clumping. We computed tree-level clumping with stem number density, height, diameter at breast height (DBH), crown length and branch biomass of individual trees in six FACE plots from McCarthy et al. (2007) and unpublished data. We obtained stem surface area \( (A_{s}(z)) \) from the height of individual trees by using a segmented polynomial taper equation (Sharma and Burkhart 2003). We calculated branch surface area \( (A_{b}(z)) \) from a combination of observation, measurements and assumptions regarding the number and dimensions of branches (for dimensional approach; see Appendix). We converted branch surface area to total branch volume and finally to biomass and we checked against a more direct and accurate estimate of total branch biomass for individual trees (McCarthy et al. 2007). The dimensional approach for estimating \( A_{b}(z) \) produced estimates of biomass larger than the direct approach, mostly due to branch loss at the bottom of the canopy. Therefore, we adjusted \( A_{b}(z) \) down as described in Appendix. When \( L \) was maximum, \( A_{s} \) and \( A_{b} \) summed to \( \sim 30\% \) of \( L \); the contribution of these components to the surface area of the canopy increased as it sheds leaves during the winter and early spring, becoming nearly equal to \( L \) when it reaches its minimum (Figure 1a–c).

In model v4, we added to v3 the same constant shoot clumping as in v2. In model v5, we used vertically variable pine shoot clumping \( (\Pi(z)) \) with spherical, constant \( x \) \( (x_{s,0}) \). The vertically variable \( \Pi(z) \) values were calculated based on four shoots harvested at the top of the canopy and four at the bottom as described in Therezien et al. (2007). In model v6, we added vertically variable \( x \). We estimated \( x \) of the pine, \( x(z) \), from pictures taken perpendicular to the shoot axis. We took five pictures at each of the top, middle and bottom layers of the canopy. We obtained the \( x \) by measuring the elevation angle of at least 40 needles oriented along the shoot axis in each picture and perpendicular to the direction the picture was taken. For the hardwood species, we assumed \( x(z) \) was similar to an oak canopy from Kull et al. (1999) and Wirth et al. (2001), i.e., changing from 1 (spherical distribution) at the top of the canopy to 2.5 at the bottom (Figure 1e). And lastly, in model v7, the most complete model, we vertically varied both \( \Pi(z) \) and \( x \).

Sensitivity analysis

For the sensitivity analysis, we calculated total \( Q_{a} \) \( (Q_{a}; \ 1 \ m \ depth) \) on the summer solstice, having the greatest zenith angle and thus making the assumptions of model v2, the most commonly used formulation in large-scale models, closest to the real conditions. Based on the seasonal dynamics of diameter increment, the growing season in the study area lasts from the beginning of April to the end of September. During the growing season, the maximum sun elevation angle ranged from 51.6° to the summer solstice angle of 77.5°. More than 50% of growing season days had maximum sun angles >70°, making the summer solstice day also reasonably similar to a large proportion of the growing season. We calculated the diurnal patterns of incoming \( Q \) during summer solstice clear day and cloudy day using the same sun angles, according to Campbell and Norman (1998; see Figure 2). We assumed the atmospheric transmittance to be 0.75 for the clear day (Campbell and Norman 1998) and 0 for the cloudy day. The maximum irradiance of \( Q \) on the clear day reached \( \sim 2100 \) versus \( \sim 790 \mu \text{mol m}^{-2} \text{s}^{-1} \) on cloudy days. On a clear day, direct light comprised the majority of total \( Q \), whereas on a cloudy day, there was no direct light (Figure 2).

To increase the generality of our findings, we used wide ranges of values for shoot clumping, \( x \), \( L \) and stand density. Shoot-level clumping ranges from 0.2 at the canopy top to 0.9 at the bottom for short-needle species versus 0.4–0.9 for long-needle species (Palmroth et al. 2002, Therezien et al. 2007). In our sensitivity analysis, we assumed \( A_{b}(z) \) and \( A_{s}(z) \) to be zero; the effect of this simplification is that changing canopy specification in our sensitivity analysis produced larger effects on \( Q_{a} \).
Figure 2. Diurnal pattern of incoming photosynthetically active radiation during the summer solstice assuming either a cloudy day with only diffuse component or a clear day with both diffuse and direct components (thick lines). These patterns were used as input to all model versions.

Table 3. Regression outputs from different model versions.

<table>
<thead>
<tr>
<th>Versions</th>
<th>Diffuse Non-interceptance (Q_{dn})</th>
<th>Photosynthetic photon flux density (Q)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>CI</td>
</tr>
<tr>
<td>1</td>
<td>1.02</td>
<td>0.07</td>
</tr>
<tr>
<td>2</td>
<td>1.03</td>
<td>0.07</td>
</tr>
<tr>
<td>3</td>
<td>1.02</td>
<td>0.07</td>
</tr>
<tr>
<td>4</td>
<td>0.98</td>
<td>0.04</td>
</tr>
<tr>
<td>5</td>
<td>0.98</td>
<td>0.04</td>
</tr>
<tr>
<td>6</td>
<td>0.98</td>
<td>0.04</td>
</tr>
<tr>
<td>7</td>
<td>0.98</td>
<td>0.04</td>
</tr>
</tbody>
</table>

CI represents 95% confidence interval and RMSE represents the root mean square error.

