Description and evaluation of the process-based forest model

4C at four European forest sites

Petra Lasch-Born1, Felicitas Suckow1, Christopher O. P. Reyer1, Martin Gutsch1, Chris Kollas1,2, Franz-Werner Badeck3, Harald K. M. Bugmann4, Rüdiger Grote5, Cornelia Fürstenau6, Jörg Schaber7

1Potsdam Institute for Climate Impact Research (PIK), Member of the Leibniz Association, P.O. Box 60 12 03, D-14412 Potsdam, Germany
2German Federal Institute for Risk Assessment, Unit 43: Epidemiology, Zoonoses and Antimicrobial Resistance, Department Biological Safety, Max-Dohrn-Straße 8-10, D-10589 Berlin, Germany
3Research Centre for Genomics and Bioinformatics, Council for Agricultural Research and Economics, via S. Protaso, 302, 1-29017 Fiorenzuola d’Arda PC, Italy
4Forest Ecology, Department of Environmental Systems Science, ETH Zürich, Universitätstrasse 16, 8092 Zürich, Switzerland
5Karlsruhe Institute of Technology (KIT), Institute of Meteorology and Climate Research (IMK-IFU), Kreuzeckbahnstr. 19, 82467 Garmisch-Partenkirchen, Germany;
6Friedrich-Schiller-Universität Jena, Institut für Informatik, Heinz Nixdorf Chair for Distributed Information Systems, Ernst-Abbe-Platz 1-4, D07743 Jena, Germany
7EXCO GmbH, Adam-Opel-Str- 9-11, D-67227 Frankenthal, Germany

Correspondence: Petra Lasch-Born (lasch@pik-potsdam.de)

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

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

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

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

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

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

The objectives of this paper are:

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

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Impact in 4C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defoliator</td>
<td>Foliage loss</td>
</tr>
<tr>
<td>Xylem clogger</td>
<td>Reduction in water supply rate</td>
</tr>
<tr>
<td>Phloem feeder</td>
<td>Carbon loss</td>
</tr>
<tr>
<td>Root disturber</td>
<td>Fine root loss</td>
</tr>
<tr>
<td>Stem rot</td>
<td>Increase in stem mortality</td>
</tr>
<tr>
<td>Mistletoe</td>
<td>Increase of tree transpiration, and carbon loss</td>
</tr>
</tbody>
</table>
The occurrence of a disturbance has to be given externally as an input time series. If a disturbance occurs, the corresponding effect is simulated (e.g. defoliator implies reduction of foliage biomass of between 0% and 100%), which then exerts its influence on the affected processes within 4C. Only in the case of simulations with disturbances, a NSC-pool (non-structural carbohydrates including starch and sugars) of the trees is activated and the carbon amount for the allocation will be enhanced by carbon from the NSC-pool as a C-reserve of the tree. The NSC-pool is assumed to be located in the biomass compartments sapwood, branch/twigs wood, and coarse root wood, which means that the maximum size of the NSC-pools is defined relative to the biomass of the corresponding compartments (differentiated for coniferous and deciduous trees and based on data reported by Hoch et al. (2003)). The surplus of carbon for allocation into damaged tissues is only available at the end of the disturbance year, while refilling of the NSC-pool can continue for many years until the pool's maximum size is reached. For more details see Lasch-Born et al. (2018).

### 2.1.3 Tree species parameterization

4C is parameterized for the most common European tree species: Common beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* Karst.), Scots pine (*Pinus sylvestris* L.), oaks (*Quercus robur* L., and *Quercus petraea* Liebl.), and birch (*Betula pendula* Roth). In addition, parameters for some species that are considered favourable under expected environmental changes or that are used for short-rotation coppices have also been tested and are readily applicable. The considered species include Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Black locust (*Robinia pseudoacacia* L.), Aleppo pine (*Pinus halepensis* Mill.), eucalypts (*Eucalyptus globulus* Labill. and *Eucalyptus grandis* W. Hill ex Maiden) and poplars (*Populus tremula* (L.), *P. tremuloides* (Michx.)).

