Challenges for evaluating process-based models of gas exchange at forest sites with fetches of various species

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Abstract

Physiologically-based (or process-based) models are commonly applied to describe plant responses mechanistically in dependence on environmental conditions. They are increasingly evaluated with eddy-covariance measurements that integrate carbon and water exchange of an area of several hectares (called the fetch). However, almost all models applied to date in such exercises have considered only the dominant tree species and neglected other species that contributed to the measured gas exchange rates-either in separate patches or in mixture. This decreases the transferability of the model from one site to another because the contributions from other species might be different. It is therefore a major challenge in modeling today to separate the measured gas exchanges by sources.

In this study, a detailed physiologically-based biosphere model is applied that allows distinguishing between tree species in mixed forests, considering them as «vegetation cohorts» that interact with each other. The sensitivity of the model to different assumptions about how different tree species contribute to an integrated measurement of stand-scale gas exchange is investigated. The model exercise is carried out for a forest site in Finland with dominant Scots pine but presence of significant amounts of Norway spruce and birch. The results demonstrate that forest structure affects simulated gas exchange rates indicating a possible importance of considering differences in physiological properties at the species level. It is argued that the variation of stand structure within the range of eddy-covariance measurements should be better accounted for in models and that inventory measurements need to consider this variation.

Key words: forest structure; understorey; physiologically-oriented model; eddy-flux measurements; sensitivity analysis.

Resumen

Retos para la evaluación de modelos basados en procesos de intercambio de gases en rodales con diversas especies

Los modelos con base fisiológica (o basados en procesos) se aplican habitualmente para describir las respuestas de la planta mecanísticamente dependiendo de las condiciones ambientales. Son evaluados cada vez más frecuentemente con mediciones de eddy-covariance que integran el intercambio de carbono y el agua de una superficie de varias hectáreas. Sin embargo, casi todos los modelos aplicados hasta la fecha han considerado sólo las especies arbóreas dominantes y se han descuidado otras especies que contribuyen a las tasas de intercambio gaseosos medidas- ya sea en zonas separadas o en mezcla. Esto disminuye la posibilidad de transferir el modelo de un sitio a otro debido a que las contribuciones de otras especies pueden ser diferentes. Por tanto, es un reto importante en la modelización separar el intercambio gaseoso medido por fuente emisora.

En este estudio, se aplica un modelo detallado con base fisiológica de la biosfera que permite distinguir entre las especies de árboles en bosques mixtos, considerándolas como «cohortes de vegetación» que interaccionan unos con otros. Se estudia la sensibilidad del modelo a los diferentes supuestos acerca de cómo contribuyen las diferentes especies de árboles a una medición integrada de intercambio de gases a escala de rodal. El estudio se lleva a cabo en un sitio forestal en Finlandia con dominancia de pino silvestre, pero con una presencia importante de piceas y abedules. Los resultados demuestran que la estructura del bosque afecta a la simulación de las tasas de intercambio gaseosos, indicando una posible importancia de considerar las diferencias en las propiedades fisiológicas a nivel de especie. Se discute como variación de la estructura de la masa dentro del rango de las mediciones de eddy-covariance debe ser tenida mejor en cuenta en los modelos y que las mediciones de los inventarios deben considerar esta variación.

Palabras clave: estructura forestal; subpiso; modelo con base fisiológica; análisis de sensibilidad; Eddy flux.

Introduction

Future changes in environmental conditions are supposed to alter vegetation dynamics, *i.e.* regarding growth and competition as well as water and carbon balances. The knowledge about these responses is of high economical and ecological interest and models are the primary tools to investigate them. These models have to be parameterized and evaluated with measurements, which is one of the main purposes of eddy-covariance sites and networks (*i.e.* FLUXNET, see Baldocchi *et al.*, 2001). Such sites are therefore usually selected in order to provide a homogenous biosphere within the fetch of the measurements – although it has been pointed out that high accuracy requires very large fetch sizes where homogeneity can seldom be ensured (Markkanen *et al.*, 2003). On the other hand, models that are evaluated with these measurements usually support only one species or plant functional type (PFT), which represents a virtual species with aggregated properties. This concept has been subject to much criticism. For example, it has recently been shown that a set of PFT parameters designed at one site is not well suited to represent photosynthesis at other sites (Groenendijk *et al.*, 2011). Thus, model parameters are often derived from measurements that do not reflect the models underlying assumptions. However, it has hardly been investigated to what degree this affects simulation results.

Here, we employ a physiologically-based model (PBM). This kind of models have been developed to describe biogeochemical properties of forests, *e.g.* to judge carbon sequestration or nitrate leaching. Therefore, they consider a multitude of environmental influences (see reviews in Constable and Friend, 2000; Landsberg, 2003; Mäkelä *et al.*, 2000). PBMs have also been introduced as management tools, particularly for plantations, where the concept of the «average tree» applies best *e.g.* Battaglia *et al.*, 2004; Landsberg *et al.*, 2001; Sievänen, 1993). The intriguing advantage of this approach is that responses to each single environmental condition can be described (in principle) over a wide range based on experiments. Thus, the overall impact may include self-emergent ecosystem properties, which are based on the underlying responses but also account for feedbacks between the major ecosystem processes (or process groups). A possible distinction of such groups into air-chemistry, micro-climate, soil properties, plant physiology, and ecosystem structure is presented in Figure 1.
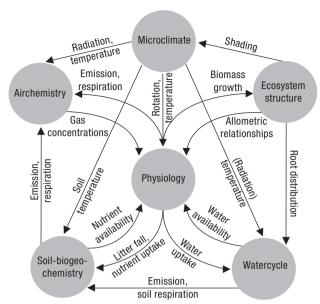

Figure 1. Ecosystem process groups (in circles) and major processes that represent linkages between them (commented arrows).

