

Individual tree branch-level simulation of light attenuation and water flow of three *F. sylvatica* L. trees

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[1] A leaf stomatal conductance model was combined with a hydrological tree and soil water flow model and a spatially explicit three-dimensional canopy light model. The model was applied to single, old-growth *Fagus sylvatica* L. trees, and the measured daily values of stem sap flux could be reproduced with a normalized root mean square error of 0.10 for an observation period of 32 days in the summer of 2009. The high temporal resolution of the model also makes it possible to simulate the diurnal dynamics of transpiration, stem sap flux, and root water uptake. We applied new data-processing algorithms to information from terrestrial laser scans to represent the canopies of the functional-structural model. The high spatial resolution of the root and branch geometry and connectivity makes the detailed modeling of the water usage of single trees possible and allows for the analysis of the interaction between single trees and the influence of the canopy light regime on the water flow inside the xylem. In addition to the laser scans of the observed trees, the model needs tree-species-specific physiological input parameters, which are easy to obtain. The model can be applied at various sites and to different tree species, allowing the up-scaling of the water usage of single trees to the total transpiration of mixed stands.

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1. Introduction

[2] Modeling the water flux and transpiration at the level of a single tree with both a high temporal and spatial resolution can give insights into species-specific strategies of water usage [Früh and Kurth, 1999; Bohrer et al., 2005; Janott et al., 2011]. An adequate geometrical representation of single trees is crucial, because the competition for resources is linked to a competition for space by both, the belowground and the aboveground parts of the tree. Because the potential evaporation of water at the leaves is strongly determined by the intensity of incoming radiation, additional simulation of the canopy light regime could further improve the model's performance and allow for the analysis of the aboveground interactions of single trees [Lorant et al., 2010; Van der Zande et al., 2009]. Especially at old-growth forests, the traditional acquisition of the tree structure is laborious and may be connected with uncertainties. Therefore, the terrestrial laser scanning (TLS) technique and data processing have recently been developed and used to

obtain the structural properties of forests [van Leeuwen and Nieuwenhuis, 2010]. The aim of this study is to present and apply a functional-structural model of the water flow of single trees that focuses on the use of TLS data for the automatic generation of structural model input information. In addition to TLS-derived detailed information on geometry, the model uses a combination of empirical and physiological species-specific parameters of stomatal behavior as well as xylem and root hydrology.

[3] Ecological functions concerning the water cycle are often determined by the properties of a particular tree species [Krämer and Hölscher, 2009]. Additionally to species-specific effects, interaction effects between single trees may have an impact on the water cycle. In general, the tree species composition of mixed forests can have a significant impact on the total stand's capacity for water storage, retention of water and groundwater recharge [Food and Agriculture Organization of the United Nations, 2005; Calder, 2007; van Dijk and Keenan, 2007]. The effect of forests diversity on ecological functions has been the focus of recent observational and modeling studies [Leuschner et al., 2009; Healy et al., 2008; Thompson et al., 2009; Scherer-Lorenzen et al., 2005; Nadrowski et al., 2010], and it was stated that biodiversity effects can be analyzed by up-scaling the information gained on an individual scale [Nadrowski et al., 2010; Kirwan et al., 2009].

[4] At some sites, the structural diversity and the spatial organization of leaves in the canopy does affect strongly the net primary production and the transpiration of the whole

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Table 1. Characteristics of Studied Trees^a

Tree	dbh (cm)	cpa ^b (m ²)	Height (m)	Leaf Area (m ²)	Maximum Canopy Xylem Water Content (l)
Bu27	58	143	28	260	2513
Bu30	47	70	26	254	1816
Bu33	45	73	25	200	1578

^aThe leaf area was calibrated using the measured stem sap flux. The maximum canopy xylem water content was calculated from the modeled canopy architecture. Dbh, diameter at breast height; cpa, crown projection area.

^bM. Jacob, unpublished data.

stand [Hardiman *et al.*, 2011]. In general, the interaction of the light regime and the hydraulic properties and structure of trees and canopies has been the focus of research [Loranty *et al.*, 2010; Campanello *et al.*, 2008]. Three-dimensional single tree functional-structural models include the structure explicitly and may be a promising approach to further understand the interaction of function and structure in forests.

[5] The Hainich forest in central Germany represents an old-growth, mixed temperate deciduous forest and has been studied in preceding studies. Large parts of the forest are dominated by *F. sylvatica*, but other tree species co-occur in some areas and allow for the analysis of the influence of tree species diversity on the water cycle of the entire stand. Here, differences in the hydraulic physiology and in the structure were found between the deciduous tree species. The structure of the old-growth beech, ash, and lime differed with respect to the leaf distribution and canopy shape [Frech *et al.*, 2003] as well as the radial fine root distribution in the soil [Meinen *et al.*, 2009]. These differences and their impact on hydrological traits have been analyzed for the xylem fraction of the stem cross section area [Gebauer *et al.*, 2008], leaf stomatal conductance [Köcher *et al.*, 2009], and root water uptake [Korn, 2004; Coners, 2001; Rewald, 2008]. Modeling studies have included these hydrological properties to simulate the soil-plant-atmosphere water cycle and quantified their influence on daily water uptake and transpiration [Bittner *et al.*, 2010]. Further, the interaction between the tree species could be analyzed at dry soil water conditions [Bittner *et al.*, 2010], and the influence of the tree structure on the water flow inside the trees was revealed [Janott *et al.*, 2011].

[6] S. Bittner (Ph.D. thesis, in preparation, 2012) applied a submodel that uses a static, TLS-derived geometry in a model that calculates the water flow through the roots, stems, and branches of single trees. Connected cylinders that could conduct water represented the tree elements. An automatic tree skeleton extraction algorithm [Xu *et al.*, 2007] was used to obtain the position of the canopy cylinders. The xylem water potential of the branches could be a sensible parameter for stomatal closure and is included in a Ball-Berry-Leuning (BBL)-type total stomatal reaction model [Leuning, 1995] in this study. In addition to the water status of the leaves, the stomatal reaction is sensitive to a set of climatic variables, of which the photosynthetically active radiation (PAR) is the most fluctuating. Therefore, a submodel to calculate the canopy PAR regime that was recently tested under controlled light conditions in a greenhouse was included in the functional-structural model.

[7] A voxel-based ray tracing algorithm was used to calculate the intensity of PAR inside the canopy [Kimes, 1984;

Cohen and Fuchs, 1987; Gastellu-Etcheberry *et al.*, 2004; Perttunen *et al.*, 2007]. Therefore, the three-dimensional space was divided into cubes of the same size (voxels) that possessed different light attenuation capabilities depending on the type of vegetation the voxel is filled with based on the information obtained by the TLS. The incoming hourly direct sun radiation, as well as the diffuse skylight, is attenuated on the path from the top of the canopy to the forest floor in these voxels, thereby including the self-shadowing of the vegetation. Finally, a PAR intensity is calculated for every voxel that contains leaves. This PAR value is one of the most sensitive parameters for the control of the stomatal behavior of the leaves and, therefore, the transfer of water from the plant to the atmosphere.

[8] To parameterize and to test models describing single tree transpiration, we performed field measurements of the stem sap flux and of stomatal conductance at three different beech trees and additionally used soil moisture and climate data.

[9] We compare two transpiration models that are based on different submodels of stomatal conductance that combine the simulations of the leaf water status and PAR with meteorological measurements of the air temperature and the vapor pressure deficit to calculate the rate of water transfer from the leaves to the atmosphere. The applied submodels are a Ball-Berry-Leuning model, and a stand level based Penman-Monteith approach. The model output was compared with the measured values of the stem xylem sap flux of three mature *F. sylvatica* trees. The Ball-Berry-Leuning model showed a good agreement with respect to the daily and diurnal dynamics of sap flux and could reduce the error of the stand level based Penman-Monteith approach by up to 40%.

[10] Moreover, by using the tested transpiration models we address the question how the 3-D canopy structure can effect the penetration of direct and diffuse radiation. We quantify the resulting increase in transpiration under higher fractions of diffuse radiation and show the significant contribution of leaf area at lower parts of the canopy. The application of the model gives further insights to the single tree water usage and to mechanisms that lead to a stomatal closure due to low leaf water contents.

2. Materials and Methods

2.1. Study Site

[11] The study was conducted in an old-growth broad-leaved forest in the Hainich National Park in central Germany (51°N 10°E). Three neighboring *F. sylvatica* trees (Table 1) were situated in an old-growth forest stand with a closed canopy. The parent rock of the site is Triassic

limestone covered with a loess layer of variable depth. The soil type is a Luvisol that dries out strongly during summer and shows stagnant properties in winter and spring, with the groundwater table found far below the rooting zone. The soil texture was characterized by a high silt content and a low sand content (silt loam to silt clay loam).

2.2. Microclimatic Measurements

[12] Hourly values of precipitation and wind speed were obtained from the weather station at Weberstedt/Hainich (Meteomedia GmbH, Bochum, Germany). Air temperature T (°) and relative air humidity H (%) were measured directly in the upper canopy using a Rotronic temperature and humidity probe (MP 100A Hygrometer, Rotronic GmbH, Ettlingen, Germany) and were used to calculate the vapor pressure deficit VPD (kPa) inside the canopy. Half-hourly values of global radiation r_g ($W\ m^{-2}$), the diffuse fraction of global radiation, and PAR ($\mu mol\ m^{-2}\ s^{-1}$) above the canopy were provided for the Hainich site by the CarboEurope research project (www.carboeurope.com) [Knohl et al., 2003]. The volumetric soil water content, θ (%), at the center of the three neighboring trees was measured using a frequency domain reflectometry (FDR) probe (Diviner 2000 FDR sensors, Sentek Pty Ltd., Stepney, Australia) at a depth of 20 cm (M. Meißner, personal communication, 2010).