Results

Model validation

All models that account for both shoot and tree clumping did similarly well—estimating light and openness down the canopy of this pine-dominated, mixed-species stand (Table 3). For example, the simulations of canopy Q_{dn} and Q on horizontal surface of the most complete model (v7) agreed well with measurements (Figure 3a and b), such that the slope of the modeled versus measured Q_{dn} (0.98, 1 SD of the parameter = 0.014) and Q (0.97, 0.021) were not different from unity, and the intercepts (0.016, 0.063, and 0.172, 0.404, respectively, the latter in μmol m⁻² s⁻¹) were not different from zero.

Sensitivity analysis

Although not statistically significant, the negative intercept observed between the modeled Q and measured values (Figure 3b) cautions of large uncertainties relative to the signal at very small values of these variables. This suggests that ratios generated by dividing outputs of various model configurations and Q distribution than if these surfaces were included because increasing the intercepting surface in the analysis has a similar effect of having higher L. Higher L tends to reduce the effect of other canopy specifications, especially in low L stands, and it is rather simple to assess the effect of such additional surfaces by moving to higher L values of the results.

We also investigated the effects of variations in x, stand density (N) and L. We evaluated the effect of constant x by assuming a spherical distribution (x = 1.0), closer to vertical (x = 0.5) or closer to horizontal (x = 3.0) distributions. We found that the additional accuracy from vertically varying I(z) and x(z) was relatively small (see Results) and thus simplified the presentation of the results of the sensitivity analysis showing estimates based on constant I(z) and x(z) throughout the canopy depth.

Given the size of the trees, set to a height of 21 m in all simulations, we evaluated the effect of stand density from a value of 100–3000 trees ha⁻¹. In addition to stand density, crown length and width influence the tree clumping factor—these properties are not independent—crown dimensions decrease with increasing density. We utilized data on open-grown P. taeda trees (Schultz 1997) to set the crown length and width of our most open stand simulation (N = 100 trees ha⁻¹). To account for the effects of stand density, we adjusted crown length based on our data, and crown radius based on an assumption that the maximum crown overlap equals 1.4 of crown radius, reflecting stand density in the following manner: length (m) = –2.08 log N + 24.12; radius (m) = –0.63 log N + 7.94, with N in trees ha⁻¹. For each stand density value, the effect of L on Q_{A} was evaluated with values ranging from 2 to 10, commonly found in stands of shade-tolerant species (Oren et al. 1986b). The vertical distribution of leaf area was assumed to follow a Weibull distribution (e.g., Mori and Hagihara 1991, Utsugi et al. 2006) with 1.5 and 3 as scale and shape parameters, respectively, generating near-normal distributions.
by the base configuration would produce volatile ratios at low light regimes, making it difficult to evaluate the effects of different simplifications on $Q_A$. Thus we limited our sensitivity analysis to conditions in which $Q$ on a horizontal surface at the bottom of any layer is estimated to be >40 $\mu$mol m$^{-2}$ s$^{-1}$. While making comparisons clearer, eliminating these ratios did not allow comparisons of the effect of all simplifications at every canopy level. We also note that we show effects of the canopy characteristics on $Q_A$ only if these were >1% of $Q$, estimated with the base scenario, and we are reminded that the effects of canopy characteristics on $Q_A$ are the likely maximum effects because we do not account for the surface area of branches and stems.

**Total absorbed $Q$**

Shoot clumping affected $Q_{AT}$ slightly less on cloudy days than on clear days, while the effect of tree clumping was slightly larger on cloudy days, but for both canopy attributes the differences between days were very small. The effect of leaf angle distribution, like that of shoot clumping, was also greater on clear days (Figure 4).

**Effect of shoot clumping**

Accounting for shoot clumping affected $Q_{AT}$ more than accounting for any of the other investigated canopy properties. As expected, $Q_{AT}$ decreased with increasing clumping especially at low $L$ (Figure 4a). Estimated $Q_{AT}$ of an open canopy ($L = 2$) of species of slightly clumped foliage ($II = 0.9$) was only 4% lower (86 versus 83 mol m$^{-2}$ day$^{-1}$) than would be estimated for a similar canopy with non-clumped shoots, but the estimate based on highly clumped shoots ($II = 0.2$), such as those found at unshaded crown tops of coniferous trees (Therezien et al. 2007 and references therein), was ~40% lower than $Q_{AT}$ in a canopy with non-clumped shoots (35 versus 86 mol m$^{-2}$ day$^{-1}$). This means that not accounting for shoot clumping in such stands would greatly overestimate $Q_{AT}$. In dense canopies ($L = 10$), the effect of these highly clumped shoots on $Q_{AT}$ was smaller, allowing only 25% of $Q$ to go unabsoed; still not accounting for shoot clumping would overestimate $Q_{AT}$ by 35% (116 versus 86 mol m$^{-2}$ day$^{-1}$). Even in more typical, less dense canopies (e.g., $L = 6$), and with a typical value of $II = 0.6$ (Therezien et al. 2007), models with non-clumped shoots would overestimate $Q_{AT}$ by >10% (113 versus 91 mol m$^{-2}$ day$^{-1}$). Thus, not accounting for shoot clumping would result in an overestimation of total $Q_A$ and canopy photosynthesis, potentially by substantial amounts, with errors increasing with decreasing canopy density.

