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Modelling age- and density-related gas exchange of *Picea abies* canopies in the Fichtelgebirge, Germany

Eva Falge*, John D. Tenhunen, Ron Ryel, Martina Alsheimer and Barbara Köstner

Biometeorology, ESPM, Univ. of California, Berkeley, CA 94720, USA

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Abstract – Differences in canopy exchange of water and carbon dioxide that occur due to changes in tree structure and density in montane Norway spruce stands of Central Germany were analyzed with a three dimensional microclimate and gas exchange model STANDFLUX. The model was used to calculate forest radiation absorption, the net photosynthesis and transpiration of single trees, and gas exchange of tree canopies. Model parameterizations were derived for six stands of *Picea abies* (L.) Karst. differing in age from 40 to 140 years and in density from 1680 to 320 trees per hectare. Parameterization included information on leaf area distribution from tree harvests, tree positions and tree sizes. Gas exchange was modelled using a single species-specific set of physiological parameters and assuming no influence of soil water availability. For our humid montane stands, these simplifying assumptions appeared to be acceptable. Comparisons of modelled daily tree transpiration with water use estimates from xylem sapflow measurements provided a test of the model. Estimates for canopy transpiration rate derived from the model and via xylem sapflow measurements agreed within $\pm 20\%$, especially at moderate to high air vapor pressure deficits. The results suggest that age and density dependent changes in canopy structure (changes in clumping of needles) and their effect on light exposure of the average needle lead to shifts in canopy conductance and determine tree canopy transpiration in these managed montane forests. Modelled canopy net photosynthesis rates are presented, but have not yet been verified at the canopy level.

norway spruce / xylem sapflow / canopy transpiration / canopy light use efficiency / biosphere-atmosphere interactions

Résumé – Effet de l'âge et de la densité sur la modélisation des échanges gazeux dans la canopée de peuplements de *Picea abies* (L.) Karst. dans le Fichtelgebirge (Allemagne). Les différences d'échange d'eau et de dioxyde de carbone au niveau de la canopée qui se produisent à la suite de changements dans la structure et la densité des arbres dans des peuplements d'Épicéa commun en zone de montagne de l'Allemagne centrale, ont été analysées selon le modèle tridimensionnel de microclimat et d'échange gazeux STANDFLUX. Le modèle a été utilisé pour calculer l'absorption du rayonnement par la forêt, le bilan photosynthétique net et la transpiration d'arbres individuels, et les échanges gazeux au niveau de la canopée. La paramétrisation du modèle a été effectuée à partir des mesures dans six peuplements de *Picea abies* (L.) Karst. dont l'âge variait de 40 à 140 ans et la densité des peuplements de 1680 à 320 arbres par hectare. La paramétrisation incluait l'information sur la distribution de la surface foliaire à partir de l'exploitation d'arbres, la position des arbres et leurs dimensions. Les échanges gazeux ont été modélisés en utilisant une série de paramètres physiologiques spécifiques de l'espèce, et en supposant qu'il n'y avait aucune influence de la disponibilité en eau. Pour les peuplements considérés en zone humide de montagne, ces hypothèses semblent acceptables. La comparaison de l'estimation par modélisation de la transpiration journalière avec l'estimation de l'eau absorbée par la mesure du flux de sève xylémique a permis de tester le modèle. L'estimation du taux de transpiration par la canopée dérivé du modèle par la mesure du flux xylémique concorde à $\pm 20\%$, spécialement lorsque les déficits de pression de vapeur sont modérés ou élevés. Les résultats suggèrent que les changements dans la structure de la canopée, dépendant de l'âge et la densité et leurs effets sur l'exposition à la lumière de l'aiguille moyenne conduisent

* Correspondence and reprints
Tel. (49) 921.55.2576; Fax. (49) 921.55.2564; e-mail: falge@uni-bayreuth.de

à un décalage dans la conductance de la canopée et déterminent la transpiration dans la canopée de l'arbre de ces forêts aménagées de montagne. Les taux de photosynthèse nette modélisés de la canopée sont présentés, mais n'ont pas encore été validés au niveau des mesures.

épicéa / modèle tridimensionnel STANDFLUX / flux de sève / transpiration de la canopée / efficacité d'utilisation de la lumière / interaction biosphère-atmosphère

1. INTRODUCTION

Long-term eddy covariance measurements over temperate forests are now more commonly used to quantify annual net ecosystem CO₂ exchange of different forest types [4, 22, 64]. It is anticipated that flux measurement networks will help clarify the role played by temperate forests in the global carbon cycle [4]. However, large variation and uncertainty exists in eddy-flux estimates obtained under seemingly similar environmental conditions. These problems may be due in part to the continuous shifts in the footprint along with the heterogeneous nature of forest ecosystems. For a better interpretation of eddy covariance signals, as well as whole ecosystem response, it is important to improve our understanding of natural variation in processes that occur within individual ecosystem compartments, e.g., to describe functional heterogeneity that occurs in the vicinity of experimental towers, to map structure within the footprint area of the towers [3, 61], and to eventually associate specific measurements of gas exchange with processes occurring at specific locations [64].

Xylem sapflow methods provide a means of characterizing local water use by the forest canopy [e.g., 16, 24, 34, 35, 40, 41, 48, 50]. Sapflow sensors were used in six spruce stands of differing ages within a montane catchment in the Lehstenbach watershed (Fichtelgebirge, Germany) in order to examine time dependent changes in tree canopy transpiration [1]. As stands age in these montane forests, density decreases from several thousand trees per hectare to only several hundred per hectare, as a result of both management activities, and natural self-thinning. Along with these structural changes, tree canopy transpiration decreases to half of the rate found in young stands even though stand total leaf area remains high [1].

A three-dimensional gas exchange model (STAND-FLUX; cf. [18]), which includes sub-models for light interception and for gas exchange of individual branches or leaves, was used to examine variation in tree canopy gas exchange of the six Norway spruce canopies. The model accounts for site-specific stand structure, and estimates gas exchange for clusters of trees, each tree with foliage distributed within vertical layers and horizontally in a series of concentric cylinders. This study investi-

gates whether the observed differences in tree transpiration result from physiological changes or due to altered clumping of the foliage in the canopy. Associated changes in canopy net photosynthesis and water use efficiencies are also predicted, but these have not yet been independently validated.

2. METHODS

2.1. Field research sites

Structural characteristics were determined for six Norway spruce stands occurring in proximity in the Fichtelgebirge in Northern Bavaria (Lehstenbach catchment, latitude 50° 9' N, longitude 11° 52' E, c.a. 775 m above sea level). The stands differed either in age and structure, in exposition, or in soil characteristics (*Table 1*). In the following text, the 40 year-old stands Weiden Brunnen, Schanze, and Schlößner Brunnen with low, medium, and high cumulative basal areas will be referred to as "40LB", "40MB", and "40HB" respectively, the older stands Süßer Schlag, Gemös, and Coulissenhieb according to their age will be referred to as "70", "110", and "140". Tree density varied between 320 and 1680 trees per ha⁻¹, average projected leaf area index (LAI) determined via harvesting methods varied between 5.3 and 7.9 m² m⁻². Average tree height in the stands is between c.a. 15 and 26 m. The soils are permeable brown earths and podsoles on phyllite and gneiss. During the period 1992 to 1994, the mean annual temperature was 5.8 °C, the mean January temperature was -1.0 °C, and the mean in July was 15.6 °C. Mean annual precipitation during this period was 885 mm.

