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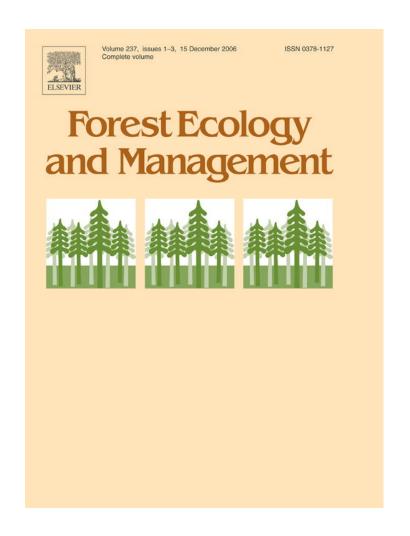
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Application of BIOME-BGC model to managed forests 2. Comparison with long-term observations of stand production for major tree species

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Abstract

In this paper, we applied the process model BIOME-BGC that was adapted to include forest management routines, to managed stands with a long-term observation of biomass production. The exercise includes a model analysis for 33 stands exemplifying typical forest management of beech, oak, pine and spruce, *i.e.*, the four major tree species important to Central-European forestry. The model analysis also included soil carbon component, which was verified using additional independent data collected from 180 forest locations. The paper builds on our companion paper that presented the sensitivity analysis and identified the key ecosystem and site parameters. The adapted model was applied to forest stands modifying only two parameters reflecting site class, namely soil depth and natural nitrogen fixation, while all other parameters were held constant across the stand sites of given species type. In this way the applied model matched the observed long-term biomass development of different stands and species with a mean relative error of 8.2%, ranging from 6.6 to 8.8% for individual tree species. The modeled litter and soil carbon pool was in line with the independent observations available at the level of species groups. Both soil depth and natural nitrogen fixation showed species-specific linear trends with site class that could potentially be utilized for simpler model application on a large scale.

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Keywords: Carbon; Biomass; Soil; Beech; Oak; Pine; Spruce; Kyoto-protocol

1. Introduction

Forest ecosystems are receiving growing attention because of their importance for mitigating environmental change. Policy making in the field of sustainable forest management, as well as climate change related agendas drive research on forest carbon budget and its interpretation. The recent adoption of the Kyoto Protocol further spurred the need of a sound understanding of carbon-related processes. For example, countries may voluntarily select forest management as an activity to offset part of its reduction target (Kyoto Protocol Art. 3.4.), although capped for the first commitment period (2008–2012). Such a decision requires thorough analysis of the likely development of forest carbon stock under the expected and/or adapted management regimes. This in turn requires the application of several types of prediction tools, which aid in

Several types of models are available to address the issues of carbon budget. They may be classified in several ways. One way is by relating them to the spatial scale distinguishing those operating at single-tree level, stand level up to regional models (e.g., Chertov et al., 1999). In terms of their ability to include causality, the models can be either empirical regression models, or so-called process models including eco-physiological processes describing ecosystem functioning in terms of key processes with their interactions. Finally, the adopted simulation system may include all kinds of combinations of approaches to fulfill the modeling goal, creating specific model hybrids. In any case, the models that build on some generalized approach to simulate ecosystem development must be parameterized for the target ecosystems.

This paper is a follow-up of the sensitivity analysis performed in our companion paper (Tatarinov and Cienciala,

making the optimal choices. This is quite a challenge as the analysis should include management regimes, species-specific differences, interactions of biomass and soil compartments, to mention at least some of the important items.

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2006) with the process model BIOME-BGC (Running and Hunt, 1993; Thornton, 1998; Thornton et al., 2002) adapted so as to include management operation. The aim of the current study is to apply the adapted model on the measured long-term production data managed stands exemplifying the typical managed forests of the four major tree species important to Central-European forestry, namely spruce, beech, pine and oak. The forestry in Central Europe has traditionally been focused on volume production. It established a clear-cut management system, creating even-age and mostly monospecific stands that have been mostly established by artificial planting after the final cut. While these systems are efficient in term of forest management operations, the current forest policies advocate changes in forest management aiming at creating multifunctional forestry, increasing biodiversity, close-to-nature management approaches with selective tree management systems and establishing structurally diverse forest stands. Still, the traditionally formed forest stands dominate in Central Europe and addressing their development under likely management scenarios remains important (e.g., Schelhaas et al., 2004).

This study and our companion paper (Tatarinov and Cienciala, 2006) have the common objective to adapt, parameterize and apply a process model with causal relationships for the conditions of Czech forestry. The previous study on parameter sensitivity (Tatarinov and Cienciala, 2006) focused specifically on the eco-physiological and site parameters that are required in BIOME-BGC. The eco-physiological and site parameters with the strongest effect on biomass production were the basis of the current analysis, in which the long-term observations of stand production for four major tree species were utilized as reference. Model prediction of soil and litter compartments was also included using independent data from forest stand sites of the analyzed tree species. The final goal of this study was to present the final sets of tree speciesspecific parameters and demonstrate model application on managed forest stands using minimal site-specific parameter adjustments. The paper also discusses some limitations of the applied model that were detected under the current analysis.

2. Material and methods

2.1. Stand growth data

A data set of stand production was obtained from the database of the permanent research plots. These plots were selected so as to represent monospecific stands of the four major tree species used in the Czech forestry, namely Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), common beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L. and *Q. petrea* L.). The criterion for plot selection was a share of basal area of above 90% for the individual species in a given stand. Secondly, each stand should contain a long series of recurring inventory measurements of growing stock. Finally, the plots were selected so as to represent different elevations and site class. The final set contained altogether 33 plots (Table 1), with 7, 6, 8 and 12 plots for beech, oak, pine and spruce, respectively, which corresponds to the species

importance and representation for forestry in the country. Each plot included data on plot position, stocking density, stand volume, age, mean stem diameter and height per species. The inventory measurements were performed for each plot repeatedly four to eight times with intervals of about 5 years. Stand characteristics for each inventory measurement were presented twice, *i.e.*, before and after thinning (being equal if no thinning occurred), which also gave information on the actual volume of thinning.

The aboveground biomass expressed in terms of carbon (C_{AB}) was calculated for each sample plot and measurement year from the stand volume using biomass expansion factors (BEFs). BEF was defined as

$$BEF = \frac{AB}{V_m} \tag{1}$$

where AB is aboveground biomass (kg), and $V_{\rm m}$ is the merchantable volume (m³). AB was calculated at the tree level using the allometric equations of Wirth et al. (2004), Cienciala et al. (2005) and Cienciala et al. (2006) for spruce, beech and pine, respectively. These species-specific BEFs were calculated so that volume and biomass were expressed on tree level, summed per plot and divided according to Eq. (1). The dependence of BEF on stand age was derived using the equation:

$$BEF = a + b \exp\left(-\frac{age}{100}\right) \tag{2}$$

where *a* and *b* are the parameters (Lehtonen et al., 2004). Values of parameters (*a*, *b*) were (0.466, 0.164) for spruce, (0.443, 0.107) for pine and (0.591, 0.194) for beech. They were derived from the database of growth and yield research plots. Since no reliable allometric equation for oak was available, BEF for oak was obtained using stand-level expansion factors (EFs) published by Pařez et al. (1990) and the conventional wood density of oak (0.58 t m⁻³, IPCC, 2003). Since data from Pařez et al. (1990) was expressed in tabular form for distinct values of mean tree diameter (DBH) of a stand, it was expressed in a functional form in relation to DBH as

$$BEF = \frac{a+b}{DBH^c}$$
 (3)

where the parameters a, b and c were 0.70, 18.69 and 1.97, respectively. Finally, C_{AB} (kg) was obtained from AB assuming a carbon fraction of 0.5.