Moreover, parameter sets for Ponderosa pine (*Pinus ponderosa* Dougl.) and Lodgepole pine (*Pinus contorta* Dougl.) exist but have not been properly tested. The oak, eucalypt and poplar parameters are derived from investigations of two species of the same genus each and are assumed to be valid for both. Besides these tree species, 4C is also parameterized for the hemiparasitic plant Mistletoe (*Viscum album* subsp. *austriacum*) and a generic grassy ground vegetation based on properties of *Calamagrostis arundinacea*. For each species, a full set of parameters comprises about 95 individual values. Some parameters do not differ across species yet, but can be potentially selected if scientific evidence becomes available. Due to the possibility of using different process descriptions for the same process in the 4C model framework (e.g. phenology) the actual number of parameters used in each simulation may vary (for the values of the parameters see Lasch-Born et al. (2018). In many cases, different physiological parameters have been determined in different environments (Kattge et al., 2011), or dependent on stand density or site fertility (e.g. Berninger et al., 2005). To account for these findings, the philosophy of 4C is to assume that species-specific parameters are genetically defined but that important tree traits (e.g. leaf area or actual electron transport capacity) can be described by acclimation processes to specific environmental conditions. Covering the most important of such processes, one parameter set for each species can be chosen that reproduces species’ growth, water and carbon cycling under a wide range of evolutionary constraints. Calibration of the parameters is therefore not usually carried out when setting up the model for a new site. However, on the one hand, ecotypes may have developed at specific sites that differ due to evolutionary developments and not acclimation so that their properties may not be sufficiently described by a common set of species properties. On the other hand, acclimation processes that are only important under specific conditions (e.g. nutrient imbalances) may not yet be adequately considered in 4C. Therefore, in recent studies, 4C has also been calibrated using a Bayesian framework (van Oijen et al., 2013; Reyer et al., 2016).
2.1.4 Input data needs

Because the smallest time step in 4C is daily, the model requires daily meteorological data (temperature, precipitation, relative humidity, air pressure, wind velocity and global radiation). Furthermore, annual CO2 concentration and nitrogen deposition are necessary inputs. Values for annual CO2 concentration can be selected from internally integrated data sources (measurements: Mauna Loa, Dr. Pieter Tans, NOAA/ESRL (www.esrl.noaa.gov/gmd/ccgg/trends/) and Dr. Ralph Keeling, Scripps Institution of Oceanography (scrippsc02.ucsd.edu)), scenarios: RCP: Meinshausen et al. (2011), SRES: Nakicenovic (2000)).

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

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

2.2 Previous model evaluations

Since the first applications of 4C, tests, evaluations and model comparisons have been carried out for various forest stands and different processes within 4C (Table 2). The evaluations find 4C applicable to a wide range of environmental conditions and research questions but also highlight deficits. Using these previous evaluations in combination with detailed results from selected ecosystems of particular properties, we will draw conclusions for further model development and improvement in the Discussion section.
Table 2 Overview of studies in which different species, processes and variables of 4C were evaluated (DBH- diameter at breast height, H height, N- stem number, AET-actual evapotranspiration, NPP- net primary production, NEE- net ecosystem exchange, TER-total ecosystem respiration, GPP-gross primary production)