**Effect of tree clumping (stand density and projected crown area)**

Stand density and associated crown dimensions (i.e., tree clumping) affected estimates of $Q_{AT}$ only at moderate-to-low densities (Figure 4c and d). Relative to scenarios without tree clumping, $Q_{AT}$ was 35–40% lower (49 versus 73 mol m$^{-2}$ day$^{-1}$ on clear days and 20 versus 33 mol m$^{-2}$ day$^{-1}$ on cloudy days) at the lowest density (100 tree ha$^{-1}$). Thus, not accounting for...
Unlike shoot and tree clumping, the relative effect of tree clumping in very open stands would result in ~70% overestimated $Q_{AT}$. With increasing stand density, the effect on estimated $Q_{AT}$ quickly diminished such that at 500 trees ha$^{-1}$ the model estimated $Q_{AT}$ only up to 18% lower (33 versus 40 mol m$^{-2}$ day$^{-1}$ on cloudy days) than $Q_{AT}$ without accounting for tree clumping (yielding 21% overestimation of $Q_{AT}$).

**Effect of leaf angle distribution**

Unlike shoot and tree clumping, the relative effect of $x$ on estimates of $Q_{AT}$ greatly differed between clear and cloudy days, but the absolute differences were much smaller. The effect of $x$ on diffuse radiation was so small (Figure 4e–h) that we will not discuss it further. On clear days, in low $L$ canopies and $\Pi = 0.6$, more vertically oriented leaves ($x_{0.5}: x = 0.5$) decreased the estimates of $Q_{AT}$ by up to 7% compared with spherical distribution ($x_{1.0}: x = 1.0$) (Figure 3c and d) and more horizontally oriented leaves ($x_{3.0}: x = 3.0$) increased $Q_{AT}$ by up to 13% (Figure 3e and f). The absolute differences in absolute $Q_{AT}$ compared with $x_{1.0}$ on a clear day were 8 and $-6$ mol m$^{-2}$ day$^{-1}$ for $x_{0.5}$ and $x_{3.0}$, respectively ($Q_{AT}$ for $x_{0.5}$, $x_{1.0}$ and $x_{3.0}$ were 86, 78 and 72 mol m$^{-2}$ day$^{-1}$, respectively). Generally, the effect of $x$ was larger and more persistent along the $L$ range where shoots are more clumped.

**Effects on the vertical distribution of $Q_A$**

The model validation (Figure 2) showed that in coniferous forests similar to the one at Duke Forest, not accounting for either shoot or tree clumping has a large impact on estimations of the vertical distribution of canopy openness and $Q_{AL}$. Sensitivity analysis of $Q_{AT}$ demonstrated that the impact of certain canopy specifications may increase or decrease with increasing $L$. We therefore proceeded with assessing the effect of varying each component on the vertical distribution of $Q_A$. To keep the comparisons manageable, we limited the stand/canopy conditions to four extreme cases, the combinations of the highest and lowest $L$ and stand densities, and we use vertically constant parameters.

Shoot clumping increases $Q_{AL}$ in deeper canopy layers by decreasing absorption in the upper layers (Figure 5a–d), and the effect increases with clumping. At low $L$, the redistribution of light benefited lower canopy strata but only at high stand densities. At high $L$, moderate-to-high shoot clumping increased light penetration and $Q_{AL}$ mid-canopy, but did not enhance absorption of $Q_{AL}$ at the bottom of the canopy. At high $L$ and stand density, absorption of $Q$ in canopies without shoot clumping was so high at the top that estimates of $Q_{AL}$ lower in the canopy were very low. We did not represent the relative effect of clumping in these situations because the $Q$ estimated based on some of the model versions was lower than our cut-off criterion ($40$ µmol m$^{-2}$ s$^{-1}$) below which ratios of $Q_{AL}$ generated with different versions are quite high and uncertain. However, these are the conditions in which shoot clumping would generate a substantial relative increase in lower canopy $Q$ conditions.

Unlike its effect on $Q_{AT}$, the effect of shoot clumping on the vertical distribution of $Q_{AL}$ was different on cloudy and clear days. During cloudy days, shoot clumping decreased $Q_{AL}$ less in the upper canopy (compared with a canopy with no shoot clumping) than during clear days, and increased $Q_{AL}$ more in mid-canopy in stands of low stand density; in high-density stands, the region of increasing $Q_{AL}$ shifted to the lower canopy. Overall, in stands of low stand and canopy density (both
low N and L), shoot clumping did not increase \( Q_{AL} \) at any layer in the canopy. At higher density of either canopy or stand, shoot clumping affected the distribution of \( Q_{AL} \) such that lower absorption in the upper canopy was compensated by higher absorption at mid-to-low canopy.

