Modeling biogeochemical cycles within old-growth forest ecosystems

Hubert Hasenauer, Katarína Merganičová and Stephan A. Pietsch

Institute of Forest Growth Research, Department of Forest and Soil Sciences, BOKU University of Natural Resources and Applied Life Science, Peter Jordan Strasse 82, A-1190 Vienna, Austria
hubert.hasenauer@boku.ac.at, katarina.merganicova@boku.ac.at, stephan.pietsch@boku.ac.at

Abstract
Old-growth forests enable us to explore the natural dynamics and equilibrium of forest ecosystems. They are characterized by a long-term balance of energy, water, carbon, nitrogen and other nutrient fluxes. One option to enhance our understanding of forest ecosystem fluxes is the application of ecosystem models. In this paper we use a species-specific adaptation of the ecosystem model BIOME-BGC to assess the biogeochemical cycle of old-growth forests and test the reliability of self initialization procedures as they are commonly applied within large-scale forest ecosystem models. We investigated the reliability of such initialization procedures by comparing the modeled equilibrium with data obtained from virgin forests in Central Europe. The results demonstrate that after some modifications the model is able to assess the flux of energy, water, nitrogen and carbon within old-growth forest ecosystems.

Keywords: old-growth forests, forest ecosystem modeling, development dynamics, mortality

1 Introduction

Most forests in Central Europe have been influenced by humans, resulting in a reduction of forest covered land area, and changes in the tree species distribution and in the soil conditions. These impacts may have resulted in site degradation and have affected the sustainability of these forests. One way to assess and study such fundamental impacts is to apply biogeochemical mechanistic ecosystem models. In combination with old-growth forests, which can be considered as a reference situation or "potential" sustainable forest ecosystem because no human interference is evident, such models may be used: (1) to understand the biogeochemistry of old-growth forest ecosystems and (2) to assess potential differences between undisturbed ecosystems and actively managed forests.

Large data requirements are thought to be the most serious drawback of mechanistic ecosystem models. Besides site characteristics (e.g. elevation, soil depth, etc.) and climate data (temperature, precipitation, air humidity and solar radiation), these models require an estimate for the initial water, carbon and nitrogen status of a given ecosystem. Unfortunately such information is usually not available for forest areas or particular forest stands. Therefore several mechanistic models (e.g. BIOME-BGC – THORNTON *et al.* 2002; LPJ – SITCH *et al.* 2003) use a so-called self-initialization procedure to obtain starting values. Only climate data and site specific conditions are required to perform a self-initialization or so-called 'spinup run' for a given site.

The mission of this paper is to apply our species-specific adaptation of the ecosystem model BIOME-BGC to old-growth forests. We are specifically interested in finding out whether the model adequately mimics the flux of carbon and nitrogen within such forests and if the currently used spin-up procedures of the model correctly mimic the natural equilibrium (VACEK 2003) of undisturbed virgin forests.

2 Material and methods

2.1 Data

Data obtained for this study came from permanent sample plots located in two Central European virgin forests in Rothwald, Austria, and Babia Hora, Slovakia. In Rothwald 18 plots, each 20 × 20 m, were measured, whereas in Babia Hora 57 circular 500 m^2 plots were established (MERGANIČ *et al.* 2003). On every plot, the site, stand and soil characteristics were recorded. Site parameters include the necessary input data for the simulations: geographic position (latitude, longitude and elevation), aspect, slope, soil depth, soil texture and average skeleton amount. The summary statistics are given in Table 1.

On each permanent sample plot, the height and diameter at breast height of all standing trees (both alive and dead) with a tree height greater than 1.3 m, as well as of stumps from decaying standing dead wood and fallen dead wood were recorded. Lying dead wood was measured if the diameter at one place along its length exceeded 20 cm (Rothwald) or 7 cm (Babia Hora). For each piece of lying dead wood, the length, diameter at both ends and in the middle (in Babia Hora only in the middle) and the deterioration or decay class were assessed and recorded according to the scale proposed by MASER *et al.* (1979) and HOLEKSA (2001).

