

BGC-model parameters for tree species growing in central European forests

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Abstract

During the last centuries forest management has changed the structure and species composition of central European forests. One option to assess forest management and how management impacts may affect forest development over time is the use of biogeochemical ecosystem simulation models. They integrate key ecosystem processes and have proven to be an appropriate diagnostic tool. If we consider that in the past, forest management has strongly affected the species distribution and the structure of central European forests, existing biogeochemical models need to integrate species-specific parameters so that they can adequately address forest management practices such as species changes, stand density etc. The purpose of this paper is to introduce species-specific parameters for one such model, Biome-BGC, for the following tree species as observed in central European forests: *Fagus sylvatica*, *Quercus robur/petraea*, *Larix decidua*, *Pinus sylvestris*, *Pinus cembra* as well as two sets of parameters for *Picea abies* growing at low and high elevations. We first evaluate and test model results obtained with parameters from the literature and single research plots. This evaluation procedure gives our final species-specific parameters that are then used in the model. Next we validate the quality of the model predictions using these parameters versus field observations covering the growing range of a given species by comparing standing tree volume, volume increment, soil carbon and soil nitrogen on 145 independent plots. Our results demonstrate that the species-specific parameters yielded consistent and unbiased predictions.

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1. Introduction

One option to assess forest ecosystem dynamics is the use of biogeochemical-mechanistic ecosystem

modeling (BGC-models) techniques. Such models integrate the main physical, biogeochemical and physiological processes based on our current understanding of key ecophysiological mechanisms. They give a mechanistic description of the interactions between the living plants and their surrounding environment (Waring and Running, 1998) and are explicitly designed to assess the cycling of energy,

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water, carbon and nutrients within a given ecosystem. Typical examples of existing and well-established models are the Lund Potsdam Jena (LPJ) model (Sitch et al., 2003) and Biome-BGC (Thornton, 1998; Thornton et al., 2002). Such models can be parameterized to capture the broad ecophysiological characteristics of plant functional types (e.g. White et al., 2000; Churkina et al., 2003), or to represent the observed characteristics of particular species (e.g. Pietsch and Hasenauer, 2002; Thornton et al., 2002; Pietsch et al., 2003).

Historic land use as well as silvicultural management practices strongly affected the species distribution and the structure of central European forests (Spiecker et al., 2004). Due to species-specific differences in litter production, chemistry and decomposition rates contributing to the quantity of nutrients cycled between vegetation and soil, different species have different impacts on site quality (Schlesinger, 1997; Finzi and Schlesinger, 2002). Hence, existing biogeochemical-mechanistic models need to integrate species-specific parameters so that they adequately address forest practice. Currently, several species belong to the same biome type but may grow in different ecological niches as for instance it is evident for *Pinus sylvestris* and *Pinus cembra*: *P. cembra* grows near the timber line in the high Alpine Mountains, whereas *P. sylvestris* grows in lower elevations on sites, which may be shallow, sandy and stony as well as water limited, or on very wet sites where other coniferous species may not grow. Hence they differ in their limits and rates of stomatal conductance, as well as in chemical composition and residence times of litter, etc.

This is also important if we want to extend biogeochemical modeling theory by integrating management practices such as tending, thinning, etc. which change the stand density within a given forest stand. The growth of the remaining stand after crown release is species sensitive and this has been extensively examined by a large number of growth and yield studies (see Assmann, 1970). Therefore species-specific parameterizations are required to estimate the effects of biomass removal due to harvesting (Merganičová et al., 2005) and to understand the effects of changing species composition on processes such as soil degradation (Pietsch and Hasenauer, 2002).

The purpose of this study is to present species-specific parameters for Biome-BGC. Our main goal is to take advantage of an extensively tested and well established model by maintaining the inner model structure as far as possible while providing parameter sets for all major tree species in central Europe. The following species have been selected: common beech (*Fagus sylvatica* L.), pedunculate/sessile oak (*Quercus robur/petraea* agg.), European larch (*Larix decidua* L.), Scots pine (*P. sylvestris* L.), cembra pine (*P. cembra* L.) as well as two sets of parameters for Norway spruce (*Picea abies* L./Karts.) growing in the lowlands (below 1000 m) and highlands. We compare simulation results using species-specific parameters with results using generalized parameters for three temperate forest biomes (evergreen needle leaf (ENF), deciduous broad leaf (DBF) and deciduous needle leaf (DNF) biome) as given in White et al. (2000), and explain the differences by species.

Our specific working steps can be summarized as follows:

1. We establish species-specific parameters using published literature and field data from intensive research plots.
2. We validate these parameter sets versus independent observations using 145 forest stands covering the growing range of each species. We determine the accuracy and precision of model predictions versus field observations for the standing timber volume, the 10-year volume increment, the soil carbon and soil nitrogen content.
3. Finally, we compare model predictions using our species-specific parameters against results obtained using generalized parameters for evergreen and deciduous forests.

2. Methods

2.1. The model

This study uses Biome-BGC Version 4.1.1 (Thornton et al., 2002). The model operates on a daily time basis and simulates the cycling of energy, water, carbon and nitrogen within a given ecosystem. Leaf area index (LAI, m² leaf area/m² ground area) is calculated by multiplying carbon allocated to leaves

times the specific leaf area (m^2 leaf area/kg leaf carbon) and controls canopy radiation absorption, water interception, photosynthesis, and litter inputs to detrital pools. Net primary production (NPP) is based on gross primary production (GPP) calculated with the Farquhar photosynthesis routine (Farquhar et al., 1980) minus the autotrophic respiration. The autotrophic respiration includes the maintenance respiration, calculated as a function of tissue nitrogen concentration (Ryan, 1991), and growth respiration which is a function of the amount of carbon allocated to the different plant compartments (leaf, root and stem).

NPP is partitioned into the leaves, roots and stems as a function of dynamic allocation patterns, considering possible limitations in the availability of nitrogen. The model requires meteorological input data, such as daily minimum and maximum temperature, incident solar radiation, vapor pressure deficit (VPD) and precipitation. Aspect, elevation, nitrogen deposition and fixation, and physical soil properties are needed to calculate: daily canopy interception, evaporation and transpiration; soil evaporation, outflow, water potential and water content; LAI; stomatal conductance and assimilation of sunlight and shaded canopy fractions; growth and maintenance respiration; GPP and NPP; allocation; litter-fall and decomposition; mineralization, denitrification, leaching and volatile nitrogen losses.

For further details concerning the theory, validation and application examples of the Biome-BGC-model and its predecessor, FOREST-BGC, we refer to Running and Coughlan (1988), Running and Gower (1991), Running and Hunt (1993), Thornton (1998),

White et al. (2000), Thornton et al. (2002), Pietsch and Hasenauer (2002), Law et al. (2003), White and Nemani (2003), Pietsch et al. (2003) and Pietsch and Hasenauer (2005).

3. Data

3.1. Evaluation data

Data for model evaluation using a given species-specific parameter set came from Austria and the Czech Republic. For *P. abies* growing below 1000 m elevation (*P. abies* lowland) data from three plots were available, for *F. sylvatica* and *Q. robur/petraea* we had two plots, for *P. sylvestris* and *P. cembra* one plot and no evaluation data were available for *P. abies* growing in high elevations (*P. abies* highland) and *L. decidua*. The type of data available for each species is given in Table 1. Two of the plots (1 beech, 1 spruce) were situated at Kreisbach ($48^{\circ}06'N$ and $16^{\circ}10'E$), 15 km southwest of St. Pölten, Austria at an elevation of 478 m. Two additional plots (1 oak, 1 spruce) came from Krivoklat ($50^{\circ}02'N$ and $13^{\circ}53'E$), 45 km north-east of Pízen, Czech Republic, with an elevation of 540 m. Another beech plot came from Hochbuch ($48^{\circ}09'N$ and $16^{\circ}10'E$), 7 km west of Vienna, Austria, at an elevation of 340 m and another oak plot was located 5 km from Lednice ($48^{\circ}48'N$ and $16^{\circ}47'E$) at the Thaya/Dyje river, flowing along the border between Austria and the Czech Republic, at an elevation of 161 m. One plot (Cembra pine) was located on Mt. Patscherkofel ($47^{\circ}N$, $11^{\circ}E$), south of

Table 1
Data available for model evaluation by species

Species Variable	<i>Fagus sylvatica</i>	<i>Quercus robur/petraea</i>	<i>Larix decidua</i>	<i>Pinus sylvestris</i>	<i>Pinus cembra</i>	<i>Picea abies</i> lowland	<i>Picea abies</i> highland
Soil temperature	–	–	–	–	Yes	–	–
Stomat. conductance	–	–	–	–	Yes	–	–
Transpiration	Yes	Yes	–	Yes	Yes	Yes	–
Soil water content	–	Yes	–	–	–	Yes	–
Water balance	Yes	Yes	–	–	–	Yes	–
LAI	Yes	Yes	–	–	–	Yes	–
Tree volume	Yes	Yes	–	–	–	Yes	–
Assimilation	Yes	–	–	–	Yes	–	–
Annual ring width	Yes	–	–	–	–	Yes	–
Soil C content	Yes	Yes	–	–	–	Yes	–
Soil N content	Yes	Yes	–	–	–	Yes	–

Innsbruck, Austria, at an elevation of 1950 m, another one (spruce) in the Zebrakovsky Creek basin (49°43'N and 15°16'E) 5 km south of Svetla, Czech Republic, at an elevation of 500 m. Finally the last plot (*P. sylvestris*) was situated at Duba (50°25'N and 14°27'E) 5 km northwest of Melnik, Czech republic, and elevation was 329 m.

3.2. Validation data

Data for independent validation of selected model outputs came from 145 plots, distributed across six different forest growth zones in Austria. The six regions represent a simplification of the nine growth districts according to Kilian et al. (1994) and characterize the major forest climate conditions within the country. Fig. 1 gives an overview of the plot distribution and the six major forest climate zones in Austria which are characterized as follows: Region (1) Central Alps, northeastern central Alps (continental and sub continental zone, high elevations, cold and wet, dominated by Norway spruce); (2) Northern Flysch Alps and calcareous Alps (sub alpine areas, oceanic influence, wet – areas with the highest precipitation rates in Austria – to moderately wet, fir in sub alpine areas, Norway spruce and common beech); (3) Hills and plains between the Alps and the Danube

(moderately wet to moderately dry, mixed common beech stands); (4) Austrian part of the Bohemian Massif (moderately wet and very cold, in winter but dry and warm during summer, mixed common beech stands); (5) Southeastern edge of the Austrian Alps (dry to moderately wet, Norway spruce, fir and common beech) and eastern pannonic semiarid region (dry and warm summer with low winter temperatures, areas with the lowest annual precipitation rates in Austria, dominated by mixed oak stands); and (6) Southern calcareous Alps (illyric climate, wet to moderately dry with long frost periods in winter).

From these sites standing timber volume, 10-year volume increment, and soil carbon and nitrogen content were available with two exceptions: no soil data were available for the 23 plots of Cembran pine and no volume increment for the 41 oak plots. Eleven of the 41 oak plots were located in wetlands with groundwater access throughout the season and three of these plots experienced flooding during 2 weeks in May. All 145 plots are fully stocked (stocking density >0.9), even-aged high forests and dominated by a single species (i.e. >90% of biomass). All stands were unfertilized and not affected by hazards like insect outbreaks or wind throw during the development of the current stand. The summarized stand and site characteristics are given in Table 2.