2.2. Observations of Sap flow

Investigations were carried out in 1994 and 1995 from the middle of April to the middle of November (see details in Alsheimer et al. [1]). In each stand, sapflow installations were made on 10 trees except in the case of the 140-year-old stand where 12 to 13 trees were examined. Two methods for measuring xylem sapflow were used: dynamic thermal flowmeters constructed according to Granier [23, 24] and the steady-state, null-balance

Table I. Stand characteristics as used in the model parameterization for six Norway spruce stands in the Lehstenbach catchment in the Fichtelgebirge, Northern Bavaria. See also Alsheimer et al. (1998).

Site	Weiden Brunnen "40LB"	Schanze "40MB"	Schlöppner Brunnen "40HB"	Süßer Schlag "70"	Gemös "110"	Coullisenhieb "140"
Stand age (years)	40	40	40	70	110	140
Exposition	southwest	northeast	south	southeast	south	southwest
Tree density (tree ha ⁻¹)	1010	1010	1680	500	450	320
Mean stand height (m)	16.1	17.8	14.7	24.1	25.7	25.2
Mean crown length (m)	10.0	7.7	6.4	11.5	13.8	11.4
Mean crown projection (m ²)	10.3	7.2	7.7	18.6	18.8	22.0
Mean circumference at breast height (cm)	60.0 (±16.3)	66.4 (±18.5)	50.5 (±19.9)	108.7 (±19.1)	107.6 (±22.4)	115.2 (±23.5)
Cumulative basal area (m ² ha ⁻¹)	30.9	37.8	39.5	48.8	42.4	35.3
LAI (m ² m ⁻²)	5.3	7.1	6.5	7.9	7.6	6.5
Understory cover (%)	66	19	23	85	76	83

method of Cermák et al. [14, 15]; Kucera et al. [37]; and Schulze et al. [62].

With the Granier methods applied in all stands, cylindrical heating and sensing elements were inserted into the trunks at breast height, one above the other c.a. 15 cm apart, and the upper element was heated with constant power. The temperature difference sensed between the two elements was influenced by the sap flux density in the vicinity of the heated element. Sap flux density was estimated via calibration factors established by Granier [23].

The steady-state, null-balance instrumentation was used to obtain an additional estimate of water use by individual trees within the 140 year-old stand. A constant temperature difference of 3K was maintained between a sapwood reference point and a heated stem section. The mass flow of water through the xylem of the heated area is proportional to the energy required in heating.

Total sapflow per tree was obtained by multiplying sap flux density by the cross-sectional area of sapwood at the level of observation [1]. Sapwood area of sample trees was estimated from regressions, relating CBH (circumference at breast height) to sapwood area determined either with an increment borer, by computer tomography [26, 27], or from stem disks of harvested trees. The up-scaling of canopy fluxes from xylem sap flow measurements was obtained by multiplying average flux densities (sapflow per sapwood area) of ten (for stand "140" 14) representative trees by total sapwood of the stand and dividing by the ground surface area. The trees were selected to best represent the CBH distribution of the canopy, and, therefore, of varying CBH and sapwood area, affecting their relative contribution to total canopy fluxes.

2.3. Model description

2.3.1. Branch gas exchange model

Photosynthesis of needed branches was described according to Farquhar et al. [21] and Harley and Tenhunen [28]. Stomatal conductance was included according to Ball et al. [5] as described in Falge et al. [17]. Details of the application are described in Appendix 1.

2.3.2. Gas exchange of individual trees and canopies

The model STANDFLUX [18] calculates water use and CO₂ fixation of individual target trees surrounded by trees of varying size and structure, considering species-specific leaf physiology, three dimensional radiation interception, and vertical microclimate gradients. One tree consists of a series of concentric cylinders and vertical layers. The resultant subsections are characterized by homogeneous leaf and stem densities as well as leaf and stem angles as derived from tree harvests. The light interception submodel calculates direct beam and sky diffuse radiation (PPFD) for each point of a cubic matrix superimposed over the tree. Single tree transpiration in STANDFLUX is calculated using a leaf area weighted sum of the rate of water use in all subsections of the tree (determined by multiplying the average transpiration rate for all matrix points in the subsection by the leaf area of the subsection and then summing subsections - see Falge et al. [18]). Details of the light interception algorithms and tree structural description are given in Ryel [57], Ryel et al. [58], and Falge et al. [18].

The contribution of the tree classes - defined by tree size - to canopy gas exchange is estimated from the frequency of occurrence of the different classes in the

canopy. With information on the (x, y) coordinates of the trees in the stand, the gas exchange of a cluster of trees with clumped leaf area similar to observation can be calculated. Such clusters of trees were the subject of sapflow observations as reported by Alsheimer et al. [1]. Thus, the model provides a good representation of the actual experimental situation. For model parameterization, structural information such as tree height, crown length, crown projection area, distribution of leaf area density (LAD), distribution of stem area density (SAD), leaf angles, and stem angles in subsections are required.

2.4. Model parameterization

2.4.1. Canopy and individual tree structure

The positions of trees in each stand and their crown projections are illustrated in *figure 1*. Shaded crowns indicate those trees on which sapflow was measured.

The frequency distribution of tree circumferences at breast height (CBH) was obtained at the six locations, and found to be normally distributed (data not shown) with the lowest mean of 50.5 at "40HB" (*table I*) and highest of 115 cm at "140". Tree heights and crown lengths were measured with a Suunto-Hypsometer (PM-5/ 1520 PCP, 02920 Espoo, Finland). Crown projection areas (CPA) were estimated from below the crown by vertical sighting at eight locations around each tree. The octagonal CPA were used to obtain circular approximations for the cylindrically modelled trees. Off-centered trunks were re-centered within the resulting CPAs to accommodate STANDFLUX. CBH was used to define five tree size classes. A representative tree from each class was harvested to estimate leaf surface and projected stem area densities within the crowns (*table II*). The harvested trees were cut into one-meter sections. From each section, a subset of sample branches were used to determine bare and needled length of branches and needle mass as related to branch basal diameter. With the

