

Combining multiple statistical methods to evaluate the performance of process-based vegetation models across three forest stands

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Abstract

Process-based vegetation models are crucial tools to better understand biosphere-atmosphere exchanges and eco-physiological responses to climate change. In this contribution the performance of two global dynamic vegetation models, i.e. CARAIB and ISBA_{CC}, and one stand-scale forest model, i.e. 4C, was compared to long-term observed net ecosystem carbon exchange (NEE) time series from eddy covariance monitoring stations at three old-grown European beech (*Fagus sylvatica* L.) forest stands. Residual analysis, wavelet analysis and singular spectrum analysis were used beside conventional scalar statistical measures to assess model performance with the aim of defining future targets for model improvement. We found that the most important errors for all three models occurred at the edges of the observed NEE distribution and the model errors were correlated with environmental variables on a daily scale. These observations point to possible projection issues under more extreme future climate conditions. Recurrent patterns in the residuals over the course of the year were linked to the approach to simulate phenology and physiological evolution during leaf development and senescence. Substantial model errors occurred on the multi-annual time scale, possibly caused by the lack of inclusion of management actions and disturbances. Other crucial processes defined were the forest structure and the vertical light partitioning through the canopy. Further, model errors were shown not to be transmitted from one time scale to another. We proved that models should be evaluated across multiple sites, preferably using multiple evaluation methods, to identify processes that request reconsideration.

Key words: singular spectrum analysis; residual analysis; wavelets; *Fagus sylvatica*; net ecosystem carbon exchange

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1. Introduction

Forest net ecosystem exchange (NEE; all abbreviations also in Table A1), the flux of carbon between the forest and the atmosphere, plays a key role in the global carbon balance (Le Quéré et al. 2016). Therefore, understanding NEE responses to environmental change, to ecosystem management and to site characteristics is essential for predicting future biogeochemical cycles (Law et al. 2002; Pan et al. 2014; Li et al. 2016). To this end, process-based vegetation models (PVMs) of varying complexity are being used, operating at varying scales (Keenan et al. 2012; Fischer et al. 2014; Reyer 2015). Dynamic Global Vegetation Models (DGVMs) are designed in order to

depict the water and carbon fluxes on a global scale (Hickler et al. 2012). On the contrary, smaller scale vegetation models commonly depict one ecosystem only, such as one particular forest stand and can be used to test different management alternatives or understand ecosystem processes at stand scale.

Insufficient knowledge about underlying processes as well as uncertainties about the parameters and the initial conditions of PVMs lead to biased and uncertain model results (Walker et al. 2003). Although more detailed processes are often implemented in the stand scale models, thus increasing confidence in the model realism, the complexity of these models may further increase uncer-

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tainty and/or bias in the results (Larocque et al. 2014). Therefore, PVMs need to be thoroughly evaluated to better understand model uncertainties and the implications for model predictions. Prominent evaluation approaches include model validation and model-model comparisons (e.g. Trudinger et al. 2007).

To achieve valuable model evaluations, the availability and the quality of long-term observational data are crucial (Hollinger & Richardson 2005) as multi-annual responses are less well captured by models than daily and seasonal changes (e.g. Braswell et al. 2005; Stoy et al. 2005; Siqueira et al. 2006). In recent years eddy covariance (EC) measurements and remote sensing data covering long periods have become increasingly available. During the last two decades, NEE has been intensively monitored by use of EC techniques across multiple ecosystems in Europe (Aubinet et al. 2000). Nonetheless, measurement errors in EC data still confine the applicability of model validation with EC data (Aubinet et al. 2012), even though measurement techniques and data processing tools are improving and increasingly standardized.

A range of statistical evaluation methods (SEM) have been used to validate and to compare the performance of process-based models. Scalar statistical measures (SSMs) of error and fit provide an indication of the overall match of model output and data, but they offer only limited insight into the potential of the model to capture the variability in the data and they neglect the temporal dimension. As residual analysis (RA) examines model errors as a function of simulated or observed data and of environmental drivers, it may reveal potential model shortcomings (Medlyn et al. 2005). More complex time series analysis techniques including wavelet analysis (WA; Stoy et al. 2005; Dietze et al. 2011) and singular spectrum analysis (SSA; Mahecha et al. 2007; Mahecha et al. 2010; Wang et al. 2012) effectively provide insight into the model fit at different time scales.

In this contribution, we used two DGVMs and one forest stand-scale model, to simulate NEE. We evaluated model results by comparing model NEE outputs with observed NEE data over a period of at least 16 years for three beech forest sites in Soroe (Denmark), Vielsalm (Belgium) and Collelongo (Italy). The SEMs currently in use, i.e. SSMs, RA, WA and SSA, were combined across multiple sites. The objectives of the study were to define environmental conditions under which the models perform poorly and to identify the related model processes that should be revised for the adequate reproduction of NEE dynamics of forest sites. Further, we aim to highlight the importance of applying multiple SEMs for multiple sites in order to perform a useful evaluation of the performance of PVMs. We focused on the consequences of the model structure on NEE simulations and did not intend a full evaluation of all possible model outputs.

2. Materials and methods

2.1. Model selection, set-up and simulation protocol

We selected three PVMs to simulate NEE for the three forest sites. The first model, CARAIB (CARbon Assimilation In the Biosphere) is a physically based DGVM developed to study the role of the vegetation in the global carbon cycle (Warnant et al. 1994; Gérard et al. 1999) and to study the vegetation distributions in the past (François et al. 1998, 2011; Henrot et al. 2016), in the present and in the future (Laurent et al. 2008; Dury et al. 2011). The second model, ISBA_{cc} (Interaction Soil–Biosphere–Atmosphere – Carbon Cycle) simulates the exchange of water, energy and carbon between the land surface and the atmosphere (Noilhan & Mahfouf 1996; Gibelin et al. 2008; Masson et al. 2013). The third model, 4C (FORESEE – FORESt Ecosystems in a changing Environment) is a stand-scale, process-based model developed to study the effects of environmental change on forest ecosystems (Bugmann et al. 1997; Suckow et al. 2001; Lasch et al. 2005). For the evaluation period, the three models, selected to represent different types of process-based models used for the simulation of the carbon balance of forests, were forced by the meteorological data measured at the sites. At the point of initialisation, models were fed with the site specific soil properties that remained constant over the simulations. For CARAIB and 4C, EC and meteorological data were obtained from the daily aggregated FLUXNET2015 data (FULLSET, <http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/fullset-data-product/>). For ISBA_{cc}, the hourly FLUXNET2015 data were used for meteorological forcing. In order to set the model's carbon pools to steady state and to obtain a mature forest at the beginning of the evaluation period, model spin-ups were run for both DGVMs, CARAIB (using ERA-Interim reanalysis; Uppala et al. 2005) and ISBA_{cc} (by cycling through the available meteorological data). The variables NEE, GPP and R_{eco} were extracted from model outputs and aggregated to daily values if the time steps were smaller, i.e. for CARAIB and ISBA_{cc}. The model parameters were not calibrated for the specific sites, since that could have concealed the actual problems in the model structure. The main features of the models can be found in Table 1 and a more extensive overview of the model processes, model input variables and model specifications for the set-up in Tables A2 (CARAIB), A3 (ISBA_{cc}) and A4 (4C).