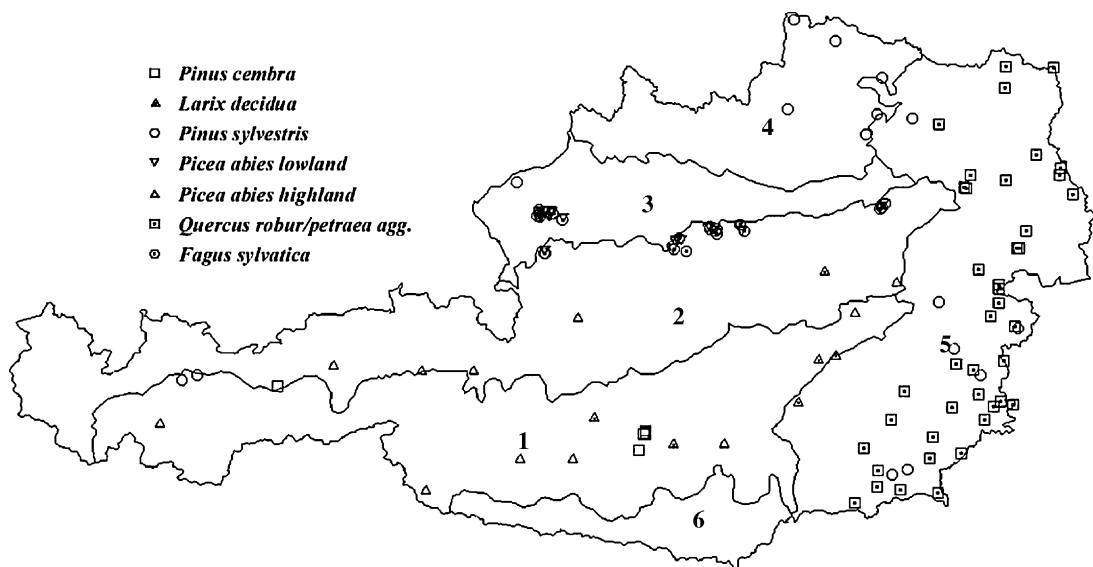


Fig. 1. Location of plots used for model validation. Numbers 1–6 represent the forest growth zones in Austria according to Kilian et al. (1994).

Table 2
Stand and site characteristics of plots used for independent model validation listed by species

Stand characteristics	<i>F. sylvatica</i> mean (min/max)	<i>Q. robur/petraea</i> mean (min/max)	<i>L. deciduas</i> mean (min/max)	<i>P. sylvestris</i> mean (min/max)	<i>P. cembra</i> mean (min/max)	<i>P. abies</i> low mean (min/max)	<i>P. abies</i> high mean (min/max)
Number of plots	20	41	6	16	23	28	11
Elevation (m)	599 (470/790)	319 (140/630)	592 (290/1020)	590 (92/1200)	1753 (1555/2050)	607 (430/750)	1385 (1050/1670)
Stand age (years)	54 (20/118)	84 (40/150)	95 (62/120)	84 (49/135)	134 (66/250)	52 (20/96)	109 (53/250)
DBH (mm)	197 (69/418)	337 (221/550)	468 (350/641)	231 (55/363)	352 (149/510)	233 (60/484)	332 (162/476)
Height (m)	19 (7/37)	25 (19/33)	26 (21/31)	17 (8/26)	15 (8/21)	24 (9/39)	25 (11/37)
Volume (m ³ ha ⁻¹)	453 (147/798)	494 (140/880)	280 (201/440)	258 (102/463)	355 (112/553)	415 (125/717)	556 (141/965)
IV (m ³ ha ⁻¹)	50.8 (19.4/136.8)	–	48.3 (17.8/65.3)	45.3 (34.3/66.3)	23.1 (6.8/39.5)	38.2 (12.0/62.2)	51.4 (23.2/76.2)
Soil C (kg m ⁻²)	5.9 (2.4/13.9)	7.2 (3.6/13.2)	5.8 (3.9/9.6)	5.7 (2.1/10.6)	–	8.7 (2.4/21.9)	10.2 (5.1/21.0)
Soil N (kg m ⁻²)	0.41 (0.22/0.84)	0.60 (0.20/1.07)	0.58 (0.38/1.00)	1.82 (0.08/0.44)	–	0.50 0.17 (1.14/)	0.52 (0.14/0.84)
SI	23.1 (9/39)	6.9 (5/10)	4.8 (2/7)	5.1 (1/8)	4.9 (1.6/7.3)	39.7 (30/48)	9.3 (2/18)
SDI	1174 (650/2374)	700 (456/1350)	645 (387/808)	635 (375/986)	626 (83/4342)	1049 (668/1608)	794 (515/1187)

DBH is the diameter at breast height, IV the 10-year volume increment, SI is the site index according to Lick (1991) for *Pinus cembra* and according to Marschall (1975) for all other species, and SDI the stand density index (Reinecke, 1933).

3.3. Climate data

Daily records of minimum and maximum temperature, precipitation, vapor pressure deficit and incident short wave radiation needed for running the model were generated using DAYMET a climate interpolation model (Thornton et al., 1997) recently adapted and validated for Austrian conditions (Hase-nauer et al., 2003). DAYMET interpolates daily minimum and maximum temperature as well as precipitation from surrounding permanent climate stations. Based on these results, missing daily solar radiation and vapor pressure data are calculated according to Thornton et al. (2000). The point version of DAYMET (Petritsch, 2002) requires longitude, latitude, elevation, slope, aspect and the horizon angle in east and west facing directions for a given plot. Climate records available for generating missing daily meteorological data were provided by the Austrian National Weather Center in Vienna (ZAMG) and include daily weather data for up to 250 stations covering years 1960–2002.

4. Simulation procedure

Mechanistic ecosystem models simulate the changes of state and flux variables over time to assess the physiology, biochemistry, structure and allocation patterns of a given ecosystem. Therefore the endpoint of any given simulation depends on the starting values of state and flux variables. For single stands, i.e. long term monitoring plots, it may be possible to acquire initial conditions from earlier measurements, but as the spatial resolution increases the data availability decreases. To circumvent this limitation, self-initialization procedures have been developed (e.g. for Biome-BBC-model Thornton et al., 2002; White et al., 2000). Within this self-initialization process or spin up run, the accumulation of soil and vegetation carbon and nitrogen pools are simulated using the available climate records repeatedly until the ecosystem reaches a steady state.

Starting with a leaf carbon pool of 0.001 kg m⁻², the spin up procedure for a plot was completed when mean soil carbon content (i.e. the last among the carbon pools to reach a steady state) did not differ by more than 0.5 g m⁻² between two successive simulations using

the same climate record. All spin up simulations were performed using pre-industrial carbon dioxide concentrations (280 ppm; IPCC WGI, 1996) and nitrogen deposition levels ($0.45 \text{ g N m}^{-2} \text{ year}^{-1}$; Ulrich and Williot, 1993). The parameter set used for the spin up simulations on a specific plot was the species-specific parameters representing potentially natural vegetation on that plot as given by Mayer (1974) for the eastern alpine region of Central Europe.

The results of the spin up procedure need to be corrected for possible degradation effects due to changes in land use and forest management. This has been proven to be very crucial for the accuracy of the modeled carbon and nitrogen sequestration (Pietsch and Hasenauer, 2002; Pietsch et al., 2003), because intensive management may have led to a decline in nutrient status and soil fertility (Mayer and Ott, 1991; Ott et al., 1997). In Central Europe intensive use of forest products has a long tradition. For example the charcoal demands from the inner alpine iron industry were fulfilled by clear cutting large forest areas (Funcke, 1998), with natural regeneration as the only source of forest reestablishment. Next, increasing population increased local demands for fuel and construction wood. Depending on tree species and growth conditions, forests were managed differently. For example oak forests in wetlands were exploited applying coppice management systems (Vicherek and Collective, 2000), common beech forests were clear cut and left for natural regeneration.

Since the exact management history for a single plot often remains unknown, we generalized human impact by region and potential natural vegetation. As natural regeneration was the only source of tree establishment prior to the 19th century, the parameter set representing the potential natural vegetation was used for simulating management and vegetation history for each single plot, whereby potential natural vegetation was taken from Mayer (1974). Management history was addressed by simulating 600 years of clear cut forest management prior to the current forest stand establishment. Rotation lengths used were 20 years for oak in wetlands (note this is a coppice forest system), 100 years for spruce, 120 for beech, 150 for dry oak stands and Scots pine, and 200 years for Cembran pine. Clear cutting was simulated by (1) removing above ground woody biomass, (2) assigning belowground woody biomass to the coarse woody

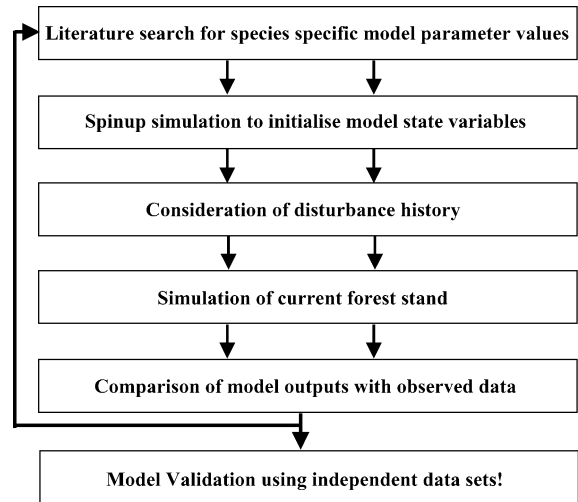


Fig. 2. Overview of working steps for achieving species-specific parameterization.

debris pool, and (3) adding leaves and fine roots to the litter pools. Successive planting was assumed by setting the starting value for leaf carbon to 10 g m^{-2} and for stem carbon to 25 g m^{-2} . All historical simulations were performed using pre-industrial CO_2 (IPCC WGI, 1996) and nitrogen deposition values (Ulrich and Williot, 1993).

For the final simulation from planting to the current forest stands we gradually increased the CO_2 concentration since planting (between 280 and 295 ppm depending on stand age) to 367 ppm in 1998 (IPCC WGI, 1996). Nitrogen deposition was increased from pre-industrial $0.45 \text{ g m}^{-2} \text{ year}^{-1}$ (Ulrich and Williot, 1993) to values between 1.6 and $3.2 \text{ g m}^{-2} \text{ year}^{-1}$ as given for different regions by Schneider (1998). Ground water access and flooding necessary for the 11 oak plots located in wetlands was simulated as described in Pietsch et al. (2003). Fig. 2 summarizes the different working steps.

5. Results

5.1. Model parameter settings

In Biome-BGC, Version 4.1.1, vegetation ecophysiology is determined by a set of 39 parameters. Starting with the general biome parameter sets, we

replaced all parameters for which we found species-specific values different from the original settings in the literature. When values reported in the literature exhibited a variation range we chose average values. All species-specific parameter values are presented in Tables A1–A7. For *P. abies* we found that two different variants may be distinguished for ensuing consistent and unbiased results: (1) spruce growing below 1000 m in elevation = lowland, and (2) spruce growing above 1000 m in elevation = highland. Note that this is consistent with reported genetic differences for *P. abies* (Schmidt-Vogt, 1977). For comparison we also provide (see Tables A8–A10) Biome-BGC parameters for deciduous broad leaf forest (DBF), deciduous needle leaf forest (DNF) and evergreen needle leaf forest (ENF) plant functional types from White et al. (2000).

5.2. Model evaluation

Our species-specific parameters were taken from the literature. Thus next we were interested in evaluating our species-specific settings using field observations available from intensive research plots (see Table 1). Evaluation consisted of non-statistical comparisons between model predictions and field observations and did not include any additional calibration process. We omitted statistical tests because each intensive research plot resembles a single sample and hence exhibits only one independent observation.

While for some variables predicted versus observed values exhibited the same units other variables such as modeled stem carbon (expressed in t ha^{-1}), differ in their units from observed standing timber volume ($\text{m}^3 \text{ha}^{-1}$). Timber volume represents an estimate of merchantable timber (the bole and branches with diameter greater or equal 6 cm) and hence only corresponds to a fraction of stem carbon content. During the optimum phase of a forest stand these fractions vary between 60 and 85%, depending on tree species. Therefore we reduced modeled stem carbon content to the merchantable timber fraction. Next we converted the remaining stem carbon to dry matter by dividing the carbon fraction of timber dry matter. Dry matter was converted to fresh weight by dividing the dry matter fraction of freshly felled timber. Dividing the fresh weight by timber density gave the modeled

timber volume which is comparable with timber volume derived from field observations. The fractions of merchantable timber, carbon in dry matter, dry matter in fresh weight and timber density for each species are given in Table 3.

