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ScienceDirect
Forest Ecology and Management 237 (2006) 267–279
Forest Ecology and Management
www.elsevier.com/locate/foreco

Application of BIOME-BGC model to managed forests 1. Sensitivity analysis

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Received 25 October 2005; received in revised form 15 June 2006; accepted 21 September 2006

Abstract

A process-based model BIOME-BGC designed for simulation of biogeochemical element cycling in terrestrial ecosystems was prepared for application to managed forest ecosystems in temperate Europe. New routines were implemented that permit specification of thinning, felling and species change when planting new forest. Other changes were implemented to water cycling routines, specifically to precipitation and evaporation, simulation of industrial nitrogen deposition and fine roots mortality. The major aim of the paper was to conduct a sensitivity analysis of the adapted model. We specifically analysed the effects of site and eco-physiological parameters on the modeled state variables (carbon pools in biomass, litter and soil and net primary production (NPP)). The analysis revealed a high sensitivity of all tested variables to the following site parameters: total precipitation, rooting depth, sand fraction (for sandy soils only), ambient CO_2 and parameters of nitrogen input. Similarly, the tested variables were shown to be highly sensitive to the following eco-physiological parameters: leaf and fine root C:N ratio, new stem C to new leaf C ratio, new fine root C to new leaf C ratio, specific leaf area, maximum stomatal conductance, fire mortality and fraction of N in Rubisco (specifically for deciduous species). Additionally, the whole plant mortality had a high effect on carbon pools, but a small effect on NPP.
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Keywords: Process model; Equilibrium; Soil carbon; Biomass; Temperate region

1. Introduction

Forest ecosystems receive growing attention because of their importance for mitigating environmental change. Specifically the carbon budget and sink capacity of forest ecosystems have become central issues in this respect. Forest carbon cycling must be understood in its interactions with changing driving forces and site conditions in order to formulate sound environmental decisions. This requires the application of advanced analytical approaches and models capable of incorporating key ecosystem processes to study and quantify interactions and responses. Additionally, for countries with a tradition of forestry it is vital that such models are capable of incorporating key forest management options.

There are several types of models that may be used in ecosystem analysis. Traditional types of models used in forestry are regression models, which are tree and stand level growth models based on empirically derived statistical relationships between biometric parameters of trees or stands, and production, which is most often expressed as height and volume growth. Such models may be used for predicting stand development under stable conditions and in regions where the built-in relationships were derived. Naturally, such models are not so useful for incorporating changing growth conditions and for spatial extrapolation. Moreover, such models remain descriptive and do not offer much explanatory power for ecosystem analysis. For this, so-called process-based models must be deployed. These models simulate ecosystem development as a result of eco-physiological processes described mechanistically. In contrast to regression models, process models usually incorporate the effect of environmental change on ecosystem functioning and are able to quantify effects of, e.g., change in climate, elevated CO_2, nitrogen deposition and land use scenarios. Moreover, ecosystem process models include both soil and biomass components and their interactions. A drawback of process-based models is that they usually require a considerable number of eco-physiological and site parameters. Therefore, a critical task for the application of a process-based model is its parameterization, including sensitivity analysis of model output to the input data and parameters.

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0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.09.085

This paper presents a sensitivity analysis and an adaptation of the BIOME-BGC process model (Running and Hunt, 1993; Thornton, 1998; Thornton et al., 2002), which was thereafter applied to managed forest ecosystems in Central-European conditions (a follow-up paper Cienciala and Tatarinov, 2006). Although BIOME-BGC was originally developed to simulate the process of natural biomes, it was also applied to managed forest ecosystems (Pietsch et al., 2003; Pietsch and Hasenauer, 2002; Churkina et al., 2003). The recent studies of Vetter et al. (2005) and Pietsch et al. (2005) already targeted the typically managed forests in German and Austrian conditions, respectively, although no explicit handling of thinning regimes was included. Our study describes a more specific model adaptation for classically managed forest ecosystems, mimicking thinning and felling regimes in even-age forests of four major tree species (beech, oak, pine and spruce) and conducts a detailed sensitivity analysis.

A model sensitivity analysis for BIOME-BGC has already been conducted by White et al. (2000). We reassess the model sensitivity for the following reasons: (1) the implemented model modifications might affect model response to some parameters, (2) parameter effects for different combinations of site and eco-physiological parameters may differ, (3) the White et al. (2000) analysis was limited to eco-physiological parameters and NPP. Our analysis also includes both eco-physiological and site parameters and their effects on vegetation, litter and soil carbon pools. It should be stressed that sensitivity analysis for eco-physiological parameters is needed, because most of them are not known with satisfactory accuracy and they may yield unrealistic results. The effect of site parameters must be examined because these are usually known for some locations and must be derived for others. It particularly concerns the driving meteorological variables, which must be commonly scaled from a known weather station to represent the location of the studied site. Finally, sensitivity analysis should also concern soil compartment, because soil exhibits different dynamics of processes when compared to the vegetation cover, and because suitable calibration data on soil carbon pools is not commonly available in comparison with regularly sampled forest volume data in forest inventories.

Hence, the aim of the current study is (1) to perform a sensitivity analysis of the key model outputs to the site and vegetation parameters under the conditions of European temperate managed forestry and (2) to describe the performed model adaptation in terms of forest management practices and other routines.

2. Material and methods

2.1. BIOME-BGC model description

The model BIOME-BGC (Running and Hunt, 1993; Thornton, 1998, 2000) is a process-based model, which operates with a daily time step and describes the dynamics of energy, water, carbon and nitrogen in a defined type of terrestrial ecosystem. Spatial variability within the simulated biome is neglected; the model operates with the pools per unit ground area. The biome gross primary production is calculated using the Farquhar photosynthesis routine (Farquhar et al., 1980) separately for illuminated and shaded foliage. Autotrophic respiration is separated into maintenance respiration calculated proportionally to nitrogen content of living tissues (Ryan, 1991) and growth respiration taken as a function of carbon allocated to the different plant compartments. The phenological block describes leaf and fine roots litterfall, foliage development and accumulation of C and N storage in the individual compartments used again the next spring. The model includes the soil block describing decomposition of litter and soil carbon and nitrogen, as well as growth limitation caused by soil water and nitrogen content. Several options of simulation runs are provided. A simulation can be performed under stable climatic conditions until a steady state is reached (spin-up simulation) or it can run for a concrete time period with specific meteorological data, background CO_2 concentrations and nitrogen deposition. The eventual climate changes can also be included.

2.2. Model parameters

The BIOME-BGC model operates with the following sets of input data:

- Initialization data file including important site and scenario parameters. The key site parameters are elevation, soil texture and effective soil depth. The important scenario parameters are length of simulation period, ambient CO_2 concentration (constant or variable), nitrogen deposition and others.
- The eco-physiological parameters characterizing the biome selected for simulation.
- A file with daily meteorological data series for the simulated site. This file can be prepared manually or using the MTClim model (Running et al., 1987; Thornton and Running, 1999) using as input the meteorological data series from a base weather station, which must include at least daily minimum and maximum temperatures and daily precipitation. MTClim generates other necessary information based on the site parameters (latitude, elevation and annual precipitation totals of base station and site, site aspect and slope) and parameters characterizing the change of temperature with elevation.
- An optional file with annual background CO_2 concentrations.

