



# A stand-level light interception model for horizontally and vertically heterogeneous canopies



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## ABSTRACT

Process-based forest growth models often rely on estimates of absorbed photosynthetically active radiation. Light absorption can easily be estimated using the Lambert–Beer law for simple homogeneous canopies composed of one layer, one species, and no canopy gaps. However, forest canopies are usually not homogenous, vertically or horizontally, and detailed tree-level models have been developed to account for this heterogeneity. These models have high input and computational demands and work on a finer temporal and spatial resolution than is often required by stand level growth models, making them impractical for this purpose. The aim of this study was to develop a stand-level “summary” light model that can account for (1) canopy gaps, (2) multiple horizontal canopy layers that may or may not overlap, and (3) multiple components (species, age classes or dominance classes). The model divides the canopy into horizontal layers that consist of a single component, or multiple components whose crowns overlap vertically. The light absorption of each layer is calculated using the Lambert–Beer law and then partitioned to each component in that layer using weightings based on the leaf area, extinction coefficients and the relative heights of each component within the layer. Canopy gaps within each layer are accounted for by assuming a Poisson-distribution of trees, while taking account of crown surface area-to-leaf area ratio and solar zenith angles, which change with latitude and season. The summary model was compared with a detailed tree-level model and performed well for stands containing up to eight components and for a wide range of stand structures, in terms of trees per ha and multiple canopy layers. For both the whole canopy and when partitioning light between individual components the summary model was nearly unbiased with low relative average errors (−0.26% and −0.30%, respectively) and high model efficiencies (0.94 and 0.87, respectively). Further improvements could be achieved by improving the ability of the model to partition light between components within a given layer. This model can be parameterised with easily obtainable information about crown sizes and extinction coefficients and could be used to examine light dynamics in complex canopies and in stand-level growth models.

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## 1. Introduction

Light is a major driver of plant growth. Many process-based forest growth models rely on the relationship between stand gross or net primary production and the amount of photosynthetically active radiation (PAR) that is absorbed by the canopy (APAR), the slope of which is a measure of light-use efficiency (Monteith, 1977). Suitably accurate estimates of APAR are critical to these models. Often, the APAR calculations are based on the turbid medium analogy, which can be described using the Lambert–Beer equation, such

that the fraction of PAR absorbed by the canopy,  $f$  (i.e. APAR/PAR), is

$$f = 1 - e^{-kL} \quad (1)$$

where  $k$  is the light extinction coefficient for the period considered, and  $L$  is the leaf area index ( $\text{m}^2 \text{m}^{-2}$ ). In this study, all  $k$  values are for the canopy as opposed to within-crown  $k$  values (e.g. Oker-Blom et al., 1989), and are therefore influenced by gaps between tree crowns, and, all  $L$  in this study are one-sided.

Eq. (1) can be used to calculate  $f$  for vertically and horizontally homogeneous canopies. However, forest canopies are often not homogeneous, and may contain multiple horizontal layers, or canopy gaps, such as in young stands before canopy closure, or following thinning or natural disturbances. Reliable values of  $k$  might also be difficult to obtain for rapidly changing canopies and complex mixed species stands where species compositions and proportions can be variable.

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Detailed, generally tree-level, light-extinction models are usually able to account for vertical and horizontal heterogeneity within the canopy, and many have been developed (Abraha and Savage, 2010; Bartelink, 1998; Brunner, 1998; Canham et al., 1999; Cescatti, 1997; Da Silva et al., 2012; Norman and Welles, 1983; Oker-Blom et al., 1989; Seidl et al., 2012; Talbot and Dupraz, 2012; Wang and Jarvis, 1990). Generally, their accuracy increases with the level of detail used to describe the tree crowns and canopy structure (Brunner, 1998; Sinoquet et al., 2000). Inputs may include the leaf area of individual tree crowns, the vertical and horizontal distribution of leaves, the leaf angle distribution, leaf transmittance and leaf and soil reflectance. These detailed models require many input parameters and a high computational effort making them unattractive for use in growth models designed to be easy to parameterise and use and quick to run at large temporal and spatial scales. As a result, stand-level light models that summarise the effect of crown architecture and stand structure on  $f$  (e.g. summary models) have been developed that use simpler descriptions of the canopy but still account for canopy gaps (Duursma and Mäkelä, 2007), multi-layered canopies or mixed-species compositions (Sinoquet and Bonhomme, 1991; Sinoquet et al., 2000; Wallace, 1997).

Several approaches have been used in summary models to account for gaps in canopies. Gaps between tree crowns can result in lower stand leaf areas,  $L$ , than closed canopy stands, thereby reducing stand APAR. On the other hand, gaps reduce inter-tree shading and increase individual tree APAR. Some models account for this horizontal variability by considering the proportion of ground area covered by the canopy and then reduce APAR, as estimated for a closed canopy, according to that proportion, or they simply use the  $L$  of the open stands (Sands, 2004; Wallace, 1997). However, while these approaches account for the reduced leaf area, they do not account for the reduced shading and increased light on the sides of tree crowns, and may therefore underestimate  $f$ .