<table>
<thead>
<tr>
<th>Process/variable</th>
<th>Validation data</th>
<th>Site</th>
<th>Species</th>
<th>Results</th>
<th>Publication</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth (DBH, H, stem volume, N)</td>
<td>Long-term permanent plot measurements; Evaluation using volume growth and survival graphs</td>
<td>Evo (Finland), Fabrikschleichach (Germany)</td>
<td>Scots pine, beech</td>
<td>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;</td>
<td>Mäkelä et al. (2000b)</td>
</tr>
<tr>
<td>Soil water content, soil temperature</td>
<td>Daily measurements of soil temperature and soil water content in different layers</td>
<td>6 Level II site² in Brandenburg (Germany)</td>
<td>Scots pine</td>
<td>Good correspondence of simulated soil water content and soil temperature with measured data for four years;</td>
<td>Suckow et al. (2001)</td>
</tr>
<tr>
<td>Management (DBH)</td>
<td>Long-term permanent plot measurements</td>
<td>Long-term management trials Chorin, Eberswalde</td>
<td>Scots pine, oak</td>
<td>Simulation of thinning preserved the diameter distribution of the residual stand and influenced the stand dynamics in the expected manner;</td>
<td>Lasch et al. (2005)</td>
</tr>
<tr>
<td>Growth (stem volume, DBH, H, N), climate sensitivity, management</td>
<td>Long-term permanent plot measurements</td>
<td>Fabrikschleichach (Bavaria, Germany), Chorin (Brandenburg, Germany), Eberswalde (Brandenburg, Germany)</td>
<td>Beech, oak, Scots pine</td>
<td>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;</td>
<td>Lindner et al. (2005)</td>
</tr>
<tr>
<td>Soil respiration, litter, DBH growth, water balance, soil temperature</td>
<td>Soil water content, soil respiration, growth parameter, tree ring data</td>
<td>Level II sites² in Germany</td>
<td>Beech, oak, Scots pine, Norway spruce</td>
<td>Realistic simulation of water balance and soil temperature; leaf mass and leaf litter simulations were valid;</td>
<td>Badeck et al. (2007)</td>
</tr>
<tr>
<td>Process/variable</td>
<td>Validation data</td>
<td>Site</td>
<td>Species</td>
<td>Results</td>
<td>Publication</td>
</tr>
<tr>
<td>------------------</td>
<td>----------------</td>
<td>------</td>
<td>---------</td>
<td>---------</td>
<td>-------------</td>
</tr>
<tr>
<td>Growth and soil processes</td>
<td>Stem biomass, foliage litter fall; soil water content and soil temperature</td>
<td>Level II sites in Germany: Kienhorst, Solling</td>
<td>Scots pine, beech</td>
<td>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.</td>
<td>Lasch et al. (2007)</td>
</tr>
<tr>
<td>Carbon balance (stem C productivity, soil C)</td>
<td>Stand level inventory data, stem wood productivity derived from yields tables</td>
<td>Forest management unit in the province of Carinthia, southern Austria</td>
<td>Norway spruce</td>
<td>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;</td>
<td>Seidl et al. (2008)</td>
</tr>
<tr>
<td>Management: thinning and conversion strategies</td>
<td>Experience from literature</td>
<td>Forest reserve Galgenberg (The Netherlands)</td>
<td>Scots pine</td>
<td>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;</td>
<td>Kint et al. (2009)</td>
</tr>
<tr>
<td>Short rotation coppice</td>
<td>Woody biomass experimental data (yields) of SRC from literature</td>
<td>Eastern Germany</td>
<td>Aspen</td>
<td>Good correspondence of simulated yields with experimental data;</td>
<td>Lasch et al. (2010)</td>
</tr>
<tr>
<td>Forest growth (stem biomass, DBH, H)</td>
<td>Long-term plot measurements</td>
<td>4 Beech stands in forest district Buchfahrt, Thuringia (Germany)</td>
<td>Beech</td>
<td>40 years of growth of the beech stands simulated very well; very good correlations between measured and simulated</td>
<td>Borys et al. (2013)</td>
</tr>
<tr>
<td>Process/variable</td>
<td>Validation data</td>
<td>Site</td>
<td>Species</td>
<td>Results</td>
<td>Publication</td>
</tr>
<tr>
<td>------------------</td>
<td>-----------------</td>
<td>------</td>
<td>------------------</td>
<td>------------------------------------------------------------------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>Stem biomass</td>
<td></td>
<td></td>
<td></td>
<td>stem biomasses for a 50-year simulation;</td>
<td>van Oijen et al. (2013)¹</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Good predictive accuracy (a likelihood value from Bayesian calibration approach) for mean tree height and DBH (before calibration);</td>
<td></td>
</tr>
<tr>
<td>Height, DBH</td>
<td></td>
<td>12 stands in Austria, Belgium, Estonia and Finland</td>
<td>Scots pine</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water and carbon fluxes, soil</td>
<td>Daily flux measurements (GPP, NPP, TER, AET), soil temperature, soil water content</td>
<td>Flux-sites: Brasschaat (Belgium), Collelongo (Italy), Hesse (France), Hyytiälä (Finland), 5 Level-II sites² in Germany</td>
<td>Beech, Scots pine, Norway spruce</td>
<td>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;</td>
<td>Reyer et al. (2014)</td>
</tr>
<tr>
<td>Transpiration, soil water, radial stem increment, root water uptake</td>
<td>Xylem sap flux, soil water content, tree ring measurements</td>
<td>Two pure pine stands and two mixed pine-oak stands in Brandenburg (Germany)</td>
<td>Scots pine, oak</td>
<td>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;</td>
<td>Gutsch et al. (2015b)</td>
</tr>
<tr>
<td>Carbon and water fluxes</td>
<td>Flux measurements (GPP, NPP, TER, AET)</td>
<td>Euroflux-site Zotino, Siberia (Russia)</td>
<td>Scots pine</td>
<td>Best results of the comparison for GPP; ecosystem respiration and actual evapotranspiration seems not so well captured; satisfactory agreement between simulated and</td>
<td>Suckow et al. (2016)</td>
</tr>
</tbody>
</table>