Tree volume of dead and living trees was calculated using the following form factor function *f:*

$$f = b_1 + b_2 \cdot \ln(DBH)^2 + b_3 / H + b_4 / DBH + b_5 /(DBH^2) + b_6 /(DBH \cdot H) + b_7 /(DBH^2 \cdot H)$$

Where DBH is the diameter at breast height in cm, and H the total tree height in m. For all trees ≥ 10.5 cm in DBH, the coefficients according to POLLANSCHÜTZ (1974) were used. For trees with a DBH 5 cm but < 10.5 cm, the same formula was used but with the coefficients according to SCHIELER (1988). For all trees with a DBH < 5 cm, we used the formula proposed by HAFELLNER (1985):

$$V = 0.5503 \cdot DBH^{1.86} \cdot H^{0.9256}$$

Where V is the tree volume (m^3), DBH the diameter at breast height (cm), and H the total tree height (m). For trees with broken crowns, which frequently occurred in both virgin forests, we first calculated the total tree height assuming no damage. We used diameter-height curves derived from undamaged trees to define the missing tree height. Next we applied the form factor function to have an estimate of the total tree volume assuming an undamaged tree. Knowing the length of the broken crown of a tree allows us to calculate the corresponding volume of the broken part. After subtracting the estimated broken proportion of volume from the total tree volume of an undamaged tree, the total tree volume for trees with broken crowns can be derived. The stump volume was estimated as the volume of a cylinder with a height equal to 0.3 m. The volume of lying dead wood (logs) was calculated as the volume of a second degree paraboloid.

Soil characteristics, such as the amount of carbon and nitrogen in the litter and soil, were assessed in the laboratory from collected field samples. In Rothwald, samples were collected from all 18 permanent sample plots, whereas in Babia Hora the samples were taken from only 19 (of 57) plots. Litter samples were taken using a 30 × 30 cm frame (Rothwald) or a 50 mm diameter litter auger (Babia Hora). Soil samples were collected using a soil auger with a diameter of 70 mm and a length of 50 cm. In Babia Hora soil sampling with the soil auger was applied only to 10 inventory plots, whereas on the other 9 plots soil pits, each at least 50 cm deep, were collected within the area of the inventory plot. Carbon amounts in litter or soil were determined from dry mass using a LECO S/C 444 infrared-spectrometer. Nitrogen amounts were estimated according to Kjeldahl (BRADSTREET 1965).

Daily climate data, i.e. daily minimum and maximum temperature, daily precipitation, air humidity and solar radiation, necessary to run the ecosystem model were obtained from nearby climate stations with long-term measurements using the climate interpolation models DAYMET (THORNTON *et al.* 1997; HASENAUER *et al.* 2003) and MT-CLIM (RUNNING *et al.* 1987) in Rothwald and Babia Hora since 1961. Average values for the required climate characteristics are given in Table 1.

Table 1. Site, soil and climate descriptors of each location. Climate parameters represent average values between 1960 and 2002. Nitrogen deposition in Rothwald was the deposition recorded in 1994 (SCHNEIDER 1998); in Babia Hora deposition was measured in 2002 (MERGANIČ *et al.* 2003).

Site characteristics	Rothwald	Babia Hora
Longitude [°,’]	15°05’ – 15°06’	19°29’ – 19°31’
Latitude [°,’]	47°46’ – 47°47’	49°33’ – 49°35’
Elevation [m a.s.l.]	1017 – 1216	1173 – 1503
Slope [°]	0 – 30	5 – 40
Aspect	E, SE, S, NW	SE, E, SW, NW
Sand %	23 ± 8	65 ± 3
Silt %	33 ± 4	27 ± 4
Clay %	44 ± 10	8 ± 5
Soil depth [m]	0.39 ± 0.10	0.17 ± 0.06
Maximum temperature [°C]	12.46 ± 9.01	5.55 ± 9.44
Minimum temperature [°C]	3.00 ± 7.09	–2.74 ± 8.27
Precipitation [mm/year]	1475 ± 233	1808 ± 285
Rainy days (>0.1mm) per year	182 ± 18	173 ± 28
Vapor pressure deficit [Pa]	543 ± 408	328 ± 299
Solar radiation [W/m^2/s]	231 ± 120	295 ± 138
Nitrogen deposition [kg/ha/year]	16	16