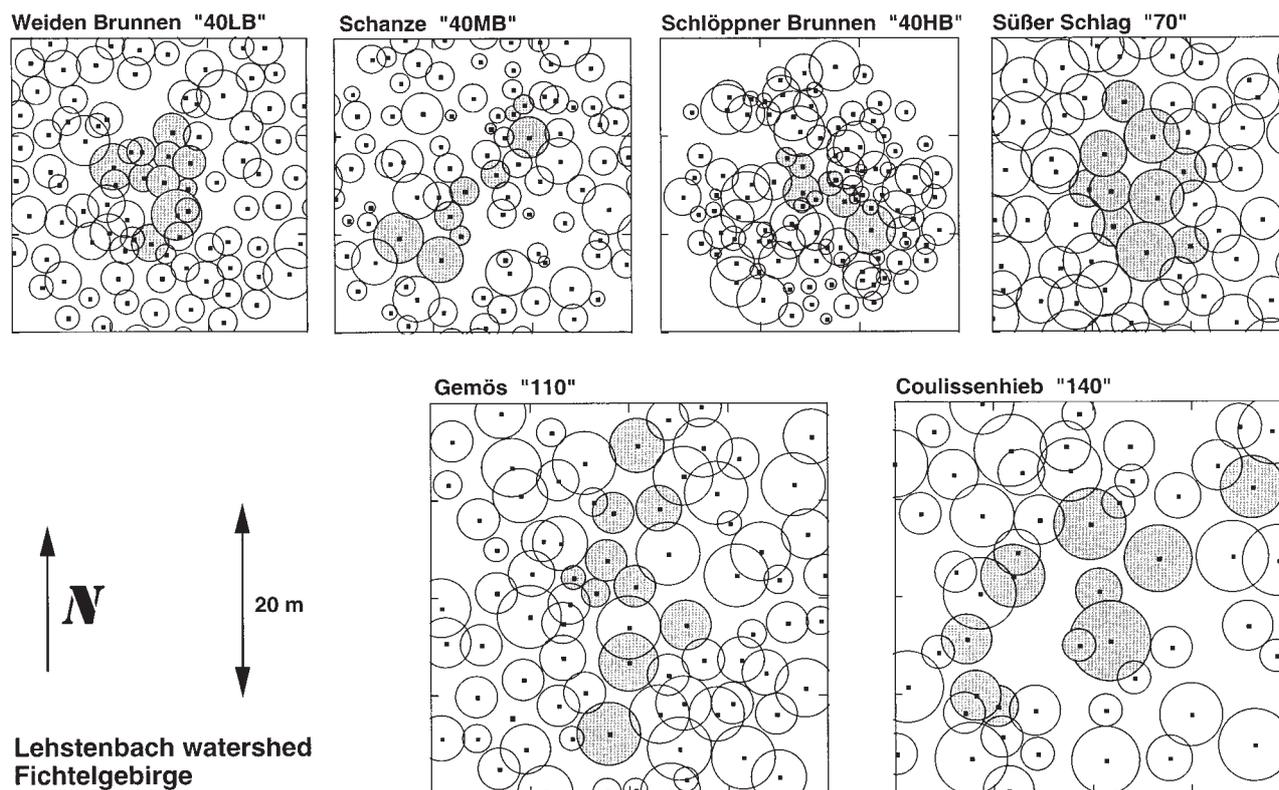


Figure 1. Relative tree positions and crown projected areas of the trees at the research sites in the Fichtelgebirge, Germany. Circular crown projections (CPA) were used to accommodate STANDFLUX; gray CPAs indicate the trees used for xylem sapflow measurements.

Table II. Coefficients of a power function to calculate average needle surface area (LSA, m² tree⁻¹) and average projected stem area (SAI, m² tree⁻¹) from the circumference at breast height (CBH, cm) for the four different age classes of Norway spruce stands, used for the STANDFLUX parameterization of leaf and stem area densities.

Sites	Number of trees <i>n</i>	LSA = $a \cdot \text{CBH}^b$ (LSA in m ² tree ⁻¹ , CBH in cm)			SAI = $a \cdot \text{CBH}^b$ (SAI in m ² tree ⁻¹ , CBH in cm)		
		<i>a</i>	<i>b</i>	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>r</i> ²
40-year-old	15	0.00116	2.81	0.93	0.000110	2.83	0.89
70-year-old	5	0.00514	2.39	0.68	0.000048	2.41	0.59
110-year-old	5	0.00520	2.39	0.83	0.000043	2.40	0.78
140-year-old	5	0.00685	2.35	0.95	0.000062	2.38	0.91

regressions obtained, the needle mass of remaining branches was estimated from their basal diameters and distributed along the tree according to mapped branch insertion points. Analogously, the branch mass and branch surface areas were determined.

Leaf area density (LAD) and stem area density (SAD) for single crown volumes were calculated from the respective absolute areas (leaf surface and stem projected area, LSA and SAI) according to the dependencies on CBH given in *table II*. The conversion used to obtain effective leaf area for light interception from LSA is given in Appendix 2. Horizontal and vertical changes in LAD and SAD in model trees were not considered in this application. Individual trees were constructed of two layers and two cylinders, but ten different tree size classes in the canopy were used. Considering the actual range of stand LAI encountered, simplification of the tree structure did not influence modelled water flux. Daily sums of transpiration are not affected at average canopy LAI above 5.3 (see sensitivity analysis in Falge et al. [18]), while underestimation of daily sums of canopy net photosynthesis increases from zero at a canopy LAI of 5.3 to 10% at a canopy LAI of 8.0 (Falge et al. [18], their *figure 5*).

2.4.2. Physiological parameterization

The physiological parameters for the Norway spruce branch gas exchange model (PSN6) were determined independently by means of cuvette gas exchange measurements of branches with up to 3 needle age classes [17] and were not adjusted in the process of examining xylem sapflow data. No information was available for needle gas exchange for trees of different age in the Fichtelgebirge, but Falge et al. [17] showed that parameters derived from 30-50 year-old spruce trees could be transferred to a 120 year-old tree in Lägeren (Switzerland), sufficiently reproducing measured gas exchange rates. In this study, the gas exchange reaction

for needles of all stands and for the entire tree crowns was described using a shade leaf parameterization determined appropriate for the Fichtelgebirge region with high LAI (*table III*). The physiological capacity of Norway spruce needles for electron transport, carboxylation, and dark respiration varies seasonally in agreement with gas exchange observations from several other tree species [10, 12, 47, 49]. We assumed that reduced soil water availability did not affect stomatal conductance during the summers 1994 and 1995 due to frequent rain events.

2.4.3. Meteorological drivers

The measurement of radiation, air temperature above and below the canopy, humidity, wind speed, CO₂ concentration, and atmospheric pressure for the modelling of the Norway spruce canopies in the Fichtelgebirge was described in Falge et al. [18]. The measurements were obtained with a 30 meter high telescope mast [32], during 1994 at "40LB", and 1995 at "140" (*figures 2 and 3*). Hourly means of the data stored at 10-minute intervals were used for the simulations. The stands "40LB" and "140" were immediately adjacent and the same meteorological conditions were used for both. For the sites "40MB", "40HB", and "70", temperature and vapor pressure deficit of the air at the top of the canopy were measured. Compared to "40LB" and "140", the temperatures at "40MB", "40HB" and "70" were about 12% lower; vapor pressure deficit of the air was on average 10% lower for "40HB" and "70", and 20% lower for "40MB", the north-east facing site. For "110" no meteorological measurements were conducted on the site and inputs to the model were assumed the same as "40LB" and "140". Differences in soil surface temperatures and canopy wind profiles were not considered in this modelling application. Although wind speed influences the boundary layer conductance of leaves or branches, the boundary layer conductance in coniferous forests is approximately an order of magnitude greater than

Table III. Constants and activation energies utilized to determine temperature and light dependent values of the photosynthesis model parameters for branches of Norway spruce in the Fichtelgebirge region. Parameters give seasonal variability of gas exchange on a needle surface area. For definition of the parameters, and carboxylase kinetics see Falge et al. [17].