2.2. Soil carbon

Soil samples from 180 permanent research plots were used as observations of soil and litter carbon to be compared with model predictions. These plots included 12, 3, 7 and 158 plots of beech, oak, pine and spruce, respectively. Since soil sampling was mostly not conducted on the plots selected for biomass inventory (Table 1), the soil observations were treated independently as groups on the level of individual tree species. On these plots, one to three measurements of soil profile depth and corresponding carbon concentration (C_{ox} , %) for mineral

Table 1 Stand characteristics of permanent research plots applied for model calibration

Species	Plot ID	Elevation (m)	Precipitation (mm/year)	Air temperature (°C)	Planting year	Age of first observ.	No. of observ.	Site index
Beech	501118	564	746	7.4	1910	62	7	4
Beech	501119	739	763	7.1	1937	35	7	6
Beech	501931	541	1023	6.359	1914	58	6	3
Beech	6020105	760	660	7.363	1899	67	6	7
Beech	6020107	735	627	6.702	1902	64	6	5
Beech	6020110	830	646	6.2	1922	44	6	5
Beech	6051405	533	744	8.0	1886	82	7	6
Oak	501068	490	578	7.4	1890	78	8	4
Oak	501069	512	569	7.7	1883	85	7	5
Oak	501855	300	613	8.1	1934	34	7	4
Oak	6011402	355	548	8.360	1898	68	6	6
Oak	6020404	565	693	7.327	1898	67	6	5
Oak	6061602	175	496	9.4	1927	43	7	1
Pine	503	402	713	10.3	1916	46	6	6
Pine	571	280	596	10.9	1936	26	6	4
Pine	573	280	625	10.9	1936	26	6	4
Pine	500622	445	592	8.103	1936	38	7	6
Pine	500625	574	524	6.833	1876	93	6	8
Pine	6010301	270	634	8.091	1899	66	7	7
Pine	6010302	270	634	8.091	1890	75	6	7
Pine	6032003	572	615	6.796	1894	72	8	8
Spruce	193	1020	1182	7.0	1926	32	7	4
Spruce	245	630	671	8.4	1911	53	6	7
Spruce	339	436	826	9.9	1912	48	7	3
Spruce	500615	436	561	7.697	1918	50	6	8
Spruce	501120	618	712	6.412	1907	61	8	4
Spruce	501121	750	1011	6.394	1937	38	6	6
Spruce	501126	585	672	6.661	1906	63	8	4
Spruce	501314	601	689	7.245	1931	38	7	3
Spruce	501621	631	647	6.7	1927	37	8	2
Spruce	501625	593	653	6.8	1907	57	8	3
Spruce	501639	697	750	6.931	1932	36	6	4
Spruce	503104	314	651	8.763	1931	38	7	4

and organic layers was available (totally 372 measurements). The carbon content of individual soil or litter layers in absolute values was calculated as

$$C_i = \rho_i d_i C_{\text{ox},i} (1 - \beta_i) \tag{4}$$

where *i* is the number of soil layer and $\rho_i d_i$, $C_{\text{ox},i}$ and β_i are the soil bulk density, thickness, portion of carbon in bulk density and portion of stones in the soil volume of the *i*th layer. Bulk density (Mg m⁻³) for mineral horizon was calculated as follows (Adams, 1973):

$$\rho = \frac{100}{(\%SOM/0.244) + ((100 - \%SOM)/MBD)}$$
 (5)

where %SOM is soil organic matter (%). %SOM is related to soil organic carbon content (C_{ox} , %) as follows: %SOM = $C_{ox} \times 1.724$. Bulk density for mineral fraction (MBD) is usually set at 1.64 Mg m⁻³ (Mann, 1986). Bulk density for the organic horizons was set at 0.140, 0.142 and 0.123 Mg m⁻³ for spruce, pine and beech stands, respectively, based on the results of the experimental data (Cienciala et al., 2006a). Bulk density of organic horizons for oak sites was set equal to that of beech sites. Soil and litter carbon pools (C_s and C_l , respectively) were obtained by summarizing C_i values

(Eq. (4)) for appropriate horizons. Organic horizons (l, h and f) were attributed to litter and the rest of the soil profile was considered as soil. One to three soil samples available on plot level were averaged and represented the single plot value. This data was compared on the level of individual species with the predicted soil carbon pool of the selected case stands (Table 1) at the age of 50 years.

2.3. Model adaptation

We used the BIOME-BGC (Running and Hunt, 1993; Thornton, 1998, 2000) model, version 4.1.1, which was specifically adapted to include key management routines, and some additional changes were made to handling interception, evaporation, throughfall, fine root mortality and industrial nitrogen deposition (Tatarinov and Cienciala, 2006). BIOME-BGC is a process-based model operating with a daily time step. It describes the distribution of energy and cycles of water, carbon and nitrogen for a specific type of terrestrial ecosystem. The calculation of biome gross primary production follows Farquhar et al. (1980), distinguishing illuminated and shaded foliage. Autotrophic respiration is separated into maintenance respiration calculated proportionally to the nitrogen content of living tissues (Ryan, 1991) and growth respiration that is handled as a function

of carbon allocated to the different plant compartments. Other details on the applied model can be found in Tatarinov and Cienciala (2006). The model requires three sets of input, namely site parameters, eco-physiological parameters and a series of daily meteorological data. The meteorological data can be extrapolated from a reference weather station at a given locality via the MTCLIM simulation model (Running et al., 1987; Thornton and Running, 1999).

The changes of the model code made within its adaptation to managed forest conditions (Tatarinov and Cienciala, 2006) were as follows:

- Forest management options were implemented, including thinning as a fraction of the tree biomass (carbon) pool harvested at a given age and an optional change of tree species following clear-cut felling.
- The routines for rainfall interception and evaporation from wet crowns were modified: (1) interception maximum was made proportional to all-sided leaf area index (LAI) only, (2) a fraction of precipitation was allowed to penetrate to the ground directly through the gaps between crowns, depending on LAI, (3) intercepted water not evaporated during the current day might remain in the canopy to evaporate the following day(s), (4) evaporation from wet canopy was simulated by Priestley—Taylor equation (Priestley and Taylor, 1972).
- Nitrogen deposition (N_d) was directly read from an input file based on the data on nitrogen emission dynamics in the Czech Republic from 1850 to 2000 of Kopaček and Veselý (2005).
- The fine roots turnover rate was made independent from foliage turnover rate and set to 0.811, 0.868 and 1.013 year⁻¹ for spruce, pine and broadleaved species, respectively (Kurz et al., 1996; Majdi, 2001).