¹ van Oijen et al. (2013)
<table>
<thead>
<tr>
<th>Process/variable</th>
<th>Validation data</th>
<th>Site</th>
<th>Species</th>
<th>Results</th>
<th>Publication</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon stock in stand and soil</td>
<td>measured data for annual values of GPP, TER, NEE, and AET (May-September);</td>
<td>Buchfahrt forest district in Thuringia (Germany), 4 beech stands</td>
<td>Beech</td>
<td>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;</td>
<td>Borys et al. (2016)</td>
</tr>
<tr>
<td>NPP</td>
<td>Static reduced models of NPP were derived from 4C simulations; comparison with results from literature showed that these functions provide meaningful estimates of NPP;</td>
<td>Representative forest stands in Germany</td>
<td>Scots pine, Norway spruce, oak, beech</td>
<td></td>
<td>Gutsch et al. (2016)</td>
</tr>
<tr>
<td>Carbon fluxes</td>
<td>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;</td>
<td>Flux-sites Sorø (Denmark), Vielsalm (Belgium) and Collelongo (Italy).</td>
<td>Beech</td>
<td></td>
<td>Horemans et al. (2017)^1</td>
</tr>
<tr>
<td>Basal area increment and</td>
<td>Simulated basal area increment (BAI)</td>
<td>Stand in the forest district Berlin-</td>
<td>Scots pine,</td>
<td></td>
<td>Kollas et al. (2018)</td>
</tr>
<tr>
<td>Process/variable</td>
<td>Validation data</td>
<td>Site</td>
<td>Species</td>
<td>Results</td>
<td>Publication</td>
</tr>
<tr>
<td>------------------</td>
<td>-----------------</td>
<td>-----------------------</td>
<td>---------</td>
<td>-------------------------------------------------------------------------</td>
<td>------------------------------------------</td>
</tr>
<tr>
<td>effect of</td>
<td></td>
<td>Müggelsee (Germany)</td>
<td>infected</td>
<td>corresponded well with BAI calculated from measured tree ring width;</td>
<td>Gutsch et al. (2018)</td>
</tr>
<tr>
<td>Mistletoe</td>
<td></td>
<td></td>
<td></td>
<td>ring width indices of both non-infected trees and trees infected from</td>
<td></td>
</tr>
<tr>
<td>infection</td>
<td></td>
<td></td>
<td></td>
<td>1994 on were found to run synchronously in relative but also in absolute</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>values; good reproduction of the absolute level of growth, of the general</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>growth trends and the pointer years;</td>
<td></td>
</tr>
<tr>
<td>Timber harvest,</td>
<td>BWI³ (forest</td>
<td>Germany</td>
<td>Scots</td>
<td>Reproduction of species-specific yields (stem increment and timber</td>
<td></td>
</tr>
<tr>
<td>stem increment</td>
<td>inventory data</td>
<td></td>
<td>pine,</td>
<td>harvest) in good correspondence with inventory data; strong</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Germany No. 3)</td>
<td></td>
<td>Norway</td>
<td>underestimation of Douglas fir stem increment, moderate overestimation</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>spruce,</td>
<td>of oak stem increment;</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>oak,</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>beech,</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>birch,</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Douglas</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>fir</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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>
<thead>
<tr>
<th>Site (Country)</th>
<th>Species Type</th>
<th>Location</th>
<th>Meteorological conditions</th>
<th>Mean temperature [°C]</th>
<th>Mean annual precipitation sum [mm]</th>
<th>Simulation time period</th>
<th>Soil type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peitz (Germany)</td>
<td>Pinus sylvestris/Scots pine</td>
<td>Long-term monitoring site</td>
<td>continental</td>
<td>9.3</td>
<td>554</td>
<td>1952-2010</td>
<td>Dystric Cambisol</td>
</tr>
<tr>
<td>Solling (Germany)</td>
<td>Picea abies/Norway spruce</td>
<td>Level II</td>
<td>maritime</td>
<td>6.8</td>
<td>1108</td>
<td>1967-2013</td>
<td>Cambisol (haplic)</td>
</tr>
<tr>
<td>Sorø (Denmark)</td>
<td>Fagus sylvatica/Common beech</td>
<td>Euroflux</td>
<td>warm temperate and fully humid</td>
<td>8.3</td>
<td>848</td>
<td>1996-2012</td>
<td>Cambisol</td>
</tr>
<tr>
<td>Hyytiälä (Finland)</td>
<td>Pinus sylvestris/Picea abies</td>
<td>Euroflux</td>
<td>continental</td>
<td>4.4</td>
<td>604</td>
<td>1996-2014</td>
<td>Haplic Podsol</td>
</tr>
</tbody>
</table>
Table 4 Stand characteristics at the beginning of the simulations/measurements

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

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

2.3.1 Climate, soil, stand, and observational data

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

2.3.2 Management

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

Table 5 Management description for all sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Number of management events</th>
<th>Type</th>
<th>Target value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peitz</td>
<td>11</td>
<td>Moderate thinning from below</td>
<td>Stem number</td>
</tr>
<tr>
<td>Solling</td>
<td>13</td>
<td>Thinning from above</td>
<td>Stem number</td>
</tr>
<tr>
<td>Sorø</td>
<td>1</td>
<td>Thinning from above</td>
<td>Stem number</td>
</tr>
<tr>
<td>Hyytiälä</td>
<td>3</td>
<td>Thinning from above</td>
<td>Stem number</td>
</tr>
</tbody>
</table>

2.4 Evaluation metrics

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

\[ NRMSE = \sqrt{\frac{1}{N} \sum_{i=1}^{N}(O_i - P_i)^2} \]

where \( \sigma_{obs} \) 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:

\[ IMV^V_{m,t} = V_{m,t} - \bar{V}_m \]

\( V_{m,t} \) – 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 \( V \):

\[ IAV^V_t = V_t - \bar{V} \]

\( V_t \) – 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).