	Parameter		Values	Units
Dark Respiration	$E_a(R_d)$	May-June	63500	J mol ⁻¹
		July-Aug. 15	64500	J mol ⁻¹
		Aug. 16-Sept.	64000	J mol ⁻¹
		Oct.-April	64000	J mol ⁻¹
	$f(R_d)$		25	
Electron transport capacity	$c(P_{ml})$	May-June	19.55	-
		July-Aug. 15	19.20	-
		Aug. 16-Sept.	19.30	-
		Oct.-April	19.35	-
			$\Delta H_a(P_{ml})$	55000
	$\Delta H_d(P_{ml})$	215000	J mol ⁻¹	
	$\Delta S(P_{ml})$	725	J K ⁻¹ mol ⁻¹	
Carboxylase capacity	$c(V_{c_{max}})$	May-June	34.50	-
		July-Aug. 15	34.25	-
		Aug. 16-Sept.	34.30	-
		Oct.-April	34.30	-
			$\Delta H_a(V_{c_{max}})$	77000
	$\Delta H_d(V_{c_{max}})$	215000	J mol ⁻¹	
	$\Delta S(V_{c_{max}})$	725	J K ⁻¹ mol ⁻¹	
Carboxylase kinetics	$f(K_c)$		31.95	-
	$E_a(K_c)$		65000	J mol ⁻¹
	$f(K_o)$		19.61	-
	$E_a(K_o)$		36000	J mol ⁻¹
	$f(t)$		-3.9489	-
	$E_a(t)$		-28990	J mol ⁻¹
Light use efficiency	α		0.015	mol CO ₂ (mol photons) ⁻¹
Stomatal conductance	g_{min}		0	mmol m ⁻² s ⁻¹
	g_{fac}		9.8	-

stomatal conductance [33], and therefore effects of changed wind profiles on canopy conductance are low.

2.5. Simulations

Simulations of canopy CO₂ and H₂O exchange were carried out for the periods May through September 1994 and April through October 1995. Since there is a time lag between the onset of transpiration in the canopy and measured flow of water in the trunk [e.g., 29], i.e., the model represents leaf responses while sapflow is influenced further by internal water storage, model validation at the individual tree level involves comparing the integrated daily sums of measured and estimated water use.

Stand level transpiration and net CO₂ fixation is estimated as the transpiration and net photosynthesis rate of the mean individual tree in each size class multiplied by the number of trees per ground area in the class, and then by integrating over all classes. Although simulations for virtual canopies showed high variation within a tree class (Falge et al. [18], their *table V*), calculations in the current application were performed only for one tree per class, namely that used for xylem sapflow measurements. This approach allowed comparisons at single tree level and reduced computer calculation time. While stand transpiration rate represents water loss through the tree crowns, net CO₂ fixation is calculated for needled branch ends, e.g., maintenance or growth respiration for the woody (bare) component of the canopy is not included.

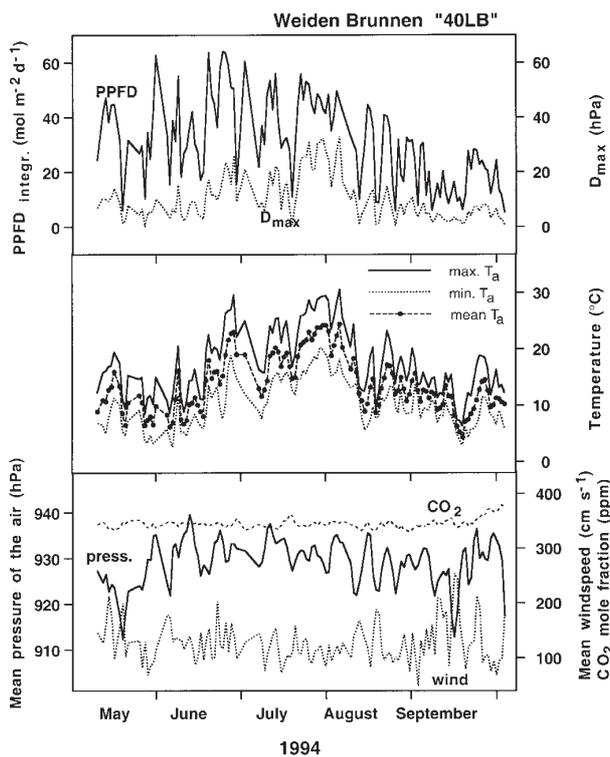


Figure 2. Daily sums of daily photosynthetic photon flux density ($PPFD_{integr.}$), maximum saturation deficit of the air (D_{max}), maximum, minimum, and mean daily temperature above the canopy (max. T_a , min. T_a , and mean T_a), atmospheric pressure, CO_2 concentration and wind speed above the Weiden Brunnen stand "40LB" from May until October 1994.

3. RESULTS

The daily integrated sums of model-estimated and measured transpiration (liters per tree and day) of ten 40-year-old individual trees at "40LB" and ten 140-year-old individual trees at "140" are compared in *figure 4* for the study periods of 1994 and 1995. The different symbols for the measurements at "140" indicate data originating from the different xylem sap flow measurement systems ("Granier" and "Cermák/Schulze", see Methods). Fluxes at "40LB" are much smaller than for "140", as the trees at "40LB" are much smaller and had less leaf area per tree (52 m^2 per tree) than those at "140" (203 m^2 per tree). The relationship between modelled daily tree transpiration and measured daily xylem sap flow was linear for most trees. However, the slope of the regression line for individual trees at Weiden Brunnen varies between 0.4 and 1.7 (with r^2 between 0.67 and 0.90), at Coulissenhieb between 0.6 and 3.2 (with r^2 between 0.74

