

## The Effect of Dynamic Mortality Incorporated in BIOME-BGC on Modelling the Development of Natural Forests

K. Merganičová<sup>1,\*</sup> and J. Merganič<sup>1,2</sup>

<sup>1</sup>Department of Forest Management and Geodesy, Faculty of Forestry, Technical University of Zvolen, Zvolen 960 53, Slovakia

<sup>2</sup>Department of Forest Management, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Praha 165 21, Czech Republic

Received 24 July 2012; revised 18 April 2013; accepted 15 October 2013; published online 09 September 2014

**ABSTRACT.** The presented paper evaluates the ability of BIOME-BGC model to simulate the small developmental cycle of natural forests after the incorporation of the dynamic mortality module. For the analysis we used the data from the Norway spruce (*Picea abies* L./Karst.) virgin forest Babia hora in Slovakia, which were equally divided into three developmental stages of virgin forests: stage of growth, optimum, and breakdown. The assessment of the simulated developmental cycle was based on the error analysis of the three main carbon pools (carbon content in stem, coarse woody debris, and soil) in individual developmental stages and the temporal performance of carbon fluxes over the whole developmental cycle. The results indicate that with the current dynamic mortality the model BIOME-BGC is capable of simulating the small developmental cycle of virgin forests.

*Keywords:* biogeochemical model, carbon cycle, developmental stage, flux dynamics, small developmental cycle, virgin forest

### 1. Introduction

It is generally known, that process-based models require a lot of input data to initialise the simulation. To overcome this disadvantage, a self-initialisation procedure has been developed and implemented in several process-based models, e.g. BIOME-BGC (Thornton, 1998). When this procedure is used, the simulation can be performed with only basic information about a forest stand, its site and soil conditions (Thornton and Rosenbloom, 2005). A self-initialisation simulation begins with 0.001 kgC m<sup>-2</sup> in leaves, 50% soil water saturation, and no soil organic matter. The main idea behind the self-initialisation procedure is that during the simulation the model gradually accumulates carbon in an ecosystem until a steady state is reached (Thornton and Rosenbloom, 2005). In the model, the steady state means that the long-term stability in all state variables has been achieved although on shorter time scales their values vary due to the variability of environmental conditions and model processes. Technically, the mean values of the soil organic matter (i.e. carbon content in soil) of the two successive periods of a certain number of years are compared. If the difference does not exceed a predefined threshold (0.0005 kg

Cm<sup>-2</sup>), it is presumed that the steady state is reached. Hence, the self-initialisation procedure of BIOME-BGC leads a forest ecosystem to climax, i.e. to a stable-end-stage (Clements, 1916). The steady state then represents the starting point for further simulations. Therefore, it is important to ensure that the steady state produced by the model represents the steady state that can be achieved in real conditions. In nature, virgin forests represent such a steady state, and hence, can be taken as a reference for the comparison with the model results. The information from virgin forests has been proven important for the validation of the simulated equilibrium for the conditions of Central Europe (Merganičová, 2004; Hasenauer et al., 2005; Pietsch and Hasenauer, 2006). The development of virgin forests can be driven either by large-scale or small-scale dynamics (Korpeľ, 1995). Large developmental cycle usually occurs after major disturbances, which radically changes the situation on the site, due to which the whole succession cycle starts with pioneer vegetation followed by subsequent developmental stages until the climax stage is achieved (Korpeľ, 1995). Small developmental cycle is characterised by small-scale dynamics caused primarily by intrinsic mortality of individual trees or small groups of trees (Korpeľ, 1995). After such events smaller or larger gaps occur within the stand, where suitable conditions are created for the establishment of new generation (Kucbel et al., 2009). The development of Central Europe has usually been considered to underlie small-scale dynamics characterised by a sequence of several developmental or succession stages (Peterken, 1996). However, nowadays

\* Corresponding author. Tel.: +421 90 4355 451; fax: +421 45 5332 654.  
E-mail address: k.merganicova@forim.sk (K. Merganičová).

this consideration has been in the centre of the scientific debate since several studies, e.g. Zielonka et al. (2009), Svoboda et al. (2012), showed that large cycle also occurs in natural forests of Central Europe.

Small-scale dynamics of forest ecosystems was studied by several authors, e.g. Leibundgut (1959), Zukrigl et al. (1963), Mayer et al. (1972), Korpel' (1995), Oliver and Larson (1996), etc. Each of the authors developed their own description and classification of natural forest development based on the results from particular forest stands. The differences between the individual classifications from the spatial and structural point of view were addressed in more detail by Král et al. (2010a, 2010b). Mathematically, fine-scale dynamics follows a U-shape distribution starting from small and young to large and old trees (Harcombe, 1987).

The original model BIOME-BGC (Thornton, 1998) accounts for fire and regular mortality (i.e. mortality caused by senescence and competition), and presumes that mortality takes place annually as a constant predefined ratio of the vegetation biomass. Both fire and regular mortality rates are set to 0.5% of vegetation biomass per year (White et al., 2000). Since according to Goldammer and Page (2000), fire does not currently play an important role in the natural dynamics of Central European forests, its effect has been excluded from the simulations in this region. However, the results of the simulations with zero fire mortality showed high overestimation of carbon content in forest ecosystems (Merganičová, 2004). A more detailed analysis of Merganičová (2004), Hasenauer et al. (2005), and Pietsch and Hasenauer (2006) documented that a simple increase of regular natural mortality from original 0.5 to 2, 3, or 6 % per year did not lead to desired results. Due to this, a dynamic mortality model was developed (Merganičová, 2004; Pietsch and Hasenauer, 2006) that incorporated a so called mosaic cycle (Remmert, 1991) of forest cyclic succession (Watt, 1947) in the model. This shift of developmental stages of a forest is characteristic of the small developmental cycle of the virgin forests (Korpel', 1995).