To account for lower leaf areas and reduced shading in open stands, Duursma and Mäkelä (2007) developed a summary model that accounts for gaps in canopies and works for single, unshaded trees, all the way to closed canopy stands. To achieve this, the model required a modified extinction coefficient. This was necessary because  $k$  can vary for a given species with changes in canopy structure and  $L$  (Binkley et al., 2013), which is influenced by factors such as age and site quality, can even change from season to season (Cannell et al., 1987), and also varies with the arrangement of leaf area, and the amount of gaps between crowns. For example, canopies clearly do not consist of trees with box-shaped crowns that fit perfectly together. Instead, crowns are shaped more like cones or ellipses, which do not fit perfectly together, and may result in some crown overlap or gaps between each crown. This clumping and variability influences  $k$  and can reduce estimates of  $f$  compared with homogenous canopies (Chen et al., 1997; Nilson, 1999; Oker-Blom et al., 1989). Despite this temporal and spatial variability in the  $k$  of a given species, many process-based models that use  $k$  to estimate APAR assume that  $k$  is static for a given species. Furthermore, the APAR predictions of such models are rarely tested against actual light data collected in the field, even when predictions of other components such as growth, evapotranspiration, nutrient availability, biomass partitioning etc. are thoroughly tested against field data. This is a particularly important consideration in mixtures because, for a given species, the sizes or shapes of crowns and the gaps between them are likely to vary between monocultures and mixtures, thereby resulting in different  $k$  (Awal et al., 2006), in addition to differences that may exist due to factors such as age and site. The summary model by Duursma and Mäkelä (2007) accounted for this variability in  $k$  by first replacing  $k$  in Eq. (1) with an extinction coefficient for a homogeneous canopy,  $k_H$ . This could be described as a canopy where all trees are the same height, have the same

live-crown length, have box-shape crowns that fit together perfectly, and also have the same leaf area density (LAD, leaf area per crown volume,  $\text{m}^2 \text{m}^{-3}$ ), leaf angle distribution, leaf reflectance, leaf transmittance etc. This  $k_H$  is independent of  $L$  or trees  $\text{ha}^{-1}$ .

Eq. (1) and  $k_H$  can be used to calculate the fraction of PAR absorbed by a homogeneous canopy,  $f_H$ , such that

$$f_H = 1 - e^{-k_H L} \quad (2)$$

Duursma and Mäkelä (2007) showed that Eq. (2) could also be applied to non-homogeneous canopies where the trees are Poisson-distributed, such that the probability that light is intercepted by any tree is independent for all trees, and when  $k_H$  is replaced with an effective extinction coefficient,  $k_{\text{eff}}$ , such that

$$f = 1 - e^{-k_{\text{eff}} L} \quad (3)$$

$$k_{\text{eff}} = \phi \frac{S_A}{L_A} (1 - e^{-k_H L_A / \phi S_A}) \quad (4)$$

where  $S_A$  is the total crown surface area of a tree ( $\text{m}^2$ ),  $L_A$  is the leaf area per tree ( $\text{m}^2$ ) and  $\phi$  is an empirical parameter that depends on the mean solar zenith angle, which itself depends on latitude and season. The  $L_A/S_A$  parameter was used to describe the tree crowns because it is well correlated with light interception efficiency for a wide range of crown architectures and integrates the effects of sizes, crown shapes and crown length-to-width ratios on light absorption (Duursma et al., 2012; Duursma and Mäkelä, 2007).

Eq. (3) was developed for monospecific stands with a single canopy layer. It can also be applied separately to any canopy layer of a mixed-species canopy if there is only one species within the layer, there is no vertical overlap with any other layer, and the PAR intercepted by higher layers is taken into account (McMurtrie and Wolf, 1983; Wallace, 1997). When there is some vertical overlap between crowns of different species, the  $f$  by each species can still be calculated using the Lambert–Beer law if the contribution of each of  $n$  species is weighted based on their  $L$  and  $k$  (Rimington, 1984; Sinoquet and Bonhomme, 1991; Sinoquet et al., 2000) such that the fraction of PAR absorbed by component  $i$ ,  $f_i$ , is given by

$$f_i = \frac{k_i L_i}{\sum_{j=1}^n k_j L_j} \left[ 1 - e^{-\left(\sum_{j=1}^n k_j L_j\right)} \right] \quad (5)$$

The fraction of PAR intercepted by the whole canopy is the term in the square brackets. Härkönen et al. (2010) combined Eqs. (3) and (5) in order to simultaneously account for species mixtures and canopy gaps. Härkönen et al. replaced  $k$  in Eq. (5) with  $k_{\text{eff}}$  (Eq. (4)) and weighted the contribution of each species using  $k_H$ ,  $k_{\text{eff}}$  and  $L$  such that

$$f_i = \frac{L_{\text{eff},i}}{\sum_{j=1}^n L_{\text{eff},j}} \left[ 1 - e^{-\left(\sum_{j=1}^n k_{\text{eff},j} L_j\right)} \right] \quad (6)$$

where  $L_{\text{eff},i} = k_{\text{eff},i} L_i / k_H$ .

Several other studies have summarised the effects of canopy structure in heterogeneous forest stands on  $f$  by calculating whole-canopy  $k$  information based on stand structure and tree dimensions (Kucharik et al., 1999; Mäkelä, 1990). However, while this provides  $f$  for the whole canopy, it does not partition the light to individual components. This can be done using Eqs. (5) and (6), but these equations do not take vertical heterogeneity into account, which can clearly have a significant effect on the partitioning of light between components of different heights that have vertically overlapping crowns (Barillot et al., 2011; Sinoquet et al., 2000; Sonohat et al., 2002; Wallace, 1997). To account for within-layer vertical heterogeneity, Wallace (1997) developed a summary model that used the relative heights of each species to describe the vertical structure of the stand and thereby to partition APAR between species. However, this approach was shown to over- or underestimate  $f$

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