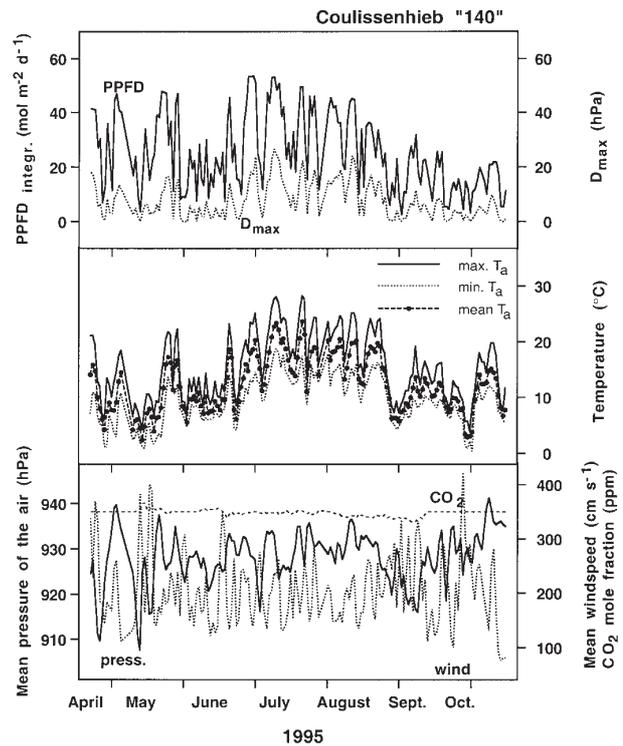


Figure 3. Daily sums of daily photosynthetic photon flux density ($PPFD_{integr.}$), maximum saturation deficit of the air (D_{max}), maximum, minimum, and mean daily temperature above the canopy (max. T_a , min. T_a , and mean T_a), atmospheric pressure, CO_2 concentration and wind speed above the Coulissenhieb stand "140" from April until October 1995.

and 0.89). Potential reasons for slopes differing from 1 are given in the discussion. Individual trees are not equally representative for the canopy (see above, Observation of Sap flow), but after weighted pooling of the results from all trees, a relatively good agreement between measured and modelled rates is found.

Figure 5 shows the comparison of modelled transpiration rates and measured xylem sap flow rates at the canopy level [1] for the six Norway spruce stands. Changes in transpiration rate due to daily variation in light, temperature and humidity are reproduced well by STANDFLUX with r^2 for the comparison regression line from 0.82 to 0.95, and slopes of the linear regression between c.a. 0.84 to 1.01 (see *table IV*). Absolute deviation of the model estimates of canopy transpiration from estimates based on xylem sapflow measurements can reach up to 0.5 mm per day (*figure 6*). However, especially when maximum daily water vapor saturation

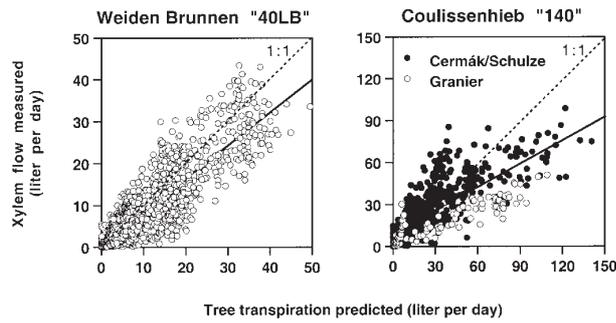


Figure 4. Comparison of daily estimates of water use obtained via xylem sap flow methods and from the canopy model for transpiration of single trees at the Weiden Brunnen "40LB" ($r^2 = 0.77$) and Coulissenhieb "140" ($r^2 = 0.64$) sites during the periods of 1994 and 1995 described in figures 2 and 3.

deficit (D_{\max}) is above 8 hPa (solid symbols), the deviation amounts to a maximum of c.a. $\pm 20\%$ of the transpiration rate. At lower values for D_{\max} , relatively large percentual over- and under-estimates of daily water use may occur (open symbols in figure 6), possibly due to lower measurement accuracy at low sap flow rates. Deviations appeared similar for both young and old stands, although transpiration rates remain much lower in the 140-year old stand.

Monthly sums of modelled canopy transpiration for the two summer periods are compared with measurements for the six Norway spruce stands in figure 7. A better agreement is found than on a daily basis due to error compensation of time integration. Observed and modelled monthly transpiration sums change in the rela-

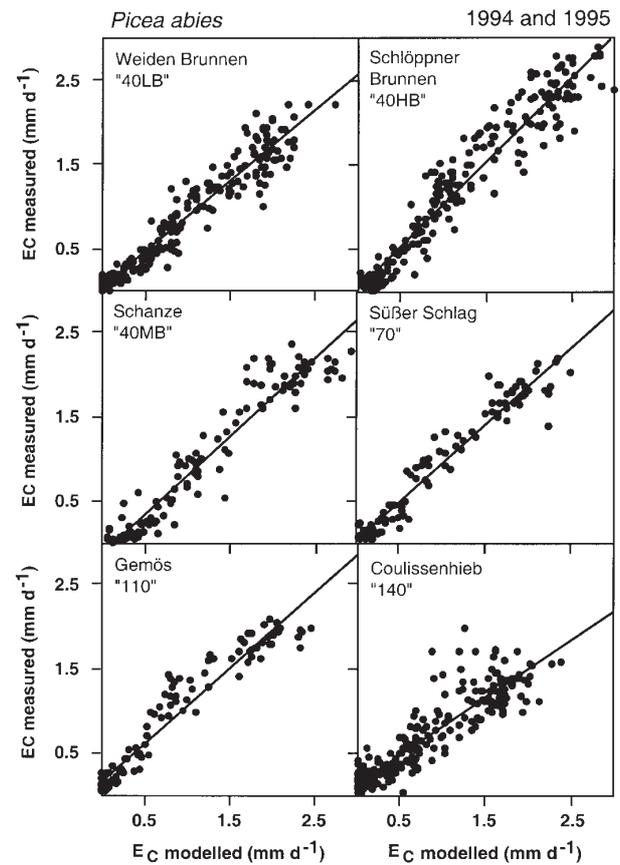


Figure 5. Comparison of measured and modelled daily canopy transpiration of the six Norway spruce canopies (see table I for stand descriptions) during the summer of 1994 ("40LB", "40HB", and "140") and 1995 (all sites). Coefficients of the regression are given separately for the six stands in table IV.

Table IV. Coefficients of a linear regression between modelled and measured daily sums of transpiration for the six Norway spruce stands in the Lehstenbach-catchment, for the vegetation period 1994 and 1995 ("40LB", "40HB", and "140") and 1995 ("40MB", "70", and "110").

$E_{c, \text{meas}} = a * E_{c, \text{mod}} + b$ (E_c in mm d^{-1})	a	b	r^2
"40LB" (Weiden Brunnen)	0.837	0.053	0.94
"40MB" (Schanze)	0.920	-0.101	0.93
"40HB" (Schlöppner Brunnen)	1.006	0.043	0.95
"70" (Süßer Schlag)	0.916	0.028	0.95
"110" (Gemös)	0.896	0.170	0.93
"140" (Coulissenhieb)	0.679	0.134	0.82

tionship to the maximum saturation deficit of the air (D_{\max}) and the level of daily radiation input (indicated as symbols in the lower panel of the figure). Monthly canopy carbon gain calculated with STANDFLUX for the six Norway spruce stands during the summer seasons of 1994 and 1995 is illustrated in figure 8. Whereas the transpiration sums increase with increase in daily mean temperature (not shown), D_{\max} , and daily radiation sum, high temperatures in the summer months are predicted to limit canopy carbon gain due to low photosynthetic activity and increases in foliage dark respiration rates. The trees of the oldest stand ("140") used less water at stand level, but are also predicted to be less efficient in carbon gain.