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

<table>
<thead>
<tr>
<th></th>
<th>Peitz</th>
<th>Solling</th>
<th>Hyytiälä Pine</th>
<th>Hyytiälä Spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td>number</td>
<td>13</td>
<td>13</td>
<td>19</td>
<td>18</td>
</tr>
<tr>
<td>DG</td>
<td>0.119</td>
<td>0.382</td>
<td>0.465</td>
<td>0.338</td>
</tr>
<tr>
<td>BM</td>
<td>0.382</td>
<td>0.772</td>
<td>0.879</td>
<td>-0.604</td>
</tr>
<tr>
<td>DBH</td>
<td>0.644</td>
<td>0.557</td>
<td>-6.064</td>
<td>-6.064</td>
</tr>
<tr>
<td>NRMSE</td>
<td>0.338</td>
<td>0.644</td>
<td>2.574</td>
<td>3.146</td>
</tr>
<tr>
<td>ME</td>
<td>0.985</td>
<td>0.964</td>
<td>0.972</td>
<td>0.985</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.988**</td>
<td>0.984**</td>
<td>0.933**</td>
<td>0.939**</td>
</tr>
</tbody>
</table>

* - $p<0.001$

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).
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).
3.2 Carbon and water fluxes

3.2.1 Evaluation over long-time scales at different time resolutions

The averages of the simulated annual fluxes in comparison with the observed averages show a good correspondence for GPP 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). 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 slightly overestimated for Hyytiälä. All statistical measures show values which indicate low performance (Table 7).

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

<table>
<thead>
<tr>
<th>Sorø</th>
<th>Annual statistics</th>
<th>Number of years</th>
<th>Observed average</th>
<th>Simulated average</th>
<th>NRMSE</th>
<th>ME</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Annual AET [mm]</td>
<td>16</td>
<td>431.3±41.2</td>
<td>313.8±22.6</td>
<td>2.977</td>
<td>-8.453</td>
<td>0.223</td>
</tr>
<tr>
<td></td>
<td>Annual NEE [g C m⁻² yr⁻¹]</td>
<td>16</td>
<td>-148.3±130.2</td>
<td>-385.8±100.3</td>
<td>2.403</td>
<td>-5.160</td>
<td>0.437*</td>
</tr>
<tr>
<td></td>
<td>Annual GPP [g C m⁻² yr⁻¹]</td>
<td>16</td>
<td>1892.5±132.4</td>
<td>1972.7±112.51</td>
<td>1.336</td>
<td>-0.902</td>
<td>0.001*</td>
</tr>
</tbody>
</table>
For the daily and monthly sums of fluxes, the evaluation metrics indicate a good model performance with monthly results showing a better fit to observations than daily results (Table 8). The evaluation metrics for Hyytiälä are slightly better than for Soro especially for AET and GPP: For Soro, 4C simulates days without any GPP, while GPP values greater than zero were observed. Daily AET is underestimated for days with a high observed AET (greater than 4 mm). For Hyytiälä, 4C clearly overestimates GPP and AET but also NEE for single days by more than 50% (Fig. 6, right). The intra-annual variability on a monthly scale in Soro for the three variables (Fig. 6, left) shows that 4C underestimates GPP from January to April but during the vegetation period the GPP is clearly overestimated (and NEE underestimated). AET is underestimated throughout the year. In Hyytiälä, 4C overestimates the monthly GPP and underestimates the NEE during the vegetation period from May until July (Fig. 7, right). The variability of the monthly GPP from May until August is higher for the simulated values than for the observed values in Soro; for Hyytiälä, it is the other way around. The monthly AET is overestimated throughout the year.

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

<table>
<thead>
<tr>
<th>Variable</th>
<th>Soro</th>
<th>Number of days</th>
<th>NRMSE</th>
<th>ME</th>
<th>R²</th>
<th>Hyytiälä</th>
<th>Number of days</th>
<th>NRMSE</th>
<th>ME</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET</td>
<td>6058</td>
<td>0.591</td>
<td>0.651</td>
<td>0.734**</td>
<td>199</td>
<td>0.508</td>
<td>0.745</td>
<td>0.884**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEE</td>
<td>6058</td>
<td>0.691</td>
<td>0.522</td>
<td>0.601**</td>
<td>199</td>
<td>0.513</td>
<td>0.735</td>
<td>0.805**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP</td>
<td>6058</td>
<td>0.718</td>
<td>0.544</td>
<td>0.743**</td>
<td>199</td>
<td>0.489</td>
<td>0.760</td>
<td>0.877**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hyytiälä</td>
<td>AET</td>
<td>3945</td>
<td>0.593</td>
<td>0.649</td>
<td>0.764**</td>
<td>136</td>
<td>0.408</td>
<td>0.833</td>
<td>0.906**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NEE</td>
<td>6170</td>
<td>0.643</td>
<td>0.587</td>
<td>0.634**</td>
<td>220</td>
<td>0.514</td>
<td>0.734</td>
<td>0.855**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>GPP</td>
<td>5398</td>
<td>0.507</td>
<td>0.743</td>
<td>0.814**</td>
<td>188</td>
<td>0.452</td>
<td>0.794</td>
<td>0.877**</td>
<td></td>
</tr>
</tbody>
</table>

