Modelling of three-dimensional, diurnal light extinction in two contrasting forests

Daniel Kükenbrink, Fabian Schneider, Bernhard Schmid, Jean-Philippe Gastellu-Etchegorry, Michael Schaepman, Felix Morsdorf

Agricultural and Forest Meteorology 296 (2021) 108230

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Modelling of three-dimensional, diurnal light extinction in two contrasting forests

Daniel Kükenbrink [*,a,b], Fabian D. Schneider [c], Bernhard Schmid [a], Jean-Philippe Gastellu-Etchegorry [d], Michael E. Schaepman [a], Felix Morsdorf [a]

[a] Remote Sensing Laboratories, Department of Geography, University of Zurich, CH-8057 Zurich, Switzerland
[b] Swiss Federal Institute WSL, Zürichstrasse 111, CH-8903 Birmensdorf, Switzerland
[c] Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA 91011, USA
[d] Centre d'Etudes Spatiales de la BIOsphère (CESBIO) - Toulouse III University (UPS, CNES, CNRS, IRD, INRA), 31401 Toulouse cedex 9, France

ARTICLE INFO

Keywords:
Light extinction
Radiative transfer
Spectroscopy
Canopy structure
Leaf optical properties
LiDAR

ABSTRACT

The three-dimensional (3D) distribution of light within forest ecosystems is a major driver for species competition, coexistence, forest ecosystem functioning, productivity, and diversity. However, accurate knowledge about the 3D distribution of light within the canopy is difficult to obtain. Recent advances in 3D forest reconstruction as well as the use of radiative transfer modelling provide new insights into spatio-temporal variations of light distribution within a forest canopy.

We used high resolution laser scanning data coupled with *in-situ* leaf optical properties (LOP) measurements to parameterize the DART radiative transfer model for a temperate deciduous forest on the Laegern mountain, Switzerland, and for a tropical rain forest located in the Lambir Hills national park, Borneo, Malaysia. Combining terrestrial and unmanned aerial vehicle (UAV) laser scanning acquisitions allowed a high detailed, 3D reconstruction of forest canopies.

We analyse the impact of the two contrasting forest canopies, both in terms of structure as well as optical properties, on the 3D extinction of photosynthetic active radiation (PAR, 400 nm - 700 nm) for a whole diurnal cycle. We show that PAR extinction is mainly driven by the canopy structure, resulting in an exponential light extinction profile for the temperate and a more linear extinction profile in the tropical site. The larger 3D heterogeneity in canopy structure for the tropical site also resulted in larger variability in light extinction throughout the whole canopy. We found that contrasting LOPs between the two forests had a minor influence on light extinction. However, approximating light extinction profiles with layered Beer-Lambert or Big-Leaf models only poorly represented the 3D heterogeneity of light extinction within the canopy, illustrating the need for more detailed 3D modelling of light distribution within forest ecosystems. This can give us important insights into light-related mechanisms driving species coexistence, competition and diversity in complex forest ecosystems.

1. Introduction

Light availability plays a major role in defining species competition and coexistence as well as forest ecosystem functioning, productivity, and diversity. Studies have shown that canopy structure strongly influences the distribution of light within the canopy and therefore also influences the within canopy variability of light-use efficiency and productivity (e.g. Morton et al., 2014; 2016; Stark et al., 2012; Widlowski et al., 2011). It is reported (e.g. Niinemets, 2007; 2012) that light availability typically varies up to 50-fold within a closed vegetation stand, and even within the crown of an isolated individual tree significant variation in light may occur (Baldocchi et al., 2002; Kükenbrink et al., 2019; Valladares, 2003). The extensive variability of light availability within the canopy induces extensive modifications of foliage structure and physiology such that it is hardly possible to find two leaves with the exact same combination of leaf-trait values (Niinemets, 2012). Seasonal and diurnal changes in light availability within the canopy promote leaf plasticity allowing for leaves to adapt to changing light conditions within the canopy (e.g. Keenan and Niinemets, 2017; Niinemets et al., 2003; Valladares et al., 2016). For a better understanding

* Corresponding author.
E-mail address: daniel.kuekenbrink@wsl.ch (D. Kükenbrink).

https://doi.org/10.1016/j.agrformet.2020.108230
Received 10 August 2020; Received in revised form 15 October 2020; Accepted 19 October 2020
Available online 5 November 2020

of ecosystem functioning and productivity of forest ecosystems, advanced knowledge of the distribution as well as the utilization of light within the canopy is vital. However, quantification of the amount of incoming light reaching the three-dimensional (3D) forest canopy is challenging. Measurement of spatially contiguous, 3D light distribution is still relatively scarce for forest canopies, mostly due to the difficult access and the high spatial and temporal variability of light distribution within the canopy. Information in the literature is mostly related to simple, one-dimensional (1D) averaged light extinction profiles that neglect the horizontal variability and 3D distribution of light within the canopy. For this reason, multiple models of varying complexity have been developed to simulate and quantify the distribution and utilization of light within the canopy.

Global and regional land surface models often employ a relatively simple assumption of an exponential decrease of incoming light within the canopy based on Beer's law of light extinction (e.g. in MOSES (Cox et al., 1999), LPJ (Sitch et al., 2003), and SiB3 (Denning et al., 2003)). This assumption, however, neglects the presence of diffuse irradiance as well as horizontal and vertical heterogeneity in canopy structure. So-called two-stream models resolve upward and downward radiation streams and differentiate between diffuse and direct radiation (Jogireddy et al., 2006). Alton et al. (2007b) further improved the two-stream model by treating the canopy as multiple discrete vertical layers and explicitly modelling leaf orientation rather than averaging irradiance into a mean light profile.

However, these radiative transfer schemes largely neglect the large impact of canopy structure and architecture on the distribution of direct and diffuse solar radiation within the canopy. Fisher et al. (2017) identified the radiative transfer component in dynamic global vegetation models (DGVMs) as one of the biggest sources of uncertainty when modelling ecosystem functioning, productivity and development. In such models, canopy architecture is represented with varying levels of detail, from big-leaf models such as the original LPJ model (Sitch et al., 2003) to cohort or even individual based parameterization (e.g. the Ecosystem Demography models ED (Moorcroft et al., 2001) or ED2 (Longo et al., 2019a; 2019b), or the LPJml-FIT model (Thonicke et al., 2020)). However, these models sometimes fail to represent the actual structural complexity found in forest ecosystems, especially those of high species richness, where species with fundamentally different architecture and leaf traits may coexist in small areas.

McElhinny et al. (2005) described the importance of the characterization of forest structure for ecosystem functioning and highlighted the link between structure and diversity. Canopy structure can affect photosynthesis within the canopy (Chen et al., 2012; Kira et al., 1969), light-use efficiency (Duursma and Mäkelä, 2007; Jia et al., 2018; Walcroft et al., 2005) and net ecosystem CO_2exchange (Baldocchi et al., 2001; Law et al., 2001) due to its influence on light interception and light distribution within the canopy. Braghiere et al. (2019) showed that DGVMs can have the problem of underestimating photosynthesis due to the simplification of vegetation structure and that photosynthesis predictions in light limited ecosystems could be improved, when considering structural parameters in the radiative transfer scheme of land surface models (Braghiere et al., 2020). Damm et al. (2020) further revealed substantial 3D heterogeneity of forest gas exchange, that cannot be represented using simplifying assumptions of the canopy structure and the radiative transfer through the canopy e.g. by using a big leaf model. An accurate description of the vertical and horizontal arrangement of vegetation material is therefore vital, while summarizing stand structural attributes such as variability in tree height, and diameter at breast height, species richness and composition falls short to provide this information.

New laser-scanning technologies, especially the cost-effectiveness and practicality of terrestrial laser scanning (TLS), introduced a new way in which we are able to quantify and understand dynamics in forest ecosystem structure and function (Danson et al., 2018; 2007). Schneider et al. (2019) showed that by combining ground based TLS measurements with above-canopy TLS measurements from a canopy crane or unmanned aerial vehicle laser scanning (UAVLS), even very complex forest structures can be represented in high detail with a minimum amount of occlusion within the canopy. Calders et al. (2018) highlighted the potential in using TLS measurements for forest reconstruction and radiative transfer modelling. Morton et al. (2016) used Airborne Laserscanning (ALS) to parameterize the DART radiative transfer model to analyse light utilization in the Amazon rain forest. However, the reduced point density of the ALS system compared with the TLS acquisitions did not allow for a detailed representation of the tropical forest as shown in e.g. Calders et al. (2018).

In this study we modeled within canopy light distribution of two contrasting forests, a temperate mixed forest site and a tropical lowland mixed rain forest. We define 'light' here as the spectrally resolved incoming radiation in the photosynthetic active radiation (PAR) region (400–700 nm) and demonstrate the effect of canopy structure and leaf optical properties on the distribution of light within the canopy, both in the vertical and horizontal as well as diurnal dimension. We use the Discrete Anisotropic Radiative Transfer model DART, parameterized with high-resolution TLS and UAVLS acquisitions and coupled with *in-situ* and *in-vivo* leaf level measurements of leaf and bark optical properties based on portable spectroradiometers (see also Schneider et al., 2014) for both canopies. Our main research questions are: (1) how do the two forest ecosystems differ in terms of canopy structure and leaf optical properties, (2) how do these structural and optical differences affect light distribution and extinction within the canopy, both under clear-sky and complete diffuse illumination conditions, and (3) how do the simulated averaged light extinction profiles compare with the ones following a Beer-Lambert approximation?

2. Materials and methods

2.1. Study sites

For the purpose of this study we analyze light extinction in two contrasting forest ecosystems (temperate and tropical) with dense and tall canopies. The temperate site is a mixed old-growth forest on the southern slope of the Laegern mountain in Switzerland (47°28′42.1″N, 8°21′51.7″E, 688 m above sea level). The entire forest is dominated by beech (*Fagus sylvatica*L.) with 12 further tree species, with about 70% deciduous broadleaf trees and about 30% evergreen coniferous trees (Schneider et al., 2017). We selected a beech dominated plot of 60 x 60 m within a non-managed 5.5 ha research area. Canopy height ranged from 30 to 40 m for the single-layer canopy. A detailed description of the Laegern study site is given in Morsdorf et al. (2020).

The tropical site is located in the Lambir Hills National Park on the island of Borneo, Malaysia (4°12′3.7″N, 114°2′20.7″E, 140 m above sea leavel). The lowland mixed rainforest at this site is the world's most diverse forest yet studied in terms of tree species richness with perhaps 2500 plant species in total (Ashton, 2005). The vegetation is classified as lowland mixed dipterocarp forest and as moist lowland tropical forest in the Holdridge system (Asner et al., 2012). The most abundant species are belonging to the Euphorbiaceae and Dipterocarpaceae families. We again selected a 60 x 60 m plot northwest of a canopy crane centered in a 4-ha research area. Manfroi et al. (2006)give a detailed description of the plot. The canopy crane is 80 m tall with a 75 m long rotating jib, providing access to all layers of the canopy from ground to above canopy level (Kenzo et al., 2006), e.g. for measurements of leaf optical properties. Canopy height ranges from 30 to 50 m with some emergent trees reaching up to 70 m (Hiromi et al., 2012).