Using the data from the Rothwald virgin forest in Austria, Pietsch and Hasenauer (2006) documented that the incorporation of the dynamic mortality model has led simulated results to the equilibrium that was comparable with observations. The previous studies (Merganičová, 2004; Pietsch and Hasenauer, 2006; Pietsch and Hasenauer, 2009; Merganičová et al., 2012) have already presented how the modelled carbon pools and fluxes develop over the whole developmental cycle. However, so far no data-supported analysis of the developmental cycle implemented in the model has been performed.

Hence, the goal of this work is to analyse if the BIOME-BGC model extended with the dynamic mortality module is capable of modelling the small developmental cycle of virgin forests. The presented paper complements the previous works by examining the accuracy of the model in simulating the sequence of individual developmental stages of the small developmental cycle as identified by Korpel' (1995). The analysis is based on the comparison of the modelled output with the data obtained in the field that represented the developmental

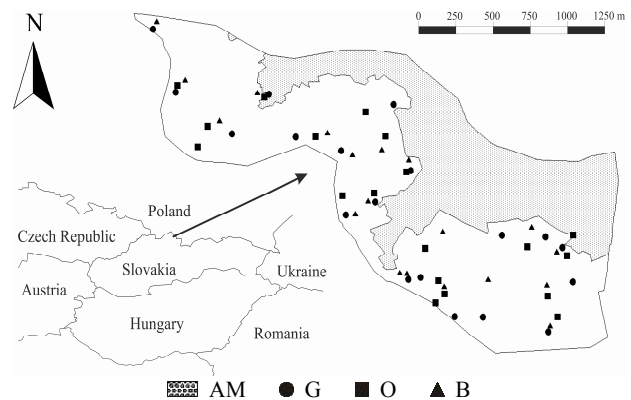
stages. The aim of the analysis is to examine which part of the modelled cycle can be assigned to the particular developmental stage. The results of the analysis are examined with regard to the common forestry knowledge about the small-scale dynamics of virgin forests in Central Europe published by e.g. Korpel' (1995). Our hypothesis is that after the incorporation of the dynamic mortality BIOME-BGC model is able to simulate the small developmental cycle reasonably well.

## 2. Material and Methods

### 2.1. Data

The data used for the study come from the Babia hora nature reserve, northern Slovakia. Babia hora is an isolated mountain massif of the outer Western Carpathian mountain range. The massif of Babia hora is built of tertiary flysch rocks, mainly sandstones, marl, claystones, slate and conglomerates. The most frequent soil type is podsol followed by raw soil, and andosol. The mean annual precipitation is 1,600 mm, and the mean annual temperature 2 °C. The forest stands are almost entirely composed of Norway spruce (*Picea abies* L./Karst.) with a small admixture of rowan (*Sorbus aucuparia* L.) and silver fir (*Abies alba* Mill.).

In 1926, a nature reserve was established to preserve natural mountainous spruce forest ecosystems in this region. Originally the area of the reserve was 117.6 ha, but in 1974 the reserve was enlarged and currently it covers 503.94 ha (Korpel', 1995), and comprises forests, dwarf mountain pine (*Pinus mugo*) stands, and sub-alpine meadows.



**Figure 1.** Location of sample plots in the Nature Reserve Babia hora (AM = alpine meadows and stands of mountain dwarf pine; G, O, B = sample plots in the developmental stage of growth, optimum, and breakdown, respectively).

Inside the forested area of the nature reserve, 57 permanent circular sample plots were established in 2002 (Merganič et al., 2003), each with an area of 0.05 ha (i.e. radius = 12.62 m). The plots are located at an elevation ranging from 1,173 m to 1,503 m above sea level, the latter representing the timber line in this region. The plots were equally divided into three developmental stages defined by Korpel' (1995): stage of growth, optimum and breakdown, i.e. each stage was represen-

ted by 19 plots distributed along the whole elevational gradient (Figure 1).

In all plots, main mensurational information was collected about living trees and dead wood with a diameter above 7 cm. For living trees and standing dead trees, tree height and diameter at breast height were assigned. In the case of lying dead wood (lying stems and their parts), its total length and diameter at ½ of its length was measured, whereas for stumps the diameter at 0.3 m height was determined. The decay class was assessed using the 8-degree scale as proposed by Holeksa (2001). The collected information was used for calculating the volume of living woody mass and dead woody mass per hectare. The volume of standing trees was calculated using an integral equation published in Merganičová et al. (2012), which was based on the models of the stem shape derived by Petráš (1986, 1989, 1990). The volume of lying deadwood was calculated using Huber's formula, while the volume of stumps was estimated as the volume of a cylinder with the height equal to 0.3 m. To enable the comparison of model output with the observed data, the volume was further transformed to carbon amount per hectare by multiplying stand wood volume, basic wood density, and fraction of carbon in woody mass. Carbon fraction was set to 50.1% of the dry mass as reported by Weiss et al. (2000) for Norway spruce in Central Europe. Basic wood density of living trees was set to 430 kg m<sup>-3</sup> as a mean of the published values (Weiss et al., 2000; Bütler et al., 2007; Morelli et al., 2007). Applied basic wood densities of deadwood for individual decay classes were derived by Merganičová and Merganič (2010).