Similar to shoot clumping, tree-level clumping decreased \( Q_{AL} \) in the upper canopy and increased it in lower canopy layers (Figure 5e–h). The effect was particularly large at stands of low stand density, especially when L was high. At stands with high stand density, the distribution of crowns approximates the continuous surface of the canopy without specification of tree clumping. The effect of tree and shoot clumping on the distribution of \( Q_{AL} \), was apparent when comparing model estimates for the same L. In all situations, the effect of tree clumping increased with decreasing shoot clumping (i.e., increasing \( \Pi \)).

Leaf angle distribution can have a large effect on the penetration of light through the canopy (Figure 6). Foliage oriented more vertically \((x = 0.5)\) than a spherical distribution \((x = 1.0)\) decreases the absorption of Q in the upper canopy, making more light available for absorption in lower canopy layers. Conversely, more horizontally oriented foliage absorbs much of the Q high in the canopy, allowing less to penetrate into the lower canopy. Under cloudy conditions, the leaf angle distribution-imposed redistribution of \( Q_{AL} \), relative to that with a spherical distribution was not very large in any combination of stand densities and L. However, on clear days, we observed very large effects in dense stands with dense canopies (Figure 6d and h), especially when foliage was not very clumped in shoots. Even in stands and canopies of lower densities, \( Q_{AL} \) redistribution generated an increase or decrease in the estimate of \( Q_{AL} > 10\% \) in some layers. In such stands, the changes were particularly large when foliage was clumped. The vertical pattern observed in \( Q_{AL} \) with changing \( x \) compared with \( Q_{AL} \) with spherical distribution was caused by reasons similar to the ones we observed when introducing shoot clumping (Figure 5a–d).

**Effects of varying shoot, tree clumping and leaf angle distribution on the vertical distribution of \( Q_{AL} \)**

In forest canopies, decreasing shoot clumping with depth in the canopy and changing leaf angle distribution should distribute light more evenly compared with the canopy with constant parameters we used in the sensitivity analysis (Stenberg 1998). For most applications, obtaining the information needed for such detailed specification of canopy attributes may be impractical.

We tested the effects of using constant versus vertically variable shoot clumping and leaf angle distribution (see Figure 1 for the parameterization); in this test, tree clumping was set higher in the subcanopy than in the canopy to reflect the large number of small individuals growing below the canopy. The results showed that, depending on the simplification and the canopy layer, estimated \( Q_{dn} \) ranged from –5 to +8% compared with the most realistic model with all parameters vertically varying (v7), while \( Q_{AL} \) ranged from –8 to +15%. Using constant values for both shoot clumping and leaf angle distribution (v4) underestimated both \( Q_{dn} \) and \( Q_{AL} \) at the top of the canopy and overestimated them at the bottom, leading to
to the worst overall agreement. Allowing $x$ to vary vertically, but keeping $\Pi$ constant ($v6$), resulted in overestimation at the top similar to that of $v4$, but a very good agreement at the bottom, and the best overall agreement with the most realistic model. Finally, allowing vertical variations in $\Pi$ but keeping $x$ constant ($v5$) produced a very close agreement with $v7$ at the top of the canopy, but the agreement deteriorated with depth in the canopy.

**Discussion**

Estimating photosynthesis in canopies of stands and forests based on semi-empirical models is commonly done by estimating $Q_{AT}$ and multiplying by potential light use efficiency reduced via stress-related modifiers (Landsberg and Waring 1997, Duursma and Mäkelä 2007, Hilker et al. 2008, Makela et al. 2008). If the potential light use efficiency is relatively invariant and the modifiers well defined (e.g., Landsberg and Waring 1997), improving estimates of $Q_{AT}$ is the only way users of these models can improve estimates of canopy photosynthesis.

We begin by describing how well the different versions of the model quantified canopy $Q_{dn}$ and $Q$ on horizontal surfaces in a stand with large spatial and seasonal variation of $L$ (McCarthy et al. 2007). We compared our simulation results with below-canopy measurements performed at various times over the year, and with measurements made from towers, representing vertical transects through the canopy. Following that, we concentrated on absorbed $Q$ ($Q_A$) of the total canopy and of each layer, calculated from mean $Q$ on horizontal surfaces through the canopy because it is the variable most often used in modeling canopy photosynthesis. We analyzed the effects of incorporating constant shoot clumping and tree clumping ($\Pi$ and $N$, respectively), and leaf angle distribution ($x$) on $Q_{AT}$ during one growing season clear day and one cloudy day. We concluded by analyzing the effect of vertically variable canopy properties on estimated $Q$ distribution in one stand.

**Model validation**

Including branch and stem area in the model was essential for reproducing the measured openness and light environment in and below the canopy, especially in the non-growing season when these surfaces were similar in quantity of $L$. For example, based on model $v7$, including the woody surfaces in the winter simulations decreased the light at the bottom of the canopy by 19%. However, in September when $L$ reaches its maximum in our stand, the relative contribution of these surfaces was smaller, reducing light by a mere 2%.

All model versions accounting for both shoot and tree clumping ($v4$–$v7$) reproduced a reasonable estimate of vertical $Q$ distribution as judged by the agreement with measurements (see Table 3). The four model configurations straddled the zero error line, meaning that overestimation at one canopy level was compensated by an underestimation lower down (Figure 3e and f).