2.2. LiDAR data

Three-dimensional measurements of canopy structure were acquired using a Riegl VZ-1000 terrestrial laser scanning (TLS) device covering an

area of 1 ha for the tropical forest site and 60 x 60 m for the temperate forest site, following a near-regular scanning pattern. To complement laser measurements from the ground, TLS scans from multiple platforms of the canopy crane were acquired in the tropical forest. For the temperate forest, we used unmanned aerial vehicle (UAV) based laser scanning for above canopy measurements. The LiDAR UAV set-up combined the OxTS xNAV550 IMU/GPS dual-GPS-antenna navigation solution and the RIEGL VUX-1UAV laser scanner mounted on the industrial Scout B1-100 UAV helicopter produced by Aeroscout GmbH, Switzerland (Morsdorf et al., 2017). For a detailed description on the acquisition and processing of the high resolution laser point cloud see Schneider et al. (2019).

2.3. Optical properties data

Leaf optical properties (LOP) for the tropical forest site were acquired using an ASD FieldSpec Pro-spectroradiometer (Analytical Spectral Devices, Boulder, Colorado) with an added plant probe and leaf-clip. The foreoptic allowed us to calculate leaf reflectance and transmittance by using a white and a black reference panel with known reflectance and by following the procedure described in Miller et al. (1992) (for a detailed description of the LOP retrieval procedure, see Kükenbrink et al. (2019)). The instrument was set to reflectance mode to acquire the LOPs. Samples of 30 individual trees of 19 different species within the reach of the canopy crane's gondola were acquired at different positions of the crown (sunlit, transitional, and shaded positions). For each of the 30 crowns, 10 leaf samples were acquired with three LOP measurements per leaf. LOP measurements of the understorey were acquired from leaves accessible from the ground.

LOP samples for the temperate study site were collected from two individual beech trees during a field campaign in 2009. Leaf samples were taken from the upper, middle, and lower part of the crown. Reflectance and transmittance were measured in the laboratory at three positions on the abaxial and adaxial side of the leaf. The measurements were performed using an integrating sphere coupled to a field spectroradiometer (ASD FieldSpec 3, Analytical Spectral Devices, Boulder, Colorado). Further details on the acquisition of LOPs for the temperate site can be found in Schneider et al. (2014).

For parameterization of the optical properties of the forest floor and bark, multiple samples of leaf litter (31 for the temperate, 54 for tropical site) and bark (31 for temperate, 17 for tropical site) were measured in the field using a field spectrometer (ASD FieldSpec Pro) coupled with a leaf-clip (for litter samples) for both study sites.

2.4. Parameterization of radiative transfer model

The radiative transfer model used in this study for light extinction modelling is the Discrete Anisotropic Radiative Transfer Model DART (v5.6.0) (Gastellu-Etchegorry et al., 2015). In this DART version three-dimensional heterogeneous landscapes are represented by a voxel grid with a predefined size (i.e. 60 x 60 m grid extent with a voxel side length of 0.25 m). Each voxel follows a turbid medium assumption (i.e., random distribution of an infinite number of infinitely small planar elements) parameterized by it's leaf area density, leaf angular distribution, and optical properties. A DART voxel can include vegetation turbid media as well as discrete triangles with an arbitrary size, independent of the voxel size to simulate objects not following the turbid medium assumption (e.g. tree trunk and branches). In ray tracing, two types of radiation interactions are simulated: volume interaction within turbid voxels (Gastellu-Etchegorry et al., 2004), and surface interaction on triangles (Gastellu-Etchegorry, 2008). Further details on the DART model can be found in (Gastellu-Etchegorry et al., 2012; 2015).

In this study, the flux tracking mode of DART was used with sun and atmosphere as the only radiation sources. The approach to parameterize the DART model is closely following the one described in Kükenbrink et al. (2019), where the irradiance field around a single isolated tree was modeled and analysed. Optical properties of tree crowns, understorey, bark, and litter were parameterized using the optical measurements described in Section 2.3. To represent the vertical variability in LOPs, the vertically distributed LOP measurements were assigned to their respective layers within the voxel grid. The forest structure and leaf area density distribution within the canopy was defined as described in Section 2.4.1 based on the TLS measurements described in Section 2.2. The leaf angle distribution for the temperate forest was defined as plagiophile, following the work by Schneider et al. (2014) on the same study site. Leaf angle distribution for the tropical site was defined as spherical following a simplifying assumption performed in many studies where actual leaf angle distributions are not known (e.g. Alton et al., 2007a; Chen et al., 2012; Mariscal et al., 2004; Vincent et al., 2017). As tree trunks and larger branches do not follow the turbid medium assumption, they were modeled as discrete, opaque objects as described in Section 2.4.2 with optical properties derived as described in Section 2.3. In order to enable a direct comparison of vertical and horizontal variation in light extinction between the two study sites, the whole canopy was normalized based on a digital terrain model (DTM) derived from the TLS point cloud. To simulate the atmosphere, DART can be used with standard gas and aerosol models as contained in the MODTRAN model (Berk et al., 1987). We used the mid-latitude summer and the tropical gas model for the temperate and tropical forest site respectively. We used the aerosol rural model with a visibility of 23 km for both sites. To reduce edge effects in modelled light extinction at the borders of the 60 x 60 m grid, DART can replicate the scene around the borders, approximating the scene to belong within a larger forest stand.

For both study sites, solar angles for a complete diurnal cycle for the northern hemisphere summer solstice (21st of June) were simulated in two-hour intervals plus additional simulations for solar noon conditions. The 3D distribution of solar irradiance of a single waveband in the photosynthetic active radiation (PAR) regime (400 - 700 nm) within the forest canopies was simulated. Here, the considered DART output is a three-dimensional radiative budget with the amount of energy (in W $m^{-2}nm^{-1}$) irradiant, absorbed and scattered at each voxel. The radiative budget can be further decomposed into direct, diffuse and coupled irradiance (irradiance after coupling with the atmosphere).

2.4.1. Plant area density estimation

Plant area density for each turbid medium voxel was estimated using the laser scanning data described in Section 2.2 (for details on processing of the data, i.e. co-registration of point clouds etc., see Schneider et al. (2019)). The plant area density value per voxel (m^2m^{-3}) was estimated using the AMAPVox Software package (version 1.0.1 r3410ffbe) developed by "botAnique Modélisation de l'Architecture des Plantes et des végétations" AMAP (Vincent et al., 2017). The AMAPVox model is tracing all laser pulses through a predefined voxel grid and calculates for each voxel the local transmittance computed from the ratio between exiting and entering energy normalized by the mean optical path length (Vincent et al., 2017). To exclude tree trunks and major branches from the plant area density estimation, as these violate the turbid medium assumption for the selected voxel size, laser returns from the tree trunks and major branches were excluded from the plant area density estimation (see also Section 2.4.2). The estimated plant area density was multiplied by the voxel height (0.25 m) to convert to the plant area index (PAI [m^2m^{-2}]) values per voxel, which is required for the parameterisation of DART.

2.4.2. Stem and branch model extraction

Laser returns from tree trunk and major branches were filtered from the co-registered point cloud based on a reflectance threshold value (-5 dB) using the RiscanPro Software suite. Woody material tends to reflect more energy in the wavelength used by the TLS (1550 nm) than leaf material, making a separation between woody material and leaf material possible, but not perfect. For the temperate forest case, an earlier

acquired TLS acquisition during leaf-off state was used to extract stems and major branches, helping with the separation between woody and foliage material. To refine the filtered point cloud it was voxelized into a voxel grid with a voxel side length of 5 cm. Voxels with a low count of high reflectance returns were filtered out (e.g. for the temperate site, only voxels with at least 5 TLS returns or 2 UAVLS returns were used. For the tropical site, a height adaptive filtering was applied with the following thresholds: minimum 5 TLS returns per voxel <15 m above ground, minimum 3 TLS returns per voxel between 15 and 25 m, and minimum 2 TLS returns per voxel between 25 and 35 m). Smaller isolated voxel clusters (less than 5 connected voxels) were excluded from the wood structure binary voxel grid. The refined binary voxel grid was then converted into a 3D mesh object and written into a wavefront object file importable into DART.

2.5. Analysis of 3D light extinction

Light extinction was calculated based on modeled PAR irradiance per voxel and the baseline irradiance modeled above the top of canopy for each simulated solar angle:

$$Extinction = 1 - \frac{E}{max(E)} \quad (1)$$

where Edenotes the simulated irradiance of the top face of each voxel and $max(E)$denotes the baseline irradiance above the canopy (i.e. the maximum possible irradiance above the forest canopy). Differences in light extinction between the temperate and tropical forest were analysed in terms of canopy structure, diurnal cycle, as well as leaf optical influences on the simulated light extinction. Additionally, the light extinction distribution under total diffuse illumination conditions was analysed and compared with the solar- and atmosphere-coupled simulations. Finally, light extinction in the proximity of larger wood structures was analysed for both study sites.

2.5.1. Comparison to Beer-Lambert approximated light extinction

Vertical canopy transmittance is commonly estimated with the so called Beer-Lambert law (Monsi and Saeki, 2005), which assumes an exponential reduction in irradiance with increasing penetration into the canopy. According to the Beer-Lambert law, vertical transmittance through the forest canopy can be written as:

$$\tau_i = \exp(-kPAI_i) \quad (2)$$

where $PAI_i$is the cumulative PAI until the i^{th}canopy layer and $k$is the attenuation coefficient. In the case of a spherical leaf angle distribution, for a solar zenith angle (θ), we have:

$$k = \frac{1}{2\cos(\theta)} \quad (3)$$

The average extinction profile based on the above Beer-Lambert approximation is finally the inverse of τ_i. The Beer-Lambert approximated light extinction curve was estimated with a vertical resolution of 0.25m, corresponding to the vertical voxel size used in the DART simulations. Additionally, a Beer-Lambert approximated light extinction profile assuming a single layer (so-called Big-Leaf model) was calculated based on the averaged vertically accumulated PAI. The layered Beer-Lambert and Big-Leaf approximated average light extinction profiles were compared to the ones based on the complex 3D representation of the canopy using the DART model.

3. Results

Fig. 1 shows the canopy structure and distribution of vegetation material inside the canopies of the two study sites for a 60 m wide and 10 m deep transect of the study sites. The temperate forest shows a very dense and horizontally homogeneous upper canopy layer, followed by a less dense, horizontally less homogeneous understorey. More than 50% of the total plant material can be found at levels higher than 20 m above ground (corresponding to the upper 40% of the canopy). For the tropical forest, however, more than 50% of the total plant material can be found at levels higher than 13 m above ground (corresponding to the upper 60% of the canopy). The canopy structure of the tropical forest is characterized by a horizontally very heterogeneous, but dense overstorey with varying tree heights, followed by a less dense, horizontally still heterogeneous mid-storey and a very dense, horizontally more homogeneous understorey. Even though the canopy structure differs drastically between the two analysed forests, the averaged vertical profiles of cumulative plant material from the top to the bottom of the canopy (quantified as plant area index (PAI)) do not differ a lot between the two ecosystems, suggesting that the difference in canopy structure between the two forests is mainly due to the different distribution of plant material rather than the total amount of plant material.