**Table 1.** Basic Stand and Soil Characteristics of the Virgin Forest Babia Hora

Stand characteristics	Developmental stage			
	Growth	Maturity	Breakdown	All
Spruce [%]	98.65	99.90	99.59	99.38
Other [%]	1.35	0.10	0.41	0.62
h [m]	11.42	21.16	18.39	16.99
DBH [cm]	18.2	36.52	28.41	27.71
V [m <sup>3</sup> ha <sup>-1</sup> ]	239.96	465.92	233.71	313.20
N [ha <sup>-1</sup> ]	1,928	714	1,115	1,253
SDI	791.96	885.97	587.73	755.23
V <sub>CWD</sub> [m <sup>3</sup> ha <sup>-1</sup> ]	95	91	248	145
C <sub>soil</sub> [kgC m <sup>-2</sup> ]	7.41	5.16	8.23	6.84

\* Spruce% and Other% represent tree species composition of spruce and other tree species, respectively, h is the mean tree height, DBH the mean quadratic diameter at breast height, V the stand volume per hectare, N the number of trees per hectare, SDI the stand density index according to Reineke (1933), V<sub>CWD</sub> the volume of coarse woody debris, and C<sub>soil</sub> carbon amount in soil.

Forest soil samples were collected from one third of all the inventory plots (i.e. 19 plots). The plots for soil sampling were selected to ensure that all developmental stages and the full elevation range were covered. Soil samples were taken to a depth of 50 cm inside the area of the inventory plots. Organic carbon content in one gram of soil was determined from the oven-dried mass (ÖNORM L 1080) by the combustion in

O<sub>2</sub>-flow and consequent measurement of CO<sub>2</sub> using the infrared-spectrometer (LECO S/C 444). The basic information about stand and soil is presented in Table 1.

The climate data used in this study consisted of daily climate data about daily minimum and maximum temperature, daily precipitation, vapour pressure deficit, solar radiation and day length. For each plot, the data were extrapolated from the base station using MT-CLIM model (Running et al., 1987) depending on the difference in elevation, slope and aspect between the base station and an extrapolated point. As a base station we used the climate station Rabča located at the southern foot of the massif of Babia hora at an elevation of 642 m above sea level. The daily data were obtained for the period from 1961 to 2002 from Slovak Hydro-meteorological institute. Mean values of climate and site characteristics are presented in Table 2.

**Table 2.** Climate and Site Description of the Virgin Forest Babia Hora

Site characteristics	Minimum - maximum Mean ± Standard deviation
Longitude	19°29' - 19°31'
Latitude	49°33' - 49°35'
Elevation [m a.s.l.]	1,173 - 1,503
Slope [°]	5 - 40
Aspect	SE, E, SW, NW
Sand [%]	65 ± 3
Silt [%]	27 ± 4
Clay [%]	8 ± 5
Effective soil depth [m]	0.17 ± 0.06
Maximum temperature [°C]	5.55 ± 9.44
Minimum temperature [°C]	-2.74 ± 8.27
Precipitation [mm year <sup>-1</sup> ]	1,808 ± 285
Vapour pressure deficit [Pa]	328 ± 299
Solar radiation [W m <sup>-2</sup> s <sup>-1</sup> ]	295 ± 138

\* Minimum and maximum temperature, vapour pressure deficit, and solar radiation are daily average values calculated from all available weather records from 1960-2002.

## 2.2. Methods

### 2.2.1. Verification of the Specified Developmental Stages for Individual Plots

As already mentioned, each inventory plot was at the time of its establishment (year 2002) assigned to one of the three developmental stages: growth, optimum, and breakdown as defined by Korpel' (1995). This classification was used because it is a commonly accepted and applied classification in Slovakia. The categorisation of the plots was based on the visual assessment of the forest structure by taking the following parameters into account: vertical structure, proportion of ingrowth and of mature trees, and dead-wood amount with regard to its decay. The developmental stage was determined as a consensus of three educated foresters. Since one may argue that such a specification of the developmental stages is observer-dependent and therefore highly subjective, we performed

an objective statistical analysis to examine the subjective influence on the classification of the developmental stages in the field. For this purpose, we applied predictive discriminant analysis (Cooley and Lohnes, 1971; Huberty, 1994; StatSoft, 2004) that classified the inventory plots into three predefined qualitative categories (developmental stages). For each developmental stage a separate discriminant equation was derived, i.e. the classification was based on the set of three equations. The assessed inventory plot is assigned the developmental stage with the maximum calculated discriminant score. All explanatory variables that enter the discriminant equations are quantitative variables. They were selected using a combination of different approaches including stepwise forward and backward method with regard to their significance in the model and their logical interpretation. The stand characteristics included in the model were: crown competition factor CCF (Krajicek et al., 1961,  $p = 0.0003$ ), sum of crown projections ( $p = 0.00016$ ), arithmetical mean of the relative tree diameter ( $p = 0.00002$ ), and volumetric proportion of early decayed deadwood ( $p = 0.00515$ ). The value of Fischer F statistics ( $F(10, 100) = 14.220$ ,  $p < 0.0000$ ) indicates that the applied discriminant model is statistically highly significant. Similarly, the value of Wilks' lambda (0.17047) suggests that the model is appropriate because it is close to 0.