2.2 Model

In this paper we use BIOME-BGC, an ecophysiological model (THORNTON *et al.* 2002) adapted for central European conditions (PIETSCH and HASENAUER 2002; PIETSCH *et al.* in press). The model estimates the cycles of carbon, nitrogen, water and energy of ecosystems based on the interactions between the atmosphere, plants and the soil. The model calculations are as follows: Leaf area index (LAI, m^2 leaf area per m^2 ground area) is calculated from carbon allocated to leaves times the specific leaf area (m^2 leaf area per kg leaf carbon). It controls canopy radiation absorption, water interception, photosynthesis, and litter inputs to detrital pools.

Net primary production (NPP) is based on gross primary production (GPP) calculated with the Farquhar photosynthesis routine (FARQUHAR *et al.* 1980) minus the autotrophic respiration. The autotrophic respiration includes the maintenance respiration calculated as a function of tissue nitrogen concentration (RYAN 1991), and growth respiration, which is a function of the amount of carbon allocated to the different plant compartments (leaf, root and stem). NPP is partitioned into the leaves, roots and stems as a function of a dynamic allocation pattern, considering eventual limitations due to the availability of and competition for nitrogen.

The model requires meteorological input data, such as daily minimum and maximum temperature, incident solar radiation, vapor pressure deficit and precipitation. Aspect, elevation, nitrogen deposition and fixation, and physical soil properties are needed to calculate: the daily canopy interception, evaporation and transpiration; soil evaporation, outflow, water potential and water content; LAI; stomatal conductance and assimilation of sunlight and shaded canopy fractions; growth and maintenance respiration; GPP and NPP; allocation; litter-fall and decomposition; mineralization, denitrification, leaching and volatile nitrogen losses. Detailed descriptions of the individual modeled processes can be found elsewhere (e.g. KIMBALL *et al.* 1997; COOPS *et al.* 2001; THORNTON *et al.* 2002 as well as PIETSCH *et al.* in press).

2.3 Simulation

The spinup starts with the assumption of no soil organic matter (SOM), very small initial carbon amounts in the leaves (0.001 kg C/m^2) and 50 % soil-water saturation. During the simulation, organic mass is accumulated. The spinup procedure stops after soil organic matter, the pool that stabilizes very slowly in an ecosystem, reaches a steady state (THORNTON *et al.* 2002). This equilibrium is dynamic with an interannual variability due to varying weather records (LAW *et al.* 2001). In BIOME-BGC, Version 4.1.1, vegetation ecophysiology is determined by a set of 39 parameters. For our simulations we use species-specific parameter sets (see PIETSCH *et al.* in press).

The initial results suggested that a constant mortality rate of 0.5 % of the total biomass, as currently used within the model, does not take into account the different successional stages of our virgin forests. Thus for each plot we used the dynamic mortality sub-model as proposed by MERGANIČOVÁ (2003). This sub-model assumes a varying mortality of the total biomass ranging between 0.3 % to 4.5 % according to the successional stages of the virgin forest.

For simulations of the forest stands in Babia Hora, we used the model parameterization for highland stands of Norway spruce *Picea abies* L. Karst. In Rothwald, a mixed beech-spruce forest, we made two different simulations, (i) one with the model parameterization for common beech *Fagus sylvatica* L. and (ii) one with the parameters suitable for highland forests of Norway spruce (PIETSCH *et al.* in press).