In order to consider potential differences in forest structure, we use a PBM that has been designed to view the forest by tree cohorts. The application of cohorts allows the differentiation of processes and responses according to a more realistic stand structure (*e.g.* over- and understory or mixed-species forests). This model is applied to a pine forest site in Finland where inventory data indicate that considerable amounts of spruce and birch are present within the fetch of an eddy-covariance tower. Our hypothesis is that it makes a difference for carbon and water flux simulations if tree species are considered either as upper- and understory or as growing in separated patches in contrast to only considering the dominant forest species.
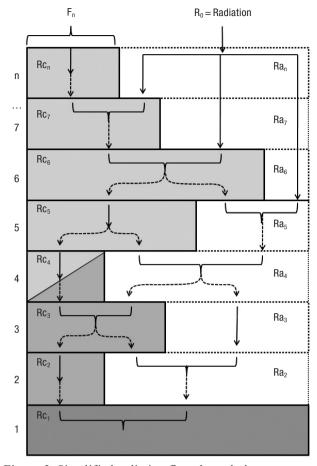
Material and methods

Model description

We applied the physiologically-based vegetation model PSIM (Physiological SImulation Model, Grote, 2007) and a newly implemented version of the biogeochemical model DNDC (De-Nitrification-De-Composition, Li *et al.*, 1992) along with models that describe micro-environmental conditions within the biosphere (*e.g.* light distribution, soil temperature development, water availability). This combination is an alternative implementation to the PnET-N-DNDC model (Li *et al.*,

2000), which has been widely used particularly to estimate trace gas emissions from forest soils (*e.g.* Butterbach-Bahl *et al.*, 2009; Kesik *et al.*, 2006). However, the PSIM model was designed for the parallel use of various vegetation cohorts from the beginning. The models were coupled within the modeling framework MoBiLE (Modular Biosphere simuLation Environment; Grote *et al.*, 2009a,b; Holst *et al.*, 2010).

In order to represent mixed forest properties with this combined model, we consider the ecosystem to consist of distinct «vegetation types» or «cohorts» that are defined by species, ground coverage and dimension. The environmental conditions experienced by a cohort are defined by the canopy- and soil layer properties that it occupies according to its height, start of the crown base, and rooting depth. Foliage and fine root biomass are explicitly distributed across the occupied layers, which are shared with other cohorts that occupy the same layers. On the other hand, tree cohorts affect the forest environment by resource use (nitrogen, water) and shading. Thus, above ground competition for a cohort is dominated by shading from other cohorts, which concentrate their foliage in higher canopy layers (asymmetric competition) while below ground competition only depends on the presence of fine roots in a particular soil layer and the species-specific uptake capacity. Assuming that a cohort occupies all soil layers if their trees are above a certain threshold height, which is assumed to be the case in the current investigation, the competition strength does not depend on the size of the trees (symmetric competition). Since the model still considers all processes as «one-dimensional», the emerging forest is still horizontally homogeneous, implicitly assuming an evenly distribution of cohorts (see Fig. 2).

The simple Empirical-based Canopy Model (ECM, Grote, 2007; Grote *et al.*, 2009a; Holst *et al.*, 2010) was applied to provide climatic information for each canopy layer. Micro-climatic conditions were calculated for a flexible number of above- as well as below-ground layers in a user-defined time resolution (hourly). The vertical light distribution was determined using a Beer-Lambert approach that was modified in order to reflect the dependence on the distribution and properties of foliage and branches in each canopy layer (see Fig. 2). In this approach the radiation intensity within the foliage (Ic) and outside the foliage (Ia) of a canopy layer is distinguished and calculated from the amount and absorption properties of the foliage within the current layer (n) and the layer immediately above ($n+1$):

Figure 2. Simplified radiation flow through the canopy as described by Eq. [1]. The shaded areas represent the relative canopy space occupied with different species represented by different shades. Each arrow represents the flow of diffuse and direct radiation. *I*: radiation intensity above the canopy (I_0), within (I_c) and outside the foliage (I_a) of each canopy layer. *F*: fraction of the canopy layer (n) that is filled with foliage.

$$Ic_n = [f(Ic_{i,n+1}) \times min(F_n, F_{n+1}) + \\ + Ia_{i,n+1} \times max(0, F_n - F_{n+1})] / F_n \quad [1a]$$

$$Ia_n = [Ia_{i,n+1} \times min(1 - F_n, 1 - F_{n+1}) + \\ + f(Ic_{i,n+1}) \times max(0, F_{n+1} - F_n) / (1.0 - F_n)] \quad [1b]$$

with:

$$f(Ic_{n+1}) = Ic_{i,n+1} \times (1 - frefl) \times exp(-FEXT_i \times PAI_{n+1})$$

$$frefl = cl \times [1 - sqrt(1 - M\ FALB)] / \\ / [1 + sqrt(1 - FALB)]$$

$$fext_{dir} = f(sin\beta)$$

$$cl = min(1, PAI_n \times 0.5)$$

F = fraction of the canopy layer that is filled with foliage.

i = distinguishing diffuse and direct radiation.

$f(Icn + 1)$ = radiation immediately above the current canopy layer.

PAI   = plant area index (foliage and branches), leaf-area weighted average of all species present in the respective canopy layer.

β   = solar elevation, calculated from latitude and day of the year (Sellers, 1965).

FEXT, FALB = leaf-area weighted average of species-specific parameters (see Table 2).

Meteorological data (air temperature and global radiation) are driving a common photosynthesis model that calculates the carbon uptake in dependence on light, temperature, and enzyme activity based on Farquhar *et al.* (1980) and the water constraint according to Ball *et al.* (1987). This approach determines carbon gain by iteratively adjusting stomata conductivity and thus transpiration demand which is then limited by water availability (see further down and Eq. [2]). The light saturated rate of carboxylation is reduced when a) nitrogen concentration in the leaf tissue is below optimum, and b) the seasonal physiological status is below 1. The latter impact is assumed to occur in deciduous species in parallel with leaf flushing and senescence and is calculated for evergreen species with the S-model approach presented in Mäkelä *et al.* (2004). Lacking other evidence, we assume the same seasonality for pine and spruce and recalibrate the saturated rate of carboxylation (*VCMAX25)* for spruce accordingly from an independently investigated spruce site-repeating the exercise described in Grote *et al.* (2011). Soil temperature which is driving biogeochemical calculations and represents a limiting condition for fine root growth and nitrogen uptake is provided by the DNDC model (Li *et al.*, 1992).