BIOME-BGC is provided with default eco-physiological parameter sets for the major biome types, such as evergreen needle-leaf and deciduous broadleaf forests (White et al., 2000; available online at http://www.ntsg.umt.edu/). We parameterized the model to be applicable for the four major tree species important for managed forests of Central Europe, including Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), common beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L. and *Quercus petrea* L.). The eco-physiological parameters for the above-mentioned species, with the exception of oak, were based on White et al. (2000). If more than one parameter value for a given species was reported, the average value was used as in White et al. (2000). The range of parameter values reported by White et al. (2000) was also used here as limits for specific parameters. If information on

some parameters was not available, we used the default values for coniferous forests (ENF; spruce and pine) or temperate broadleaved forests (DBF; beech) reported by White et al. (2000). As for oak, the eco-physiological parameters from Pietsch et al. (2003) were applied. In order to obtain the final parameterization, the simulated values of the aboveground carbon pool (C_{ab}) were validated using the measured data from selected permanent forest inventory plots (see Cienciala and Tatarinov, 2006). For spin-up-simulations, fire and whole plant mortality parameters are specifically important, these were set twice as big compared to White et al. (2000). With these parameter values, the equilibrium carbon pools reasonably matched the potential soil and vegetation carbon pools for temperate regions as described by Adams (1997). Besides the data from White et al. (2000), we compiled the following sources of eco-physiological parameters for individual species: Antunez et al. (2001), Bartelink (1997, 1998), Bauer et al. (1997), Broadmeadow and Jarvis (1999), Cermak (1998), Cermak et al. (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), and Ross et al. (1986). The final parameter sets applied for the four studied species are presented in Table 1.

2.3. Modification of the model source code

2.3.1. Forest management options

Since the original version of the model does not include forest management, several new routines were implemented. These include:

- Thinning and felling: cutting a prescribed fraction of trees in a given year, simulated as a proportional decrease of the variables describing carbon and nitrogen pools in the tree biomass;
- Species change: when final cut (100% cutting) is performed, an optional choice of regenerating/planted tree species is available. This routine selects and applies the appropriate species-specific eco-physiological parameter set.

When a given fraction of stand biomass is cut, it is assumed that the same portion of foliage and fine root, C and N pools, is translocated to litter, while the same fraction of coarse roots is translocated into a coarse woody debris pool. The corresponding portion of stem wood is harvested (removed from the biome). In the case of final cut, the whole stem wood is removed, while the coarse root pool enters the coarse woody debris and the pool of foliage and fine root enters litter.

2.3.2. Modification of rainfall interception, evaporation and troughfall

Some changes were made to model processes concerning the water regime, which were identified during the analytical work with the model (for more information see Section 4).

In the original model version, the maximum canopy water interception was calculated as $I_{max} = k_p p \mathrm{LAI}_{all}$, where k_p is the interception coefficient (0.04–0.05 $\mathrm{LAI}^{-1}\,\mathrm{day}^{-1}$ for different biomes according to White et al. (2000)), p is daily precipitation and LAI_{all} is the all-sided LAI. Thus, I_{max} is proportional to the precipitation. We altered this algorithm as follows: $I_{max} = k_p \mathrm{LAI}_{all}$, where k_p taken as 0.3 (Cienciala et al., 1994) represents the maximum amount of water that can be instantly absorbed per unit LAI.

The daily evaporation from moist canopy was originally calculated by a modified Penman–Monteith equation with canopy conductance to evaporated water vapor set equal to $g_{bl}\mathrm{LAI}$, where g_{bl} is leaf area boundary layer conductance and LAI is the projected LAI. We implemented the Priestley–Taylor equation (Priestley and Taylor, 1972) for wet canopy evaporation.

In the original model code, the intercepted water that did not evaporate during the simulated day was routinely passed to the soil compartment. In our version, if evaporation does not deplete the entire intercepted water amount, the remaining quantity is left to evaporate during the following day or days.

The handling of free throughfall was also changed. Originally, precipitation could reach the ground only if daily precipitation was larger than I_{max}, i.e., assuming absolute effectiveness of canopy to intercept precipitation. In the modified model version, a throughfall coefficient (p_t) was introduced. This allows a fraction of rainfall to reach the ground without hitting the canopy (Gash, 1979). We set p_t to depend on projected LAI as $p_t = e^{-k\mathrm{LAI}}$ (Dijk, 2002), where k is the light extinction coefficient.

2.3.3. Modification of nitrogen industrial deposition

In the original model version the industrial nitrogen deposition (N_{di}) increased proportionally with ambient CO_2 concentration. This routine was modified in the following way. The relative industrial nitrogen deposition (from 0 to 1) for individual years was directly read from a specific file. The data on actual nitrogen emission dynamics in the Czech Republic in 1850–2000 were taken from Kopaček and Veselý (2005). Providing that the dynamics of relative emission and relative deposition match, we applied the data of Kopaček and Veselý (2005) to approximate the relative N_{di} during 1850–2000. N_{di} was extrapolated back to year 1200 and forward until 2050 supposing no industrial N deposition in 1200 and 20% decrease of N_{di} during 2000–2050.

2.3.4. Independent fine root turnover rate

In the original model version the fine root turnover rate was set equal to that of the foliage. However, since these rates can considerably differ, fine root turnover rate was specifically prescribed in the eco-physiological parameter file. The applied fine root turnover rates in this study were 0.811, 0.868 and 1.013 year^{-1} for spruce, pine and broadleaved, respectively (Kurz et al., 1996; Majdi, 2001).

2.4. Sensitivity analysis

The sensitivity analysis was focused on the effect of input parameters used in MTCLIM and/or BIOME-BGC on the

Table 1
Applied parameterization of single tree species

Parameter description	Symbol	Units	Beech	Oak	Pine	Spruce
Transfer growth period as fraction of growing season	T_t	Prop.	0.17	0.25	0.3	0.3
Litterfall as fraction of growing season	T_{lf}	Prop.	0.2	0.3	0.3	0.3
Annual leaf turnover fraction	m_l	$Year^{-1}$	1	1	0.39	0.24
Annual fine root turnover fraction	m_{fr}	$Year^{-1}$	1.023	1.023	0.868	0.811
Annual live wood turnover fraction	m_w	$Year^{-1}$	0.7	0.7	0.7	0.7
Annual whole-plant mortality fraction (steady state)	m_t	$Year^{-1}$	0.01	0.01	0.01	0.01
Annual fire mortality fraction (steady state)	m_f	$Year^{-1}$	0.01	0.01	0.005	0.005
Allocation new fine root C:new leaf C	FRC:LC	Ratio	1.10	1.20	1.00	0.66
Allocation new stem C:new leaf C	SC:LC	Ratio	2.71	1.70	2.12	2.20
Allocation new live wood C:new total wood C	LWC:TWC	Ratio	0.160	0.160	0.076	0.100
Allocation new croot C:new stem C	CRC:SC	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	$C:N_{leaf}$	kg C/kg N	27.0	27.2	36.0	43.0
C:N of leaf litter, after retranslocation	$C:N_{lit}$	kg C/kg N	49.8	64.1	122.0	83.0
C:N of fine roots	$C:N_{fr}$	kg C/kg N	72.0	73.5	49.0	42.0
C:N of live wood	$C:N_{lw}$	kg C/kg N	70.0	73.5	58.0	37.1
C:N of dead wood	$C:N_{dw}$	kg C/kg N	520	451	730	730
Leaf litter labile proportion	FR_{lab}	DIM	0.12	0.20	0.26	0.28
Leaf litter cellulose proportion	FR_{cel}	DIM	0.56	0.56	0.49	0.38
Leaf litter lignin proportion	FR_{lig}	DIM	0.32	0.24	0.25	0.34
Fine root labile proportion	L_{lab}	DIM	0.30	0.34	0.23	0.23
Fine root cellulose proportion	L_{cel}	DIM	0.45	0.44	0.41	0.41
Fine root lignin proportion	L_{lig}	DIM	0.25	0.22	0.36	0.36
Dead wood cellulose proportion	DW_{cel}	DIM	0.75	0.75	0.70	0.70
Dead wood lignin proportion	DW_{lig}	DIM	0.25	0.25	0.30	0.30
Canopy water interception coefficient[a]	W_{int}	(mm/LAI)	0.3	0.3	0.3	0.3
Canopy light extinction coefficient	k	DIM	0.50	0.54	0.495	0.50
All-sided to projected leaf area ratio	$LAI_{all:proj}$	DIM	2.0	2.0	2.6	2.6
Canopy average specific leaf area (SLA)[b]	SLA	m^2/kg C	35.0	34.5	9.5	7.8
Ratio of shaded SLA:sunlit SLA	$SLA_{shd:sun}$	DIM	2	2	2	2
Fraction of leaf N in Rubisco	N_R	DIM	0.100	0.088	0.055	0.055
Max. stomatal conductance[b]	$g_{s,max}$	m s^{-1}	0.0050	0.0050	0.0025	0.0020
CUTICULAR conductance[b]	g_{cut}	m s^{-1}	6E−05	6E−05	6E−05	6E−05
Boundary layer conductance[b]	g_{bl}	m s^{-1}	0.010	0.005	0.010	0.009
Leaf WP: start of conductance reduction	LWP_i	MPa	−0.34	−0.50	−0.50	−0.50
Leaf WP: complete conductance reduction	LWP_f	MPa	−2.2	−3.5	−2.5	−2.5
VPD: start of conductance reduction	VPD_i	Pa	600	200	600	610
VPD: complete conductance reduction	VPD_f	Pa	3000	2550	2500	3100