The predictions based on the most complete model (Figure 3a and b) demonstrate that our 1-D model fed with architectural specification of a complex broadleaf and needle-leaf canopy, and a broadleaf subcanopy, was able to reproduce the combined effects of the individual components on $Q$ averaged on horizontal surfaces just as well as 3-D models (considering typical published statistics; compared with, e.g., Stadt and Lieffers 2000, Mariscal et al. 2004, Möttus 2004).
Not accounting for either shoot and/or tree clumping resulted in a large overestimation of light absorption high in the canopy and underestimation of light levels in all lower canopy layers. A number of 3-D radiation transfer models can predict well the vertical distribution of mean $Q$ in the canopy (Wang and Baldocchi 1989, Brunner 1998, Canham et al. 1999, Gersonde et al. 2004, Mariscal et al. 2004), including in mixed-species canopies (Stadt and Liefers 2000). It is noteworthy that even 3-D model-based estimates poorly reproduce point-by-point measured $Q$, because small errors in canopy element positions can translate into large errors in estimated $Q$ (e.g., Mariscal et al. 2004). Our 1-D model reproduced the mean $Q$ in the canopy well in both mixed-species (Figure 3a and b) and single-species stands (see closed circles during the non-growing season when broadleaved species are leafless in Figure 3a and b, making it essentially a pine stand, and a poplar stand in Kim et al. 2008). However, unlike 3-D models requiring spatially explicit information on tree crowns, our model operates based on more readily obtained statistical representation of the canopy (Figure 1).

**Sensitivity analysis**

**Total absorbed $Q$**

The pattern of $Q_{AT}$ with $L$ observed at stands with low stand densities compared with modeling the stand as randomly distributed shoots in the canopy (i.e., no tree clumping) reflects the combined effect of a number of processes. Starting at low $L$, increasing canopy leaf area in stands with tree clumping increases the density of shoots in the crowns of a few trees, which is not as effective for intercepting $Q$ as the same increase in $L$ randomly distributed throughout the whole canopy. At high $L$, randomly distributed canopies that do not account for tree clumping reach a point at which most $Q$ is already absorbed, and further increase generates a very little gain in $Q_{AT}$. Thus, even small increases in $Q_{AT}$ with the additional $L$ crammed in crowns of few trees helps close the $Q_{AT}$ gap with canopies of randomly distributed canopy elements, resulting in the upturn of the ratios observed in Figure 4c and d.

As demonstrated by this (Figure 4c and d) and earlier studies (Oker-Blom et al. 1989, Brunner 1998, Duursma and Mäkelä 2007), tree clumping affects $Q_{AT}$ by controlling the spatial distribution of canopy elements through crown dimensions and stand density, which are highly variable among species and affected by stand conditions.

With increasing $L$, the absolute differences in $Q_{AT}$ were of similar sign to the relative effects when considering shoot clumping, were of opposite sign when considering tree clumping, and could go either way when considering $x$ due to the small effects involved with this property. Thus, for example, where shoot clumping is $I = 0.2$, in stands of $L = 2$, $Q_{AT}$ was 51 mol m$^{-2}$ day$^{-1}$ or $\sim$60% less compared with non-clumped foliage, and in stands of $L = 10$, $Q_{AT}$ was 32 mol m$^{-2}$ day$^{-1}$ or $\sim$30% less. However, the effect of tree clumping was not similar in relative and absolute terms. For example, where $N = 100$ trees ha$^{-1}$, in stands of $L = 2$, $Q_{AT}$ was 24 mol m$^{-2}$ day$^{-1}$ or $\sim$35% less than that of non-clumped stands, and in stands of $L = 10$, it was 39 mol m$^{-2}$ day$^{-1}$ less, still $\sim$35% reduction in $Q_{AT}$.

More generally, the effect of tree clumping on $Q_{AT}$ can be viewed via the area shaded by the trees, which reflects stand and crown characteristics and the sun angle. When and where the shade area equals the ground area ($N \times S = 1.0$ in Equation 3), canopy elements are presumably positioned in the way of incoming light anywhere in the stand. However, the Poisson distribution of crowns means that there is a crown overlap and estimated $Q_{AT}$ increases less with $L$ when tree clumping is imposed (Figure 7). A similar pattern emerges with $N \times S < 1.0$, but the stable minimum decreases. As $N \times S$ increases $>1.0$, even randomly positioned crowns will approach complete cover, especially early and late in the day when the sun elevation angle is low. In open stands, as the sun elevation angle steepens, the solitary crowns will fail to intercept much of the light, but as stand density increases (especially for species that can maintain large crowns in dense stands), $N \times S$ will be much greater than 1.0 all day, and interception will approach that estimated without accounting for tree clumping (Figure 7). The ratios presented in Figure 4c and d, produced from daily...
integrated sums, smooth over the different patterns representing changing $N \times S$ with diurnal changes in sun angle.