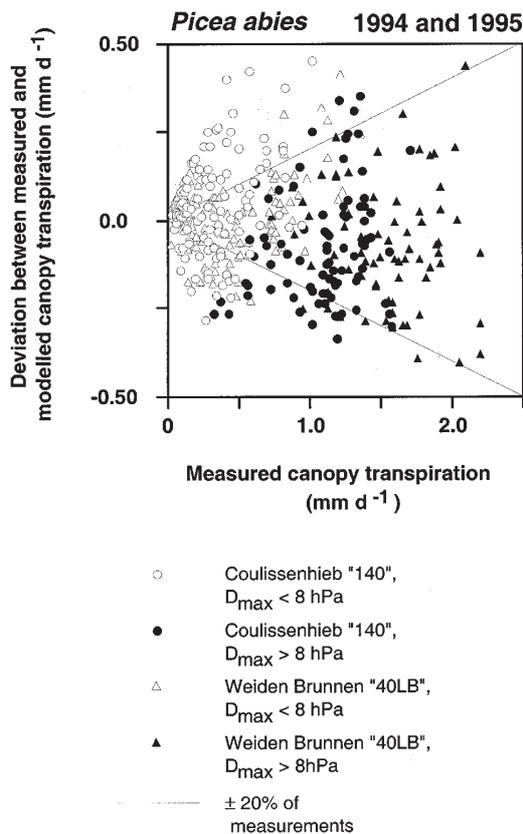


Figure 6. Differences between the model estimates and sap flow estimates of daily canopy transpiration of the 40-year-old Norway spruce canopy Weiden Brunnen "40LB" (triangles) and the 140-year-old Norway spruce canopy Coulissenhieb "140" (circles) plotted versus canopy transpiration from sap flow monitoring. Open symbols indicate days on which maximum daily water vapor saturation deficit was less than 8 hPa, solid symbols are for days with greater D_{\max} . Negative values describe an over-estimation of the measurements by the model. The lines delimit the area corresponding to a measuring accuracy of $\pm 20\%$.

4. DISCUSSION AND CONCLUSIONS

Gas exchange rates of the six Norway spruce canopies were described with the three dimensional gas exchange model STANDFLUX with one species-specific set of physiological parameters neglecting effects of tree or needle age (see below), and assuming no influence of soil water availability at the selected research sites (constant stomatal sensitivity to aboveground microclimate factors). Estimates for canopy transpiration rate derived from the model and via xylem sap flow measurements in these managed montane Norway spruce forest agree

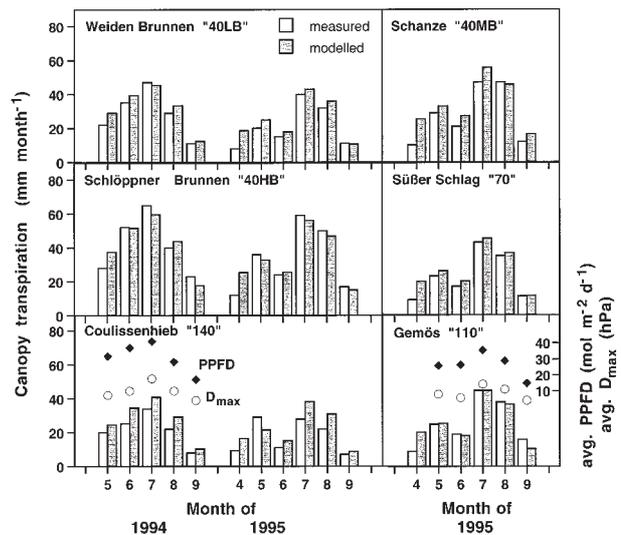


Figure 7. Monthly sums of modelled and measured canopy transpiration based on square meter ground area for six Norway spruce stands in the Lehstenbach catchment from May to September 1994 and April to September 1995. Average daily sums of photosynthetic photon flux density (PPFD, solid diamond) and average daily maximum saturation deficit of the air (D_{\max} , open circles) as measured above "40LB" (1994) and "140" (1995) are indicated in the lower panels of the figure.

within $\pm 20\%$, especially at moderate to high air vapor pressure deficits. Good agreement was found in the seasonal patterns for water use obtained by both methods.

Leaf area index, or more specifically the three-dimensional distribution of foliage density in a vegetation canopy, is a critical factor determining the average light intensity to which foliage elements are exposed, and therefore the degree to which foliage photosynthetic capacity is utilized, i.e., the foliage distribution determines the gas exchange rate of the average needle in these spruce stands. Since the physiological capacities of all needles were considered to be the same in STANDFLUX, the large differences in modeled gas exchange can only be ascribed to structural effects on foliage distribution (cf. figure 1) and the resulting influences on light distribution. The results suggest strongly that age and density dependent changes in canopy structure (changes in clumping of needles) and their effect on light exposure of the average needle lead to shifts in canopy conductance and determine tree canopy transpiration in these managed montane forests. Spruce stands 70-years-old and older were characterized by fewer trees per hectare, only 70 to 90% canopy closure, relatively high leaf area indices (≥ 6.5), and high per tree leaf areas

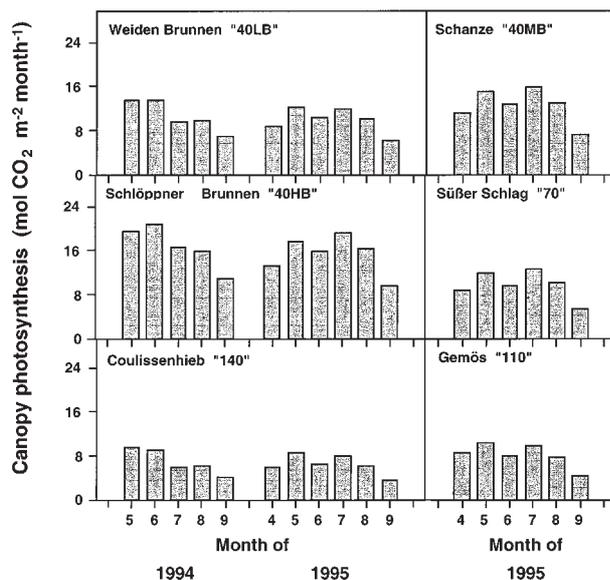


Figure 8. Monthly sums of modelled canopy carbon gain based on square meter ground area for six Norway spruce stands in the Lehstenbach catchment from May to September 1994, and April to September 1995. Carbon gain is obtained with the exclusion of aboveground woody respiration as described in the methods.