"DIM" means dimensionless.
[a] The meaning of this coefficient differs from the original model; see the explanation in the text.
[b] On projected area basis.

biome state variables under steady state. The effects of the individual site and eco-physiological parameters were assessed on the set of the key output variables. They included carbon content in plants, litter and soil and total carbon content (abbreviated as C_p, C_l, C_s, C_t, respectively), maximum annual leaf area index (LAI, L_{max}), soil mineral nitrogen (N_s) and mean daily net primary production (NPP). All tests were performed using spin-up simulations, i.e., for steady state variable values. Carbon pools under the spin-up simulation started to grow from its minimum and reached a steady state after several hundreds to several thousand years of simulation depending on the applied parameter set (for studied species and sites). However, additional normal simulations starting with clear-cutting of original virgin forest were performed in order to study the implemented model changes on simulation results.

For the purposes of sensitivity analysis the spin-up simulation was always run up to the maximum spin-up period (6000 years), even after the prescribed tolerance limit for soil carbon pool change (0.05% per year) was reached. This was to minimize the effects of different time to reach steady state conditions on ecosystem carbon stock pools. The output variables under the steady state used in the sensitivity procedure were the average of 15 years to reduce the effect of annual variability in the input climate driving files.

The sensitivity of output variables (y) to input parameters (x) (or the effect of parameter x on the variable y), $\Delta y/\Delta x$ was calculated as a ratio of output variable change to parameter

change (both in %). To interpret these sensitivity values, one may say that a negative ratio means a variable decrease with an increasing parameter value and vice versa. As for the absolute quantity ($|\Delta y/\Delta x|$), the parameters were ranked in terms of their effect on the modeled variable as (i) parameters a with strong effect ($|\Delta y/\Delta x|$ larger than 0.2), (ii) parameters with a medium effect ($|\Delta y/\Delta x|$ between 0.1 and 0.2) and (iii) parameters with low effect ($|\Delta y/\Delta x|$ less than 0.1). Effects of the site and eco-physiological parameters were examined on single-species stands of Norway spruce (*Picea abies* (L.) Karst.) and common beech (*Fagus sylvatica* L.), the most important coniferous and broadleaf species in Central-European conditions, respectively. Two other important tree species, namely Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L. and *Q. petrea* L.), were also occasionally used in the analysis.

The default site parameterization reflected a site with an altitude of 450 m, no slope and soil containing 30% sand, 50% silt and 20% clay.

2.4.1. Effect of site parameters

The simulation experiment required a preparation of a test driving file. For this, a 23-year record of basic meteorological data was used. Measurements from a meteorological station located in Southern Bohemia (station Bolevec) at an elevation of 328 m were used. The record contained daily minimum and maximum temperatures and precipitation totals. The remaining variables required by BIOME-BGC were calculated by the MTCLIM climatic generator. The recalculation of the meteorological variables for other elevations was also performed using the above data from the MTCLIM model. The driving data series was replicated for as long as required to create a long-term driving data of any length for the BIOME-BGC runs.

It should be noted that MTCLIM output affects the BIOME-BGC model predictions and in this way MTCLIM is considered as part of the model, in particular for the purpose of sensitivity analysis.

We assessed the effect of the following input parameters: site elevation (H, m), soil texture described as a fraction of sand particles (β_s, %), site slope (φ) and aspect (S or N), tree species, albedo (α), precipitation ratio P (ratio of site and base annual precipitation totals applied within the MTCLIM model for calculating the site precipitation), nitrogen input (N_d, kg N m^{-2} year^{-1}) composed from nitrogen background and industrial deposition and nitrogen fixation and effective soil depth (d, m). The effect of ambient CO_2 concentration (C_A) was studied in spin-up simulations with different constant C_A values. The effect of N_d was tested in a similar way, i.e., by varying background nitrogen input under spin-up simulations. All the parameters were varied within the span typical for the region under study.

2.4.2. Effect of eco-physiological parameters

The eco-physiological parameters (Table 1) and their effect on state variables were tested individually with 10% variation of each parameter in both directions from its prescribed value.

3. Results

3.1. Effect of model code changes

During the analysis of model output related to water cycling, we observed unrealistically high daily evaporation and interception values when the canopy was wet. The revised handling of wet canopy evaporation using the Priestley–Taylor equation and changed interception resulted in more realistic quantities. We suspect that particularly the boundary layer conductance (g_{bl} = 0.09 m s^{-1}) was set too high in the original parameterization for conifers (see Section 4 for further details). During tests on coniferous forest ecosystems represented by an adult spruce stand with stabilized leaf area index (LAI), the simulation using Priestley–Taylor equation resulted in transpiration and wet canopy evaporation representing 42 and 26% of precipitation, respectively. The original model yielded values of 39 and 38%, respectively. This means that the new evaporation routine had basically no effect on transpiration, but strongly affected the wet canopy evaporation. The maximum simulated daily wet canopy evaporation with the original model and boundary layer from the default ENF parameter set was 22.4 mm day^{-1}, while with the new evaporation and interception routine it reached a maximum of only 4.0 mm day^{-1}. Since g_{bl} for broadleaves was smaller (0.01 m s^{-1}, White et al., 2000) this difference was considerably smaller for deciduous stands and the new routines did not result in significant changes in long-term daily average values. Hence, the original model routines for spruce with reduced g_{bl} (0.009 m s^{-1}, Table 1), also yielded similar values as the new adaptation applied here. However, the simulated maximum evaporation from wet canopy in beech was also considerably smaller using the new evaporation and interception routines. While the original model gave a daily maximum wet evaporation of 9.0 mm day^{-1}, the adapted model resulted in a daily maximum of 3.1 mm day^{-1}.

The above described changes in evaporation routines affect not only the water balance, but also carbon pools. Demonstrated on a normal simulation run initiated with new stand planting for coniferous and broadleaved stands, plant biomass production increased when applying the modified version. For stands of 40 years and older, the ratio of modified to original simulation of plant carbon pools became about 1.16 for spruce and 1.06 for beech (Fig. 1). Another model change concerned the independent input of fine root turnover rate (m_{fr}). It had no significant effect on biomass carbon pools of broadleaf species because the applied value (1.023 year^{-1}) was similar as the leaf turnover rate (m_l, 1 year^{-1}). However, for spruce and pine, m_{fr} was 4.4 and 2.2 times higher than m_l, respectively, and the effect of the model change was significant. The increase of m_{fr} led to some decrease of root biomass and increase of litterfall. In its turn, the increase of litterfall evoked an increase in the soil carbon pool and, consequently, an increase in production. As a result, the aboveground biomass also increased (Fig. 2).