Accounting for stand density ($N$) thus including tree-level clumping in the model had a substantial effect on $Q_{AI}$. In contrast, the interaction effect between TD and $L$ is small, causing <3% difference between maximum and minimum $Q_{AI}$ estimated at each stand density along the wide range of $L$. We feel that, given the model complexity, it is important to provide a physical explanation for each observed phenomenon, including the contrasting single effect of $N$ versus the joint effect of $N \times L$. Recognizing that stand density affects crown surface area and, thus, stand density and $L$ determine tree leaf area per crown surface area ($L_{A}/S_{A}$), we assessed our model's ability to reproduce the effective extinction coefficient of the canopy ($k_{eff}$) based on a new structural parameter, $L_{A}/S_{A}$, recently proposed by Duursma and Mäkelä (2007; see their equation 9b). Our sensitivity analysis covers the range of values of $L_{A}/S_{A}$ in their analysis and extends it further to much higher values.

The relationship between $k_{H}$ and $L_{A}/S_{A}$ implies a lumped parameter $k_{H}$, the extinction coefficient of the homogeneous canopy (Duursma and Mäkelä (2007), which depends on the zenith angle ($\theta$) and on shoot characteristics and was derived from simulations done with a detailed 3-D model. We simulated $Q$ attenuation with our model parameterized with their shoot clumping, but with $k_{H}$ reflecting our latitude, and thus angular distribution of incoming $Q$ ($k_{H} = -0.29$). In the simulations we used two representations of $L_{A}/S_{A}$ of the P. taeda stand: (i) annual mean $L_{A}/S_{A}$ of 1.55, and (ii) dynamic $L_{A}/S_{A}$ reflecting the dynamics of leaf area and crown dimensions in the stand. We simulated our stand with all inputs kept constant except for varying crown width to generate a range of $L_{A}/S_{A}$.

The $k_{eff}$ that we extracted from either the annual mean or dynamic $L_{A}/S_{A}$ was higher than the one predicted from Duursma and Mäkelä (2007; see Figure 8a), shifting our points upwards. The shift is due in part to a different way of accounting for shoot clumping (fixed $k$ in their paper and $\Pi \times G$ as a function of $\theta$ in our model), and was described well by running their general (not their 3-D) model without tree clumping, resulting in $k_{H} = -0.34$ (rather than $-0.29$) for our stand. Thus, not only did our model recover the same shape of the relationship between $k_{eff}$ and $L_{A}/S_{A}$ as depicted in Duursma and Mäkelä (2007), but also the explanation for the difference in the position of the lines is straightforward, lending confidence in the response of $Q_{AI}$ to stand density along a range of $L$.

Although changing $k_{H}$ shifted the relationship between $k_{eff}$ and $L_{A}/S_{A}$ in our model compared with that of Duursma and Mäkelä (2007), it did not change its curvature. In other words, there is little effect of shoot clumping and zenith angle on the relationship, and the ratio of the two estimates of $k_{eff}$ (our model divided by that of Duursma and Mäkelä 2007) along the range of $L_{A}/S_{A}$ averaged 1.199 with a very small variance (SD = 0.004). There is, however, an effect of $\Pi$ and $\theta$ on $k_{H}$ (Figure 8b) because $G$ in our model depends on $\theta$ (Equation 5b). We ran the model for a range of shoot clumping values representing a large number of species (Therezien et al. 2007) over a latitudinal range of 10°–65° (reflected in a range of mean $\theta$ in Figure 8), and found that the latitudinal influence on $k_{H}$ increases with decreasing shoot clumping (i.e., increasing $\Pi$; Figure 8c). Because the relationship for each $\Pi$ can be approximated as linear, considering the range in values (Figure 8b), we described the model results as linear (Figure 8c), extracted the intercept and slope of the relationship between $k_{H}$ and zenith angle at $\Pi$ ranging by 0.1 from 0.2 to 0.9, and produced a relationship between the two parameters and $\Pi$ (Figure 8d). Note the two parameters are linearly related: slope $= -4.463$; intercept $= +0.020$. Therefore, it is possible to estimate $k_{H}$ for canopies of any shoot clumping positioned in any zenith angle ($k_{H} = 1.808\Pi + 0.081 \theta - 0.405\Pi \theta - 0.022$), thus allowing generalization of the Duursma and Mäkelä (2007) approach globally and across forest types.

Finally, $Q_{AI}$ was also somewhat affected by leaf angle distribution ($x$). The difference in $Q_{AI}$ between non-spherical and spherical distribution increased with sun angle (data not shown), meaning that our results from the summer solstice.
showed the maximum $x$ effect. Considering that the study site was located at the southern region of temperate forest, the results also show the higher end of the $x$ effect in temperate forests. Because solar angle decreases with latitude from the equator, the effect of $x$ will be smaller at higher latitudes and higher at lower latitudes than at ours.