Further vegetation processes are calculated with PSIM model that simulates phenology (Lehning *et al.*, 2001; Grote, 2007), plant respiration (Thornley and Cannell, 2000), senescence and allocation of carbon and nitrogen (Grote, 1998), as well as nitrogen uptake (separately accounting for ammonia and nitrate). The latter is assumed to be restricted either by availability, plant uptake capacity or demand. The availability of ammonium and nitrate is again calculated with the DNDC model, which accounts for the mineralization of litter, transport between the soil layers and losses by leaching and trace gas emission. Nitrogen availability is thus the same for any vegetation type (given that rooting depth is the same). Total plant uptake capacity is determined by fine root biomass and specific uptake capacity (per root biomass). It thus depends on the seasonal biomass development as well as the spatial distribution of fine roots throughout the root profile. The demand for nitrogen is calculated as the difference between optimum and actual nitrogen concentration summed up over all tissues (see Table 2).

We also used the DNDC model for simulating water balance processes, including potential transpiration and soil water availability in each soil layer. Potential transpiration (water demand for each cohort) is determined from the daily amount of assimilated carbon within one vegetation cohort by multiplying with the species-specific water-use-efficiency variable that increases with decreasing water availability from *WUECmin to WUECmax* (see Table 2 for both parameters). The actual water uptake, however, is restricted by the availability of soil water, which is the sum of water in the rooted soil.

Finally, the drought stress factor of a cohort is calculated from the ratio between water content and water holding capacity in each soil layer. The average of this ratio, weighted by fine root biomass in each soil layer, is used to restrict stomata opening if it falls below a species specific threshold according to:

$$gs' = gs \times min\{1.0; [1.1 - p1 \times exp(-p2 \times RWC/FRWC)]\} \quad [2]$$

with:

gs   = stomata conductance (mmol m^{-2} s^{-1}).

RWC   = relative volumetric soil water content (= actual/maximum water content in the rooted soil volume) (–).

FRWC = relative water content below which the electron transport rate is affected (see Table 2).

*p*1 and *p*2 *b*eing parameter fixed to the value of 0.8 and 2.2, respectively.

Additional model procedures described mortality and dimensional growth from carbon allocation into stem wood. Mortality is simply assumed as a decrease of living biomass by a certain percentage that depends on stand density following a concept proposed by Bossel (1996). Since we apply the model to a managed forest, we assume that all aboveground stem wood that died naturally or due to thinning is exported out of the forest, whereas the below ground part of the stem and the branches are considered as litter. Diameter and height growth are calculated from the carbon allocated to the wood compartment using the taper functions presented in Dik (1984) (cit. in Zianis *et al.*, 2005). A

more detailed description and evaluations for various tree species can be found in Miehle *et al.* (2010) and Grote *et al.* (2011). Based on the height of trees, crown length and foliage distributions are calculated. While crown length is defined as a species-specific fraction of the total height *h* (after reaching a minimum absolute crown length), crown ground coverage and vertical foliage biomass distribution are calculated from height and crown length for each tree cohort according to Grote (2003). The sum of the coverage of all trees in a given layer is equal to the foliated fraction F in this layer (see Fig. 2). Leaf area within a canopy layer that is used as the main determinant for *PAI* in Eq. [1] is calculated from foliage biomass (*mfol*), specific leaf area parameters (see Table 2) and relative crown height according to:

$$lai_{vt,n} = mfol_{vt,n} \times [SLAmax - (SLAmax - SLAmin) \times h_n / h] \qquad [3]$$

with h_n indicating the middle height of a particular canopy layer

Foliage biomass develops dynamically in relation to the sum of «growing degree days» (calculated from the average temperature within the canopy space occupied by the respective cohort) after a species-specific threshold had been reached. It increases up to the maximum value *MFOLpot* (Table 2), given that crown length is above a minimum value and crown area is fully covering the ground.

Although meteorological input data may only been available in a daily timestep resolution, the Farquhar photosynthesis routine is run in a sub-daily timestep. The specific time step is selected by the user and is set here to one hour. Input data are daily temperature and radiation values. Hourly weather conditions for photosynthesis are internally calculated from sinusoidal distribution schemes for temperature (De Wit, 1978) and radiation (Berninger, 1994). Phenology, carbon and nitrogen allocation and loss, water balance, and biogeochemical processes are run in daily time steps. Coverage and dimension of each tree cohort is calculated annually.

Simulations

Description of site properties and measurements

To investigate the sensitivity of gas flux simulations to stand structure, we selected the forest at the SMEAR II site in Hyytiälä, southern Finland (61.15N, 24.17E, 160-180 m above sea level) that has been under long-term observation. The site is covered with dominant Scots pine (*Pinus sylvestris*) and has been considered before as homogeneous forest. It has been described in detail by Kolari *et al.* (2004) and Hari and Kulmala (2005). However, in the footprint area of a tower equipped with eddy-covariance instruments, up to ten different tree species have been recorded (Ilvesniemi *et al.*, 2009). We used this inventory but aggregated the recorded biomasses into the most prominent species Scots pine, Norway spruce (*Picea abies*), and birch (*Betula pubescens* and *B. pendula*).