The implemented prescribed input of industrial nitrogen deposition also increased production and consequently carbon

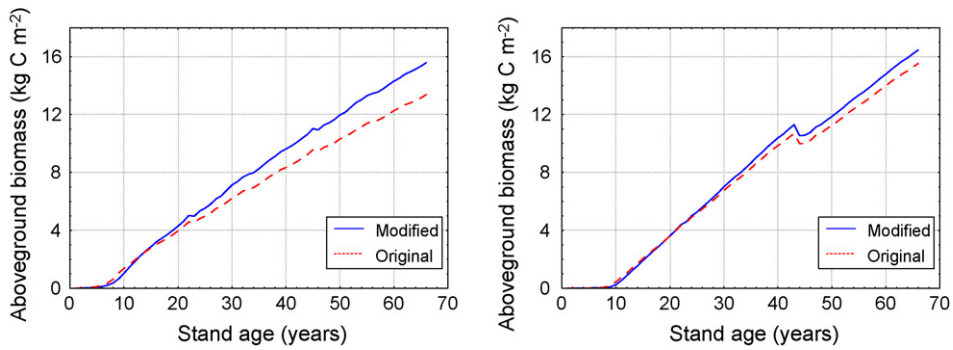

Fig. 1. Dynamics of stand aboveground biomass under original and modified models of precipitation interception and evaporation for spruce (left) and beech (right) stands, showing normal simulation after clear-cut.

pools under normal simulation (Fig. 2). The reasons will be discussed in Section 4.

3.2. Effect of site parameters

The assessed effects $\Delta y/\Delta x$ of the sensitivity analysis are presented in Table 2. The negative sign of $\Delta y/\Delta x$ means that an increase of the parameter leads to a decrease of the variable.

The ambient CO_2 concentration (C_A) and precipitation ratio (P) had the strongest effect on all considered biome state variables, reaching absolute values up to 1.3. Whereas the effect of both parameters on plant carbon (C_p) was always positive, the effect of P on soil and litter carbon was positive for beech and negative for other species. Effective soil depth (d) had a strong effect on beech and a medium effect on spruce (Fig. 3). In contrast, nitrogen input (N_d) had a strong effect on spruce and a medium effect on beech. The effect of soil texture (sand fraction) was strong and negative only on sandy soils ($\beta_s > 50\%$). The effects of elevation and slope were medium or small depending on the parameter value, species and output variable (Table 2). A strong effect of elevation on C_p (negative, for beech) or C_s (positive, for spruce) was observed only for elevations above 800 m. The effect of albedo was small. The effect of nitrogen input was strong for small N_d values (below 0.0004 kg N m^{-2} year^{-1}) and rapidly decreasing with N_d (Fig. 3).

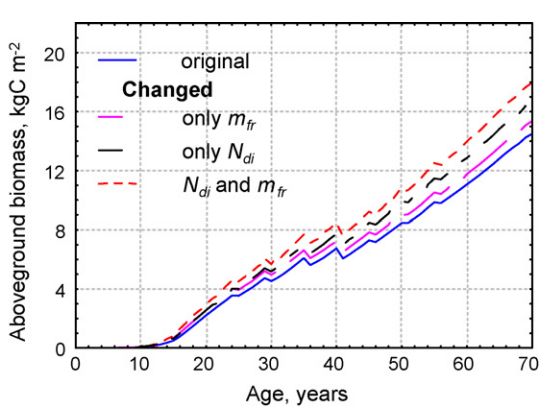

Fig. 2. Impact of changes of model industrial nitrogen deposition (N_{di}) and fine root turnover (m_{fr}) routines on aboveground biomass of spruce (stand planted in 1932).

3.3. Effect of eco-physiological parameters

Generally the effect of eco-physiological parameters on NPP and output carbon pools was weaker than the effect of site parameters. The effect of individual parameters considerably differed for beech and spruce and for individual output variables, being generally higher for beech, than for spruce (Table 3). Generally, a strong or medium effect on both species and most output variables was observed for C:N ratios of leaves and fine roots (C:N_{fr} and C:N_{leaf}) and maximum stomatal conductance ($g_{s,max}$). The effect of fire mortality, new fine roots carbon to new leaves carbon (FRC:LC) and new stem carbon to new leaves carbon (SC:LC) allocation ratios was strong on carbon pools, but small or medium for NPP. The effect of whole plant mortality (m_t) was strong for plant carbon (C_p) only. The effect of SLA on C_p and NPP was strong or medium for both spruce and beech. However, this effect on C_l and C_s for beech was small. A medium effect of light extinction coefficient (k) and leaf turnover rate was observed on carbon pools and NPP for spruce. The effect of nitrogen content in Rubisco (PLNR) was strong for beech and small or medium for spruce. For beech, a medium effect on some output variables was observed also for vapor pressure deficit values of complete conductance reduction (VPD_f) and the period of litterfall. The effect of other eco-physiological parameters was small.

Among the parameters with strong or medium effect, only PLNR and fine root C:N had positive effects, whereas fire mortality, FRC:LC and k had negative effect on all output carbon pools and NPP. The effect of leaf C:N was positive for spruce and negative for beech. Other parameters had effects of different sign for different variables. In particular, SLA and m_t had a negative effect on C_p and NPP and a positive effect on C_l and C_s, whereas for leaf turnover rate the opposite was the case.

3.4. Carbon pools in steady state

Steady state carbon pools with the proposed parameterization sets (Table 1) reached values comparable to those reported for temperate forest ecosystems by Adams (1997). On the contrary, carbon pools of plants under initial whole plant and fire mortality values proposed by White et al. (2000) were significantly larger for all tested parameterizations (Table 4). This difference was related to differences in the applied whole-

Table 2
Sensitivity (expressed as ratio (% of variable change)/(% of parameter change)) of selected model output variables to quantitative site parameters: elevation (H), sand fraction (β_s), slope (φ), albedo (α), soil depth (d), precipitation ratio (P) ambient CO_2 (C_A) and nitrogen input (N_d)