In summary, our analysis shows that $Q_{AT}$ was most affected by shoot clumping (Figure 4a and b). Because leaves are less clumped on shoots of broadleaved species than on shoots of conifers (Niinemets et al. 2004, Therezien et al. 2007), shoot clumping affected $Q_{AT}$ much less than tree clumping in a dense, high $L$ poplar plantation ($N = 3175$ trees ha$^{-1}$, e.g., Kim et al. 2008). However, most widely used growth and ecosystem carbon dynamics models do not account for either variable (e.g., Running and Coughlan 1988, Landsberg and Waring 1997). Incorporating shoot and tree clumping into models to improve estimates of $Q_{AT}$ and canopy photosynthesis should not be particularly difficult. Shoot clumping has been quantified for many conifer species (see Therezien et al. 2007), and stand density, useful for estimating $Q_{AT}$ in both types of forest, is commonly available from stand inventories and can be obtained for larger scale applications from certain remotely sensed products (Lefsky et al. 2002).

**Effects on the vertical distribution of $Q_A$**

Because the greatest effect on the vertical distribution of $Q$ is realized once shoot and tree clumping are incorporated, either as constant or vertically varying quantity, we concentrated our sensitivity analysis on the effects of including these factors in the simplest, constant form. We concluded with an analysis of the relative deterioration of accuracy of predictions of the vertical distribution of $Q$ caused by holding each canopy property constant in the test stand instead of allowing them to vary vertically. We restricted this analysis to a coniferous (needle-leaf) canopy because of the added complexity of their shoot level clumping.

Shoot clumping increases $Q_A$ in deeper canopy layers by decreasing absorption in the upper layers (Figure 5a–d), and the effect increased with clumping as has been demonstrated in earlier modeling studies (e.g., Stenberg 1998, Niinemets et al. 2004) and was limited to stands of high density. Moderate-to-high shoot clumping increased light penetration and $Q_A$ to greater depths with decreasing $L$. At high $L$ and stand density, $Q_A$ in canopies without shoot clumping is so high at the top that estimates of $Q_A$ lower in the canopy were extremely low. Thus, there are conditions in which shoot clumping would generate a substantial relative increase in lower canopy $Q$ conditions. Accounting for shoot clumping under such conditions would be essential to correctly estimate the carbon balance that permits trees to hang onto lower branches and for the success of recruitment and subcanopy species (Brunner 1998, Kull and Kruijt 1998, Kim et al. 2008).

Similar to shoot clumping, tree-level clumping decreased $Q_{AL}$ in the upper canopy and increased it in lower canopy layers (Figure 5e–h), an effect that was particularly large in stands of low stand density, high $L$ and low shoot clumping (i.e., as $II$ increased). Thus, accounting for the organization of foliage into crowns has an increasing effect on $Q_{AL}$ distribution with decreasing shoot clumping, and the effect is larger on cloudy than on clear days. Indeed, accounting for tree-level clumping when computing $Q_{AL}$ and its vertical distribution is most important in stands of broadleaved species where leaves are not very clumped on shoots (Chen et al. 1996, Niinemets et al. 2004, Kim et al. 2008), and optical estimates of total clumping reflect clumping at scales larger than that of the shoot (Chen et al. 1996, Nilson 1999, Mottus 2004, Niinemets et al. 2004). However, in stands of high $L$, an accurate estimation of $Q_{AL}$ distribution requires that stand density be explicitly incorporated in the model, even in coniferous forests with highly clumped shoots.

Orienting foliage vertically in open stands resulted in a reduced $Q_{AL}$ at all canopy layers, much like having highly clumped foliage on shoots. On the other hand, horizontal orientation in such stands increased absorption of $Q$ at all layers, regardless of the shoot clumping, but the effect was largest in canopies with highly clumped shoots. Among the published results on the effects of $x$ on $Q_{AL}$ and vertical $Q$, some show a small effect (Oker-Blom and Kellomäki 1982, Goudriaan 1988) and others a relatively large effect (Stadt and Lieffers 2000, this study). This disagreement likely reflects the amount and direction of the difference between the modeled and actual $x$ in the canopy (Thomas and Winner 2000, Wirth et al. 2001), and the mean sun angle (Oker-Blom and Kellomäki 1982). Moreover, as we show here, the effect of shoot clumping must also be considered.

Vertically varying the architectural parameters was apparently not especially important for estimating daily or yearly $Q_{AT}$.
and, thus, possibly canopy photosynthesis. However, the vertical distribution of openness and light was somewhat sensitive to whether the parameters are held constant representing the average used for pine canopies in the literature (and close to our stand’s average), or vertically varying similarly to true canopies (Figure 9). Holding the parameters constant average means that, relative to true canopies, the upper canopy is estimated to be less or similarly open, and the lower canopy is more or similarly open, depending on the parameter. This translated, for example, to the upper layers of the most realistic canopy (v7) enjoying 1600 mmol m⁻² day⁻¹ higher Q than a canopy specified with constant clumping and spherical distribution, but having 6 mmol m⁻² day⁻¹ less at the bottom layers of canopy. Summed over the upper third of the canopy, the more realistic canopy was estimated to have 3 mol m⁻² day⁻¹ higher Q and the lower third of the canopy 0.04 mol m⁻² day⁻¹ lower Q.