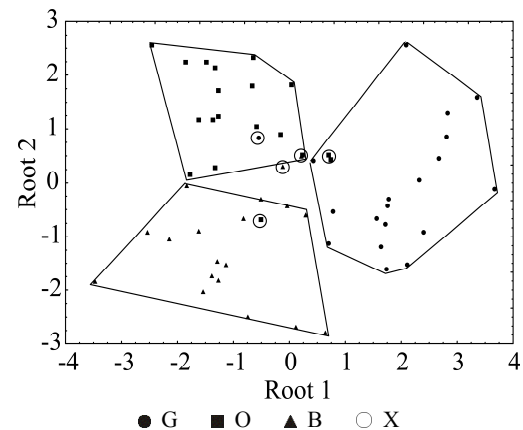
The coincidence between the visual classification and the classification with the discriminant model was 89.5%. This means that for 6 out of 57 inventory plots the developmental stage assigned by the model differed from the visual classification in the field. Figure 2 presents the graphical interpretation of the classification of the developmental stages on the base of the canonical analysis and the misclassified plots. This type of graph is useful for determining how each discriminant function contributes to the discrimination between groups (StatSoft, 2004).

If the discriminant model was extended with additional mensurational and geomorphological variables, namely elevation, and stand density index SDI (Reineke, 1933), the statistical classification coincided with the visual classification in the field in 96.5% cases, i.e. only two plots were classified differently in the field versus with the discriminant model. The two plots as well as 5 plots out of the total 6 plots classified differently with the discriminant model with only significant characteristics included are situated at the upper timber line, where the differences between the individual developmental stages diminish due to the limiting growing conditions (Merganič et al., 2003). On the base of the presented results we can state that the visual classification of the developmental stages in the field was objective and hence, can be taken as a basis for our analysis.

### 2.2.2. Model

The model BIOME-BGC is a biogeochemical model that simulates daily cycling of energy, water, carbon and nitrogen within an ecosystem (Thornton, 1998). For this study we used an extended version of BIOME-BGC developed by Pietsch et

al. (2003, 2005) and Pietsch and Hasenauer (2006) that is species-specific, accounts for the hydrology of flood-plains and presumes dynamic regular mortality.



**Figure 2.** Graphical interpretation of the classification of the developmental stages using canonical analysis (G, O, B = sample plots in the developmental stage of growth, optimum, and breakdown, respectively; X = plots for which the developmental stage classified in the field was different from the stage classified with the discriminant model).

The model requires input information about climate (daily values of minimum and maximum temperature, daily sum of precipitation, incident solar radiation, vapour pressure deficit), site (aspect, elevation, soil depth, soil texture), nitrogen deposition and fixation, prevailing tree species, and the specification of the length of the whole developmental cycle, the length of the high mortality phase, and minimum and maximum annual mortality rates. Pietsch and Hasenauer (2006) describe the applied dynamic mortality module in detail. It is a theoretical model of regular mortality driven by intrinsic ecosystem processes (competition and senescence).

### 2.2.3. Analysis of the Developmental Cycle Simulated by the Model BIOME-BGC

The analysis of the simulated developmental cycle was based on the comparison of the modelled average values with the observed average values of the three carbon pools: carbon content in stem, carbon content in coarse woody debris, and in soil separately for each developmental stage along the whole mortality cycle. This was performed in order to examine which part of the modelled cycle can be assigned to the particular developmental stage. In the analysis we compared the sequence of stages obtained for the modelled cycle with the theoretical expectations according to the common forestry knowledge about the small developmental cycle as presented e.g. in Korpel' (1995). The analysis was performed as follows.

First, all 57 inventory plots were simulated using Norway spruce ecophysiological parameterisation of BIOME-BGC (Pietsch et al., 2005), plot-specific site characteristics (i.e. latitude, elevation, soil depth, soil texture, see Table 2) and plot-specific daily climate data (Table 2), and constant

mortality settings derived for Norway spruce virgin forests of the Babia hora region by Merganičová et al. (2012). The length of the developmental cycle was set equal to 300 years, and the length of the high mortality phase was equal to 75 years based on Korpel' (1995). Minimum and maximum mortality rates were equal to 0.74 and 6%, respectively, since this combination was found to produce non-significant modelled values for the examined carbon pools by Merganičová et al. (2012). The simulation of each plot was performed in two steps. First, the self-initialisation procedure was run until the steady state was reached. Afterwards, each plot was simulated for another three hundred years representing one whole developmental cycle.

From the simulations we obtained the annual model output for each of 57 plots over the whole developmental cycle, i.e. 300 years. For the analysis we selected 7 model output variables: carbon content in stem (Cstem), carbon content in coarse woody debris, carbon content in soil, annual natural mortality rate, net primary production (NPP), heterotrophic respiration (Rh), and net ecosystem production (NEP). Hence, for each plot we obtained seven curves each representing the temporal performance of one of the seven variables over the whole developmental cycle.

Next, we calculated the average modelled temporal performance of the seven model output variables from the total of 57 inventory plots. In this way we obtained 7 curves representing average model performances of each of the 7 output variables (Cstem, carbon content in coarse woody debris, and in soil, annual natural mortality rate, NPP, Rh, and NEP) over the whole developmental cycle. These curves represent average temporal development of the seven variables under the average conditions of Babia hora nature reserve over the whole developmental cycle, i.e. 300 years.

For the analysis of the model versus observations we selected three variables, i.e. carbon content in stem, soil and coarse woody debris, for which we had information about both modelled and observed values. We calculated an average modelled temporal performance of every examined variable for each of the three individual developmental stages over the whole developmental cycle. This was calculated from 19 plots assigned to the same developmental stage. Hence, for every variable we obtained three curves, each representing one developmental stage. Likewise, each developmental stage was characterised by three curves representing the average modelled temporal performance of the three variables (Cstem, Ccwd, and Csoil) and each consisting of 300 annual average modelled values of the particular variable.