[13] In the model, other environmental drivers than the PAR such as the temperature and the VPD are assumed to be homogenous inside the canopy. One way to include inhomogeneities is to adapt existing models of the vertical canopy profiles of temperature [Siqueira et al., 2003], VPD [Poggi et al., 2004] and wind speed [Massman and Weil, 1999] to sub-canopy single tree levels. Another way could be the direct use of the three-dimensional canopy voxel model to calculate the intracanopy distribution of the environmental drivers [Bienert et al., 2010]. High-resolution large-eddy simulations of the canopy are another possibility for a dynamic three-dimensional description of the canopy microclimate [Yue et al., 2007; Dupont and Brunet, 2008, 2009; Bohrer et al., 2009] and could easily be coupled to our model.

2.3. Xylem Sap Flux Measurements

[14] At the three study trees, the sap flux density in the stem was monitored with the constant-heat method proposed by Granier [1987]. Two 20 mm-long Granier type probes were inserted at a distance of 15 cm from each other into the stem at 1.3 m height. The upper probe was constantly heated (200 mW), while the lower one served to monitor the reference temperature of the stem. The temperature difference between the heated and the reference probe was recorded continuously and related to the maximum temperature difference occurring at predawn, when minimum or no flow occurred. Sap flux density (J_s , $gm^{-2}\ s^{-1}$) was calculated according to the empirical equation given by Granier [1987]. We used data from a prior study [Gebauer et al., 2008] that investigated radial patterns and changes in sapwood area with tree size of the same tree species at the same forest site to calculate the total stem sap flux of a single tree (S_s , $l\ d^{-1}$). Sap flux data were logged every 30 s and a mean value was recorded every 30 min over the whole vegetative period of 2009. After the leaves had developed in spring, the

logger provided continuous, reliable data for the period from 5/22/2009 to 6/22/2009 (observation period) for the beech trees Bu27, Bu30, and Bu33.

2.4. Terrestrial Laser Scans and Voxel Representation of the Canopy

[15] The Riegl VZ-400 (Riegl GmbH, Horn, Austria) terrestrial laser scanner was used to scan the foliated canopies of the trees in September 2010 at nearly windless weather conditions. The scanner has a range precision of 3 mm and a beam divergence of 0.3 mrad, and the angular spacing between two laser beams was set to 0.002° . The Riegl VZ-400 scanner records the full waveform of multiple target echoes. The full waveform of the echoes was used to filter artifacts using the RiscanPro (Riegl GmbH, Horn, Austria) software. Multiple target echoes were included in the final point clouds, which resulted in a high point density even in the deeper and higher parts of the canopy. To further decrease the effect of shadowing, 4 scans were made at different positions around the tree group. All scan setup positions were then referenced in a local coordinate system using reflectors and reference targets with a positional average standard deviation of less than 8 mm.

[16] A Voxel-based canopy architecture model was obtained from the TLS measurements using the cloud of three-dimensional points that resulted from reflections of the laser beam at the surface of the trees. The region of interest was divided into three-dimensional small cubes (voxels), and the canopy of each of the three trees was represented by a set of k voxels $V = \{v_1 \dots v_k\}$ containing at least one of the TLS reflection points. The voxels were further divided into voxels that contain woody material and into voxels that contain leaves (Figure 1) by visual inspection. The region of interest was defined by all points that were inside a cylinder with the center of the group of the neighboring three *F. sylvatica* trees and a diameter of 51.2 m. In this way, edge effects could be avoided because, in addition to the three analyzed *F. sylvatica* trees, the neighboring trees were included in the model. The edge length of the voxels was set to be 0.1 m. The resulting voxel representation of the tree group served as the input for the light regime submodel (section 2.7), assuming a static architecture of the old-growth trees.

2.5. Water Exchange Model of the Soil-Plant-Atmosphere System

[17] A hydrological model of water flow on a single tree scale has been recently developed [Bohrer et al., 2005; Aumann and Ford, 2002; Janott et al., 2011]. The water flow inside the tree is driven by the transpiration of water at the leaves, which leads to a gradient of xylem water potential between the fine branches and the root system and results in a water uptake of available soil water by the roots. The flow of water along the hydrological pathway of the roots, stem, and branches is driven by the hydraulic gradient according to the cohesion-tension theory [Tyree and Zimmermann, 2002] and is calculated using the non-linear Darcy equation for the flow of water in a porous media. By adding a sink-source term to represent transpiration and root water uptake, we get the following one-dimensional Richards equation, as outlined in detail by [Janott et al., 2011]. This equation can then

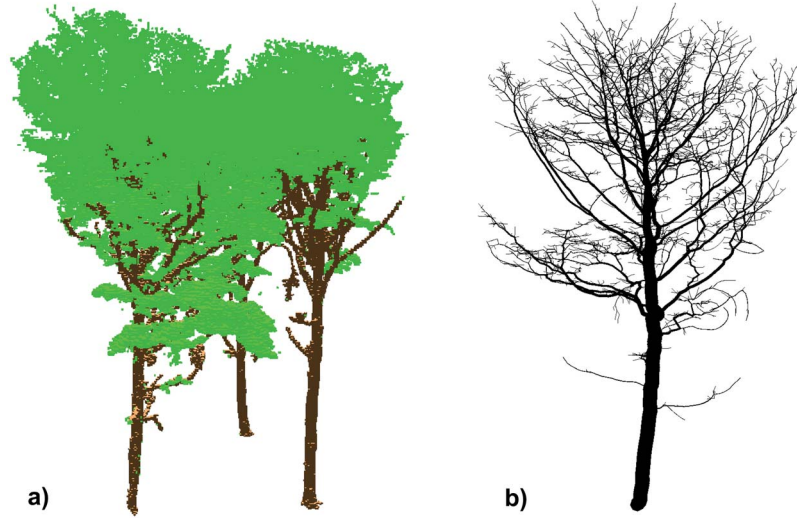


Figure 1. (a) Voxel representation of the *F. sylvatica* trees with the distinction of woody material and leaves. (b) Canopy representation of connected cylinders obtained by a skeleton extraction algorithm. The position and connectivity of the cylinders gives the potential pathway of the water flow through the tree.

be solved on the domain given by the graph, which represents the plant xylem porous medium by straight lines aboveground for stem and branches and below-ground for roots:

$$\frac{\partial \theta_x(\psi_x)}{\partial t} = \frac{\partial}{\partial z} \left[k_x(\psi_x) \left(\frac{\partial \psi_x}{\partial z} + \cos \alpha_x \right) \right] - S_x \quad (1)$$

where for all of the tree elements represented by straight lines θ_x denotes the volumetric water content ($\text{m}^3 \text{m}^{-3}$) of the xylem as function of the xylem matric potential ψ_x (mm). The xylem matric potential is given on a weight basis, i.e., it is expressed as hydraulic head (mm). The letter t denotes the time (s), z the height or depth (mm) of the element, and $k_x(\psi_x)$ represents the xylem hydraulic conductivity (mm s^{-1}) defined as function of the xylem matric potential using the maximal xylem cross sectional area as reference surface of the water flux. The vertical position is given by the height above (positive upward) or the depth below the soil surface (negative downward). For a branch or root element α_x is the zenith angle ($^\circ$) and S_x (s^{-1}) the sink or source term, which stands in case of roots for the root water uptake and in case of outer branches for the transpiration.

[18] Here, the volumetric xylem water content and the xylem axial hydraulic conductivity depend non-linearly on the xylem water potential. The xylem elements have the maximal axial hydraulic conductivity at the xylem water potential $\psi_x = 0$. At higher negative values of ψ_x , the diameter of the cylinder elements is reduced, resulting in a lower area of water conducting xylem and, therefore, in a decrease in the conductance. Below the air entry value $\psi_x < a$ (mm), air enters into single xylem vessels, which leads to a strong decrease in the xylem hydraulic conductance. The resulting xylem water curves for the volumetric

xylem water content, θ_x ($\text{mm}^3 \text{mm}^{-3}$), and the xylem hydraulic conductivity, $k_x(\psi_x)$ (mm s^{-1}), are given by

$$\theta_x(\psi) = \begin{cases} (\epsilon - \theta_x(a)) \left(\frac{a - \psi_x}{a} \right) + \theta_x(a) & \psi_x \geq a \\ \theta_x(a) \left(\frac{\psi_x}{a} \right)^\lambda & \psi_x < a, \end{cases} \quad (2)$$

and

$$k_x(\psi_x) = k_{\max} \begin{cases} \frac{\theta_x(a)}{\epsilon} + \left(1 - \frac{\theta_x(a)}{\epsilon} \right) \left(\frac{a - \psi_x}{a} \right)^2 & \psi_x \geq a \\ \left(\frac{\psi_x}{a} \right)^{-\lambda_{BC}\eta} & \psi_x < a, \end{cases} \quad (3)$$

with $k_{\max}$ (mm s^{-1}), the specific axial hydraulic conductivity, the Brooks and Corey [Brooks and Corey, 1966] exponent $\lambda_{BC}(-)$, and $\eta := 2/\lambda_{BC} + 1$. Here, the xylem sapwood porosity ϵ ($\text{mm}^3 \text{mm}^{-3}$) is defined as the ratio of the maximal volume of xylem water at saturation to the maximal total volume of the xylem sapwood in the tree element, and the elastic modulus of the xylem sapwood E (mm) is defined by $\theta_x(a) = \epsilon + \frac{a}{E}$. The total conductance of a cylinder element $K(\psi_x)$ ($\text{mm}^3 \text{s}^{-1}$) is given by multiplication of the specific conductivity with the hydroactive xylem area A_x (mm^2) of the element. A mathematically rigorous description of the xylem water retention curve and the xylem conductance curve is given in [Janott et al., 2011].