2.4. Meteorology and other input variables to BIOME-BGC

The simulation by the BIOME-BGC model requires input of a series of meteorological data including minimum and maximum daily temperatures and daily precipitation. The meteorological data was taken from 40 weather stations situated all over the Czech Republic with available data series from 1961 to 2000. Meteorological data for a given plot was obtained using the nearest weather station available. The extrapolation of meteorological data from station to plot was done by the MTCLIM model (Running et al., 1987; Thornton and Running, 1999). The maximum and minimum temperature lapse rates for MTCLIM simulations were estimated using the data from these stations and were set to -6.0 and -2.0 K km⁻¹. The mean annual precipitation totals for each plot required by MTCLIM for the extrapolation of the actual precipitation from the base station to the individual plots were obtained from the spatial data set of the annual mean temperatures and precipitation totals all over the Czech Republic with a regular grid of 1–1 km (Květoň, 2001). The ratio $P(H_{base})/P(H_{site})$ obtained using the grid data as noted above was applied in the MTCLIM simulations to adjust daily precipitation from the base station to the site under simulation.

Besides the meteorological data, the information about environmental change including CO_2 concentration and nitrogen deposition, as well as site elevation and soil texture was used in the model runs. The ambient CO_2 concentration for each simulation year was taken from the Mauna Loa record (since 1959, Keeling and Whorf, 2004) and from Law Dome ice cores (before 1959, Etheridge et al., 1998). The actual N_d for a given plot and year was obtained from the N-deposition matrix for 2002 (Czech Hydrometeorological Institute, 2003) and historical development of nitrogen emissions (Kopaček and Veselý, 2005). If soil texture was unavailable for a certain site, it was derived for model simulation from the mean values of the plot soil type (P. Vopenka, unpublished results).

2.5. Modeling procedure

The BIOME-BGC simulation procedure contained three steps: (1) the full meteorological data set for the given plot was generated by the MTCLIM model using the plot elevation and the measured meteorological data series from the nearest weather station. (2) The spin-up (self-initialization) simulation was performed using the prepared meteorological data and ecophysiological parameters file corresponding to the given species. (3) The normal simulation started with the steady-state soil and litter C and N pools obtained at the previous step but with the stand felling in the first year of simulation.

To apply the model to the actual sites of managed ecosystems, both the current and historical management scenarios must be specified as input information to the model. The applied scenarios are described below.

2.6. Current management regimes

Since all the selected stands were managed, the applied management scenario including intensity and timing of thinning events was adjusted so as to correspond to the prescribed management regime as given by the Czech Forestry Act. The timing (stand age) and thinning intensity was derived from the recorded data from the individual plots and complemented by the Czech growth and yield tables (Černý et al., 1996) for the earlier period of stand development that was not covered by the long-term inventory. We converted thinning volumes to a corresponding share of biomass removed from the sample plot at a given age. Besides the thinning regime, mortality rates were changed for the current stand generation: fire mortality was set to zero and the whole plant mortality rate was reduced to 0.002 year⁻¹. This expressed the partial compensation of natural mortality by the imposed thinning regime.

2.7. Historical management scenarios

BIOME-BGC is a dynamic model including feedback between carbon pools in biomass and soil, which uses so-called spin-up simulation to reach equilibrium of carbon pools under given growth (climate and site) conditions. After that, a specific historical management may be applied that corresponds to the site history of the studied site and region. In the territory of The Czech Republic, the primary virgin forests were cut at the lower elevations during the 13th and 14th centuries (Nožička, 1957), then partially transformed into agricultural lands, while other parts remained as forested lands with more or less regular harvesting (Pietsch et al., 2003; Güde, 1960). Large areas of agricultural land were abandoned and consequently reforested during the 30-years War (1618–1648). Their regular utilization restarted only in 18th century (Nožička, 1957). At higher elevations, the regular forest harvesting started later, namely during 18–19th centuries. Regular forest management, strongly promoting the replacement of the original mixed species stands by Norway spruce, started in the middle of 18th century (Spiecker, 2000; Nožička, 1957). The simulation by BIOME-BGC that included several forest rotation cycles showed that

soil and litter carbon pools as well as the biomass growth rate usually decreased from cycle to cycle (Pietsch et al., 2003; Pietsch and Hasenauer, 2002, 2005).

To reflect management history of the studied sites on this study, we applied two management scenarios, namely:

- 1. Clear-cut in the Middle Ages (14th century) with temporal transformation of forest into grassland, followed by the forest restoration in 18th century with four 100-year long rotations for coniferous forests or three 120-year long rotations for deciduous forests—applicable to sites with elevation below 800 m.
- 2. Two 100-year long rotations for coniferous forests or one 120-year long rotation for deciduous forests starting in 18–19th centuries—applicable to sites with elevation above 800 m.

Table 2
The final parameter sets for the individual tree species

The final parameter sets for the individual tree species					
Parameter description	Beech	Oak	Pine	Spruce	
Transfer growth period as fraction of growing season (prop.)	0.17	0.25	0.3	0.3	
Litterfall as fraction of growing season (prop.)	0.2	0.3	0.3	0.3	
Annual leaf turnover fraction (year ⁻¹)	1	1	0.39	0.24	
Annual fine root turnover fraction (year ⁻¹)	1.023	1.023	0.868	0.811	
Annual live wood turnover fraction (year ⁻¹)	0.7	0.7	0.7	0.7	
Annual whole-plant mortality fraction (steady state) (year ⁻¹)	0.01	0.01	0.01	0.01	
Annual whole-plant mortality fraction (historical) (year ⁻¹)	0.005	0.006	0.005	0.005	
Annual whole-plant mortality fraction (actual) (year ⁻¹)	0.002	0.002	0.002	0.002	
Annual fire mortality fraction (steady-state) (year ⁻¹)	0.01	0.01	0.005	0.005	
Annual fire mortality fraction (historical) (year ⁻¹)	0.005	0.005	0.0025	0.0025	
Annual fire mortality fraction (actual) (year ⁻¹)	0	0	0.002	0.001	
Allocation new fine root C:new leaf C (ratio)	1.10	1.20	1.00	0.66	
Allocation new stem C:new leaf C (ratio)	2.71	1.70	2.12	2.20	
Allocation new live wood C:new total wood C (ratio)	0.160	0.160	0.076	0.100	
Allocation new root C:new stem C (ratio)	0.15	0.26	0.44	0.21	
Allocation current growth proportion (prop.)	0.5	0.5	0.5	0.5	
C:N of leaves (kg C/kg N)	27.0	27.2	36.0	43	
C:N of leaf litter, after retranslocation (kg C/kg N)	49.8	64.1	122.0	83.0	
C:N of fine roots (kg C/kg N)	72.0	73.5	49.0	42.0	
C:N of live wood (kg C/kg N)	70.0	73.5	58.0	37.1	
C:N of dead wood (kg C/kg N)	520	451	730	730	
Leaf litter labile proportion	0.12	0.20	0.26	0.28	
Leaf litter cellulose proportion	0.56	0.56	0.49	0.38	
Leaf litter lignin proportion	0.32	0.24	0.25	0.34	
Fine root labile proportion	0.30	0.34	0.23	0.23	
Fine root cellulose proportion	0.45	0.44	0.41	0.41	
Fine root lignin proportion	0.25	0.22	0.36	0.36	
Dead wood cellulose proportion	0.75	0.75	0.70	0.70	
Dead wood lignin proportion	0.25	0.25	0.30	0.30	
Canopy water interception coefficient ^a (mm/LAI)	0.3	0.3	0.3	0.3	
Canopy light extinction coefficient	0.45	0.54	0.495	0.50	
All-sided to projected leaf area ratio	2.0	2.0	2.6	2.6	
Canopy average specific leaf area (SLA) ^b (m ² /kg C)	35.0	34.5	9.5	7.8	
Ratio of shaded SLA:sunlit SLA	2	2	2	2	
Fraction of leaf N in Rubisco	0.100	0.088	0.055	0.053	
Maximum stomatal conductance ^b (m/s)	0.0050	0.0050	0.0025	0.0020	
Cuticular conductance (m/s)	6E-05	6E-05	6E-05	6E-05	
Boundary layer conductance ^b (m/s)	0.010	0.005	0.010	0.009	
Leaf WP: start of conductance reduction (MPa)	-0.34	-0.50	-0.50	-0.50	
Leaf WP: complete conductance reduction (MPa)	-2.2	-3.5	-0.50 -2.5	-2.5	
VPD: start of conductance reduction (Pa)	600	200	600	610	
VPD: complete conductance reduction (Pa)	3000	2550	2500	3100	
VFD. complete conductance reduction (Pa)	3000	2550	2300	3100	