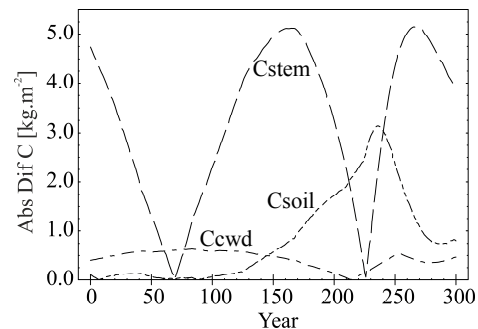
The annual average modelled values of an analysed variable were compared with the average observed value of the particular developmental stage. Note that each developmental stage was characterised by a single value of a specific variable calculated from 19 plots representing the developmental stage (Table 1). Thus, we obtained the differences between the annual modelled and the observed values for each variable and each developmental stage along the whole simulated cycle.

Next, the absolute values of the differences of the three variables were summed up in each year of the developmental cycle to obtain the total average absolute difference for each year and each developmental stage, from which the temporal performance of the differences over the whole developmental cycle was derived.

The temporal performances of the total average absolute differences of all three developmental stages were graphically analysed. Specifically, we examined in which period and for which developmental stage the total absolute differences are at minimum. The periods with minimum total absolute differences were then analysed with regard to the model performance of the seven output variables.

### 3. Results

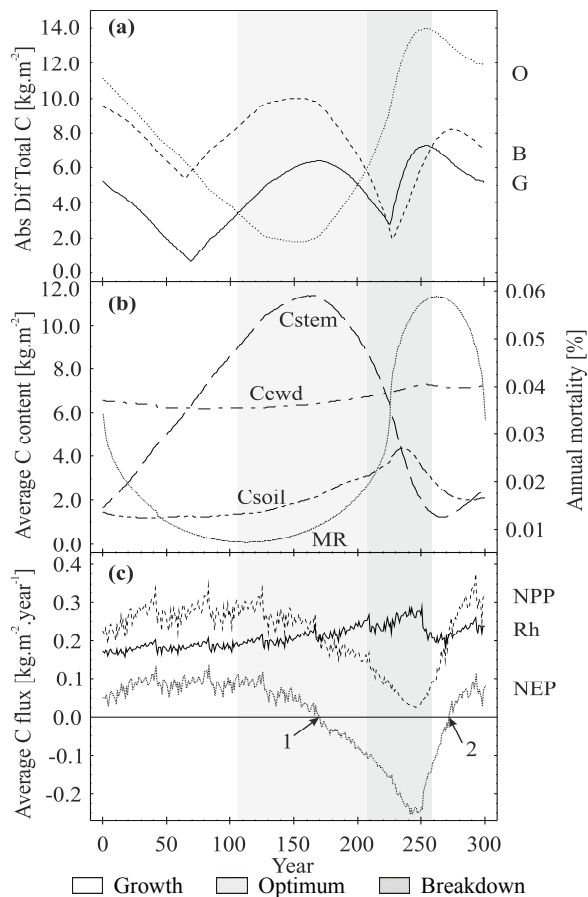
The analysis of the small developmental cycle simulated by BIOME-BGC after the incorporation of the dynamic mortality module in the model was based on the comparison of the observed values with the modelled values over the whole simulated cycle, i.e. 300 years. Figure 3 shows the differences between the modelled annual values and the average observed value of the three analysed variables for the stage of growth. The total average absolute differences for each developmental stage obtained as the sum of the absolute values of the three variables are presented in Figure 4A. Figures 4B and 4C show the average temporal performance of 7 output variables: carbon content in stem (Cstem), in coarse woody debris, and in soil, annual natural mortality rate, net primary production (NPP), heterotrophic respiration (Rh), and net ecosystem production (NEP) over the whole cycle.



**Figure 3.** The absolute differences between the modelled annual average values and the observed average value for the developmental stage of growth and three carbon pools along the whole developmental cycle (Cstem = carbon content in stem, Ccwd = carbon content in coarse woody debris, Csoil = carbon content in soil).

From Figure 4A we can see that in the period 0-106 years of the cycle, minimum absolute differences between the model and the observation were found for the stage of growth. This corresponds with the increasing carbon content in stem, decreasing mortality (Figure 4B) and positive NEP, i.e.  $NPP > Rh$  (Figure 4C). In the period from 106 to 207 years of the

cycle, the stage of optimum is characteristic by minimum absolute differences between the model and the observation (Figure 4A). As can be seen from Figure 4C, this stage covers the first transition point of NEP, when  $NPP = Rh$ .



**Figure 4.** Temporal development of absolute total differences in ecosystem carbon content between the model and observations (a) and of the simulated output (b and c). a: Absolute differences in carbon content in an ecosystem for the stage of growth (G), optimum (O), and breakdown (B). b: carbon content in stem (Cstem), carbon content in coarse woody debris (Ccwd), carbon content in soil (Csoil), and annual regular mortality rate (MR). c: Net primary production (NPP), heterotrophic respiration (Rh), net ecosystem production (NEP), numbers 1 and 2 indicate 1st and 2nd transition points, respectively. Background colours indicate the developmental stages determined on the base of the absolute differences in carbon content in an ecosystem.