2.2. Flux data

2.2.1 Site selection

We used data from three FLUXNET sites: Soroe (Denmark), Vielsalm (Belgium) and Collelongo (Italy). At all sites the dominating vegetation type consisted of mature beech (*Fagus sylvatica* L.) forest (from 76 years to 106

Table 1. Short description of the main features of the models used in this study three.

Model characteristics	CARAIB	ISBAcc	4C
Spatial scale	grid or point scale	grid or point scale	stand-scale
Smallest temporal scale	2-hourly	hourly	daily
Spin up	yes	yes	no
Plant functional type options	multiple	multiple	only tree species
Number of PFT dependent parameters	55	40	99
Number of calibrated tree (PFT) species	15 (26)	8	14
Forest structure	one layer of trees and one layer containing herbs and shrubs	one layer of trees	cohorts with different tree characteristics
Driving variables	CO ₂ , air temperature, amplitude of air temperature (T _{day_{max}} – T _{day_{min}}), precipitation, air relative humidity, short-wave incoming radiation, wind velocity	CO ₂ , air temperature, precipitation, air relative humidity, short-wave incoming radiation, long-wave incoming radiation, wind velocity	CO ₂ , air temperature, precipitation, air relative humidity, net radiation, wind velocity
Developed in	University of Liège, Belgium	Météo France/CNRS, Toulouse, France	Potsdam Institute for Climate Impact Research, Germany

years old), with different soil and environmental characteristics. EC data were available for a 16-year period (1997–2012) for Soroe and for an 18-year period (1997–2014) for Vielsalm and Collelongo. A detailed description of the sites including stand and soil characteristics is provided in Table 2.

2.2.2 Eddy covariance measurements

The NEE measurements, i.e. the time series of the carbon exchange between ecosystems and the atmosphere, were monitored at a 10 Hz sampling frequency and aggregated to 30-min averages. NEE measurements were processed using a constant friction velocity threshold across years with the reference selected based on model efficiency. Time series of GPP and R_{eco} were calculated by the partitioning of NEE based on nighttime NEE values (Reichstein et al. 2005). Based on the dataset of observations the random uncertainty and the joint uncertainty in NEE were calculated according to the FLUXNET2015 pro-

ocols (<http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/data-processing/>). An extensive description of the partitioning of the NEE flux and measurement errors, as well as of the EC flux calculation and processing protocols has been previously published (Aubinet et al. 2012)

2.3. Model evaluation methods

The performance of the three models was evaluated by four SEMs, i.e. SSM, RA, WA and SSA.

2.3.1 Scalar statistical measures

Three fit statistics were used. Firstly, the coefficient of determination (R^2), secondly, R^2 multiplied by the slope of the regression line between simulations and observations (bR^2), allowing to account for the systematic discrepancy in the magnitude of two signals as well as for the proportion of variance in the observations pre-

Table 2. Descriptions of the three beech-dominated sites investigated in the current study.

	Soroe	Vielsalm	Collelongo
Location			
Country (region)	Denmark	Belgium (Ardennes)	Italy (Abruzzo)
Lat [deg N]	55.5	50.2	41.9
Long [deg E]	11.7	6	13.6
Elevation [m]	40	450	1550
Climate			
Average daily temperature [°C]	8.4	8.3	7.43
Average yearly sum precipitation [mm]	872	964	1159
Average daily relative humidity [%]	82.6	80.6	72.6
Average daily irradiation [J cm ⁻²]	988	991	1489
Soil			
Soil type	Alfisol or mollisol	Dystric cambisol	Humic alisol -calcarous
Clay in top soil [%]	14.2	15.7	14.2
Sand in top soil [%]	59.2	25	55.3
Average C content of root zone [g m ⁻²]	1963	2457	2605
Average N content of root zone [g m ⁻²]	125.2	113	213.1
Average field capacity [vol%]	19.2	30.8	50.1
Average wilting point [vol%]	9.2	12	26.9
Soil density mineral [g cm ⁻²]	1.6	2.65	0.8
Rooting depth [cm]	75	60	86.5
Stand characteristics			
Year of plantation	1921	1908	1891
Age at the beginning of the study period [yrs]	76	88	106
Age at the end of the study period [yrs]	89	103	122
Initial forest density [trees ha ⁻¹]	354	243	900
Initial average diameter at breast height [cm]	38	31.79	20.2
Initial average height [m]	25	26.79	17.3
Initial average basal area [cm ²]	48.77	19.76	28.86

dicted by the simulation results (Krause et al. 2005), and thirdly, the Nash-Sutcliffe efficiency (NSE), providing the relative magnitude of the residual variance compared to the measured data variance (Nash & Sutcliffe 1970). Two scalar error estimates were calculated, the normalized root mean squared error (RMSE) and the more robust normalized euclidean error (NMEE; Li & Zhao 2006; Mahecha et al. 2010).

2.3.2 Residual analysis

The residuals were calculated as the daily simulated values minus the observed values. The following moments of their distribution were calculated: the mean, here called the mean error (ME), the standard deviation (sdR), expressing the variability in the model errors, the skewness (skR; when skR is between -0.5 and 0.5 the distribution is approximately symmetric) and the excess kurtosis (kurR; positive kurR means fat-tailed and negative kurR means thin-tailed distribution). We analyzed the time course of the residuals and their relation with respect to the observed values. The correlation coefficients between the residuals and the observed values (CorrO) as well as between the residuals of the different models (CorrE) were also calculated.

The relation between the residuals and a number of meteorological variables, i.e. air temperature (T), incoming solar radiation (RAD), vapour pressure deficit (VPD) and the modelled drought index (DRI) were studied. A third order polynomial function was fitted through the daily residuals as a function of each of the meteorological variables to analyze the model performance over the range of those variables. DRI was not an observed variable, but calculated by 4C as the daily ratio of water uptake and demand as follows. The potential canopy transpiration demand (D_{tr}) is calculated from the potential evapotranspiration reduced by the interception evaporation (E_{int}), the unstressed stomatal conductance (g_{tot}) and the maximum stomatal conductance (g_{max}) of the forest canopy [Eq. 1]. The transpiration demand of each cohort is derived by considering its relative conductance. The water uptake per cohort is calculated from the soil water availability, itself depending of the daily precipitation and the relative share of fine roots, and is limited by the transpiration demand of the cohort (D_{tr}^c). The DRI of a cohort is defined as the average of the ratios of uptake and demand over the time period of interest (number of days).

$$D_{tr} = E_{int} * \alpha_m * \left(1 - e^{-\left(\frac{g_{tot}}{g_{max}}\right)} \right) \quad [1]$$

In addition, the residuals of the centered and normalized observed and simulated time series (Res_{cn}) were calculated. The centering and the normalization eliminated the effect of consistent model biases and differences

in variance amplitude, respectively (Dietze et al. 2011). The day of the year (DOY) averages of Res_{cn} over the whole study period were calculated to check for systematic asynchronies between simulations and observations, and were compared with the intra-annual NEE evolution represented in the same way.

