



1 Description and evaluation of the process-based forest model 2 4C at four European forest sites

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26 **Abstract.** The process-based model 4C (FORESEE) has been developed over the past twenty years. The
27 objective of this paper is to give a comprehensive description of the main features of 4C and to present an
28 evaluation of the model at four different forest sites across Europe. The evaluation was focused on growth
29 parameters, carbon, water and heat fluxes. The main data source for the evaluation was the PROFOUND
30 database. We applied different statistical metrics of evaluation and compared the inter-annual and inter-monthly
31 variability of observed and simulated carbon and water fluxes. The ability to reproduce forest growth differs
32 from site to site and is best for the pine stand site Peitz. The model's performance in simulating carbon and water
33 fluxes was very satisfactory on daily and monthly time scales in contrast to the annual time scale. This
34 underlines the conclusion that processes that are either not represented in dependence on on medium- to long-
35 term dynamic influences such as allocation, or those that are not represented at all but may have a large impact at
36 specific sites – such as the dynamics of non-structural carbohydrates (NSC) and ground vegetation growth –
37 need to be elaborated for general forest growth investigations under climate change. On the other hand, 4C has
38 shown a great potential for improvement since it emphasizes the representation of boundary conditions such as
39 soil temperature at different depths. Therefore, more spatial differentiation of processes such as organ-specific
40 respiration should easily be accomplished. Nonetheless, by using the PROFOUND database we were able to
41 demonstrate the applicability and reliability of 4C.



42 1 Introduction

43 Forest modelling has a long tradition in forest science and ecology, and is of central importance to understanding
44 forest functioning and dynamics, but also for planning forest management and assessing forest product and
45 service provisioning (Pretzsch, 2010). While climate change has often put **emphasize** on long-term forest
46 developments, nowadays the changing variability of environmental conditions **and** has provoked a wider interest
47 in the sustainability of various ecosystem services from current forests. There is also an increasing demand for
48 estimating the sensitivity of forests to disturbance events as well as the mitigation options of management. This
49 makes it necessary to account for a high degree of complexity in forest ecosystems and thus demand forest
50 models that can capture numerous interactions between air, soil and vegetation. For this reason, stand-scale
51 process-based forest models (PBM) have been developed over the past 30 years that try to explain forest growth
52 and development based on an ecological understanding (Fontes et al., 2010; Landsberg, 2003; Mäkelä et al.,
53 2000a; Medlyn et al., 2011). Many of these models were developed to study climate change impacts on forest
54 productivity (see review by Reyer (2015)) or matter dynamics (water, carbon, nitrogen) (Cameron et al., 2013;
55 Constable and Friend, 2000; Kramer et al., 2002), or the effects of forest management (Fontes et al., 2010; Porte
56 and Bartelink, 2002; Pretzsch et al., 2008) or natural disturbances (Seidl et al., 2011) on forests. One such model
57 is the forest model “FORESt Ecosystems in a changing Environment”, in short ‘FORESEE’ and even shorter
58 ‘4C’, developed at the Potsdam Institute for Climate Impact Research in Germany.

59 The development of the forest model 4C started in the 1990s (Bugmann et al., 1997), at a time when
60 environmental change, and especially climate change, had been hypothesized to provoke major changes in forest
61 ecosystems that could not be covered by traditional statistics-based forest models. The main idea was to develop
62 a forest model that describes individual forest stands and has the following characteristics:

- 63 – represents our knowledge of the main mechanisms of forest functioning such as photosynthesis,
64 allocation, water relations etc. (i.e. is process-based)
- 65 – is responsive to changing environmental conditions
- 66 – is generic in its structure
- 67 – is applicable to forests world-wide
- 68 – respects the principle of parsimony (a minimum number of parameters that need to be estimated for
69 each species).

70 The model’s objectives include scenario analyses regarding (i) Impacts of climate change including other
71 changing environmental conditions (e.g., CO₂, N-deposition) on forest growth and matter balance (carbon, water,
72 nitrogen), (ii) Effects of forest management on forest ecosystem functioning, and (iii) Impacts of biotic
73 disturbances.

74 The concept underlying 4C and its salient features were outlined by Bugmann et al. (1997) and partly by Lasch
75 et al. (2002), Lasch et al. (2005) and Reyer et al. (2010). Here, we present the model in more detail and illustrate
76 **these** features with examples of model runs compared with observed data using the PROFOUND database
77 (Reyer et al., in preperation), see also <http://cost-profound.eu/site/outcomes/data/>.

78 The objectives of this paper are:

- 79 (1) To provide a comprehensive description of the structure and the processes of 4C
- 80 (2) To evaluate the model’s performance in reproducing growth and carbon and water fluxes as well as soil
81 temperature and water content for typical European forest stands



(3) To discuss the general applicability of the model and to highlight potential future improvements.

2 Methods

2.1 Model 4C

In the following we briefly present the main features of the process-based forest model 4C. More details on all processes, state variables and parameterization are given in the model description (Lasch-Born et al., 2018) and also on the website: <http://www.pik-potsdam.de/4c/>.

2.1.1 Model structure

4C describes tree species composition, forest growth and structure as well as the whole carbon, water, and nitrogen balance of a forest stand on an area basis. Thus it can be applied for patches of various sizes. The model mechanistically describes forest responses to climate, nitrogen, and CO₂, and accounts for realistic representation of forest management (Bugmann et al., 1997; Lasch et al., 2005). A forest stand is represented by a number of tree cohorts, each of which with a specific number of trees. All trees within a cohort share the same characteristics which are species, age, tree dimensions (height, height of crown base (or bole height), and diameter at breast height), biomass differentiated into various compartments (foliage, fine roots, sapwood, and heartwood) and stage of phenological development. The tree cohorts compete for light, water and nutrients. Their relative success in this competition determines their performance in terms of growth and mortality. Establishment of new cohorts is simulated with a regeneration module. Each cohort is represented in the model as horizontally homogeneous, i.e. the model is distance independent. The vertical structure of crown space and rooting zone is represented by a resolution into vertical layers. The model requires the following input data: daily meteorological data, a detailed description of the physical and chemical characteristics of each soil layer and an initialization of cohort properties (see section 2.1.4).

Different time scales are used for the sub-models, ranging from a daily time step for e.g. soil water dynamics, phenology, and for photosynthesis (based on weekly averaged daily climate data), to an annual time step for tree carbon allocation, dimensional growth and mortality (Fig. 1). For several key processes, 4C provides alternative descriptions to enable an uncertainty analysis across different model assumptions or for selecting processes at different levels of detail depending on data availability for parametrization or stand initialization. For example, evapotranspiration can be calculated using approaches by Turc and Ivanov (Dyck and Peschke, 1995; DVWK, 1996), Penman-Monteith (Monteith and Unsworth, 1990), or Priestley-Taylor (Priestley and Taylor, 1972). Each of these process descriptions is suited for different applications. The Turc-Ivanov procedure is a simple estimate which requires the least input data whereas Penman-Monteith uses a full range of meteorological variables but is based on physical knowledge which allows for more precise estimates (Kingston et al., 2009). Hence 4C is not only a forest model but a forest modelling framework. For more details see Lasch-Born et al. (2018).

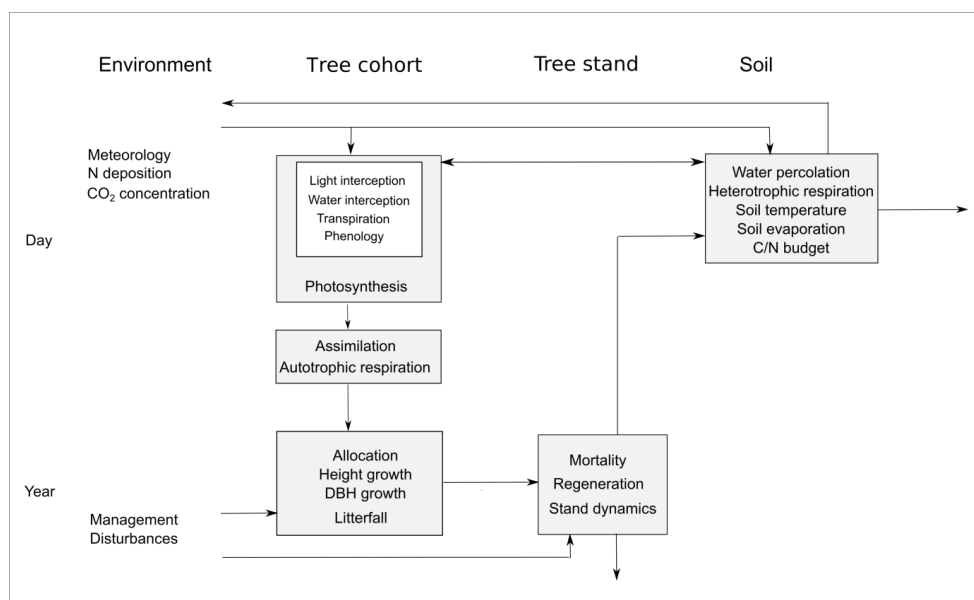


Figure 1. Structural scheme of 4C.

2.1.2 Main processes and sub-models

2.1.2.1 Light competition

The cohorts compete for light and the fraction of photosynthetically active radiation absorbed by each cohort is calculated based on the Lambert-Beer law (Haxeltine and Prentice, 1996b; Monsi and Saeki, 2005). Four different approaches for light transmission are implemented in 4C. All approaches calculate the absorbed photosynthetically active radiation for each cohort in each layer of the canopy between height and bole height of the trees, but differ in the way light is transmitted through the canopy and in the consideration of sun inclination (see Lasch-Born et al. (2018)). The daily total radiation absorbed by the canopy is mainly used for calculating photosynthesis and potential evapotranspiration.

2.1.2.2 Phenology

For deciduous tree species, 4C models bud burst to determine the start of the vegetation period. Bud burst is calculated according to three different approaches driven by temperature and photoperiod (day length) as described by Schaber (2002) and Schaber and Badeck (2003). The date of leaf fall is fixed. For coniferous tree species the length of the vegetation period is one year. For more details see Lasch-Born et al. (2018).

2.1.2.3 Production, allocation and growth

The annual course of net photosynthesis and net primary productivity is simulated for each cohort with a mechanistic formulation of net photosynthesis as a function of environmental influences (temperature, water and nitrogen availability, radiation, and CO₂) where the physiological capacity (maximal carboxylation rate) is calculated based on optimization theory (modified after Haxeltine and Prentice (1996b) and Haxeltine and Prentice (1996a)). The actual calculation is based on the mechanistic photosynthesis model of Farquhar et al. (1980) as simplified by Collatz et al. (1991). The competition of cohorts for water and nutrients is modelled via absorption of water and nitrogen by the fine roots in proportion to the fine root mass of the individual cohorts in a specific soil layer. Water limitation of photosynthesis is calculated per cohort by the ratio of cohort water



supply and cohort transpiration demand. Nitrogen limitation is described as a function of the C/N ratio of the soil and the species-specific photosynthesis response to nitrogen. Elevated CO₂ affects photosynthesis by an increase of the internal partial pressure of CO₂ which increases light-use efficiency and gross assimilation and reduces stomatal conductance as well as the potential water demand for transpiration. Therefore, water-use efficiency is increased with increasing CO₂ (Haxeltine and Prentice, 1996a).

The total tree, cohort and stand respiration is calculated as a constant annual fraction of gross primary productivity (GPP) as proposed by Landsberg and Waring (1997). Therefore, the net primary production (NPP) is also a constant fraction of GPP (Waring et al., 1998).

The allocation of annual net primary productivity to different tree organs (sapwood, heartwood, foliage, and fine root biomass) and dimensional tree growth is modelled by combining the pipe model theory (Shinozaki et al., 1964), the functional balance hypothesis (Davidson, 1969), and ideas presented by Mäkelä (1990) to make the model sensitive to resource availability and varying demand with increasing dimensions. Height growth is coupled to the growth of foliage mass and depending on **intra canopy shading** (Reyer et al., 2010). The diameter is calculated annually after allocation of NPP and height growth using the **sapwood and heartwood area** and the length of sapwood pipes. For more details see Lasch-Born et al. (2018).

2.1.2.4 Mortality and senescence

Cohort mortality is described on an annual time scale and two kinds of mortality are considered. The so-called 'age related' mortality is based on tree life span and corresponds to the intrinsic mortality described by Botkin (1993). In addition, the reduction of the number of trees due to limitation of resources and resulting growth suppression is described as carbon-based stress mortality according to Keane et al. (1996). If a tree cohort is not able to reproduce foliage biomass losses within a year, this period counts as a stress year. Successive stress years increase the probability of mortality. Stress-related mortality is species-specific, since the sensitivity to stress years is directly related to the **parametrized shade tolerance** of a tree species as well as the abundances of disturbances (see chapter 2.1.2.9), see also Lasch-Born et al. (2018). Both types of mortality can be combined or applied separately. Additionally, tree mortality can be superimposed by prescribed mortality events originating from thinning or harvests (see also chapter 2.1.2.7)

Annual senescence rates for the biomass compartments foliage, fine roots and sapwood of a cohort are species-specific and calculated from the corresponding fixed parameterized relative senescence rates. They deliver the litter input to the soil and the transformation of sapwood in heartwood.

2.1.2.5 Water balance

The following processes are considered for the calculation of the water balance: interception of precipitation, actual evapotranspiration, percolation and snowmelt. Intercepted water of the canopy as well as the ground vegetation is calculated depending on the leaf area and a species-specific interception capacity (Jansson, 1991). The potential evapotranspiration (PET) that is needed to define the evaporation demand of the forest stand is calculated by approaches of Turc and Ivanov from air temperature and global radiation or relative humidity, respectively (Dyck and Peschke, 1995; DVWK, 1996; Lasch-Born et al., 2015). Further approaches (i.e. Penman-Monteith, Priestley-Taylor) can be selected and are described in more detail in Lasch-Born et al. (2018). The potential evapotranspiration limits the evaporation demand of intercepted and soil water as well as the transpiration of trees and ground vegetation. The actual water uptake of each cohort depends on its transpiration demand and the available water in the soil layers and is proportional to its relative share of fine roots in each soil



layer. Snowmelt is estimated from the actual air temperature greater than a threshold temperature with a linear approach suggested by Koitzsch and Günther (1990).

2.1.2.6 Soil temperature, water, carbon and nitrogen

The transport of heat and water in a multi-layered soil is explicitly calculated, as well as carbon and nitrogen dynamics based on the decomposition and mineralisation of organic matter (Grote and Suckow, 1998; Grote et al., 1998; Kartschall et al., 1990). The soil of a forest stand is divided into different layers with optional thickness defined based on the horizons of the soil profile. Each layer, the humus layer as well as the deeper mineral layers, is assumed to be homogeneous concerning its physical parameters. Water content and soil temperature of each soil layer are estimated as functions of soil parameters, air temperature, and stand precipitation. They control the decomposition and mineralisation of organic matter. The carbon and nitrogen dynamics are driven by the litter input which is separated into five fractions for each species (stems, twigs and branches, foliage, fine roots, and coarse roots). The turnover of all litter fractions and of the soil organic matter compartment is described as a first order reaction (Grote and Suckow, 1998; Post et al., 2007). These processes are controlled by matter- and species-specific reaction coefficients and modified by soil moisture, temperature and pH value. For more details see Lasch-Born et al. (2018).

2.1.2.7 Management

4C simulates management of mono- and mixed-species forests automatically based on rules that are selected by the user. For this purpose, a variety of management routines are implemented to mimic thinning, harvesting and planting. Thinning is defined mainly by intensity, given by a fixed portion of biomass or stem number removed per year, and type such as thinning from above or below realized by means of stochastic approaches based on a Weibull distribution applied to the cohorts, similar to Lindner (2000); for more details see Lasch-Born et al. (2018).

Planting of seedlings includes the generation of a variety of seedling cohorts of a specific tree species differing in height and number of seedlings. Further seedling characteristics are derived from empirical relationships available in the literature (Hauskeller-Bullerjahn, 1997; Schall, 1998; Van Hees, 1997) which are also used for seedling growth. If the height of a seedling cohort exceeds a threshold value, the entire cohort is then transformed into a regular tree cohort. 4C allows the management of short rotation coppices with Aspen and Black locust, see Lasch-Born et al. (2018).

2.1.2.8 Wood product model and socio-economic analysis

A wood product model (WPM) is integrated in 4C. It is based on a concept introduced by Karjalainen et al. (1994) and further developed by Eggers (2002). The WPM simulates carbon pools and fluxes in the forest sector. The parameters are based on aggregated values of the German timber market reports, available regional data and parameters according to Eggers (2002). The WPM allows the grading of the harvested and standing timber, the processing of the timber and allocation of timber to wood products, and includes the retention period of timber in the final products and later on landfills. Finally, a socio economic analysis tool (SEA) (Fürstenau et al., 2007) calculates costs, revenues and subsidies of forest management and furthermore the net present value (NPV) and the liquidation value of the standing stock (Fig. 2).