3.1. Three-dimensional light extinction in a temperate vs. tropical forest

The difference in canopy structure between the two study sites clearly has an influence on the light distribution inside the canopy. Fig. 2 shows the average diurnal extinction of PAR for the same transect as shown in Fig. 1 together with four horizontal slices (Figs. 2(c), 2(d)) through the canopy at 0, 25, 50, and 75% canopy height and one vertically averaged profile (right panel of Figs. 2(a) and 2(b)). Due to the very dense and homogeneous upper layer in the temperate forest, most of the incoming PAR is already extinct across the entire horizontal area after just few meters into the canopy (top right panel in Fig. 2(c)). Only the few canopy gaps within the study site allow for more radiation passing into the lower canopy parts. These canopy gaps also allow more light to pass into lower strata during specific solar positions, which can be seen by brighter linear features protruding into the canopy at certain angles especially in Fig. 2(a). The dense and horizontally homogeneous upper canopy layer in the temperate forest averages to a typical

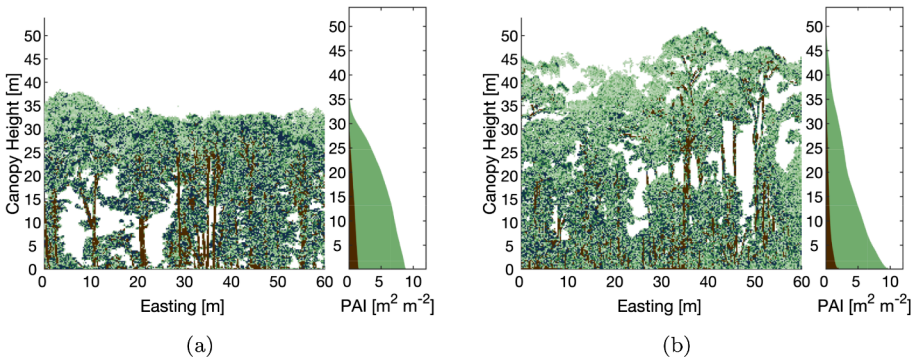


Fig. 1. Vegetation density grids of a 60 m wide and 10 m deep transect for the (a) temperate (Northing: 10 - 20 m) and (b) the tropical (Northing: 40 - 50 m) study site. The two-dimensional projection shows vegetation area volume densities [m^2m^{-3}] at 25 cm voxel resolution from low (light green) to high (dark green). The right panel shows the cumulative plant area index (PAI) averaged across the 60x10 m area (all 10 m deep transects are shown in the supplementary material), with brown color for wood material and green color for leaf elements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

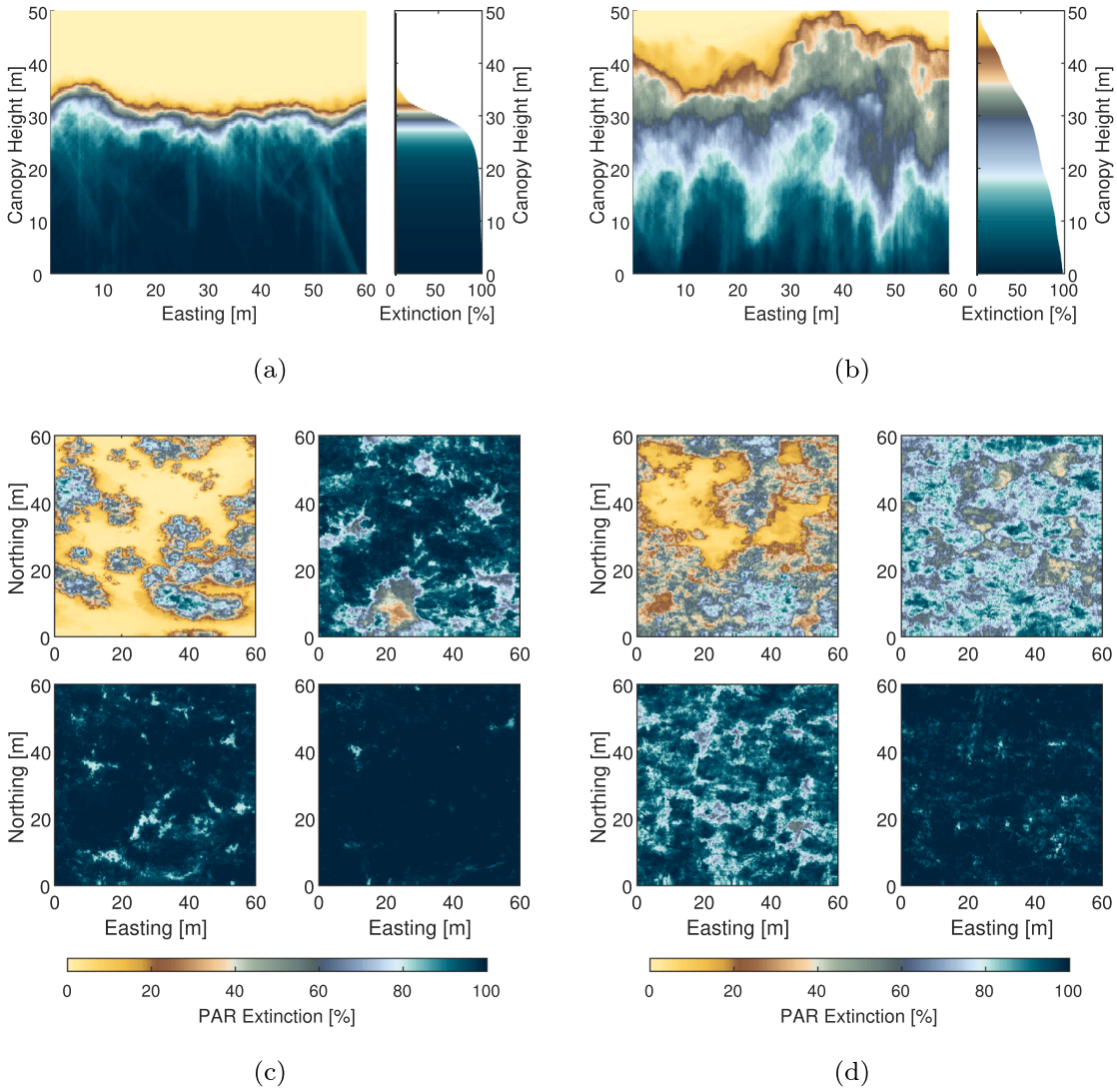


Fig. 2. Average diurnal light extinction for a 10 m deep transect for the temperate (a) and tropical (b) study site. The 10 m deep transect is oriented East-West and is located between Northings 10 - 20 m and 40 - 50 m for the temperate and tropical study site, respectively. The right panel shows the average light extinction profile for the entire transect (all 10 m deep transects are shown in the supplementary material). The lower panel shows four horizontal slices through the entire 60 x 60 m study sites at the temperate (c) and tropical (d) forest. The slices were taken at 75% (top left), 50% (top right), 25% (bottom left) and 0% (bottom right) of the total canopy height of the respective forest, where 0% denotes the forest floor and 100% maximum canopy height.

exponential light extinction curve as shown in Fig. 3(a) (DART modelled, layered Beer-Lambert and Big-Leaf approximated light extinction profiles). The tropical forest on the other hand shows a much more heterogeneous distribution of PAR extinction throughout the whole canopy, mainly due to the many vertical and horizontal canopy gaps caused by the large horizontal variance in tree height allowing the light to pass into lower strata of the canopy. This results in a light extinction profile for the whole study site that is on average more linear

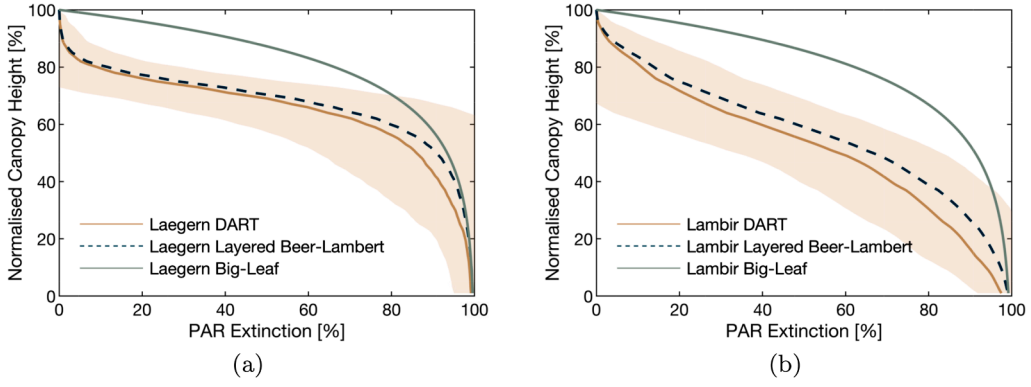


Fig. 3. DART modelled vs. layered Beer-Lambert approximated average light extinction profiles and Big Leaf approximated average light extinction profile for the temperate (3 a) and tropical forest (3 a) for the entire 60 x 60 m study plots. The shaded areas denote the standard deviation in light extinction for the DART modelled extinction. 100% canopy height denotes maximum canopy height of the entire plot to enable a comparison with the Big-Leaf approximated light extinction profiles. Comparison is shown for solar noon conditions.

but at the same time horizontally more variable than that of the temperate forest as shown in Fig. 3(a) (DART modelled, layered Beer-Lambert and Big-Leaf approximated light extinction profiles). For the temperate study site, already 86% of the incoming irradiance is extinct at 50% canopy height, whereas for the tropical case only 58% of the incoming light is extinct at the same height level.

Fig. 3 shows the comparison between the DART simulated average light extinction profiles for the temperate and tropical study site and a multi-layered Beer-Lambert approximated extinction profile as well as a single layer Beer-Lambert approximation as often assumed in so-called Big-Leaf models, where the whole forest canopy is approximated by a single layer defined by the vertical accumulated average LAI. Fig. 3 highlights the large discrepancies between the DART simulated light extinction profile compared with the single layer Big-Leaf model, especially in the upper and mid canopy. For estimations of light extinction at the bottom of the canopy, the Big-Leaf model performs quite accurately (relative difference to DART simulated extinction: 0.52% and 5.8% at 10% canopy height for temperate and tropical site respectively). If the vertical distribution of canopy material is more accurately represented with a layered Beer-Lambert approach, the average light extinction profile can be approximated more accurately, closely following the DART simulated light extinction profile, generally overestimating extinction within the canopy. The difference to the DART simulated extinction is higher in the upper crown layer (up to 30% difference in the upper 20% of the canopy height) and gets smaller towards the bottom of the canopy (0.5% and 3.8% at 10% canopy height for temperate and tropical site respectively).

3.2. Diurnal variation in light extinction

For the diurnal variation in PAR distribution, multiple simulations have been conducted in two-hour intervals between 15 minutes after sunrise and 15 minutes before sunset for the respective study sites, plus a simulation at solar maximum for the date of the northern hemisphere solstice (21st of June). Fig. 4 shows the vertical change in light extinction over the course of a single day (northern hemisphere solstice) for the two study sites. The average light extinction profile per study site was calculated for each simulation. Light extinction profiles between simulated solar angles were linearly interpolated. Due to the multiple vertical gaps in the canopy of the tropical forest larger variations in light extinction can be observed with changing solar angles. For both study sites, minimum extinction for all canopy layers can be observed during mid-day, whereas maximum extinction for all height layers are only observed at low solar angles, once the direct component of incoming sunlight on top of canopy has a larger component relative to the diffuse sky light. This is usually the case several minutes after sunrise or before sunset.