The spinup procedures include the following steps: First, the system was brought to steady state using the pre-industrial carbon dioxide concentration of 280 ppm (IPPC WGI 1996) and a nitrogen deposition level of 0.0001 kg N/m^2/yr (HOLLAND *et al.* 1999). After the equilibrium was reached, another 237 to 624 years were simulated to account for industrial influences starting in 1765 (IPCC WGI 1996). The length of this auxiliary simulation differed from plot to plot and was set to such a value that for the last 40 years of the simulation the climate records were used, e.g. for the simulation of the year 2002 climate data from that year were used. This ensures that the modeled development stage for a given plot is similar to the recorded current virgin forest development stage.

Since 1765 atmospheric carbon dioxide has gradually increased to current values according to the scenario provided by the IPCC (IPCC WGI 1996). In addition, nitrogen deposition has increased from pre-industrial to current deposition rates according to the pattern of CO_2 increase (THORNTON *et al.* 2002).

3 Results

A comparison of the model output with plot measurements revealed unbiased estimates for the stand volume and soil carbon in both virgin forests (Table 2). In Babia Hora, the modelled amount of dead wood did not differ significantly from observations. Litter carbon and nitrogen in both virgin forests were underestimated, while soil nitrogen was overestimated (Table 2).

Since the data collected in the two virgin forests refer to a specific point in time, we evaluated temporal model behavior according to different key ecophysiological parameters. Annual mortality is assumed to be dynamic and ranges from 0.3 to 4.5 % of the total biomass according to the successional stage of the forest (see also MERGANIČOVÁ 2003). Results are presented in Figure 1.

As shown in Figure 1, litter carbon has a developmental pattern similar to dead wood (compare Fig. 1C and 1B), including one significant maximum reached at the same time that the coarse woody debris reaches its first peak. Nitrogen in litter does not have a particular maximum during the development cycle, but it does have a distinct minimum at the same time that litter carbon is at its lowest level (Fig. 1C). Except for the maximum of litter carbon, the patterns of both litter parameters examined follow those of the stem carbon changes.

The levels of carbon and nitrogen in the soil (Fig. 1E and 1F) differ from litter characteristics. They reach their highest values after 200 years when litter variables are at their lowest levels, shortly after the dead wood reaches its maximum, and several years before maximum mortality is evident. After the peak is reached they quickly decline to previous values.

Table 2. Mean and the standard deviation (Stdev.) of the model predictions vs. the observations for each of the two virgin forests Rothwald and Babia Hora. V is the volume per hectare, C_{CWD} the amount of carbon in coarse woody debris, C_{Litter} the carbon and N_{Litter} the nitrogen contents in the litter; C_{Soil} the carbon and N_{Soil} the nitrogen contents in the soil. Δ is the difference between predicted and observed values. Note that a paired t-test was applied.
* significant at • = 0.05

Variable	Rothwald					Babia Hora				
		Predicted	Observed	Δ			Predicted	Observed	Δ	
	N	Mean (Stdev.)	Mean (Stdev.)	Mean (Stev.)	t-test	N	Mean (Stdev.)	Mean (Stdev.)	Mean (Stdev.)	t-test
V (m^3/ha)	18	633.3 (301.6)	559.2 (280.0)	74.1 (167.7)	1.87	57	294.3 (142.0)	313.2 (230.0)	–18.93 (156.98)	0.91
C_{CWD} (tC/ha)	18	26.50 (12.90)	86.14 (19.83)	–59.64 (19.14)	13.2*	57	19.53 (10.21)	20.31 (22.57)	–0.77 (16.86)	0.35
C_{Litter} (kg/C/m^2)	18	0.697 (0.540)	0.952 (0.445)	–0.253 (0.732)	1.47	19	0.344 (0.185)	5.139 (1.927)	–6.54 (1.47)	19.4*
N_{Litter} (kgN/m^2)	18	0.0038 (0.0006)	0.0319 (0.0142)	–0.0281 (0.0143)	8.32*	19	0.0023 (0.0004)	0.228 (0.074)	–0.292 (0.054)	23.7*
C_{Soil} (kgC/m^2)	18	8.609 (1.048)	8.263 (3.090)	0.346 (2.812)	0.52	19	6.918 (1.244)	6.840 (3.253)	–1.255 (2.116)	2.59*
N_{Soil} (kgN/m^2)	18	0.859 (0.105)	0.484 (0.187)	0.375 (0.175)	9.08*	19	0.690 (0.124)	0.373 (0.188)	0.249 (0.158)	6.87*