Parameter (range)	Species	Sensitivity (% of variable change)/(% of parameter change)						
		Maximum LAI	Content of carbon (kg C m^{-2})				Mean NPP (kg C m^{-2} day^{-1})	Soil mineral N (kg N m^{-2})
			Plant	Litter	Soil	Total		
H 250–350 m	Spruce	0.02	0.02	0.10	0.10	0.05	0.02	−0.05
H 350–450 m	Spruce	0.00	0.00	0.09	0.09	0.04	0.03	0.45_2
H 450–600 m	Spruce	0.02	0.01	0.14_1	0.14_1	0.07	0.04	0.26_2
H 600–800 m	Spruce	0.03	0.03	0.20_1	0.20_1	0.10	0.03	−0.01
H 800–1100 m	Spruce	0.00	0.00	0.23_2	0.23_2	0.11_1	0.04	-0.27_2
H 350–450 m	Beech	−0.07	−0.07	0.02	0.02	−0.04	−0.02	−0.05
H 450–600 m	Beech	-0.15_1	-0.14_1	−0.06	−0.06	-0.11_1	−0.03	0.08
H 600–800 m	Beech	-0.19_1	-0.19_1	−0.08	−0.08	-0.15_1	−0.06	−0.03
H 800–1100 m	Beech	-0.21_2	-0.21_2	−0.06	−0.05	-0.15_1	-0.11_1	-0.22_2
β_s (0–10%)	Spruce	0.00	0.00	0.01	0.01	0.00	0.00	0.00
β_s (10–30%)	Spruce	−0.02	−0.02	0.06	0.06	0.01	−0.02	0.00
β_s (30–50%)	Spruce	−0.05	−0.05	0.09	0.09	0.01	−0.07	−0.07
β_s (50–80%)	Spruce	−0.01	0.01	0.22_2	0.24_2	0.11_1	-0.21_2	0.12_1
β_s (80–100%)	Spruce	-0.57_2	-0.54_2	-0.32_2	-0.31_2	-0.44_2	-0.63_2	-0.62_2
β_s (0–10%)	Beech	0.00	0.00	0.02	0.02	0.01	0.00	0.00
β_s (10–30%)	Beech	−0.05	−0.04	0.03	0.03	−0.02	−0.04	−0.03
β_s (30–50%)	Beech	-0.12_1	-0.11_1	0.01	0.02	−0.07	−0.10	−0.07
β_s (50–80%)	Beech	-0.36_2	-0.35_2	-0.24_2	-0.22_2	-0.30_2	-0.28_2	-0.13_1
β_s (80–100%)	Beech	-1.16_2	-1.09_2	-1.05_2	-1.03_2	-1.07_2	-0.85_2	-1.13_2
φ (0–10°), N	Spruce	0.00	0.00	−0.02	−0.02	−0.01	−0.01	0.00
φ (10–20°), N	Spruce	−0.08	−0.08	-0.17_1	-0.18_1	-0.13_1	−0.03	-0.11_1
φ (20–30°), N	Spruce	0.01	0.01	-0.12_1	-0.11_1	−0.04	−0.08	−0.01
φ (30–40°), N	Spruce	0.01	0.02	−0.21	-0.18_1	−0.06	-0.15_1	−0.01
φ (20–30°), N	Beech	0.04	0.04	−0.02	−0.02	0.02	−0.03	0.01
φ (10–20°), S	Spruce	0.00	0.00	0.01	0.01	0.00	0.00	−0.01
α (0.15–0.2)	Beech	0.09	0.09	0.05	0.05	0.07	−0.01	0.05
α (0.15–0.2)	Spruce	0.02	0.02	−0.08	−0.07	−0.02	−0.05	0.13
d (0.3–0.5 m)	Spruce	0.12_1	0.11_1	0.09	0.07	0.09	0.30_2	−0.04
d (0.5–0.7 m)	Spruce	0.12_1	0.11_1	0.01	0.01	0.07	0.19_1	-0.18_1
d (0.7–1.0 m)	Spruce	0.11_1	0.08	0.00	0.00	0.05	0.09	-0.11_1
d (0.3–0.5 m)	Beech	0.46_2	0.44_2	0.53_2	0.52_2	0.47_2	0.40_2	0.14_1
d (0.5–0.7 m)	Beech	0.42_2	0.39_2	0.44_2	0.43_2	0.41_2	0.41_2	0.06
d (0.7–1.0 m)	Beech	0.28_2	0.29_2	0.29_2	0.29_2	0.29_2	0.29_2	−0.09
d (1.0–1.3 m)	Beech	0.22_2	0.27_2	0.37_2	0.36_2	0.30_2	0.16_1	0.15_1
P 0.8–1.0	Spruce	0.47_2	0.45_2	-0.47_2	-0.60_2	−0.02	1.09_2	0.66_2
P 1.0–1.2	Spruce	0.05	0.03	-0.87_2	-0.94_2	-0.36_2	0.71_2	0.18_1
P 0.8–1.0	Beech	0.84_2	0.88_2	0.59_2	0.56_2	0.77_2	0.81_2	0.89_2
P 1.0–1.2	Beech	0.64_2	0.68_2	0.34_2	0.30_2	0.55_2	0.72_2	0.59_2
P 0.8–1.0	Oak	1.02_2	1.08_2	−0.07	-0.16_1	0.53_2	1.10_2	0.92_2
P 1.0–1.2	Oak	0.45_2	0.38_2	-0.62_2	-0.66_2	−0.04	0.55_2	0.46_2
P 0.8–1.0	Pine	0.53_2	0.48_2	-1.37_2	-1.44_2	-0.37_2	1.10_2	0.47_2
P 1.0–1.2	Pine	0.26_2	0.27_2	-0.72_2	-0.70_2	−0.09	0.35_2	0.47_2
C_A 298–330 ppm	Spruce	0.18_1	0.18_1	0.34_2	0.25_2	0.22_2	0.01	0.18_1
C_A 330–350 ppm	Spruce	0.16_1	0.16_1	0.32_2	0.23_2	0.20_1	0.01	0.17_1
C_A 350–370 ppm	Spruce	0.16_1	0.16_1	0.30_2	0.22_2	0.19_1	0.01	0.16_1
C_A 298–325 ppm	Beech	0.53_2	0.52_2	0.73_2	0.72_2	0.59_2	0.08	0.65_2
C_A 325–350 ppm	Beech	0.44_2	0.43_2	0.60_2	0.59_2	0.49_2	0.05	0.52_2
C_A 350–370 ppm	Beech	0.41_2	0.41_2	0.56_2	0.55_2	0.46_2	0.04	0.50_2
N_d (0.3–0.5)[a]	Spruce	0.87_2	0.85_2	1.11_2	1.19_2	0.97_2	0.25_2	1.16_2
N_d (0.5–0.7)[a]	Spruce	0.86_2	0.86_2	1.08_2	1.19_2	0.99_2	−0.05	0.98_2
N_d (0.7–1.1)[a]	Spruce	0.26_2	0.27_2	0.31_2	0.37_2	0.31_2	−0.04	0.61_2
N_d (1.1–1.5)[a]	Spruce	0.02	0.04	0.03	0.05	0.04	0.00	0.11_1
N_d (0.3–0.5)[a]	Beech	0.36_2	0.36_2	0.46_2	0.50_2	0.40_2	0.07	0.56_2
N_d (0.5–0.7)[a]	Beech	0.09	0.09	0.09	0.12_1	0.10	0.01	0.33_2
N_d (0.7–1.1)[a]	Beech	0.04	0.04	0.04	0.05	0.04	0.00	0.20_1
N_d (1.1–1.5)[a]	Beech	0.08	0.08	0.09	0.11_1	0.09	0.01	0.48_2

The following default values of parameters were applied: $\beta_s = 30\%$, $\varphi = 0$, $\alpha = 0.2$, $H = 450$ m, $d = 0.5$ m, $C_A = 298$ ppm. The bottom index indicates the ranking of sensitivity (0.1–0.2—index 1, medium sensitivity, above 0.2—index 2, high sensitivity).

[a] Total nitrogen deposition + fixation (in g N m^{-2} year^{-1}).