(between 158 and 203 m² per tree). Such trees had denser foliage clumping on individual branches and denser crowns, two factors leading to increased self-shading. Thus, even on an individual tree basis, water use was reduced due to a high degree of self-shading. Decreased tree transpiration in the old stands was associated with a simultaneous decrease in sapwood area per LAI or per hectare [1]. Not surprisingly, understory cover (mainly *Deschampsia flexuosa*, *Calamagrostis villosa*, and *Vaccinium myrtillus*) exceeded 75% in these stands (see table I).

Silvicultural measures such as thinning will reduce the leaf area of the stand but not the clumping of foliage in the crown and self-shading. Spruce trees with their strong apical control are less able to exploit the patchy light distribution in forest canopies, and as trees age, the ability to respond to light gaps decreases. Tree architecture limits growing new leaves in areas with high light availability [7, 51]. Due to these architectural restrictions, the older spruce crowns were less able to exploit the available crown space in terms of light interception, and as a result, transpiration and photosynthesis were reduced compared to younger stands. Contrary to our view, other authors [30, 55] have discussed decreased hydraulic conductivity in older stands as the limiting fac-

tor of canopy gas exchange, whereas our results suggested an important influence of crown architecture.

Based on the modelling results as well as foliage removal experiments on young spruce trees under controlled conditions [8], it seems likely that foliage loss that occurs in the Fichtelgebirge as a consequence of acid deposition and Mg deficiency [63] may initially lead to only small decreases in carbon gain at the tree level, since the light climate of remaining needles may be improved. Together with increased nitrogen availability, increases in growth (as reported in Pretzsch [52]) are potentially supported.

The parameter to which single tree gas exchange rate is most sensitive is the leaf area assumed for the tree. The leaf area included for model trees are derived from their circumference using a function derived from the leaf area of harvested trees (table II). Difficulties in determining this regression, the natural variability of the leaf area of similar-sized trees, together with potential errors in sap flow estimation (assumed radial homogeneity, heat storage in the trunk, etc.) are reflected in the comparison of transpiration rates on a single tree basis (figure 4). Furthermore, hydraulic limitations and daily depletion of water stored in the trunk or branches may add an additional restriction on actual water use and an overestimation in the calculated estimate [36, 56, 60, 67]. Pooling daily results from all trees, a relatively good agreement between measured and modelled daily rates is found, indicating that up-scaled cuvette gas exchange measurements at branch level and xylem sap flow measurements deliver consistent data. For a discussion of time lags in diurnal courses of sap flow and upscaled cuvette data due to capacitances see Hinckley et al. [29].

All model applications in this study were carried out under the assumption that the canopies were sufficiently supplied with water at the Fichtelgebirge sites in 1994 and 1995. Strong decreases in stomatal conductance of Norway spruce stands were found by Biron [9] when large negative soil matrix potentials (−0.7 to −0.8 MPa) occurred at 105 cm depth and soil water storage in the profile was low (< 150 mm in the first 90 cm). Soil matrix potentials at 35 cm depth at “40LB” decreased after periods without rain in 1994 to values as low as −0.6 MPa and in 1995 at 20 cm depth as low as −0.3 MPa. At “140”, soil matrix potentials more negative than −0.8 MPa occurred occasionally at 20 cm depth during 1994, but potentials at 90 cm depth decreased only to approximately −0.45 MPa. In 1995, soil matrix potential at 20 cm depth decreased only to −0.6 MPa, and at 90 cm depth was never more negative than −0.1 MPa. An examination of the deviations between modeled and measured daily canopy transpiration showed no correlation with measured soil water potentials at 35 cm depth

at "140" and "40LB". As soil water availability decreases, water potential in stem, branches and leaves as part of the potential gradient from soil to the atmosphere is expected to drop. In a recent publication, Bauerle et al. [6] emphasize the utility of the cohesion theory in interpretation of water potential gradients in trees. More generally, predawn water potential of leaves or needled branch ends serve as an integrated measure for the water status of the plant. Decreases in stomatal conductance of Norway spruce branches have been reported along with decreases in predawn water potential of branch ends to -0.7 to -0.8 MPa [25, 40]. At our study sites in the Fichtelgebirge, predawn water potential more negative than -0.5 MPa was never recorded during 1994 and 1995 [1]. Thus, we conclude that the deviations between model and measured estimates of transpiration were not influenced by water stress phenomena.

Although a single leaf physiology was assumed in the modelling and the results demonstrated a primary role for changing tree structure in determining canopy gas exchange, decreases in needle gas exchange in the Fichtelgebirge are well documented in response to needle aging and the turnover of magnesium [39]. Older needles can show a reduction of photosynthesis and conductance of up to 50%. The shade needle parameterization derived for 0-2 year-old needles applied in the current study could mean that gas exchange rates in the older stands is overestimated as leaf area accumulates in older needle classes. Approximately 25% of the needles at "140" are older than four years, while four-year-old needles were seldom found at "40LB". Alternatively, occurrence of sun or high-light adapted needles in the exposed outer crown could lead to compensating effects [38] and a good average prediction of tree gas exchange.

The current study which helps clarify heterogeneity for Norway spruce forest in the water flux contribution from the tree canopy compartment with sap flow methods must be complemented by direct measurements of evapotranspiration from the soil surface and understory. The soil surface flux varies strongly with age due to differences in stand density and radiation penetration through the stand to the ground. The view obtained of compensatory water loss from these compartments can aid in deciding whether to consider the total flux of water to the atmosphere from forest stands as a conservative process *sensu* Roberts [53]. Alternatively, shifts in activity from the tree canopy layer to the ground surface and understory could mean that total fluxes also change due to altered characteristics in their regulation by the organisms present.

Changes in total fluxes with alterations in stand structure seem even more likely for total CO_2 flux than for evapotranspiration. Carbon dioxide exchange primarily

regulated by spruce needle physiology in young spruce stands with a closed canopy will decrease with stand aging, while CO_2 exchange by grasses invading gaps will increase, as will the activity of microorganisms in response to altered soil environment (warmer but possibly drying in a different time dependent manner). The CO_2 exchange of clear-cut areas and mature closed forests provides estimates of the extremes that occur for measured fluxes, it is important to increase our understanding of flux variation that occurs in intermediate stages and with intermediate forest structures, as shown for instance by Buchmann et al. [13]. Based on measurements of needle gas exchange [17] and gas exchange of branches without needles and trunks [42], we have obtained a view on changing activity in carbon gain of the tree canopy compartment with stand age for Norway spruce as well as for water use. It should be possible to verify these changes with a skillful application of eddy covariance techniques above and below the canopy, such that the difference is directly comparable to the output of STANDFLUX. This must be complemented with systematic investigations of CO_2 exchange by the understory plants and soil compartment of the spruce forest ecosystem.

Spruce forest density is a critical factor determining forest/atmosphere exchange, but it is also a characteristic easily determined by remote sensing. Furthermore, managed spruce forest is a landscape element with wide distribution within Europe. Thus, the results from our study, appropriately coupled to below canopy fluxes, may be generalized over larger areas, e.g., in determining water use of forested catchments. For such applications, we must still determine the potential effect of additional factors such as soil water availability or variation in leaf physiological parameters in response to gradients in temperature, N-deposition, etc.