ns - not significant  
N - normal distribution  
** - p<0.001  
* - p<0.05
Figure 6. Simulated versus observed daily GPP, NEE and AET in Sorø (left) and Hyytiälä (right). The black line shows a 1:1 relationship.
3.2.2 Inter-monthly (IMV) and inter-annual variability (IAV)

The simulated and observed inter-annual variability is nearly in the same order of magnitude for both sites and for the three variables except for a few years for Soro (1997: GPP, NEE) and Hyytiälä (1997-1998, GPP, 2006 AET) (Fig. 8). The signs of IAV were best captured for Hyytiälä with 82 % for GPP, 65 % for NEE and 70 % of the years for AET. In Soro, the signs 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 except for AET (63 %).
The analysis of inter-monthly variability with the normalized IMV data shows similar inter-quartile ranges for simulated and observed IMV but a clearly higher range of the IMV of GPP and NEE for Soro (Fig. 9, left). The IMV of AET differs in the interquartile ranges for simulated and observed data but the range is similar. The simulated variables for Hyytiälä show less variability especially for NEE but also for AET (Fig. 9, right) and a smaller range of the inter-monthly variability in the case of GPP.

Figure 8. Inter-annual variability of GPP, NEE and AET (sim - simulated and obs - observed) in Soro (left) and Hyytiälä (right).
3.3 Soil temperature and water content

The simulated soil temperature (ST) fits the observed data very well in Soro (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 Soro, 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>
<thead>
<tr>
<th></th>
<th>Daily</th>
<th>Monthly</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>NRMSE</td>
</tr>
<tr>
<td>ST 2 cm</td>
<td>6073</td>
<td>0.370</td>
</tr>
<tr>
<td>ST 10 cm</td>
<td>6073</td>
<td>0.283</td>
</tr>
<tr>
<td>SWC 8 cm</td>
<td>5645</td>
<td>1.175</td>
</tr>
</tbody>
</table>

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hyytiälä</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ST organic layer</td>
<td>6828</td>
</tr>
<tr>
<td></td>
<td>ST 5 cm</td>
<td>6828</td>
</tr>
<tr>
<td></td>
<td>ST 18 cm</td>
<td>6560</td>
</tr>
<tr>
<td></td>
<td>ST 50 cm</td>
<td>6560</td>
</tr>
<tr>
<td></td>
<td>SWC organic layer</td>
<td>6438</td>
</tr>
<tr>
<td></td>
<td>SWC 5 cm</td>
<td>6438</td>
</tr>
<tr>
<td></td>
<td>SWC 18 cm</td>
<td>6309</td>
</tr>
<tr>
<td></td>
<td>SWC 50 cm</td>
<td>6438</td>
</tr>
</tbody>
</table>

- *P<0.001
- ** not significant

---

Manuscript under review for journal Geosci. Model Dev.
Discussion started: 15 January 2019
© Author(s) 2019. CC BY 4.0 License.
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 series of observed and simulated daily soil water content at 8 cm depth (below) in Sorø for the period 1996-2012. For Hyytiälä, the results are similar (Fig. 12). The visual inspection for two layers shows a similar picture to Sorø: an underestimation during winter time and a more frequent exhaustion of the soil water during summer. The observed water 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 and August of 2006 with only one third and a half of the precipitation sum of the long-term mean. The interquartile ranges and the ranges of outliers of soil water content are mostly higher for the simulated values than for the measured (Fig. 13, right).
Figure 11. Time series of observed and simulated daily soil temperature for the organic layer and at 5, 18, and 50 cm depth in Hyytiälä for the period 1996-2014.
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 for the period 1996-2014.
Discussion