2.3.3 Wavelet analysis

A discrete as well as a continuous wavelet transformation (based on the non-orthogonal Morlet mother wavelet function), were performed on the observed meteorological data (T, RAD, wind velocity (u), VPD, DRI) and on the observed and simulated time series of the ecosystem fluxes (package WaveletComp in R version 3.1.2). With this analyses the model's performance to reproduce the spectral properties of the observed fluxes was quantified. The minimum period in the analysis was two days and the maximum was 6475 days (5844 for Soroe). In order to check the significance of the average power on each frequency of the series, a low resolution (1/20) was used. In addition, a WA was performed on Res_{cn} . More details about the wavelet method can be found in Lau & Wang (1995) and Torrence & Compo (1997). The scaling exponent, which is the slope of the regression of the log-log relation between the time period and the wavelet power calculated for the normalized residuals ((simulated-observed)/observed) was calculated to check if errors at one scale were correlated with errors at larger scales (cfr. Richardson et al. 2008).

2.3.4 Singular spectral analysis

We conducted an SSA that quantified the relative amount of variance in the time series explained by specifically defined frequency bins (package Rssa in R version 3.1.2). The following frequency (period) bins were defined: 0 – 0.002 (infinity-500 days, multi-annual trend, bin 1), 0.002 – 0.004 (500 – 250 days, yearly variability, bin 2), 0.004 – 0.006 (250 – 166 days, half-yearly variability, bin 3), 0.006 – 0.009 (166 – 111 days, seasonal variability, bin 4) and 0.009 – 0.015 (111 – 66 days, inter-weekly variability, bin 5) and 0.015 – 0.05 (66 to two days, day to day variability, bin 6). Some of these bins were linked to the evolution of meteorological variables and consequently to physiological processes; others appeared as powerful spectrum peaks for one or more of the environmental variables during the wavelet analysis. A full description with implementation guidance of the SSA method is available (Golyandina & Zhigljavsky 2013). The NMEE quantified the goodness of fit between observed and simulated time series for each of the bins (cfr. Mahecha et al. 2010). To include the uncertainty on the EC data, the SSA was also performed for the observed value plus and minus its joint uncertainty. Additionally, the significance of the extracted subsignals (bins) was tested by a red noise test

(package *dpIR* in R version 3.1.2). Based on the Lomb-Scargle Fourier Transform 1000 surrogate time series were generated within the borders of a first order autoregressive (AR(1)) spectrum. Assuming that the background noise could be approximated by an AR(1) model, the hypothesis of a spectrum being purely appointed to noise could be rejected at the chosen confidence levels (95% and 99%). For a detailed description of the method see Schultz & Mudelsee (2002).

3. Results

3.1. Observed NEE values and scalar statistical measures

NEE values diverged largely between the three FLUXNET sites. In Soroe, the annual averages were close to zero, and even positive in the first three years of the study, with an average net carbon storage rate of $-0.42 \mu\text{mol m}^{-2} \text{s}^{-1}$. The other forests were more productive with an average storage rate of $1.26 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Vielsalm and of $1.97 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Collelongo (see Table 3). The evolution of NEE over the year clearly differed between sites, with less extreme values in summer and a longer growing season in Vielsalm compared to the other two sites. In Collelongo and Soroe, the maximum carbon

uptake rate occurred at the same time of the year (absolute maximum on DOY 165 in Soroe and on DOY 173 in Collelongo), but overall, Collelongo was a more active carbon sink than Soroe with a higher maximum and a less rapid activity decline. Although GPP was highest in Soroe (avg. of $234.8 \text{ gC m}^{-2} \text{y}^{-1}$), the extremely high $R_{\text{eco}}/\text{GPP}$ ratio (0.92 for the mean yearly values) undermined the net storage of carbon. For Vielsalm this $R_{\text{eco}}/\text{GPP}$ ratio was 0.74 and for Collelongo 0.48. Under similar meteorological conditions (Table 3) GPP at Vielsalm was approximately 10% lower and R_{eco} 30% lower as compared to Soroe, resulting in a higher carbon storage rate in Vielsalm. The three models underestimated yearly averages of R_{eco} for Soroe consistently over the whole study period. For Collelongo (a forest at high altitude with a high tree density) CARAIB and 4C constantly overestimated R_{eco} . For Vielsalm, 4C and ISBA_{CC} strongly and systematically underestimated R_{eco} , while CARAIB overestimated it for the first 11 years, and turned it into an underestimation later on when the observed R_{eco} values strongly increased (yearly values not shown).

The model-site dependent errors in the simulations for either GPP or R_{eco} or both, resulted in diverged biases and random errors in the NEE simulations (Fig. 1). Overall, ISBA_{CC} and CARAIB underestimated the net storage of carbon for Vielsalm and Collelongo (positive

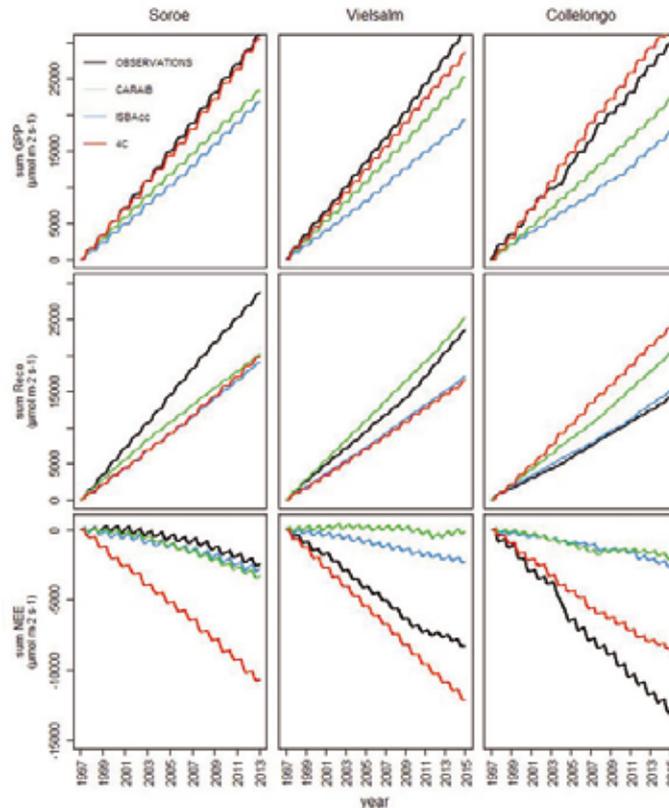


Fig. 1. Cumulative plots of the daily observed and simulated gross primary production (GPP; top), ecosystem respiration (R_{eco} ; middle) and net ecosystem exchange (NEE; bottom) for the study sites Soroe (1997–2012), Vielsalm and Collelongo (both 1997–2014).