In Biome-BGC rates and limitations of stomatal conductance regulate the trade off between carbon gain and water losses. Therefore we present as an evaluation example predicted versus observed daily transpiration rates. Besides the absolute values of daily transpiration, we were also interested in the seasonal pattern of the day to day variations between predicted and observed values (see Fig. 3), because this helps to identify inconsistencies in the modeled phenology regarding the onset and termination of the growing season.

Next we show stomatal conductance observations for the Cembran pine stand at Mt. Patscherkofel (Wieser, 1997) which were overestimated by the model during the winter time (see Fig. 4A). In the model, stomatal conductance is regulated between 0 and its maximum value by three multipliers. These multipliers linearly reduce conductance predictions if the boundaries for conductance reduction according to vapor pressure deficit (VPD), leaf water potential (LWP, set equal to predawn soil water potential) or previous night minimum temperature are exceeded. Since during winter time neither VPD nor LWP reach limiting values, the limits for conductance reduction due to previous night minimum temperature were readjusted. We moved these boundaries to the parameter file to allow species-specific adjustment. The success of this step is shown in Fig. 4B and the results for evergreen tree species improved. For deciduous species no readjustment of minimum temperature regulation was necessary because trees have no leaves during the cold winter season.

Another important result of our evaluations is shown in Fig. 5. Transpiration estimates may be of good quality in 1 year and relatively poor in the following year. This illustrates that the model does not reproduce the full variation range as observed in different seasons.

5.3. Model validation

Single plots are not enough for a thorough validation of our species-specific model settings.

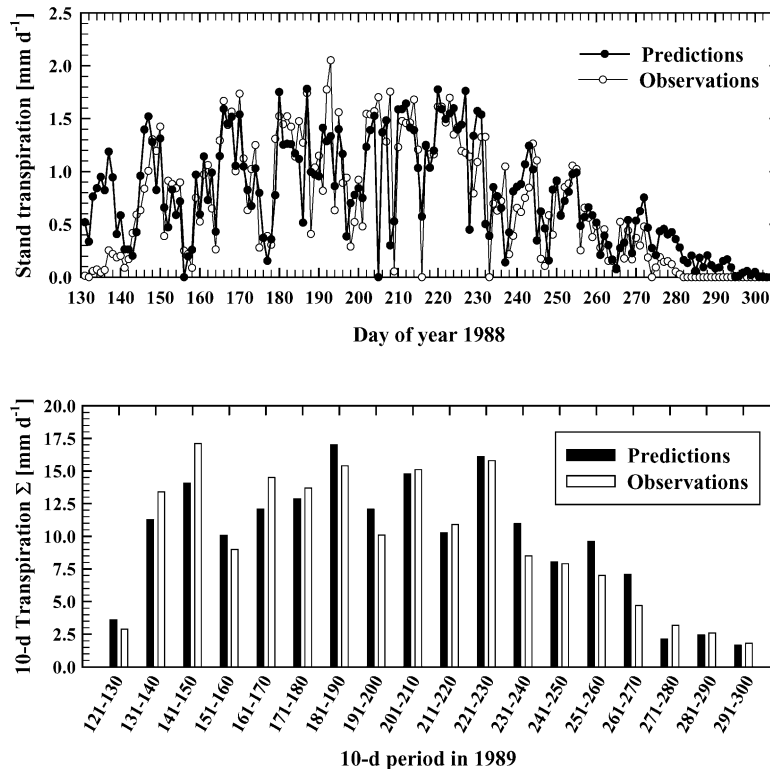


Fig. 3. Predicted and observed daily transpiration rate 1988 (upper graph) and 10 day transpiration totals 1989 (lower graph) from a *Quercus petraea* stand near Krivoklat, CZ. Observed values come from sap flow measurements according to the heat balance method (Čermák et al., 1973).

They provide only limited information on whether unbiased and consistent simulation results will be produced in repeated model applications. Therefore we obtained data from 145 independent plots covering the growing conditions of the different species in Austria (see Fig. 1). The plots varied by species, site index, stand density and stand age. On each plot, observations on soil carbon and soil nitrogen as well as merchantable tree volume and 10-year volume increment were available. The only exceptions were the validation data for *P. cembra* where no soil and for *Q. robur/petraea* agg. where no volume increment information was available. The data represent an excellent source for model validation (see Table 2).

With validation we refer to a comparison of predicted versus observed values to assess the accuracy and precision of our model predictions in using the different species and general biome parameter settings (see Appendix A) under current

environmental conditions. The model accuracy is the measure of the coincidence between the mean of the predictions versus the mean of the observations. The model precision is a measure for assessing the range of single differences between predictions versus observations and may be considered as the distribution range of errors.

We first assessed the relationship between predicted and observed volume, 10-year volume increment, soil carbon and soil nitrogen content. Table 4 gives the results of the correlation analysis by species. Volume and volume increment exhibited the best correlations (see Table 4). Species where no evaluation data were available (*L. decidua*, *P. abies* highland), and therefore no evaluation and model adjustments were possible (see Fig. 2), exhibited the lowest correlations (see Table 4).

Next we were interested in comparing our species-specific parameter settings versus using the general-

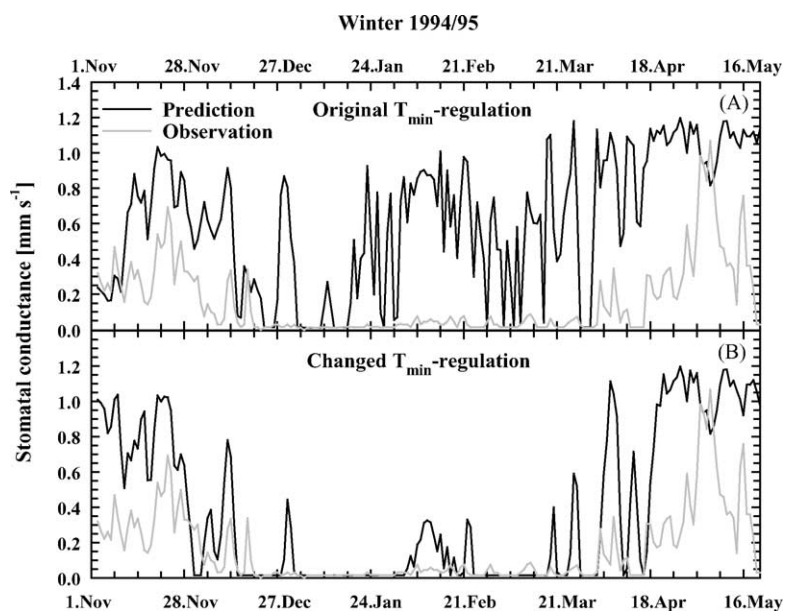


Fig. 4. Predicted and observed daily mean stomatal conductance from the *Pinus cembra* plot at Mt. Patscherkofel during winter 1994/1995. (A) With standard minimum temperature regulation settings. (B) With adjusted previous night minimum temperature regulation. Observations were taken from Wieser (1997).

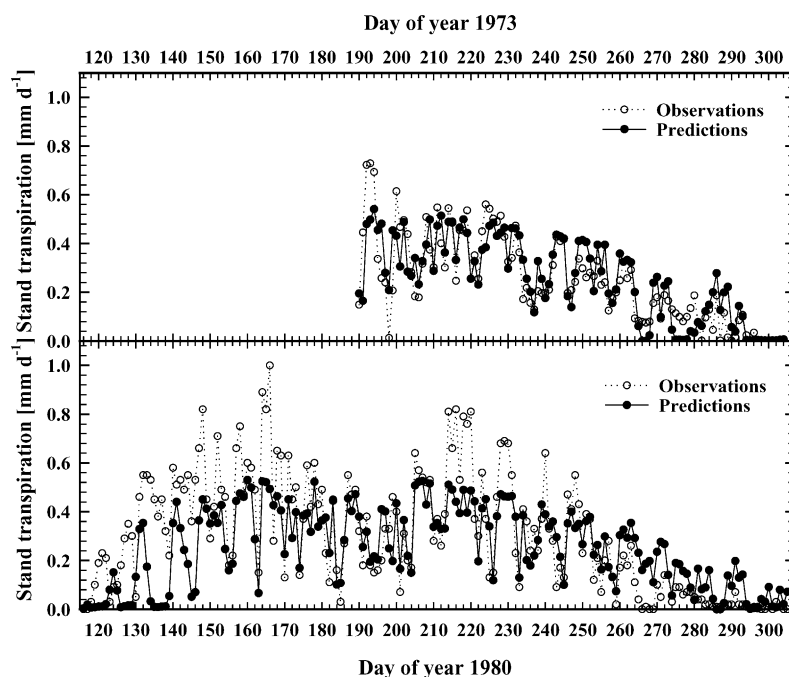


Fig. 5. Predicted and observed daily stand transpiration rates vs. day of year for 1979 (upper graph) and 1980 (lower graph) from the *Pinus sylvestris* plot in Duba, CZ. Observed values come from sap flow measurements according to the heat balance method (Čermák et al., 1973).

Table 3

Fractions of commercial timber, carbon in dry matter and dry matter in fresh weight as well as timber density

Species	Merchantable timber fraction	Dry matter carbon fraction	Fresh weight dry matter fraction	Timber density (kg m ⁻³)
<i>F. sylvatica</i>	0.825	0.486	0.440	950
<i>Q. robur/petraea</i>	0.760	0.504	0.500	1000
<i>L. deciduas</i>	0.850	0.503	0.440	800
<i>P. sylvestris</i>	0.694	0.500	0.500	820
<i>P. cembra</i>	0.694	0.500	0.500	820
<i>N. spruce</i> lowland	0.850	0.503	0.440	800
<i>N. spruce</i> highland	0.700	0.503	0.440	800

Values for *F. sylvatica* were taken from Hochbichler et al. (1994), for *Q. robur/petraea* from Hochbichler (1993), for *P. cembra* and *P. sylvestris* from Sekot (1982) and for *L. decidua* and *P. abies* from Hager (1988).

ized biome parameters as given in White et al. (2000). We additionally performed all model runs using the generalized parameters (see Tables A8–A10). For both model predictions (species-specific and the biome parameters) the same conversion factors for timber volume by species (see Table 3) were applied to compare the modeling results with field observations. Fig. 6 gives the results for predicted versus observed tree volume and 10-year volume increment using the species-specific and the standard biome parameters for evergreen needle forests (ENF). Fig. 8 shows the results for the deciduous broad leaf forest and deciduous needle forest. Because data from different species are plotted (see Figs. 6 and 8) we only give the

1:1 reference line. The species-specific correlation diagnostics are presented in Table 4.