The stage of breakdown (B) was found to have the lowest differences between the modelled and the observed values between years 224 and 259 (Figure 4A). This period is characteristic by minimum NPP and negative NEP (Figure 4C), maximum CWD, increasing mortality rate that is approaching its maximum, and the steepest decline of Cstem (Figure 4B). In the last period of the developmental cycle (259 ~ 300 years), minimum differences were again found for the stage of

growth. During that period, mortality rate reaches its maximum and begins to decrease, while Cstem reaches its minimum and begins to rise (Figure 4B), NEP passes through the second transition point and becomes positive again (Figure 4C).

Carbon content in stem is analogous to a forestry characteristic stand volume. During the first 100 years of the developmental cycle, carbon content in stem increases steadily in an almost linear pattern. This steady increase is coupled with the decrease of mortality rate (Figure 4B). However, their transition points, where the courses of mortality and carbon content in stem change in the opposite direction, do not coincide. Carbon content in stem continues to increase even after the mortality rate starts to increase, although the annual increase slows down (in our case for approximately 60 years starting from 110 to 170 years of the developmental cycle). The increase in carbon content in stem stops when NPP equals heterotrophic respiration (Figures 4B and C). After this point, both carbon content in stem and NPP begin to decrease. The decline of carbon content in stem continues until the second transition point at approximate age of 270 years. At this age, mortality rate reaches its maximum and begins to decrease. The second transition point of the course of carbon content in stem again coincides with the time when NPP equals Rh (Figures 4B and C).

#### 4. Discussion and Conclusion

From the curves representing the temporal behaviour of the particular variable we can conclude that the performance of carbon in stem in time coincides with the curves of stand volume performance hypothesised and presented by e.g. Korpel' (1995) for virgin forests of Central Europe. Our distinction of the individual developmental stages on the base of the differences between the model and the observations differs from the one by Pietsch and Hasenauer (2009) performed on the base of the modelled values. These authors also identified 3 developmental stages, while they placed the borders between the individual developmental stages in the two transition points, when NEP changes from being positive to being negative or vice versa (see Figure 4C), since in these points the ecosystem changes its position in the carbon balance system, i.e. it becomes a carbon source (after 1<sup>st</sup> transition point) or a carbon sink (after 2<sup>nd</sup> transition point). These carbon balance stages (Figure 4C) do not correspond with the developmental stages commonly applied in forestry (Figure 4A). This is because the definition of forestry developmental stages is based on forestry characteristics, e.g. stand volume, stand increment, diameter and height distribution, mortality, regeneration (e.g. Korpel', 1995; Podlaski, 2006; Král et al., 2010a), i.e. on the characteristics which are observable and measurable in the field, rather than on carbon balance of the ecosystem.

Hence, 1<sup>st</sup> transition point (when NEP changes from being positive to being negative, i.e. ecosystem becomes carbon source) occurs within the stage of optimum (Figure 4). From the forestry point of view, this stage represents maturity, when

the stand volume reaches its maximum, volume growth is decelerated, and mortality rate begins to increase (Korpel', 1995). This description coincides with the pattern of Cstem, mortality and NEP within the given period (Figures 4B and C). Similarly, the description of the stage of breakdown found in Korpel' (1995) corresponds with the model behaviour, i.e. stand volume decreases rapidly, mortality is high, the amount of C-WD is at its maximum (Figure 4). During the stage of growth, mortality rate decreases and carbon content in stem increases (Figure 4), which coincides with the verbal description of this stage by Korpel' (1995) who characterised it by steadily increasing stand volume, and low mortality rate.

In spite of this good coincidence of model behaviour with the verbal description of developmental stages by Korpel' (1995), the analysis also revealed some minor inconsistencies, particularly in the period between years 210 and 225, when unexpectedly the stage of growth was found to have the smallest absolute differences between the model and the observations (Figure 4). However, the differences between the stage of growth and breakdown in this period are not significant (Figure 4) and can be caused by the fact that the infield-assigned developmental stage of 2-6 plots did not correspond with the discriminant analysis of the stages. These results might also indicate that using only three developmental stages as proposed by Korpel' (1995) is not sufficient and more than 3 stages are needed to describe the dynamics of a forest ecosystem more precisely. In fact, most predecessors and contemporaries of Korpel' distinguished more than 3 phases, e.g. Leibundgut (1959) and Hillgarter (1976) defined 5 developmental phases, while Mayer et al. (1972) distinguished 6 different phases. The same trend has also been observed in several recent works dealing with the dynamics of natural forests (e.g. Emborg et al., 2000; Král et al., 2010a), which on the base of more sophisticated methods (e.g. diameter distribution, artificial neural network, etc.) specified 4-5 developmental stages or phases. Similarly, when analysing the attractor of the model dynamics, Pietsch and Hasenauer (2009) distinguished 5 developmental stages. The change of the applied classification would require a proper comparison of the individual existing classification schemes used in the research of natural forests and their harmonisation especially at a spatial scale, which was found to be crucial for addressing the representativeness of the plots (Král et al., 2010b). However, this task is out of the scope of the presented paper, which aimed at the analysis of the model capability to simulate the development of forest ecosystems driven by intrinsic processes.