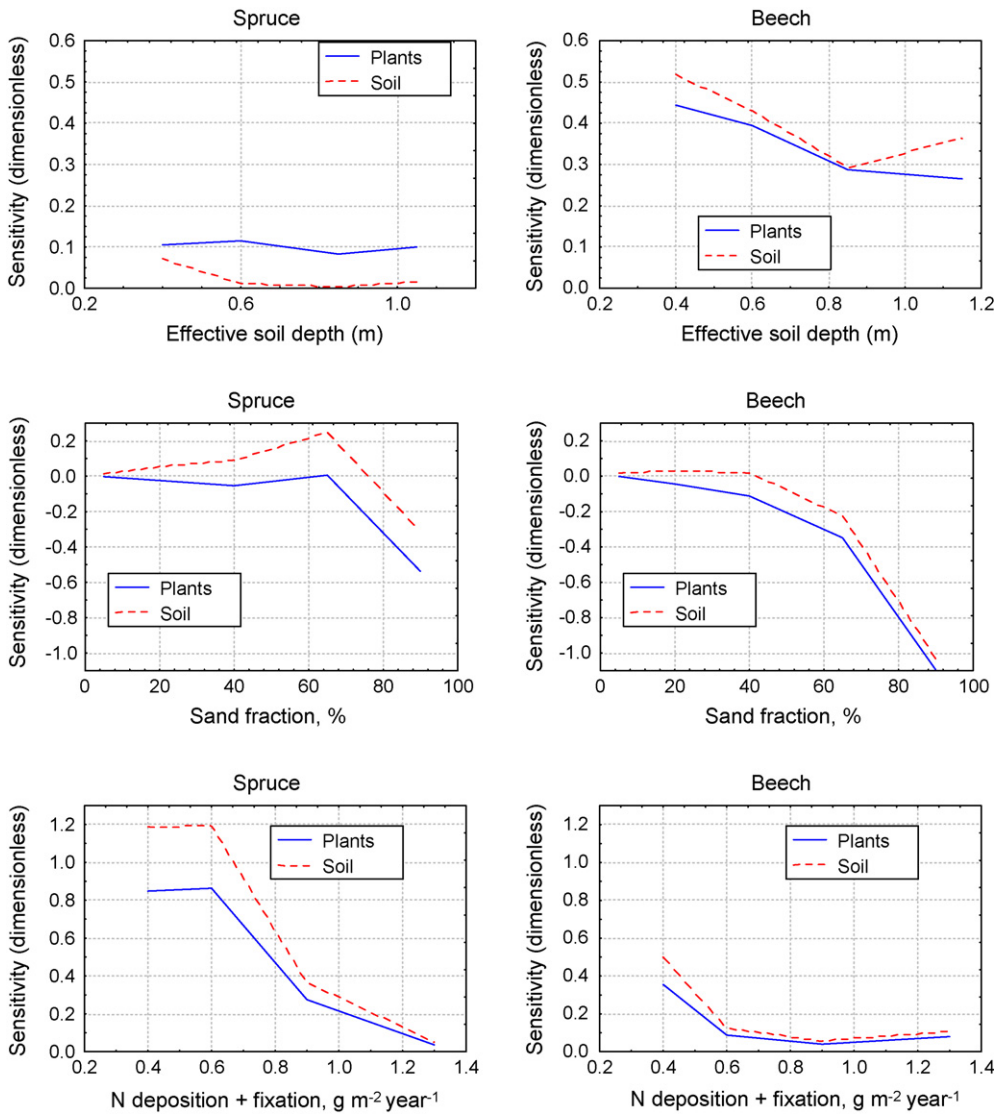

Fig. 3. Sensitivity of plant and soil carbon pools to the selected site variables for spruce and beech stands.

plant and fire mortality values. While this study applied a steady state whole plant mortality of 0.01 year^{-1} for all species and fire mortality of 0.005 year^{-1} for deciduous and 0.01 year^{-1} for coniferous species, White et al. (2000) used values smaller by 50% for all cases listed above.

4. Discussion

4.1. Source code changes

Apart from newly implemented forest management options, the processes related to water cycling were also changed. These also have an impact on carbon cycling, and therefore should receive appropriate attention.

Firstly, in the original model version, the maximum canopy water interception (I_{max}) was taken as proportional to the precipitation. In such a case the amount of intercepted water is theoretically unlimited and becomes unrealistic under high precipitation. In particular, the maximum daily precipitation was about 80–130 mm for different sites within the Czech Republic during the last 20 years, which for a full-grown stand gives I_{max} of about 20–30 mm. We set $I_{max} = k\text{LAI}$, where $k = 0.3$ mm supposing that the evaporation during rainfall is negligible. In the modified version, the value of I_{max} below 2 mm is more realistic.

Secondly, the daily evaporation from moist canopy was originally calculated by a modified Penman–Monteith equation with canopy conductance to evaporated water vapor set equal to g_{bl}LAI, where g_{bl} is leaf area boundary layer conductance and LAI is the projected LAI. This may create situations with unrealistically high evaporation. For example, with the parameterization proposed by White et al. (2000), $g_b = 0.01$ and 0.09 m s^{-1} for deciduous broadleaf forest (DBF) and evergreen needleleaf forest (ENF), respectively, the maximum potential evaporation from wet canopy of a full-grown stand would reach about 90 mm day^{-1} for ENF and about 10 mm day^{-1} for DBF. The real evaporation was limited by the interception, but using overestimated I_{max} values (see

Table 3
Sensitivity of simulated carbon pools, net primary production (NPP) and soil mineral N in a steady state, to single eco-physiological parameters

Parameter under study	Mean value	Effect (% of variable change to % of parameter change)						
		Maximum LAI	Content of carbon (kg C m^{-2})				NPP (kg C m^{-2} $year^{-1}$)	Mineral N (kg N m^{-2})
			Plants	Litter	Soil	Total		
Beech								
Litterfall period	0.2	-0.16_1	−0.09	-0.13_1	-0.13_1	−0.10	−0.09	−0.09
Fine root turnover	1.023	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total mortality	0.005	0.01	-0.65_2	0.06	0.05	-0.41_2	0.02	0.05
Fire mortality	0.0025	−0.05	-0.37_2	-0.12_1	-0.11_1	-0.28_2	−0.05	−0.10
New fine root C:new leaf C	1.1	-0.30_2	-0.30_2	-0.38_2	-0.19_1	-0.28_2	−0.09	-0.16_1
New stem:leaf C	2.71	-0.54_2	0.47_2	0.21_2	-0.16_1	0.29_2	0.06	-0.14_1
New coarse root C:new stem C	0.15	−0.07	0.06	0.03	−0.02	0.04	0.01	−0.02
Leaf C:N	27	-0.40_2	-0.38_2	-0.58_2	-0.54_2	-0.44_2	-0.40_2	-0.54_2
Fine root C:N	72	0.33_2	0.32_2	0.44_2	0.44_2	0.36_2	0.33_2	0.38_2
Live wood C:N	70	0.05	0.05	0.07	0.07	0.06	0.05	0.06
Light extinction	0.5	−0.09	−0.09	−0.03	−0.02	−0.07	−0.09	−0.03
SLA	35	0.77_2	-0.24_2	0.02	0.04	-0.14_1	-0.23_2	0.00
N in Rubisco	0.1	0.54_2	0.53_2	0.75_2	0.74_2	0.60_2	0.55_2	0.66_2
Maximum stomatal conductance	0.005	-0.29_2	-0.30_2	-0.13_1	-0.11_1	-0.24_2	-0.30_2	-0.13_1
Boundary layer conductance	0.01	0.01	0.01	0.04	0.04	0.02	0.01	0.04
Leaf WP—start of reduction	0.34	−0.02	−0.02	−0.02	−0.02	−0.02	−0.02	−0.02
Leaf WP—full reduction	2.2	0.05	0.05	0.14_1	0.14_1	0.08	0.05	0.08
VPD—start of reduction	600	−0.07	−0.07	−0.04	−0.03	−0.06	−0.07	−0.03
VPD—full reduction	3000	-0.17_1	-0.17_1	−0.08	−0.07	-0.13_1	-0.17_1	−0.06
Spruce								
Leaf turnover	0.24	-0.75_2	0.20_1	-0.18_1	−0.10	0.07	0.22_2	−0.02*n*
Fine root turnover	0.81	0.05	0.04	0.08	0.07	0.05	0.04	0.05
Total mortality	0.005	0.01	−0.45	0.08	0.07	−0.24	0.04	0.07
Fire mortality	0.005	-0.25_2	-0.62_2	-0.37_2	-0.38_2	-0.53_2	-0.23_2	-0.31_2
New fine root C:new leaf C	0.66	-0.18_1	-0.17_1	−0.26	−0.08	-0.15_1	−0.02	−0.01
New stem C:leaf C	2.2	-0.46_2	0.52_2	0.23_2	−0.08	0.31_2	0.18_1	-0.12_1
New coarse root C: new stem C	0.21	−0.08	0.09	0.04	−0.02	0.05	0.03	0.01
Leaf C:N	43	0.12_1	0.11_1	0.07	0.16_1	0.12_1	0.10	0.11_1
Fine root C:N	42	0.11_1	0.11_1	0.19_1	0.16_1	0.14_1	0.11_1	0.12_1
Live wood C:N	37.1	0.03	0.03	0.02	0.04	0.03	0.02	0.03
Light extinction	0.5	-0.11_1	-0.11_1	-0.18_1	-0.17_1	-0.14_1	-0.11_1	0.19_1
Water extinction	0.3	−0.04	−0.04	0.04	0.04	−0.01	−0.04	−0.04
SLA	7.8	0.89_2	-0.12_1	0.31_2	0.26_2	0.04	-0.14_1	0.27_2
N in Rubisco	0.055	0.08	0.09	0.18_1	0.13_1	0.11_1	0.08	0.09
Maximum stomatal conductance	0.002	-0.11_1	-0.12_1	0.37_2	0.32_2	0.06	-0.14_1	0.00
Boundary layer conductance	0.009	0.02	0.02	0.00	0.00	0.01	0.02	0.01
Leaf WP—start of reduction	−0.5	−0.01	0.00	0.01	0.01	0.00	−0.01	0.00
Leaf WP—full reduction	−2.5	0.01	0.01	0.08	0.07	0.03	0.01	0.03
VPD—start of reduction	610	−0.03	−0.03	0.08	0.07	0.01	−0.03	0.00
VPD—full reduction	3100	−0.06	−0.06	0.16_1	0.13_1	0.02	−0.07	−0.01