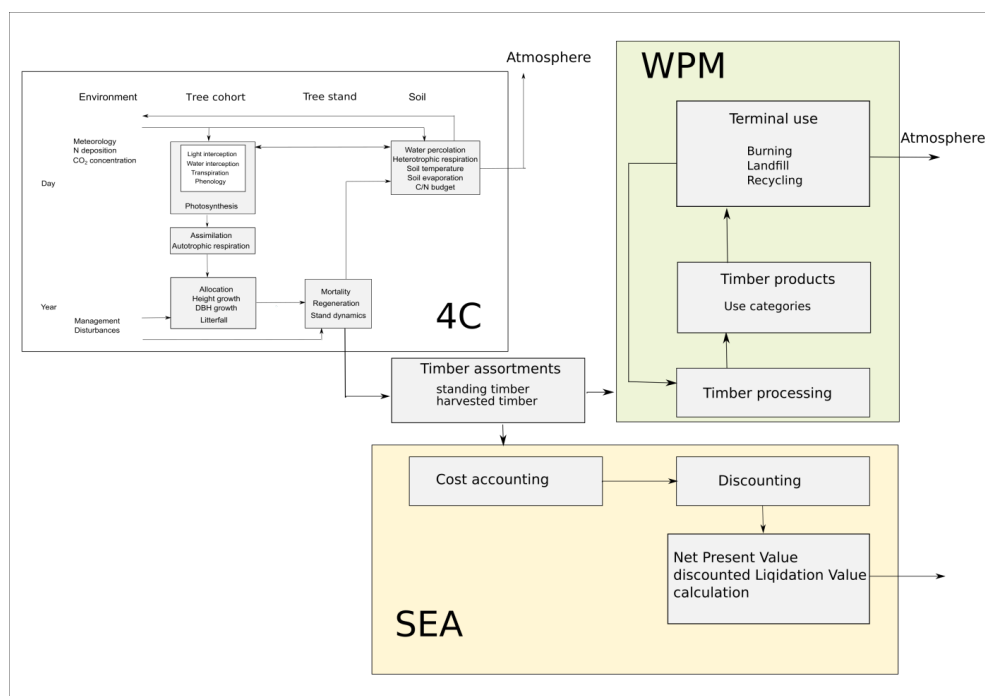


Figure 2. Model system 4C (as presented in Fig. 1) coupled with the Wood Product Model (WPM) and Socio-economic Analysis-tool (SEA) (Eggers, 2002; Fürstenau et al., 2007).

2.1.2.9 Disturbances

The implementation of biotic disturbances follows a specific framework of modelling functional groups of biotic agents (defoliator, root disturber, stem rot, xylem clogger, and phloem feeder) proposed by Dietze and Matthes (2014). In this framework, insects and pathogens are clustered upon their damaging action and abstracted on the level of functional groups. In addition, we also implemented growth and impacts of the hemiparasitic European mistletoe (*Viscum album* L.) (Kollas et al., 2018) (Table 1).

Table 1 Six functional groups which are currently implemented in 4C with their corresponding impacts in the model.

Functional group	Impact in 4C
Defoliator	Foliage loss
Xylem clogger	Reduction in water supply rate
Phloem feeder	Carbon loss
Root disturber	Fine root loss
Stem rot	Increase in stem mortality
Mistletoe	Increase of tree transpiration, and carbon loss



229 The occurrence of a disturbance has to be given externally as an input time series. If a disturbance occurs, the
230 corresponding effect is simulated (e.g. defoliator implies reduction of foliage biomass of between 0% and
231 100%), which then exerts its influence on the affected processes within 4C.

232 Only in the case of simulations with disturbances, a NSC-pool (non-structural carbohydrates including starch
233 and sugars) of the trees is activated and the carbon amount for the allocation will be enhanced by carbon from
234 the NSC-pool as a C-reserve of the tree. The NSC-pool is assumed to be located in the biomass compartments
235 sapwood, branch/twigs wood, and coarse root wood, which means that the maximum size of the NSC-pools is
236 defined relative to the biomass of the corresponding compartments (differentiated for coniferous and deciduous
237 trees and based on data reported by Hoch et al. (2003)). The surplus of carbon for allocation into damaged
238 tissues is only available at the end of the disturbance year, while refilling of the NSC-pool can continue for many
239 years until the pool's maximum size is reached. For more details see Lasch-Born et al. (2018).

240 2.1.3 Tree species parameterization

241 4C is parameterized for the most common European tree species: Common beech (*Fagus sylvatica* L.), Norway
242 spruce (*Picea abies* L. Karst.), Scots pine (*Pinus sylvestris* L.), oaks (*Quercus robur* L., and *Quercus petraea*
243 Liebl.), and birch (*Betula pendula* Roth). In addition, parameters for some species that are considered favourable
244 under expected environmental changes or that are used for short-rotation coppices have also been tested and are
245 readily applicable. The considered species include Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Black
246 locust (*Robinia pseudoacacia* L.), Aleppo pine (*Pinus halepensis* Mill.), eucalypts (*Eucalyptus globulus* Labill.
247 and *Eucalyptus grandis* W. Hill ex Maiden) and poplars (*Populus tremula* (L.), *P. tremuloides* (Michx.)).
248 Moreover, parameter sets for Ponderosa pine (*Pinus ponderosa* Dougl.) and Lodgepole pine (*Pinus contorta*
249 Dougl.) exist but have not been properly tested. The oak, eucalypt and poplar parameters are derived from
250 investigations of two species of the same genus each and are assumed to be valid for both. Besides these tree
251 species, 4C is also parameterized for the hemiparasitic plant Mistletoe (*Viscum album* subsp. *austriacum*) and a
252 generic grassy ground vegetation based on properties of *Calamagrostis arundinacea*. For each species, a full set
253 of parameters comprises about 95 individual values. Some parameters do not differ across species yet, but can be
254 potentially selected if scientific evidence becomes available. Due to the possibility of using different process
255 descriptions for the same process in the 4C model framework (e.g. phenology) the actual number of parameters
256 used in each simulation may vary (for the values of the parameters see Lasch-Born et al. (2018)).

257 In many cases, different physiological parameters have been determined in different environments (Kattge et al.,
258 2011), or dependent on stand density or site fertility (e.g. (Berninger et al., 2005)). To account for these findings,
259 the philosophy of 4C is to assume that species-specific parameters are genetically defined but that important tree
260 traits (e.g. leaf area or actual electron transport capacity) can be described by acclimation processes to specific
261 environmental conditions. Covering the most important of such processes, one parameter set for each species can
262 be chosen that reproduces species' growth, water and carbon cycling under a wide range of evolutionary
263 constraints. Calibration of the parameters is therefore not usually carried out when setting up the model for a new
264 site. However, on the one hand, ecotypes may have developed at specific sites that differ due to evolutionary
265 developments and not acclimation so that their properties may not be sufficiently described by a common set of
266 species properties. On the other hand, acclimation processes that are only important under specific conditions
267 (e.g. nutrient imbalances) may not yet be adequately considered in 4C. Therefore, in recent studies, 4C has also
268 been calibrated using a Bayesian framework (van Oijen et al., 2013; Reyer et al., 2016).



269 **2.1.4 Input data needs**

270 **Because** the smallest time step in 4C is daily, the model requires daily meteorological data (temperature,
271 precipitation, relative humidity, air pressure, wind velocity and global radiation). Furthermore, annual CO₂
272 concentration and nitrogen deposition are necessary inputs. Values for annual CO₂ concentration can be selected
273 from internally integrated data sources (measurements: Mauna Loa, Dr. Pieter Tans, NOAA/ESRL
274 (www.esrl.noaa.gov/gmd/ccgg/trends/) and Dr. Ralph Keeling, Scripps Institution of Oceanography
275 (scrippsco2.ucsd.edu/), scenarios: RCP: Meinshausen et al. (2011), SRES: Nakicenovic (2000)).

276 The information about the forest can be provided at two levels of detail: At the stand level, average values of
277 diameter at breast height (DBH), height, stem number or basal area, age and species type are needed. From these
278 data tree cohorts are generated using distribution functions. The cohorts together represent these average values.
279 At tree level, individual tree measurements (DBH, height, height of the crown base, species, age) are needed and
280 used to aggregate cohort data. The individual tree data are better suited for initializing 4C because the cohorts
281 can be estimated more realistically from individual tree data.

282 The description of the soil layers follows the soil horizons. At least the thickness and texture of the horizons are
283 required as well as their carbon and nitrogen content. Further important variables are pH, bulk density, pore
284 volume, field capacity, and wilting point. If the last three entries are missing, they can also be estimated via
285 pedotransfer functions from texture (Russ and Riek, 2011; Wösten et al., 2001).

286 **2.2 Previous model evaluations**

287 Since the first applications of 4C, tests, evaluations and model comparisons have been carried out for various
288 forest stands and different processes within 4C (Table 2). The evaluations find 4C applicable to a wide range of
289 environmental conditions and research questions but also highlight deficits. Using these previous evaluations in
290 combination with detailed results from selected ecosystems of particular properties, we will draw conclusions for
291 further model development and improvement in the Discussion section.

292



293

294 **Table 2 Overview of studies in which different species, processes and variables of 4C were evaluated (DBH- diameter**
 295 **at breast height, H height, N- stem number, AET-actual evapotranspiration, NPP- net primary production, NEE- net**
 296 **ecosystem exchange, TER-total ecosystem respiration, GPP-gross primary production)**

Process/ variable	Validation data	Site	Species	Results	Publication
Growth (DBH, H, stem volume, N)	Long-term permanent plot measurements; Evaluation using volume growth and survival graphs	Evo (Finland), Fabrikschleichach (Germany)	Scots pine, beech	Satisfactory results for volume growth in tree size classes; underestimation of height growth; underestimation of growth of smaller tree cohorts; overestimation of mortality of smaller tree cohorts;	Mäkelä et al. (2000b) ¹
Soil water content, soil temperature	Daily measurements of soil temperature and soil water content in different layers	6 Level II site ² in Brandenburg (Germany)	Scots pine	Good correspondence of simulated soil water content and soil temperature with measured data for four years;	Suckow et al. (2001)
Management (DBH)	Long-term permanent plot measurements	Long-term management trials Chorin, Eberswalde	Scots pine, oak	Simulation of thinning preserved the diameter distribution of the residual stand and influenced the stand dynamics in the expected manner;	Lasch et al. (2005)
Growth (stem volume, DBH, H, N), climate sensitivity, management	Long-term permanent plot measurements	Fabrikschleichach (Bavaria, Germany), Chorin (Brandenburg, Germany), Eberswalde (Brandenburg, Germany)	Beech, oak, Scots pine	Strong sensitivity of growth to the level of precipitation; sensitivity to drought larger for beech than for oak; simulated diameter development was slightly overestimated by the model, and height growth was slightly underestimated in most management scenarios;	Lindner et al. (2005) ¹
Soil respiration, litter, DBH growth, water balance, soil temperature	Soil water content, soil respiration, growth parameter, tree ring data	Level II sites ² in Germany	Beech, oak, Scots pine, Norway spruce	Realistic simulation of water balance and soil temperature; leaf mass and leaf litter simulations were valid;	Badeck et al. (2007) ¹



Process/ variable	Validation data	Site	Species	Results	Publication
Growth and soil processes	Stem biomass, foliage litter fall; soil water content and soil temperature	Level II sites in Germany: Kienhorst, Solling	Scots pine, beech	Good correspondence for stem biomass; slight overestimation of foliage litter fall; good correspondence of simulated and observed soil temperature and soil water content in two depths (Kienhorst); deviation of simulated soil water content from observed data at the end of the dry year 2003 and in 2004.	Lasch et al. (2007)
Carbon balance (stem C productivity, soil C)	Stand level inventory data, stem wood productivity derived from yields tables	Forest management unit in the province of Carinthia, southern Austria	Norway spruce	Realistically captured interactions between stand structure and forest floor C as represented in a local empirical model; simulated Norway spruce stem C productivity compared well to the observed values;	Seidl et al. (2008) ¹
Management: thinning and conversion strategies	Experience from literature	Forest reserve Galgenberg (The Netherlands)	Scots pine	Effects of different thinning types (from above and from below) and thinning intensities on stand structural characteristics such as tree density, spatial point pattern and diameter and height differentiation, were consistent with reported effects in various Scots pine conversion stands;	Kint et al. (2009)
Short rotation coppice	Woody biomass experimental data (yields) of SRC from literature	Eastern Germany	Aspen	Good correspondence of simulated yields with experimental data;	Lasch et al. (2010)
Forest growth (stem biomass, DBH, H)	Long-term plot measurements	4 Beech stands in forest district Buchfahrt, Thuringia (Germany)	Beech	40 years of growth of the beech stands simulated very well; very good correlations between measured and simulated	Borys et al. (2013)



Process/ variable	Validation data	Site	Species	Results	Publication
	Height, DBH	12 stands in Austria, Belgium, Estonia and Finland	Scots pine	stem biomasses for a 50-year simulation; Good predictive accuracy (a likelihood value from Bayesian calibration approach) for mean tree height and DBH (before calibration);	van Oijen et al. (2013) ¹
Water and carbon fluxes, soil	Daily flux measurements (GPP, NPP, TER, AET), soil temperature, soil water content	Flux-sites: Brasschaat (Belgium), Collelongo (Italy), Hesse (France), Hyytiälä (Finland), 5 Level-II sites ² in Germany	Beech, Scots pine, Norway spruce	Carbon fluxes: low normalized errors and the Nash-Sutcliffe, model efficiency and the correlation coefficients are high; Hyytiälä: soil temperature follows the annual course of the measured values, no systematic bias exists; the soil water content in the organic layer is mostly not correctly simulated;	Reyer et al. (2014)
Transpiration, soil water, radial stem increment, root water uptake	Xylem sap flux, soil water content, tree ring measurements	Two pure pine stands and two mixed pine-oak stands in Brandenburg (Germany)	Scots pine, oak	For water uptake with low root resistance overestimation of tree transpiration and good accordance of simulated and observed soil water content; for water uptake with high root resistance high correlation between observed and simulated tree ring growth, better match of observed transpiration but overestimation of soil water content;	Gutsch et al. (2015b)
Carbon and water fluxes	Flux measurements (GPP, NPP, TER, AET)	Euroflux-site Zotino, Siberia (Russia)	Scots pine	Best results of the comparison for GPP; ecosystem respiration and actual evapotranspiration seems not so well captured; satisfactory agreement between simulated and	Suckow et al. (2016)



Process/ variable	Validation data	Site	Species	Results	Publication
				measured data for annual values of GPP, TER, NEE, and AET (May-September);	
Carbon stock in stand and soil		Buchfahrt forest district in Thuringia (Germany), 4 beech stands	Beech	Successfully simulated past growth of four study sites independent of their thinning regime with 4C and WPM; validation on the level of the forest district: overestimation of the absolute C-stock in the biomass in comparison to the estimates based on inventory (using biomass functions); development of forest stands and harvests at forest district level were depicted;	Borys et al. (2016)
NPP	NPP from references	Representative forest stands in Germany	Scots pine, Norway spruce, oak, beech	Static reduced models of NPP were derived from 4C simulations; comparison with results from literature showed that these functions provide meaningful estimates of NPP;	Gutsch et al. (2016)
Carbon fluxes	Flux measurements (NEE)	Flux-sites Sorø (Denmark), Vielsalm (Belgium) and Collelongo (Italy).	Beech	Overestimation of NEE in periods of very high carbon uptake and mostly underestimation in periods of carbon release; asynchrony between simulations and observations was large in spring and autumn, dropping to lower levels in full summer and full winter; often overestimation of the importance of high frequency variability (inter-monthly to inter-daily) in NEE;	Horemans et al. (2017) ¹
Basal area increment and	Tree ring measurements	Stand in the forest district Berlin-	Scots pine,	Simulated basal area increment (BAI)	Kollas et al. (2018)



Process/ variable	Validation data	Site	Species	Results	Publication
effect of Mistletoe infection		Müggelsee (Germany)	infected with Mistletoe	corresponded well with BAI calculated from measured tree ring width; ring width indices of both non-infected trees and trees infected from 1994 on were found to run synchronously in relative but also in absolute values; good reproduction of the absolute level of growth, of the general growth trends and the pointer years;	
Timber harvest, stem increment	BWI ³ (forest inventory data Germany No. 3)	Germany	Scots pine, Norway spruce, oak, beech, birch, Douglas fir	Reproduction of species- specific yields (stem increment and timber harvest) in good correspondence with inventory data; strong underestimation of Douglas fir stem increment, moderate overestimation of oak stem increment;	Gutsch et al. (2018)

¹ – model comparisons; ² – ICP Forests intensive monitoring plots



2.3 Test sites, data and simulation setup

To evaluate the current version of 4C regarding long-term growth, water and carbon fluxes we selected four sites representing the main central European tree species from the PROFOUND database (Reyer et al., in preparation) and additional sources (Table 3, Table 4, Supplement Table S1). For Peitz (Scots pine), Solling (Norway spruce) and Hyytiälä (mixed stand of Scots pine and Norway spruce) we evaluated forest growth by stem biomass (BM) and diameter at breast height (DBH) or geometric mean diameter (DG) measurements. These data were not available for Sorø from real measurements. The availability of diameter variables differs from site to site in the PROFOUND database (see also Supplement Table S2). Furthermore, for Hyytiälä and Sorø (Common beech) flux data were available. We selected these sites to represent the main tree species under a wide range of environmental conditions. We did not calibrate species-specific parameters for the considered sites.