3.3. Light extinction - the role of LOP

In order to analyse how leaf optical properties affect light distribution within the canopy we ran two simulations at solar noon, where we assigned the tropical LOPs to the temperate forest canopy and vice versa. Fig. 5 shows the four light extinction profiles for the 60 x 60 m study plots with their proper LOPs and with the exchanged ones from the other forest. The extinction decreases slightly (<5% below 80% canopy height) in the temperate case when we assign LOPs from the tropical test site. The biggest difference can be observed in the upper canopy layer with an increase in available light of up to 12% (upper 2% of the canopy). By assigning the temperate forest LOPs at the tropical forest site we observe a much larger change in light distribution throughout the whole canopy. We observe an increase in extinction of more than 5% above 40% canopy height and even more than 12% above 80% canopy height. Therefore, the beech-dominated optical properties of the temperate forest site absorbed much more incoming solar radiation, than the optical properties of the tropical forest, adding to the explanation for the differences in light extinction profiles of the two test sites.

Fig. 5 (c) shows the measured leaf reflectance and transmittance for the two study sites in the simulated spectral region between 400 and 700 nm. The LOPs for the temperate and the tropical site were acquired differently with an integrating sphere and a leaf-clip, respectively (see Section 2.3). As the LOPs for the temperate study site are dominated by beech trees, the variance in LOP within this single species is relatively small compared with the observed variance at the tropical site caused by the high species richness with highly diverse optical characteristics of the leaves. For both study sites, larger differences between leaves from the upper and lower parts of the crowns or understory can be observed for the transmittance, whereas the difference in reflectance between leaves of the two vertical canopy compartments are smaller.

3.4. Light extinction - diffuse illumination conditions

The radiative transfer through the forest canopies at complete diffuse illumination conditions (i.e. complete overcast skies) were simulated within DART by not simulating the radiative transfer through the atmosphere and defining the diffuse irradiance fraction to the total irradiance to be 1. In that way, no direct irradiance from the sun is simulated and the only illumination source is the diffuse sky illumination. Fig. 6 shows the diffuse PAR extinction for the same transects as shown in Fig. 2. Due to the missing direct irradiance part, the light distribution

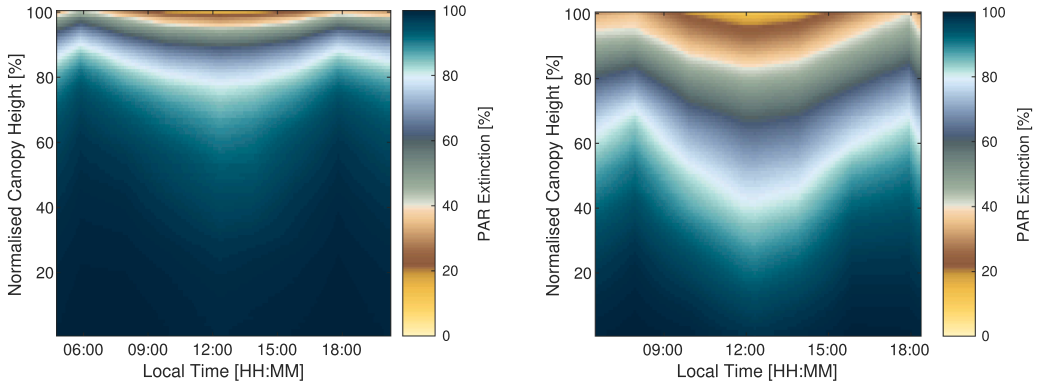


Fig. 4. Vertical diurnal changes in light extinction for the temperate (a) and tropical (b) study site. For each simulated solar angle, the average light extinction per height level for the whole 60 x 60 m was calculated. Light extinction profiles between simulated solar angles were linearly interpolated. 100% canopy height denotes the height of the convex surface fitted to the digital surface model (DSM).

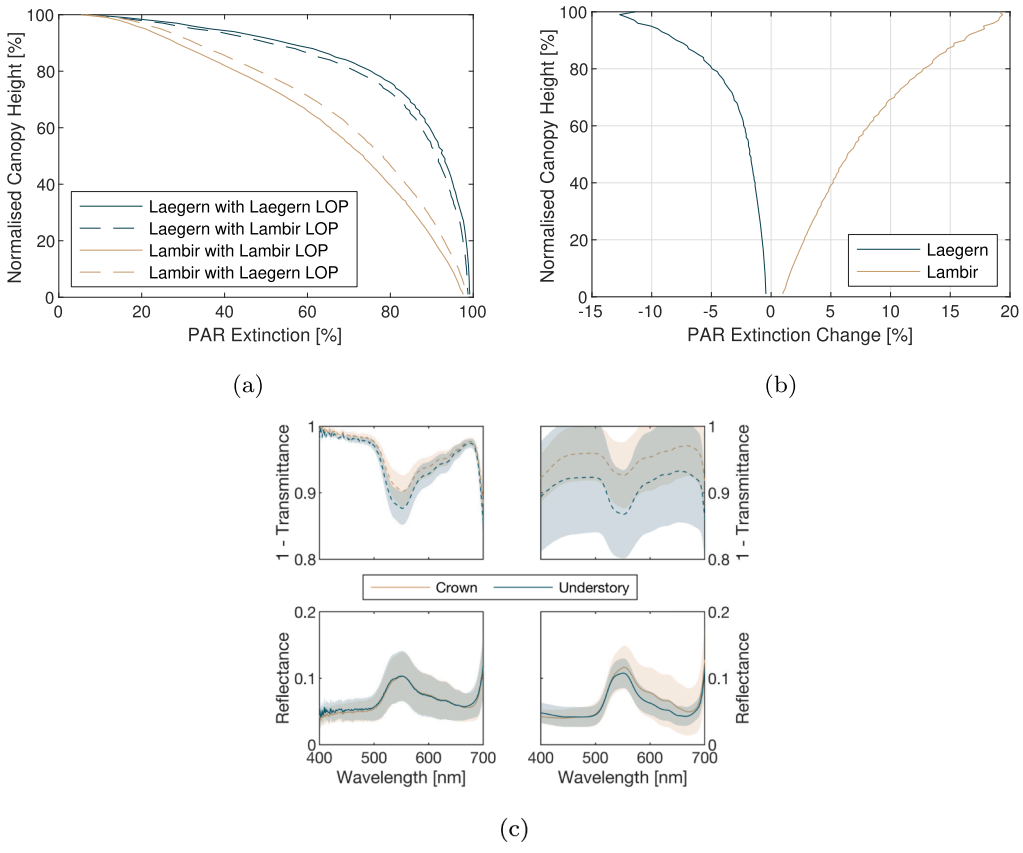


Fig. 5. Sensitivity of light extinction profiles due to change in LOP. (a) Absolute change in PAR extinction when we exchange the LOPs of the two study sites. Solid lines denote the light extinction profile if the proper LOPs are assigned, dashed lines denote the light extinction profile with LOPs of the other study site assigned. (b) shows the relative change compared to the initial simulation with the properly assigned LOPs. Results are based on solar noon simulations. The average light extinction for the entire 60 x 60 m plots is shown. 100% canopy height denotes the height of the convex surface fitted to the digital surface model (DSM). (c) shows the average reflectance and transmittance used for parameterization of the DART model for the temperate (left) and tropical (right) study site respectively.

within the canopy is much more homogeneous with well defined layering. However, the average light extinction profiles for the shown transects (Figs. 6(a) and 6 b) as well as for the whole study plots (Fig. 6 (c)) do not differ much from the case where we have direct solar irradiance from the sun and diffuse sky light. Due to the more homogeneous distribution of the light within the canopy, also the variance in light extinction per height layer was decreased (shown as the standard deviation of the light extinction as shaded areas in Fig. 6(c)).

3.5. Light extinction in wood proximity

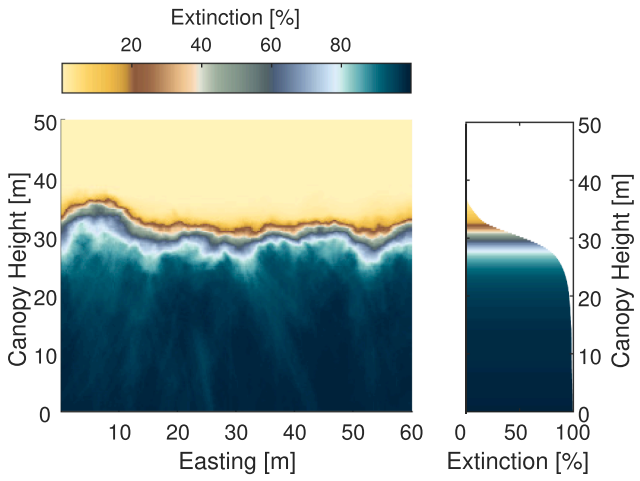
Based on the wood structure model derived as described in Section 2.4.2 we were able to analyse the light extinction as a function of distance from larger wood bodies (tree trunks and major branches). Fig. 7 shows the relation of extinction to distance of larger wood bodies at different canopy height layers (between 2 m and 31 m or 47 m above canopy for the temperate and the tropical site, respectively, in 5 m height intervals). Wood bodies generally had a larger influence on extinction in the upper canopy layers mainly due to the higher overall irradiance levels. Due to the already largely extinct light in the lower canopy layers, the distance to wood bodies does not strongly affect simulated irradiance. Nevertheless, between 2 m and 7 m above ground, the average light extinction difference between < 1m and > 3m distance was 2.6% and 6% for the temperate and tropical study plots, respectively. With increasing height above ground, the differences in extinction with increasing distance from wood material become larger. Between 17 m and 22 m above ground, the average light extinction difference between $< 1$and > 3m distance was 15.5% and 17% for the temperate and tropical study plots, respectively.

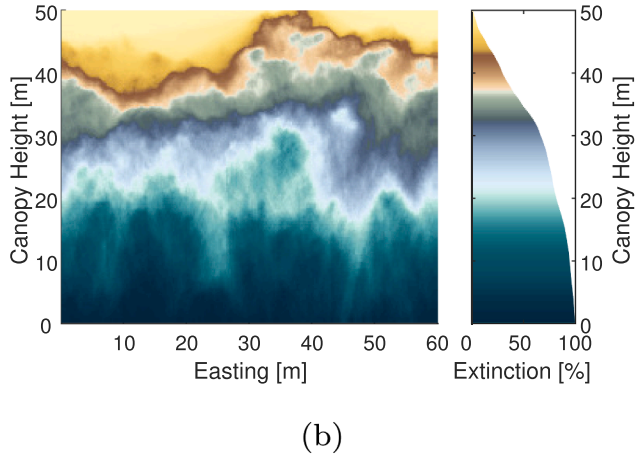
4. Discussion

4.1. Three-dimensional light extinction in a temperate vs. tropical forest

The comparison of light extinction between a temperate forest patch dominated by a single species and a species-rich tropical forest patch has shown that the contrasting canopy structure is fundamental for explaining the distribution of light within the canopy. The heterogeneous distribution of canopy material in the tropical forest allows more light to pass into lower strata, possibly explaining the abundance of shade tolerant species in the middle- and understorey of the canopy. Williams et al. (2017) showed that a mixture of species shows larger crown-complementarity (i.e. vertically non-overlapping crowns) compared with forests dominated by a single species as found in our temperate study site. According to Williams et al. (2017), crown complementarity is a mechanism related to light interception and use that links biodiversity with ecosystem productivity. Williams et al. (2017) showed that greater crown complementarity found in species-rich canopy mixtures lead to increased stem biomass overyielding. Therefore a mixture of fast growing shade-intolerant species with slow-growing shade-tolerant species can enhance productivity in forests (Huang et al., 2018; Kelty, 1989; Morin et al., 2011; Schmid and Niklaus, 2017; Williams et al., 2017), but also leads to a more heterogeneous distribution in canopy material and intercepted light, shown in this paper's comparison.