^a Meaning of this coefficient differs from the original model code: see model description.

^b On projected leaf area basis.

Mortality parameters for steady-state run were set as in our companion paper (Tatarinov and Cienciala, 2006). For the period of historical management and current rotation, we applied reduced mortality values as shown in Table 2. The two latter parameter sets differ because no thinning was applied during historical management, but it was applied for the current rotation.

The default forest biome species for spin-up simulation was set as oak, beech and spruce for the elevations below 400 m, between 400 and 900 m and above 900 m, respectively, according to the Czech typological classification (Průša, 2001). For sandy soils (sand fraction above 80%) at the elevations below 400 m, the default biome species was pine.

2.8. Model parameterization

The strategy of model parameterization was to start with the default parameter sets for broad categories of temperate forests (broadleaved and coniferous) applied on medium site class and test them against the verification data set, consisting of the observed long-term wood production in the research (growth and yield) plots. This analysis was linked to our companion study on sensitivity analysis (Tatarinov and Cienciala, 2006), which identified the key parameters in terms of their effect on carbon pools. The analyses made for both papers resulted in basic tree species-specific parameter sets. As for the sitespecific parameters, the modeled aboveground biomass (C_{AB}) was compared to the observed production data. In Czech forestry, 11 site classes are used, ranging from 9– (the lowest) to 1+ (the highest). With the aim of applying minimal possible tuning, we used only two site parameters to vary across the sites depending on site class within each forest species. These parameters were natural nitrogen fixation and effective soil depth. The range of likely natural nitrogen fixation values was based on the data of Jurgensen et al. (1990) and Perez et al. (2003). Soil depth ranged from 0.3 to 1.5 m for individual sites and species. All other vital site parameters were either specifically known for the given site or held constant across species type. The latter include initial foliage carbon pool (set to $0.001~\mathrm{kg}~\mathrm{C}~\mathrm{m}^{-2}$ for deciduous and $0.002~\mathrm{kg}~\mathrm{C}~\mathrm{m}^{-2}$ for coniferous species) and initial stem carbon pool (set to 0.002 kg C m⁻² for all species).

With respect to other parameter resources used for the above described parameterization procedure, the default eco-physiological parameters for the studied species, except for oak, were obtained mostly from White et al. (2000), using the species-specific mean of the reported parameter values. If some parameters for a given species were missing, the default value for evergreen needle-leaf forest (ENF, for spruce and pine) or deciduous broadleaf forest (DBF, for beech) was used. The eco-physiological parameter set for oak was mostly taken from Pietsch et al. (2003). Besides the data of White et al. (2000), we used the following sources of eco-physiological parameters for individual species for establishing the range and mean parameter values (Antunez et al., 2001; Bartelink, 1997, 1998; Bauer et al., 1997; Broadmeadow and Jarvis, 1999; Cermak, 1998; Churkina et al., 2003; Gay et al., 1994;

Helmisaari et al., 2002; Jach and Ceulemans, 1997, 1999; Laitat et al., 1999; Lefevre et al., 1999; Marek and Kalina, 1996; Niinemets and Kuul, 1995; Nilson et al., 1999; Ross et al., 1986).

The simulation accuracy was evaluated by classical regression analysis with relative error (ER) of prediction calculated as

$$ER = \frac{C_{AB,simulated} - C_{AB,observed}}{C_{AB,observed}} \times 100\%$$
 (6)

where the additional subscript with C_{AB} indicates the simulated and observed aboveground carbon.

3. Results

The result section refers to BIOME-BGC model predictions obtained using the final parameter sets for the four studied species as shown in Table 2.

3.1. Aboveground biomass

The fit of the model simulation of carbon pool in aboveground biomass (C_{AB}) to the observed data was strong: for the whole set of analyzed plots (Table 1, n = 32 plots excluding oak plot no. 6061602) combining all species, the coefficient of determination (r^2) reached 0.91 for n = 213 points with the estimated standard error (S.E.) of 1.19 kg C m⁻² (Fig. 1). For individual species of beech, oak, pine and spruce, the $r^2 = 0.92$ corresponding coefficients were S.E. = 0.88 kg C m^{-2}), $0.90 (n = 35, \text{ S.E.} = 1.00 \text{ kg C m}^{-2})$, 0.92 $(n = 51, 0.49 \text{ kg C m}^{-2})$ and $r^2 = 0.86$ $(n = 83, 0.49 \text{ kg C m}^{-2})$ S.E. = 1.40 kg C m^{-2}), respectively. For all the mentioned cases P < 0.001. The slope of the regression line for the total set of observed data was 0.92. The slope parameter and

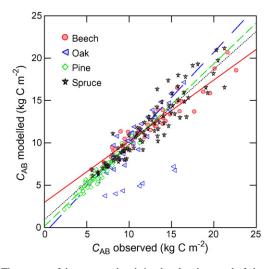


Fig. 1. The scatter of the measured and simulated carbon pool of aboveground tree biomass ($C_{\rm AB}$) for the analyzed permanent research plots of beech, oak, pine and spruce; the regression lines approximate all data per species. Excluded from the regression are the points of the oak plot no. 6061602 situated in a floodplain area (empty triangles).

coefficient of determination for the model approximation of the observed $C_{\rm AB}$ for individual plots are listed in Table 3. The mean absolute value of ER (Eq. (6) for the total set (excluding oak plot no. 6061602) reached 8.2%; the corresponding errors for the individual species of beech, oak, pine and spruce were 8.7, 8.4, 6.6 and 8.8%, respectively.