[19] Similar to the water flow through the tree, the soil water flow was calculated by solving the Richards equation describing the soil water flow in porous media [Richards, 1931]:

$$\frac{\partial \theta_s(\psi_s)}{\partial t} = \frac{\partial}{\partial z} \left[k_s(\psi_s) \left(\frac{\partial \psi_s}{\partial z} - 1 \right) \right] - S_w \quad (4)$$

where θ_s is the volumetric soil water content ($\text{m}^3 \text{m}^{-3}$) as a function of the soil matric potential ψ_s (mm), t (s) denotes time and z (mm) soil depth (here positive downward). $k_s(\psi_s)$ (mm s^{-1}) is the soil hydraulic conductivity which is given as a function of the soil matric potential. Both soil hydraulic property functions θ_s and k_s are described by parameterisations according to [van Genuchten, 1980]. The last term S_w (s^{-1}) represents the sink term of root water uptake (per unit soil depth). Typical boundary conditions of the flow equation are a mixed boundary condition at the soil surface to represent atmospheric conditions leading either to infiltration, evaporation or water ponding and a free drainage condition at the bottom boundary [Priesack and Gayler, 2009; Simunek et al., 2008].

[20] The coupling between the plant and the soil is achieved by the possible water exchange between the tree roots and one-dimensional soil layers by a Darcy flux driven by a possible water potential difference between the soil and the roots, which further depends on the tree hydraulic properties, such as the radial root water conductivity [Janott et al., 2011]. For a detailed description of the hydraulic properties of the soil and the calculation of the infiltration of water after rain, see Bittner et al. [2010].

[21] The radial volumetric flux j_r ($\text{mm}^3 \text{s}^{-1}$) between the soil-root interface that describes the amount of water exchanged between a root element and the one-dimensional soil layer is driven by the difference of the water potentials of the soil, ψ_s (mm), and water potentials of the soil and the root xylem, ψ_x (mm),

$$j_r = Lp_r s_r [\psi_s - \psi_x], \quad (5)$$

where s_r (mm^2) is the surface of the root element, Lp_r (s^{-1}) is the radial conductivity between the root xylem and the soil.

[22] The calculated flux j_r into or out of the root element is then used to calculate the below-groundwater uptake sink or source terms S_x and S_w of the Richards equations of xylem and soil water flow. The below-ground xylem sink or source term S_x ($\text{mm}^3 \text{mm}^{-3} \text{s}^{-1}$) is obtained by relating the fluxes to the corresponding xylem volumes $V_x = s_{x,\max}(z)l_x$ of the root elements of maximal xylem sapwood area $s_{x,\max}$ (mm^2) and element length l_x (mm) and by building the sum over the root elements:

$$S_x(z) = \sum \frac{j_r(z)}{s_{x,\max}(z)l_x} \quad (6)$$

[23] In an analogous way by summing up the parts of the root elements that intersect with the soil layer i , the sink term $S_{w,i}$ is obtained for each numerical soil layer i [Janott et al., 2011].

[24] We used a geometrically explicit model of the potential pathway of tree water flow. Therefore, the xylem is represented by connected cylinder elements with specific hydrological properties, such as the axial conductivity and the water retention curves of the xylem. We used laser scans of the unfoliated canopy from Spring 2010 as the input for a tree skeleton extraction algorithm [Verrout and Lazarus, 2000; Xu et al., 2007] to derive the position of the stem and branches from the three dimensional point cloud. The algorithm could give a more detailed representation of the

canopy when laser scans of the unfoliated canopy were used than the laser scans from Summer 2010 because the fine branches in the higher canopy were more shaded in the scans of the foliated canopy due to the reflection of the laser beams at the leaves. The canopies of the three trees consisted of 2255, 2754, and 6591 cylinder elements with a length of 0.25 m (Figure 1). The root architecture of the trees was simulated using available experimental data on the vertical and horizontal fine root distribution, the root area index and the rooting depth that were measured at the study site [Meinen et al., 2009]. The taproot system of beech was strongly influenced by the site soil conditions, leading to a narrow rooting zone with approximately 80% of the fine root biomass in the upper 40 cm of the soil profile.

[25] The water flow in the model is driven by the transpiration at the leaf scale; therefore, the modeling of the actual transpiration is crucial. A first approach could be to use a stand-level scale to calculate the potential transpiration and then downscale this value to the single tree and the leaf scales. Down-scaling to the leaf scale is especially difficult, as the microclimate at the leaf scale shows a high spatial variation. In forests that are well coupled to the atmosphere, the spatially most heterogeneous parameter that influences the potential transpiration is the incoming PAR. Therefore, we first calculated the light regime inside the tree canopies (see section 2.7), which serves as input for the leaf stomatal conductance model (see section 2.6). In addition to the PAR, the stomatal conductance model includes the reaction of the leaves to the air temperature, T , and the VPD . By applying the calculated leaf stomatal conductance in conjunction with the simulation of the xylem water potential, the actual transpiration, i.e., the water that is exchanged between the single branch elements and the atmosphere, is calculated and drives the water flux inside the tree and the uptake of the roots.

2.6. Transpiration Model

[26] We tested two models describing the reaction of the transpiration rates to environmental conditions. The first model is the stand-level Penman-Monteith reference evapotranspiration on an hourly timestep that describes the leaf-atmosphere water exchange per unit area of canopy covered soil. This model does not make use of an explicit three-dimensional light distribution of the voxel-approach. Therefore, the Penman-Monteith evapotranspiration can be seen as a reference model to the other model, a BBL type model, that includes the spatial light distribution inside the canopy. We applied the BBL model on every voxel of the canopy representation and then scaled the voxel values up to the total single tree transpiration. In this way, the BBL model uses the simulated three-dimensional light regime inside the canopy.

[27] In this study we used the area of canopy covered soil (Penman-Monteith) respectively the leaf area (BBL) of the trees as calibration factors in the models to reproduce the mean value of the measured stem sap flux. The quality of the two models is then compared based on the daily and hourly dynamics of the modelled and measured stem sap flux.

2.6.1. Down-Scaling of the Penman-Monteith Reference Evapotranspiration

[28] The standardized reference evapotranspiration Penman-Monteith equation on an hourly basis [Allen, 2005] is used

to calculate the potential transpiration $E_{r,pot}$ (mm s^{-1}). $E_{r,pot}$ reflects the atmospheric demand for water including climatic input data such as wind speed, air temperature, relative humidity, and the global radiation.

[29] To account for the stomatal response of the leaves to low water potentials, the model considers a reduction of the potential transpiration based on the stomatal closure of the leaves. The potential tree transpiration is distributed homogeneously to the k voxels of the canopy model and reduced by a voxel-specific reduction factor f_{ψ_x} , that is explained below (see equation (10)) to get the actual transpiration rate of the tree

$$E_r = \sum_{i=1}^k E_{r,i} f_{ds} = \sum_{i=1}^k f_{\psi_x,i} \frac{E_{r,pot}}{k} f_{ds}. \quad (7)$$

[30] The values given by the Penman-Monteith equation correspond to a potential evapotranspiration per square meter of canopy covered soil. They are reduced to represent the actual transpiration and are converted to actual tree transpiration rates by the down-scaling factor f_{ds} (mm^2) representing the hydraulic area of the single tree. For each single tree this scaling-factor is obtained by calibration to the mean values of the measured sap flux.

2.6.2. Ball-Berry-Leuning-Type Model of Leaf Stomatal Conductance

[31] The semi-empirical Ball-Berry-Leuning (BBL) model was proposed by Leuning [1995] as a modification of the earlier model of Ball *et al.* [1987]. The BBL model follows a semi-mechanistic approach and includes the leaf physiology by coupling models of stomatal behaviour and photosynthesis. The model describes the reaction of the leaf conductance g_{CO_2} ($\text{mol m}^{-2} \text{s}^{-1}$) in dependence of the atmospheric CO_2 concentration and further environmental conditions by

$$g_{CO_2,i} = g_0 + \frac{a_1 A_i (T, VPD, PAR)}{(c_s - \Gamma(T))(1 + VPD/D_0)}, \quad (8)$$

with the CO_2 concentration at the leaf surface c_s (mol mol^{-1}), the CO_2 compensation point Γ (mol mol^{-1}), the assimilation rate per voxel A_i ($\text{mol m}^{-2} \text{s}^{-1}$), the vapor pressure deficit VPD (kPa), and two empirical parameters a_1 (—) and D_0 (kPa). The summation index i indicates values that are voxel-specific and the value of the whole canopy is calculated by the sum over all voxels. A detailed description of the calculation of the CO_2 compensation point Γ and the assimilation rate A_i is given by Leuning [1995].