Table 3 Site characteristics, data source: PROFOUND database

Site	Species	Type	Lon [°]	Lat [°]	Alt. [m]	Meteorological conditions	Mean temperature [°C]	Mean annual precipitation sum [mm]	Simulation time period	Soil type
Peitz (Germany)	<i>Pinus sylvestris</i> / Scots pine	Long-term monitoring site	14. 35	51. 92	50	continental	9.3	554	1952- 2010	Dystic Cambisol
Solling (Germany)	<i>Picea abies</i> / Norway spruce	Level II	9.5 7	51. 77	50 4	maritime	6.8	1108	1967- 2013	Cambisol (haplic)
Sorø (Denmark)	<i>Fagus sylvatica</i> / Common beech	Euroflux	11. 64	55. 49	40	warm temperate and fully humid	8.3	848	1996- 2012	Cambisol
Hyytiälä (Finland)	<i>Pinus sylvestris</i> / <i>Picea abies</i>	Euroflux	24. 29	61. 85	18 5	continental	4.4	604	1996- 2014	Haplic Podsol



316

317

318 **Table 4** Stand characteristics at the beginning of the simulations/ measurements

Site	Species	Age	Mean H [m]	Mean DBH [cm]	Number of trees per ha
Peitz	<i>Pinus sylvestris</i>	53	7.4	9.1	3860
Solling	<i>Picea abies</i>	85	23.9	30.2	595
Sorø ¹	<i>Fagus sylvatica</i>	77	25.0	38.0	426
Hyytiälä	<i>Pinus sylvestris</i>	34	10.9	12.7	870
	<i>Picea abies</i>	34	4.1	3.7	967

319 H – height, DBH – diameter at breast height, ¹ – source: derived from Horemans et al. (2017)

320 2.3.1 Climate, soil, stand, and observational data

321 Climate, stand, soil data, and observational data for model evaluation were available from the PROFOUND database (Reyer
 322 et al., under review). In addition to the gap-filled half-hourly flux data from the PROFOUND database we used the monthly
 323 and annual aggregated data from FLUXNET (<http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>). We checked the half-
 324 hourly flux data and removed implausible data on a daily basis. Some additional data are used for the initialization of the soil
 325 profile for Hyytiälä which are based on Haataja and Vesala (1997).

326 2.3.2 Management

327 All sites were simulated considering management according to the inventory records. Therefore, the time of occurrence and
 328 the intensity of thinnings have been prescribed for the respective runs. Thinnings from above or from below indicate an
 329 imbalance of stem number and biomass removal which leads to mathematically changed average dimensions after the event
 330 (Table 5).

331 **Table 5** Management description for all sites

Site	Number of management events	Type	Target value
Peitz	11	Moderate thinning from below	Stem number
Solling	13	Thinning from above	Stem number
Sorø	1	Thinning from above	Stem number
Hyytiälä	3	Thinning from above	Stem number

332 2.4 Evaluation metrics

333 For the evaluation of growth at the sites Peitz, Solling and Hyytiälä we selected the variables arithmetic mean diameter at
 334 breast height (DBH) or the diameter of the geometric mean diameter (DG) and stem biomass (BM), which were analysed
 335 with an annual time step. Using different diameter based variables is explained by the availability in the used database. We
 336 applied regression analysis between observed and simulated values to determine the regression coefficient R^2 and its
 337 significance (with SigmaPlot), and the model efficiency (ME) (Loague and Green, 1991):



$$ME = 1 - \frac{\sum_{i=1}^N (O_i - P_i)^2}{\sum_{i=1}^N (O_i - \bar{O})^2}$$

where O_i are observation values, P_i are simulation values, \bar{O} is the mean of observation values, and N is the number of values. ME estimates the proportion of variance of the data explained by the 1:1 line and is an overall indication of goodness of fit (Mayer and Butler, 1993); a positive value indicates that the simulated values describe the trend in the measured data better than the mean of the observations (Medlyn et al., 2005a; Smith et al., 1997). Furthermore, we calculated the normalized root mean square error (Keenan et al., 2012):

$$NRMSE = \frac{\sqrt{\frac{1}{N} \sum_{i=1}^N (O_i - P_i)^2}}{\sigma_{obs}}$$

where σ_{obs} represents the standard deviation of the observation values.

Where available, we evaluated carbon (net ecosystem exchange (NEE), gross primary production (GPP)) and water fluxes (actual evapotranspiration (AET)), soil temperature (ST) and soil water content (SWC) in different layers using the same statistical measures on daily and monthly (and annual) time scales.

We also analysed the inter-monthly and inter-annual variability of the carbon and water fluxes. At this end we applied the method described by Keenan et al. (2012) and Vetter et al. (2008) to the monthly and annual time series of observed and simulated GPP, NEE and AET. The inter-monthly variability (IMV) is calculated as follows:

$$IMV_{m,t}^V = V_{m,t} - \bar{V}_m$$

$\bar{V}_{m,t}$ – monthly variable (GPP; NEE, AET) (sum) of month m and year t

\bar{V}_m – long-term monthly mean of the variable V for month m ($m=1, 12$)

The inter-annual variability (IAV) is calculated for the annual time series of the considered variables V :

$$IAV_t^V = V_t - \bar{V}$$

V_t – annual V of year t

\bar{V} – long-term mean of V

The resulting monthly and annual ‘normalized’ times series (observed and simulated) were compared and subjected to statistical and graphical analyses.

3 Results

3.1 Forest growth

Judging from the statistical measures, 4C shows the best performance in terms of ME of DG and BM for Peitz. For Solling the model performance is less good than for Peitz (Table 6). For Hyytiälä, the model performance (ME) for DBH of pine is better than for spruce, and their performance measures for stem biomass are low. The negative values indicate that the residual variance (observed minus simulated) is greater than the variance of the observed values. For Peitz, 4C overestimated stem biomass (Fig. 3) whereas it overestimated DBH for Solling (Fig. 4).

The measure of deviation between observed and simulated data (NRMSE) and the ME show for Peitz and Hyytiälä better results for DBH/DG than for stem biomass. The stem biomass simulations are less precise because biomass simulation depends on simulated height increment and NPP allocation to sapwood and the sapwood senescence rate. The large negative ME values for DBH and BM of spruce at the site Hyytiälä indicate a poor result of the model. 4C underestimated the BM



and overestimated DBH of spruce in this forest (Fig. 5). The values of R^2 are very high for all variables and sites but do not give a good measure of model performance (Medlyn et al., 2005b).

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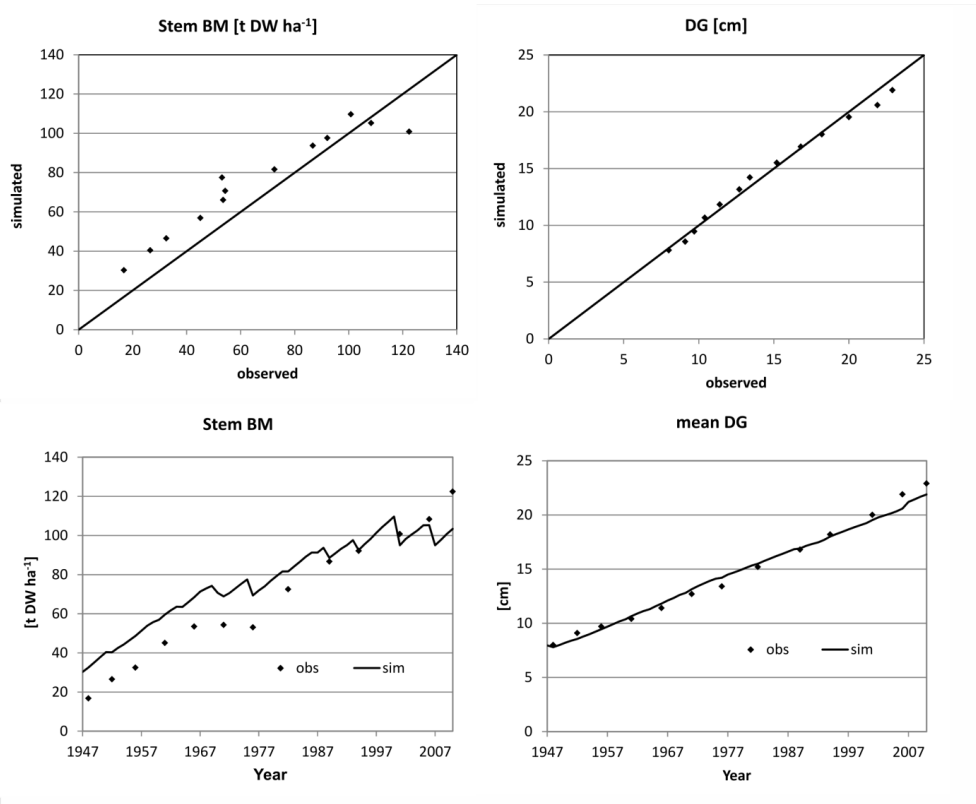
Table 6 Statistics for the three sites (DG – geometric mean diameter, DBH – diameter at breast height, BM – stem biomass, number – number of values)

	Peitz		Solling		Hyytiälä Pine		Hyytiälä Spruce	
	DG	BM	DBH	BM	DBH	BM	DBH	BM
number	13	13	19	18	16	16	16	16
NRMSE	0.119	0.382	0.465	0.338	0.644	1.049	2.574	3.146
ME	0.985	0.842	0.772	0.879	0.557	-6.064	-6.064	-9.560
R^2	0.988**	0.964**	0.984**	0.933**	0.983**	0.939**	0.972**	0.985**

** - $p < 0.001$

373

374



375

Figure 3. Simulated (sim) versus observed (obs) DG and stem biomass BM for Peitz. The plots show scatter plots with a 1:1 line (upper row) and time series (lower row).

378

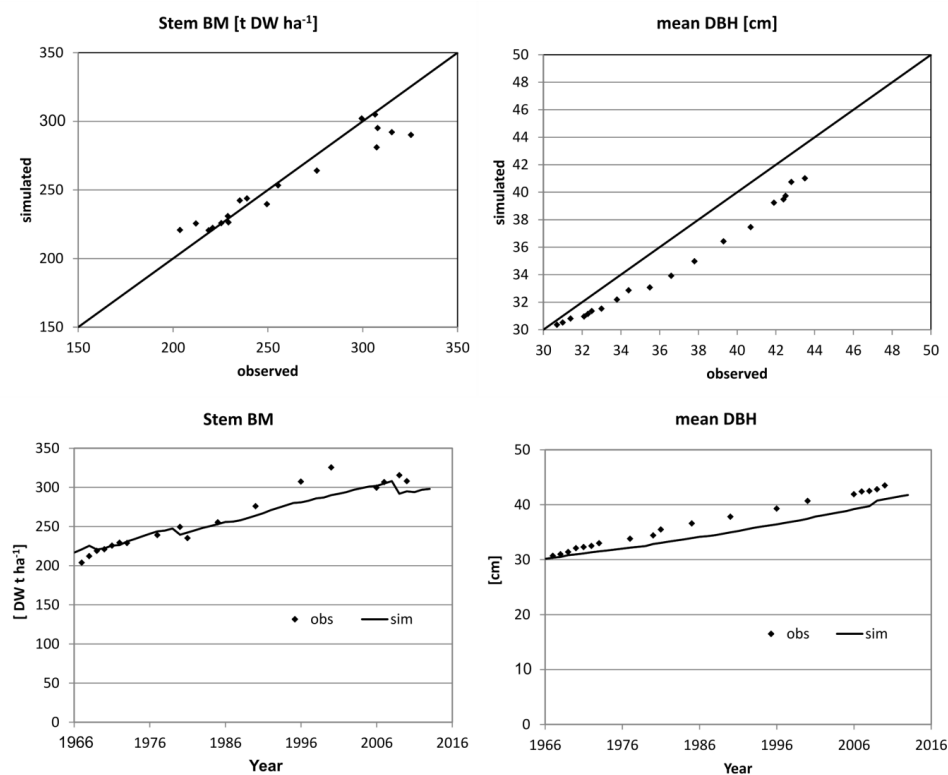
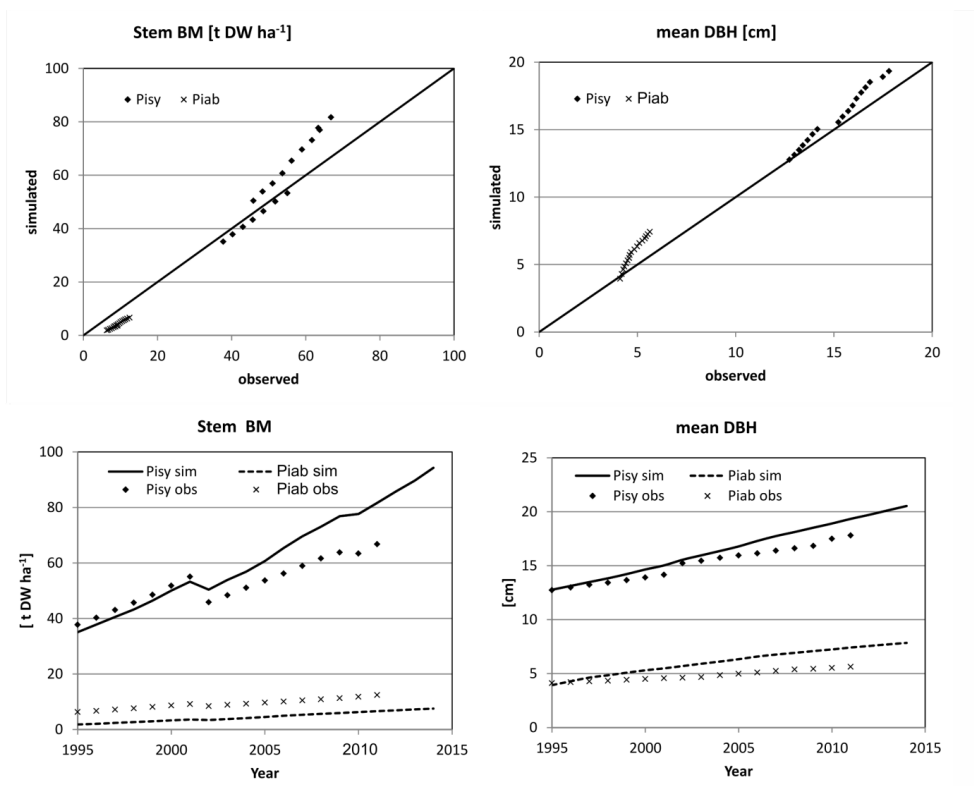


Figure 4. Simulated (sim) versus observed (obs) DBH and stem biomass BM for Solling. The plots show scatter plots with a 1:1 line (upper row) and time series (lower row).



383

384 **Figure 5.** Simulated (sim) versus observed (obs) DBH and stem biomass BM for Hyytiälä (Pisy – pine, Piab – spruce). The plots
 385 show scatter plots with a 1:1 line (upper row) and time series (lower row).

386 3.2 Carbon and water fluxes

387 3.2.1 Evaluation over long-time scales at different time resolutions

388 The averages of the simulated annual fluxes in comparison with the observed averages show a good correspondence for GPP
 389 for Sorø and Hyytiälä. In Sorø, 4C overestimates the long-term average of GPP by 3.7 % and in Hyytiälä by 3.5 % (Table 7).
 390 The NEE is clearly underestimated in Sorø and Hyytiälä on long-term average. The same is true for the AET in Sorø but it is
 391 slightly overestimated for Hyytiälä. All statistical measures show values which indicate low performance (Table 7).