The differences in species composition, crown complementarity and canopy structure and ultimately available light within the canopy will further influence the development of the two showcased forests. In the old-growth forest found at the temperate study site, there is no particular gain for a single individual to grow in size to capture more light. According to King (1990), this forest patch already reached the so-called evolutionary stable state (ESS), where a gain in canopy height of a single individual is not favorable anymore. In the tropical site, however,





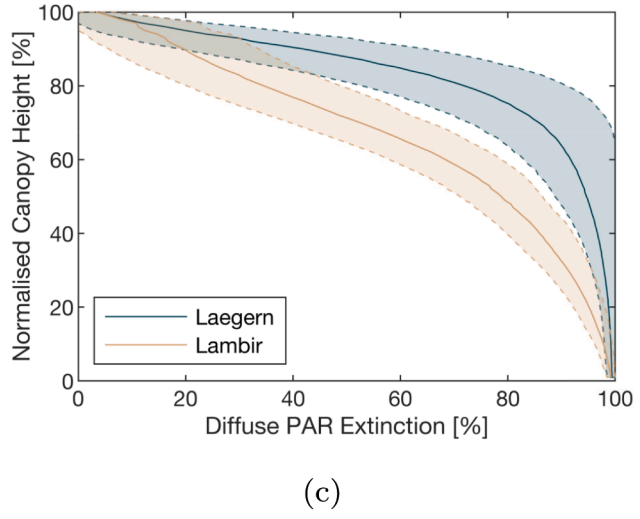


Fig. 6. Diffuse light extinction for the corresponding transects shown in Fig. 1 and 2 for the temperate (a) and the tropical (b) study site. The average diffuse light extinction of the 10 m deep transect is shown. The right panel shows the average diffuse light extinction profile for the entire transect (all 10 m deep transects are shown in the supplementary material). The average diffuse light extinction profile for both study sites is shown in (c). The shaded areas in (c) denotes the variance in diffuse light extinction for the respective height level. 100% canopy height denotes the height of the convex surface fitted to the digital surface model (DSM).

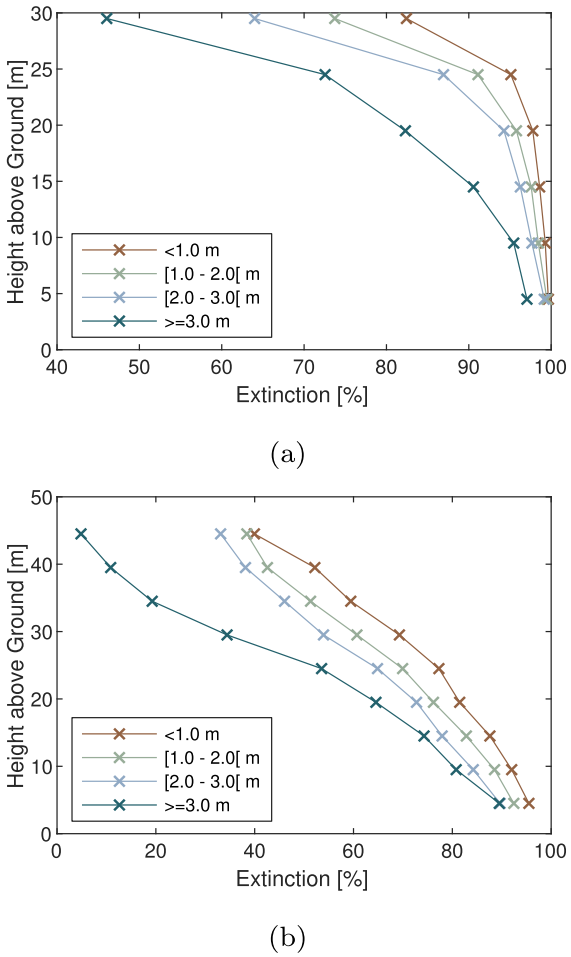


Fig. 7. Extinction profiles as a function of distance from wood material for the temperate (a) and tropical (b) study plots.

where multiple species compete for light, evolutionary considerations are more complex, because different species may use different strategies to capture light and allocate biomass to plant organs. Therefore, it is harder to predict how a multi-species ESS vertical canopy profile should look like and conceivably it might be more heterogeneous than for monocultures. An indication for this has been observed in a grassland biodiversity experiment by Wacker et al. (2009).

The heterogeneous canopy structure found in the tropical case is both the result of the high diversity of tree species present and allows for more niches of additional species with varying resource-use strategies to find their matching biotope space to thrive. The more complex canopy structure may therefore also be used as an indicator for high diversity (see also McElhinny et al., 2005). The question to which degree a heterogeneous canopy structure is a consequence or cause (via feedback effects) of diversity is largely unexplored (see e.g. Sapijanskas et al., 2014).

Zellweger et al. (2019) showed that vegetation structure not only drives the interception of solar radiation, but also affects microclimatic conditions within the canopy on temporal and spatial scales. However, information on the 3D distribution of light, vital for analysing microclimatic conditions within the forest, is still rare. We show that with the proposed approach a modelling of the light regime in any forest canopy is possible in unprecedented detail. The high level of detail has a large impact on computational costs, limiting the size of forest patches that can be analyzed. However, as Fig. 3 shows, the DART-simulated light extinction profiles also differ largely from the layered Beer-Lambert or Big-Leaf approximated light extinction profiles. The layered

Beer-Lambert approximated light extinction profiles are based on an average vertical vegetation density profile with a vertical resolution of 0.25 m, matching the voxel size of the DART simulations. By increasing the height of the vertical layers, the discrepancies to the DART modeled light extinction profiles increases up to the extent shown in the Big-Leaf approximated profiles assuming a single canopy layer covering the whole canopy extent (see Fig. 3). Additionally, with the layered Beer-Lambert or Big-Leaf approximated light extinction we are missing the information on horizontal variations in light extinction within the whole canopy which can be analysed by the 3D DART light extinction simulations. Additionally, the Beer-Lambert approximation does not account for diffuse irradiance nor for multiple scattering, therefore not allowing for assessments in small scale variations of the irradiance field due to the heterogeneity of the canopy (see also Kükenbrink et al. (2019)). This underlines the need for such high detailed modelling of the light regime in forest ecosystems. Especially as the radiative transfer through the forest ecosystems is recognized as one of the largest sources of uncertainty in dynamic global vegetation models (DGVMs), where often simplifying assumptions about the distribution of plant material are made (e.g. Big Leaf assumption) (Alton et al., 2007a; Fisher et al., 2017). These simplifying assumptions on canopy structure could then lead to large uncertainties in predicted photosynthesis (e.g. Braghiere et al., 2019; 2020; Rosati et al., 2020) or in the assessment of forest gas exchange (e.g. Damm et al., 2020). The proposed approach could be used as a benchmark for DGVMs to assess the level of detail needed for an accurate simulation of the 3D radiative transfer through the canopy, possibly allowing for more accurate modelling of the radiative transfer also on larger scales. With data from NASA's Global Ecosystem Dynamics Investigation (GEDI) instrument, more wide spread (however without wall-to-wall global coverage) information regarding the distribution of vegetation material can be gained. From this we could improve our understanding of the differences in canopy structure of different forest canopies, further improving the parameterization of forest structure in DGVMs.

Even though the proposed approach can deliver 3D light extinction maps at high level of detail, they are still based on simplifying assumptions (e.g. turbid medium assumption, neglecting the specular reflectance term of leaves, as further discussed in Section 4.3, use of standard atmosphere models etc.), which may add sources of uncertainty in the modeled light extinction products. However, the proposed approach using the DART model was reported to deliver accurate estimates for 3D irradiance fields compared with *in-situ* measurements (Kükenbrink et al., 2019) as well as in simulating imaging spectroscopy data when compared with actual at-sensor radiance measurements (Schneider et al., 2014). The inherent complexity of instantaneous, 3D irradiance measurements within a forest canopy (e.g. through quickly changing irradiance conditions caused by moving clouds or tree crowns) makes an accurate validation of the modelled 3D light distribution difficult to achieve. Measurements of the light distribution along a single vertical profile are sensitive to the proximity to major tree branches and trunks and are likely not representative for larger forest stands (see Sections 3.5 and 4.5). Nevertheless, the modelled light extinction corresponds well with the measured and published light extinction profiles for a mature beech forest stand in Southern Germany (Leuchner et al., 2011). For the site at the Lambir Hills National Park, Yoshimura and Yamashita (2014) and Kenzo et al. (2015) measured vertical extinction profiles through canopy gaps with quantum sensors mounted on the gondola of the canopy crane. The measured light extinction profiles show a slightly more exponential characteristic compared with the more linear shape of the modelled light extinction profiles of this study. However, Yoshimura and Yamashita (2014) stated the difficulties in measuring these light extinction profiles due to quickly changing irradiance conditions and reported large variance in light extinction over the whole vertical profile. Furthermore, as the canopy crane mounted gondola is only able to penetrate through the canopy within canopy gaps, the plot-averaged measured extinction profiles might not be directly comparable to our modelled extinction profiles, as sampling only in larger gaps might introduce a bias. A direct comparison of single measured light profiles with modelled ones was not possible due to spatial and temporal differences between the data sets (Yoshimura, pers. comm.). The modelled high extinction of up to 99% close to the canopy floor for both study sites also corresponds well to the measured light extinction for a mature beech forest as reported in Leuchner et al. (2011) or for the same temperate forest plot as in this study as reported in Damm et al. (2020) and for the same tropical rain forest site as in this study as reported in Yoshimura and Yamashita (2014) or Kenzo et al. (2015). Rissanen et al. (2019) also reported reduced light interception with increasing structural complexity of the canopy in their study on the biodiversity experiment located on the Macdonald Research Farm at McGill University, Canada. Therefore, we argue that the proposed approach delivers information about the 3D light distribution in forest ecosystem in a complexity and at a level of detail we have not yet seen. However, the approach should be further tested in additional forest ecosystems to fully analyse the potential of the approach and to cover a larger range in forest structure and ecosystems. The modelling environment we present would as well be ideal to test sampling approaches of light extinction in terms of representativeness, as is done for terrestrial laser scanning in respect to forest inventory use (Abegg et al., 2017).

4.2. Diurnal variation in light extinction

Vegetation structure further affects light interception and distribution over the whole diurnal cycle. Due to the heterogeneous canopy structure found in the tropical forest, an increased variability in available light for any canopy layer can be observed compared with the temperate forest. This assures that also species in lower canopy strata receive enough light over the diurnal cycle to be productive and competitive. In the case of the temperate forest on the other hand, the variability in available light over the whole diurnal cycle within the lower stratum of the canopy is minimal, reducing the opportunities for competing species to grow. However, the seasonal leaf-fall pattern in the temperate forest allows some early-growing understorey herbs to coexist with the large canopy trees.