[32] We calculated the conductance of the leaves to water g_c (mm s^{-1}) by

$$g_c = \frac{1}{k} \sum_{i=1}^k 1.56 u g_{CO_2,i} f_{\psi_x,i}(\psi_x), \quad (9)$$

with the reduction factor $f_{\psi_x}(\psi_x)$ (—) to leaf water status ψ_x (mm), the empirical coefficient of 1.56 as described by Leuning [1995], and a unit conversion factor $u = 24.39 \cdot 10^6 \text{ mm}^3 \text{ mol}^{-1}$.

[33] The stomatal reduction of the leaves to the leaf water status is given by

$$f_{\psi_x}(\psi_x) = \max \left[0.1, \exp \left(- \left(\frac{-\psi_x}{St_b} \right)^{St_c} \right) \right], \quad (10)$$

with the parameters St_b (mm) and St_c [1] describing the stomatal response to branch xylem water potentials following the approach of Bohrer *et al.* [2005] and are estimated using empirical vulnerability curves for leaf conductance [Köcher *et al.*, 2009]. We further assumed that the water potential of the leaf is equal to the water potential of the corresponding branch. Therefore, every voxel containing leaves was assigned to a cylinder element of the canopy using the smallest distance in the tree-dimensional space among all canopy cylinder elements.

2.6.3. Up-Scaling From Leaf Stomatal Conductance to Actual Tree Transpiration

[34] The BBL model gives an expressions for the stomatal conductance to water g_c (equation (9)). The stomatal conductance is converted into the actual leaf transpiration rate E_l (mm s^{-1}) to give the amount of water that is exchanged with the atmosphere per unit leaf area. For vegetation showing a high coupling to the atmosphere, the tree transpiration rate per unit leaf area E_r (mm s^{-1}) can be calculated by [Köstner *et al.*, 1992]

$$E_l = \frac{VPD g_c}{\rho G_V T}, \quad (11)$$

with the air vapor pressure deficit VPD (kPa), the air temperature T (K), the density of water ρ (kg m^{-3}), the gas constant for water vapor G_V ($\text{kPa kg}^{-1} \text{K}^{-1}$), and the tree canopy average of the stomatal conductance per unit leaf area g_c (mm s^{-1}). The advantage of this simplification of assuming a high coupling of the vegetation to the atmosphere is that no further information on the wind profile inside the canopy is needed.

[35] Theoretical [Jarvis and McNaughton, 1986] and observational [McDowell *et al.*, 2008; Gao *et al.*, 2002] studies show that it is appropriate to assume a high coupling to the atmosphere of the canopy for some tree species, especially in old-growth stands and coniferous forests. The degree of the coupling of the canopy to the atmosphere can be expressed by the dimensionless omega coefficient Ω , and a value of $\Omega < 0.2$ is often chosen as a threshold for the simplified calculation of the canopy transpiration. A strong coupling is reported in the literature for mature *F. sylvatica* stands ($\Omega = 0.1$, [Jarvis and McNaughton, 1986]; $\Omega \in 0.05..0.2$, depending on wind speed [Granier *et al.*, 2000]; $\Omega = 0.2$, [Herbst, 1995]), as well as for various other broad leaved forest stands [Granier and Bréda, 1996]. Therefore, we used equation (11) to calculate E_l .

[36] To quantify the tree's total water usage, the rate of water volume that is actually evaporated by the tree E_r ($\text{mm}^3 \text{s}^{-1}$) is given by multiplying E_l (mm s^{-1}) with the total leaf area, LA (mm^2), of the canopy. In section 3, we compare the measured and the modeled stem sap flux of water ($\text{mm}^3 \text{s}^{-1}$), and we used the LA as a calibration factor for the model in such a way that the mean value of the daily modeled stem sap flux values equaled the mean value of the measured daily values of the stem sap flux. When measurements or

estimations of LA are available, the model can use the LA as an input parameter and could then calculate the transpiration rate of single trees without the need for calibration to sap flux measurements. In section 2.8, we discuss measurements and estimations of the LA using a terrestrial laser scanner.

2.7. Light Model

2.7.1. Voxel Ray Tracer

[37] A voxel-based representation of the canopy is a way to obtain a detailed envelope of the canopy [Kimes, 1984; Cohen and Fuchs, 1987; Gastellu-Etcheberry et al., 2004; Perttunen et al., 2007], and the use of terrestrial laser scans allows the usage of a small voxel size and therefore a high spatial resolution of the geometrical model [Van der Zande et al., 2009]. The combination of a TLS-derived voxel representation and a ray tracing algorithm results in low requirements for computational time and computer memory consumption and is capable of reproducing the distribution of PAR inside the canopy and at the forest floor.

[38] The incoming light is represented by line segments, R_i , which are each defined by a starting point S_i , an ending point E_i , and a starting intensity, I_0^i . The line segments are referred to hereafter as rays and may intersect voxels of the canopy. The starting points of the rays were given by the position of the sun and 99 additional random positions in the hemisphere. In this way, the direct sunlight and the diffuse skylight in the field conditions were included. The center of all voxels that contained leaves of the three observed *F. sylvatica* trees, were the end points of the rays, which resulted in a number of $N = 100 n_l$ rays per time step (time step of 1 h), with n_l being the number of leaf voxels. The intensity of the ray that represents the direct sunlight is calculated by using the measured fraction of the direct radiation multiplied by the measured total incoming PAR. The initial intensities of the diffuse rays were calculated using the CIE standard general sky model, which is described below.

[39] To couple the voxel representation with the rays, we applied the Amanatides-Woo algorithm [Amanatides and Woo, 1987] to calculate the set of n_i voxels $A^i = \{a_j^i\}$ with $j \in \{1, \dots, n_i\}$ and $a_j^i \in \{v_1 \dots v_m\}$ that intersect the ray R_i as well as the intersection length d_j^i of the ray R_i and every intersected voxel a_j^i . The attenuation of light can then be calculated at every position in the canopy by using Beer's law

$$I(d) = I_0 \exp(-\lambda d), \quad (12)$$

with the incoming light intensity above the canopy I_0 ($\mu\text{mol m}^{-2} \text{s}^{-1}$), the attenuation coefficient, λ (m^{-1}), and the attenuation length, d (m), which is the sum of the intersection length of the intersected voxels between the starting point of the ray and the regarded position. Thus, the light intensity I_j^i ($\mu\text{mol m}^{-2} \text{s}^{-1}$) after intersecting the voxel, a_j^i , is given by

$$I_j^i = I_0^i \exp\left(-\lambda \sum_{c=1}^j d_c^i\right). \quad (13)$$

Voxels, that contained woody material, such as the stem or coarse branches, could not transmit any light and the intensity of a ray that intersected such was completely attenuated in the model.

[40] Light models that describe the canopy by an envelope that attenuates light according to a Lambert-Beer law often include the measured leaf angle distribution and a leaf distribution function in the expression for the light attenuation factor (see Baldocchi and Harley [1995]). This is important when the leaves are clumped in old-growth forests and when the expression for the light attenuation factor is derived by physical and geometrical approaches. Here the question arises, if an empirical and constant light attenuation factor that is used in this study is adequate to simulate the light regime.

[41] By analyzing digitalized and simulated tree architectures, Sinoquet et al. [2005] could show that the clumping effect should be included in models that work on coarse envelopes of the canopy but can be neglected if a voxel representation of the canopy with a small voxel size is used. The authors state that decreasing the voxel size generally increases the fraction of the inhomogeneity of the spatial leaf distribution accounted for by the space division into voxels with the optimal voxel size similar to the leave size. Wang [2003] states that a constant light attenuation factor that is independent of the leaf angle distribution and leaf clumping is accurate if the model considers the direct and the diffuse radiation separately. We successfully tested the voxel ray tracer model in a preceding study by simulation and measuring the three-dimensional PAR regime of an artificial stand of young beech trees in a greenhouse (S. Bittner, Ph.D. thesis, in preparation, 2012).

[42] Therefore, we assume that the simple Lambert-Beer absorption is adequate to simulate the light regime, because the direct and diffuse radiation is simulated explicitly by the CIE model and because the size of the voxel that describe the canopy envelope is very small and similar to the size of single leaves. Nevertheless, the model could be extended by including more complex absorption laws.

2.7.2. CIE Standard General Sky

[43] The diffuse part of the PAR is distributed over the sky hemisphere according to the standard general sky as defined by the Commission Internationale de l'Eclairage (see "Spatial distribution of daylight-CIE standard general sky" (CIE ISO 15469 / CIE S011/E-2003), at <http://www.cie.co.at>). This standard defines 15 luminance distributions (sky types) that depend on weather and climate and change during the course of a day with the position of the sun. The aim of this standard is to model the sky under a wide range of climatic conditions ranging from an overcast sky to cloudless weather. The 15 sky types can be divided into luminance distributions of overcast skies (CIE types 1–5), transitional skies (CIE types 6–10), and clear skies (CIE types 11–15). In this study, the hourly CIE sky types were derived from the measured total global radiation and diffuse global radiation according to Kittler and Danda [2000].

2.8. Parameter Values

[44] The model input parameter values that were used in the light regime, stomatal conductance, and tree hydrodynamical submodels are listed in Table 2. Additional model parameters were needed for the submodel of the water flow in the soil. Values for the soil water retention curves and other soil property parameters can be found in Bittner et al. [2010].