To conclude we can state that the assessment of the temporal performance of carbon fluxes in forest ecosystems revealed that with the incorporated dynamic mortality module BIOME-BGC model is capable of simulating the small dynamic developmental cycle of virgin forests in Central Europe reasonably well. Hence, the model can be applied to studies analysing the changes of carbon storage in natural forest ecosystems that have not been directly influenced by human interventions or those that have been left to self-development and undergo small-developmental cycle. The prerequisite for its application outside the Central Europe or for different species

is the calibration of the dynamic mortality module, as the model requires a priori information about the length of the developmental cycle and the length of the high mortality phase. The incorporated dynamic mortality module is not suitable for simulating the regions where large-scale dynamics prevails, because it does not account for disturbances caused by extrinsic factors, such as wind or bark beetle outbreak. For this, other approaches presented e.g. in Seidl et al. (2012) should be applied and coupled with the current model.

**Acknowledgments.** This work was financed by the Centre of Excellence "Decision support in forest and country", ITMS 26220120069 supported by the Research and Development Operational Programme funded by the ERDF. We thank two anonymous reviewers and our colleagues Stephan Pietsch, Hubert Hasenauer and Róbert Sedmák for their valuable comments that helped us to improve the manuscript, and Stanislav Kucbel for his helpful comments on the developmental cycle of virgin forests.

## References

- Bütler, R., Patty, L., Le Bayon, R.C., Guenat, C., and Schlaepfer, R. (2007). Log decay of *Picea abies* in the Swiss Jura Mountains of central Europe. *For. Ecol. Manage.*, 242, 791-9. <http://dx.doi.org/10.1016/j.foreco.2007.02.017>
- Clements, F.E. (1916). *Plant succession: An analysis of the development of vegetation*. Carnegie Institute, Washington, DC, No. 242.
- Cooley, W.W., and Lohnes, P.R. (1971). *Multivariate data analysis*. Wiley, New York.
- Emborg, J., Christensen, M., and Heilmann-Clausen, J. (2000). The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.*, 126, 173-189. [http://dx.doi.org/10.1016/S0378-1127\(99\)00094-8](http://dx.doi.org/10.1016/S0378-1127(99)00094-8)
- Goldammer, J. G., and Page, H. (2000). Fire History of Central Europe: Implications for prescribed burning in landscape management and nature conservation. BALTEX FIRE, Finland, June 2000. <http://www.fire.uni-freiburg.de/programmes/natcon/BAL-PAP3-2.PDF>
- Harcombe, P.A. (1987). Tree life tables: Simple birth, growth, and death data encapsulate life histories and ecological roles. *BioScience*, 37(8), 557-568. <http://dx.doi.org/10.2307/1310666>
- Hasenauer, H., Merganičová, K., and Pietsch, S.A. (2005). Modeling biogeochemical cycles within old-growth forest ecosystems. *For. Snow Landscape Res.*, 79 (1/2), 81-90.
- Hillgarter, F.W. (1976). Beitrag zur Methodik der Erfassung und Beschreibung von Urwaldphasen. In: Mayer H. (Ed.) XVI. IUFRO World-Congress, 20.6.-2.7.1976, Oslo, Norway, Institut für Waldbau, BOKU Wien, 79-83.
- Holeksa, J. (2001). Coarse woody debris in a Carpathian subalpine spruce forest. *Forstw. Cbl.*, 120, 256-270. <http://dx.doi.org/10.1007/BF02796097>
- Huberty, C.J. (1994). *Applied discriminant analysis*. Wiley, New York.
- Korpel', Š. (1995). *Die Urwälder der Westkarpaten*. G. Fischer, Stuttgart.
- Krajicek, J.E., Brinkman, K.A., and Gingrich, S.F. (1961). Crown competition-A measure of density. *For. Sci.*, 7, 35-42.
- Král, K., Vrška, T., Hort, L., Adam, D., and Šamonil, P. (2010a). Developmental phases in a temperate natural spruce-fir-beech forest: determination by a supervised classification method. *Eur J For Res.*, 129 (3), 339-351. <http://dx.doi.org/10.1007/s10342-009-0340-0>
- Král, K., Janík, D., Vrška, T., Adam, D., Hort, L., Unar, P., and Šamonil, P. (2010b). Local variability of stand structural features in bee-