The simulated $C_{\rm AB}$ during the course of the actual stand rotation for two selected sample plots for each tree species is shown in Fig. 2. For each case, the simulated line of $C_{\rm AB}$ shows a typical pattern of managed stands with thinning events seen as dips in some years. The simulated $C_{\rm AB}$ approximated the observed values satisfactorily, except of the oak plot no. 6061602 located in a floodplain region, the case of which is further discussed below. On the other hand, the simulated biomass production of other plots matched the observations well (Table 3; Fig. 2). In the case of beech, it is interesting to note that the production of younger stand with lower site class came close to that observed for the older stand with higher site class. The case of pine plots (Fig. 2, bottom left) demonstrates the effect of good and poor site classes. The modeled biomass matched both observed

situations well, with the coefficient of determination reaching 0.995 and 0.977 for the two plots, respectively (Table 3). The pair of selected spruce plots illustrates the effect of different management timing and intensity (Fig. 2, upper left).

3.2. Soil and litter carbon

The observed soil carbon pool (C_s) assessed from the measurements on individual plots, ranged from 2.0 to 37.5 kg C m⁻² with the mean value of 13.1 and median of 11.6 kg C m⁻². Classified by tree species, the median observed values of C_s were 13.2, 7.7, 4.0 and 11.9 for beech, oak, pine and spruce locations, respectively. The species-specific median values of C_s simulated by BIOME-BGC for the set of analyzed sites (Table 1) were 10.6, 11.0, 6.4 and 9.7 kg C m⁻² for beech, oak, pine and spruce sites, respectively. The *t*-test showed that all differences between observed and predicted C_s values were statistically insignificant for all species-specific locations, apart from those of pine (ANOVA, F = 6.011, p = 0.023, Fig. 3 left). This is further discussed below.

Table 3 Site parameters of permanent research plots applied for model calibration and the results of a comparison of simulated and observed aboveground biomass values (C_{AB})

Species P	Plot ID	Soil depth (m)	Sand fraction (%)	N fixation (g m ⁻² year ⁻¹)	N deposition (g m ⁻² year ⁻¹)	Approximation of observed C_{AB}		
						Slope	r^2	ER (%)
Beech	501118	1.1	44	0.7	0.77	0.938	0.952	5.681
Beech	501119	0.8	45	0.5	0.89	0.822	0.988	6.109
Beech	501931	1.1	82	0.8	1.17	0.494	0.923	12.664
Beech	6020105	0.7	40	0.4	1.31	0.578	0.915	7.909
Beech	6020107	0.8	40	0.55	1.11	0.525	0.935	8.763
Beech	6020110	0.8	40	0.55	1.04	0.483	0.791	25.119
Beech	6051405	0.8	40	0.5	0.94	0.659	0.976	10.433
Oak	501068	0.9	40	0.7	1.35	0.847	0.948	9.445
Oak	501069	0.7	40	0.6	1.35	0.734	0.952	7.82
Oak	501855	0.9	40	0.7	0.65	0.774	0.942	10.779
Oak	6011402	0.6	40	0.4	1.55	0.958	0.909	4.364
Oak	6020404	0.7	82	0.6	1.39	0.89	0.86	9.555
Oak	6061602	1.5	40	0.8	1.19	0.410	0.972	53.111
Pine	503	0.9	40	0.5	0.92	0.803	0.976	4.887
Pine	571	1.2	40	0.7	0.6	0.978	0.989	10.965
Pine	573	1.2	40	0.7	0.63	1.133	0.995	5.697
Pine	500622	0.9	79	0.5	0.65	0.804	0.984	5.121
Pine	500625	0.3	53	0.1	0.75	0.817	0.885	9.651
Pine	6010301	0.3	82	0.15	0.75	0.736	0.906	5.659
Pine	6010302	0.3	82	0.15	0.75	0.916	0.922	3.383
Pine	6032003	0.3	40	0.1	1.3	0.989	0.977	7.05
Spruce	193	0.7	40	0.4	0.57	0.772	0.996	7.35
Spruce	245	0.6	60	0.3	0.8	0.565	0.95	6.748
Spruce	339	0.8	40	0.5	1.4	0.788	0.988	7.868
Spruce	500615	0.61	43	0.2	0.63	0.721	0.995	4.376
Spruce	501120	0.7	50	0.4	0.8	0.785	0.932	8.508
Spruce	501121	0.63	62	0.4	0.97	0.664	0.99	13.251
Spruce	501126	0.7	50	0.4	1.12	1.063	0.765	9.382
Spruce	501314	0.8	40	0.5	0.8	0.79	0.946	18.59
Spruce	501621	0.8	40	0.5	1.02	1.235	0.98	6.283
Spruce	501625	0.8	40	0.5	1.02	1.055	0.935	6.836
Spruce	501639	0.7	40	0.4	1.26	0.908	0.98	3.634
Spruce	503104	0.7	21	0.4	0.68	0.596	0.965	11.473

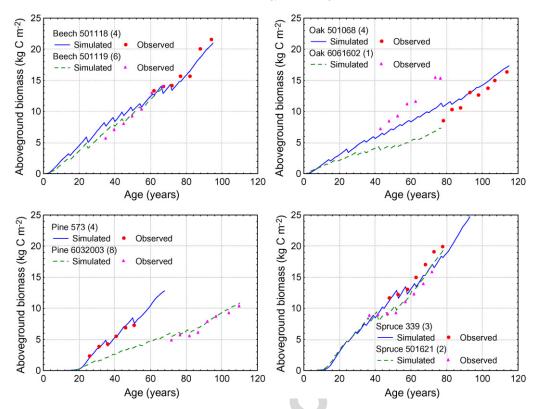


Fig. 2. Simulated and observed aboveground biomass pool of carbon against stand age—for each species, two plots are selected, with plot ID and site class noted in the parenthesis, respectively. In the case of oak plot no. 6061502 is also shown.

The observed litter carbon pool (C_1) ranged from 0.0 to 4.9 kg C m⁻² with the mean value of 1.41 and median of 1.25 kg C m⁻². The median observed values of C_1 reached 0.67, 0.20, 1.15 and 1.30 kg C m⁻² for beech, oak, pine and spruce sites, respectively. The median simulated litter carbon pool for the analyzed sites of individual species at stand age of 50 was 0.92, 1.03, 0.64 and 1.05 for beach, oak, pine and spruce, respectively. No significant difference between observed and predicted values was observed for any species (Fig. 3 right). The simulated litter pool always reached its maximum shortly

after the imposed felling, and it stabilized after ca. 40 years (see also the example in Fig. 6).