Figs. 7 and 9 give the distribution of standardized differences between predicted and observed values for volume and volume increment versus stand age, site index, stand density index (SDI), elevation, slope, aspect and the predictor. No trends were evident, neither for the species-specific nor for the standard biome parameter sets, except a shift towards negative residuals for the latter. Such analyses are important because the relative proportion of model residuals may vary with site and stand variation parameters. Specific trends versus a particular site parameter would indicate that the modeling system is biased due to

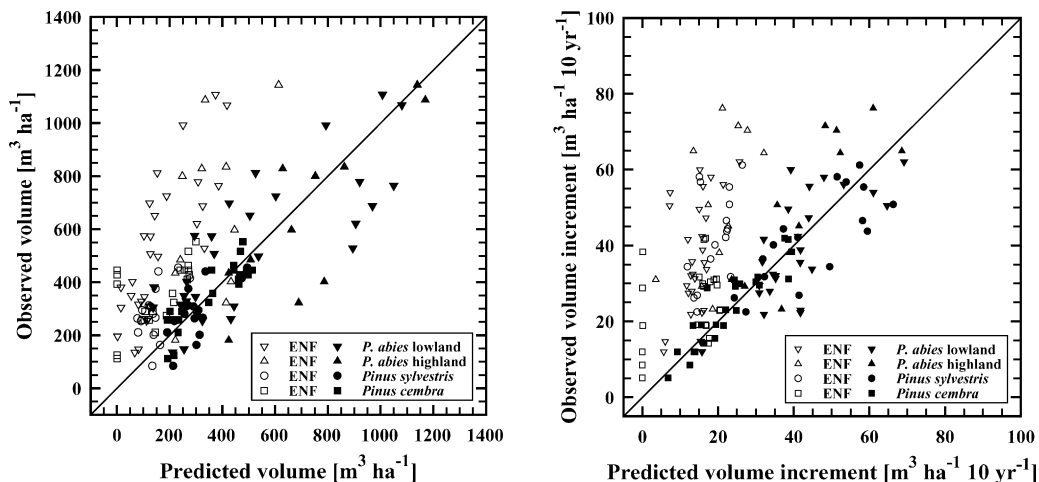


Fig. 6. Predicted vs. observed stand volume (left hand graph) and 10-year volume increment (right hand graph) for the *Picea abies* lowland, *Picea abies* highland, *Pinus sylvestris*, and *Pinus cembra* parameter sets together with the respective results using the standard evergreen needle leaf forest (ENF) parameterization. The parameters are listed in Appendix A.

Table 4

Results of the correlation analyses of predicted vs. observed values, where 10-year IV is 10-year increment in merchantable timber, soil C is soil carbon content and soil N is soil nitrogen content

Species parameter	Intercept	Regression coefficient	Standard error of estimates	Correlation coefficient	F-value	α
<i>Fagus sylvatica</i> (n = 20)						
Volume (m ³ ha ⁻¹)	104.4	0.85	109.3	0.87	53.5	<0.01
10-year IV (m ³ ha ⁻¹)	0.48	0.75	3.30	0.86	47.7	<0.01
Soil C (kg m ⁻²)	-4.2	1.74	3.31	0.45	4.65	<0.05
Soil N (kg m ⁻²)	-0.04	0.78	0.17	0.40	3.49	>0.05
<i>Quercus robur/petraea</i> (n = 41)						
Volume (m ³ ha ⁻¹)	6.5	0.90	74.9	0.85	100.3	<0.01
Soil C (kg m ⁻²)	3.9	0.46	1.47	0.67	31.5	<0.01
Soil N (kg m ⁻²)	0.21	0.60	0.14	0.67	31.0	<0.01
<i>Larix decidua</i> (n = 6)						
Volume (m ³ ha ⁻¹)	47.1	0.86	82.1	0.55	1.74	>0.05
10-year IV (m ³ ha ⁻¹)	-8.86	1.27	13.0	0.81	7.69	>0.05
Soil C (kg m ⁻²)	6.04	-0.05	2.37	0.04	0.01	>0.90
Soil N (kg m ⁻²)	0.35	0.35	0.25	0.27	0.32	>0.50
<i>Pinus sylvestris</i> (n = 16)						
Volume (m ³ ha ⁻¹)	42.9	0.82	76.0	0.68	11.8	<0.01
10-year IV (m ³ ha ⁻¹)	9.9	0.83	8.7	0.77	20.0	<0.01
Soil C (kg m ⁻²)	11.0	-1.37	2.31	0.50	4.8	<0.05
Soil N (kg m ⁻²)	0.66	-0.98	0.09	0.73	15.6	<0.01
<i>Pinus cembra</i> (n = 23)						
Volume (m ³ ha ⁻¹)	13.9	0.93	56.2	0.89	76.2	<0.01
10-year IV (m ³ ha ⁻¹)	1.7	0.97	4.1	0.91	103.9	<0.01
<i>Picea abies</i> lowland (n = 28)						
Volume (m ³ ha ⁻¹)	182.5	0.69	169.1	0.78	39.1	<0.01
10-year IV (m ³ ha ⁻¹)	3.16	0.88	9.5	0.76	32.9	<0.01
Soil C (kg m ⁻²)	-11.9	6.1	4.39	0.53	10.4	<0.01
Soil N (kg m ⁻²)	-0.21	2.1	0.20	0.43	5.96	<0.01
<i>Picea abies</i> highland (n = 11)						
Volume (m ³ ha ⁻¹)	-105.4	1.03	187.6	0.82	19.1	<0.01
10-year IV (m ³ ha ⁻¹)	0.8	1.15	11.3	0.83	19.5	<0.01
Soil C (kg m ⁻²)	14.9	-0.64	5.4	0.26	0.63	>0.1
Soil N (kg m ⁻²)	0.92	-0.54	0.19	0.54	3.7	>0.05

the impact of this parameter, while a trend versus the predictor reveals a general failure. Similar results were obtained for soil carbon and nitrogen content (graphs not shown, but see Table 4).

Neither correlation statistics (Table 4) nor analysis for residuals (Figs. 7 and 9) provides any information about the consistency of future model predictions. Thus we conducted paired *t*-tests for predictions versus observations and an extensive error analysis according to Reynolds (1984). Table 5 gives the mean of the observations and the mean and standard deviation of the differences between predicted and observed values. Positive differences indicate overestimation and nega-

tive underestimation. Note that statistics for volume are given in percent since volume increases with stand age. For the species-specific parameter sets *t*-statistics indicated significant differences for three of the 25 tested variables (see Table 5: soil N for beech and soil C and N for lowland stands of spruce). For the standard biome parameter sets 17 of the 25 tested variables were significantly biased (see Table 5).

One possibility to determine the limits and range of errors in future predictions is to calculate the confidence, prediction and tolerance intervals (Reynolds, 1984). The confidence interval, CI for the mean of the differences, *D* (predicted – observed), can be

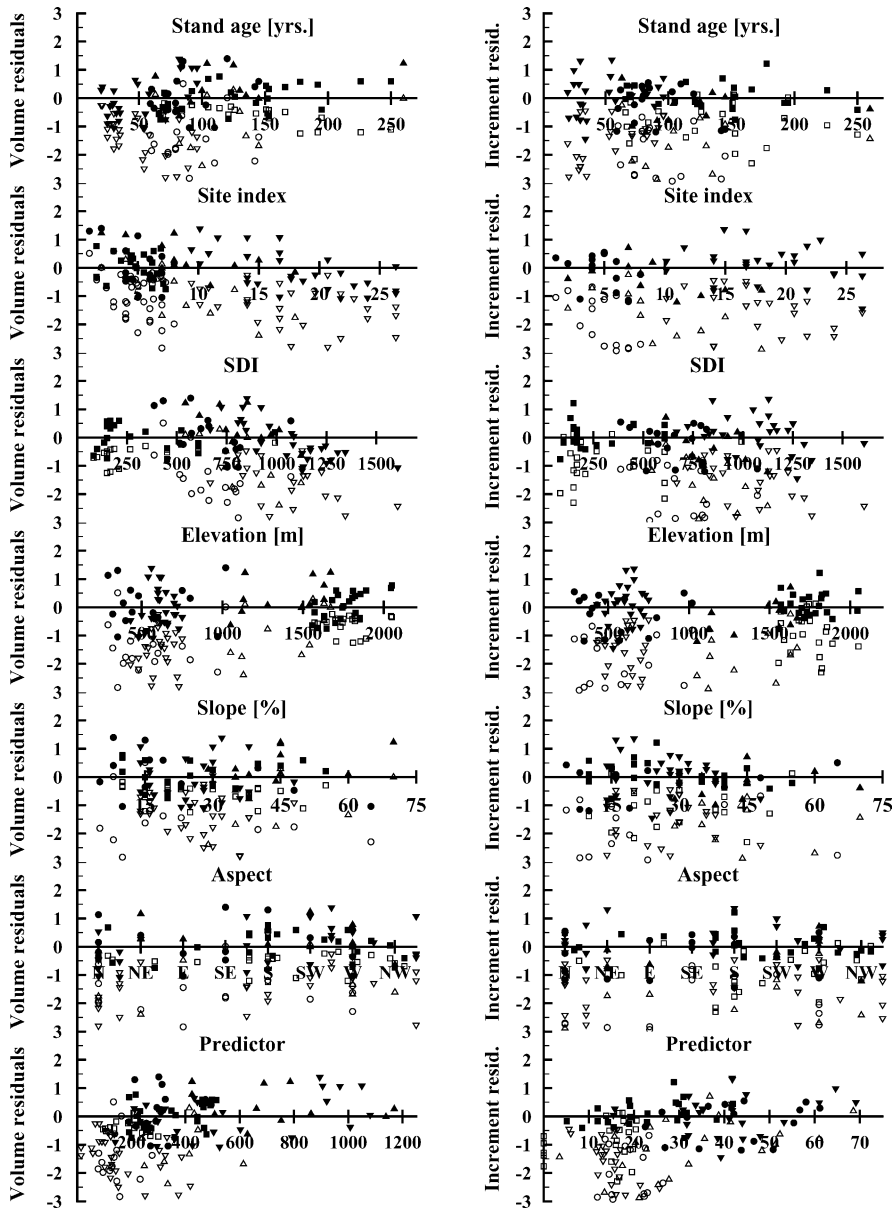


Fig. 7. Standardized residuals for tree volume (left hand graphs) and volume increment (right hand graphs) vs. stand age, site index, stand density index (SDI, Reinnecke, 1933), elevation, slope, aspect and predictor for the *Picea abies* lowland (closed upward triangles), *Picea abies* highland (closed downward triangles), *Pinus sylvestris* (closed circles), and *Pinus cembra* (closed squares) parameter sets together with the respective results using the standard evergreen needle leaf biome (open symbols) parameterization (symbols as in Fig. 5).

used to evaluate discrepancies between the expected difference and the estimator \bar{D} (Reynolds, 1984):

$$CI = \bar{D} \pm \frac{s_D}{\sqrt{n}} t_{1-\alpha/2(n-1)} \quad (1)$$

where \bar{D} is the mean, s_D the standard deviation of the D_i differences, n is the sample size and t is the $1 - \alpha/2$ quantile of the t -distribution with $n - 1$ degrees of freedom.

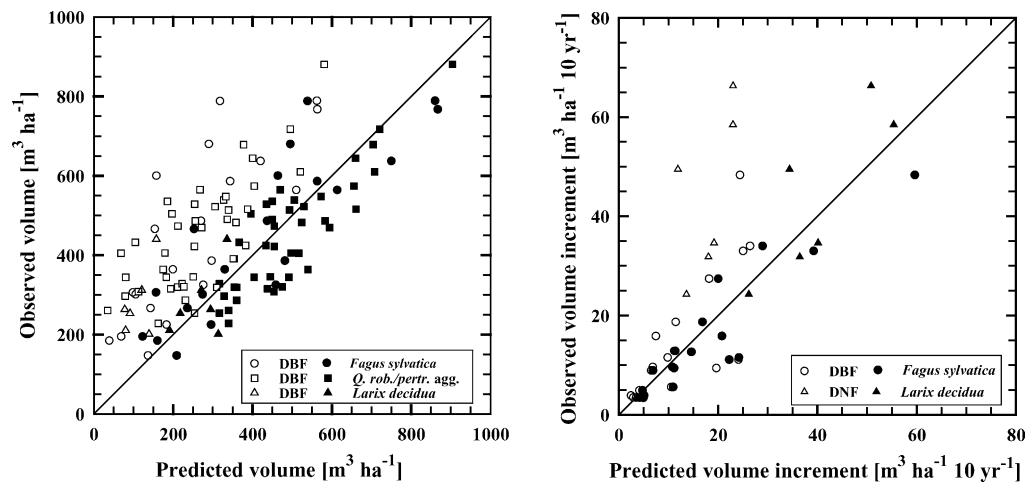


Fig. 8. Predicted vs. observed stand volume and 10-year volume increment for the *Fagus sylvatica*, *Quercus robur/petraea* agg. and *Larix decidua* parameter sets together with the respective results using the standard deciduous broad leaf (DBF) and deciduous needle leaf (DNF) biome parameterization.