392

393 **Table 7** Annual long-term means (+/- standard deviation) and evaluation metrics of water and carbon fluxes in Sorø (1997-2012)
 394 and Hyytiälä (1996-2014)

Sorø	Annual statistics					
	Number of years	Observed average	Simulated average	NRMSE	ME	R ²
Annual AET [mm]	16	431.3±41.2	313.8±22.6	2.977	-8.453	0.223 ^{nsN}
Annual NEE [g C m ² yr ⁻¹]	16	-148.3±130.2	-385.8±100.3	2.403	-5.160	0.437**N
Annual GPP [g C m ² yr ⁻¹]	16	1892.5±132.4	1972.7±112.5.1	1.336	-0.902	0.001 ^{nsN}



Hyytiälä						
Annual AET [mm]	11	320.6±38.1	381.6±41.0	2.039	-3.5748	0.0328 ^{nsN}
Annual NEE [g C m ² yr ⁻¹]	17	-213.65±53.8	-348.03±45.4	2.764	-7.1188	0.0172 ^{nsN}
Annual GPP [g C m ² yr ⁻¹]	17	1160.80±102.4	1209.2±157.8	1.304	-0.8066	0.3435 ^{ns}

395 ** - p<0.001

396 * - p<0.05

397 ^{ns} - not significant

398 ^N - normal distribution

399

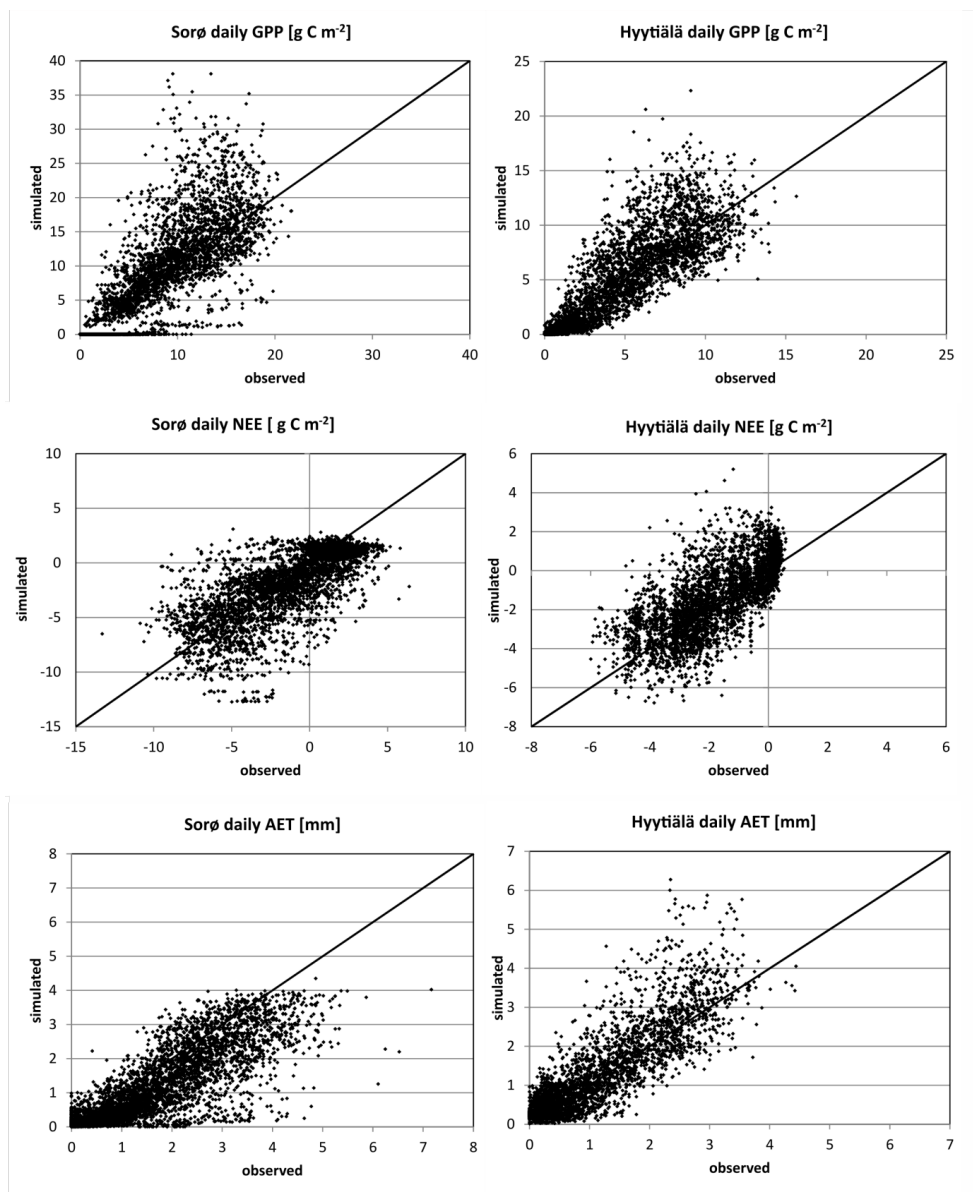
400 For the daily and monthly sums of fluxes, the evaluation metrics indicate a good model performance with monthly results
 401 showing a better fit to observations than daily results (Table 8). The evaluation metrics for Hyytiälä are slightly better than
 402 for Sorø especially for AET and GPP: For Sorø, 4C simulates days without any GPP, while GPP values greater than zero
 403 were observed. Daily AET is underestimated for days with a high observed AET (greater than 4 mm). For Hyytiälä, 4C
 404 clearly overestimates GPP and AET but also NEE for single days by more than 50% (Fig. 6, right). The intra-annual
 405 variability on a monthly scale in Sorø for the three variables (Fig. 6, left) shows that 4C underestimates GPP from January to
 406 April but during the vegetation period the GPP is clearly overestimated (and NEE underestimated). AET is underestimated
 407 throughout the year. In Hyytiälä, 4C overestimates the monthly GPP and underestimates the NEE during the vegetation
 408 period from May until July (Fig. 7, right). The variability of the monthly GPP from May until August is higher for the
 409 simulated values than for the observed values in Sorø; for Hyytiälä, it is the other way around. The monthly AET is
 410 overestimated throughout the year.

411

412 **Table 8 Evaluation metrics for daily and monthly sums of AET, NEE and GPP for Sorø (1996-2012) and Hyytiälä (1996-2014)**

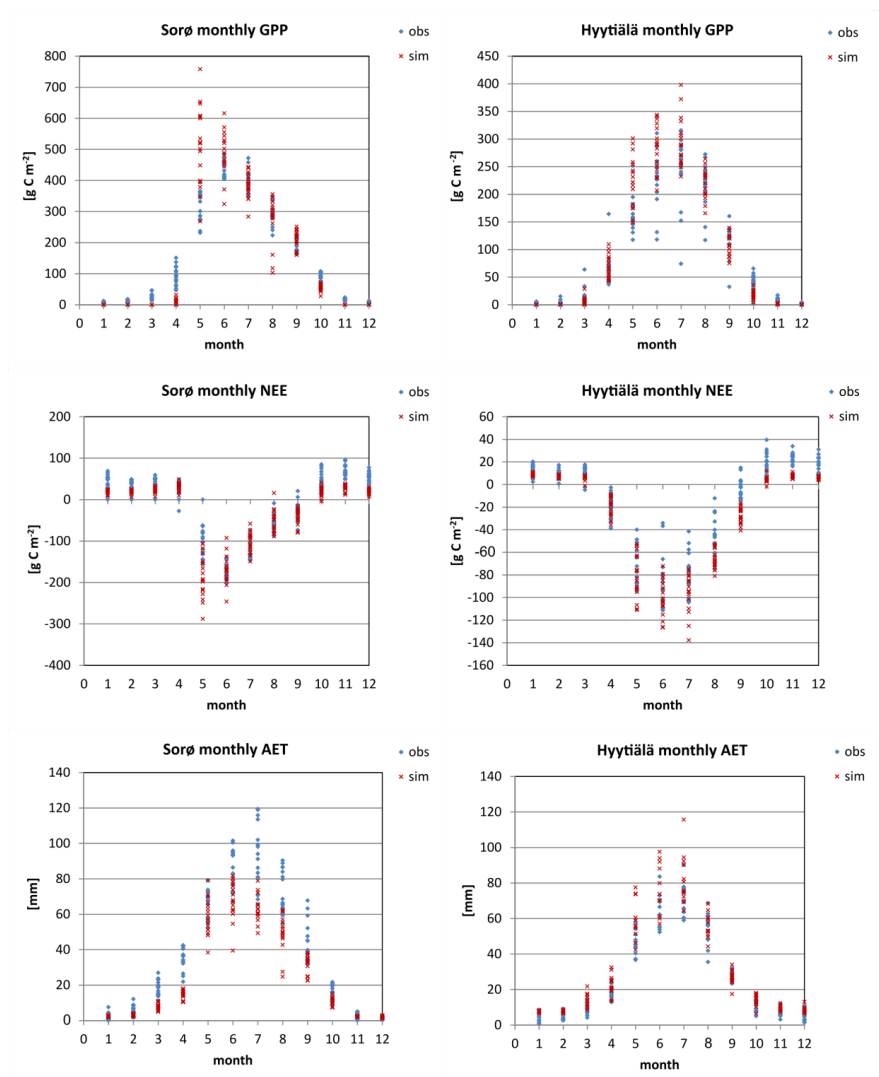
	Daily				Monthly			
Sorø	Number of days	NRMSE	ME	R ²	Number of month	NRMSE	ME	R ²
AET	6058	0.591	0.651	0.734**	199	0.508	0.745	0.884**
NEE	6058	0.691	0.522	0.601**	199	0.513	0.735	0.805**
GPP	6058	0.718	0.544	0.743**	199	0.489	0.760	0.877**
Hyytiälä								
AET	3945	0.593	0.649	0.764**	136	0.408	0.833	0.906**
NEE	6170	0.643	0.587	0.634**	220	0.514	0.734	0.855**
GPP	5398	0.507	0.743	0.814**	188	0.452	0.794	0.877**

413 *** - p<0.001



414

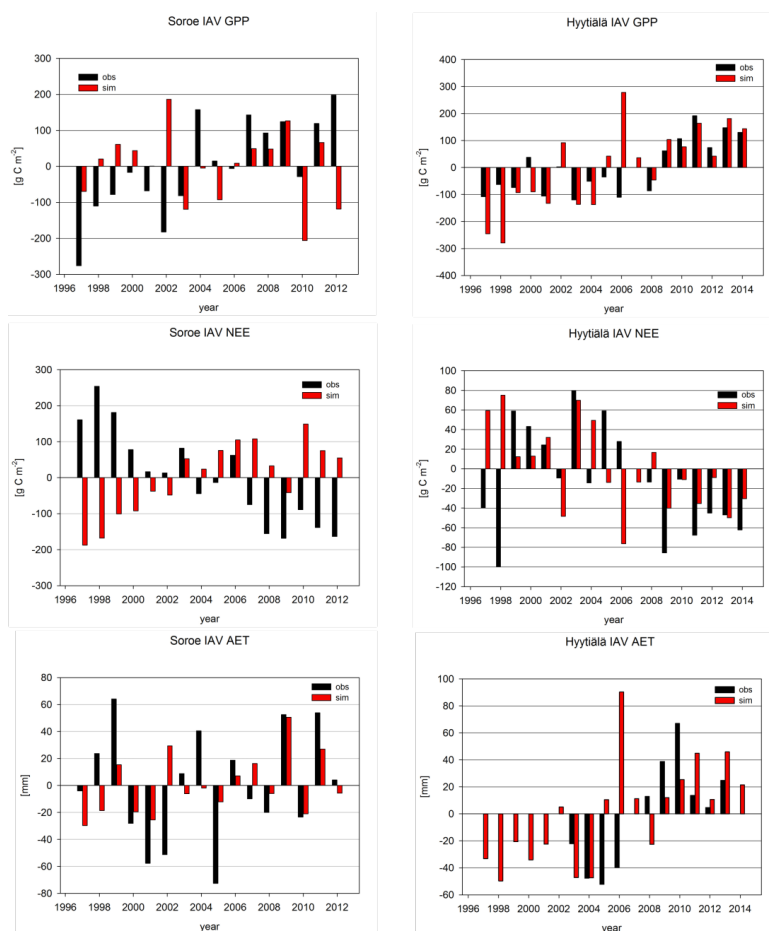
415 **Figure 6.** Simulated versus observed daily GPP, NEE and AET in Sorø (left) and Hyytiälä (right). The black line shows a 1:1
416 relationship.



417
 418 **Figure 7. Seasonal cycle of monthly GPP, NEE and AET values (obs - observed, sim - simulated) in Sorø (left) and Hyytiälä (right).**

419 3.2.2 Inter-monthly (IMV) and inter-annual variability (IAV)

420 The simulated and observed inter-annual variability is nearly in the same order of magnitude for both sites and for the three
 421 variables except for a few years for Sorø (1997: GPP, NEE) and Hyytiälä (1997-1998, GPP, 2006 AET) (Fig. 8). The signs
 422 of IAV were best captured for Hyytiälä with 82 % for GPP, 65 % for NEE and 70 % of the years for AET. In Sorø, the signs
 423 of IAV of GPP and NEE is not really captured by the model, in most of the years the signs are opposite to observed IAV
 424 except for AET (63 %).



425

426 **Figure 8. Inter-annual variability of GPP, NEE and AET (sim - simulated and obs - observed) in Sorø (left) and Hyttiälä (right).**

427 The analysis of inter-monthly variability with the normalized IMV data shows similar inter-quartile ranges for simulated and
 428 observed IMV but a clearly higher range of the IMV of GPP and NEE for Sorø (Fig. 9, left). The IMV of AET differs in the
 429 interquartile ranges for simulated and observed data but the range is similar. The simulated variables for Hyttiälä show less
 430 variability especially for NEE but also for AET (Fig. 9, right) and a smaller range of the inter-monthly variability in the case
 431 of GPP.

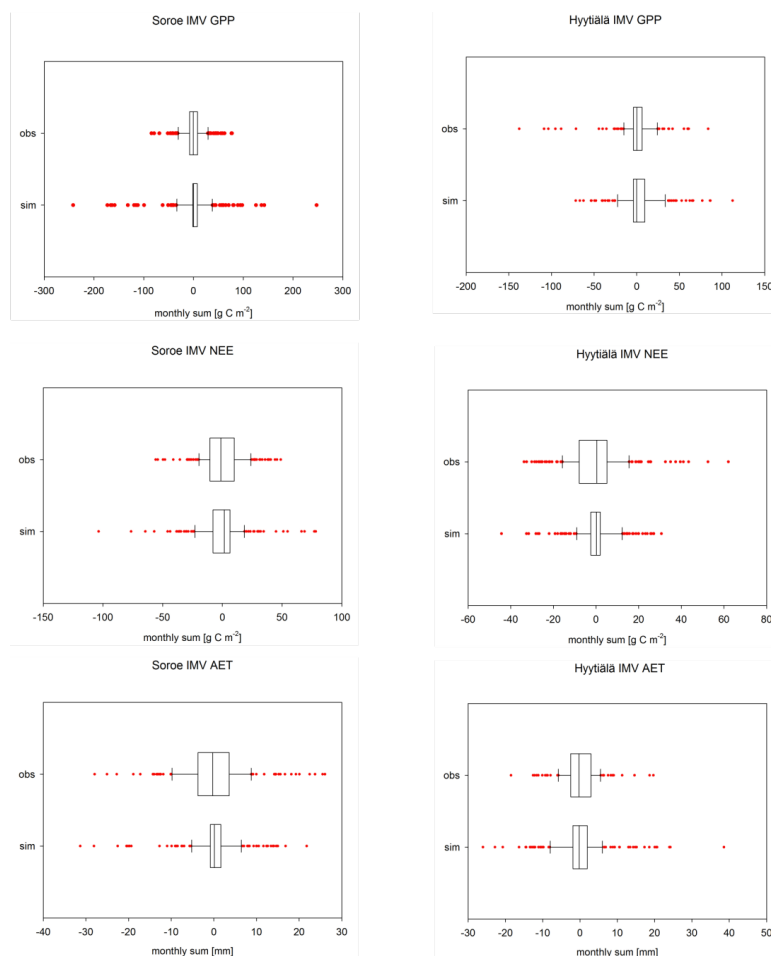


Figure 9. Distribution of the magnitude for the inter-monthly variability values (IMV) of observed (obs) and simulated (sim) monthly sums of GPP, NEE and AET in Sorø (left) and Hyytiälä (right). The graphs show the median, the 25th and 75th percentile (box), the 10th and 90th percentile (whiskers) and the outliers.

3.3 Soil temperature and water content

The simulated soil temperature (ST) fits the observed data very well in Sorø (Fig. 10, top and middle) and Hyytiälä (Fig. 11). With increasing soil depth, the bias between simulated and observed values decreases, which is reflected in a decreasing NRMSE and an increasing ME and R^2 (Table 9). This applies for the daily and monthly statistics with the statistics on monthly level being slightly better than on daily level in most cases. In Hyytiälä, the simulated soil temperature in winter is lower than the observed temperature for the years 1996 until 2005 and consequently also the simulated depth of frost (Fig. 11). In contrast, the simulation of the soil water content (SWC) is less accurate for both sites. Comparing simulated and observed soil water content for all soil layers leads to very low R^2 values and also low model efficiencies ME (Table 9). In Sorø, the model underestimates the water content in the upper mineral layer especially in winter time (Fig. 10, below). During summer, the model simulates an exhaustion of the soil water content up to the wilting point for several days and more often than observed. Altogether, the model responds to precipitation faster than indicated by measurements.