3.3. Parameterization of site classes

As mentioned, the model calibration for individual sites concerned two parameters, namely nitrogen fixation and soil depth, which were allowed to vary to reflect the specific site class conditions. Both parameters had a strong positive effect on the simulated aboveground biomass (Fig. 4). However,

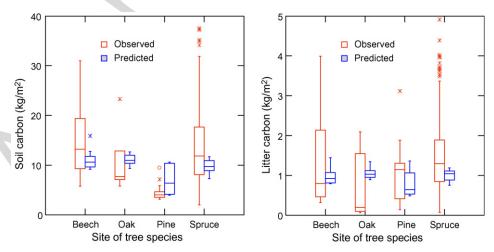


Fig. 3. Box plot of the observed and predicted soil (left) and litter (right) carbon pools for sites of individual tree species. The centerline marks the median of the sample. The box length shows the central 50% of the values with box edges at the first and third quantiles. The differences between the observed and predicted pools were insignificant for all litter pools and for all soil pools apart from that of pine (p = 0.023).

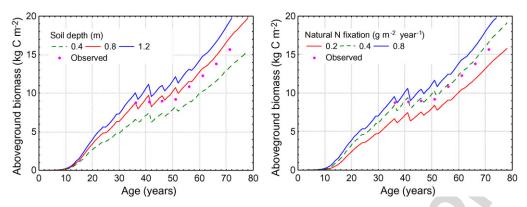


Fig. 4. Effect of effective soil depth (left) and natural nitrogen fixation (right) on aboveground biomass simulated using different parameter values; the observed data are from the spruce plot no. 501621 (site index 2).

under high parameter values this effect decreased. It became apparent that this calibration produced a rather strong linear dependence of both parameters on site class for each tree species analyzed here (Fig. 5, Table 4).

4. Discussion

4.1. Aboveground biomass

The overall match of model simulations with the long-term observation of C_{AB} (Figs. 1 and 2) is considered as very good for several reasons. First, it must be noted that the identical set of eco-physiological parameters was used across all sites of individual species. Basically all these parameters were retained within the ranges reported in the literature. One exception was nitrogen fraction in Rubisco beech (0.1; dimensionless), which was slightly higher than the value of 0.088 reported for deciduous species by White et al. (2000). Secondly, the runs were performed under very uncertain information on land-use history, which was only roughly derived from scarce literature evidence and historical maps (Nožička, 1957). Thirdly, the observations of stem biomass (or carbon) increment, which served as the critical reference for model performance used in this study, were typically available only for a fraction of the actual stand rotation: this data was spread across three or four decades only. Finally, other vital site-specific information was limited and in many instances had to be derived, e.g., soil

texture. Soil depth and total nitrogen input are among the most important site parameters needed for a more reliable model prediction as was also previously demonstrated in model sensitivity analysis (Tatarinov and Cienciala, 2006). These two parameters were also adjusted to reflect site class conditions. The effect of these parameters will be further discussed below.

Nevertheless, the inclined slope of the common regression line observed for individual species (Fig. 1) reveals that relative to the observed values, C_{AB} tended to be overestimated for the early period of stand development, while it became somewhat underestimated when the stand was old. This observation was similar for all species, but most pronounced for beech. This prediction pattern can be detected on Figures for individual plots, such as for spruce plot no. 339 or beech plot no. 501119 (Fig. 2). The quantitative indicator of this trend for individual plots is the slope between the simulated and measured C_{AB} that was commonly less than 1 (Table 3). The posing explanation of this observation is the frequently discussed evidence of increased growth, which is in the current research focus (e.g., Karjalainen et al., 2002; Mellert et al., 2004). It remains unclear what the decisive factor of the increased growth is; however, it becomes evident that nitrogen may have the dominant role, with additional contribution of increased temperature and CO₂ concentration (Karjalainen, 2002). Although the model included the specific pattern of increased deposition observed in the country based on Kopaček and Veselý (2005), the actual effect on growth might have been

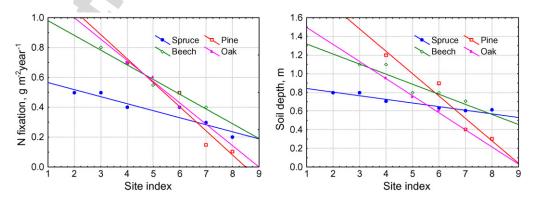


Fig. 5. Dependence of site parameters applied for model calibration on site index. Oak plot no. 6061502 of site class 1 is not shown.

Table 4 Parameters of linear regression (y = a + bx) of site parameters applied for calibration on site index

Species	Parameter	а	b	r^2
Beech	N fixation	1.1000	0.1000	1.000
Oak	N fixation	1.2857	-0.1429	0.952
Pine	N fixation	1.1571	-0.1371	0.914
Spruce	N fixation	0.6125	-0.0471	0.863
Beech	Soil depth	1.4263	-0.1079	0.819
Oak	Soil depth	1.5143	-0.1571	0.960
Pine	Soil depth	2.2286	0.2486	0.890
Spruce	Soil depth	0.8800	-0.0388	0.853

stronger than that simulated by the model. This issue deserves a more detailed analysis than allowed within the scope of this paper.

The model underestimation of $C_{\rm AB}$ for oak plot no. 6061602 is shown in Fig. 2 to exemplify that this modeling tool cannot handle very specific ecosystems. The plot mentioned is situated in a floodplain region with a considerable rainfall deficit, which is counterbalanced by utilizing the abundant ground water supply. This mechanism was not built in to the current model, but an adequate model adaptation was already successfully tested for this ecosystem (Pietsch et al., 2003). Since such an ecosystem is scarce in the conditions of this country, we have not attempted to include this rather demanding adaptation into our model.

4.2. Soil and litter carbon

Soil compartment is one of the key components of the ecosystem carbon budget. As BIOME-BGC includes feedback mechanisms between soil and vegetation, both ecosystem pools must be predicted with confidence in order to obtain a meaningful ecosystem carbon budget. The match found between the modeled soil and litter carbon ($C_{\rm s}$ and $C_{\rm l}$, respectively) and available observations of $C_{\rm s}$ and $C_{\rm l}$ was considered satisfactory for all species. In the case of pine, the inconsistency between the two data sets was partly attributed to the elevation effect. Once the effect of altitude was considered in the analysis of covariance (ANCOVA), the differences between the modeled and observed soil carbon decreased from p=0.023 to 0.015.

In general, the analysis of soil and litter carbon suffers from a limited sample size of observations, which applies for all species apart from spruce. Therefore, the analysis of the modeled and observed C_s and C_l is used as complementary information on model performance and to provide a complete picture of the forest carbon budget. Anyway, it is obvious that soil carbon will remain one of the most uncertain components of the carbon budget, because verification data is either scarce or highly variable, and the driving processes are slow with long-term residual effects (see below). Actually, no other published reference shows a similar comparison of observed and BIOME-BGC-simulated C_s for different forest ecosystems. Thürig (2005) compared two modeling approaches, namely BIOME-BGC and YASSO in combination with empirical model

MASSIMO. They reported larger differences in predicted $C_{\rm s}$ as compared to the predicted biomass between the two models. Generally, the simulated and observed soil carbon pools in this study were somewhat smaller as compared to the data of Jobbágy and Jackson (2000), who reported the soil carbon pool in the upper 1 meter of soil as 17.4 and 14.5 kg m⁻² for temperate deciduous and evergreen forests, respectively, with corresponding standard deviations of 10.8 and 8.4 kg m⁻².