Table 2. Model Input Parameters of the Light Regime Submodel and the Stomatal Conductance Submodel^a

Symbol	Description	Unit	Value
λ	Light attenuation factor	m^{-1}	2.5
St_b	Parameter of stomatal response to leaf water potential ^b	MPa	2.25
St_c	Parameter of stomatal response to leaf water potential ^b	(–)	3.5
g_0	Stomatal conductance at light compensation point ^c	$\text{mol m}^{-2} \text{s}^{-1}$	0.05
D_0	Parameter of the BBL model of stomatal response to VPD	kPa	0.2
a_1	Parameter of the BBL model ^c	(–)	10.0
$k_{\text{max,root}}$	Axial specific hydraulic conductivity of roots	$10^{-2} \text{ mm s}^{-1}$	13.0
$k_{\text{max,branch}}$	Axial specific hydraulic conductivity of branches	$10^{-2} \text{ mm s}^{-1}$	1.7
Lp_r	Radial root hydraulic conductivity ^d	$10^{-8} \text{ m MPa}^{-1} \text{s}^{-1}$	4.7
ε	Xylem porosity ^b	$\text{mm}^3 \text{mm}^{-3}$	0.52
A_x/A_b	Xylem area to basal area ^c	(–)	0.75
E	Elastic modulus ^f	10^6 mm	3.5
a	Xylem air entry value ^f	MPa	3.1
λ_{BC}	Brooks and Corey parameter ^f	(–)	0.86

^aHerbst [1995].^bS. Bittner (Ph.D. thesis, in preparation, 2012).^cLeuning [1995].^dKorn [2004].^eGebauer et al. [2008].^fOertli [1993].

2.8.1. Stomatal Conductance Parameter Values

[45] BBL model parameters for the CO_2 compensation point and the assimilation rates are taken from Leuning [1995]. The simulated assimilation rates were not sensitive to the choice of the parameter values if taken within the range given values in [Leuning, 1995] and [Knobl and Baldocchi, 2008]. This may be due to the rather narrow range of the parameter sets and due to the climate conditions during the simulated period.

2.8.2. Light Attenuation Factor

[46] The submodel to calculate the PAR regime inside the canopy needs the light attenuation factor λ as a single input when the size of the voxels is fixed. Usually no measurements of the PAR profiles are available to calibrate λ , but it is possible to estimate the value in different ways. In this study, we used the fraction of PAR that reaches the forest floor to obtain a value of $\lambda = 2.5 \text{ m}^{-1}$. A preceding model analysis by S. Bittner (Ph.D. thesis, in preparation, 2012) of the light regime submodel at an artificial stand of young *F. sylvatica* trees in a greenhouse found an optimal value of $\lambda = 2.7 \text{ m}^{-1}$ for a voxel size of 0.1 m, which is similar to the value used in the present study on an old-growth stand. Thus, species-specific values of λ may be found, but the analysis of more sites is needed to test this assumption.

[47] A third way to obtain λ may be to vary its value in a prescribed range and analyze the model performance. This sensitivity analysis of the error between the simulated and measured daily values of the stem sap flux to λ could give optimal values of λ for the trees Bu30 and Bu33 in the range of $\lambda = 2.5\text{--}4.0 \text{ m}^{-1}$ (Figure 2). Therefore, the estimation of λ using a model performance optimization strategy might be appropriate when no other parameterization is possible.

2.8.3. Leaf Area

[48] Next to the canopy conductance, the LA is the most crucial value for calculating the total tree transpiration. In this study, we calibrated the LA using the measured stem sap flux in such a way that the mean value of the daily modeled stem sap flux values equals the mean value of the measured

daily values of the stem sap flux. The calibrated value of the LA of all three trees ($LA = 714 \text{ m}^2$) was similar to the value that was calculated using the litter that was collected at the center of the tree group using a litter collector with an area of 28 cm^2 in Autumn of 2008 ($LA = 684 \text{ m}^2$, D. Hertel, personal communication). Because of the uncertainties of the litter collection method, we did not use the observed LA as the model input. Methods to derive the LA from TLS measurements have been recently proposed for coniferous and broad-leaved forests. We tested the voxel-based method of Hosoi and Omasa [2006] at our site, but the calculated LA was not invariant when voxel size changed, which is a sign that the resolution of our laser scans is too low for this method. In our case, a voxel-size of $<1 \text{ cm}$ could not be achieved because of the angular step width of the laser beams, 0.002° and the large distance to the tree canopies. Nevertheless, the use of an estimation of the LA has advantages compared to the calibration to stem sap flux measurements because the measurements are often not available for a large number of trees and require a careful calibration to the stand and the tree species [Bush et al., 2010].

3. Results

3.1. Sky Luminance and Canopy Light Regime

[49] The measured daily maxima of above-canopy PAR ranged from $430\text{--}1920 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the observation period, and the direct fraction of global radiation was 0.6. All 15 CIE sky types were observed during the vegetative period of 2009 in the model. The most frequent CIE sky types were type 12 (CIE standard clear sky) and type 9 (partly cloudy, with the obscured sun) with a proportion of 24%, followed by sky type 10 (partly cloudy, with brighter circumsolar region, 19%). The five CIE overcast sky types had a proportion of 11%, the five transitional sky types had a proportion of 46%, and the five clear sky types had a proportion of 43%.

[50] The vertical distribution profiles inside the canopy can be derived by building the mean values of the PAR

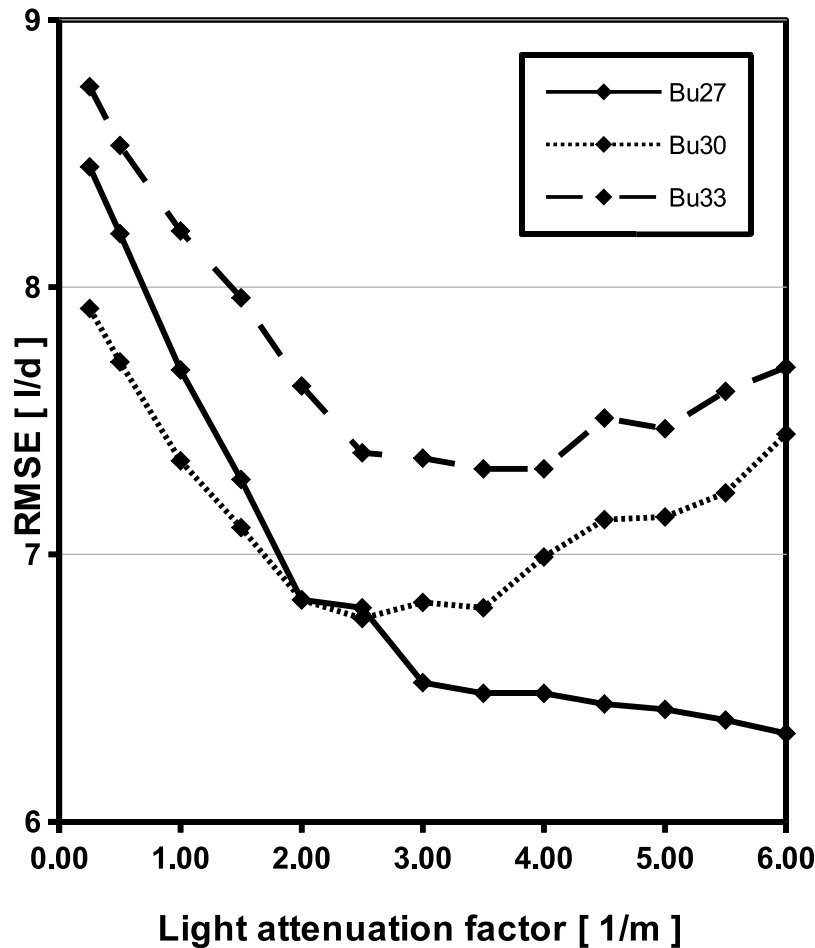


Figure 2. Root mean square error (RMSE) of the simulated and measured daily stem sap flux for different values of the light attenuation factor λ .

intensity of all voxels with the same height (Figure 3a). Approximately 80% of the incoming PAR is attenuated at the highest 5 m of the canopies. Below the onset of the canopy, more than 95% of the incoming PAR was attenuated. In comparison with the direct sunlight, the diffuse skylight penetrated the canopy deeper (Figure 3b).

3.2. Volumetric Soil Water Content

[51] During the observation period, the measured volumetric soil water content at a depth of 20 cm varied between 35% and 38%, indicating wet soil water conditions with enough soil water available to the plants. The simulated values of the volumetric soil water content were similar to the measured values, and the root mean square error of the observation period was below 2%. The linear fit equation between the simulated volumetric soil water content θ_{sim} (%) and the measured soil water content θ_{meas} (%) was $\theta_{sim} = 0.96 \theta_{meas} + 0.8$ ($R^2 = 0.88$; $p < 0.0001$).

3.3. Xylem Water Potential

[52] An important model state-variable is the xylem water potential, which is calculated for every cylinder element at every time step. The gradient of lower values of the xylem water potential in the fine branches and higher values in the

root system is a result of the gravitation gradient and the depletion of branch xylem water caused by the daily transpiration. Following the diurnal changes in transpiration, the highest gradient of xylem water potential is observed in the afternoon (Figure 4). During the night, the tree takes up water from the soil and after filling only a xylem water potential difference between the cylinder elements due to the gravity potential is observed.