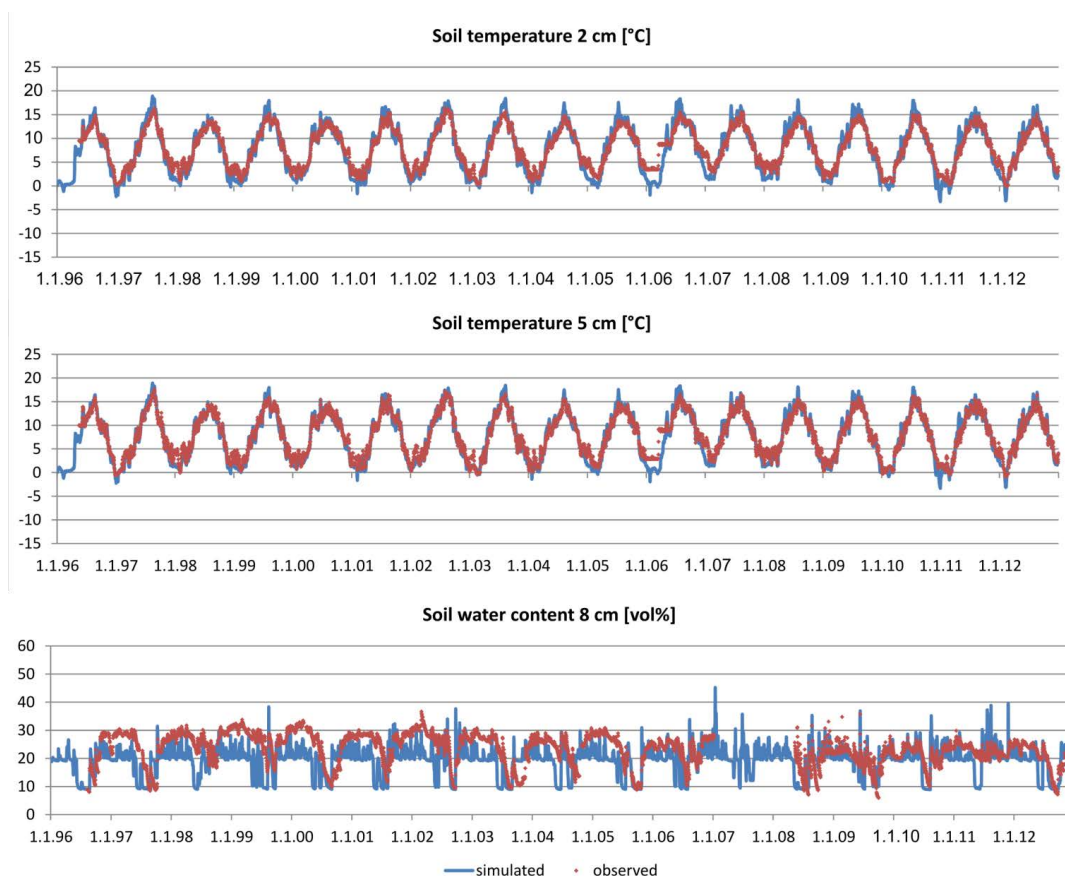
Table 9 Daily and monthly statistics of soil temperature (ST) and soil moisture (SWC), Sorø 1996-2012 and Hyytiälä (1996-2014)



Sorø	Daily				Monthly			
	Number	NRMSE	ME	R ²	Number	NRMSE	ME	R ²
ST 2 cm	6073	0.370	0.863	0.942**	199	0.169	0.887	0.959**
ST 10 cm	6073	0.283	0.920	0.951**	199	0.130	0.943	0.972**
SWC 8 cm	5645	1.175	-0.382	0.286**	183	0.261	-0.414	0.288**
Hyttälä								
ST organic layer	6828	0.338	0.886	0.914**	225	0.259	0.974	0.948**
ST 5 cm	6828	0.346	0.880	0.913**	225	0.253	0.916	0.941**
ST 18 cm	6560	0.250	0.937	0.943**	216	0.178	0.954	0.959**
ST 50 cm	6560	0.263	0.931	0.943**	216	0.167	0.947	0.958**
SWC organic layer	6438	0.978	0.043	0.167**	216	0.311	0.062	0.118**
SWC 5 cm	6438	1.196	-0.431	0.176**	216	0.328	-0.299	0.128**
SWC 18 cm	6309	0.861	0.259	0.337**	211	0.261	0.217	0.269**
SWC 50 cm	6438	0.983	0.034	0.129**	213	0.303	-0.192	0.261**

450 ** - P<0.001

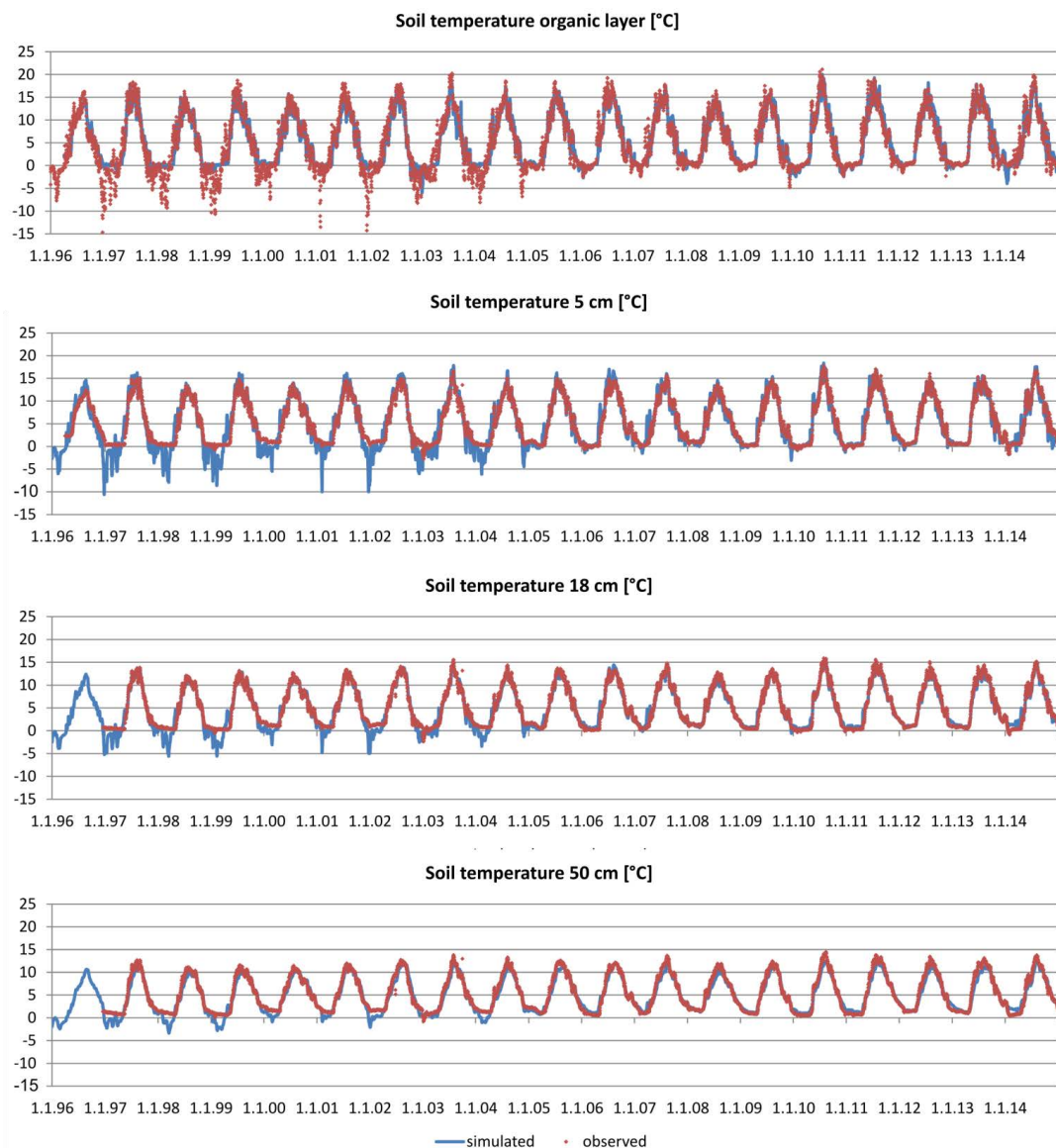
451 ns - not significant



452

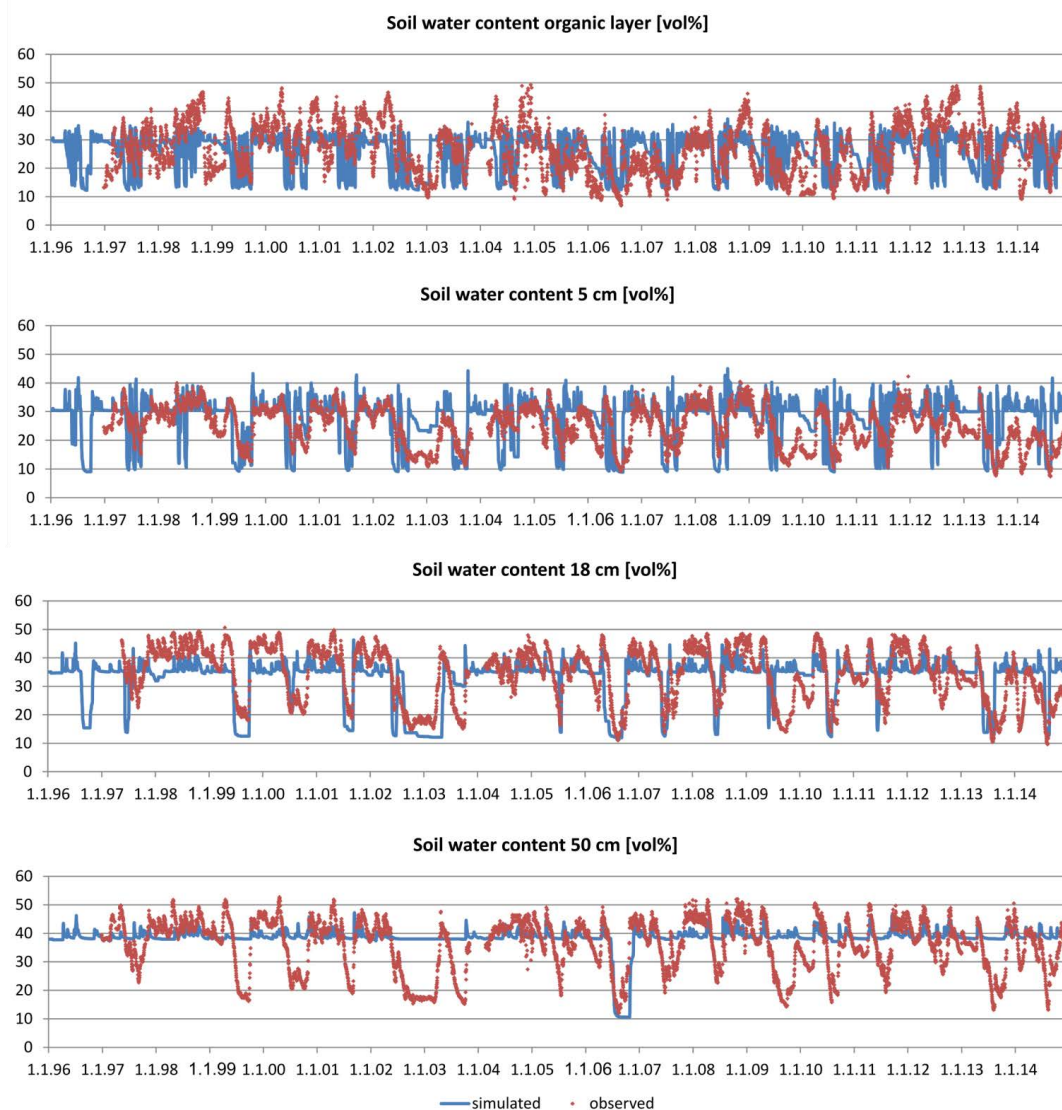
453 **Figure 10.** Time series of observed and simulated daily soil temperature at 2 cm and 10 cm depth (at the top and middle) and time
454 series of observed and simulated daily soil water content at 8 cm depth (below) in Sorø for the period 1996-2012.

455 For Hyytiälä, the results are similar (Fig. 12). The visual inspection for two layers shows a similar picture to Sorø: an
456 underestimation during winter time and a more frequent exhaustion of the soil water during summer. The observed water
457 uptake drops to a depth of 50 cm while the simulated water uptake reaches a maximum depth of 50 cm in the very dry July
458 and August of 2006 with only one third and a half of the precipitation sum of the long-term mean. The interquartile ranges
459 and the ranges of outliers of soil water content are mostly higher for the simulated values than for the measured (Fig. 13,
460 right).



461

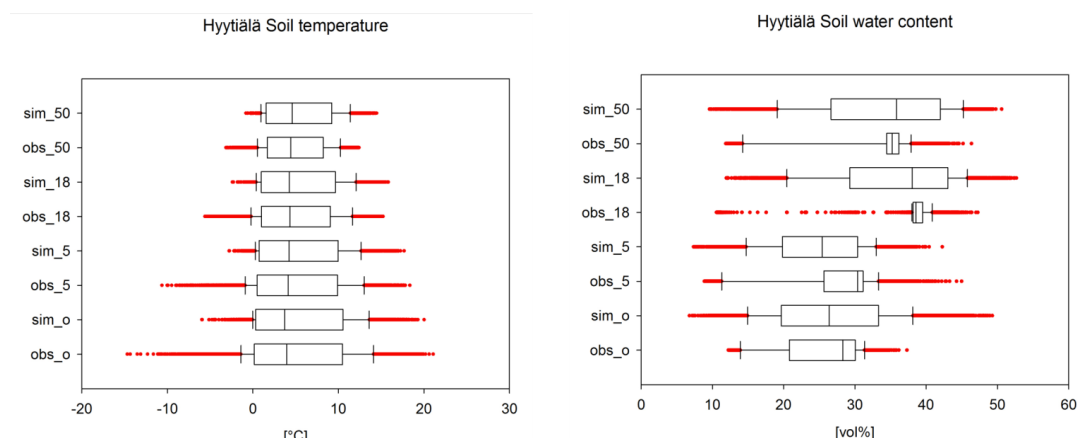
462 **Figure 11. Time series of observed and simulated daily soil temperature for the organic layer and at 5, 18, and 50 cm depth in**
 463 **Hyttälä for the period 1996-2014.**



464

465 **Figure 12 Time series of observed and simulated daily soil water content at organic layer and at 5, 18, and 50 cm depth in Hyytiälä**
466 **for the period 1996-2014.**

467



468

469 **Figure 13. Distribution of magnitude of daily soil temperature and soil water content (observed and simulated) in different soil**
 470 **layers (organic layer, layer in 5, 18, and 50 depth) in Hyytiälä. The graph shows the median, the 25th and 75th percentiles (box), the**
 471 **10th and 90th percentiles (whiskers) and the outliers.**

472 4 Discussion

473 We analyse the capability of 4C to reproduce growth, carbon and water fluxes as well as soil water content and soil
 474 temperature in different layers on different time scales and resolutions for four forest stands throughout Europe. This will
 475 also be done in light of previous evaluations in order to depict the importance of specific processes that may vary with
 476 boundary conditions, respectively site properties. Depending on data availability, not all processes can equally be judged for
 477 all sites and scales, which is a common challenge for the evaluation of complex stand-scale forest models. Yet, for each of
 478 the sites and variables we have selected here, there is clearly important information gained about the applicability of 4C

479 4.1 Evaluation of forest growth

480 Overall, the ability of 4C to reproduce the dynamics of forest growth differs clearly from site to site. 4C performs best for the
 481 mono-specific, coniferous stands Solling and Peitz independent of the evaluation metrics. In particular for Peitz, which
 482 features the longest observational time series of Scots pine growth, we observe the best agreement between model and data
 483 (Fig. 3). For Solling 4C underestimates the development of DBH (Fig. 4). Ibrom (2001) and Ellenberg et al. (1991) found
 484 similar carbon storage in this spruce stand in 1967 of 9314 g C m^{-2} initialized by 4C based on tree dimensions
 485 (10840 g C m^{-2}), indicating that basic assumptions about stem form and wood density are appropriate. Our initialization
 486 prescribes the same number of trees (595 ha^{-1}) as observed but strongly underestimates foliage (needle) mass (4C:
 487 422.5 g C m^{-2} vs. 868 g C m^{-2} found by Ellenberg et al. (1991)). We applied the fixed parameter η_s (foliage to sapwood area
 488 relationship) to estimate foliage mass, which could lead to this underestimation. Furthermore, the estimation of sapwood area
 489 from DBH used for initialization is also uncertain. Consequently, our initialization leads to a smaller leaf area index (LAI) of
 490 $5.1 \text{ m}^2 \text{ m}^{-2}$ in 1990 compared to a value of $7 \text{ m}^2 \text{ m}^{-2}$ reported by Ibrom (2001) for the same year. In 4C, the initialization of
 491 the foliage biomass as well as fine root biomass is estimated via a function depending on sapwood area and a parameter
 492 describing the foliage to sapwood area relationship. The sapwood area. Therefore, it is possible that 4C's underestimation of
 493 DBH growth is due to the underestimation of foliage biomass during initialization. While foliage is underestimated, the
 494 initialization works well for DBH. Ibrom (2001) gives the values for mean DBH (35 cm) and mean top height (28 m) which
 495 are nearly matched by 4C with a DBH of 35 cm and mean top height of 31.8 m. The initialization of height of tree cohorts
 496 uses height-diameter relationships from various yield tables which can lead to deviations in comparison to reality.