- ch dominated natural forests of Central Europe: Implications for sampling. *For Ecol Manage.*, 260, 2196-2203.
- Kucbel, S., Jaloviari, P., Saniga, M., Vencurik, J., and Klimaš, V. (2010). Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *Eur J Forest Res.*, 129(3), 249-259. <http://dx.doi.org/10.1007/s10342-009-0322-2>
- Leibundgut, H. (1959). Über Zweck und Methodik der Struktur und Zuwachsanalyse von Urwäldern. *Schweizerische Zeitschrift für Forstwesen*, 110 (3), 111-124.
- Mayer, H., Schenker, S., and Zukrigl, K. (1972). Der Urwaldrest Neuwald beim Lahnsattel. *Centralblatt des gesamten Forstwesens*, 89 (3), 147-190.
- Merganič, J., Vorčák, J., Merganičová, K., Ďurský, J., Miková, A., Škvarenina, J., Tuček, J., and Mind'áš, J. (2003). Diversity monitoring in mountain forests of Eastern Orava. EFRA, Tvrdošín: 200pp. (in Slovak).
- Merganičová, K., Merganič, J., and Hasenauer, H. (2012). Assessing the carbon flux dynamics within virgin forests: The Case Study 'Babia hora' in Slovakia. *Austr. J of For Sci.*
- Merganičová, K., and Merganič, J. (2010). Coarse woody debris carbon stocks in natural spruce forests of Babia hora. *J For Sci.*, 56(9), 397-405.
- Merganičová, K. (2004). Modelling forest dynamics in virgin and managed forest stands, PhD. thesis, University of Natural Resources and Applied Life Sciences Vienna, Austria.
- Morelli, S., Paletto, A., and Tosi, V. (2007). Deadwood in forest stands: assessment of wood basic density in some tree species, Trentino, Italy. *Forest*, 4(4), 395-406. <http://dx.doi.org/10.3832/efor0492-0040395>
- Oliver, C.D., and Larson, B.C. (1996). Forest stand dynamics. New York, John Wiley and Sons, Inc.
- Peterken, G.F. (1996). Natural woodland: Ecology and conservation in northern temperate regions. Cambridge, Cambridge University Press.
- Petráš, R. (1986). Mathematical model of stem shape. *Lesnícky časopis*, 32(3), 223-236 (in Slovak).
- Petráš, R. (1989). Mathematical model of stem shape of coniferous tree species. *Lesnictví*, 35(10), 867-878 (in Slovak).
- Petráš, R. (1990). Mathematical model of stem shape of broadleaved tree species. *Lesnícky časopis*. 36(3), 231-241 (in Slovak).
- Pietsch, S.A., Hasenauer H., and Thornton, P.E. (2005). BGC-model parameter sets for central European forest stands. *For. Ecol. Manage.*, 211, 264-295. <http://dx.doi.org/10.1016/j.foreco.2005.02.046>
- Pietsch, S.A., Hasenauer H., Kučera J., and Čermák, J. (2003). Modelling effects of hydrological changes on the carbon and nitrogen balance of oak in floodplains. *Tree Physiol.*, 23, 735-746. <http://dx.doi.org/10.1093/treephys/23.11.735>
- Pietsch, S.A., and Hasenauer, H. (2006). Evaluating the self-initialisation procedure of large scale ecosystem models. *Global Change Biol.*, 12, 1658-1669. <http://dx.doi.org/10.1111/j.1365-2486.2006.01211.x>
- Pietsch, S.A., and Hasenauer, H. (2009). Photosynthesis within large-scale ecosystem models. In: Laisk, A., Nedbal, L., Govindjee (eds.): Photosynthesis in silico: Understanding Complexity from Molecules to Ecosystems, 441-464.
- Podlaski, R. (2006). Suitability of the selected statistical distributions for fitting diameter data in distinguished development stages and phases of near-natural mixed forests in the Świętokrzyski National Park (Poland). *For. Ecol. Manage.* 236 (2-3), 393-402. <http://dx.doi.org/10.1016/j.foreco.2006.09.032>
- Reineke, L.H. (1933). Perfecting a stand-density index for even-aged forest. *J of Agri. Res.*, 46, 627-638.
- Remmert, H. (1991). The mosaic cycle concept of ecosystems. *Ecological Studies* 85. Springer Verlag, Berlin. [http://dx.doi.org/10.1007/978-3-642-75650-4\\_1](http://dx.doi.org/10.1007/978-3-642-75650-4_1)
- Running, S.W., Nemani, R.R., and Hungerford, R.D. (1987). Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Can J For Res.*, 17. 472-483. <http://dx.doi.org/10.1139/x87-081>
- Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., Netherer, S., Arpacı, A., Bontemps, J.D., Bugmann, H., Olabarria, J.R.G., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.J., and Mohren, F. (2011). Modelling natural disturbances in forest ecosystems: a review. *Ecol. Model.*, 222(4), 903-924. <http://dx.doi.org/10.1016/j.ecolmodel.2010.09.040>
- StatSoft, Inc. (2004). STATISTICA Cz [Software], Version 7.
- Svoboda, M., Janda, P., Nagel, T.A., Fraver, S., Rejzek, J., and Bače, R. (2012). Disturbance history of an old-growth sub-alpine Picea abies stand in the Bohemian Forest, Czech Republic. *J. Veg. Sci.*, 23(1), 86-97. <http://dx.doi.org/10.1111/j.1654-1103.2011.01329.x>
- Thornton, P.E. (1998). Description of a numerical simulation model for predicting the dynamics of energy, water, carbon and nitrogen in a terrestrial ecosystem. PhD. thesis. University of Montana, Missoula, MT, USA.
- Thornton, P.E., and Rosenbloom, N.A. (2005). Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecol. Model.*, 189, 25-48. <http://dx.doi.org/10.1016/j.ecolmodel.2005.04.008>
- Watt, A.S. (1947). Pattern and process in the plant community. *J. Ecol.*, 35, 1-22. <http://dx.doi.org/10.2307/2256497>
- Weiss, P., Schieler, K., Schadauer, K., Radunsky, K., and Englisch, M. (2000). Die Kohlenstoffbilanz des österreichischen Waldes und Betrachtungen zum Kyoto-Protokol. Federal Environment Agency, Wien, Monographie 106.
- White, M.A., Thornton, P.E., Running, S.W., and Nemani, R.R. (2000). Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls. *Earth Interact.*, 4(3), 1-85. [http://dx.doi.org/10.1175/1087-3562\(2000\)004<0003:PASAOT>2.0.CO;2](http://dx.doi.org/10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2)
- Zielonka, T., Holeksa, J., and Malcher, P. (2009). Disturbance events in a mixed spruce-larch forest in the Tatra Mts., Western Carpathians-a tentative reconstruction. *Balt. For.*, 15(2), 161-167.
- Zukrigl, K., Eckhart, G., and Nather, J. (1963). Standortkundliche und waldbauliche Untersuchungen in Urwaldresten der niederösterreichischen Kalkalpen. Mitteilungen der forstlichen Bundesversuchsanstalt Mariabrunn 6.