3.4. Daily and Diurnal Stem Sap Flux

[53] During the observation period the mean value $\bar{S}$ of the measured daily stem sap flux was 69 l d^{-1} for *Bu27*, 65 l d^{-1} for *Bu30*, and 80 l d^{-1} for *Bu33*. The highest value of 138 l d^{-1} was measured for *Bu33* on 6/2/2009. The differences between the measured and the simulated stem sap flux are expressed by three statistical criteria: the root mean square error $RMSE$ (l d^{-1}), the normalized root mean square error $NRMSE = \frac{RMSE}{\bar{S}}$ and the Nash-Sutcliffe model efficiency NSE [Nash and Sutcliffe, 1970] (Table 3, Figure 5). The values for the BBL model indicate a good model performance with a higher quality than the Penman-Monteith simulations.

[54] The simulated diurnal dynamics of stem sap flow were similar to the measured half-hourly values (Figure 6).

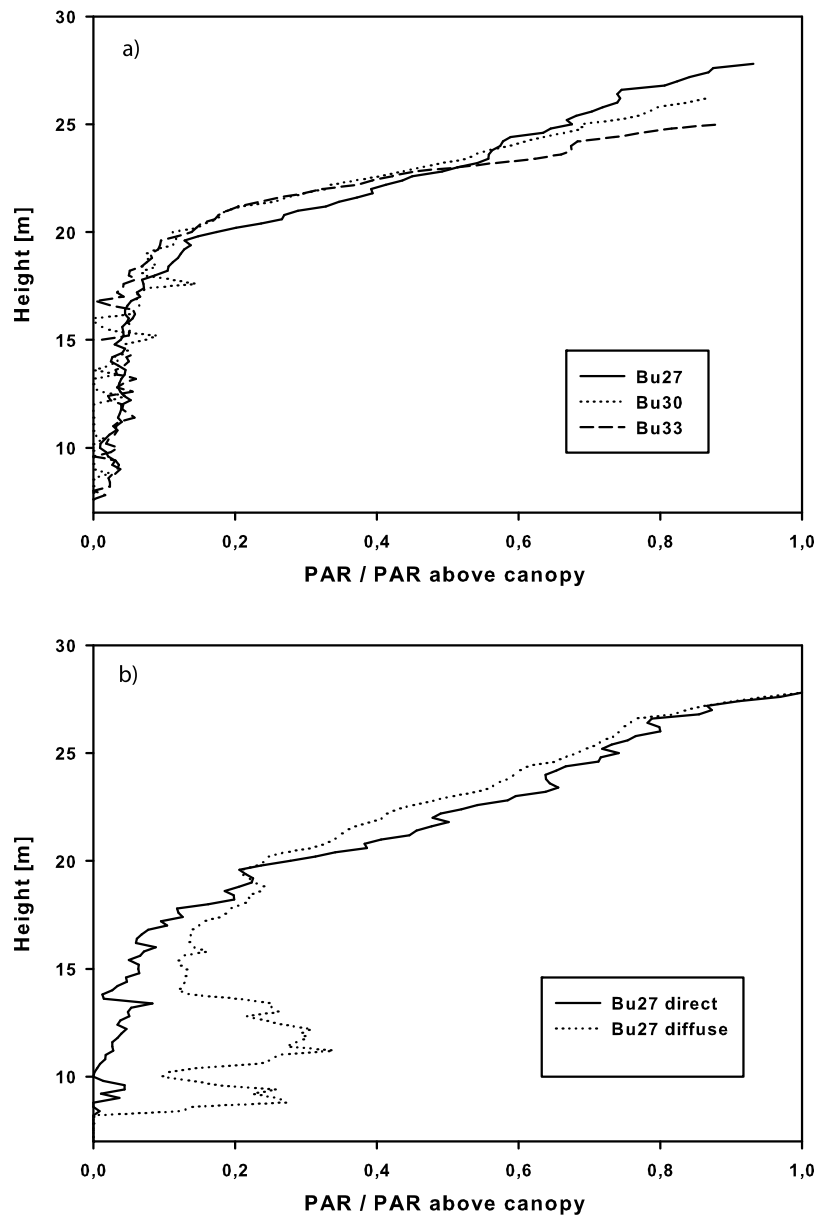


Figure 3. (a) Vertical distribution of photosynthetically active radiation (PAR) in the canopies of the three beech trees at noon at CIE standard clear sky. (b) Vertical distribution of direct sunlight and diffuse skylight PAR in the canopy of *Bu27* at noon at CIE sky type 5 (standard sky of uniform luminance).

The simulated values of stem sap flux of the Jarvis-type and BBL-type stomatal reaction models were different compared to the stand-level simulations of transpiration applying the down-scaling of the Penman-Monteith reference method, although the simulations were calibrated to the mean value of the sap flux. The onset of the simulated sap flux in the morning hours was up to 1 h later when using the stomatal reaction models compared to the model based on the Penman-Monteith approach. This was because the models based on the up-scaling of stomatal conductance included the incoming light, which was low inside the canopy of the three *F. sylvatica* trees because the angle between the direct sunlight and the horizon was low in the morning hours, which resulted in a high shadowing of the canopy. Another

difference was observed on days with a low *VPD*. For example, on the rainy day of 5/28/2009, the Penman-Monteith approach overestimated the transpiration rate of all three trees.

3.5. Stomatal Closure Due to Low Branch Water Status

[55] Only on hot and sunny days with a high transpiration, water stress was observed in the simulation. The lowest ratio of daily actual and potential transpiration was 0.98 for *Bu27* and *Bu30*, and 0.95 for *Bu33* on 6/2/2009. On branch level, the restriction of the transpiration by low water status of the leaves is described by the reduction factor $f_{\psi_x}(\psi_x) \in [0.1 \dots 1.0]$, with a value of 1.0 indicating no closure of the stomata due to a low leaf water content. The water stress is

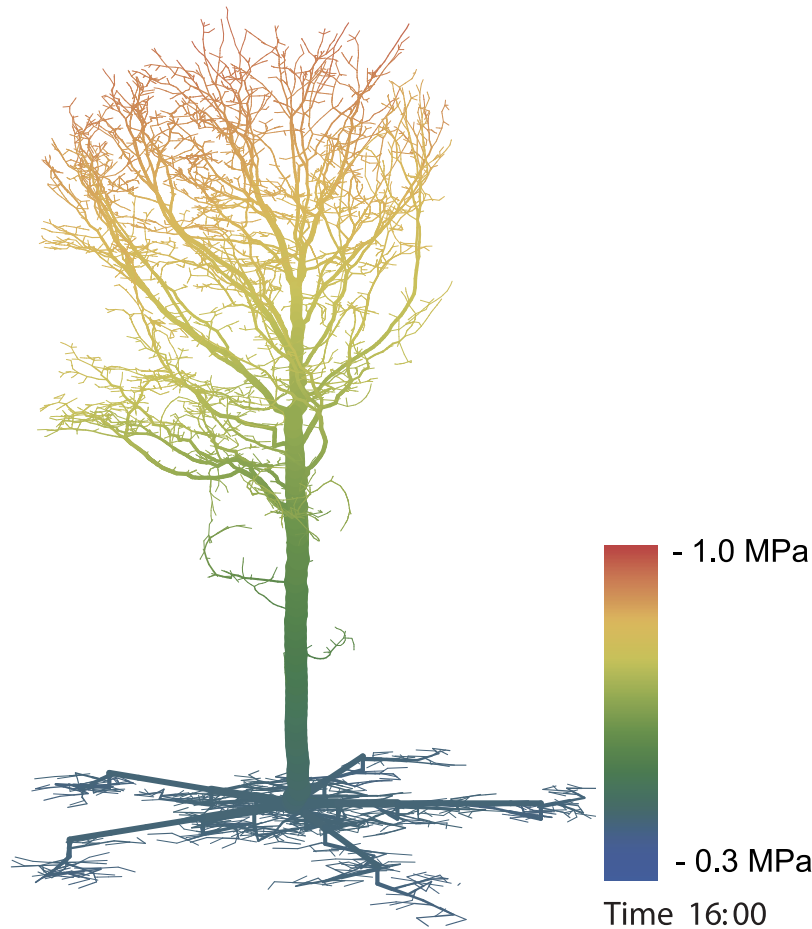


Figure 4. Xylem water potential of the model xylem cylinder elements at the observation day 6/2/2009, 16:00 LT at the tree *Bu27*. The visualization shows a simplified root system with fewer elements than are actually used in the model.

higher for branch elements that are higher and increases with the length of the water path (Figure 7). Single branches with similar path lengths and with a similar height can show different patterns of water stress as a result of the total leaf area that is attached to the branches and the distribution of the leaf area. The light regime had also an influence on the stomatal closure. In a model scenario, the fraction of direct radiation is set to 1.0 and the resulting distribution of the potential transpiration over the branch elements is applied with the total amount of potential transpiration kept unchanged. The water stress is increased in this scenario of a regime of direct light with the lowest ratio of daily actual and potential transpiration of 0.92 (*Bu33*).

[56] Next to the reduction factor of the canopy elements, the model provides the volumetric and total xylem water content, the xylem water potential and the water flux between connected cylinder elements. These hydrodynamic state variables are provided in a high spatial and temporal resolution and make an analysis of the mechanisms that lead to water stress possible. As a result of the high availability of soil water during the whole observation period, the water status of the leaves was not restricted by the water uptake rates of the roots. At hot days with a high potential transpiration the simulation revealed another process that led to a

stomatal closure due to a low xylem water content of the branches. The water status of the leaves was restricted by the axial hydraulic conductivity of the roots and branches and the resulting capability to supply the fine branches at the top of the canopy with enough water after the diurnal transpiration rates were highest and the water reserves of the xylem were exhausted.