ME and skR, Table A5), but not for Soroe. Even though the DGVMs exhibited higher R^2 values for those two sites as compared to 4C, larger biases were observed (lower bR^2 and higher ME). For Soroe all models overestimated the carbon storage over time leading to large values for ME, NRMSE and NMEE and low NSE for the NEE simulations of 4C. For the two other models, however, the combined effect of underestimating both R_{eco} and GPP resulted in an apparently adequate fit with NEE. Although the NEE simulations by ISBA_{cc} and CARAIB were similar, the simulations of its underlying components (GPP and R_{eco}) diverged.

this sink performance of the forests, while, in contrast, at low or negative carbon storage capacity, the models tend to overestimate the carbon uptake. The observed NEE value for which NEE was correctly simulated differed between models. Minimum yearly average residuals were observed for mean yearly NEE values around $-1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 4C and around $-0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for ISBA_{cc} and CARAIB. This similar model behaviour indicated some degree of equifinality in the model results on a yearly time scale. Remarkably, for all models, at the onset of the growing season, Res_{cn} started to increase and reached a maximum when NEE values were at half their minimum yearly value, to be low during the small period of minimum NEE (highest carbon uptake). In full sum-

Table 3. Observed and simulated average values of daily net ecosystem exchange (NEE), gross primary production (GPP) and ecosystem respiration (R_{eco}) with their range (of averages over different years; within brackets). The simulations were made with three different models, i.e. 4C, CARAIB and ISBA_{cc} for the three forest sites. All values are in $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. The dimensionless ratio of R_{eco}/GPP is also indicated.

		NEE		GPP		Reco		R_{eco}/GPP
Soroe	Observations	-0.42	[-0.88, 0.24]	5.32	[4.29, 6.75]	4.9	[4.31, 5.59]	0.92
	4C	-1.84	[-2.43, -1.41]	5.23	[4.08, 6.75]	3.39	[2.65, 4.32]	0.65
	CARAIB	-0.56	[-0.97, -0.13]	4	[3.79, 4.28]	3.43	[4.01, 3.43]	0.86
	ISBA _{cc}	-0.47	[-0.84, -0.13]	3.73	[2.97, 4.49]	3.26	[2.77, 3.75]	0.87
Vielsalm	Observations	-1.26	[-1.89, -0.48]	4.82	[4.18, 5.44]	3.57	[2.81, 4.65]	0.74
	4C	-1.85	[-2.09, -1.49]	4.35	[3.78, 4.93]	3.57	[2.81, 4.65]	0.57
	CARAIB	-0.01	[-0.67, 0.43]	3.84	[3.25, 44.26]	2.5	[2.10, 2.85]	1
	ISBA _{cc}	-0.34	[-0.61, -0.01]	2.94	[2.42, 3.37]	3.83	[3.56, 4.58]	0.89
Collelongo	Observations	-1.97	[-3.69, -0.94]	4.55	[1.44, 7.71]	2.6	[2.33, 2.95]	0.48
	4C	-1.3	[-2.06, -0.66]	4.94	[3.76, 6.62]	2.16	[1.72, 2.67]	0.74
	CARAIB	-0.3	[-0.73, 0.31]	3.39	[2.75, 4.01]	3.09	[2.68, 3.54]	0.91
	ISBA _{cc}	-0.4	[-1.00, 0.07]	2.69	[1.90, 4.00]	2.3	[1.89, 3.00]	0.85

3.2. Residual analysis

For none of the models the daily residuals were normally distributed, with skR and sdR depending on the site. The density distribution of the daily residuals showed high kurR, indicating that a large part of the variance was explained by more extreme values. Overall, the sdR values were highest for Soroe, while skR and kurR were maximum for Collelongo for the three models. 4C differed from the other models in Soroe by producing very high kurR and skR values here, too (Table A5; Fig. 2, top row). The correlations between the daily NEE residuals of the different models were high for some model-site combinations, but not very consistent over sites and models within each site (CorrE in Table A5).

The average yearly residuals changed with time and had a large range including both negative and positive biases (Fig. 2, middle row). The mean yearly bias differed between the models, but the relative size of the residuals fluctuated in parallel. In other words, the models reacted with a comparable magnitude and in the same direction to inter-annual environmental changes. Overall, the average yearly residuals of all models were negatively correlated with the average yearly observed NEE (Table A5; Fig. 3, bottom row). When high yearly carbon storages were observed, the models consistently underestimated

mer (July–September), the carbon storage rate slowed down and Res_{cn} decreased sharply (Fig. 3). However, neither average yearly simulated NEE values nor average yearly NEE residuals were directly correlated with the average yearly or seasonal T, RAD, VPD and DRI (correlations not shown).

On a daily time scale the univariate relation between the NEE residuals and the observed climate variables, i.e. T, RAD, VPD and DRI could not be unambiguously interpreted. These relations were neither consistent between models, nor for each model between sites (Fig. 4). The effect of T on the residuals was low up to temperatures of 10 °C. For higher T, site and model dependent changes in residuals were observed. For Collelongo all models strongly overestimated NEE for high temperatures. The relation between residuals and RAD was less site dependent, although in Collelongo the summer days with high RAD values led again to underestimations of net carbon storage (Fig. 4). Site-to-site inconsistency was also observed for the dependence of the model residuals on VPD observations. However, for each site individually, the models largely reacted in the same way. ISBA_{cc} and CARAIB performed independently of DRI, while 4C residuals varied as a function of DRI.

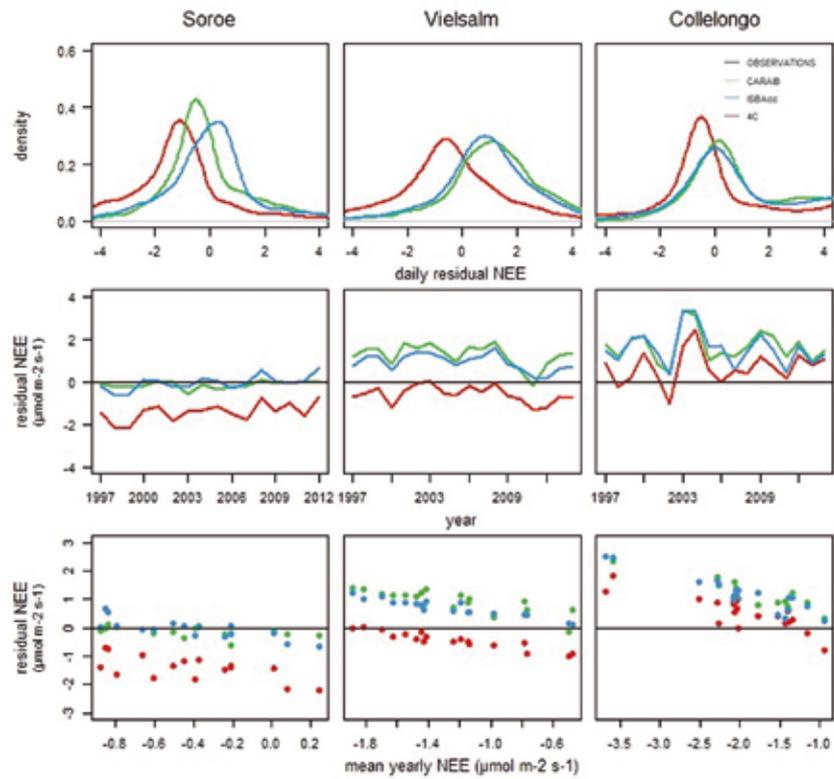


Fig. 2. For the three study sites: (i) the distribution density of the daily net ecosystem exchange (NEE) residuals (top row), (ii) the yearly averaged residuals over the whole study period (middle row), and (iii) yearly average residuals versus average yearly observed values (bottom row).