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

4.1 Evaluation of forest growth

Overall, the ability of 4C to reproduce the dynamics of forest growth differs clearly from site to site. 4C performs best for the mono-specific, coniferous stands Solling and Peitz independent of the evaluation metrics. In particular for Peitz, which features the longest observational time series of Scots pine growth, we observe the best agreement between model and data (Fig. 3). For Solling, 4C underestimates the development of DBH (Fig. 4). Ibrom (2001) and Ellenberg et al. (1991) found similar carbon storage in this spruce stand in 1967 of 9314 g C m\(^{-2}\) initialized by 4C based on tree dimensions (10840 g C m\(^{-2}\)), indicating that basic assumptions about stem form and wood density are appropriate. Our initialization prescribes the same number of trees (595 ha\(^{-1}\)) as observed but strongly underestimates foliage (needle) mass (4C: 422.5 g C m\(^{-2}\) vs. 868 g C m\(^{-2}\) found by Ellenberg et al. (1991)). We applied the fixed parameter \(\eta\) (foliage to sapwood area relationship) to estimate foliage mass, which could lead to this underestimation. Furthermore, the estimation of sapwood area from DBH used for initialization is also uncertain. Consequently, our initialization leads to a smaller leaf area index (LAI) of 5.1 m\(^2\) m\(^{-2}\) in 1990 compared to a value of 7 m\(^2\) m\(^{-2}\) reported by Ibrom (2001) for the same year. In 4C, the initialization of the foliage biomass as well as fine root biomass is estimated via a function depending on sapwood area and a parameter describing the foliage to sapwood area relationship. The sapwood area Therefore, it is possible that 4C’s underestimation of DBH growth is due to the underestimation of foliage biomass during initialization. While foliage is underestimated, the initialization works well for DBH. Ibrom (2001) gives the values for mean DBH (35 cm) and mean top height (28 m) which 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 uses height-diameter relationships from various yield tables which can lead to deviations in comparison to reality.
The quality of growth simulation in Hyytiälä differs for the two species. For Norway spruce, which is present in the
understorey of this pine-dominated stand, stem biomass initialization is underestimated but growth is realistic, whereas the
stem biomass growth of pine is slightly overestimated (Fig. 5). Due to thinning according to given stem numbers the stem
biomass is again overestimated after thinning because maybe other trees were harvested in the model stand as in the real
stand. Comparing simulated biomass data of foliage for the mixed stand Hyytiälä with measurements (personal
communication by Fredrik Lagergren) for the initialization year 1995 we find that pine stem biomass is in accordance with
measurement while spruce stem biomass is clearly underestimated (see Fig. 5).

Earlier model evaluation of stand dynamics for different species such as pine, spruce and beech in Germany by Lasch et al.
(2005); Lasch et al. (2007); Lindner et al. (2005) demonstrated a sufficient ability of the model to reproduce forest growth in
terms of DBH, height and biomass. Thus, while in general we have confidence in the ability of 4C to simulate forest growth,
it is important to keep in mind that 4C works with a site-independent species parameter set and we did not calibrate any of
the parameters locally. Simulating a Scots pine stand in Germany or Finland could therefore clearly differ, depending on
parameter uncertainty for different genera (Collalti et al., 2016). For example, trees in Finland often develop crown shapes
that are more adapted to reducing snow damage – this is an example for an adaptive trait that is evolutionary and is not
considered in the model.

4.2 Evaluation of carbon and water fluxes

We analysed the model’s performance to simulate carbon and water fluxes using statistical measures on different time scales.
For Sorø and Hyytiälä, 4C performed best when comparing simulation results with observational data on daily and monthly
scales for GPP, NEE and AET (Table 8). Collalti et al. (2016) also found a better performance for their 3D-CMCC-FEM
model on a monthly scale for these sites.

For both sites, 4C overestimated GPP and underestimated NEE on long-term average. This could be caused by the simplified
simulation of ecosystem respiration in 4C (see section 2.1.2.3). Because organ-specific, dynamic respiration rates are hard to
parameterize due to a lack of data, the respiration rate in 4C is a fixed fraction of GPP following an approach of Landsberg
and Waring (1997). However, caution is needed as errors of flux measurements could also be a reason for deviations
between observed and simulated values on all time scales (e.g. Brændholt et al. (2018); Rannik et al. (2006)). The standard
deviations of the annual GPP are of similar magnitude for observations and simulation data, which indicates high variability
from year to year in both data sets. For Sorø, the standard deviations of NEE are also very high for simulated and observed
annual values whereas for Hyytiälä the standard deviations are of a lower order of magnitude.

The annual course of GPP and NEE in Sorø shows a sharp increase of GPP with the start of the vegetation period (bud burst)
which is faster than the simulated flushing. For one reason, the phenological model of 4C (Schaber and Badeck, 2003;
Schaber, 2002) for beech was derived from long-term observational data in Germany and hence the model parameters might
not represent the phenology of beech in Denmark. In fact, the 4C average generated day of bud break for 1999-2009 is
DOY 120, while (Pilegaard et al., 2011) found values between 118 and 134 with a mean being DOY 129. Furthermore, we
did not consider ground vegetation because ground vegetation implemented in 4C is not suitable for beech stands (see
section 2.1.3) Therefore, the simulated GPP during winter time is zero and the NEE is underestimated during this time period
(Fig. 7, left). The mismatches in phenology were also discussed by Collalti et al. (2016). For Sorø, Horemans et al. (2017)
discussed in great detail the differences between simulated and observed NEE for 4C and concluded that 4C overestimates
the importance of high frequency variability because 4C uses the daily temperature to redistribute the weekly calculated
NEE and the applied dependency is possibly too sensitive. These daily calculated values are only used for comparison
reasons.