The diurnal simulations have shown that for both study sites, minimum extinction throughout the whole canopy can be observed during mid-day at solar maximum conditions. However, interestingly, maximum extinction is not observed right after sunrise or before sunset for both study sites as stated in Section 3.2. This could be explained by the fact that light extinction, as defined in this paper, is a relative term based on the maximum solar irradiance observed above the forest canopy. Due to the low solar angle at the beginning and end of the day, nearly 100% of the radiation is diffuse-sky illumination rather than direct solar irradiance, reducing the total incoming radiation on the top of canopy to a minimum. This also reduces the difference in light conditions between the top of and within the canopy, resulting also in lower light extinction throughout the canopy. The distribution of leaf angles also affects the diurnal distribution of light within the canopy, as certain leaf and solar angle combinations will promote or prevent the distribution of light within the canopy (e.g. Wang et al., 2007). In this study, a single leaf angle distribution function per study site (i.e. plagiophile for temperate and spherical for tropical forest) was used to parameterize the forest canopy, which could lead to a bias when simulating light extinction. Measuring accurate 3D leaf angle distribution functions is still a challenge, notwithstanding the fact that leaves may adjust their angles diurnally. However, recent studies have shown the potential of high resolution TLS measurements for the retrieval of momentarily accurate leaf angle distributions (e.g. Li et al., 2018; Liu et al., 2019; Vicari et al., 2019).

Seasonal differences in light extinction were not analysed in this study. An analysis of the seasonal variation in light extinction would require multiple laser scanning and LOP acquisitions distributed across

the year in order to adequately represent seasonal changes in canopy structure and LOP. However, especially in the case of the temperate, deciduous forest site, seasonal changes in canopy structure and leaf-optical properties can have large impacts on the distribution of light within the canopy, allowing seasonal growing periods for certain species (e.g. wild garlic, *Allium ursinum* L., in early spring). These seasonal changes in light conditions should be addressed in future studies. Morton et al. (2016) analysed diurnal and seasonal variability in light utilization in an Amazon forest, however they assumed a constant canopy structure and constant LOPs over the year.

4.3. Light extinction - the role of LOP

Compared with structural vegetation characteristics, leaf optical properties only had a small influence on the distribution of light within the canopy. The change in simulated light extinction when we exchanged LOPs of the two study sites depended on the canopy height and was generally smaller for the temperate than for the tropical study site. However, this observed change was purely based on differences in the measured reflectance and transmittance values, which do not account for specular components of the LOPs. Due to the entirely different anatomical and morphological structures of temperate and tropical leaves (i.e. waxy leaf surface found in the tropics), it is believed that larger differences in specular reflectance could exist, probably resulting in a bigger influence of the leaves' optical properties on the distribution of light within the canopy. The specular reflectance distribution functions of leaves were neither measured nor modelled in this study. We emphasize the need for further analysis of the influence of the specular term on the light distribution and suggest future studies on the matter, including geometrical-optical modelling of small leaves including a specular component.

Another source of uncertainty in the modeled light extinction could be due to the assignment of the LOP onto the virtual forest canopy. The leaf optical properties for the temperate and tropical site were acquired using two different approaches (Laboratory measurement with integrating sphere for the temperate forest vs. non-destructive LOP sampling using a leaf-clip add-on to the ASD spectroradiometer for the tropical forest), possibly leading to some systematic differences between measured LOPs with the different approaches. Hovi et al. (2017) found that reflectance measured using a leaf-clip is on average 14% higher compared with measurements using a single integrating sphere. As it was not possible to assign LOP to the different tree species within the DART scene, we opted for a random assignment of the measured LOPs to the vegetation turbid medium voxels.

We argue that the above stated sources of uncertainty only have a minor influence on the modeled light extinction. The findings in this study showed that substantially different LOPs only resulted in relatively small changes in modeled light extinction of up to 10–15% at the top of canopy and less than 3% below 20% of the normalised canopy height. This assumption is also supported by the findings of Kükenbrink et al. (2019) and Stuckens et al. (2009), where differences in simulated irradiance or reflectance values were small when LOPs were varied within realistic boundaries.

In this study, we only analysed light extinction within the PAR spectral region between 400 and 700 nm, as the majority of light harvested for photosynthesis is located within these wavelengths. However, Chen and Blankenship (2011) found that under light-limiting conditions, certain plants adapted to deep shade also can use wavelengths greater than 700 nm for photosynthesis due to a modification in the plant's chlorophyll (Chen and Blankenship, 2011; Chen et al., 2010; Miyashita et al., 1996). However, when light interception is studied in relation to plant health and growth, an analysis based on photon flux density (i.e. measured in mol $m^{-2}s^{-1}$) might be better suited because the rate of photosynthesis depends on the number of photons received, rather than photon energy (i.e. measured in W m^{-2}) (Jones et al., 2003).

4.4. Light extinction - diffuse illumination conditions

Especially in the tropics, diffuse-sky irradiance is the dominant illumination source rather than direct sunlight due to high cloud coverage. Therefore it is important to also analyse the distribution of light within the canopy under diffuse illumination conditions. Alton et al. (2007b) found that light-use efficiency (LUE) is increased by 28% to 33% for a temperate and tropical forest, respectively, under diffuse illumination conditions. It is believed that the LUE enhancement under diffuse illumination is due to a sharing of the canopy radiation-load. Alton et al. (2007b) argue that, under direct sunlight, a sizeable fraction of the foliage is either light-saturated or not receiving enough sunlight to photosynthesize efficiently. Our simulation with total diffuse irradiance conditions showed that the distribution of light within the canopy was much more homogeneous at both sites compared with conditions under direct sunlight. A more even distribution of light within the canopy could potentially be a further explanation for an increased LUE and productivity of a forest.

4.5. Light extinction in wood proximity

Due to the separation of wood and leaf material in the laser acquisitions, it is possible to analyse light extinction in the vicinity of major trunks and branches. This analysis further highlights the complexity of radiation measurements within the canopy, as wood material can have an effect on observed incoming radiation at several meters distance from the tree trunk or major branches. In this study, we modeled the 3D wood structure based on the amount of detected laser returns from wood material within each voxel. This can result in discontinuous trunk and branch structures within the model due to occlusion effects caused by dense understorey (especially in the tropical site) or trunks and branches (Kükenbrink et al., 2017; Schneider et al., 2019). A continuous representation of the wood structure could have been achieved by using a quantitative structure model (QSM) as introduced by Raumonen et al. (2013) and already employed by Calders et al. (2018) to reconstruct a temperate forest for radiative transfer modelling. However, a successful performance of the QSM model requires a highly detailed representation of the wood structure. Missing parts of branches or trunks can cause the QSM model to fail, which would have been especially a problem in the tropical site, where dense understorey often obstructed a clear view of the lower trunk area. We therefore opted for the stated simpler approach for representing the wood structure within the DART model.

5. Conclusion

We conclude that a detailed three-dimensional forest reconstruction is essential for accurate modelling of the light distribution within a forest canopy. In this study we developed an approach to model and analyse the spatial heterogeneity of light distribution at high levels of detail in the vertical, horizontal and temporal domains. We showed that the radiative transfer of photons through the forest canopy was mainly driven by characteristics of the canopy structure, whereas optical properties of leaves had a smaller impact on the distribution of light within the canopy. The comparison of the simulated light extinction profiles with the ones produced using a Beer-Lambert approximation revealed the necessity of such a complex representation of the 3D canopy structure in order to accurately represent the 3D radiative transfer of photons through the forest canopy. The proposed approach may serve as a benchmark to assess the impact of level of detail necessary to represent a forest canopy structure as well as optical characteristics in a radiative transfer model. This will further improve radiative transfer approximations in dynamic global vegetation models (DGVMs), further advancing the understanding of the importance of light distribution within a forest canopy. This is particularly important when DGVMs shall represent a high level of detail allowing to assess primary productivity and other processes well. For this it is important that photosynthetic

light curves are not linear and thus for accurate prediction light distributions cannot be averaged or aggregated across canopy parcels before simulating assimilation. The presented study allows such accurate estimates of photosynthesis and primary productivity. High resolution 3D laser-scanning data with *in-situ* and *in-vivo* measured optical characteristics in combination with a 3D radiative transfer model reveal insights of small scale variability of light availability and distribution within a canopy and therefore advance our understanding of light-matter interactions driving species coexistence, competition and diversity in complex forest canopies. In this study we only analysed 3D light extinction for two forest ecosystems with contrasting canopy structure and physiological characteristics. In future studies, additional forest ecosystems should be analysed regarding the 3D light distribution and its effect on ecosystem functioning. Furthermore, possibilities to simplify the modelling approach and to validate modelled 3D light distributions should be assessed.

CRediT authorship contribution statement

Daniel Kükenbrink: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Fabian D. Schneider:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft. **Bernhard Schmid:** Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft. **Jean-Philippe Gastellu-Etchegorry:** Conceptualization, Writing - original draft. **Michael E. Schaepman:** Conceptualization, Writing - original draft. **Felix Morsdorf:** Conceptualization, Formal analysis, Project administration, Writing - original draft.

Declaration of Competing Interest

The authors declare no conflict of interest.

Acknowledgement

This study has been supported by the University of Zurich Research Priority Program on Global Change and Biodiversity (URPP GCB). The research carried out at the Jet Propulsion Laboratory, California Institute of Technology, was under a contract with the National Aeronautics and Space Administration (80NM0018D0004). Government sponsorship is acknowledged. Daniel Kükenbrink has been additionally supported by the Swiss National Forest Inventory. We thank Dr. Tomoaki Ichie, Dr. Eri Yamasaki and Prof. Dr. Kentaro Shimizu for their support in organizing and performing the field work at the Lambir Hills NP. Permits and access to the Lambir Hills National Park research site (Miri Division, Sarawak) have been granted by the Forest Department Sarawak, as with research permit no. NCCD.907.4.4(JLD.13)-181 and park permit no. 128/2016. UAVLS flight operations and data processing were performed by Aeroscout, Switzerland. We thank the anonymous reviewers for their valuable comments.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at 10.1016/j.agrformet.2020.108230.

References

Abegg, M., Kükenbrink, D., Zell, J., Schaepman, M.E., Morsdorf, F., 2017. Terrestrial laser scanning for forest inventories-tree diameter distribution and scanner location impact on occlusion. Forests 8 (6), 1–29. https://doi.org/10.3390/f8060184.

Alton, P.B., Ellis, R., Los, S.O., North, P.R., 2007. Improved global simulations of gross primary product based on a separate and explicit treatment of diffuse and direct sunlight. Journal of Geophysical Research Atmospheres 112 (7), 1–12. https://doi.org/10.1029/2006JD008022.

Alton, P.B., North, P.R., Los, S.O., 2007. The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. Glob Chang Biol 13 (4), 776–787. https://doi.org/10.1111/j.1365-2486.2007.01316.x.

Ashton, P.S., 2005. Lambir's Forest: the World's Most Dive Known Tree Assemblage? Pollination Ecology and the Rain Forest. Springer-Verlag, New York, pp. 191–216. https://doi.org/10.1007/0-387-27161-9_17.

Asner, G.P., Martin, R.E., Suhaili, A.B., 2012. Sources of canopy chemical and spectral diversity in lowland Bornean forest. Ecosystems 15 (3), 504–517. https://doi.org/10.1007/s10021-012-9526-2.

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, U.K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-Scale carbon dioxide, water vapor, and energy flux densities. Bull. Am. Meteorol. Soc. 82 (11), 2415–2434. https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2.

Baldocchi, D.D., Wilson, K.B., Gu, L., 2002. How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest - An assessment with the biophysical model CANOAK. Tree Physiol. 22 (15–16), 1065–1077. https://doi.org/10.1093/treephys/22.15-16.1065.

Berk, A., Bernstein, L., Robertson, D., 1987. MODTRAN: A Moderate Resolution Model For LOWTRAN. Technical Report. Spectral Sciences. Inc., Burlington.