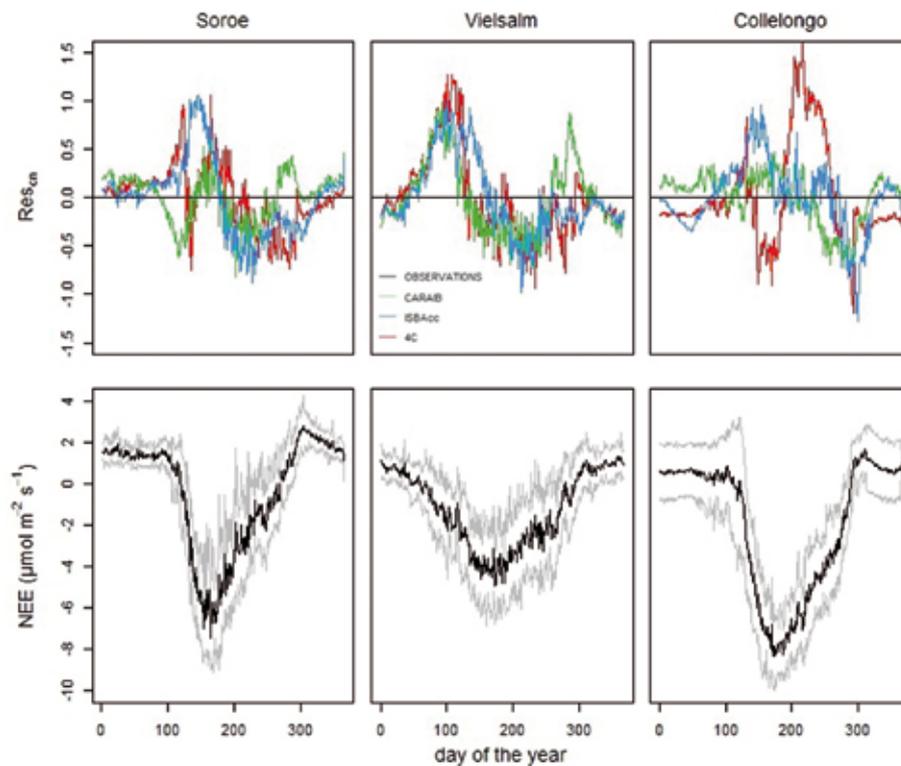


Fig. 3. Day of the year averages of the residuals of the centered and normalized simulations and observations (1997–2012 for Soroe; 1997–2014 for Vielsalm and Collelongo) for the three study sites and for each of the models (top row) and the day of the year averages of the NEE observations (black line) with their standard deviations (grey lines). NEE: net ecosystem exchange.

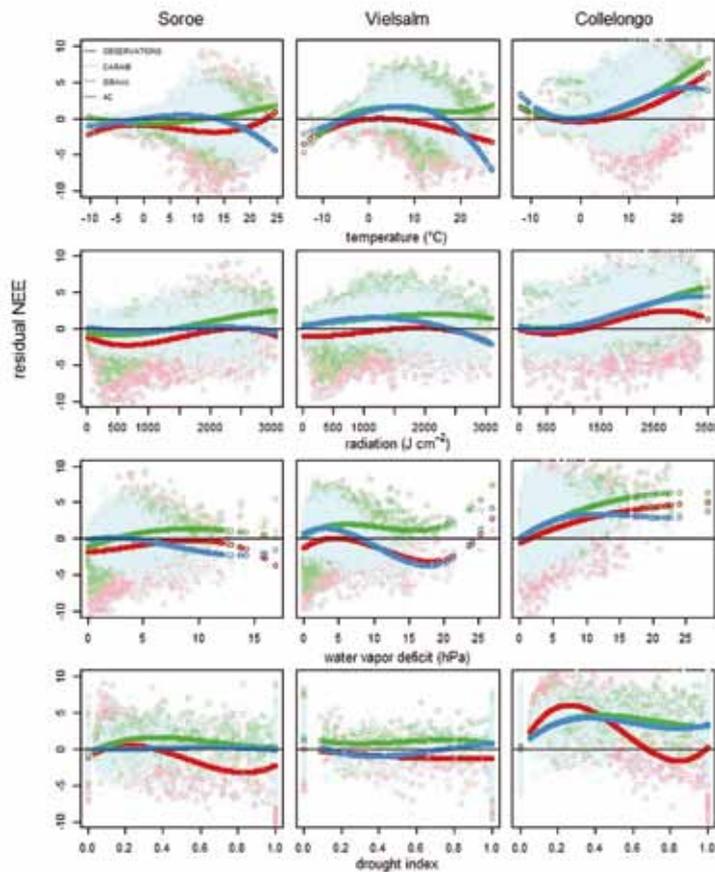


Fig. 4. Daily residuals (light colored circles) of net ecosystem exchange (NEE) as a third order polynomial function (the dots represent the individual daily values) of daily observations of air temperature (top row), incoming radiation (second row from top), vapor pressure deficit (third row from top) and drought index (bottom row) for the three models at the three study sites.

3.3. Wavelet analysis

The meteorological variables T, RAD, u, VPD as well as the DRI all gave, as expected, a significant yearly signal, being least pronounced for u and VPD. For u there was a significant recurrent pattern for higher frequencies (between a few days and two weeks), reflecting the well-known 4-day peak of meteorological processes (Vinichenko 1970). The DRI showed a significant signal around 128 days meaning that there was a pattern in drought peaks approximately three times a year. In Collelongo, a significant half-yearly VPD signal was present (Fig. 5, top row).

The strong power of the yearly signal in NEE observations was depicted by all models (Fig 5, middle row). 4C and ISBA_{cc} underestimated the strength of this yearly signal for Collelongo; CARAIB slightly overestimated its strength at all sites as did 4C for Vielsalm. The strength of the signal simulated by ISBA_{cc} seemed exactly right in Soroe and Vielsalm. A recurrent half-yearly pattern in NEE was furthermore simulated for all sites and was observed in Soroe and Collelongo (Fig. 5, middle row). The inter-site differences in intra-annual observed NEE variability were obvious from the power spectra plotted

in the time-frequency domain (Fig. 6). In Vielsalm there was a higher power at the half-yearly time scale in some of the years, while for the other two sites it was present every year. For Collelongo, the strength of the half-yearly signal simulated by ISBA_{cc} and 4C seemed to be close to the observed one, while CARAIB underestimated this temporal variability (Fig. 5, middle row). For Soroe, 4C underestimated the half-yearly signal and in Vielsalm all models overestimated the intra-annual variability leading to a false half-yearly signal in the simulations. 4C overestimated the strength of the spectral power in the NEE time series at higher frequency (inter-monthly to inter-weekly) at all sites, but especially for Collelongo. There was also a significant NEE signal for Soroe and for Collelongo at four months (period approximately 128 days). For periods below one month there were no significant signals for any of the sites.