All simulations were performed for elevation 450 m, soil depth 0.5 m and soil texture with 30% of sand and no slope. The bottom index indicates the sensitivity ranking (the same as in Table 2). Units are shown in Table 1.

above), evaporation occasionally reached values between 10 and 20 mm day^{-1}. The accurate estimation of conductance for the parameterization of the Penman–Monteith equation requires data on wind speed and canopy height that are not handled by BIOME-BGC. Another factor helping to avoid overestimation of evaporation would be the feedback between the evaporation rate and VPD, which is not included in BIOME-BGC. The application of the Priestley–Taylor equation (Priestley and Taylor, 1972) for the wet canopy evaporation strongly decreased the overall model sensitivity to g_{bl}. Under high g_{bl} values such as those applied by White et al. (2000) and Churkina et al. (2003), application of the Priestley–Taylor equation made the prediction of water balance more realistic. The recent study of Pietsch et al. (2005) used 10 times smaller g_{bl} for coniferous stands. We observed that this value also stabilized the simulated evaporation fluxes under the original model equation (see Thornton, 1998).

The applied modification of antropogenic nitrogen deposition based on the data of Kopaček and Veselý (2005) had the following reasons. The dynamics of N_{di} considerably differs from the dynamics of ambient CO_2. N_{di} consists of two components: NH_3-N and NO_x-N. NH_3-N originating mostly from livestock-raising and partially (in the last century) from mineral fertilizers. The latter was already considerable in the

Table 4
Steady state carbon pool content for selected biomes simulated using either the current parameterization sets (Table 1), default parameters for deciduous broadleaf forest (DBF) and coniferous evergreen forest (ENF) of White et al. (2000) or the current parameters with mortality of White et al. (2000)

Biome type	Content of carbon (kg C m^{-2})			
	Plants	Litter	Soil	Total
Simulations with current mortality parameterization				
Beech	19.9	5.1	15.2	40.2
Oak	16.5	4.1	14.2	34.8
Pine	17.6	4.5	13.8	35.9
Spruce	16.0	4.6	13.4	34.0
Simulations with mortality parameterization of White et al. (2000)				
DBF	31.9	3.7	11.0	46.6
Beech	41.1	5.4	16.2	62.6
Oak	30.2	4.5	15.4	50.0
ENF	28.4	4.4	14.8	47.5
Pine	43.6	6.4	19.7	69.8
Spruce	41.4	7.0	20.9	69.4
Potential ecosystem carbon storage (Adams, 1997)				
Warm temperate forest	19.0	3.6	14.5	37.1
Cool temperate forest	16.0	2.5	14.0	32.5

The spin-up simulations were run for a site with elevation of 450 m, soil depth 0.5 m, soil texture with 30% of sand and no slope.

middle of the XIX century representing about 16% of the maximum total N_{di} and increased very slowly until the end of the XIX century (Kopaček and Veselý, 2005). Consequently it could have had a significant level from the beginning of livestock-raising, i.e., since the middle-age colonisation of the territory. On the other hand, the peak of nitrogen emission in the region was reached in late the 1980s and then it fell approximately two times during the 1990s of the XX century. In contrast, the increase of ambient CO_2 started later and continued monotonously. Consequently, when linking N_{di} with ambient CO_2 level and taking the reference N_{di} value around the year 2000 we considerably underestimate its value.

4.2. Sensitivity analysis

Our analysis showed a high negative effect of new fine roots carbon to new leaves carbon allocation ratio (FRC:LC), specific leaf area (SLA) and maximum stomatal conductance ($g_{s,max}$) and a strong positive effect of C:N ratio of fine roots ($C:N_{fr}$) on NPP (Table 3). In spruce the significant effect of leaf turnover rate (m_l) was also observed ($m_l \equiv 1$ for deciduous), being positive for C_p and NPP and negative for C_l and C_s. This corresponds with the results of White et al. (2000) and was discussed in their study. The separated fine root turnover rate had only a small positive effect in spruce. A positive effect on NPP was also observed for nitrogen content in Rubisco (N_R) for all species under consideration, similarly to White et al. (2000). This effect follows from the fact that maximum rate of carboxylation in the model is proportional to N_R. However, for spruce it was small.

The effect of the C:N ratio of leaves ($C:N_{leaf}$) was different for different species: it was high and negative for beech, medium and positive for spruce and small for pine. This is in contrast with White et al. (2000), who found, that the increase of $C:N_{leaf}$ decreased NPP in all woody biomes and had the opposite effect for grasslands. Such an ambivalent effect of $C:N_{leaf}$ is explained by the trade-off between the increase of photosynthesis and foliage respiration with an increasing foliage nitrogen content.

Additionally, a high positive effect of new stem carbon to new leaf carbon allocation ratio (SC:LC) on carbon pools was observed for both beech and spruce. However, the effect of SC:LC on NPP was medium for spruce and small for beech. The reason for this effect is the redistribution of biomass into the woody compartment with a low turnover rate (equal to whole plant mortality). Fire mortality of spruce and pine also had a high negative effect on NPP, whereas in deciduous it had no effect on NPP. This may be explained in the following way. Fire mortality in the model is applied for each day of the year. In the coniferous species the foliage is present during the whole year, whereas in deciduous it is absent during the winter season, i.e., it is affected by fire mortality for a shorter time. This leads to a higher decrease of foliage biomass (see data on LAI in Table 3) and consequently photosynthesis in the coniferous compared to deciduous species. These effects were not observed by White et al. (2000).

The values of some of the eco-physiological parameters with a strong effect on the simulated carbon (as m_l, SC:LC, SLA) reported by different authors for the same species differ by up to several times (see, for example, White et al., 2000). Other parameters, for example the fraction of nitrogen content in Rubisco (N_R), have only a few references. In the studies with BIOME-BGC different authors applied for the stands of the same or similar type the values of parameters differing by up to 10 times. In particular, Pietsch and Hasenauer (2005) applied a 6 times smaller value of $g_{s,max}$ (0.001 and 0.006 m s^{-1}, respectively) and 10 times smaller value of boundary layer conductance (g_{bl}) (0.009 and 0.09 m s^{-1}, respectively) for Scots pine than White et al. (2000) for evergreen coniferous forests (ENF). Churkina et al. (2003) applied for ENF the value of N_R 0.07 in contrast with 0.033 in White et al. (2000). Pietsch et al. (2005) applied an N_R value of 0.162 for beech, which is almost twice as much as White et al. (2000) for DBF. This is why it is advised, that the key parameters initially taken from literature should be then specified by means of calibration for a given species and region.