The model simulation of litter carbon (C_1) was actually in line with the independent observations, although the variability was also high. Vetter et al. (2005) showed that for coniferous forests in Thuringia, Germany, C_1 was probably underestimated. Our simulated values of C_1 were higher than those generated in the study of Vetter et al. (2005), although still below their reported measurements (from 2.2 to 3.6 kg m⁻²). We assume that this might be due to a different litter definition applied in that study.

It should be noted that the distinction between litter and soil in the BIOME-BGC model is not clear enough. Litter is defined in the model in terms of its chemical composition (soluble fraction, cellulose and lignin), but not in terms of soil horizons (Thornton, 1998, 2000). Therefore, attributing the model soil and litter pools to the observed data remains arbitrary. This may also be why several studies with BIOME-BGC do not really clarify how the observation of litter and soil attribution was performed (e.g, Pietsch and Hasenauer, 2002; Pietsch et al., 2003; Vetter et al., 2005). Merganičová (2005) considered horizons l, f, h as litter and the mineral horizons as soil. In our study we treated the observed litter and soil in the same way.

4.3. Considering site-specific conditions

The specific site conditions strongly affect the carbon budget and therefore will always be critical for a successful model prediction. The model, on the other hand, must include routines and functional relationships to permit generalization and application over larger scales. BIOME-BGC has the following major parameters driving the site growth conditions: soil texture, effective soil depth, nitrogen input and initial vegetation carbon pools. Other site parameters affect the BIOME-BGC prediction indirectly via the calculation of site meteorological data series using the MTCLIM model. These include in particular latitude, elevation above sea level, site exposition and slope and annual precipitation total. Our earlier analysis (Tatarinov and Cienciala, 2006) showed a high model sensitivity to soil depth, nitrogen input and site precipitation total. Latitude and elevation for a given site were known and could be directly fed into the model as independent variables. Precipitation totals and industrial nitrogen deposition were taken from base station data and grid interpolation. Input data on soil texture may be aggregated from sufficient sampling schemes (e.g., Vetter et al., 2005) or they can be derived from soil maps as applied here, when soil texture information was not available for most of the growth and yield plots. Hence, the two important parameters of site conditions, soil depth and nitrogen fixation, remained uncertain and were used to tune the model for specific sites.

Soil depth (d) may substantially affect model simulation (Fig. 4, right). It strongly affects water budget, influencing transpiration and hence also growth, whereas soil microbial activity and soil respiration directly affect soil carbon pools and site carbon budget. It must be noted that soil hydrology is very much simplified in the current model version. Since the model does not consider groundwater supply and drainage, d simply determines soil water capacity, supposing that all incoming water is distributed within this volume, except for the surplus precipitation that runs off. It is evident that this concept would be important for flat regions and floodplain areas as discussed above for the case of the oak plot no. 6061602 and shown in Fig. 2. In floodplain areas, the local precipitation may not meet the evaporation demand and high forest production can only be granted by the availability of underground water (Pietsch et al., 2003; Molchanov and Molchanova, 2000). The importance of drainage was shown to be important, e.g., for a landscape in Central Russia, where a minor slope would result in more productive stands as compared to those in flat watersheds (Schultze et al., 2002). On the other hand, such situations are not common in the more or less hilly forested landscape of the Czech Republic, the subject of the current study. Soil depth is therefore rather strongly coupled to forest biomass production, which has also been confirmed by the linear relationships of soil depth with forest site class that was observed for all tree species under current study (Fig. 5, Table 4).

Another important site driver affecting biomass prediction is nitrogen. It represents the only nutrient element incorporated in the model, while other important nutrients such as phosphorus and potassium are not included in the model routines. While nitrogen deposition can reasonably be extracted from extrapolation of available observation sites, the information on actual natural nitrogen fixation ($N_{\rm f}$) for sample plots is not commonly known. This parameter can vary considerably in relation to local microclimatic conditions and management scenarios (Gessler et al., 2005). It is usually higher for deciduous than for coniferous stands (Jurgensen et al., 1990; Perez et al., 2003). Evidently, the effect of $N_{\rm f}$ on the modeled biomass production is strong, as it was demonstrated on the case of spruce plot no. 501621 (Fig. 4, left). The effect of $N_{\rm f}$ on $C_{\rm AB}$ is particularly strong for small $N_{\rm f}$ values, while it becomes

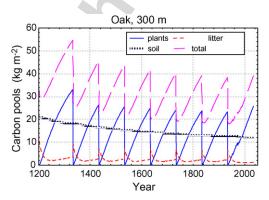
smaller for high $N_{\rm f}$ values (Tatarinov and Cienciala, 2006). The observed relationship of $N_{\rm f}$ with forest site class further confirmed the close dependence of biomass production on nutrients in the model, which was apparent for all species under study (Fig. 5, Table 4).

The above observations on parameters reflecting forest site class are vital for a large-scale model application, where site-specific conditions require attention and must be reasonably generalized. A good example of landscape categorization by site conditions for large-scale simulation purposes was recently shown by Vetter et al. (2005). In our approach, this may be addressed by utilizing the apparent linear trends between site class and both soil depth and nitrogen fixation.

As for the other site parameters that may affect the model prediction of biomass, we noted a specific importance of initial vegetation (stem and leaf) carbon. The initial vegetation carbon in a planted stand may be adjusted so as to reflect tree species and the age of plant seedlings for the given site, i.e., it corresponds to forest planting management and it is not related to site growing conditions. A larger value results in earlier, and therefore also larger, biomass accumulation at any time of a rotation period. Therefore, site-specific values would often have helped to improve the match between the modeled and observed biomass carbon accumulation (production). However, focusing on a robust model prediction and more widely applicable parameters, we applied identical initial values of stem and leaf carbon across deciduous and coniferous species. In any case, it would be advisable to seek average initial leaf carbon, generalized at least, at the level of tree species.

4.4. Effect of land-use management

It must be understood that any land management will affect ecosystem carbon pools. Hence, land-use history is vital for the analysis of current stand rotation and its carbon pools. Specifically, $C_{\rm s}$ requires a particularly long time to reach a new equilibrium after the imposed management regime. Fig. 6 shows two examples of such effect on the oak stand grown at an elevation of 300 m and exemplified by the research plot no. 501855 (Table 1). For this case, the long-term simulation, since 13th century, using 100-year-long rotation cycles showed that



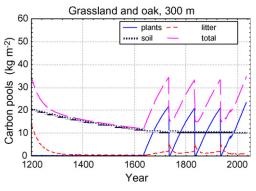


Fig. 6. Effect of land-use management scenarios on carbon pools: (1) Virgin forest felled in 13th century followed by a rotation cycle of 100 years (left); (2) Virgin forest felled in 13th century, replaced by grassland and afforested in the middle of 17th century with forest of 100 year long rotation cycle (right). These examples were generated for the example oak site and the permanent research plot no. 501855 (Table 1).

the C_s stabilized only after seven rotations (Fig. 6, left). Under the last rotation, a further decrease was observed due to an imposed thinning regime. It can be expected that C_s would stabilize faster if thinning and/or wood removal was prescribed for all stand rotations. Note that for managed stands the wholeplant mortality fraction was always reduced (Table 2) as the thinning regime to some degree substituted the natural mortality in unmanaged ecosystems. This is an absolutely crucial mechanism distinguishing conditions of managed stands. If natural mortality were preserved, the effect of thinning would have been reinforced. If natural mortality were used to mimic thinning (as e.g., Vetter et al., 2005), litter input to soil compartment would have been significantly enhanced, which does not correspond to the real situation of a thinning regime with wood removal. Additionally, using mortality to mimic a thinning regime would mean applying identical thinning fraction during whole stand rotation. This is undesirable, because in managed stands the prescribed fraction of biomass removed by thinning considerably decreases with stand age (Černý et al., 1996). Actually, the latter approach was used, e.g., by Vetter et al. (2005). That study, however, was primarily concerned with biomass carbon budget.