The results of the WA for the observed and simulated values showed that the yearly peak, driven by the annual solar cycle, was properly modeled, but the same analysis on the Res_{cn} showed a dominating asynchrony between simulations and observations on this time scale (Fig. 6, bottom row). The annual signal as well as the half-yearly and the quarterly signal observed for NEE and

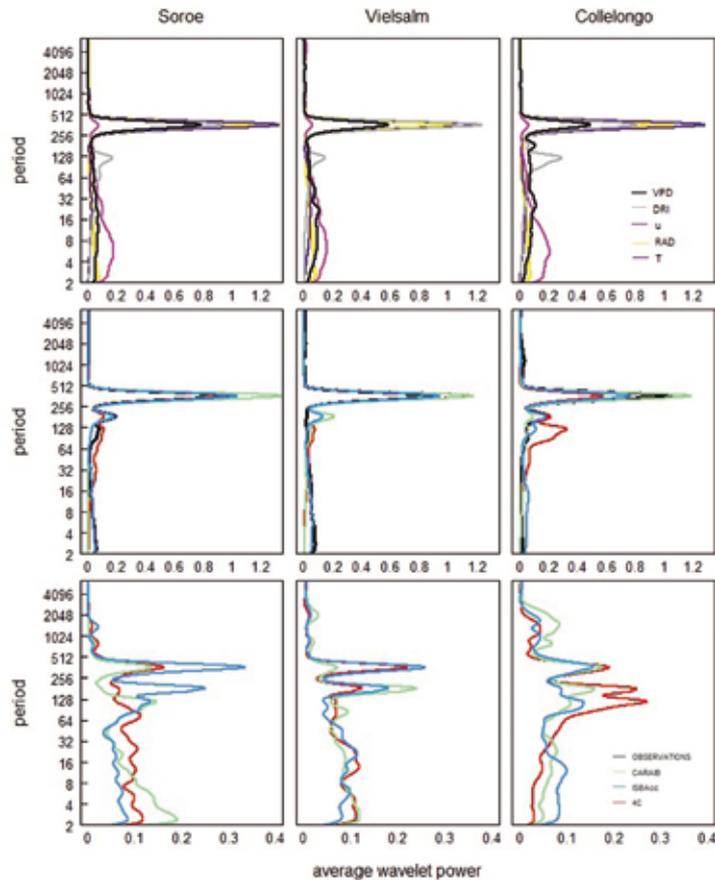


Fig. 5. Average power of the wavelet transform for the three study sites. Top row: as a function of the period for the observed meteorological variables, i.e. temperature (T), incoming radiation (RAD), wind speed (u), vapor pressure deficit (VPD) and drought index (DRI). Middle row: for net ecosystem exchange (NEE) simulated by the three models and from observations. Bottom row: power spectra of the wavelet analysis of the residuals of the centered and normalized simulated and observed values of NEE for the three models.

the meteorological variables were clearly visible in the power spectra of Res_{cn} . The spectral power of the half-yearly asynchronies between simulations and observations were almost as important as that on the yearly time scale. This could not directly be linked to the seasonal pattern of drought neither to the power spectrum of any other environmental variable studied here. Also on higher frequencies (inter-monthly and inter-weekly), where more precipitation related processes and time lagged responses occurred, the model results all significantly deviated from the observed power spectrum. At a frequency of approximately 128 days, where a drought peak was present on all sites, significant shortcomings in model performance were found at two of the three sites, but not in Vielsalm. Since the Res_{cn} for evapotranspiration (data not shown) did not show this 128-days signal but NEE did, the model shortcoming might be linked to an incorrect incorporation of the effects of drought on NEE. For periods between 16 and 64 days, where T, RAD as well as the observed NEE values lacked significant power, unexplained significant periodicity in Res_{cn} still remained. For time periods shorter than 16 days the

power spectra were no longer significant. The calculated scaling exponents were between -1 and -1.16 meaning that there was no memory of errors over time scales, i.e. errors were independent on different time-scales.

3.4. Singular spectrum analysis

The red noise test showed that there was no significant recurrent pattern on the multi-annual NEE time series, but the SSA allocated high variabilities to bin 1. The variability on this time scale was poorly assessed by the models: the variance that was attributed to this bin was incorrect (Fig. 7) and the NMEE values between the bin specific simulations and the observations were large (Table 4). For Soroe less variance was explained by the multi-annual variability than for the other sites. For this site, the variance explained by the multi-annual signal was overestimated by 4C, leading to high NMEE values (Table 4). For Vielsalm and Collelongo, the variance attributed to long-term changes in NEE was generally underestimated, but less by 4C than by the

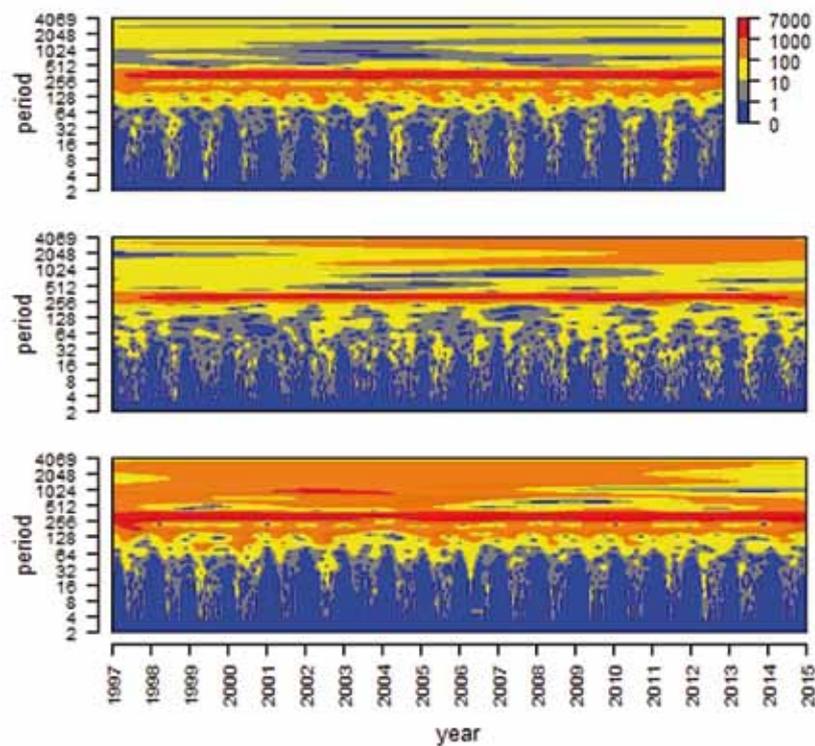


Fig. 6. Plots of the spectral power (colors) as a function of time and period for the three models for the observed net ecosystem exchange at the three study sites i.e. Soroe (top), Vielsalm (middle) and Collelongo (bottom).