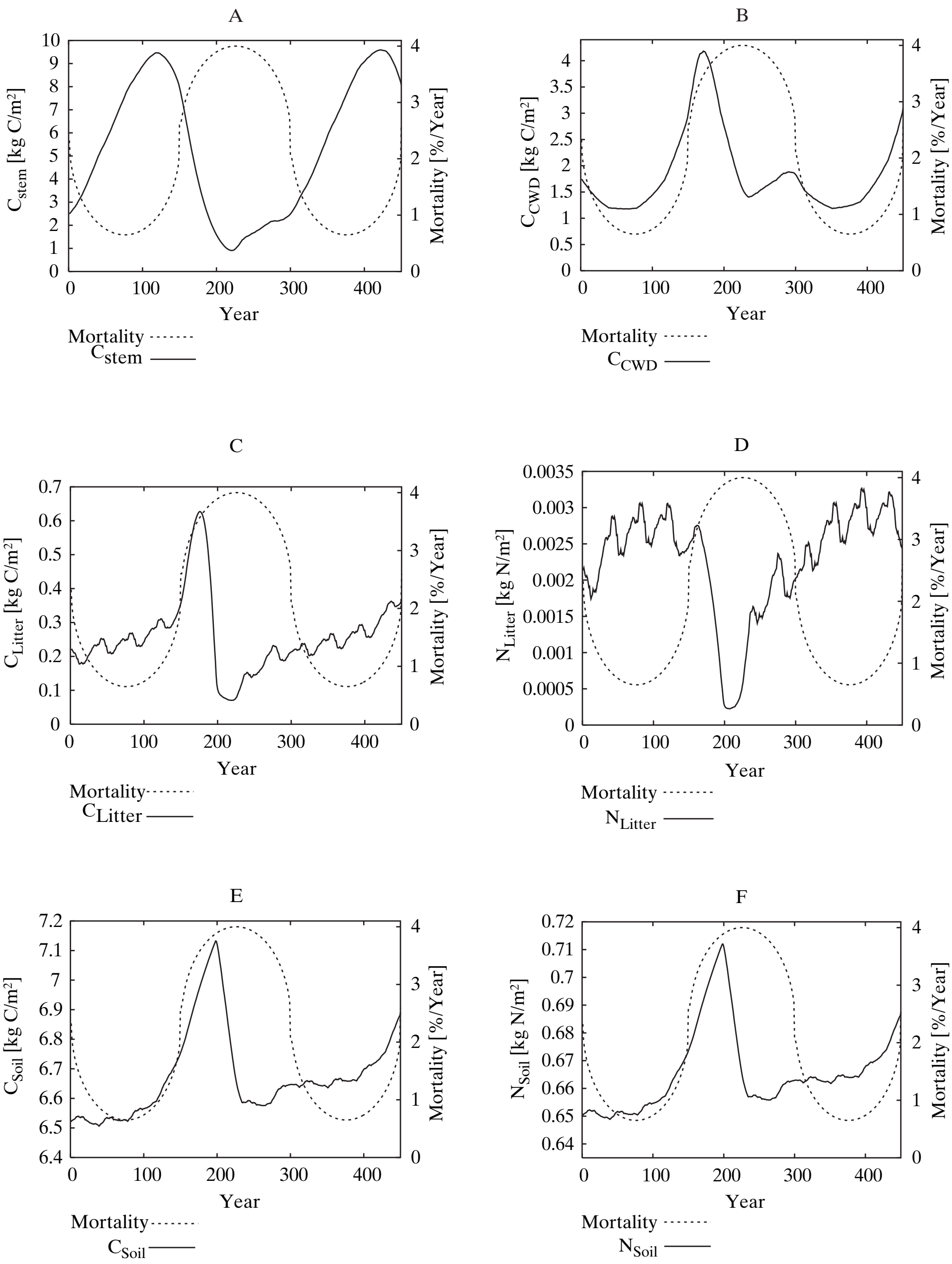

Fig. 1. Temporal development of selected model state variables (solid lines) versus annual mortality rates (dotted lines). C_{Stem} is the modeled amount of carbon in the stem representing the stand volume, C_{CWD} the amount of carbon in the coarse woody debris, C_{Litter} and N_{Litter} the amounts of carbon and nitrogen in the litter, and C_{Soil} and N_{Soil} the amounts of carbon and nitrogen in the soil, respectively. The soil carbon and soil nitrogen development show an almost identical pattern (see E and F) due to their close relationship within the model. Only one respiration function is used, which assumes that carbon will be respired as long as nitrogen is available.

4 Discussion

The ecosystem model BIOME-BGC was able to mimic the ecosystem fluxes of old-growth forests after we had replaced the constant mortality rate of 0.5 % with a dynamic mortality rate ranging between 0.3 to 4.5 % of the biomass, depending on the successional stage of the forest. With these changes we were able to show that the self initialization procedure as used within the ecosystem model produces reliable results.

Consistent estimates were produced between predicted and observed volumes for both virgin forests. Dead wood, or coarse woody debris, are adequately simulated in Babia Hora, while in Rothwald these parameters are underestimated (Table 2). We assume that this difference is mainly due to the fact that there was four times as much dead wood observed in Rothwald as in Babia Hora due to the several wind-throws that occurred in the 2nd half of the last century in 1966, 1976 and 1990 (NEUMANN 1978; SCHREMPF 1985; Splechtna 2003, pers. communication).