Braghiere, R.K., Quaife, T., Black, E., He, L., Chen, J.M., 2019. Underestimation of global photosynthesis in earth system models due to representation of vegetation structure. Global Biogeochem Cycles 33 (11), 1358–1369. https://doi.org/10.1029/2018GB006135.

Braghiere, R.K., Quaife, T., Black, E., Ryu, Y., Chen, Q., De Kauwe, M.G., Baldocchi, D., 2020. Influence of sun zenith angle on canopy clumping and the resulting impacts on photosynthesis. Agric For Meteorol 291 (May), 108065. https://doi.org/10.1016/j.agrformet.2020.108065.

Calders, K., Origo, N., Burt, A., Disney, M., Nightingale, J., Raumonen, P., Åkerblom, M., Malhi, Y., Lewis, P., 2018. Realistic forest stand reconstruction from terrestrial LiDAR for radiative transfer modelling. Remote Sensing 2018, Vol. 10, Page 933 10 (6), 933. https://doi.org/10.3390/RS10060933.

Chen, J.M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., Chan, D., 2012. Effects of foliage clumping on the estimation of global terrestrial gross primary productivity. Global Biogeochem Cycles 26 (1), 1–18. https://doi.org/10.1029/2010GB003996.

Chen, M., Blankenship, R.E., 2011. Expanding the solar spectrum used by photosynthesis. Trends Plant Sci. 16 (8), 427–431. https://doi.org/10.1016/j.tplants.2011.03.011.

Chen, M., Schliep, M., Willows, R.D., Cai, Z.-L., Neilan, B.A., Scheer, H., 2010. A red-shifted chlorophyll. Science 329 (5997), 1318–1319. https://doi.org/10.1126/science.1191127.

Cox, P.M., Betts, R.A., Bunton, C.B., Essery, R.L.H., Rowntree, P.R., Smith, J., 1999. The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. Clim Dyn 15 (3), 183–203. https://doi.org/10.1007/s003820050276.

Damm, A., Paul-Limoges, E., Kükenbrink, D., Bachofen, C., Morsdorf, F., 2020. Remote sensing of forest gas exchange: considerations derived from a tomographic perspective. Glob Chang Biol 26 (4), 2717–2727. https://doi.org/10.1111/gcb.15007.

Danson, F.M., Disney, M.I., Gaulton, R., Schaaf, C., Strahler, A., 2018. The terrestrial laser scanning revolution in forest ecology. Interface Focus 8 (2), 20180001. https://doi.org/10.1098/rsfs.2018.0001.

Danson, F.M., Hetherington, D., Morsdorf, F., Koetz, B., Allgower, B., 2007. Forest canopy gap fraction from terrestrial laser scanning. IEEE Geosci. Remote Sens. Lett. 4 (1), 157–160. https://doi.org/10.1109/LGRS.2006.887064.

Denning, S.A., Nicholls, M., Prihodko, L., Baker, I., Vidale, P.-L., Davis, K., Bakwin, P., 2003. Simulated variations in atmospheric CO2 over a Wisconsin forest using a coupled ecosystem-atmosphere model. Glob Chang Biol 9 (9), 1241–1250. https://doi.org/10.1046/j.1365-2486.2003.00613.x.

Duursma, R.A., Mäkelä, A., 2007. Summary models for light interception and light-use efficiency of non-homogeneous canopies. Tree Physiol. 27 (6), 859–870. https://doi.org/10.1093/treephys/27.6.859.

Fisher, R.A., Koven, C.D., Anderegg, W.R.L., Christoffersen, B.O., Dietze, M.C., Farrior, C., Holm, J.A., Hurtt, G., Knox, R.G., Lawrence, P.J., Lichststein, J.W., Longo, M., Matheny, A.M., Medvigy, D., Muller-Landau, H.C., Powell, T.L., Serbin, S.P., Sato, H., Shuman, J., Smith, B., Trugman, A.T., Viskari, T., Verbeeck, H., Weng, E., Xu, C., Xu, X., Zhang, T., Moorcroft, P., 2017. Vegetation demographics in earth system models: a review of progress and priorities. Glob Chang Biol (August), 1–20. https://doi.org/10.1111/gcb.13910.

Gastellu-Etchegorry, J., Grau, E., Lauret, N., 2012. DART: a 3D model for remote sensing images and radiative budget of earth surfaces. In: Alexandru, C. (Ed.), Modeling and Simulation in Engineering. CESBIO - CNES, CNRS (UMR 5126), IRD, Universite de Toulouse, Toulouse, France, pp. 1–40.

Gastellu-Etchegorry, J.P., 2008. 3D modeling of satellite spectral images, radiation budget and energy budget of urban landscapes. Meteorol. Atmos. Phys. 102 (3–4), 187–207. https://doi.org/10.1007/s00703-008-0344-1.

Gastellu-Etchegorry, J.P., Martin, E., Gascon, F., 2004. DART: a 3D model for simulating satellite images and studying surface radiation budget. Int J Remote Sens 25 (1), 73–96. https://doi.org/10.1080/0143116031000115166.

Gastellu-Etchegorry, J.-P., Yin, T., Lauret, N., Cajgfinger, T., Gregoire, T., Grau, E., Feret, J.-B., Lopes, M., Guilleux, J., Dedieu, G., Malenovský, Z., Cook, B., Morton, D., Rubio, J., Durrieu, S., Cazanave, G., Martin, E., Ristorcelli, T., 2015. Discrete anisotropic radiative transfer (DART 5) for modeling airborne and satellite spectroradiometer and LIDAR acquisitions of natural and urban landscapes. Remote Sens (Basel) 7 (2), 1667–1701. https://doi.org/10.3390/rs70201667.

Hiromi, T., Ichie, T., Kenzo, T., Ninomiya, I., 2012. Interspecific variation in leaf water use associated with drought tolerance in four emergent dipterocarp species of a tropical rain forest in borneo. Journal of Forest Research 17 (4), 369–377. https://doi.org/10.1007/s10310-011-0303-4.

Hovi, A., Forsström, P., Mõttus, M., Rautiainen, M., 2017. Evaluation of accuracy and practical applicability of methods for measuring leaf reflectance and transmittance spectra. Remote Sens (Basel) 10 (2), 25. https://doi.org/10.3390/rs10010025.

Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., Li, Y., Härdtle, W., Von Oheimb, G., Yang, X., Liu, X., Pei, K., Both, S., Yang, B., Eichenberg, D., Assmann, T., Bauhus, J., Behrens, T., Buscot, F., Chen, X.Y., Chesters, D., Ding, B.Y., Durka, W., Erfmeier, A., Fang, J., Fischer, M., Guo, L.D., Guo, D., Gutknecht, J.L., He, J.S., He, C.L., Hector, A., Hönig, L., Hu, R.Y., Klein, A. M., Kühn, P., Liang, Y., Li, S., Michalski, S., Scherer-Lorenzen, M., Schmidt, K., Scholten, T., Schuldt, A., Shi, X., Tan, M.Z., Tang, Z., Trogisch, S., Wang, Z., Welk, E., Wirth, C., Wubet, T., Xiang, W., Yu, M., Yu, X.D., Zhang, J., Zhang, S., Zhang, N., Zhou, H.Z., Zhu, C.D., Zhu, L., Bruelheide, H., Ma, K., Niklaus, P.A., Schmid, B., 2018. Supplementary material for: impacts of species richness on productivity in a large-scale subtropical forest experiment. Science 362 (6410), 80–83. https://doi.org/10.1126/science.aat6405.

Jia, W., Coops, N.C., Tortini, R., Pang, Y., Black, T.A., 2018. Remote sensing of variation of light use efficiency in two age classes of douglas-fir. Remote Sens Environ 219 (September), 284–297. https://doi.org/10.1016/j.rse.2018.10.017.

Jogireddy, V., Cox, P.M., Huntingford, C., Harding, R.J., Mercado, L.M., 2006. An improved description of canopy light interception for use in a GCM land-surface scheme: calibration and testing against carbon fluxes at a coniferous forest. Hadley Centre technical note 63, 1–13.

Jones, H.G., Archer, N., Rotenberg, E., Casa, R., 2003. Radiation measurement for plant ecophysiology. J. Exp. Bot. 54 (384), 879–889. https://doi.org/10.1093/jxb/erg116.

Keenan, T.F., Niinemets, Ü., 2017. Global leaf trait estimates biased due to plasticity in the shade. Nat Plants 3 (1), 16201. https://doi.org/10.1038/nplants.2016.201.

Kelty, M.J., 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage. 28, 237–257.

Kenzo, T., Ichie, T., Watanabe, Y., Yoneda, R., 2006. Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest changes in photosynthesis and leaf characteristics with tree height in. Tree Physiol. 26 (September), 865–873. https://doi.org/10.1093/treephys/26.7.865.

Kenzo, T., Inoue, Y., Yoshimura, M., Yamashita, M., Tanaka-Oda, A., Ichie, T., 2015. Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. Oecologia 177 (1), 191–202. https://doi.org/10.1007/s00442-014-3126-0.

King, D.A., 1990. The adaptive significance of tree height. Am. Nat. 135 (6), 809–828. https://doi.org/10.1086/285075.

Kira, T., Shinozaki, K., Hozumi, K., 1969. Structure of forest canopies as related to their primary productivity. Plant and Cell Physiology 10 (36), 129–142.

Kükenbrink, D., Hueni, A., Schneider, F.D., Damm, A., Gastellu-Etchegorry, J.-P., Schaepman, M.E., Morsdorf, F., 2019. Mapping the irradiance field of a single tree: quantifying vegetation-Induced adjacency effects. IEEE Trans. Geosci. Remote Sens. 1–18. https://doi.org/10.1109/TGRS.2019.2895211.

Kükenbrink, D., Schneider, F.D., Leiterer, R., Schaepman, M.E., Morsdorf, F., 2017. Quantification of hidden canopy volume of airborne laser scanning data using a voxel traversal algorithm. Remote Sens Environ 194 (Special Issue of the SilviLaser 2015 Conference), 424–436. https://doi.org/10.1016/j.rse.2016.10.023.

Law, B.E., Cescatti, A., Baldocchi, D.D., 2001. Leaf area distribution and radiative transfer in open-canopy forests. Tree Physiol. 21 (12/13), 777–788.

Leuchner, M., Hertel, C., Menzel, A., 2011. Spatial variability of photosynthetically active radiation in European beech and norway spruce. Agric For Meteorol 151 (9), 1226–1232. https://doi.org/10.1016/j.agrformet.2011.04.014.

Li, Y., Su, Y., Hu, T., Xu, G., Guo, Q., 2018. Retrieving 2-D leaf angle distributions for deciduous trees from terrestrial laser scanner data. IEEE Trans. Geosci. Remote Sens. 56 (8), 4945–4955. https://doi.org/10.1109/TGRS.2018.2843382.

Liu, J., Skidmore, A.K., Wang, T., Zhu, X., Premier, J., Heurich, M., Beudert, B., Jones, S., 2019. Variation of leaf angle distribution quantified by terrestrial LiDAR in natural European beech forest. ISPRS J. Photogramm. Remote Sens. 148 (May 2018), 208–220. https://doi.org/10.1016/j.isprsjprs.2019.01.005.