Measurements of CO_2 and water exchange rates (fluxes) by means of eddy covariance (EC) technique were available starting at the year 1996 (Vesala *et al.*, 2005). The EC fluxes were calculated according to commonly accepted procedures (*e.g.* Aubinet *et al.*, 2000) and updated methodologies (*e.g.* Mammarella *et al.*, 2009). Total ecosystem respiration (TER) and GPP were extracted from the measured NEE as described in Mäkelä *et al.* (2006). EC flux measurements used in this study for model evaluation have also been published in Suni *et al.* (2003), Ilvesniemi *et al.* (2009), and Ilvesniemi *et al.* (2010). Soil temperature and soil water content were measured at four different soil horizons (with two replicates in depth of 4, 16, 29, and 46 cm) using silicon-based temperature sensors and time-domain reflectometer, respectively. Wind speed, relative humidity and air temperature were measured at the SMEAR II station tower. Precipitation data used was from the weather station of the Finnish Meteorological Institute, approximately 300 m west from the station. Additionally, data from forest inventories were available for initialization.

Model settings and simulation setup

The model was set up for three different runs representing different stand structures: 1) a homogenous pine stand (PP), where all trees were assumed equal in size and represented the total biomass of the inventory, 2) three homogenous stands each with a different tree species (pine, spruce, birch) that are equal in dimensions (ED); simulation results are pooled and weighted according to the relative stem biomasses from the inventory which is consistent with current approaches of mixed forest representations for regional applications (*e.g.* Coops and Waring, 2001; Kimball *et al.*,

Table 1. Simulation settings to investigate different stand structural assumptions

Acronym	Species considered	Stand structure	Post processing
PP	Pine	Homogenous (1 cohort)	Direct output
ED	Pine, spruce, birch	Homogenous (1 cohort)	Weighted from 3 runs
MS	Pine, spruce, birch	Mixed (3 cohorts of different sizes)	Direct output

2000; Mickler *et al.*, 2002), and 3) the three tree species are initialized according to the average dimension indicated by inventory data and are assumed to grow together in a mixed stand (MS). See also Table 1.

To adjust the model to the GPP and TER data observed at the site, we assumed that the forest consists of pine only as was also the standard assumption in other modeling attempts at this site (Kramer *et al.*, 2002; Mäkelä *et al.*, 2008; Hari *et al.*, 2009). Then we modified three parameters of Scots pine physiology: 1) potential carboxylation capacity at 25°C as used in the Farquhar model (*VCMAX25*), 2) Michaelis-Menten coefficient at 20°C in the model presented by Thornley and Cannell (2000) (*KM20*), and 3) minimum temperature in the temperature response function of plant respiration (*TRmin*). Other species-specific parameters that are used for the description of gas exchange of all three species are taken from literature reviews, if possible from authors describing northern forest ecosystems (see Table 2). Based on this parameterization, we derived all the statistical properties for the simulation.

The simulation was initialized with measured soil data and forest inventory information and run with daily weather data input (radiation, temperature) from 1996 to 2007. Soil data included the relative content of carbon, nitrogen, clay, and stones as well as pH, saturated conductivity, field capacity and wilting point for the litter layer and each of four soil strata.

The four strata covered a depth of about 0.6 m which is the average depth for the area as has been defined based on soil radar measurements and is also assumed to represent rooting depth. Because the different carbon pools used in the soil model can only be estimated with high uncertainty, they eventually show a very dynamic behavior in the beginning of a simulation that is exponentially approaching an approximate equilibrium. In order to avoid potentially erroneous respiration rates that accompany such rapid pool changes, the first two years of simulation have been excluded from the analysis. Total carbon and nitrogen pools reached an approximate equilibrium already during the first year, although some litter-pool shifts continued throughout several more years. However, this had hardly any effect on soil respiration and nutrient availability (not shown). Additionally, it was assumed that the nitrogen deposition rate is 0.56 mg L^{-1} precipitation (representing both dry and wet deposition), which results in an average annual deposition rate of 5.5 kgN ha^{-1} (Flechard *et al.*, 2011). The forest experienced a thinning during the simulation period, where approximately one fifth of the stand volume had been removed. This has been reflected in the simulation as the death of 20% of all tissues at the first day of March in 2002, where only the above ground (branch free) stem wood was exported from the forest. All other tissues were added to the respective litter pools.

Results

Water balance

The relative water content between field capacity ($RWC = 1$) and wilting point ($RWC = 0$) at which the stomata conductance of Scots pine trees is affected has been determined from specific years where this effect could be seen on eddy-flux derived total evapotranspiration rates (Fig. 3b). We thus used a *FRWC* value of 0.65 as parameter for pine, assuming that the observed value is representative. The sensitivity of the water fluxes on forest structure is indicated further down and in Table 3. Together with other literature derived parameters, soil water content in 30 cm, which is an important indicator for drought stress could be represented by the model remarkably well (Fig. 3c). We observed only a small overestimation of water content in the uppermost layers, while in the other layers soil water supply is slightly underestimated (not shown). Despite the good correlation for the soil water dynamics, the overall simulated evaporation (transpiration, interception and soil evaporation) is between 19 and 26% larger than indicated by eddy-covariance presented in Ilvesniemi *et al.* (2010) (Fig. 4, Fig. 3a, Table 3).