The detected underestimation of litter nitrogen is probably caused by an incomplete assessment of the modeled litter pools. In the model litter consists of only dead leaf and fine root biomass plus fragmented dead wood, while in nature litter also includes other kinds of dead organic material, e.g. pieces of bark, buds, etc., which can make up 20 to 40 % of the dry litter mass. In contrast to litter, soil nitrogen was slightly overestimated in both virgin forests.

No repeated measurements were available for our plots. Thus it was not possible to compare the stand dynamics with the model simulations, although we were interested in seeing whether model predictions under the current model logic correctly mimic the observed data. The difficulty is that observations may be strongly affected by random measurement errors or simply by the random behavior of nature. Therefore, we examined the individual parameters by comparing mortality rates with other variables (see Fig. 1). For example, we expected stand volume (stem carbon) development to follow the reverse order of mortality. As shown in Figure 1, maximum stem carbon occurs when mortality rates increase and only a small increment of stem carbon was reached during the following 80 years. This differs from published findings in the stand volume development for Central European virgin forests, e.g. KORPEL (1995). Moreover the dynamics of natural forests are mainly based on existing knowledge and practical experience but not on long-term field experiments. In Central Europe the longest time series from undisturbed forest ecosystems covers only 30 to 50 years (SANIGA 1999; SANIGA and SCHÜTZ 2001a, b), which is too short to evaluate these concepts.

Coarse woody debris exhibited a minimum when the mortality reached its maximum. This is consistent with the development of stem carbon. At this point stem carbon is also very low, which indicates that a high relative mortality rate results in a low input of biomass into the coarse woody debris pool.