[57] About 19% of the amount of the transpiration is contributed by the depletion of canopy xylem water. The lowest canopy xylem water content was simulated between 14:00 and 15:00 LT and about 2 h after the peak of the transpiration at noon. At this time the ratio of actual and

Table 3. Model Performance Over the Observation Period (BBL Model/Penman-Monteith Model)^a

Statistical Criterion	<i>Bu27</i>	<i>Bu30</i>	<i>Bu33</i>
<i>RMSE</i> (l d^{-1})	6.6 / 10.2	7.4 / 14.0	6.8 / 9.6
<i>NRMSE</i> (–)	0.10 / 0.15	0.09 / 0.18	0.11 / 0.15
<i>NSE</i> (–)	0.93 / 0.82	0.99 / 0.97	0.94 / 0.88

^aThe simulated daily stem sap flux is compared to the measured daily stem sap flux. *RMSE*, root mean square error; *NRMSE*, normalized root mean square error; *NSE*, Nash-Sutcliffe index.

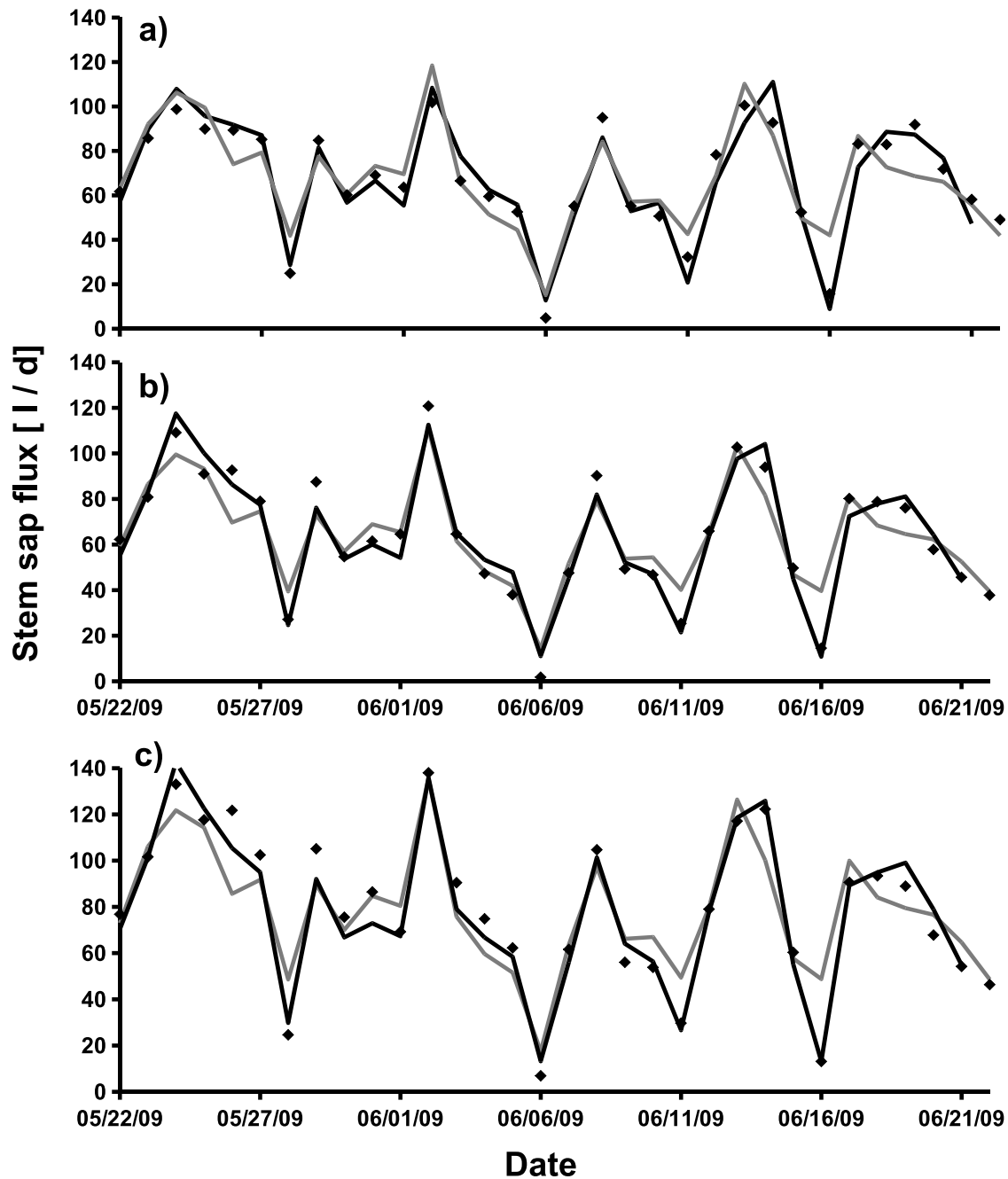


Figure 5. Daily values of measured stem sap flux (dots) and simulated stem sap flux (black solid line shows BBL model results; gray solid line shows down-scaled Penman-Monteith model results): (a) *Bu27* (b) *Bu30* (c) *Bu33*.

potential transpiration was 0.93 for *Bu33*. The xylem water content is depleted mostly till noon. After noon, the leaf demand for water has to be supplied by the water transport inside the tree which may lead to limiting leaf water contents. A similar behaviour is observed in the simulation at other days with high rates of potential transpiration rates.

3.6. Influence of Direct Sunlight and Diffuse Skylight on the Transpiration

[58] In a model scenario we quantified the differences of the influence of the direct and the diffuse PAR on the

transpiration rate of the whole canopy. Using the *CIE* distributions of the intensity of the diffuse skylight in the hemisphere can reproduce the omnidirectional penetration of skylight into the canopy. In the scenario we used the measured total values of incoming PAR and the daily dynamics of PAR and compared the transpiration rates that resulted of using the fraction of direct PAR radiation of 1.0 and 0.0. All other environmental drivers such as the temperature and the vapour pressure deficit were kept as measured.

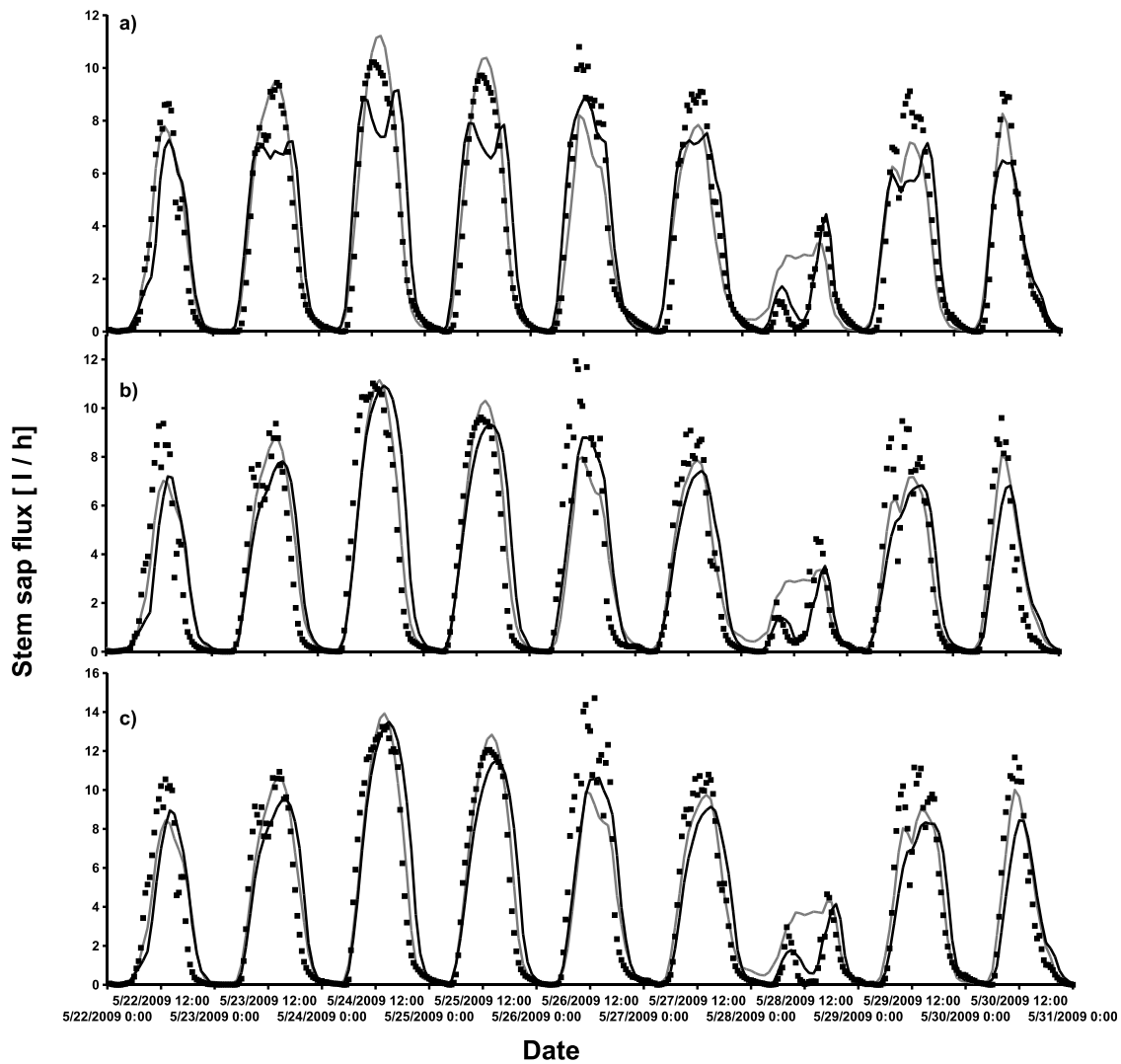


Figure 6. Diurnal values of measured stem sap flux (dots) and simulated stem sap flux (black solid line shows BBL model results). The gray solid line gives the simulated values of sap flux using the down-scaled Penman-Monteith reference potential evapotranspiration model instead of the BBL-type model of stomatal reaction: (a) *Bu27* (b) *Bu30* (c) *Bu33*.