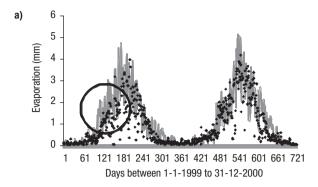Because the long-term precipitation and potential

Table 2. Parameters affecting the simulation of radiation regime and gas exchange
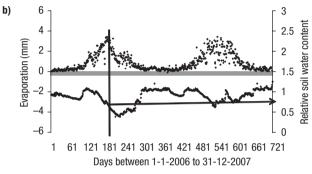
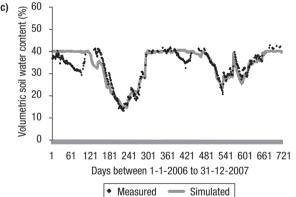| Variable	Description	Pine	Spruce	Birch	References (pine, spruce, birch)
Light extinction					
FALB	Foliage albedo	0.11	0.06	0.31	Perttu *et al.*, 1980; Jarvis *et al.*, 1976; Montheith and Unsworth, 1990
FEXT	Light extinction factor	0.5	0.67	0.44	Sampson *et al.*, 2006; Pietsch *et al.*, 2005; Aubinet *et al.*, 2000
Farquhar model					
KC25	Michaelis-Menten constant for CO_2	405	460	275	Wang *et al.*, 2003; Farquhar *et al.*, 1980; Aalto and Juurola, 2001
KO25	Michaelis-Menten constant for O_2	279	330	420	Wang *et al.*, 2003; Farquhar *et al.*, 1980; Aalto and Juurola, 2001
QVOVC	Relation between saturated rate of oxygenation and carboxylation	0.21	0.21	0.21	Long 1991 (gen., all)
QJVC	Relation between maximum electron transport rate and RubP saturated rate of carboxylation	2.5	2.5	2.4	Sampson *et al.*, 2006; Bergh *et al.*, 2003 (avg.); Aalto and Juurola 2001
QRD25	Relation between dark respiration rate and carboxilytion capacity	0.028	0.011	0.017	Wang *et al.*, 1996; Farquhar *et al.*, 1980; Aalto and Juurola, 2001
AEKC	Activation energy for Michaelis-Menten constant for CO_2 ($J mol^{-1}$)	59,400	65,000	80,500	Medlyn *et al.*, 2002; Falge *et al.*, 1997; Aalto and Juurola, 2001
AEKO	Activation energy for Michaelis-Menten constant for O_2 ($J mol^{-1}$)	36,000	36,000	14,500	Medlyn *et al.*, 2002; Falge *et al.*, 1997; Aalto and Juurola, 2001
AERD	Activation energy for dark respiration ($J mol^{-1}$)	45,000	63,500	26,000	Aalto *et al.*, 2002; Falge *et al.*, 1997; Aalto and Juurola, 2001
AEVC	Activation energy for photosynthesis ($J mol^{-1}$)	50,000	75,750	64,500	Aalto *et al.*, 2002; Falge *et al.*, 1997; Aalto and Juurola, 2001
AEVO	Activation energy for RubP oxygenation ($J mol^{-1}$)	37,530	37,530	37,530	Long 1991 (gen., all)
AEJM	Activation energy for electron transport ($J mol^{-1}$)	61,650	28,000	50,400	Wang *et al.*, 1996; Long 1991 (gen.); Aalto and Juurola, 2001
THETA	Curvatur parameter	0.7	0.9	0.93	Aalto *et al.*, 2002; Thornley 2002 (gen.); Aalto and Juurola, 2001
GSmax	Maximum stomata conductivity (mmol $H_2O m^{-2} s^{-1}$)	148	125	405	Kellomäki and Wang, 1997; Sellin and Kupper, 2004; Uddling *et al.*, 2005 (avg)
GSmin	Minimum stomata conductivity (mmol $H_2O m^{-2} s^{-1}$)	10	10	10	Medlyn *et al.*, 1999 (gen., all)
S_M	Slope of stomata response in BERRY-BALL model	5.0	6.5	9.4	Thum *et al.*, 2007; Falge *et al.*, 1996; Medlyn *et al.*, 2001

Table 2 (cont.). Parameters affecting the simulation of radiation regime and gas exchange

Variable	Description	Pine	Spruce	Birch	References (pine, spruce, birch)
Seasonality of photosynthesis					
NCFO-Lopt	Optimum nitrogen concentration of foliage (%)	1.5	1.5	2.5	Alriksson and Eriksson, 1998 (all)
WUEC-max	Maximum water use efficiency (mg H_2O g C^{-1})	10.0	7.3	12.2	Wang *et al.*, 2003; Kram *et al.*, 1999; Maurer and Matyssek, 1997
WUEC-min	Minimum water use efficiency (mg H_2O g C^{-1})	4.1	5.5	3.5	Thum *et al.*, 2007; Grote *et al.*, 2011; Maurer and Matyssek, 1997
FRWC	Relative available soil water content at which stomata closure starts	0.65	0.4	0.25	This study. Havranek and Benecke, 1978; Richardson *et al.*, 2004
NCFO-Lopt	Optimum nitrogen concentration (gN gDW^{-1})	0.014	0.015	0.025	Jacobsen *et al.*, 2003; Wang *et al.*, 2003; Uri *et al.*, 2007
VCMAX-25	Saturated rate of carboxylation (μmol m^{-2} s^{-1})	110	70	26.7	This study. Recalibrated from Grote *et al.*, 2011*; Aalto and Juurola, 2001
Phenology (foliage development)					
GDDF0	Temperature sum for foliage activity onset (°C)	279	290	111	Linkosalo *et al.*, 2006; Bergh *et al.*, 1998; Linkosalo *et al.*, 2006
NDFLUSH	Time interval necessary to complete flushing of foliage (days)	50	90	32	Jach and Ceulemans 1999; Bergh *et al.*, 1998; Richardson *et al.*, 2006
DFSHED	Total leaf longvity from the first day of the emergend year on (days)	1,065	1,815	315	This study
NDMORT	Time interval necessary to complete litterfall of foliage (days)	220	590	120	This study
SLAmax	Specific leaf area in the shade (m^2 kg^{-1})	9.1	6.3	17.0	Moren *et al.*, 2000; Meir *et al.*, 2002; Portsmuths and Niinemets, 2006
SLAmin	Specific leaf area in full light (m^2 kg^{-1})	3.4	4.2	7	Moren *et al.*, 2000; Meir *et al.*, 2002; Portsmuths and Niinemets, 2006
MFOL-pot	Foliage biomass for mature stands under closed canopy condition (kg m^{-2})	0.64	1.66	0.24	Kuuluvainen, 1991; Mund *et al.*, 2002; Uri *et al.*, 2007 (avg.)
Plant respiration					
KM20	Maintenance coefficient at reference temperature	1.0	0.8	0.1	This study. Recalibrated from Grote *et al.*, 2011*; Thornley and Cannell, 2000 (gen.)
TRmax	Maximum temperature for plant respiration	45	45	45	Thornley and Cannell, 2000 (all)
TRopt	Optimum temperature for plant respiration	20	20	20	Thornley and Cannell, 2000 (all)
TRmin	Minimum temperature for plant respiration	−7	−7	−7	This study (all)

* Recalibration was necessary because the model did not account for the seasonality of enzyme activity before [gen. = author(s) indicated this value for a group of species; all: used for all species here; avg: average value obtained from a range of conditions].