We expected that the temporal pattern of litter carbon and nitrogen would be identical, since these variables are closely related. The development of carbon litter (Fig. 1) is similar to that of the coarse woody debris. This is due to the flow of the decomposed dead wood into the litter. Since coarse woody debris is known to have a large C : N ratio, its accumulation has a much lower effect on litter nitrogen than on litter carbon. Therefore, unlike litter carbon or dead wood, litter nitrogen exhibited no distinct maximum. In our simulations the climate recorded for the last 41-year period was repeatedly used. Consequently the similarity in the soil characteristics with the temporal climate variation suggests that litter and soil parameters are strongly related to annual weather patterns.

The important findings of this study are that according to the successional stage, forest ecosystems are dynamic systems. This needs to be taken into account (e.g. by using a dynamic mortality model) within ecosystem modeling to ensure unbiased and consistent simulations of such forests and to ensure reliable self-initialization runs.

Acknowledgements
The field work was funded by a grant from the BOKU University of Natural Resources and Applied Life Sciences Vienna. The model adaptation was supported by the Austrian Ministry of Science and Education, and the Austrian Ministry of Forestry, Agriculture and Environment, as well as by an ÖAD scholarship for Katarina Merganičová. Helpful review comments were provided by Bruce Mitchie and two anonymous referees.

5 References

BRADSTREET, R.B., 1965: The Kjeldahl method for organic nitrogen. New York, Academic Press. 239 pp.

COOPS, N.C.; WARING, R.H.; BROWN, S.R.; RUNNING, S.W., 2001: Comparisons of predictions of net primary production and seasonal patterns in water use derived with two forest growth models in Southwestern Oregon. Ecol. Model. 142: 61–81.

FARQUHAR, G.; VON CAEMMENER S.; BERRY, J., 1980: A Biochemical model of photosynthesis CO_2 fixation in leaves of C_4 species. Planta 149: 78–90.

HAFELLNER, W., 1985: Studie über Entwicklung und Struktur der forstlichen Biomasse in Fichtendickungen nach unterschiedlich starken Stammzahlreduktionen. Diplomarbeit Universität Bodenkultur, Wien. 94 pp.

HASENAUER, H.; MERGANIČOVÁ, K.; PETRITSCH, R.; PIETSCH, S.A.; THORNTON, P.E., 2003: Validating daily climate interpolation over complex terrain in Austria. Agric. For. Meteorol. 119: 87–107.

HOLEKSA, J., 2001: Coarse woody debris in a Carpathian subalpine spruce forest. Forstwiss. Cent.bl. 120: 256–270.

HOLLAND, E.A.; DENTENER, F.J.; BRASWELL, B.H.; SULZMAN J.M., 1999: Contemporary and pre-industrial global nitrogen budgets. Biogeochemistry 46: 7–43.

IPCC WGI 1996: Technical Summary. In: HOUGHTON J.T.; MEIRA FILHO, L.G.; CALLANDER, B.A.; HARRIS, N.; KATTENBERG, A.; MASKELL, K. (eds) Climate change 1995 – the science of climate change: contribution of the working group I to the second assessment report of the intergovernmental panel on climate change. Cambridge, Cambridge University Press. 9–50.

KIMBALL, J.S.; THORNTON, P.E.; WHITE, M.A.; RUNNING, S.W., 1997: Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region. Tree Physiol. 17: 589–599.

KORPEL, Š., 1995: Die Urwälder der Westkarpaten. Stuttgart, Fischer. 310 pp.

LAW, B.E.; THORNTON, P.E.; IRVINE, J.; ANTHONI, P.M.; VAN TUYL, S., 2001: Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Glob. Chang. Biol. 7: 755–777.

MASER, C.; ANDERSON, R.G.; CROMACK, K. JR.; WILLIAMS, J.T.; MARTIN, R., 1979: Dead and down woody material. In: WARD, J. (ed) Wildlife Habitats in managed forests. Washington D.C., U.S. Printing Office. 512 pp.