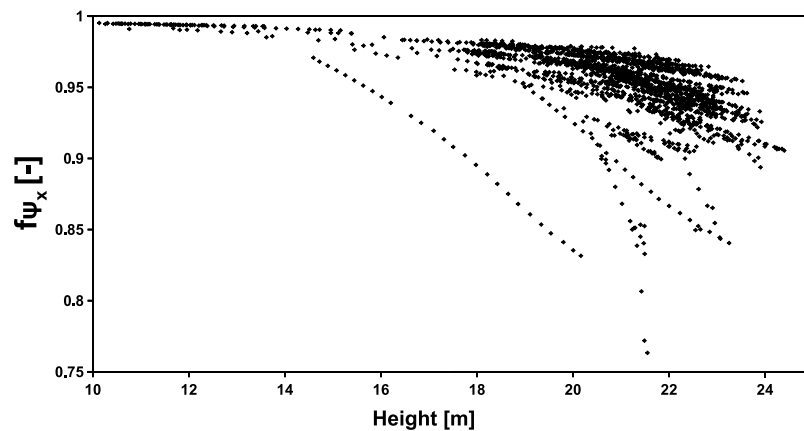


Figure 7. Reduction factor $f_{\psi_x}(\psi_x)$ of stomatal conductance due to low branch matric water potential of all canopy cylinder elements of *Bu33* that are attached to leaves (6/2/2009, 15:00 LT). A value of $f_{\psi_x}(\psi_x) = 1.0$ indicates no water stress.

[59] The diffuse radiation results in 17%–19% higher transpiration rates than the rates of direct sunlight, depending on the *CIE* sky type. *CIE* sky types with a homogenous distribution of the intensity in the hemisphere show the highest transpiration rates. The transpiration rates of the clear sky types are lower, because these *CIE* types show a large intensity gradient of skylight toward the direction of the sun.

[60] The increase of the simulated transpiration rates can be explained by the deeper penetration of the omnidirectional diffuse skylight (Figure 3b). The deeper penetration of light increased the transpiration rates of the lower branches strongly, because the light curve of the BBL-model is steep for low PAR intensities.

4. Discussion

4.1. Sky Luminance and Canopy Light Regime

[61] A database of daylight information such as the half-hourly *CIE* sky types has been made available for western and central Europe via the *Satel-light* project (www.satel-light.com) [Fontoyne et al., 1999]. The daylight information within this framework is completely derived from *Meteosat* satellite imagery of the years 1996–2000. The proportions of the derived *CIE* types for the Hainich site are 24% overcast sky types, 40% transitional sky types, and 36% clear sky types. These are similar to the *CIE* type frequencies that we have derived from micrometeorological measurements for the year 2009.

[62] The modeled vertical distribution of PAR is similar to the vertical PAR regime that were observed at *F. sylvatica* forests with a similar structure [Leuchner et al., 2005; Hansen et al., 2002].

4.2. Xylem Water Potential

[63] The simulated diurnal change of the xylem water potential is observed in field measurement. Observed values of the daily leaf water potential ψ_l ranged from -2.5 to -1.4 MPa at sun-exposed leaves at noon and from -1.8 to -0.3 MPa at predawn [Köcher et al., 2009]. The observed fine root xylem water potential ranged from -1.5 to -0.5 MPa [Korn, 2004]. The values are similar to observations of broad-leaved old-growth trees at other temperate sites; for an overview over the observed values, see Korn [2004].

4.3. Daily and Diurnal Stem Sap Flux

[64] The application of the stomatal conductance models could improve the model performance of the simulated daily sap flux compared to the down-scaling of the Penman-Monteith estimate of the potential transpiration. This is in accordance with Loranty et al. [2010], who achieved a similar model error using a simpler representation of the canopy and light attenuation. Therefore, the good performance of the functional-structural model presented in this study has to be compared to the performance of other simpler models. Here we observed that a stand-level estimation of the potential transpiration using the Penman-Monteith reference evapotranspiration method in combination with a geometrically explicit tree water flow model could already adequately reproduce the measured values of actual evapotranspiration [Janott et al., 2011]. The Jarvis-type and BBL-

type models of stomatal reaction performed better than the down-scaling approach, especially on days with a low Penman-Monteith potential transpiration, because the Penman-Monteith approach tends to overestimate the potential transpiration under these weather conditions at forest sites [David et al., 1997].

[65] This raises the question whether the voxel-based light model and the Jarvis or BBL type models of stomatal response are an adequate way (with respect to the model complexity) to describe the water use of single trees. First, it has to be stated that the additional model input parameters, such as the light attenuation factor or the parameters for the stomatal reaction, are easily estimated (see section 2.8) and can be found in the literature for many species. If laser scans of the canopy are available, the algorithms to extract the voxel and the cylinder element representations work automatically and require little user interaction. In this way, TLS is an elegant way to provide the functional-structural model of single tree water flow with detailed structural information on the aboveground part of the trees, as was suggested by Loranty et al. [2010]. Second, the simulation of tree water flux at high temporal and spatial resolutions allows the analysis of the influence of the light regime on the water usage, the interaction of the light regime and the hydraulic architecture, and the interaction with single neighboring trees.

[66] The influence of a low leaf water status at noon on the closure of the stomata was low during the observation period, with a maximal daily decrease of 5%. The inclusion of a detailed tree hydraulic model and a root water uptake model is nevertheless crucial because the impact of the leaf water status could be higher under different climatic and site conditions. The sensitivity of the stomatal conductance to the leaf water status is highly determined by the structure and height of the stand [Novick et al., 2009; Janott et al., 2011], and is significantly higher for ring-porous species [Bittner et al., 2012]. Furthermore, the Hainich site shows dry soil water conditions and long drought periods in some years, leading to a significant decrease in transpiration at nonoptimal soil water conditions [Hölscher et al., 2005; Köcher et al., 2009; Gebauer, 2010].

[67] Using measurements of radiation and vegetation-atmosphere energy fluxes at the Hainich forest, Knohl and Baldocchi [2008] analyzed the influence of the fraction of diffuse skylight of total incoming radiation on photosynthesis and tree transpiration. They found a sensitive dependency of the total stand-atmosphere gas exchange on the fraction of diffuse radiation at forests with a heterogeneous canopy as a result of a higher penetration into the canopy of diffuse radiation than direct radiation [Leuchner et al., 2005]. Therefore, a detailed simulation of the skylight using the *CIE* model is adequate, especially for heterogeneous canopies of mixed or uneven-aged forests.

[68] This study focused on the simulation of *F. sylvatica* trees, but the application on other tree species is possible. A preceding study had applied the soil-plant water flow model to *F. sylvatica*, *T. cordata*, and *F. excelsior* species and was able to simulate the species-specific water balances [Bittner et al., 2012]. Thus, an up-scaling of the simulations of the single trees to a mixed stand seems to be possible by applying the model on tree groups that consist of different species.

4.4. Influence of Direct Sunlight and Diffuse Skylight on the Transpiration

[69] The difference of CO_2 and water exchange under direct or diffuse radiation has been described in modeling [Knobl and Baldocchi, 2008] and observational [Urban et al., 2007] studies. The authors state that the deeper penetration of diffuse light into the canopy may be the main reason for higher observed gas exchange at days with a low fraction of direct radiation. The leaves that are in lower parts of the canopy are shaded and the PAR intensity is in the linear part of the light curve that is used to calculate the assimilation rate and the stomatal conductance. The increase of the light intensities in the lower parts of the canopy has a high positive effect on the total canopy transpiration rate. The sunlit leaves at the top of the canopy are exposed to higher PAR intensities and are in less steep regions of the light curve (saturation). The light penetration effect is overlaid by other possible indirect effects [Knobl and Baldocchi, 2008; Urban et al., 2007]. On days with a low fraction of direct radiation, the total incoming radiation is usually lower, which makes a quantification of the light penetration effect difficult in observational studies. The model scenario analysis of direct and diffuse radiation could reveal the deeper penetration of diffuse light into the canopy as the main effect that increased the simulated transpiration rates.

5. Conclusion

[70] A functional-structural model that is capable of simulating the water flux in single trees at a high temporal and spatial resolution was presented. Using the information of the TLS combined with a root architecture model, it is possible to analyze the water flux through single root elements and branches. The model combines physiological tree properties with the structure of the trees and allows us to describe the interaction of function and structure and to quantify the influence of single species-specific hydraulic traits. In its present form, the model may be useful for analyzing the interactions of neighboring trees and their competition for available soil water and sunlight. By up-scaling the hydrological properties of different tree species of a mixed forest, this model can be used to analyze the effect of biodiversity on the water cycles of the entire stand.

[71] The geometrical input was derived from point clouds provided by terrestrial laser scans. The data processing algorithms to convert the point clouds into voxels and into cylinder elements require minimal user input and are applicable for various tree sizes and species.

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