497 The quality of growth simulation in Hyytiälä differs for the two species. For Norway spruce, which is present in the
498 understorey of this pine-dominated stand, stem biomass initialization is underestimated but growth is realistic, whereas the
499 stem biomass growth of pine is slightly overestimated (Fig. 5). Due to thinning according to given stem numbers the stem
500 biomass is again overestimated after thinning because maybe other trees were harvested in the model stand as in the real
501 stand. Comparing simulated biomass data of foliage for the mixed stand Hyytiälä with measurements (personal
502 communication by Fredrik Lagergren) for the initialization year 1995 we find that pine stem biomass is in accordance with
503 measurement while spruce stem biomass is clearly underestimated (see Fig. 5).
504 Earlier model evaluation of stand dynamics for different species such as pine, spruce and beech in Germany by Lasch et al.
505 (2005); Lasch et al. (2007); Lindner et al. (2005) demonstrated a sufficient ability of the model to reproduce forest growth in
506 terms of DBH, height and biomass. Thus, while in general we have confidence in the ability of 4C to simulate forest growth,
507 it is important to keep in mind that 4C works with a site-independent species parameter set and we did not calibrate any of
508 the parameters locally. Simulating a Scots pine stand in Germany or Finland could therefore clearly differ, depending on
509 parameter uncertainty for different genera (Collalti et al., 2016). For example, trees in Finland often develop crown shapes
510 that are more adapted to reducing snow damage – this is an example for an adaptive trait that is evolutionary and is not
511 considered in the model.

512 4.2 Evaluation of carbon and water fluxes

513 We analysed the model's performance to simulate carbon and water fluxes using statistical measures on different time scales.
514 For Sorø and Hyytiälä, 4C performed best when comparing simulation results with observational data on daily and monthly
515 scales for GPP, NEE and AET (Table 8). Collalti et al. (2016) also found a better performance for their 3D-CMCC-FEM
516 model on a monthly scale for these sites.
517 For both sites, 4C overestimated GPP and underestimated NEE on long-term average. This could be caused by the simplified
518 simulation of ecosystem respiration in 4C (see section 2.1.2.3). Because organ-specific, dynamic respiration rates are hard to
519 parameterize due to a lack of data, the respiration rate in 4C is a fixed fraction of GPP following an approach of Landsberg
520 and Waring (1997). However, caution is needed as errors of flux measurements could also be a reason for deviations
521 between observed and simulated values on all time scales (e.g. Brændholt et al. (2018); Rannik et al. (2006)). The standard
522 deviations of the annual GPP are of similar magnitude for observations and simulation data, which indicates high variability
523 from year to year in both data sets. For Sorø, the standard deviations of NEE are also very high for simulated and observed
524 annual values whereas for Hyytiälä the standard deviations are of a lower order of magnitude.
525 The annual course of GPP and NEE in Sorø shows a sharp increase of GPP with the start of the vegetation period (bud burst)
526 which is faster than the simulated flushing.. For one reason, the phenological model of 4C (Schaber and Badeck, 2003;
527 Schaber, 2002) for beech was derived from long-term observational data in Germany and hence the model parameters might
528 not represent the phenology of beech in Denmark. . In fact, the 4C average generated day of bud break for 1999-2009 is
529 DOY 120, while (Pilegaard et al., 2011) found values between 118 and 134 with a mean being DOY 129. Furthermore, we
530 did not consider ground vegetation because ground vegetation implemented in 4C is not suitable for beech stands (see
531 section 2.1.3) Therefore, the simulated GPP during winter time is zero and the NEE is underestimated during this time period
532 (Fig. 7, left). The mismatches in phenology were also discussed by Collalti et al. (2016). For Sorø, Horemans et al. (2017)
533 discussed in great detail the differences between simulated and observed NEE for 4C and concluded that 4C overestimates
534 the importance of high frequency variability because 4C uses the daily temperature to redistribute the weekly calculated
535 NEE and the applied dependency is possibly too sensitive. These daily calculated values are only used for comparison
536 reasons.
537 4C simulates the AET quite well except on the annual scale. For Hyytiälä the statistics show a better correspondence of daily
538 and monthly observed and simulated AET than for Sorø, where the long-term annual amount as well as the daily AET values



are underestimated (Fig. 6, Table 8). The annual course of AET for Sorø shows a large underestimation of AET during the vegetation period in contrast to a slight overestimation at Hyytiälä (Fig. 7). At Hyytiälä Grote et al. (2011) come to a similar result for the simulation period 1996–2007 with a slightly lower R^2 . But also from January until May, before bud break, the monthly AET is underestimated in Sorø (see Supplement Fig. S3), possibly because ground vegetation is neglected in this 4C version. In the model we assume that there is no transpiration when there are no leaves. But in Sorø ground vegetation consisting of *Anemone nemorosa* L. and *Mercurialis perennis* L. exists before bud break (Pilegaard et al., 2001) and in that time the AET is underestimated clearly by the model. High values of observed AET of more than 4 mm per day show almost no correlation to radiation and only weak correlation to air temperature, but the approach of Penman-Monteith used in 4C calculates the potential evapotranspiration in dependence on radiation and air temperature. Obviously, there are other factors that influence the AET. Furthermore, the soil data for field capacity, wilting point, pore volume and percolation were only estimated by pedotransfer functions. This estimation might explain the underestimation of water supply causing the deviations in AET simulations from observations. In contrast, for Hyytiälä these data were available from measurements leading to a better simulation of AET.

Model validation with eddy covariance data is known to have some inherent problems (Medlyn et al., 2005b; Robinson et al., 2005). Therefore, we performed informal interpretation of graphs regarding the residuals (Supplement Fig. S1, S4), showing for all variables (GPP, NEE, AET) correlations to the observed and simulated data. This indicates that high simulated values of GPP and AET are overestimated at both sites. Considering the statistical measures, for instance, the good accuracy of simulated AET at the daily and monthly scale shows that the model is able to describe the day to day and seasonal variability. On one hand, the good accuracy on these scales does not imply good accuracy on an annual scale due to the nonlinear relationships between the statistical measures. On the other hand, at the annual scale more modelled processes influence the AET, GPP and NEE, in particular the length of the growing season, the ground vegetation and the tree growth (e.g. leaf area). The seasonality on an intra-annual scale is described sufficiently by the model but on the inter-annual scale the seasonality is lost due to the aggregation.

We also analysed the inter-annual variability (IAV) with so-called normalized time series indicating the variation from year to year between the observed and simulated annual values of GPP, NEE and AET. At both sites the magnitude of inter-annual variability is similar between observations and simulations for all variables except for some years (Fig. 8). The signs of the IAV differed clearly more often for Sorø than for Hyytiälä. However, for both sites the signs of simulated as well as observed GPP IAV are negative in the extremely dry year 2003 (Granier et al., 2007). For the AET this is only the case for Hyytiälä. This underlines a serious problem in simulating AET for the beech stand, due to missing consideration of ground vegetation even though the statistical measures on daily and monthly time scale are sufficiently good (Table 8).

4C reproduced IAV of GPP, NEE and AET clearly better for Hyytiälä than for Sorø. The lower performance in Sorø could be explained by the imprecise simulation of evapotranspiration and available water at Sorø which, in turn, influences the NEE via a water limitation factor.

The IAV of the observations is caused by a high number of physical, biological and anthropogenic factors affecting the photosynthesis, respiration and water fluxes of forest ecosystems (Lagergren et al. (2008)). The reproduction of the IAV by the model requires information about these factors and model approaches describing these known but often not observed factors. This deficit could also contribute to the inconsistency of the simulated IAV with the observed timing of variability (Keenan et al., 2012).

Overall, our results are in accordance with the finding of Baldocchi et al. (2018) showing from analysis of flux data a clearly higher IAV of NEE in a temperate deciduous forest than in a boreal evergreen forest. They explained the variability in ecosystem photosynthesis as the more dominant factor causing IAV in net ecosystem carbon exchange which is confirmed by our results.



Analysing the distribution of the magnitude of inter-monthly variability (IMV) for AET shows obviously smaller ranges for the observed than for the simulated IMV in Sorø but the variation of the IMV outliers is similar (Fig. 9). This result underlines the previously discussed problem of simulating evapotranspiration for the beech stand. For GPP and NEE the distribution of IMV values shows similar patterns for the inter-quartile ranges but the range of the outliers is higher for the simulated values.

For Hyytiälä the interquartile ranges of observed IMV are smaller not only for AET but also for NEE in comparison to simulated IMV. The latter could be caused by the ecosystem respiration (soil and stand). The IMV of monthly simulated NEE is clearly lower than the IMV of the observed NEE (Fig. 9) during the vegetation period. In Sorø it is the other way around (see Fig. 9). GPP shows the same pattern. We suspect that this behaviour could be caused by differences in the length of vegetation period between coniferous and deciduous species as well as different climatic conditions. Discussions about the ability of models to reproduce flux variability are hampered by the problem that flux data are subject to random error roughly in proportion to the size of flux, especially during summer (Keenan et al., 2012). Another major source of data uncertainty is related to the technique of eddy covariance measurements (Medlyn et al., 2005b). The higher observed fluxes at the deciduous forest site in this period could lead to higher random errors in the observations.

4.3 Evaluation of soil water content and soil temperature

Our results show that 4C is able to reproduce soil temperature in different depths at Sorø and Hyytiälä very well (Fig. 10 top and middle, Fig. 11). The implemented soil temperature model (Suckow, 1986) is physically based and gives trustworthy results, as former model evaluations have confirmed (e.g. Reyer et al. (2014)). The statistics of soil temperature match results obtained in a modelling study with the CoupModel in Hyytiälä (Wu et al., 2011, 2012). In Hyytiälä, 4C did not simulate a snow pack until 2005 potentially because snow cover is underestimated due to unrealistic low winter precipitation (Supplement Fig. S7). Hence the simulated soil temperature of the upper layer is much lower than the observed values and thus the freezing depth is greater than observed. Starting from 2006, winter precipitation data seem more realistic and the model simulated a snow pack leading to a much better fit of the simulated and observed soil temperatures.

The evaluation of the soil water model is more difficult. Wu et al. (2011) stated that the performance of soil moisture was poorer than soil temperature performance in their modelling study at Hyytiälä with calibrated parameters. The minimum R^2 ranges between 0.03 and 0.27 in the different soil layers and is in the same order of magnitude as in our simulations. The model is able to reproduce the intra-annual cycle of soil water content with low values during vegetation time and clearly higher values during winter time (Fig. 10 below, Fig. 12). The negative ME values for three different depths at both sites (Table 9) means that the mean square error exceeds the variance of the observed data and that the model is not consistent with the observed data. In detail, the model reproduced the lowest values during summer time in Sorø and Hyytiälä for the three upper layers caused by the water uptake of the trees, but underestimated the soil water content during winter at both sites. In Sorø the groundwater table rises in winter up to 20 cm and falls in the summer down to 2 m below the surface (Pilegaard et al., 2011). The model 4C does not consider fluctuating groundwater level and is parametrized with a constant ground water depth of 2 m at this site. Therefore the observed high water content in winter time due to the high ground water level cannot be reproduced by the simulation. In Hyytiälä the observed water uptake reaches up to a depth of 75 cm, but the simulation results show that the water uptake from the deeper layers is not needed to satisfy the simulated transpiration demand with the exception of the dry summer 2006 (Fig. 12).

The uncertainty of simulated soil water content is mainly determined by the parameterization of the soil profile and its approach to calculate the potential evapotranspiration and the water demand. The soil parameters field capacity and wilting point are hard to determine exactly for all soil layers (Supplement Table S1). Furthermore, the parameter rooting depth and the distribution of fine roots in the layers are often not accurately known, but they control the water uptake (Medlyn et al., 2011). Another component of the water balance is the ground vegetation which is not considered in the model for these two



623 sites. Former evaluation of the soil water model at other sites (e.g. ICP-Forests level II monitoring plots) achieved better
624 statistical results (Reyer et al., 2014) which may depend on the soil type, the soil parameterization and the quality of soil
625 water content measurements. A former analysis comparing the applied water uptake approach in 4C with a more process-
626 based approach indeed indicated that missing data on root length densities might be crucial (Gutsch et al., 2015b).

627 4.4 Applicability and Reliability of 4C

628 Analysing the model results for four sites across Europe, Peitz (pine), Solling (spruce), Sorø (beech) and Hyytiälä (mixed
629 pine spruce), underlines the ability of 4C to describe growth as well carbon and water fluxes at stand scale with sufficient
630 accuracy. In comparison to former evaluations of the model (Reyer et al., 2014) we not only compared observed and
631 simulated data but used further methods to analyse biases in annual and monthly variability. These methods allowed us also
632 to evaluate the ability of 4C to reproduce extreme years like 2003 as shown for GPP simulated in Hyytiälä (see section 4.2).
633 We aimed for a model which simulates forest growth in terms of height, diameter and biomass as well as the water, nitrogen
634 and carbon fluxes without any site-specific calibration. Even though uncertainties in model parametrization for all species
635 and the uncertainties in model structure contribute to partly insufficient results (Medlyn et al., 2005b) we argue that it is
636 encouraging to see how well 4C performs overall across these very different sites. In agreement with other recent studies
637 with 4C (Borys et al., 2016; Gutsch et al., 2015a; Gutsch et al., 2016), this study underlines the applicability of 4C to its
638 main research areas: (1) studies on climate impacts on managed forest ecosystems, (2) trade-off studies on forest-based
639 ecosystem services, (3) studies on forest management strategies and risk analysis, (4) carbon accounting of forest-based
640 bioenergy, and (5) studies on understanding the underlying functioning of forest ecosystems.
641 Yet our results clearly show that representation of some processes in 4C should be improved, e.g. the phenology sub-model
642 and the description of ground vegetation as an important element in the water balance. Moreover, the way respiration is
643 modelled was identified as a major uncertainty. A new model version including a non-structural carbohydrates (NSC) pool in
644 a changed allocation scheme is currently under development. This version will allow calculation of the organ-specific
645 respiration and will possibly improve the calculation of ecosystem respiration. Furthermore, by considering this pool in the
646 carbon balance the model will be able to react to biotic disturbances and will be able, e.g., to describe the effects of
647 defoliators on the forest ecosystem.
648 Parameter calibration is possible with 4C if it is supported by data, as carried out by Reyer et al. (2016) and van Oijen et al.
649 (2013). Application of generic calibration could improve model results at various stands as shown by Minunno et al. (2016)
650 by a site-specific calibration, and Peltoniemi et al. (2015) for the site Hyytiälä. Molina-Herrera et al. (2015) confirmed that
651 site-specific and multi-site calibration leads to a model parameterization that is best suited for simulating daily carbon fluxes
652 with a forest growth model (Pnet).

653 5 Conclusions

654 4C shows good performance in reproducing growth and carbon and water fluxes as well as soil temperature and water
655 content of typical European forest stands. Nevertheless, various opportunities for the improvement of model processes and
656 parameterization exist. The drought-stress effect on tree growth has to be improved and validated with tree-ring width and
657 isotope data. The discussion on tree mortality as an important demographic process (Neumann et al., 2017; Anderegg et al.,
658 2016; Manusch et al., 2012) underlines the need for improvement of mortality modelling in 4C. Further, new stand-level
659 approaches regarding light interception have been published (Forrester, 2014), which may improve the modelling of
660 vertically or horizontally diverse structured mixed forests.



A variety of species-specific parameters should be improved using the TRY database (Kattge et al., 2011) and updated phenological data. Additionally, further tree species can be parameterized using Bayesian calibration and measurement data and the TRY database if their use is necessary.

Nevertheless, the current version of 4C is applicable for a wide range of research questions related to both process-relevant aspects and adaptive management and ecosystem services. Using the PROFOUND database was helpful in proving this applicability.

Code and data availability. The detailed model description (<https://dx.doi.org/10.2312/pik.2018.006>), the model source code and the simulation results are available in the Gitlab repository <https://gitlab.pik-potsdam.de/foresee/4C>.

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6 References

- Anderegg, W. R. L., Martinez-Vilalta, J., Cailleret, M., Camarero, J. J., Ewers, B. E., Galbraith, D., Gessler, A., Grote, R., Huang, C.-y., Levick, S. R., Powell, T. L., Rowland, L., Sánchez-Salguero, R., and Trotsiuk, V.: When a Tree Dies in the Forest: Scaling Climate-Driven Tree Mortality to Ecosystem Water and Carbon Fluxes, *Ecosystems*, 1-15, doi:10.1007/s10021-016-9982-1, 2016.
- Badeck, F. W., Beese, F., Berthold, D., Einert, P., Jochheim, H., Kallweit, R., Konopatzky, A., Lasch, P., Meesenburg, H., Meiwes, K.-J., Puhlmann, M., Raspe, S., Schulte-Bisping, H., Schulz, C., and Suckow, F.: Parametrisierung, Kalibrierung und Validierung von Modellen des Kohlenstoffumsatzes in Waldökosystemen und deren Böden, Bayerische Landesanstalt für Wald und Forstwirtschaft (LWF), Institut für Bodenkunde und Waldernährung der Universität Göttingen (IBW), Landesforstanstalt Eberswalde (LFE), Leibniz-Zentrum für Agrarlandschaftsforschung (ZALF), Nordwestdeutsche Forstliche Versuchsanstalt (NW-FVA), Potsdam-Institut für Klimafolgenforschung (PIK), 110, 2007.
- Baldocchi, D., Chu, H., and Reichstein, M.: Inter-annual variability of net and gross ecosystem carbon fluxes: A review, *Agric. For. Meteorol.*, 249, 520-533, doi:10.1016/j.agrformet.2017.05.015, 2018.