Figure 3. a) Comparison of simulated and measured ecosystem evaporation (circle indicates warm period before flushing). b) Relative water content at which evaporation starts to decrease based on measured soil water content in 30 cm depth and evaporation derived from latent heat measurements. c) Simulated and measured soil water content of the whole rooted soil profile (assumed 0.6 m deep) estimated as weighted average values from 3 depth (4 cm, 31 cm, 46 cm) for two consecutive years. Measurements are indicated with black dots, simulations are presented with grey lines. All simulation results for the PP run.

evaporation are approximately the same, the soil water required for transpiration at the site is generally available. Nevertheless, summer drought occurs occasionally. If forest structure is not considered, which means that pine is given more weight, total simulated evaporation (transpiration, interception, and soil evaporation) is

larger and ground water supply (runoff/percolation) smaller (Table 3). This indicates that a homogeneous canopy of pine is overall less water conservative than a more structured forest.

Carbon balance

The comparison of simulated and measured (= derived from measured net exchange) daily GPP and TER fluxes shows high correlation with R^2 values of about 0.9 for all simulation runs and slopes very close to 1 (Table 4 and Fig. 5). Generally, simulated daily GPP fluxes are somewhat too small during flushing, which is compensated by an overestimation in summer. TER is overestimated for a short period in early summer (after flushing) which is compensated by a small but prolonged underestimation in autumn. NEE reflects both of these biases as is demonstrated in Figure 6. Simulated seasonal NEE development for the three model set-ups are significantly different (according to a paired two sample t-test for mean values and referring to a 5% confidence interval). Thus we can conclude that the result of both biases is smallest when all species are separately calculated assuming that they are all the same size (ED run). This indicates that the contribution of spruce and birch to total fluxes at the site Hyytiälä may be best described by their relative volume fraction.

Compared with other long-term eddy-flux data sets (*e.g.* Duursama *et al.*, 2009; Grote *et al.*, 2011; Rodrigues *et al.*, 2011), the variation of the overall in- and outflow of carbon between the years is mostly small, indicating that drought plays only a minor role as a limiting condition at this site. Although *RWC* frequently drops below the threshold value in summer (most frequent in the pure stand, least often in the mixed stand), it falls only seldom below 0.5 [in average 17 (PP), 5 (ED), and 9 (MS) days per year]. Only in the very dry year 2006, *RWC* fell below 0.2. During this year, the annual GPP was about 10% higher in the mixed forest simulation than in the other runs, reflecting the model assumption that a structured stand is less water consuming (and thus have more water available) under high temperature conditions because a higher fraction of leaves are located in the shade. However, the actual measurements did not indicate such an effect (see Table 5). Instead, total GPP was again best represented by the ED simulations, indicating the importance to take the higher drought sensitivity of spruce into account.
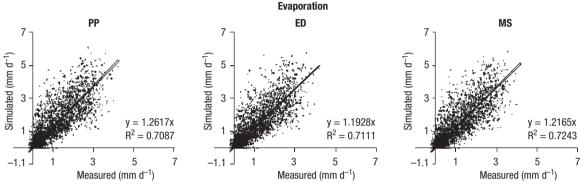
Table 3. Water balance for the period 1998 to 2006. Average annual water fluxes (avg.) and standard deviation (sd) are given in mm a^{-1}. Additionally, the importance of the flux relative to total precipitation is given in percent (%)

	PP			**MS**			**ED**			**Ilvesniemi *et al.*, 2010***		
	Avg.	**sd**	**%**	**Avg.**	**sd**	**%**	**Avg.**	**sd**	**%**	**Avg.**	**sd**	**%**
Total evaporation	395	26	59	373	25	55	379	21	56	295	42	43
Total runoff + storage change	279	76	41	300	106	45	294	102	44	397	108	57

* Water loss from Ilvesniemi *et al.* (2010) is calculated as the difference between precipitation and evaporation measured using eddy-covariance. The sum of both water balance terms between the simulation (673 mm) and measurements (692) differ slightly due to differences between this study and Ilvesniemi *et al.* (2010) in gap filling procedures (the new method was used because it better reflects the actual rainfall pattern).

Figure 4. Measured and simulated daily evaporation (transpiration + evaporation from ground and leaves) for different stand structures. Tree species composition is regarded as pure pine (PP), as weighted average of three simulations pine, spruce and birch (ED), and as perfectly mixed considering different sized tree cohorts (MS). Simulations results cover the period from 1998 to 2007.