Table 5

Results of the error analysis for the deciduous tree species *Fagus sylvatica*, *Quercus robur/petraea* and *Larix decidua* as well as the results using the standard biome parameter settings for deciduous broad leaf forest (DBF), deciduous needle leaf forests (DNF), and evergreen needle forest (ENF)

Species parameter	$\overline{\text{obs}}$	$\overline{D_i}$	S.D.	t	CI	PI	TI
<i>Fagus sylvatica</i> (n = 20)							
Volume ($\text{m}^3 \text{ha}^{-1}$)	453	−5.5%	25.2%	0.98	−17.3 to 6.3%	−59.6 to 48.5%	−63.8 to 52.8%
10-year IV ($\text{m}^3 \text{ha}^{-1}$)	50.8	2.29	5.33	1.87	−0.2 to 4.8	−9.1 to 13.7	−10.0 to 14.6
Soil C (kg m^{-2})	5.93	−0.20	3.29	0.27	−1.74 to 1.34	−7.26 to 6.86	−7.80 to 7.41
Soil N (kg m^{-2})	0.41	0.17	0.17	4.40*	0.08 to 0.24	−0.20 to 0.53	−0.22 to 0.55
DBF							
Volume ($\text{m}^3 \text{ha}^{-1}$)	453	−43.4%	28.5%	6.81*	−56.7 to −30.1%	−104.4 to −17.6%	−109.2 to −22.4%
10-year IV ($\text{m}^3 \text{ha}^{-1}$)	50.8	2.39	7.87	2.17*	−3.5 to −1.3	−19.3 to 14.5	−20.6 to 15.8
Soil C (kg m^{-2})	5.93	0.67	3.37	0.89	−0.91 to 2.24	−6.55 to 7.88	−7.11 to 8.44
Soil N (kg m^{-2})	0.41	−0.25	0.18	6.35*	0.17 to 0.34	−0.13 to 0.63	−0.16 to 0.66
<i>Quercus robur/petraea</i> (n = 41)							
Volume ($\text{m}^3 \text{ha}^{-1}$)	449	−0.9%	20.3%	1.36	−7.2 to 5.3%	−41.4 to 39.5%	−49.0 to 47.1%
Soil C (kg m^{-2})	7.31	0.05	2.11	0.16	−0.61 to 0.72	−4.27 to 4.37	−5.08 to 5.18
Soil N (kg m^{-2})	0.60	0.04	0.16	1.68	−0.01 to 0.09	−0.28 to 0.37	−0.35 to 0.43
DBF							
Volume ($\text{m}^3 \text{ha}^{-1}$)	449	−41.2%	20.9%	6.03*	−47.4 to −34.3%	−83.4 to 1.6%	−91.3 to 9.6%
Soil C (kg m^{-2})	7.31	0.63	2.55	1.58	−1.43 to −0.32	−5.85 to 4.59	−6.83 to 5.57
Soil N (kg m^{-2})	0.60	0.05	0.21	1.47	−0.02 to 0.11	−0.83 to 0.49	−0.46 to 0.56
<i>Larix deciduas</i> (n = 6)							
Volume ($\text{m}^3 \text{ha}^{-1}$)	280	−3.5%	26.4%	0.32	−14.2 to 7.3%	−52.7 to 105.5%	−71.5 to 124.3%
10-year IV ($\text{m}^3 \text{ha}^{-1}$)	48.3	−3.4	12.1	0.68	−8.4 to 1.6	−24.3 to 48.7	−33.0 to 57.3

Table 5 (Continued)

Species parameter	$\overline{\text{obs}}$	\overline{D}_i	S.D.	t	CI	PI	TI
Soil C (kg m ⁻²)	5.75	0.63	2.96	0.52	-0.58 to 1.84	-5.92 to 11.83	-8.02 to 13.94
Soil N (kg m ⁻²)	0.58	0.09	0.26	0.84	-0.02 to 0.19	-0.51 to 1.03	-0.69 to 1.21
DNF							
Volume (m ³ ha ⁻¹)	280	-60%	26.0%	5.67*	-71.1 to -49.8%	-138.6 to 17.8%	-157.2 to 36.4%
10-year IV (m ³ ha ⁻¹)	48.3	-26.4	17.0	3.81*	-33.4 to 19.5	-77.3 to 24.5	-89.4 to 36.6
Soil C (kg m ⁻²)	5.75	0.63	2.97	0.15	-1.03 to 1.39	-8.71 to 9.08	-10.82 to 11.19
Soil N (kg m ⁻²)	0.58	0.18	0.26	0.40	-0.06 to 0.14	-0.72 to 0.81	-0.91 to 0.99
<i>Pinus sylvestris</i> (n = 16)							
Volume (m ³ ha ⁻¹)	289	4.0%	25.9%	0.63	-9.7 to 17.9%	-52.9 to 61.0%	-65.4 to 73.5%
10-year VI (m ³ ha ⁻¹)	45.3	2.99	8.65	1.37	-7.6 to 1.6	-22.0 to 16.1	-26.2 to 25.2
Soil C (kg m ⁻²)	5.7	-1.6	3.10	2.01	-3.3 to 0.1	-8.5 to 5.2	-10.0 to 6.8
Soil N (kg m ⁻²)	0.27	0.08	0.18	2.06	-0.02 to 0.17	-0.32 to 0.48	-0.40 to 0.57
ENF							
Volume (m ³ ha ⁻¹)	289	51.2%	29.4%	6.98*	-66.9 to -35.6%	-115.7 to 13.2%	-130.0 to 27.4%
10-year VI (m ³ ha ⁻¹)	45.3	-26.14	14.09	8.68*	-71.8 to 1.6	-22.0 to 16.1	-26.2 to 25.2
Soil C (kg m ⁻²)	5.7	-2.4	3.12	3.06*	-4.0 to -0.7	-9.1 to 4.4	-10.6 to 5.9
Soil N (kg m ⁻²)	0.27	0.06	0.20	1.17	-0.04 to 0.16	-0.37 to 0.49	-0.47 to 0.58
<i>Pinus cembra</i> (n = 16)							
Volume (m ³ ha ⁻¹)	355	5.5%	25.3%	0.59	-4.8 to 8.7%	-32.0 to 36.1%	-41.2 to 45.1%
10-year VI (m ³ ha ⁻¹)	23.1	1.06	5.3	1.06	-0.8 to 2.6	-7.7 to 9.56	-9.9 to 11.7
ENF							
Volume (m ³ ha ⁻¹)	355	57.4%	31.7%	8.69*	-70.8 to -44.0%	-124.0 to 9.5%	-141.0 to 25.9%
10-year VI (m ³ ha ⁻¹)	23.1	10.51	8.31	5.27*	-14.2 to -6.8	-28.88 to 7.85	-33.50 to 12.47
<i>Picea abies</i> lowland (n = 28)							
Volume (m ³ ha ⁻¹)	415	-0.7%	32.0%	0.62	-13.1 to 11.8%	-67.5 to 66.2%	-83.2 to 81.9%
10-year VI (m ³ ha ⁻¹)	38.2	3.71	10.01	0.97	-0.2 to 7.6	-17.2 to 24.6	-22.1 to 27.6
Soil C (kg m ⁻²)	8.55	-4.78	4.47	5.64*	-6.2 to -2.7	-13.8 to 4.8	-16.0 to 7.0
Soil N (kg m ⁻²)	0.50	-0.16	0.20	4.13*	-0.24 to -0.07	-0.58 to 0.26	-0.67 to 0.36
ENF							
Volume (m ³ ha ⁻¹)	415	-68.4%	15.2%	10.40*	-74.3 to -62.5%	-100.1 to -36.7%	-107.6 to -29.2%
10-year VI (m ³ ha ⁻¹)	38.2	-19.12	6.65	9.74*	-21.8 to -16.6	-33.1 to -5.3	-36.4 to -2.0
Soil C (kg m ⁻²)	8.55	-5.21	4.91	5.73*	-7.1 to -3.3	-0.58 to 0.26	-17.9 to 7.4
Soil N (kg m ⁻²)	0.50	-0.16	0.21	4.20*	-0.24 to -0.08	-0.59 to 0.27	-0.69 to 0.37
<i>Picea abies</i> highland (n = 11)							
Volume (m ³ ha ⁻¹)	647	10.8%	42.8%	1.57	-17.9 to 39.6%	-88.9 to 110.5%	-134 to 156%
10-year VI (m ³ ha ⁻¹)	51.4	-7.3	10.9	2.20	-14.6 to 0.04%	-32.7 to 16.0%	-44.2 to 29.6
Soil C (kg m ⁻²)	10.2	-2.7	6.2	1.49	-6.9 to 1.4	-17.2 to 10.4	-23.7 to 18.1
Soil N (kg m ⁻²)	0.52	0.22	0.37	1.95	-0.02 to 0.17	-0.32 to 0.48	-0.40 to 0.57
ENF							
Volume (m ³ ha ⁻¹)	647	-35.7%	33.1%	3.45*	-58.0 to -13.5%	-113 to 41.3%	-148 to 76.2%
10-year VI (m ³ ha ⁻¹)	51.4	-31.5	16.2	6.46*	-21.8 to 10.6	-35.6 to 3.2	-44.3 to 11.9
Soil C (kg m ⁻²)	10.2	-3.0	6.1	1.66	-7.1 to 1.0	-17.2 to 11.1	-23.6 to 17.5
Soil N (kg m ⁻²)	0.52	0.19	0.36	1.77	-0.04 to 0.16	-0.37 to 0.49	-0.47 to 0.58

Where $\overline{\text{obs}}$ is the mean of observations, \overline{D}_i the mean of the differences between predicted and observed values, S.D. the standard deviation of the differences and t the value from paired t -statistics. CI, PI and TI are the confidence, prediction and tolerance intervals of the error (Reynolds, 1984). IV is 10-year increment in merchantable timber, soil C is soil carbon content and soil N soil nitrogen content.

* Significant at alpha = 0.05.