A complementary problem is the parameterization of fire mortality $(m_{\rm f})$. We assumed that $m_{\rm f}$ of managed stand was reduced by fire protection measures and hence it was set lower (Table 2). It is necessary to notice, that when zero $m_{\rm f}$ is used (e.g., Pietsch et al., 2005) and applied also for spin-up simulation, the steady-state carbon pools would be considerably larger (up to two times). Consequently, the model would require a considerably longer period to stabilize soil carbon pools under the conditions of forest management, extending for more than five stand rotations. Therefore, the solution of applying different mortality values for different periods of landuse management seems more adequate.

When the land-use scenario included grassland, $C_{\rm s}$ always stabilized sooner compared to managed forest due to significantly smaller litter-fall during the intermezzo of grassland regime (Fig. 6, right). As expected, other ecosystem pools (litter and biomass) exhibited much faster turnover compared to $C_{\rm s}$ (Fig. 6).

It is obvious that reliable detection of carbon stock changes in forest ecosystems remains challenging, both on local and, even more so, on larger spatial scales. The latest Good Practice Guidance for reporting emissions from the Land-use, land-use change and forestry sector (IPCC, 2003) under the Climate Convention (UNFCCC, United Nations Framework Convention on Climate Change) and its Kyoto Protocol asks for either including soil carbon stock changes in reports or proving that carbon is not being lost from the ecosystem. Our simulation exercise confirms that both requirements represent a very challenging task, as the residual effect of historical land use is likely to mask the effect of current management practices on the soil carbon pool. The same concern applies for practicable discerning of contributing processes, which was also stated by the recent expert evaluation of IPCC (Apps et al., 2003). In the recent elegant application of BIOME-BGC, Vetter et al. (2005) concluded that they were able to distinguish direct and indirect human impacts on carbon sequestration in a managed coniferous forest, referring to accounting requirements of Art. 3.4 of the Kyoto Protocol. However, since the reporting is required by five pools, soil should also be explicitly considered. The study of Vetter et al. (2005) does not discuss soil carbon issues, but it includes the information on area averaged soil and litter accumulation rates, which were mostly negative, i.e., these compartments were loosing carbon. On the other hand, these quantities were insignificant as compared to the biomass accumulation rates reported.

4.5. Other notes on model concept

Biome-BGC remains sufficiently general considering the amount of processes included. Several minor issues have been identified that could be improved, such as handling of interception and evaporation from wet crown (Tatarinov and Cienciala, 2006) and ground water utilization (Pietsch et al., 2003). A more significant conceptual improvement should include handling of multilayer vegetation, which is specifically needed for the transition between old and newly planted stands, as well as for natural succession and stands of mixed species. An important study in this direction was performed by Bond-Lamberty et al. (2005), who successfully adapted BIOME-BGC to support multiple interacting vegetation types.

One important feature worth paying attention to was the pattern of NPP during the stand development. Typically for

Dead woody tissues (kg C m-2)

니 100

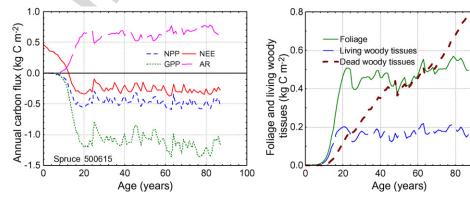


Fig. 7. (Left) Annual biomass carbon fluxes; (right) development of foliage, living and dead woody tissues during one stand rotation (example shown: spruce stand no. 500615).

conifers, the simulated NPP (and GPP) increased dramatically for about 20 years and thereafter it leveled off, although some oscillations remained due to changing weather conditions or imposed thinning regime (Fig. 7, left). NPP should basically mimic current increment, which usually reaches its maximum when stand age is about 50 years and then gradually decreases as the stand becomes older. Associate with older stands is increased respiration, higher hydraulic resistance and perhaps other mechanisms (e.g., Ryan et al., 1997), which are not included in the model. Hence, the pattern demonstrated in Fig. 7 does not correspond to the expected development. The reason for such model behavior is as follows. The model divides woody biomass (both aboveground and belowground) into two compartments, namely that of living (sapwood) and dead (heartwood) woody tissues. The growth of living woody tissues is determined by GPP (i.e., by LAI), whereas its transformation into dead woody tissues is determined by a constant fraction of 0.7 per year (White et al., 2000). The simulated LAI for spruce reaches a plateau about 20 years after stand planting, which approximately corresponds to real observations (a slight further increase of foliage biomass at the age of about 60 years was likely evoked by the increase of CO2 concentration and nitrogen deposition). After that, growth of living woody tissues level off (Fig. 7, right). Since the rate of transformation of living into dead woody tissues is set proportional to the amount of living woody tissues, the pool of living woody tissues becomes constant soon after the stabilization of LAI. On the contrary, dead woody tissues that do not respire continue growing (Fig. 7, right). Consequently, AR remains close to constant once LAI becomes stable. There is no additional age-related decline mechanism built in to the model. On the other hand, age-related changes of NPP are not critically important for intensively managed stands with relatively short rotation periods (about 100 years). Some modification of living wood to dead wood transformation routine implicitly or explicitly taking into consideration true allometric relations, would likely improve biomass prediction. On the other hand, this would require a substantial change of the code, similar to that performed by Bond-Lamberty et al. (2005).

5. Conclusions

We conclude that BIOME-BGC may be applied to managed forest ecosystems once it is enhanced with forest management options as implemented here. This was demonstrated on the long-term observation of biomass accumulation (production) for stands of four major tree species. The model prediction of soil carbon was also addressed using independent observation data. The current model is sufficiently robust to simulate carbon budget development of managed, even-aged and monospecific stands, which still strongly dominate Central-European forestry. Production site class could be reflected by changes in two parameters, namely soil depth and natural nitrogen fixation. Both parameters indicated a positive linear dependence with site class quality. The model simulations respected the historical land-use management and long-term observation of N deposition. This makes the model potentially suitable for a

large-scale grid application and analysis of ecosystem responses to environmental changes under different management scenarios.

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