Among the site parameters, those affecting temperature or solar radiation, i.e., elevation, albedo, aspect and slope, usually had little effect, which is related to the moderate climate conditions of the region. One exception was the observed strong positive effect of elevation on C_l and C_s under the highest elevation values. The last effect was related to the slowing down of soil and litter decomposition under lower temperature values.

In contrast, the site parameters affecting water, carbon and nitrogen regime (soil depth (d) and texture, precipitation ratio (P), ambient CO_2 and N_d) generally had high or medium effect. However, their effects considerably varied within the studied parameter spans, decreasing for high soil depth and N_d and for low sand fraction.

The soil texture is applied in the model to calculate the dependence of soil water pressure and volume. Soil water pressure is further applied to modify the rates of transpiration,

photosynthesis and decomposition. This explains the high effect of soil texture on output variables.

It is important to note that the precipitation dependence can pose difficulties for result extrapolation over an area with complex terrain. On the other hand, the low effect of site aspect and slope permits a safe extrapolation over a hilly territory with slopes up to 20°. Hence, the extrapolation to large forested areas can safely be performed if relief (elevation distribution) is known, together with tree species distribution and regional precipitation dependence on elevation.

As root water uptake processes are not simulated in the model, the effective soil depth set in the model determines only the potential soil water storage. If the soil water potential exceeds maximum, all additional water from precipitation represents run-off. The decrease of d leads to the decrease of the soil water storage and consequently to the decrease in the biomass production during the periods with the deficit of precipitation. This explains the high effect of soil depth on the model state variables. The effects of P and d considerably interacted. Under low d the effect of P rapidly decreases with P because under low soil volume the additional precipitation flows out. In contrast, under high d the effect of P remains significant within a larger span of P. The model block describing soil water includes considerable simplifications. In reality, the rooted zone of the soil can be supplied by water not only from precipitation, but also from capillary lift of underground water. Secondly, water run-off depends not only on soil water content, but also on drainage, in particular on slopes. Hence, an improvement of model soil block is desirable, for example, in such a way as was done by Pietsch et al. (2003), where the flooding events and the infiltration of groundwater into the rooting zone were introduced into the model.

The strong effect of nitrogen input on beech was observed only for small N_d values, namely below 0.0005 kg N m^{-2} year^{-1}. However this value, composed from 0.0001 kg N m^{-2} year^{-1} of natural nitrogen deposition and 0.0004 kg N m^{-2} year^{-1} of nitrogen fixation with no industrial deposition, was set as default in the example of site parameterization by the authors of the model (available online at http://www.ntsg.umt.edu/). Under the actual nitrogen deposition load in the Czech Republic (from 0.0005 to 0.0015 kg N m^{-2} year^{-1} for most of the territory, Czech Hydrometeorological Institute, 2001) the effect of N_d was low. However, in spruce the strong effect of N_d was observed up to N_d = 0.0011 kg N m^{-2} year^{-1}, i.e., the industrial nitrogen deposition can considerably affect growth. In contrast with N_d the ambient CO_2 had several times higher effect on the considered output variables for beech, than for spruce. This effect was high or medium for both species within the whole considered span of CO_2 concentration (298–370 ppm).

4.3. Steady state carbon pools

The comparison with the evaluations of Adams (1997) for potential forest carbon showed that when applying the original mortality parameterization of White et al. (2000), the steady state simulation gave considerably larger (up to 2.5 times) plant carbon pools (Table 4). The soil and litter carbon pools were larger as well (up to 2.3 times for litter and up to 1.5 times for soil). This led to a long-term decrease of C_l and C_s after imposing land-use management after steady state conditions. This was also noted by other authors (e.g., Pietsch and Hasenauer, 2005; Pietsch et al., 2005). With steady state mortality parameterization as applied in this study, a new equilibrium of C_s under land-use management was reached considerably earlier. White et al. (2000) based their parameterization of whole plant and fire mortalities, each on one reference only. It must be noted that the assessment of whole plant mortality remains difficult, because it includes mortality of whole individuals, branches, coarse roots, etc. However, the mortality rates of individual tree components may differ by up to several times and depend on tree age (Schlehaas et al., 2004). One way of assessing mortality rates might give the volume share of so-called salvage logging in relation to total growing stock in the managed forests ecosystems. In the case of the Czech Republic, this share has recently been oscillating around 1% (data not shown). In any case, the application of corresponding mortality parameters in the present study resulted in steady state vegetation carbon pool values matching other assessments for temperate forest ecosystems (Adams, 1997).

4.4. Long-term dynamics

The test simulation of long-term biomass production after a single imposed clear-cut (with the same mortality as that under spin-up simulation) showed that the simulated carbon pools, including vegetation, started to stabilize approximately 150 years after the clear-cut (data not shown). When applying the mortality parameterization of White et al. (2000), the rate of carbon accumulation rapidly decreased after 300 years, but a slow accumulation continued until approximately 4000 years.

The simulated litter and soil carbon pools reached their maximum during the first and fourth year after clear-cutting, respectively, due to the input of foliage and roots of harvested trees. C_l and C_s then gradually decreased due to the imbalance between small litterfall from the new growing stand and high rate of litter and humus decomposition, which depends on actual C_l and C_s values. C_l reached a minimum 20–60 years after clear-cut and then stabilized after a certain increase. The dynamics of C_s was considerably dependent on fire mortality (see Table 3). Under m_f = 0.005 year^{-1} C_s reached a minimum 250–300 years after felling and then gradually increased, whereas under m_f = 0.01 year^{-1} it decreased continuously with a tendency towards stabilization.

One problem associated with the correct prediction of carbon budget may be the fact that BIOME-BGC does not include any population dynamics: vegetation is described by carbon and nitrogen pools in the different plant compartments. When the simulation is performed for one generation only (or for several rotations of managed stand), population dynamics may be neglected and the monotone biomass growth within one generation, reproduced by the model, is realistic enough. However, for natural stand and long-term prediction, the population and succession dynamics become of crucial

importance. Biomass development becomes significantly non-monotone due to the uneven decline of old tree cohorts, natural change of species composition etc. The simulation of such processes requires models with a more detailed description of stand structure and competition, such as gap-models (Shugart, 1984).

5. Conclusions

The study identified key site and eco-physiological parameters of a process model BIOME-BGC based on a detailed sensitivity analysis. The model was adapted for application to managed forests in temperate regions. Additional changes to rainfall interception and nitrogen deposition routines made the model better suited for long-term application under changes in environmental conditions.

Among the site parameters, ratio of site and base station precipitation, ambient CO_2 concentration, nitrogen deposition, effective soil depth and texture had a strong effect on the simulated carbon pools. On the other hand, the effect of albedo, slope and exposition was small. Among the eco-physiological parameters, nitrogen content in Rubisco, new fine roots carbon to new leaves carbon allocation ratio, fire mortality and the C:N ratio of foliage and fine roots showed the strongest effect on simulated carbon pools and net primary production (NPP). Whole plant mortality and new stem to new leaf carbon allocation ratio had a strong effect on state variables only and did not significantly affect NPP. The magnitude of these effects commonly varied between coniferous and broadleaved tree species.

Commonly, the model prediction is nonlinearly affected by several parameters. Consequently the effect of a certain parameter can considerably vary within its considered range and it is also dependent on the values of other parameters. We recommend distinguishing parameter sets by tree species and verifying them using experimental data. This is the content of our companion paper (Cienciala and Tatarinov, 2006).

Acknowledgements

Biome-BGC version 4.1.1 was provided by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana. NTSG assumes no responsibility for the proper use of Biome-BGC by others. The authors gratefully acknowledge the support of the Czech Science Foundation (GAČR), Grant number 526/03/1021 (CzechRECAF) and of the Czech Ministry of Environment (VaV/640/18/03-CzechCARBO).

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