4C simulates the AET quite well except on the annual scale. For Hyytiälä the statistics show a better correspondence of daily
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 R². But also from January until May, before bud break, the monthly AET is underestimated in Soro (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 Soro 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 Soro 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 Soro. The lower performance in Soro could be explained by the imprecise simulation of evapotranspiration and available water at Soro 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 (Lagren 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 R²
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
sites. Former evaluation of the soil water model at other sites (e.g. ICP-Forests level II monitoring plots) achieved better statistical results (Reyer et al., 2014) which may depend on the soil type, the soil parameterization and the quality of soil water content measurements. A former analysis comparing the applied water uptake approach in 4C with a more process-based approach indeed indicated that missing data on root length densities might be crucial (Gutsch et al., 2015b).

4.4 Applicability and Reliability of 4C

Analysing the model results for four sites across Europe, Peitz (pine), Solling (spruce), Sorø (beech) and Hyytiälä (mixed pine spruce), underlines the ability of 4C to describe growth as well carbon and water fluxes at stand scale with sufficient accuracy. In comparison to former evaluations of the model (Reyer et al., 2014) we not only compared observed and simulated data but used further methods to analyse biases in annual and monthly variability. These methods allowed us also to evaluate the ability of 4C to reproduce extreme years like 2003 as shown for GPP simulated in Hyytiälä (see section 4.2). We aimed for a model which simulates forest growth in terms of height, diameter and biomass as well as the water, nitrogen and carbon fluxes without any site-specific calibration. Even though uncertainties in model parametrization for all species and the uncertainties in model structure contribute to partly insufficient results (Medlyn et al., 2005b) we argue that it is encouraging to see how well 4C performs overall across these very different sites. In agreement with other recent studies with 4C (Borys et al., 2016; Gutsch et al., 2015a; Gutsch et al., 2016), this study underlines the applicability of 4C to its main research areas: (1) studies on climate impacts on managed forest ecosystems, (2) trade-off studies on forest-based ecosystem services, (3) studies on forest management strategies and risk analysis, (4) carbon accounting of forest-based bioenergy, and (5) studies on understanding the underlying functioning of forest ecosystems.

Yet our results clearly show that representation of some processes in 4C should be improved, e.g. the phenology sub-model and the description of ground vegetation as an important element in the water balance. Moreover, the way respiration is modelled was identified as a major uncertainty. A new model version including a non-structural carbohydrates (NSC) pool in a changed allocation scheme is currently under development. This version will allow calculation of the organ-specific respiration and will possibly improve the calculation of ecosystem respiration. Furthermore, by considering this pool in the carbon balance the model will be able to react to biotic disturbances and will be able, e.g., to describe the effects of defoliators on the forest ecosystem.

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. (2013). Application of generic calibration could improve model results at various stands as shown by Minunno et al. (2016) by a site-specific calibration, and Peltoniem et al. (2015) for the site Hyytiälä. Molina-Herrera et al. (2015) confirmed that site-specific and multi-site calibration leads to a model parameterization that is best suited for simulating daily carbon fluxes with a forest growth model (Pnet).

5 Conclusions

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

Author contributions. P. Lasch-Born wrote the manuscript with contribution from co-authors, performed simulations, contributed to data analysis and co-developed the model code, F. Suckow contributed to the manuscript, co-developed the model code, performed the simulations, and contributed to data analysis. C.O.P. Reyer contributed to the manuscript, M. Gutsch contributed to the manuscript and co-developed the model code, R. Grote contributed to the manuscript and co-developed the model code. F.-W. Badeck, H. K. M. Bugmann, J. Schaber and C. Fürstenau co-developed the model code. All authors contributed to the model description.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. This paper was supported partly by the EU project SilviStrat (Silvicultural Strategies to Climatic Change in Management of European Forests, 2000-2003), the BMBF project OakChain (Nachhaltige Bewirtschaftung von Eichen-Kiefern-Mischbeständen im subkontinentalen Nordostdeutschen Tiefland, 2005-2009), the EU-funded project MOTIVE (Models for Adaptive Forest Management, 2009-2013) of the 7th FP, the BMBF project CC-LandStraD (Climate Change - Land Use Strategies, 2010-2015) the projects WAHYKLIMA (Waldhygienische Klimaanpassungsstrategien, 2014-2017) and DENDROKLIMA (Jahrringanalysen auf dem Telegrafenberg (Potsdam) - Nutzung dendrochronologischer Daten Deutschlands zur modell-basierten Analyse der Wirkung von Klimaänderungen auf Waldökosysteme, 2016-2019 both funded by the Waldklimafonds (BMEL, BMU). We thank Ylva Hauf for her great support in preparing figures and data and Alison Schlums for great editorial help.

6 References