Longo, M., Knox, R.G., Medvigy, D.M., Levine, N.M., Dietze, M.C., Kim, Y., Swann, A.L., Zhang, K., Rollinson, C.R., Bras, R.L., Wofsy, S.C., Moorcroft, P.R., 2019. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the ecosystem demography model, version 2.2-Part 2: model evaluation for tropical south america. Geosci. Model Dev. 12 (10), 4309–4346. https://doi.org/10.5194/gmd-12-4309-2019.

Longo, M., Knox, R.G., Medvigy, D.M., Levine, N.M., Dietze, M.C., Kim, Y., Swann, A.L.S., Zhang, K., Rollinson, C.R., Bras, R.L., Wofsy, S.C., Moorcroft, P.R., 2019. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically- and horizontally-heterogeneous ecosystems: the ecosystem demography model, version 2.2 part 1: model description. Geosci. Model Dev. Discuss. (March), 1–53. https://doi.org/10.5194/gmd-2019-45.

Manfroi, O.J., Kuraji, K., Suzuki, M., Tanaka, N., Kume, T., Nakagawa, M., Kumagai, T., Nakashizuka, T., 2006. Comparison of conventionally observed interception evaporation in a 100-m2 subplot with that estimated in a 4-ha area of the same Bornean lowland tropical forest. J Hydrol (Amst) 329 (1–2), 329–349. https://doi.org/10.1016/j.jhydrol.2006.02.020.

Mariscal, M., Martens, S., Ustin, S., Chen, J., Weiss, S., Roberts, D., 2004. Light-transmission profiles in an old-growth forest canopy:simulations of photosynthetically active radiation by using spatially explicit radiative transfer models. Ecosystems 7 (5), 454–467. https://doi.org/10.1007/s10021-004-0137-4.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2005. Forest and woodland stand structural complexity: its definition and measurement. For. Ecol. Manage. 218 (1–3), 1–24. https://doi.org/10.1016/j.foreco.2005.08.034.

Miller, J.R., Steven, M.D., Demetriades-Shah, T.H., 1992. Reflection of layered bean leaves over different soil backgrounds: measured and simulated spectra. Int J Remote Sens 13 (17), 3273–3286. https://doi.org/10.1080/01431169208904118.

Miyashita, H., Ikemoto, H., Kurano, N., Adachi, K., Chihara, M., Miyachi, S., 1996. Chlorophyll d as a major pigment. Nature 383 (6599), 402.

Monsi, M., Saeki, T., 2005. On the factor light in plant communities and its importance for matter production. 1953. Ann. Bot. 95 (3), 549–567. https://doi.org/10.1093/aob/mci052.

Moorcroft, A.P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics : the ecosystem demography model (ED). Ecol Monogr 71 (4), 557–585.

Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol. Lett. 14, 1211–1219. https://doi.org/10.1111/j.1461-0248.2011.01691.x.

Morsdorf, F., Eck, C., Zgraggen, C., Imbach, B., Schneider, F.D., Kükenbrink, D., 2017. UAV-based LiDAR acquisition for the derivation of high-resolution forest and ground information. The Leading Edge 36 (7), 566–570. https://doi.org/10.1190/tle36070566.1.

Morsdorf, F., Schneider, F.D., Gullien, C., Kükenbrink, D., Leiterer, R., Schaepman, M.E., 2020. The Laegeren site: an augmented forest laboratory. In: Cavender-Bares, J., Gamon, J., Townsend, P.A. (Eds.), Remote Sensing of Plant Biodiversity. Springer, Cham.

Morton, D.C., Nagol, J., Carabajal, C.C., Rosette, J., Palace, M., Cook, B.D., Vermote, E.F., Harding, D.J., North, P.R.J., 2014. Amazon forests maintain consistent canopy structure and greenness during the dry season. Nature 506 (7487), 221–224. https://doi.org/10.1038/nature13006.

Morton, D.C., Rubio, J., Cook, B.D., Gastellu-Etchegorry, J.P., Longo, M., Choi, H., Hunter, M., Keller, M., 2016. Amazon forest structure generates diurnal and seasonal variability in light utilization. Biogeosciences 13 (7), 2195–2206. https://doi.org/10.5194/bg-13-2195-2016.

Niinemets, Ü., 2007. Photosynthesis and resource distribution through plant canopies. Plant, Cell & Environment 30 (9), 1052–1071. https://doi.org/10.1111/j.1365-3040.2007.01683.x.

Niinemets, U., 2012. Optimization of foliage photosynthetic capacity in tree canopies: towards identifying missing constraints. Tree Physiol. 32 (5), 505–509. https://doi.org/10.1093/treephys/tps045.

Niinemets, Ü., Valladares, F., Ceulemans, R., 2003. Leaf-level phenotypic variability and plasticity of invasive Rhododendron pontificum and non-... Plant Cell Environ 941–956.

Raumonen, P., Kaasalainen, M., Åkerblom, M., Kaasalainen, S., Kaartinen, H., Vastaranta, M., Holopainen, M., Disney, M., Lewis, P., 2013. Fast automatic precision tree models from terrestrial laser scanner data. Remote Sens (Basel) 5 (2), 491–520. https://doi.org/10.3390/rs5020491.

Rissanen, K., Martin-Guay, M.-O., Riopel-Bouvier, A.-S., Paquette, A., 2019. Light interception in experimental forests affected by tree diversity and structural complexity of dominant canopy. Agric For Meteorol 278 (July 2018), 107655. https://doi.org/10.1016/j.agrformet.2019.107655.

Rosati, A., Wolz, K.J., Murphy, L., Ponti, L., Jose, S., 2020. Modeling light below tree canopies overestimates net photosynthesis and radiation use efficiency in understory crops by averaging light in space and time. Agric For Meteorol 284 (January), 107892. https://doi.org/10.1016/j.agrformet.2019.107892.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M., 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. Ecology 95 (9), 2479–2492.

Schmid, B., Niklaus, P.A., 2017. Complementary canopies. Nature Ecology and Evolution 1 (4). https://doi.org/10.1038/s41559-017-0104.

Schneider, F.D., Kükenbrink, D., Schaepman, M.E., Schimel, D.S., Morsdorf, F., 2019. Quantifying 3D structure and occlusion in dense tropical and temperate forests using close-range lidar. Agric For Meteorol 268 (2019), 249–257. https://doi.org/10.1016/j.agrformet.2019.01.033.

Schneider, F.D., Leiterer, R., Morsdorf, F., Gastellu-Etchegorry, J.-P., Lauret, N., Pfeifer, N., Schaepman, M.E., 2014. Simulating imaging spectrometer data: 3D forest modeling based on LiDAR and in situ data. Remote Sens Environ 152, 235–250. https://doi.org/10.1016/j.rse.2014.06.015.

Schneider, F.D., Morsdorf, F., Schmid, B., Petchey, O.L., Hueni, A., Schimel, D.S., Schaepman, M.E., 2017. Mapping functional diversity from remotely sensed morphological and physiological forest traits. Nat Commun 8 (1), 1441. https://doi.org/10.1038/s41467-017-01530-3.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Glob Chang Biol 9 (2), 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x.

Stark, S.C., Leitold, V., Wu, J.L., Hunter, M.O., de Castilho, C.V., Costa, F.R., Mcmahon, S.M., Parker, G.G., Shimabukuro, M.T., Lefsky, M.A., Keller, M., Alves, L. F., Schietti, J., Shimabukuro, Y.E., Brandão, D.O., Woodcock, T.K., Higuchi, N., de Camargo, P.B., de Oliveira, R.C., Saleska, S.R., 2012. Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. Ecol. Lett. 15 (12), 1406–1414. https://doi.org/10.1111/j.1461-0248.2012.01864.x.

Stuckens, J., Somers, B., Delalieux, S., Verstraeten, W.W., Coppin, P., 2009. The impact of common assumptions on canopy radiative transfer simulations: a case study in citrus orchards. J. Quant. Spectrosc. Radiat. Transfer 110 (1–2), 1–21. https://doi.org/10.1016/j.jqsrt.2008.09.001.

Thonicke, K., Billing, M., von Bloh, W., Sakschewski, B., Niinemets, Ü., Peñuelas, J., Cornelissen, J.H.C., Onoda, Y., van Bodegom, P., Schaepman, M.E., Schneider, F.D., Walz, A., 2020. Simulating functional diversity of European natural forests along climatic gradients. J. Biogeogr. (December 2019), 1069–1085. https://doi.org/10.1111/jbi.13809.

Valladares, F., 2003. Light Heterogeneity and Plants: from ecophysiology to species coexistence and biodiversity. In: W. B., Esser, F.H.K., Lüttge, U. (Eds.), Progress in botany. Springer Berlin Heidelberg, pp. 439–471.

Valladares, F., Laanisto, L., Niinemets, Ü., Zavala, M.A., 2016. Shedding light on shade: ecological perspectives of understorey plant life. Plant Ecology & Diversity 9 (3), 1–15. https://doi.org/10.1080/17550874.2016.1210262.

Vicari, M.B., Pisek, J., Disney, M., 2019. New estimates of leaf angle distribution from terrestrial LiDAR: comparison with measured and modelled estimates from nine broadleaf tree species. Agric For Meteorol 264 (September 2018), 322–333. https://doi.org/10.1016/j.agrformet.2018.10.021.

Vincent, G., Antin, C., Laurans, M., Heurtebize, J., Durrieu, S., Lavalley, C., Dauzat, J., 2017. Mapping plant area index of tropical evergreen forest by airborne laser scanning. a cross-validation study using LAI2200 optical sensor. Remote Sens Environ 198, 254–266. https://doi.org/10.1016/j.rse.2017.05.034.

Wacker, L., Baudois, O., Eichenberger-Glinz, S., Schmid, B., 2009. Effects of plant species richness on stand structure and productivity. Journal of Plant Ecology 2 (2), 95–106. https://doi.org/10.1093/jpe/rtp010.

Walcroft, A.S., Brown, K.J., Schuster, W.S., Tissue, D.T., Turnbull, M.H., Griffin, K.L., Whitehead, D., 2005. Radiative transfer and carbon assimilation in relation to canopy architecture, foliage area distribution and clumping in a mature temperate rainforest canopy in new zealand. Agric For Meteorol 135 (1–4), 326–339. https://doi.org/10.1016/j.agrformet.2005.12.010.

Wang, W.-M., Li, Z.-L., Su, H.-B., 2007. Comparison of leaf angle distribution functions: effects on extinction coefficient and fraction of sunlit foliage. Agric For Meteorol 143 (1–2), 106–122. https://doi.org/10.1016/j.agrformet.2006.12.003.

Widlowski, J.L., Pinty, B., Clerici, M., Dai, Y., De Kauwe, M., De Ridder, K., Kallel, A., Kobayashi, H., Lavergne, T., Ni-Meister, W., Olchev, A., Quaife, T., Wang, S., Yang, W., Yang, Y., Yuan, H., 2011. RAMI4PILPS: an intercomparison of formulations for the partitioning of solar radiation in land surface models. Journal of Geophysical Research: Biogeosciences 116 (2). https://doi.org/10.1029/2010JG001511.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nature Ecology and Evolution 1 (4). https://doi.org/10.1038/s41559-016-0063.

Yoshimura, M., Yamashita, M., 2014. A consideration for the light environmental modeling under tropical rainforest canopies. International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives 40 (7), 217–220. https://doi.org/10.5194/isprsarchives-XL-7-217-2014.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., Coomes, D., 2019. Advances in microclimate ecology arising from remote sensing. Trends in Ecology & Evolution xx, 1–15. https://doi.org/10.1016/j.tree.2018.12.012.