In contrast to the year-to-year variation of GPP and TER, the simulated variability of fluxes into the different carbon storages is very high (see standard deviation in Table 5). While the average simulated belowground carbon sequestration is about 60 g C m^{-2} a^{-1}, it may vary between approximately 18 (1999, PP) and 140 (ED, 2006). The differences between the simulations are small, with the PP run showing the smallest belowground and the highest above ground carbon sequestration, while the ED run shows the highest belowground sequestration of the three simulation runs.
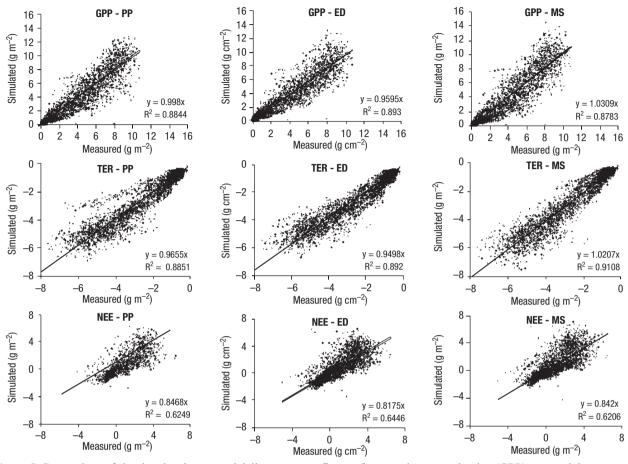
Discussion

Overall, similarities as well as some differences to previously estimated water (Ilvesniemi *et al.*, 2010)

Table 4. Statistical properties of daily aggregated results from simulation runs
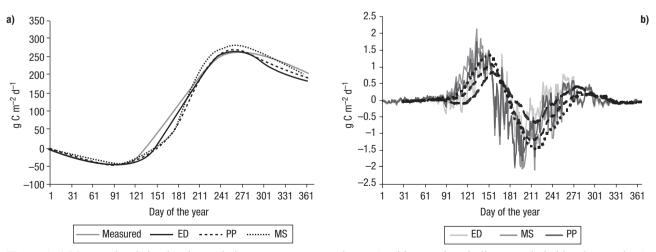
		Slope	**R²**	**SE**	**ME**	**RMSE**
Pure pine (PP)	GPP	1.01	0.90	0.98	−0.01	1.04
	TER	0.99	0.92	0.50	0.05	0.51
	NEE	0.83	0.62	1.02	0.02	1.10
Equal dimensions (ED)	GPP	0.96	0.89	1.01	0.07	1.03
	TER	0.95	0.90	0.57	0.00	0.57
	NEE	0.82	0.65	0.98	0.05	1.04
Mixed forest (MS)	GPP	1.03	0.88	1.08	−0.05	1.21
	TER	1.02	0.91	0.54	0.05	0.58
	NEE	0.84	0.62	1.01	−0.02	1.09

SE: standard error. ME: mean error. RMSE: root mean square error.

Figure 5. Comparison of simulated and measured daily ecosystem fluxes of gross primary production (GPP), terrestrial ecosystem respiration (TER), and the net ecosystem exchange (NEE) for the Hyytiälä site regarding three species composition as pure pine (PP), as a weighted average of three runs assuming homogenous conditions and equal dimensions for each species (ED), and as a perfectly mixed forest of different sized tree cohorts (MS). Simulations results cover the period from 1998 to 2007. Further statistics are presented in Table 4.

Figure 6. a) Measured and simulated cumulative net ecosystem exchange (positive numbers indicate a gain in biosphere carbon). Each data point is the average of ten simulated values throughout the period from 1998 to 2007. b) Differences between measured and simulated net ecosystem exchange rates. The black lines refer to smoothed 30 day averages of simulations obtained with different stand structural assumptions (same line structure as in figure above).

Table 5. Average annual carbon balance for the period 1998 to 2007. Average annual carbon fluxes (avg.) and standard deviation (sd) are given in g C m^{-2}. Simulations also provide the separation of TER and NEE into heterotrophic and autotrophic, respectively above- and belowground components. The export of carbon is representing the averaged above ground stem wood that died naturally and by thinning

	Measured		PP		ED		MS	
	Avg.	sd	Avg.	sd*	Avg.	sd*	Avg.	sd*
GPP	1,035	55	1,031	96	1,009	52	1,054	107
TER	−830	37	−825	79	−829	64	−849	85
Soil (heterotrophic)			−189	15	−206	22	−165	16
Vegetation			−636	73	−623	53	−683	91
Below ground			−401	42	−388	43	−374	24
Above ground			−424	42	−442	32	−475	66
NEE	199	40	206	41	180	34	205	49
Soil (heterotrophic)			56	27	43	25	47	27
Vegetation			72	25	57	34	68	27
Below ground			56	27	66	39	60	30
Above ground			72	25	35	19	55	21
Export			−78	—	−79	—	−90	—

* Neglecting the harvest year 2002.

and carbon balances (Ilvesniemi *et al.*, 2009) have been simulated based on literature derived physiological parameters for the Hyytiälä site. The current estimates of total evaporation are considerably larger than indicated by Ilvesniemi *et al.* (2010). Since the soil water content is correctly reflected in the model, the reason is either an underestimation of runoff or that measurements do not refer to the same site conditions. Both may be true to some degree. Ilvesniemi *et al.* (2010) already noted that the sum of estimated interception and transpiration, scaled from independent measurements of individual trees from the same site, resulted in a larger total evaporation than estimated from the catchment outflow measurements. Additionally, it should be noted that the positive deviations of simulations from measurements occurred predominantly during warm periods in spring (see Fig. 3a), vegetation dynamics that affect transpiration and ground evaporation might thus be insufficiently captured, possibly due to missing ground vegetation processes. However, soil water balance has been reproduced remarkably well. The deviations between measured and simulated soil water content only occur in the winter period, where the measurements indicate a loss of water that is probably related to freezing processes. Thus, we assume that the drought stress component of the carbon gas exchange has also been represented sufficiently accurate.

The *VCMAX25* estimates for pine obtained by the iterative process ended up being a reasonable number compared to what is known from literature. The derived value for Scots pine of 110 μmol m^{-2} s^{-1} at the leaf scale amounts to a maximum value at the canopy scale (considering seasonality and spatial distribution within the canopy) between 66 (in 1998) and 82 (in 2006), obtained only during a very short summer period. The average value throughout the year is 29 and throughout the vegetation period (mid May to mid September) it is 55. For comparison, the ECOCRAFT data base (Medlyn *et al.*, 1999) gives a range of 57 to 163 μmol m^{-2} s^{-1}. For boreal sites, Aalto *et al.* (2002) reported 48 and Kellomäki and Wang (1997) measured a *VCMAX25* of 52.