DGVMs. For each site, 4C attributed more variance to this bin 1 than the other models. For other frequency bins the NMEE values were site and model dependent without clear patterns. Approximately half of the total variance of the observed NEE time series could be attributed to the annual variability at all sites (bin 2; Fig. 7). CARAIB always overestimated the contribution of the annual variability. However, this did not lead to very high NMEE values (Table 4). ISBA_{cc} overestimated the percentage explained by the yearly signal for Soroe and Vielsalm, while 4C underestimated it for Soroe and Collelongo. Bin 3 (the half-yearly signal) was significant for the observations in Soroe (10.12%) and Collelongo (7.80%). In Vielsalm this bin only explained 0.45% of the observed variance in the NEE time series. Nevertheless, the models did simulate a significant half-yearly signal for Vielsalm. While in the WA the half-yearly signal seemed to be better simulated by ISBA_{cc} and 4C, the variance they attributed to bin 3 was not closer to the observed variance than the variance of that bin estimated by CARAIB. In Soroe bin 4 (inter-monthly or seasonal variability) was significant, even if it explained only 3.90% of the total variance. Higher frequency bins explained small parts of the variance and were not significant for the observations at any of the sites. 4C, giving significant signals for bin 4 and 5 systematically overestimated the variance explained by high frequency bins. CARAIB and ISBA_{cc} had no significant signal in bins 4, 5 and 6.

4. Discussion

4.1. NEE values and scalar statistical measures

This study focused on NEE. This variable is directly measured by EC techniques but the models computed NEE as the net result of R_{eco} and GPP. The NEE values were not always correctly simulated by the models, but the observed model errors for NEE could be caused by either wrongly simulated GPP or R_{eco} values or both. Sometimes NEE values seemed to be adequately simulated, while it was actually the net result of simulated GPP and R_{eco} values, both not completely correctly simulated.

A combination of SSMs showed that the model's predictive ability and their relative error compared to the other models were dependent on the site. None of the models had the best or the worst fit for all three sites. This could partly be due to auto- and heterotrophic respiration processes incorporated in the models. The former is modelled by 4C using the fixed fraction calculation method (Landsberg & Waring 1997), that yields important differences in model results as compared to models (e.g. ISBA_{cc} and CARAIB) incorporating maintenance respiration separate from photosynthesis (Hickler et al. 2015). Generally, there is a lack in our understanding of the soil C–climate interactions, especially over the longer term (Crowther et al. 2016). The models evaluated in this contribution simulated

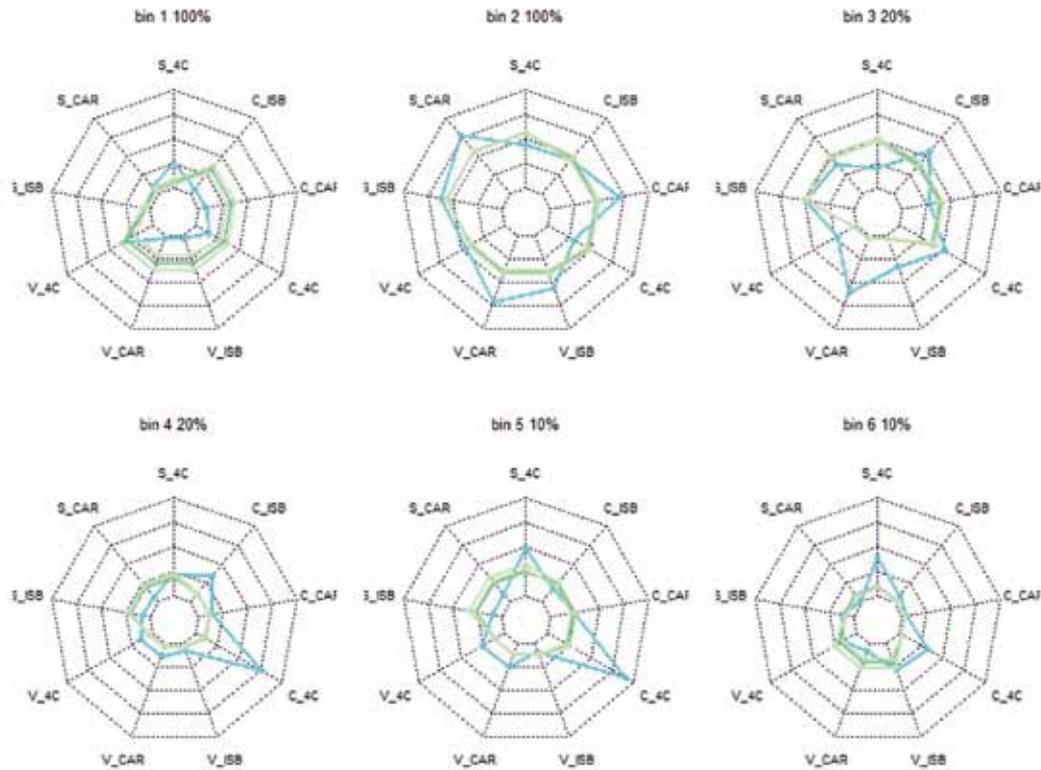


Fig. 7. Radar plot of the singular spectrum analysis for the simulated net ecosystem exchange (NEE) in blue, for the observed NEE (green), and for the observed NEE plus and minus the joint uncertainty (light green). S: Soroe, V: Vielsalm, C: Collelongo, CAR: CARAIB, ISB:ISBA_{CC}.

Table 4. Normalized median Euclidean error (NMEE) for the six bins of the singular spectrum analysis for the three models at the three sites.

	Soroe			Vielsalm			Collelongo		
	4C	CARAIB	ISBA _{CC}	4C	CARAIB	ISBA _{CC}	4C	CARAIB	ISBA _{CC}
bin 1	4.52	0.5	0.52	1.38	3.28	2.37	1.26	1.84	1.78
bin 2	0.27	0.19	0.31	0.42	0.15	0.36	0.44	0.5	0.54
bin 3	0.3	0.35	0.63	3.43	4.18	3.45	0.7	0.66	0.5
bin 4	0.38	0.72	0.59	1.89	1.02	0.98	1.75	0.46	0.73
bin 5	0.73	0.63	0.6	1.14	0.97	0.67	1.03	0.59	0.75
bin 6	1.61	0.68	0.93	1.04	0.76	0.98	2.32	0.46	0.99

soil respiration in different ways. Other processes as the coupling of transpiration and photosynthesis, allocation rules and the sink activity of the trees, as well as the effect of nutrient availability are also of prominent importance for reliable carbon exchange simulations (Hickler et al. 2015). Although some SSMs are more robust than others (Li & Zhao 2006) and give a first impression of how well the simulations fit with the observations, none of them provides information about the specific timing of these model errors and the environmental situations in which they occur. Therefore, more advanced evaluation methods as the ones discussed below, should be used in addition to SSMs for more reliable model evaluations.

4.2. Residual analysis

The different model-data asynchronies between the models partly resulted from the different ways in which the evolution of LAI and of phenology is represented in the different models. Although the included processes were different, all three models showed high NEE residuals at moments of transition phases. Another reason for the asynchronies could be that parameter values are often representing adult leaves and the physiological responses of both young or senescing leaves were not well represented.