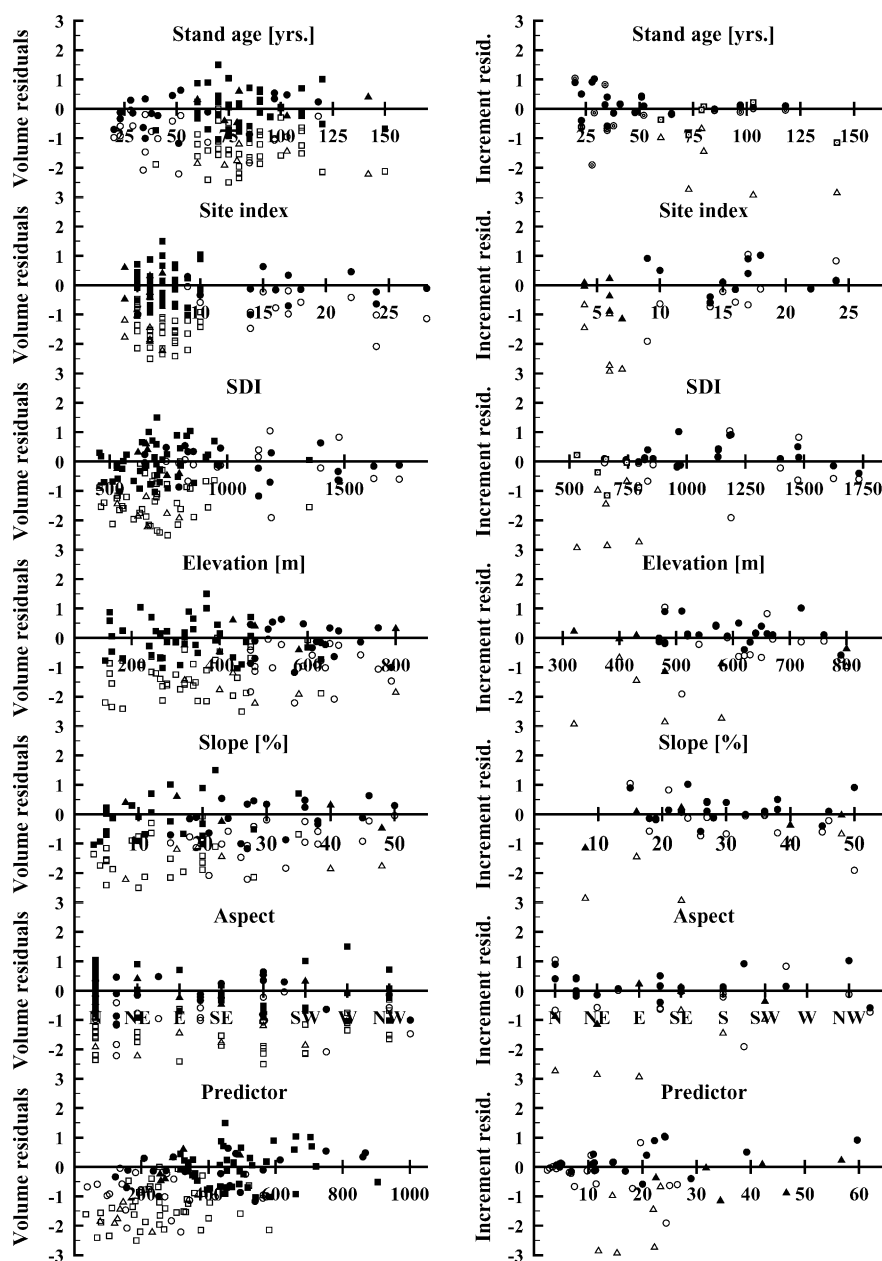


Fig. 9. Standardized residuals for tree volume (left hand graphs) for *Fagus sylvatica* (closed circles), *Quercus robur/pertraea* agg. (closed squares) and *Larix decidua* (closed upward triangles) and volume increment (right hand graphs) for *Fagus sylvatica* and *Larix decidua* vs. stand age, site index, SDI, elevation, slope, aspect and predictor together with the respective results using the standard deciduous broad leaf (DBF, open circles) or deciduous needle leaf (DNF, open upward triangles) biome parameterization (symbols as in Fig. 8).

The prediction interval PI gives the range of the differences (D_i) among predictions versus observations and is defined as:

$$PI = \bar{D} \pm \sqrt{1 + \frac{1}{n}} S_D t_{1-\alpha/2(n-1)} \quad (2)$$

Finally, the tolerance interval TI provides the limit that contains a specified portion (e.g. 95%) of the distribution of the differences when the model is used repeatedly (Reynolds, 1984):

$$TI = \bar{D} \pm S_D g_{1-\gamma, n, 1-\alpha} \quad (3)$$

The tolerance factor ($g_{1-\gamma, 1-\alpha}$) for the normal distribution accounting for the probability that $(1 - \gamma)100\%$ of the distribution D is within a probability of $1 - \alpha$, can easily be obtained from statistical tables (e.g. Sachs, 1999). For details and prerequisites for this procedure we refer to Reynolds (1984).

To apply Eqs. (1)–(3) the differences D_i must be distributed normally. A Kolmogorov Smirnov test ($\alpha = 0.05$) found no significant differences from normality. The results of the paired t -test as well as the resulting confidence, prediction and tolerance interval by species and variable are given in Table 5. For comparison we also provide the results for the standard Biome-BGC settings DBF (deciduous broad leaf forest), DNF (deciduous needle leaf forest) and ENF (evergreen needle leaf forest). Statistics for the 10-year IV (10-year volume increment) predictions in $\text{m}^3 \text{ha}^{-1}$ for *Fagus sylvatica*, e.g. can be interpreted as follows: with a probability of 95% we are confident that for the mean, the bias is between -0.2 and $4.8 \text{ m}^3 \text{ha}^{-1}$ and thus not significantly different from zero (= unbiased). With a probability of 95% we can be confident that a single future difference in the 10-year volume increment predictions of *Fagus* will be between -9.1 and $13.7 \text{ m}^3 \text{ha}^{-1}$. In repeated model applications, most of the errors (95%) will be between -10.0 and $14.6 \text{ m}^3 \text{ha}^{-1}$.

6. Discussion and conclusion

Species-specific parameters are presented for *F. sylvatica*, *Q. robur/petraea* agg., *L. decidua*, *P. sylvestris*, *P. cembra*, as well as for two variants of *P. abies* – lowland and highland (see Appendix A). The main changes versus the general biome settings for

evergreen needle leaf forests, deciduous broad leaf forests and deciduous needle leaf forests as published in White et al. (2000) (see Appendix A) can be summarized as follows.

We reduced maximum stomatal conductance from 6 mm s^{-1} as suggested for all forest biomes by Körner (1994) to lower values (see, e.g. Appendix A: Table A4: 1 mm s^{-1} for *P. sylvestris*). We changed the boundaries for conductance reduction due to leaf water potential, the effect of vapor pressure deficit, and for the evergreen species, the reduction caused by the previous night minimum temperature. Allocation ratios to leaves, to fine roots and to the living and dead fractions of stem and coarse root wood were changed for each species. Fractions of lignin, cellulose and labile material in litter, fine roots and deadwood were changed. We adjusted the C/N ratios of leaves, falling leaf litter, fine roots and living and dead wood fractions for each species. Among the canopy parameters we reassessed the water and light extinction coefficients, the average specific leaf area, the ratios of all sided to projected LAI and the fraction of leaf nitrogen in ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO), to determine the amount of this key carbon fixing enzyme. All details are listed in Appendix A.

For simplicity we provide only one parameter set for *Q. robur* and *Q. petraea* because no improvements in the resulting predictions using different parameters were detectable (data not shown). This is supported by plant systematics, treating the two species as an aggregate (Aas, 1993; Samuel et al., 1995).

The opposite was evident for *P. abies*, where we first started our analyses with one parameter set across the whole growing range of the species. However several test runs suggested that two different variants for *P. abies* are needed to ensure consistent and unbiased results. Tables A6 and A7 give the different parameter sets for *P. abies* growing in an elevation above (highland variant) and below 1000 m (lowland variant). This distinction is also supported by several research studies which report physiological differences of *P. abies* growing in higher ($>1000 \text{ m a.s.l.}$) versus lower elevations ($<800 \text{ m a.s.l.}$) (see Schmidt-Vogt, 1977). For instance Cieselar (1895) found that *P. abies* growing in lower elevations exhibits a timber weight to leaf weight ratio of 1.65 g g^{-1} whereas highland variants show a ratio of 1.16 g g^{-1} . This

suggests that lowland *P. abies* may produce a higher LAI or a lower specific leaf area, but most likely a combination of both. Neuwirth (1968) interpreted these findings as an adaptation of the assimilation potential to shorter growing seasons in higher elevations. This is supported by the higher nitrogen content of needles from highland variants (Fober and Giertych, 1971).

In the model the differences between low and highland *P. abies* are addressed by different allocation ratios, differences in the C/N ratio of leaves, leaf litter, fine roots and different litter qualities defined by the ratios of lignin, cellulose and labile material in litter (see Tables A6 and A7). Model parameter settings for the highland variant allocate 15% more carbon to leaves and fine roots, twice as much carbon to coarse roots and about 20% less carbon to the stem pool versus the lowland variant (see Tables A6 and A7). Nevertheless *P. abies* growing in higher elevations exhibit a higher amount of total carbon allocation to timber. Obviously the shorter growing season is compensated for by a higher leaf mass. The lower light extinction coefficient used for the highland variant has the following reasons: (1) Stands growing in higher elevations exhibit a higher reflectance due to a cuticle with a thicker wax layer. This reduces water losses because at higher elevations vapor pressure deficit is also higher due to higher diurnal temperature differences. (2) These differences can be seen as an adaptation to protect the photosynthetic apparatus from the higher radiation loads at noon resulting from the lower solar distance and the lower light interception by the less dense atmosphere.

The detailed evaluation data (see Table 1) enabled us to judge and perform test runs of model output by species as obtained with different combinations of parameter values found in the literature. With evaluation we refer to limited but detailed observations to test key model output of state and flux variables as they are important for characterizing a species. Figs. 3 and 5, for example, give the daily transpiration rates for *Quercus petraea* (Fig. 3) and *P. sylvestris* (Fig. 5) over the growing season. Although no seasonal trends are detectable it is important to note that inter-annual variations may exist (see Fig. 5), between the modeled versus observed values. Fig. 4 shows the improvement of stomatal conductance predictions for *P. cembra* upon species-specific adjustment of conductance reduction

due to previous night minimum temperature (see Fig. 4B). This has been changed for all evergreen needle trees (see Appendix A).

Validation runs for each species-specific parameter set using 145 plots not used for model initialization (see Table 2) exhibited unbiased and consistent results. A comparison between predicted and observed volume and 10-year volume increment (see Figs. 6 and 8) and a residual analysis versus the main stand or site characteristics such as stand age, site index, stand density (SDI), elevation, slope, aspect as well as the predictor for volume and 10-year volume increment (see Figs. 7 and 9), suggest that no trends or bias are detectable.

An important part of our analysis was to ensure consistent future model predictions for each species and to provide a range of errors in future predictions including their limits by calculating the confidence prediction and tolerance interval for the standing tree volume, 10-year volume increment, soil carbon and soil nitrogen predictions by species.

The results given in Table 5 exhibited no significant differences. Only the soil nitrogen predictions for *F. sylvatica*, as well as the soil carbon and soil nitrogen predictions for *P. abies* lowland exhibited significant differences in the confidence intervals. All other confidence intervals suggest (Table 5) that with a probability of 95% we can be confident that for the mean volume, 10-year volume increment, soil carbon and soil nitrogen the bias is not significantly different from zero (unbiased). In addition Table 5 gives the predictions intervals which assess single future differences between predicted and observed values as well as the range of a single future difference of repeated model applications. With a probability of 95% they are not significantly different from zero.

Comparing the results using the species-specific parameter sets versus the general biome parameters for evergreen needle leaf biome, deciduous broad leaf biome as well as deciduous needle leaf biome trees (see Appendix A and White et al., 2000) suggests that within our application area significant differences in the resulting model predictions exist for the general biome settings. The results (see Figs. 6–9, Tables 4 and 5) demonstrate systematic trends (see Figs. 6–9) and that most of the confidence intervals, a measure for assessing the mean of the differences between predicted and observed values, differed significantly.

Although the prediction and tolerance intervals for volume estimates using the *L. decidua* and *P. abies* highland parameters cover a broader range as compared to the DNF or ENF initialization, the confidence intervals confirm that the species-specific parameters produce unbiased results while the corresponding biome does not (see Table 5). Switching from DNF to *L. decidua* or from ENF to the *P. abies* highland model decreases the precision but increases the accuracy of resulting model predictions. For regional applications we suggest that an increase in accuracy is more important than a decrease in the precision because systematic trends may occur.

With this study we demonstrate that the biogeochemical-mechanistic ecosystem model Biome-BGC can be extended to all major species in central Europe. This is essential to further develop and enhance mechanistic modeling theories by taking advantage of a general ecosystem modeling theory but also addressing the species-specific growth patterns. This is important for assessing species impacts (Spiecker et al., 2004) but also silvicultural management issues such as thinning intensity, harvesting, biomass removal, etc. (Merganičová et al., 2005). Furthermore, it will allow us to link biogeochemical-mechanistic modeling theory with other modeling concepts such as

tree growth models, which are explicitly designed for assessing silvicultural practices

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Appendix A

Tables with species-specific and general biome parameter sets (Tables A1–A10).