- 702 Berninger, F., Coll, L., Vanninen, P., Mäkelä, A., Palmroth, S., and Nikinmaa, E.: Effects of tree size and position on pipe
703 model ratios in Scots pine, Canadian Journal Of Forest Research-Revue Canadienne De Recherche Forestiere, 35, 1294-
704 1304, doi:10.1139/X05-055, 2005.
- 705 Borys, A., Lasch, P., Suckow, F., and Reyer, C.: Kohlenstoffspeicherung in Buchenbeständen in Abhängigkeit von
706 Waldpflege und Klimawandel, Allg. Forst- u. J.-Ztg., 184, 26-35, 2013.
- 707 Borys, A., Suckow, F., Reyer, C., Gutsch, M., and Lasch-Born, P.: The impact of climate change under different thinning
708 regimes on carbon sequestration in a German forest district, Mitig Adapt Strateg Glob Change, 21, 861-881,
709 doi:10.1007/s11027-014-9628-6, 2016.
- 710 Botkin, D.: Forest Dynamics: An Ecological Model, Oxford University Press, Oxford & New York, 309 pp., 1993.
- 711 Brændholt, A., Ibrom, A., Larsen, K. S., and Pilegaard, K.: Partitioning of ecosystem respiration in a beech forest, Agric.
712 For. Meteorol., 252, 88-98, doi:10.1016/j.agrformet.2018.01.012, 2018.
- 713 Bugmann, H., Grote, R., Lasch, P., Lindner, M., and Suckow, F.: A new forest gap model to study the effects of
714 environmental change on forest structure and functioning, in: Impacts of Global Change of Tree Physiology and Forest
715 Ecosystem. Proceedings of the International Conference on Impacts of Global Change on Tree Physiology and Forest
716 Ecosystems, held 26-29 November 1996, Wageningen, edited by: Mohren, G. M. J., Kramer, K., and Sabate, S., Forestry
717 Science, Kluwer Academic Publisher, Dordrecht, 255-261, 1997.
- 718 Cameron, D. R., Van Oijen, M., Werner, C., Butterbach-Bahl, K., Grote, R., Haas, E., Heuvelink, G. B. M., Kiese, R., Kros,
719 J., Kuhnert, M., Leip, A., Reinds, G. J., Reuter, H. I., Schelhaas, M. J., De Vries, W., and Yeluripati, J.: Environmental
720 change impacts on the C- and N-cycle of European forests: a model comparison study, Biogeosciences, 10, 1751-1773,
721 doi:10.5194/bg-10-1751-2013, 2013.
- 722 Collalti, A., Marconi, S., Ibrom, A., Trotta, C., Anav, A., D'Andrea, E., Matteucci, G., Montagnani, L., Gielen, B.,
723 Mammarella, I., Grunwald, T., Knohl, A., Berninger, F., Zhao, Y., Valentini, R., and Santini, M.: Validation of 3D-CMCC
724 Forest Ecosystem Model (v.5.1) against eddy covariance data for 10 European forest sites, Geosci. Model Dev., 9, 479-504,
725 doi:10.5194/gmd-9-479-2016, 2016.
- 726 Collatz, G. J., Ball, J. T., Grivet, C., and Berry, J. A.: Physiological and Environmental-Regulation of Stomatal Conductance,
727 Photosynthesis and Transpiration - a Model That Includes a Laminar Boundary-Layer, Agric. For. Meteorol., 54, 107-136,
728 doi:10.1016/0168-1923(91)90002-8, 1991.
- 729 Constable, J. V. H., and Friend, A. L.: Suitability of process-based tree growth models for addressing tree response to
730 climate change, Environmental Pollution, 110, 47-59, doi:10.1016/S0269-7491(99)00289-4, 2000.
- 731 Davidson, R. L.: Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover, Ann.
732 Bot., 33, 561-569, doi:10.1093/oxfordjournals.aob.a084308, 1969.
- 733 Dietze, M. C., and Matthes, J. H.: A general ecophysiological framework for modelling the impact of pests and pathogens on
734 forest ecosystems, Ecol. Lett., 17, 1418-1426, doi:10.1111/ele.12345, 2014.
- 735 DVWK: Ermittlung der Verdunstung von Land- und Wasserflächen, DVWK - Merkblätter zur Wasserwirtschaft, edited by:
736 Deutscher Verband für Wasserwirtschaft und Kulturbau e. V., Wirtschafts- und Verlagsgesellschaft Gas und Wasser mbH
737 Bonn, Bonn, 134 pp., 1996.
- 738 Dyck, S., and Peschke, G.: Grundlagen der Hydrologie, 3 ed., Verlag für Bauwesen GmbH, Berlin, 536 pp., 1995.
- 739 Eggers, T.: The impacts of manufacturing and utilization of wood products on the European carbon budget, European Forest
740 Institute, Joensuu, Internal report 9 9, 90, 2002.
- 741 Ellenberg, M., Mayer, R., and Schauermaun, J. (Eds.): Ökosystemforschung, Ergebnisse des Sollingprojekts. 1966 - 1986. ,
742 Ulmer Eugen Verlag, 1991.
- 743 Farquhar, G. D., Caemmerer, S. V., and Berry, J. A.: A Biochemical-Model of Photosynthetic CO₂ Assimilation in Leaves of
744 C-3 Species, Planta, 149, 78-90, doi:10.1007/BF00386231, 1980.



- 745 Fontes, L., Bontemps, J.-D., Bugmann, H., van Oijen, M., Gracia, C. A., Kramer, K., Lindner, M., Rötzer, T., and
746 Skovsgaard, J. P.: Models for supporting forest management in a changing environment, *For. Syst.*, 19, 8-9, 2010.
- 747 Forrester, D. I.: A stand-level light interception model for horizontally and vertically heterogeneous canopies, *Ecological*
748 *Modelling*, 276, 14-22, doi:10.1016/j.ecolmodel.2013.12.021, 2014.
- 749 Fürstenau, C., Badeck, F., Lasch, P., Lexer, M., Lindner, M., Mohr, P., and Suckow, F.: Multiple-use forest management in
750 consideration of climate change and the interests of stakeholder groups, *European Journal of Forest Research*, 126, 225-239,
751 doi:10.1007/s10342-006-0114-x, 2007.
- 752 Granier, A., Reichstein, M., Breda, N., Janssens, I. A., Falge, E., Ciais, P., Grunwald, T., Aubinet, M., Berbigier, P.,
753 Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Kostner, B.,
754 Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer,
755 M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., and
756 Wang, Q.: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year:
757 2003, *Agric. For. Meteorol.*, 143, 123-145, doi:10.1016/j.agrformet.2006.12.004, 2007.
- 758 Grote, R., and Suckow, F.: Integrating dynamic morphological properties into forest growth modeling. I. Effects on water
759 balance and gas exchange, *For. Ecol. Manage.*, 112, 101-119, doi:10.1016/S0378-1127(98)00329-6, 1998.
- 760 Grote, R., Suckow, F., and Bellmann, K.: Modelling of carbon-, nitrogen-, and water balances in pine stands under changing
761 air pollution and deposition, in: *Changes of Atmospheric Chemistry and Effects on Forest Ecosystems. A Roof Experiment*
762 *Without Roof*, edited by: Hüttel, R. F., and Bellmann, K., *Nutrients in Ecosystems*, Kluwer, Dordrecht, 251-281, 1998.
- 763 Grote, R., Korhonen, J., and Mammarella, I.: Challenges for evaluating process-based models of gas exchange at forest sites
764 with fetches of various species, *For. Syst.*, 20, 389-406, doi:10.5424/fs/20112003-11084, 2011.
- 765 Gutsch, M., Lasch-Born, P., Lüttger, A. B., Suckow, F., Murawski, A., and Pilz, T.: Uncertainty of biomass contributions
766 from agriculture and forestry to renewable energy resources under climate change, *Meteorologische Zeitschrift*, 24, 1-11,
767 doi: 10.1127/metz/2015/0532, 2015a.
- 768 Gutsch, M., Lasch-Born, P., Suckow, F., and Reyer, C.: Modeling of Two Different Water Uptake Approaches for Mono-
769 and Mixed-Species Forest Stands, *Forests*, 6, 2125-2147, doi:10.3390/f6062125, 2015b.
- 770 Gutsch, M., Lasch-Born, P., Suckow, F., and Reyer, C. P. O.: Evaluating the productivity of four main tree species in
771 Germany under climate change with static reduced models, *Annals of Forest Science*, 73, 401-410, doi:10.1007/s13595-015-
772 0532-3, 2016.
- 773 Gutsch, M., Lasch-Born, P., Kollas, C., Suckow, F., and Reyer, C. O. P.: Balancing trade-offs between ecosystem services in
774 Germany's forests under climate change., *Environmental Research Letters*, 13, 045012, doi:10.1088/1748-9326/aab4e5,
775 2018.
- 776 Haataja, J., and Vesala, T. (Eds.): *SMEAR II. Station for measuring forest ecosystem - atmosphere relation*, University of
777 Helsinki, Department of Forest Ecology, Helsinki, 1997.
- 778 Hauskeller-Bullerjahn, K.: *Wachstum junger Eichen unter Schirm*, Forschungszentrum Waldökosysteme der Universität
779 Göttingen, Göttingen, *Berichte des Forschungszentrums Waldökosysteme, Reihe A Bd. 147*, 1997.
- 780 Haxeltine, A., and Prentice, I. C.: BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological
781 constraints, resource availability and competition among plant functional types, *Global Biogeochemical Cycles*, 10, 693-709,
782 doi:10.1029/96GB02344, 1996a.
- 783 Haxeltine, A., and Prentice, I. C.: A general model for the light-use efficiency of primary production, *Functional Ecology*,
784 10, 551-561, doi:10.2307/2390165, 1996b.
- 785 Hoch, G., Richter, A., and Körner, C.: Non-structural carbon compounds in temperate forest trees, *Plant, Cell &*
786 *Environment*, 26, 1067-1081, doi:10.1046/j.0016-8025.2003.01032.x, 2003.



- 787 Horemans, J., A., Henrot, A., Delire, C., Kollas, C., Lasch-Born, P., Reyer, C., Suckow, F., François, L., and Ceulemans, R.:
788 Combining multiple statistical methods to evaluate the performance of process-based vegetation models across three forest
789 stands, *Central European Forestry Journal*, 63, 153-172, doi:10.1515/forj-2017-0025, 2017.
- 790 Ibrom, A.: Die biophysikalische Steuerung der Kohlenstoffbilanz in einem Fichtenbestand im Solling, Habilitationsschrift,
791 Berichte des Forschungszentrums Waldökosysteme der Universität Göttingen, Reihe A, 236 Seiten, 2001.
- 792 Jansson, P.-E.: Simulation model for soil water and heat conditions. Description of the SOIL model, Report, Swedish
793 University of Agricultural Sciences, Department of Soil Sciences, Division of Agricultural Hydraulics, Uppsala, 1991.
- 794 Karjalainen, T., S., K., and A., P.: Role of wood-based products in absorbing atmospheric carbon, *Silva Fennica*, 28, 67-80,
795 1994.
- 796 Kartschall, T., Döring, P., and Suckow, F.: Simulation of Nitrogen, Water and Temperature Dynamics in Soil, *Syst. Anal.*
797 *Model. Simul.*, 7, 33-40, 1990.
- 798 Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J.,
799 Cornelissen, J. H. C., Violle, C., Harrison, S. P., van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A.,
800 Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond,
801 W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin, F. S., Chave, J., Coomes,
802 D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F.,
803 Fang, J., Fernandez-Mendez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M.,
804 Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A.,
805 Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kuhn, I., Kurokawa, H.,
806 Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusia, J., Louault, F., Ma, S., Mahecha,
807 M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., Muller, S. C., Nadrowski, K., Naeem, S.,
808 Niinemets, U., Nollert, S., Nuske, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordonez, J., Overbeck, G.,
809 Ozinga, W. A., Patino, S., Paula, S., Pausas, J. G., Penuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod,
810 P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negre, B., Sardans, J., Shiodera, S.,
811 Shipley, B., Siefert, A., Sosinski, E., Soussana, J. F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M.,
812 Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., and Wirth, C.: TRY - a global database
813 of plant traits, *Global Change Biology*, 17, 2905-2935, doi:10.1111/j.1365-2486.2011.02451.x, 2011.
- 814 Keane, R. E., Morgan, P., and Running, S. W.: FIRE-BGC - A mechanistic ecological process model for simulating fire
815 succession on coniferous forest landscapes of the northern Rocky Mountains, United States Department of Agriculture,
816 Forest Service, Intermountain Research Station, Ogden, UT, Research Paper INT-RP-484, 1996.
- 817 Keenan, T. F., Baker, I., Barr, A., Ciais, P., Davis, K., Dietze, M., Dragoni, D., Gough, C. M., Grant, R., Hollinger, D.,
818 Hufkens, K., Poulter, B., McCaughey, H., Raczka, B., Ryu, Y., Schaefer, K., Tian, H., Verbeeck, H., Zhao, M., and
819 Richardson, A. D.: Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO₂ exchange,
820 *Global Change Biology*, 18, 1971-1987, doi:10.1111/j.1365-2486.2012.02678.x, 2012.
- 821 Kingston, D. G., Todd, M. C., Taylor, R. G., Thompson, J. R., and Arnell, N. W.: Uncertainty in the estimation of potential
822 evapotranspiration under climate change, *Geophysical Research Letters*, 36, doi:10.1029/2009GL040267, 2009.
- 823 Kint, V., Lasch, P., Lindner, M., and Muys, B.: Multipurpose conversion management of Scots pine towards mixed oak-
824 birch stands--A long-term simulation approach, *For. Ecol. Manage.*, 257, 199-214, doi:10.1016/j.foreco.2008.08.031, 2009.
- 825 Koitzsch, R., and Günther, R.: Modell zur ganzjährigen Simulation der Verdunstung und der Bodenfeuchte
826 landwirtschaftlicher Nutzflächen mit und ohne Bewuchs, *Arch. Acker- Pflanzenbau Bodenkd*, 34, 803-810, 1990.
- 827 Kollas, C., Gutsch, M., Hommel, R., Lasch-Born, P., and Suckow, F.: Mistletoe-induced growth reductions at the forest
828 stand scale, *Tree Physiol*, 38, 1-10, doi:10.1093/treephys/tpx150, 2018.