Conclusions

Our validation exercise showed that in a stand with a canopy dominated by pine with a substantial component of broadleaved species, and a subcanopy composed entirely of broadleaved species, accounting for mean shoot and tree clumping was not needed for estimating $Q_{\text{AT}}$ in October when plant area index was high (~6.82 ± 0.77 (SD))—both simple (v1–v3) and complex models estimated correctly that most light is absorbed. However, in March, when plant area index was low (~2.96 ± 0.43 (SD)), the simple models continued to estimate that nearly 98% of the light was absorbed, while the more realistic models estimated ~83% absorption, similar to measured values. Indeed, our sensitivity analysis showed a potential for large overestimation of $Q_{\text{AT}}$ when the effect of shoot clumping is not incorporated, with errors increasing with decreasing canopy leaf area, and when the effect of stand density is not considered in low-density stands regardless of canopy leaf area. Accounting for shoot and tree clumping was also necessary to reproduce measured $Q_{\text{AL}}$ and Q gradient with depth in the canopy. Further improvements incorporating vertically variable leaf angle and shoot clumping made only small additional changes in the vertical distribution of $Q_{\text{AL}}$.

Where $L$ is high, estimation errors of $Q_{\text{AT}}$ are likely to be small even without accounting for shoot and tree clumping. However, the distribution of Q within the canopy is very important for correct estimations of canopy photosynthesis—even at a given total absorption—because of the non-linear dependence of leaf photosynthesis on Q. This study demonstrates that the vertical gradient of Q did depend strongly on incorporating detailed canopy characteristics.

Altogether, accounting for tree clumping is most important in stands composed of species of which leaves are not very clumped on shoots (e.g., most broadleaved species). Yet, even in forests composed of species of highly clumped shoots (e.g., most coniferous forests), accurate estimation of $Q_{\text{AL}}$ distribution requires that stand density is explicitly incorporated in the model where the leaf area index is high. At present, information on both variables, stand density and shoot characteristics, are commonly available and their incorporation into canopy photosynthesis models should be relatively straightforward.

Acknowledgements

We thank two anonymous reviewers and the handling Editor for their insightful comments.

Funding

This research was supported by the United States Department of Energy (DOE) through the Office of Biological and Environmental Research (BER) Terrestrial Carbon Processes (TCP) program (FACE: DE-FG02-95ER62083).

Appendix: the dimensional approach of branch and stem area

For the dimensional approach, we estimated the number of whorls in the live crown from the crown length; we first estimated the live crown length from the diameter and height of individual trees using a regression model developed from measurements made at the end of the 2005 and 2006 growing seasons (McCarthy et al. 2007). We estimated the number of whorls within the live crown from crown length and tree average height growth, which varies by dominance class. The average annual height growth for pine trees was ~1 m over 3-year periodic measurements. We calculated height growth of subcanopy species from annual diameter increment and the relationship between height and diameter. We found that intra-whorl branches were few, small and short lived, and thus we ignored their contribution to $A_{\text{sh}}(z)$. We also found that, on average, branches bifurcated three times, with a fifth-year length increment rarely exceeding 1% of the total branch length, and only occurring on a few shoots. We considered a branch of any order dead and gone once its youngest bifurcation was older than 4 years. We set the first-year length increment of branch originating at the main stem to ~90% of the height increment during that year. A second-year length increment along the branch axis was 90% of the previous year’s length, and that of the two laterals was 90% of this year’s axial increment. We replicated this procedure for the second bifurcation (third-year growth) and third bifurcation for three axial and six lateral branches, at which point we recorded no further branch length increment for that whorl. Using this design, we computed the total length of the main branches originating from the stem based on their age.

We calculated the diameter of each branch by assuming that, due to lower hydraulic conductivity at the branch base, the
sum of branch sapwood area at the base of branches exceeds the sapwood area of the stem supporting these branches (Oren et al. 1986b). Knowing the taper of the stem allows calculation of the sapwood area below and above a whorl, with the reduction in sapwood area assumed to be divided among the four branches and then increased to account for the effect of reduced hydraulic conductivity at the junction. Thus, excluding bark thickness, the sapwood area of current year stem and branches was ~14% larger than the previous year’s stem sapwood. We used the same method to calculate the diameter of higher order branches.

We estimated both the branch surface area and the volume of an idealized branch in each whorl based on the basal diameter and length of each branch order, and multiplied the results by 4 to obtain the average number of branches per whorl. For the correction described in the Materials and methods section, we converted branch volume to biomass using wood density interpolated between 0.37 g cm$^{-3}$ at the topmost and 0.52 g cm$^{-3}$ at the bottommost whorl (McCarthy et al. 2007). Summing provided the total branch mass, which we compared with the estimate from the direct method. Given all the assumptions in the dimensional approach, many sources of uncertainty caused a 50% higher biomass estimate than the direct approach, reflecting lower self-pruning in various layers in the canopy than competition imposes in the actual stand and deviations from assumed architecture. We reduced the dimensional estimate by removing branches from each layer, if necessary, until both total biomass from the direct estimate and a known vertical profile of relative branch biomass distribution (Pataki et al. 1998, Blazier et al. 2002) matched, and recalculated $A_0(2)$ from the remaining branches. Our approach removed some branches at most layers except those of the upper canopy, matching the likelihood of self-pruning.

References