MERGANIČ, J.; VORČÁK, J.; MERGANIČOVÁ, K.; DURSKÝ, J.; MIKOVÁ, A.; ŠKVARENINA, J.; TUČEK, J.; MIND'ÁŠ, J., 2003: Monitoring of diversity in mountain forests of Eastern Orava. EFRA, Tvrdošín. 200 pp. http://www.efra.sk/projekt.php?w=d&pr=2

MERGANIČOVÁ, K., 2003: Modeling forest dynamics in virgin and managed forest stands. Ph.D. Thesis. Vienna, BOKU University of Natural Resources and Applied Life Sciences. 155 pp.

NEUMANN, M., 1978: Bestandesstruktur und Entwicklungsdynamik im Urwald Rothwald, NÖ und im Urwald Corkova Uvala, Kroatien. Dissertation Universität Bodenkultur Wien. 132 pp.

PIETSCH, S.A.; HASENAUER, H., 2002: Using mechanistic modeling within forest ecosystem restoration. For. Ecol. Manage. 159: 111–131.

PIETSCH, S.A.; HASENAUER, H.; THORNTON, P.E.: BGC-Model parameters for tree species growing in central European forests. For. Ecol. Manage. (in press).

POLLANSCHÜTZ, J., 1974: Formzahlfunktionen der Hauptbaumarten Österreichs. Allg. Forst Z. Waldwirtsch. Umweltvorsorge 85: 191–194.

SCHIELER, K., 1988: Methodische Fragen in Zusammenhang mit der Österreichischen Forstinventur. Diplomarbeit Universität Bodenkultur Wien. 99 pp.

RUNNING, S.W.; NEMANI, R.R.; 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.

RYAN, M.G., 1991: Effects of climate change on plant respiration. Ecol. Appl. 1: 157–167.

SANIGA, M., 1999: Structure, production conditions and regenerative processes in the Badín virgin forest. Journal of Forest Science 45, 3: 121–130.

SANIGA, M.; SCHÜTZ, J.P., 2001a: Dynamik des Totholzes in zwei gemischten Urwäldern der Westkarpaten im pflanzengeographischen Bereich der Tannen-Buchen- und Buchenwälder in verschiedenen Entwicklungsstadien. Schweiz. Z. Forstwes. 152, 10: 407–416.

SANIGA, M.; SCHÜTZ, J.P., 2001b: Dynamic changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle. J. For. Sci. 47, 12: 557–565.

SCHNEIDER, J., 1998: Kartierung der nassen Deposition in Österreich. Wien, Umweltbundesamt. 24 pp.

SCHIELER, K., 1988: Methodische Fragen in Zusammenhang mit der Österreichischen Forstinventur. Diplomarbeit Universität für Bodenkultur Wien. 99 pp.

SCHREMPF, W., 1985: Waldbauliche Untersuchungen im Fichten-Tannen-Buchen-Urwald Rothwald und in Urwald-Folgebeständen. Dissertation, Universität Bodenkultur Wien. 177 pp.

SITCH, S.; SMITH, B.; PRENTICE, I.C.; ARNETH, A.; BONDEAU, A.; CRAMER, W.; KAPLAN, J.O.; LEVIS, S.; LUCHT, W.; SYKES, M.T.; THONICKE, K.; VENEVSKY, S., 2003: Evaluation of ecosystem dynamic, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Glob. Chang. Biol. 9: 161–185.

THORNTON, P.E.; RUNNING, S.W.; WHITE, M.A., 1997: Generating surfaces of daily meteorological variables over large regions of complex terrain. J. Hydrol. 190: 214–251.

THORNTON, P.E.; LAW, B.E.; GHOLZ, H.L.; CLARK, K.L.; FALGE, E.; ELLSWORTH, D.S.; GOLDSTEIN, A.H.; MONSON, R.K.; HOLLINGER, D.; FALK, M.; CHEN J.; SPARKS, J.P., 2002: Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agric. For. Meteorol. 113: 185–222.

VACEK, S., 2003: Minimum area of forests left to spontaneous development in protected area. J. For. Sci. 49, 8: 349–358.

Accepted April 21, 2005