Despite the overall very good match between simulated and measured carbon fluxes, we detected three problems that should be subject to further investigations:

— In order to represent the winter respiration rates, the minimum temperature for respiration (*TRmin*, see Table 2) had to be decreased from 0 (Thornley and Cannell (2000) to −7. The resulting shift in the response curve increases respiration mostly between 0 and 10°C, which indicates that the shape of the response curve as proposed by Thornley and Cannell (2000) should probably be improved.

— On average over the whole simulation period, we underestimated GPP during the flushing period. This may be due to an inappropriate seasonality algorithm, but may also hint to a possible contribution of

ground vegetation (mainly mosses) that are more active during the spring time due to favorable water conditions (Kolari *et al.*, 2006).

— Measured respiration peaked in early summer during a relatively short period (1-2 weeks), which could not be fully reflected in the model. An adjustment of the respiration coefficient to meet the measured annual TER resulted in simulated respiration rates that were somewhat too high during prolonged periods in summer. Since there is no indications in soil chamber measurements about any particularly high respiration rates from the ground (Korhonen *et al.*, 2009), we can only speculate that the increased respiration might be related to specific physiological reactions such as nitrogen mobilization in plant tissues (Vose and Ryan, 2002). However, it also cannot be excluded that this may be due to problems of the technique deriving respiration rates from the measurements, which is prone to several uncertainties (see *e.g.* Mammarella *et al.*, 2007, Rannik *et al.*, 2006, Van Gorsel *et al.*, 2009).

If simulations are run with the same parameters but assuming different stand structures —as was the case in the presented exercise— , the rates of carbon in- and output fluxes are higher in a mixed forest, indicating a positive effect of niche-differentiation (see *e.g.* Silverton, 2004). Under the common practice that a site which exhibits several tree species in uneven proportions is described as a patchwork of mono-specific stands, the total carbon exchange will be different from the case that all trees are perfectly mixed (MS approach). This is because the gas exchange of the smaller trees will be partially suppressed by larger trees of the dominant species. Thus, the physiological parameters of the dominant species (PP approach) that determine the exchange rates (*i.e. VCMAX25, KM20*) describe to the overall response rate better than a proportional weighting (ED approach). It is remarkable though that the ED approach yields the least deviations, indicating that it might reflect the actual stand conditions best. Indeed, a distinct pattern of pine, spruce and deciduous species is apparent within the investigated fetch (Ilvesniemi *et al.*, 2009). Nevertheless, the conclusion for this site is that it is more important to improve the physiological processes rather than stand structure. However, it has to be considered that spruce and birch are representing only minor portions at Hyytiälä so that this conclusion cannot be extended to all mixed forests.

Finally, it has to be admitted that the approach of using literature based parameterization is uncertain, because parameters from different sources may vary considerably (see *e.g.* Medlyn *et al.*, 1999). Therefore, it can be assumed that a more precise adjustment, *i.e.* to phenological observations, would bring the simulation closer to measurements. Such a procedure may be justified by the assumption that the same species might occur in different ecotypes and that the physiology is thus actually different. However, it should be kept in mind that a major reason for modeling based on physiological processes is that the approach should be generally applicable across a wide range of environmental conditions which would be counteracted by a site specific parameterization (see *e.g.* Delagrange, 2011). For this reason we used a parameterization for spruce that is also valid to describe a mono-specific stand in central Germany. For a reliable parameterization of pines and birches a test with mono-specific stands of these species would be desirable. Any parameter adjustment —or selection of parameters within a range of possibilities presented by literature sources— should thus be checked regarding its impact on physiological responses in other environments.

Despite the relative similarity of the gas exchanges obtained by different stand structural assumptions, the explicit consideration of stand structure can be of critical importance under changing environmental conditions. In such cases, specific properties of different tree species might result in a shift of relative competition strength with possible feedback effects on resource availability and susceptibility to disturbances. This would also affect gas exchange and carbon balances. The combination of physiological process description and individual (or cohort) dimensional development represents a potential advantage compared to empirically based competition models, because multiple resource distribution is described in dependence on forest dynamics. Thus, the challenge is to provide appropriate tools that consider energy and resource distribution within a forest in dependence on a crown and root system that is dynamically developing according to the micro-climatic conditions. Particularly, the experience of drought under shaded conditions should be more thoroughly investigated.

Currently, we are aware of only few approaches of physiologically-based cohort-models, none of which has been applied to temperate or boreal mixed forests development. The most common application is for tropical forests (*e.g.* Ditzer *et al.*, 2000; Tietjen and Huth 2006), where the physiological description has to be relatively crude since the parameterization cannot

be done on the level of species, but is aggregated to describe plant functional types. Another development is the 4C model (*e.g.* Lasch *et al.*, 2005), which has been applied to estimate regional forest production in Germany and describes tree cohorts, but up to date has focused on mono-specific stands. A more recent development has been presented by Deckmyn *et al.* (2007, 2009, 2011), highlighting the ability of cohort models to represent air pollution impacts and wood quality in structured forests.

Forest management puts a lot of emphasize on developing sustainable strategies that are suitable to cope with environmental changes (climate change, varying deposition regime). The emerging strategies generally include a higher proportion of uneven-aged mixed forests that are supposed to be less susceptible to possible negative effects (see *e.g.* Keskitalo, 2011). Given that very little is known about the actual responses of these kinds of forests under changed conditions, we feel that there is a large potential for applications of physiologically based cohort models today. For this purpose, the model presented will be further developed and evaluated in order to be more generally applicable for stand-structure related forestry questions.

Acknowledgements

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