Importantly, it should be recognized that STANDFLUX is too costly in parameterization and computation time to be used directly for landscape and regional applications. Direct spatial application of the three-dimensional model is necessary to achieve better understanding of fluxes from different sources in the vicinity of a tower for eddy covariance measurements, but landscape level estimates of gas exchange will be better achieved through use of homogeneous-layered models describing vegetation light interception, canopy microclimate, and canopy gas exchange that have been in use for several decades [e.g., 45, 43, 46, 54, 59, 66]. The question that must be answered is how to correctly parameterize such models for the complex structural situation found in forest stands. We might expect the answer to this question to be provided by combining information from direct eddy covariance measurements which

provide the ultimate calibration and test data sets and from analyses and principles determined from models such as STANDFLUX. By comparing the output of different types of models to measured flux data, “equivalent descriptions” may be achieved [65] and the simpler layered models can then be used in designing strategies for generalizing biological information for landscapes and regions.

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Appendix 1

The branch gas exchange model PSN6

The model PSN6 is based on the enzyme kinetics of ribulose-1,5-bisphosphate carboxylase-oxygenase (RubisCO) describing net photosynthesis as a function of internal CO₂ partial pressure [20, 21] and includes the Ball et al. [5] empirical model of stomatal conductance. Model parameterization is described in detail in Harley and Tenhunen [28]. In the current study, an analytical solution for leaf net photosynthesis, for stomatal conductance, and for leaf internal and leaf surface CO₂ concentration was used (Baldocchi 1994). Four basic equations were combined in a cubic equation for net photosynthesis (np , in $\mu\text{mol m}^{-2} \text{s}^{-2}$) which is solved according to the scheme of Bronstein and Semendjajew [11].

At low CO₂ pressure and light saturation, CO₂ fixation is limited by the potential rate of fixation by RubisCO (w_c), and at high CO₂ pressure, by the potential rate of electron transport or the regeneration of ribulose-1,5-bisphosphate (RuBP) (w_j). Thus net photosynthesis (np) may be expressed as

$$np = \left(1 - \frac{\Gamma^*}{c_i}\right) \cdot \min\{w_c, w_j\} - 0.5 \cdot r_d \quad (\text{A.1})$$

where $0.5 \cdot r_d$ is the dark respiration assumed to continue in the light ($\text{mmol m}^{-2} \text{s}^{-1}$), c_i is leaf internal CO₂ partial pressure and Γ^* the CO₂ compensation point in the absence of r_d . Following Baldocchi [2], equation (A.1) is solved for c_i :

$$c_i = \frac{a \cdot d + b \cdot (np + 0.5 \cdot r_d)}{a - e \cdot (np + 0.5 \cdot r_d)} \quad (\text{A.2})$$

If $w_c < w_j$, the coefficients a , b , d , and e are replaced by $V_{c_{\max}}$ (the maximum carboxylation velocity for the actual temperature), $K_c (1 + \text{O}_2/\text{K}_o)$ (considering oxygen concentration, and Michaelis-Menten constants for carboxylation and oxygenation), Γ^* , and 1, respectively. If $w_c > w_j$, the coefficients a , b , d , and e correspond to $4 P_m$ (the maximum electron transport rate at actual light and temperature), $8 \Gamma^*$, Γ^* , and 4.

Additional equations are needed to calculate leaf surface CO₂ concentration c_s , and leaf-internal CO₂ concentration c_i assuming molecular diffusion in the boundary layer:

$$c_s = c_a - \frac{1.6 \cdot np \cdot 1000}{g_a} \quad (\text{A.3})$$

$$c_i = c_s - \frac{1.6 \cdot np \cdot 1000}{g_s} \quad (\text{A.4})$$

where c_a is the CO₂ concentration of the air. The factor 1000 derives from balancing the differing units used for np and the boundary layer conductance, g_a , calculated as described below, or the stomatal conductance, g_s , both in $\text{mmol m}^{-2} \text{s}^{-1}$. The factor 1.6 is the ratio of the diffusivities of water vapor and CO₂ in air [19].

Laminar flow in the boundary layer, which would reduce the factor 1.6 in equation (A.3) to 1.3, was neglected.

Stomatal conductance is calculated as:

$$g_s = g_{\min} + \frac{g_{\text{fac}} \cdot 1000 \cdot (np + 0.5 \cdot r_d) \cdot h_s}{c_s} \quad (\text{A.5})$$

where g_{\min} is the minimum conductance, h_s is relative humidity (as a decimal fraction), and g_{fac} is an empirically determined constant. The factor 1000 adjusts for the different units of g_s and $(np + 0.5 \cdot r_d)$.

For coniferous needles the calculation of g_a according to Nobel [44] was modified using so-called σ -factors of Jarvis et al. [31], for definition and measurements see Appendix 2). First, the thickness of the boundary layer (dbl) is determined after Nobel [44], his equation (7):

$$dbl = 0.004 \cdot \sqrt{\frac{w}{u}} \quad (\text{A.6})$$

with w the width of leaf (in m), and u the wind speed on the leaf surface (in m s^{-1}). The temperature dependence (temperature in $^{\circ}\text{C}$) of d_{wv} , the coefficient of diffusivity

for water vapor (in $\text{m}^2 \text{s}^{-1}$), is calculated according to Nobel [44], his Appendix 2:

$$d_{wv} = 2.126 \cdot 10^{-5} + 1.48 \cdot 10^{-7} \cdot T_c. \quad (\text{A.7})$$

Calculation of the boundary layer conductance, g_a in $\text{mmol m}^{-2} \text{s}^{-1}$, (numerator as in Nobel [44], his Eqs. (8.3) and (8.8) denominator according to Jarvis et al. [31]) with consideration of the clumping of the needles on the branch gives:

$$g_a = \frac{\frac{d_{wv}}{dbl} \cdot 1000 \cdot \frac{P}{R \cdot T_k}}{1.67 \cdot \sigma^{0.43}} \quad (\text{A.8})$$

with P pressure of the air (in Pa), T_k leaf temperature (in K) and R the gas constant ($8.31 \text{ J K}^{-1} \text{ mol}^{-1}$).

Appendix 2

The definition and determination of σ -factors

The σ -factors were used to estimate leaf boundary layer conductance (Eq. A.8), as well as to convert LAD (leaf area per volume crown section) for individual needles to the density for projected areas of intact twigs, e.g., the effective leaf area for light interception:

$$\sigma = \frac{A_n + A_t}{A_s} \quad (\text{A.9})$$

where A_n is the projected area of all needles laid out separately, A_t is the projected area of the twig, and A_s the projected area of the intact twig. Measurements of A_s , A_t and A_n were obtained with a Delta-T Image Analysis System (Delta-T Devices LTD, Cambridge, England). For the determination of the σ -factors for each meter section of the harvested tree, three 2nd or 3rd order twigs were randomly selected. The σ -factors reflect the morphological light acclimation, and decrease with depth in the canopy (data not shown).

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