- 829 Kramer, K., Leinonen, I., Bartelink, H. H., Berbigier, P., Borghetti, M., Bernhofer, C., Cienciala, E., Dolman, A. J., Froer,
830 O., Gracia, C. A., Granier, A., Grunwald, T., Hari, P., Jans, W., Kellomäki, S., Loustau, D., Magnani, F., Markkanen, T.,
831 Matteucci, G., Mohren, G. M. J., Moors, E., Nissinen, A., Peltola, H., Sabate, S., Sanchez, A., Sontag, M., Valentini, R., and
832 Vesala, T.: Evaluation of six process-based forest growth models using eddy-covariance measurements of CO₂ and H₂O
833 fluxes at six forest sites in Europe, *Global Change Biology*, 8, 213-230, doi:10.1046/j.1365-2486.2002.00471.x, 2002.
- 834 Lagergren, F., Lindroth, A., Dellwik, E., Ibrom, A., Lankreijer, H., Launiainen, S., MÖLder, M., Kolari, P., Pilegaard, K. I.
835 M., and Vesala, T.: Biophysical controls on CO₂ fluxes of three Northern forests based on long-term eddy covariance data,
836 *Tellus B*, 60, 143-152, doi:10.1111/j.1600-0889.2006.00324.x, 2008.
- 837 Landsberg, J.: Modelling forest ecosystems: state of the art, challenges, and future directions, *Canadian Journal of Forest*
838 *Research-Revue Canadienne De Recherche Forestiere*, 33, 385-397, 2003.
- 839 Landsberg, J. J., and Waring, R. H.: A Generalised Model of Forest Productivity Using Simplified Concepts of Radiation-
840 Use Efficiency, Carbon Balance and Partitioning, *Forest Ecology & Management*, 95, 209-228, doi:10.1016/S0378-
841 1127(97)00026-1, 1997.
- 842 Lasch-Born, P., Suckow, F., Gutsch, M., Reyer, C., Hauf, Y., Murawski, A., and Pilz, T.: Forests under climate change:
843 potential risks and opportunities, *Meteorologische Zeitschrift*, 24, 157-172, doi:10.1127/metz/2014/0526, 2015.
- 844 Lasch-Born, P., Suckow, F., Badeck, F.-W., Schaber, J., Bugmann, H., Fürstenau, C., Gutsch, M., Kollas, C., and Reyer, C.
845 P. O.: 4C model description, PIK, Potsdam, 133, <https://dx.doi.org/10.2312/pik.2018.006>, 2018.
- 846 Lasch, P., Badeck, F.-W., Lindner, M., and Suckow, F.: Sensitivity of simulated forest growth to changes in climate and
847 atmospheric CO₂, *Forstwiss. Centralblatt*, 121, Supplement 1, 155-171, 2002.
- 848 Lasch, P., Badeck, F. W., Suckow, F., Lindner, M., and Mohr, P.: Model-based analysis of management alternatives at stand
849 and regional level in Brandenburg (Germany), *For. Ecol. Manage.*, 207, 59-74, doi:10.1016/j.foreco.2004.10.034, 2005.
- 850 Lasch, P., Suckow, F., and Badeck, F.-W.: Analyses of forest ecosystems' response to climate change at level II monitoring
851 sites, in: *Symposium: Forests in a Changing Environment - Results of 20 years ICP Forests Monitoring Göttingen*, 25.-
852 28.10.2006, edited by: Eichhorn, J., *Schriften aus der Forstlichen Fakultät der Universität Göttingen und der*
853 *Nordwestdeutschen Forstlichen Versuchsanstalt*, J.D. Sauerländer's Verlag Frankfurt am Main, Göttingen, 136-141, 2007.
- 854 Lasch, P., Kollas, C., Rock, J., and Suckow, F.: Potentials and impacts of short-rotation coppice plantation with aspen in
855 Eastern Germany under conditions of climate change, *Reg Environ Change*, 10, 83-94, doi:10.1007/s10113-009-0095-7,
856 2010.
- 857 Lindner, M.: Developing adaptive forest management strategies to cope with climate change, *Tree Physiol.*, 20, 299-307,
858 doi:10.1093/treephys/20.5-6.299, 2000.
- 859 Lindner, M., Lasch, P., Badeck, F.-W., Beguiristain, P. P., Junge, S., Kellomäki, S., Peltola, H., Gracia, C., Sabate, S., Jäger,
860 D., Lexer, M., and Freeman, M.: Chapter 4: *SilviStrat Model Evaluation Exercises*, in: *Management of European Forests*
861 *under Changing Climatic Conditions*, edited by: Kellomäki, S., and Leinonen, S., University of Joensuu, Faculty of
862 *Forestry*, Joensuu, 117-157, 2005.
- 863 Loague, K., and Green, R. E.: Statistical and graphical methods for evaluating solute transport models: Overview and
864 application, *Journal of Contaminant Hydrology*, 7, 51, doi:10.1016/0169-7722(91)90038-3, 1991.
- 865 Mäkelä, A.: Modeling structural-functional relationships in whole-tree growth: resource allocation, in: *Process modeling of*
866 *forest growth responses to environmental stress*, edited by: Dixon, R. K., Meldahl, R. S., Ruark, G. A., and Warren, W. G.,
867 *Timber Press*, Portland, Oregon, 81-95, 1990.
- 868 Mäkelä, A., Landsberg, J., Ek, A. R., Burk, T. E., Ter-Mikaelian, M., Agren, G. I., Oliver, C. D., and Puttonen, P.: Process-
869 based models for forest ecosystem management: current state of the art and challenges for practical implementation, *Tree*
870 *Physiol.*, 20, 289-298, 2000a.



- 871 Mäkelä, A., Sievänen, R., Lindner, M., and Lasch, P.: Application of volume growth and survival graphs in the evaluation of
872 four process-based forest growth models, *Tree Physiol.*, 20, 347-355, doi:10.1093/treephys/20.5-6.347, 2000b.
- 873 Manusch, C., Bugmann, H., Heiri, C., and Wolf, A.: Tree mortality in dynamic vegetation models - A key feature for
874 accurately simulating forest properties, *Ecological Modelling*, 243, 101-111, doi:10.1016/j.ecolmodel.2012.06.008, 2012.
- 875 Mayer, D. G., and Butler, D. G.: Statistical Validation, *Ecological Modelling*, 68, 21-32, doi:10.1016/0304-3800(93)90105-
876 2, 1993.
- 877 Medlyn, B. E., Berbigier, P., Clement, R., Grelle, A., Loustau, D., Linder, S., Wingate, L., Jarvis, P. G., Sigurdsson, B. D.,
878 and McMurtrie, R. E.: Carbon balance of coniferous forests growing in contrasting climates: Model-based analysis, *Agric.*
879 *For. Meteorol.*, 131, 97-124, doi:10.1016/j.agrformet.2005.05.004, 2005a.
- 880 Medlyn, B. E., Robinson, A. P., Clement, R., and McMurtrie, R. E.: On the validation of models of forest CO₂ exchange
881 using eddy covariance data: some perils and pitfalls, *Tree Physiol.*, 25, 839-857, doi:10.1093/treephys/25.7.839, 2005b.
- 882 Medlyn, B. E., Duursma, R. A., and Zeppel, M. J. B.: Forest productivity under climate change: a checklist for evaluating
883 model studies, *Wiley Interdisciplinary Reviews: Climate Change*, 2, 332-355, doi:10.1002/wcc.108, 2011.
- 884 Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J. F., Matsumoto, K., Montzka, S. A.,
885 Raper, S. C. B., Riahi, K., Thomson, A., Velders, G. J. M., and van Vuuren, D. P. P.: The RCP greenhouse gas
886 concentrations and their extensions from 1765 to 2300, *Clim. Change*, 109, 213-241, doi:10.1007/s10584-011-0156-z, 2011.
- 887 Minunno, F., Peltoniemi, M., Launiainen, S., Aurela, M., Lindroth, A., Lohila, A., Mammarella, I., Minkinen, K., and
888 Mäkelä, A.: Calibration and validation of a semi-empirical flux ecosystem model for coniferous forests in the Boreal region,
889 *Ecological Modelling*, 341, 37-52, doi:10.1016/j.ecolmodel.2016.09.020, 2016.
- 890 Molina-Herrera, S., Grote, R., Santabárbara-Ruiz, I., Kraus, D., Klatt, S., Haas, E., Kiese, R., and Butterbach-Bahl, K.:
891 Simulation of CO₂ Fluxes in European Forest Ecosystems with the Coupled Soil-Vegetation Process Model
892 "LandscapeDNDC", *Forests*, 6, 1779-1809, doi:10.3390/f6061779, 2015.
- 893 Monsi, M., and Saeki, T.: On the Factor Light in Plant Communities and its Importance for Matter Production, *Annals of*
894 *Botany*, 95, 549-567, doi:10.1093/aob/mci052, 2005.
- 895 Monteith, J. L., and Unsworth, M. H.: Principles of environmental physics, second ed., Edward Arnold, London, 1990.
- 896 Nakicenovic, N.: Greenhouse gas emissions scenarios, *Technological Forecasting and Social Change*, 65, 149-166,
897 doi:10.1016/s0040-1625(00)00094-9, 2000.
- 898 Neumann, M., Mues, V., Moreno, A., Hasenauer, H., and Seidl, R.: Climate variability drives recent tree mortality in
899 Europe, *Global Change Biology*, 23, 4788-4797, doi:10.1111/gcb.13724, 2017.
- 900 Peltoniemi, M., Pulkkinen, M., Aurela, M., Pumpanen, J., Kolari, P., and Makela, A.: A semi-empirical model of boreal-
901 forest gross primary production, evapotranspiration, and soil water - calibration and sensitivity analysis, *Boreal Environ.*
902 *Res.*, 20, 151-171, 2015.
- 903 Pilegaard, K., Hummelshøj, P., Jensen, N. O., and Chen, Z.: Two years of continuous CO₂ eddy-flux measurements over a
904 Danish beech forest, *Agric. For. Meteorol.*, 107, 29-41, doi:10.1016/s0168-1923(00)00227-6, 2001.
- 905 Pilegaard, K., Ibrom, A., Courtney, M. S., Hummelshøj, P., and Jensen, N. O.: Increasing net CO₂ uptake by a Danish beech
906 forest during the period from 1996 to 2009, *Agric. For. Meteorol.*, 151, 934-946, doi:10.1016/j.agrformet.2011.02.013, 2011.
- 907 Porte, A., and Bartelink, H. H.: Modelling mixed forest growth: a review of models for forest management, *Ecological*
908 *Modelling*, 150, 141-188, doi:10.1016/S0304-3800(01)00476-8, 2002.
- 909 Post, J., Krysanova, V., Suckow, F., Mirschel, W., Rogasik, J., and Merbach, I.: Integrated ecohydrological modelling of soil
910 organic matter dynamics for the assessment of environmental change impacts in meso- to macro-scale river basins,
911 *Ecological Modelling*, 206, 93-109, doi:10.1016/j.ecolmodel.2007.03.028, 2007.
- 912 Pretzsch, H., Grote, R., Reineking, B., Rotzer, T., and Seifert, S.: Models for forest ecosystem management: A European
913 perspective, *Annals Of Botany*, 101, 1065-1087, doi:10.1093/aob/mcm246, 2008.



- 1914 Pretzsch, H.: Forest Dynamics, Growth and Yield, Springer Berlin, Germany, 664 pp., 2010.
- 1915 Priestley, C. H. B., and Taylor, R. J.: On the assessment of surface heat flux and evaporation using large-scale parameters,
- 1916 Monthly weather review, 100, 81-92, doi:10.1175/1520-0493(1972)100<0081:OTAOSH>2.3.CO;2, 1972.
- 1917 Rannik, Ü., Kolari, P., Vesala, T., and Hari, P.: Uncertainties in measurement and modelling of net ecosystem exchange of a
- 1918 forest, Agric. For. Meteorol., 138, 244-257, doi:10.1016/j.agrformet.2006.05.007, 2006.
- 1919 Reyer, C., Lasch, P., Mohren, G. M. J., and Sterck, F. J.: Inter-specific competition in mixed forests of Douglas-fir
- 1920 (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change - a model-based analysis, Annals Of
- 1921 Forest Science, 67, doi:10.1051/forest/2010041, 2010.
- 1922 Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., and Pilz, T.: Projections of regional changes in forest net
- 1923 primary productivity for different tree species in Europe driven by climate change and carbon dioxide, Annals Of Forest
- 1924 Science, 71, 211-225, doi:10.1007/s13595-013-0306-8, 2014.
- 1925 Reyer, C.: Forest Productivity Under Environmental Change—a Review of Stand-Scale Modeling Studies, Curr Forestry
- 1926 Rep, 1-16, doi:10.1007/s40725-015-0009-5, 2015.
- 1927 Reyer, C. P. O., Flechsig, M., Lasch-Born, P., and van Oijen, M.: Integrating parameter uncertainty of a process-based
- 1928 model in assessments of climate change effects on forest productivity, Clim. Change, 137, 395-409, doi:10.1007/s10584-
- 1929 016-1694-1, 2016.
- 1930 Robinson, A. P., Duursma, R. A., and Marshall, J. D.: A regression-based equivalence test for model validation: shifting the
- 1931 burden of proof, Tree Physiol., 25, 903-913, doi:10.1093/treephys/25.7.903, 2005.
- 1932 Russ, A., and Riek, W.: Pedotransferfunktionen zur Ableitung der nutzbaren Feldkapazität – Validierung für Waldböden des
- 1933 nordostdeutschen Tieflands, Waldökologie, Landschaftsforschung und Naturschutz, 5-17, 2011.
- 1934 Schaber, J.: Phenology in Germany in the 20th century: methods, analyses and models, Math.-Nat. Fakultät, Universität
- 1935 Potsdam, Potsdam, 164 pp., 2002.
- 1936 Schaber, J., and Badeck, F.-W.: Physiology based phenology models for forest tree species in Germany, Intern. J.
- 1937 Biometeorol., 47, 193-201, doi:10.1007/s00484-003-0171-5, 2003.
- 1938 Schall, P.: Ein Ansatz zur Modellierung der Naturverjüngungsprozesse im Bergmischwald der östlichen bayrischen Alpen,
- 1939 Forschungszentrum Waldökosysteme, GöttingenReihe A Bd 155, 1998.
- 1940 Seidl, R., Rammer, W., Lasch, P., Badeck, F. W., and M.J., L.: Does conversion of even-aged, secondary coniferous forest
- 1941 affect carbon sequestration? A simulation study under changing environmental conditions, Silva Fennica, 42, 369-386,
- 1942 doi:10.14214/sf.243, 2008.
- 1943 Seidl, R., Fernandes, P. M., Fonseca, T. F., Gillet, F., Jönsson, A. M., Merganicová, K., Netherer, S., Arpaci, A., Bontemps,
- 1944 J.-D., Bugmann, H., González-Olabarria, J. R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J., and Mohren, F.:
- 1945 Modelling natural disturbances in forest ecosystems: a review, Ecological Modelling, 222, 903-924, doi:
- 1946 10.1016/j.ecolmodel.2010.09.040, 2011.
- 1947 Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T.: A quantitative analysis of plant form - the pipe model theory. I. Basic
- 1948 analysis., Jap. J. of Ecology, 14, 97-105, 1964.
- 1949 Smith, P., Smith, J. U., Powlson, D. S., McGill, W. B., Arah, J. R. M., Chertov, O. G., Coleman, K., Franko, U., Frohling, S.,
- 1950 Jenkinson, D. S., Jensen, L. S., Kelly, R. H., Klein-Gunnewiek, H., Komarov, A. S., Li, C., Molina, J. A. E., Mueller, T.,
- 1951 Parton, W. J., Thornley, J. H. M., and Whitmore, A. P.: A comparison of the performance of nine soil organic matter models
- 1952 using datasets from seven long-term experiments, Geoderma, 81, 153-225, doi:10.1016/S0016-7061(97)00087-6, 1997.
- 1953 Suckow, F.: Ein Modell zur Berechnung der Bodentemperatur unter Brache und unter Pflanzenbestand, Akademie der
- 1954 Landwirtschaftswissenschaften der DDR, Berlin, 1986.
- 1955 Suckow, F., Badeck, F.-W., Lasch, P., and Schaber, J.: Nutzung von Level-II-Beobachtungen für Test und Anwendungen
- 1956 des Sukzessionsmodells FORESEE, Beitr. Forstwirtschaft. u. Landsch.ökol., 35, 84-87, 2001.



- 957 Suckow, F., Lasch-Born, P., Gerstengarbe, F.-W., Werner, P., and Reyer, C. P. O.: Climate change impacts on a pine stand
958 in Central Siberia, *Reg Environ Change*, 16, 1671-1683, doi:10.1007/s10113-015-0915-x, 2016.
- 959 Van Hees, A. F. M.: Growth and Morphology of Pedunculate Oak (*Quercus Robur* L) and Beech (*Fagus Sylvatica* L)
960 Seedlings in Relation to Shading and Drought, *Annales des Sciences Forestieres*, 54, 9-18, doi:10.1051/forest:19970102,
961 1997.
- 962 van Oijen, M., Reyer, C., Bohn, F. J., Cameron, D. R., Deckmyn, G., Flechsig, M., Härkönen, S., Hartig, F., Huth, A.,
963 Kiviste, A., Lasch, P., Mäkelä, A., Mette, T., Minunno, F., and Rammer, W.: Bayesian calibration, comparison and
964 averaging of six forest models, using data from Scots pine stands across Europe, *For. Ecol. Manage.*, 289, 255-268,
965 doi:10.1016/j.foreco.2012.09.043, 2013.
- 966 Vetter, M., Churkina, G., Jung, M., Reichstein, M., Zaehle, S., Bondeau, A., Chen, Y., Ciais, P., Feser, F., Freibauer, A.,
967 Geyer, R., Jones, C., Papale, D., Tenhunen, J., Tomelleri, E., Trusilova, K., Viovy, N., and Heimann, M.: Analyzing the
968 causes and spatial pattern of the European 2003 carbon flux anomaly using seven models, *Biogeosciences*, 5, 561-583,
969 doi:10.5194/bg-5-561-2008, 2008.
- 970 Waring, R. H., Landsberg, J. J., and Williams, M.: Net Primary Production of Forests - a Constant Fraction of Gross Primary
971 Production?, *Tree Physiol.*, 18, 129-134, doi:10.1093/treephys/18.2.129, 1998.
- 972 Wösten, J. H. M., Pachepsky, Y. A., and Rawls, W. J.: Pedotransfer functions: bridging the gap between available basic soil
973 data and missing soil hydraulic characteristics, *Journal of Hydrology*, 251, 123-150, doi:10.1016/S0022-1694(01)00464-4,
974 2001.
- 975 Wu, S. H., Jansson, P.-E., and Kolari, P.: Modeling seasonal course of carbon fluxes and evapotranspiration in response to
976 low temperature and moisture in a boreal Scots pine ecosystem, *Ecological Modelling*, 222, 3103-3119,
977 doi:10.1016/j.ecolmodel.2011.05.023, 2011.
- 978 Wu, S. H., Jansson, P.-E., and Kolari, P.: The role of air and soil temperature in the seasonality of photosynthesis and
979 transpiration in a boreal Scots pine ecosystem, *Agric. For. Meteorol.*, 156, 85-103, doi:10.1016/j.agrformet.2012.01.006,
980 2012.
- 981