Table A1
Species-specific parameters for *Fagus sylvatica*

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	20	%	Given as fraction of the growing season
Litterfall period	20	%	
Annual turnover rates			
Leaves and fine roots	1.0	year ⁻¹	
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	0.545	DIM	Ellenberg et al. (1986)
Stem C/leaf C	3.8	DIM	Nihlgard (1972), Kestemont (1975)
Live wood C/total wood C	0.154	DIM	Panshin et al. (1964)
Coarse root C/stem C	0.115	DIM	Ellenberg (1981)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	26.9	DIM	Jose and Gillespie (1996)
C/N of falling leaf litter	44.0	DIM	Bocock (1964)
C/N of fine roots	47.6	DIM	Vogt et al. (1986)
C/N of live wood	50.0	DIM	
C/N of dead wood	550	DIM	Allison et al. (1963)
Leaf litter proportions			
Labile proportion	0.124	DIM	Cortez et al. (1996)
Cellulose proportion	0.561	DIM	
Lignin proportion	0.315	DIM	
Fine roots proportions			
Labile proportion	0.34	DIM	
Cellulose proportion	0.44	DIM	
Lignin proportion	0.22	DIM	
Dead wood proportions			
Cellulose proportion	0.77	DIM	Panshin and de Zeeuw (1980)
Lignin proportion	0.23	DIM	Panshin and de Zeeuw (1980)
Canopy parameters			
Water interception coefficient	0.034	LAI ⁻¹ d ⁻¹	Klaasen et al. (1996)
Light extinction coefficient	0.6	DIM	Waring and Schlesinger (1985)
Average specific leaf area	48.0	m ² kg ⁻¹ C	Bauer et al. (1997)
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.0	DIM	
Fraction of leaf N in RubisCO	0.162	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.006	m s ⁻¹	
Cuticular conductance	0.00006	m s ⁻¹	
Boundary layer conductance	0.01	m s ⁻¹	
Boundaries for conduction reduction			
Leaf water potential: start of reduction	-340	kPa	Ni and Pallardy (1991)
Leaf water potential: complete reduction	-1700	kPa	Ni and Pallardy (1991)
VPD: start of reduction	600	Pa	Kerstiens (1995)
VPD: complete reduction	3000	Pa	Kerstiens (1995)
Night temperature: start of reduction	-0	°C	
Night temperature: complete reduction	-8	°C	

No entry in the reference column indicates that the default values for deciduous broad leaf biomes (DBF) as given in Table A8 are used.

Table A2

Species-specific parameters for *Quercus robur/petraea*

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	25	%	Given as fraction of the growing season
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	1.0	year ⁻¹	
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	1.2	DIM	Harris et al. (1973)
Stem C/leaf C	1.32	DIM	
Live wood C/total wood C	0.16	DIM	
Coarse root C/ stem C	0.26	DIM	van der Drift (1981)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	27.2	DIM	Jose and Gillespie (1996)
C/N of falling leaf litter	64.1	DIM	Bocock (1964)
C/N of fine roots	73.5	DIM	Joslin and Henderson (1987)
C/N of live wood	73.5	DIM	
C/N of dead wood	451	DIM	Allison et al. (1963)
Leaf litter proportions			
Labile proportion	0.20	DIM	Cortez et al. (1996)
Cellulose proportion	0.56	DIM	Cortez et al. (1996)
Lignin proportion	0.24	DIM	Cortez et al. (1996)
Fine roots proportions			
Labile proportion	0.34	DIM	Stump and Binkley (1993)
Cellulose proportion	0.44	DIM	Stump and Binkley (1993)
Lignin proportion	0.22	DIM	Stump and Binkley (1993)
Dead wood proportions			
Cellulose proportion	0.75	DIM	Wise and Jahn (1952)
Lignin proportion	0.25	DIM	Wise and Jahn (1952)
Canopy parameters			
Water interception coefficient	0.038	LAI ⁻¹ d ⁻¹	Klaasen et al. (1996)
Light extinction coefficient	0.54	DIM	Li et al. (1997)
Average specific leaf area	34.5	m ² kg ⁻¹ C	Abrams et al. (1994)
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.0	DIM	
Fraction of leaf N in RubisCO	0.088	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.0024	m s ⁻¹	Gross et al. (1973)
Cuticular conductance	0.00006	m s ⁻¹	
Boundary layer conductance	0.005	m s ⁻¹	Nobel (1999)
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−500	kPa	Vivin et al. (1993)
Leaf water potential: complete reduction	−3500	kPa	Vivin et al. (1993)
VPD: start of reduction	200	Pa	Infante et al. (1997)
VPD: complete reduction	2550	Pa	Infante et al. (1997)
Night temperature: start of reduction	−0	°C	
Night temperature: complete reduction	−8	°C	

No entry in the reference column indicates that the default values for deciduous broad leaf biomes (DBF) as given in Table A8 are used.

Table A3
Species-specific parameters for *Larix decidua*

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	20	%	Given as fraction of the growing season
Litterfall period	20	%	
Annual turnover rates			
Leaves and fine roots	1.0	year ⁻¹	
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	1.0	DIM	Havranek (1982)
Stem C/leaf C	2.2	DIM	
Live wood C/total wood C	0.1	DIM	Havranek (1982)
Coarse root C/ stem C	0.23	DIM	Havranek (1982)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	25.8	DIM	Kloeppel et al. (1998)
C/N of falling leaf litter	111.9	DIM	Kloeppel et al. (1998)
C/N of fine roots	42.0	DIM	Nambiar (1987)
C/N of live wood	42.0	DIM	Nambiar (1987)
C/N of dead wood	442	DIM	Allison et al. (1963)
Leaf litter proportions			
Labile proportion	0.39	DIM	Aber et al. (1990)
Cellulose proportion	0.44	DIM	Aber et al. (1990)
Lignin proportion	0.17	DIM	Stohlgren (1988)
Fine roots proportions			
Labile proportion	0.30	DIM	
Cellulose proportion	0.45	DIM	
Lignin proportion	0.25	DIM	
Dead wood proportions			
Cellulose proportion	0.76	DIM	Timmell (1967)
Lignin proportion	0.24	DIM	Timmell (1967)
Canopy parameters			
Water interception coefficient	0.041	LAI ⁻¹ d ⁻¹	
Light extinction coefficient	0.51	DIM	Pierce and Running (1988)
Average specific leaf area	20.3	m ² kg ⁻¹ C	Gower and Richards (1990)
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.6	DIM	
Fraction of leaf N in RubisCO	0.075	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.0022	m s ⁻¹	Wieser (1999)
Cuticular conductance	0.000022	m s ⁻¹	See White et al. (2000)
Boundary layer conductance	0.009	m s ⁻¹	Nobel (1999)
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−700	kPa	Häsler (1991)
Leaf water potential: complete reduction	−2600	kPa	Häsler (1991)
VPD: start of reduction	800	Pa	Wieser (1999)
VPD: complete reduction	3200	Pa	Wieser (1999)
Night temperature: start of reduction	0	°C	
Night temperature: complete reduction	−8	°C	

No entry in the reference column indicates that the default values for deciduous needle leaf biomes (DNF) as given in Table A9 are used.

Table A4
Species-specific parameters for *Pinus sylvestris*

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	30	%	Given as fraction of the growing season
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	0.18	year ⁻¹	Satoo (1971)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	0.523	DIM	Linder and Axelsson (1982)
Stem C/leaf C	2.5	DIM	Alvera (1981)
Live wood C/total wood C	0.059	DIM	Panshin et al. (1964)
Coarse root C/stem C	0.29	DIM	Ellenberg (1981)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	33.1	DIM	Berg and Ekbohm (1991)
C/N of falling leaf litter	132.0	DIM	Berg et al. (1984)
C/N of fine roots	38.0	DIM	Nadelhoffer et al. (1985)
C/N of live wood	50.0	DIM	
C/N of dead wood	1400	DIM	Fahey et al. (1985)
Leaf litter proportions			
Labile proportion	0.257	DIM	Berg et al. (1984)
Cellulose proportion	0.493	DIM	Berg et al. (1984)
Lignin proportion	0.25	DIM	Berg et al. (1984)
Fine roots proportions			
Labile proportion	0.252	DIM	Aber et al. (1990)
Cellulose proportion	0.495	DIM	Aber et al. (1990)
Lignin proportion	0.253	DIM	Aber et al. (1990)
Dead wood proportions			
Cellulose proportion	0.71	DIM	Wise and Jahn (1952)
Lignin proportion	0.29	DIM	Wise and Jahn (1952)
Canopy parameters			
Water interception coefficient	0.051	LAI ⁻¹ d ⁻¹	Gash et al. (1999)
Light extinction coefficient	0.51	DIM	Pierce and Running (1988)
Average specific leaf area	13.0	m ² kg ⁻¹ C	Reich et al. (1995)
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.6	DIM	Fassnacht et al. (1994)
Fraction of leaf N in RubisCO	0.0457	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.0010	m s ⁻¹	Čermák personal communication
Cuticular conductance	0.00001	m s ⁻¹	See White et al. (2000)
Boundary layer conductance	0.009	m s ⁻¹	Nobel (1999)
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−500	Pa	DeLucia and Schlesinger (1990)
Leaf water potential: complete reduction	−2200	Pa	DeLucia and Schlesinger (1990)
VPD: start of reduction	50	Pa	Kellomäki and Wang (1997)
VPD: complete reduction	2500	Pa	Kellomäki and Wang (1997)
Night temperature: start of reduction	5	°C	Personal assessment
Night temperature: complete reduction	1	°C	Personal assessment

No entry in the reference column indicates that the default values for evergreen needle leaf biomes (ENF) as given in Table A10 are used.

Table A5
Species-specific parameters for *Pinus cembra*

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	30	%	Given as fraction of the growing season
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	0.18	year ⁻¹	Satoo (1971)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	1.65	DIM	Linder and Axelsson (1982)
Stem C/leaf C	2.0	DIM	Mälkönen (1974)
Live wood C/total wood C	0.076	DIM	Panshin et al. (1964)
Coarse root C/stem C	0.29	DIM	Ellenberg (1981)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	33.1	DIM	Berg and Ekbohm (1991)
C/N of falling leaf litter	93.8	DIM	Stump and Binkley (1993)
C/N of fine roots	58.0	DIM	
C/N of live wood	50.0	DIM	
C/N of dead wood	730	DIM	Allison et al. (1963)
Leaf litter proportions			
Labile proportion	0.257	DIM	Berg et al. (1984)
Cellulose proportion	0.493	DIM	Berg et al. (1984)
Lignin proportion	0.25	DIM	Berg et al. (1984)
Fine roots proportions			
Labile proportion	0.252	DIM	Aber et al. (1990)
Cellulose proportion	0.495	DIM	Aber et al. (1990)
Lignin proportion	0.253	DIM	Aber et al. (1990)
Dead wood proportions			
Cellulose proportion	0.71	DIM	Wise and Jahn (1952)
Lignin proportion	0.29	DIM	Wise and Jahn (1952)
Canopy parameters			
Water interception coefficient	0.036	LAI ⁻¹ d ⁻¹	Kelliher et al. (1992)
Light extinction coefficient	0.51	DIM	Pierce and Running (1988)
Average specific leaf area	13.0	m ² kg ⁻¹ C	Reich et al. (1995)
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.6	DIM	Fassnacht et al. (1994)
Fraction of leaf N in RubisCO	0.0457	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.0014	m s ⁻¹	Wieser (2000)
Cuticular conductance	0.000014	m s ⁻¹	See White et al. (2000)
Boundary layer conductance	0.009	m s ⁻¹	Nobel (1999)
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−1000	Pa	DeLucia and Schlesinger (1990)
Leaf water potential: complete reduction	−2000	Pa	DeLucia and Schlesinger (1990)
VPD: start of reduction	100	Pa	Kellomäki and Wang (1997)
VPD: complete reduction	1900	Pa	Kellomäki and Wang (1997)
Night temperature: start of reduction	0.8	°C	Personal assessment
Night temperature: complete reduction	−2.5	°C	Personal assessment

No entry in the reference column indicates that the default values for evergreen needle leaf biomes (ENF) as given in Table A10 are used.

Table A6

Species-specific parameters for *Picea abies* (lowland)

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	30	%	Given as fraction of the growing season
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	0.195	year ⁻¹	Satoo (1971)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	0.622	DIM	Nadelhoffer et al. (1985)
Stem C/leaf C	3.03	DIM	Nihlgard (1972), Hager (1988)
Live wood C/total wood C	0.076	DIM	Panshin et al. (1964)
Coarse root C/ stem C	0.19	DIM	Ellenberg (1981)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	58.8	DIM	Axelsson and Berg (1988)
C/N of falling leaf litter	116	DIM	Berg and McClaugherty (1989)
C/N of fine roots	58.0	DIM	
C/N of live wood	50.0	DIM	
C/N of dead wood	535	DIM	Hager (1988)
Leaf litter proportions			
Labile proportion	0.44	DIM	Berg and McClaugherty (1989), Taylor et al. (1991)
Cellulose proportion	0.35	DIM	
Lignin proportion	0.21	DIM	
Fine roots proportions			
Labile proportion	0.427	DIM	Stump and Binkley (1993)
Cellulose proportion	0.381	DIM	Stump and Binkley (1993)
Lignin proportion	0.192	DIM	Stump and Binkley (1993)
Dead wood proportions			
Cellulose proportion	0.71	DIM	Panshin and de Zeeuw (1980)
Lignin proportion	0.29	DIM	Panshin and de Zeeuw (1980)
Canopy parameters			
Water interception coefficient	0.036	LAI ⁻¹ d ⁻¹	Kelliher et al. (1992)
Light extinction coefficient	0.67	DIM	Sampson and Allen (1998)
Average specific leaf area	10.2	m ² kg ⁻¹ C	Gower and Richards (1990)
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.6	DIM	Fassnacht et al. (1994)
Fraction of leaf N in RubisCO	0.0457	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.002	m s ⁻¹	Day (2000)
Cuticular conductance	0.00006	m s ⁻¹	
Boundary layer conductance	0.009	m s ⁻¹	Nobel (1999)
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−500	Pa	Goldstein et al. (1985)
Leaf water potential: complete reduction	−2500	Pa	Goldstein et al. (1985)
VPD: start of reduction	50	Pa	Eastmann and Camm (1995)
VPD: complete reduction	1500	Pa	Eastmann and Camm (1995)
Night temperature: start of reduction	−2	°C	Personal assessment
Night temperature: complete reduction	−10	°C	Personal assessment

No entry in the reference column indicates that the default values for evergreen needle leaf biomes (ENF) as given in Table A10 are used.

Table A7

Species-specific parameters for *Picea abies* (highland)

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	30	%	Given as fraction of the growing season
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	0.195	year ⁻¹	Satoo (1971)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	0.762	DIM	Vogt et al. (1990)
Stem C/leaf C	2.09	DIM	Satoo (1971)
Live wood C/total wood C	0.059	DIM	Panshin et al. (1964)
Coarse root C/ stem C	0.23	DIM	Nihlgard (1972)
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	42.0	DIM	Taylor et al. (1991)
C/N of falling leaf litter	87.7	DIM	
C/N of fine roots	42.4	DIM	
C/N of live wood	50.0	DIM	Nambiar (1987)
C/N of dead wood	535	DIM	
Leaf litter proportions			
Labile proportion	0.35	DIM	Berg and McClaugherty (1989), Stump and Binkley (1993)
Cellulose proportion	0.40	DIM	
Lignin proportion	0.25	DIM	
Fine roots proportions			
Labile proportion	0.427	DIM	Stump and Binkley (1993)
Cellulose proportion	0.381	DIM	Stump and Binkley (1993)
Lignin proportion	0.192	DIM	Stump and Binkley (1993)
Dead wood proportions			
Cellulose proportion	0.71	DIM	Panshin and de Zeeuw (1980)
Lignin proportion	0.29	DIM	Panshin and de Zeeuw (1980)
Canopy parameters			
Water interception coefficient	0.031	LAI ⁻¹ d ⁻¹	Kaliuzhny et al. (1979)
Light extinction coefficient	0.51	DIM	Pierce and Running (1988)
Average specific leaf area	9.4	m ² kg ⁻¹ C	Bauer et al. (1997)
Ratio of sunlit to shaded LAI	1.8	DIM	Personal assessment
Ratio of all sided to projected LAI	2.6	DIM	Fassnacht et al. (1994)
Fraction of leaf N in RubisCO	0.035	DIM	See White et al. (2000)
Conductance parameters			
Maximum stomatal conductance	0.002	m s ⁻¹	Day (2000)
Cuticular conductance	0.00002	m s ⁻¹	See White et al. (2000)
Boundary layer conductance	0.009	m s ⁻¹	
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−500	Pa	Goldstein et al. (1985)
Leaf water potential: complete reduction	−2500	Pa	Goldstein et al. (1985)
VPD: start of reduction	50	Pa	Eastmann and Camm (1995)
VPD: complete reduction	1500	Pa	Eastmann and Camm (1995)
Night temperature: start of reduction	−2	°C	Personal assessment
Night temperature: complete reduction	−10	°C	Personal assessment

No entry in the reference column indicates that the default values for evergreen needle leaf biomes (ENF) as given in Table A10 are used.

Table A8

Values of Biome-BGC parameters for the deciduous broad leaf forest (DBF) as published in [White et al. \(2000\)](#)

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	20	%	White et al. (2000)
Litterfall period	20	%	
Annual turnover rates			
Leaves and fine roots	1.0	year ⁻¹	White et al. (2000)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	1.2	DIM	White et al. (2000)
Stem C/leaf C	2.2	DIM	
Live wood C/total wood C	0.16	DIM	
Coarse root C/stem C	0.22	DIM	
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	25.0	DIM	White et al. (2000)
C/N of falling leaf litter	55.0	DIM	
C/N of fine roots	48.0	DIM	
C/N of live wood	50.0	DIM	
C/N of dead wood	550	DIM	
Leaf litter proportions			
Labile proportion	0.38	DIM	White et al. (2000)
Cellulose proportion	0.44	DIM	
Lignin proportion	0.18	DIM	
Fine roots proportions			
Labile proportion	0.34	DIM	White et al. (2000)
Cellulose proportion	0.44	DIM	
Lignin proportion	0.22	DIM	
Dead wood proportions			
Cellulose proportion	0.77	DIM	White et al. (2000)
Lignin proportion	0.23	DIM	
Canopy parameters			
Water interception coefficient	0.045	LAI ⁻¹ d ⁻¹	White et al. (2000)
Light extinction coefficient	0.54	DIM	
Average specific leaf area	32.0	m ² kg ⁻¹ C	
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.0	DIM	
Fraction of leaf N in RubisCO	0.088	DIM	
Conductance parameters			
Maximum stomatal conductance	0.006	m s ⁻¹	White et al. (2000)
Cuticular conductance	0.00006	m s ⁻¹	
Boundary layer conductance	0.009	m s ⁻¹	
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−334	kPa	White et al. (2000)
Leaf water potential: complete reduction	−2200	kPa	
VPD: start of reduction	1100	Pa	
VPD: complete reduction	3600	Pa	
Night temperature: start of reduction	0	°C	
Night temperature: complete reduction	−8	°C	

Table A9

Values of Biome-BGC parameters for the deciduous needle leaf forest (DNF) as published in White et al. (2000)

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	20	%	White et al. (2000)
Litterfall period	20	%	
Annual turnover rates			
Leaves and fine roots	1.0	year ⁻¹	White et al. (2000)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	1.4	DIM	White et al. (2000)
Stem C/leaf C	2.2	DIM	
Live wood C/total wood C	0.071	DIM	
Coarse root C/ stem C	0.29	DIM	
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	42.0	DIM	White et al. (2000)
C/N of falling leaf litter	93.0	DIM	
C/N of fine roots	58.0	DIM	
C/N of live wood	50.0	DIM	
C/N of dead wood	730	DIM	
Leaf litter proportions			
Labile proportion	0.31	DIM	White et al. (2000)
Cellulose proportion	0.45	DIM	
Lignin proportion	0.24	DIM	
Fine roots proportions			
Labile proportion	0.34	DIM	White et al. (2000)
Cellulose proportion	0.44	DIM	
Lignin proportion	0.22	DIM	
Dead wood proportions			
Cellulose proportion	0.71	DIM	White et al. (2000)
Lignin proportion	0.29	DIM	
Canopy parameters			
Water interception coefficient	0.041	LAI ⁻¹ d ⁻¹	White et al. (2000)
Light extinction coefficient	0.51	DIM	
Average specific leaf area	8.2	m ² kg ⁻¹ C	
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.6	DIM	
Fraction of leaf N in RubisCO	0.033	DIM	
Conductance parameters			
Maximum stomatal conductance	0.006	m s ⁻¹	White et al. (2000)
Cuticular conductance	0.00006	m s ⁻¹	
Boundary layer conductance	0.009	m s ⁻¹	
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−630	Pa	White et al. (2000)
Leaf water potential: complete reduction	−2300	Pa	
VPD: start of reduction	610	Pa	
VPD: complete reduction	3100	Pa	
Night temperature: start of reduction	0	°C	
Night temperature: complete reduction	−8	°C	

Table A10

Values of Biome-BGC parameters for the evergreen needle leaf biome (ENF) as published in White et al. (2000)

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	30	%	White et al. (2000)
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	0.26	year ⁻¹	White et al. (2000)
Live wood	0.7	year ⁻¹	
Whole plant mortality	0.005	year ⁻¹	
Fire mortality	0.0	year ⁻¹	
Allocation ratios			
Fine root C/leaf C	1.4	DIM	White et al. (2000)
Stem C/leaf C	2.2	DIM	
Live wood C/total wood C	0.071	DIM	
Coarse root C/stem C	0.29	DIM	
Growth C/storage C	0.5	DIM	
C/N ratios			
C/N of leaves	42.0	DIM	White et al. (2000)
C/N of falling leaf litter	93.0	DIM	
C/N of fine roots	58.0	DIM	
C/N of live wood	50.0	DIM	
C/N of dead wood	730	DIM	
Leaf litter proportions			
Labile proportion	0.31	DIM	White et al. (2000)
Cellulose proportion	0.45	DIM	
Lignin proportion	0.24	DIM	
Fine roots proportions			
Labile proportion	0.34	DIM	White et al. (2000)
Cellulose proportion	0.44	DIM	
Lignin proportion	0.22	DIM	
Dead wood proportions			
Cellulose proportion	0.71	DIM	White et al. (2000)
Lignin proportion	0.29	DIM	
Canopy parameters			
Water interception coefficient	0.041	LAI ⁻¹ d ⁻¹	White et al. (2000)
Light extinction coefficient	0.51	DIM	
Average specific leaf area	8.2	m ² kg ⁻¹ C	
Ratio of sunlit to shaded LAI	2.0	DIM	
Ratio of all sided to projected LAI	2.6	DIM	
Fraction of leaf N in RubisCO	0.033	DIM	
Conductance parameters			
Maximum stomatal conductance	0.006	m s ⁻¹	White et al. (2000)
Cuticular conductance	0.00006	m s ⁻¹	
Boundary layer conductance	0.009	m s ⁻¹	
Boundaries for conduction reduction			
Leaf water potential: start of reduction	−630	Pa	White et al. (2000)
Leaf water potential: complete reduction	−2300	Pa	
VPD: start of reduction	610	Pa	
VPD: complete reduction	3100	Pa	
Night temperature: start of reduction	0	°C	
Night temperature: complete reduction	−8	°C	

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