Surprisingly, the correlations between residuals and yearly NEE were negative for all models. The models overestimated NEE in periods of extreme large carbon uptake and mostly underestimated in periods of carbon release. This could cause problems for predicting NEE

in more extreme environments and under future climate change scenarios. Since the residuals of the three models were not systematically cross-correlated, we can not conclude that the observed NEE values contained errors caused by the assumptions in data processing.

Since the PVM processes and the errors on their outcome are neither linearly nor univariately related to climate variables, we might get incomplete and possibly misleading information using univariate relations. Responses to environmental input variables are hard to interpret due to multicollinearity between model structure and parameters; a univariate study could reflect the result of the multicollinearity rather than the cause of model errors. The dependence of the model error on the meteorological input variables were highly site dependent, meaning that such relations were strongly affected by the quality of the site characteristic data, the model context and by the inherent differences of the different forest systems. This site dependency calls for caution in the interpretation of such univariate relations and clearly illustrates the need to evaluate models for several sites, even more with the ambition for long-term prediction. Responses to meteorological variables do not only directly influence modelled NEE, but also leaf development and senescence. A thorough improvement of the physiological and phenological process description during these periods and also of winter activity will be helpful. Further, residual analysis techniques including bivariate plots, added variable plots (Medlyn et al. 2005) or principal component analysis, could improve our understanding of the environmental dependency of the model errors on NEE simulations.

4.3. Spectral analyses

Spectral analyses are in use to detect and to quantify temporal patterns in model simulations, in observations (cfr. Stoy et al. 2005), in their dissimilarities (cfr. Dietze et al. 2011) and to test the statistical significance of those patterns (Mahecha et al. 2010). On the multi-annual time scale, we found high bin-specific model errors (NMEE), as did also other authors (e.g. Braswell et al. 2005; Sequera et al. 2006), which were linked to the correlation between residuals and observed NEE values. Apparently, certain modelled negative feedback mechanisms affecting NEE were overestimated with respect to reality, where more extreme values occurred. The effect of nitrogen limitation or of stimulation on photosynthesis is very important on the long-term time-scale and needs further investigation. Models not incorporating this effect might overestimate GPP values as a result of CO₂ fertilization, an effect that is often overestimated by PVMs (Anav et al. 2015). Nitrogen limitation effects were only incorporated by 4C, as was also the effect of forest management during the study period. Eventual forest disturbances (e.g. pest plagues) were included in none of the models. On stand scale, such local high impact events and their

lag-effects have a high impact on the long-term evolution of the carbon balance (Anav et al. 2015). On the multi-annual time scale, the spectral power was shown to be often improperly simulated by PVMs (e.g. Braswell et al. 2005). Furthermore, the extraction reliability of the SSA method for low-frequency modes is low (Mahecha et al. 2010). Finally, the time series were not centered before the SSA analysis; the NMEE values did thus not only reflect asynchronies but the entire model error including the model bias.

Regarding the observed and simulated half-yearly spectral peaks, a link to phenology and LAI development was suggested because it more often appears in deciduous forests than in evergreen forests (Mahecha et al. 2010; Dietze et al. 2011). Indeed, Vielsalm consists for one third of conifers. In this study however, the stand was modelled as a mono-species beech forest. Our study, using the longest available EC time series, supports the hypothesis that the asynchrony between simulations and observations was large in spring and autumn, dropping to lower levels in full summer and full winter (see Fig. 2). Inter-annual phenology variability might explain a large part of yearly NEE fluctuations (Keenan et al. 2012) and the way it is incorporated in simulation models affects model performance (Richardson et al. 2012). Further research on this intra-annual variability of carbon exchange and especially on the effect of both transition phases, remains necessary to improve model performance.

4C often overestimated the importance of high frequency variability (inter-monthly to inter-daily) in NEE. The dependence on T which is used to redistribute weekly simulated NEE values to daily values could be too sensitive. Other reasons for asynchrony on smaller frequency bins, by all models, could possibly be ascribed to the simplifications of the forest structure and the vertical radiation partitioning through the canopy, affecting photosynthesis as well as respiration on small time scales. One possible cause for the significant periodicity in Res_{cn} for periods between 16 and 64 days, could be the influence of VPD (Dietze et al. 2011). Also, NEE observations and model input variables measured at the site are prone to random and/or systematic measurement errors. The former might have large effects on the time scale specific analyses of the highest frequencies (Hollinger & Richardson, 2005). An important part of the uncertainty in NEE observations is ascribed to the assumptions in the NEE calculation procedure (Aubinet et al. 2012). Since observational data are often incomplete and models show context errors, it is important to evaluate the models for several sites to discover the real systematic problems in the model structure. While model residuals were shown to maintain a certain temporal correlation structure varying over sites (Richardson et al. 2008), the scaling exponent from our WA of the normalized residuals did not give evidence for a lingering effect of errors over time scales.

5. Conclusions

This study proved the added value of using a set of different statistical evaluation methods and data from multiple sites (without site-specific calibration) for long-term model evaluations. The evaluation methods not only confirm each other but also lead to new insights. Aspects for which one method only provides speculative evidence can be specified using another method. Our study highlighted the need for reviewing the accuracy of the models at the time of canopy closure in spring and canopy shed in autumn and points to other processes to be reconsidered. The study confirmed the confining effect of model complexity on the model evaluation process. In order to evaluate each proposed model process in depth, we advise to perform additional techniques including parameter sensitivity tests and the evaluation of structural changes in the models on long-term data across different sites.

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References

- Anav, A., Frielingstein, P., Beer, C., Ciais, P., Harper, A., Jones, C. et al., 2015: Spatio-temporal patterns of terrestrial gross primary production. *Reviews of Geophysics*, 53:785–818.
- Aubinet, M., Grelle, A., Ibrom, A., Rannik, U., Moncrieff, J., Foken, T. et al., 2000 : Estimates of the annual net carbon and water exchange of forests: The EUROFLUX methodology, *Advances in Ecological Research*, 30:113–175.
- Aubinet, M., Heinesch, B., Perrin, D., Moureaux, C., 2005: Discriminating net ecosystem exchange between different vegetation plots in a heterogeneous forest. *Agricultural and Forest Meteorology*, 132: 315–328.
- Aubinet, M., Vesala, T., Papale, D. (eds.), 2012: *Eddy Covariance: A Practical Guide to Measurement and Data Analysis*. Springer Atmospheric Sciences, Dordrecht, Netherlands, 424 p.
- Botkin, D., 1993: *Forest Dynamics: An Ecological Model*. Oxford University Press, Oxford & New York, UK. 309 p.
- Braswell, B. H., Sacks, W. J., Linder, E., Schimel, D. S., 2005: Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology*, 11:335–355.
- Bugmann, H., Grote, R., Lasch, P., Lindner, M., Suckow, F., 1997: A new forest gap model to study the effects of environmental change on forest structure and functioning. In: Mohren, G. M. J., Kramer, K., Sabate, S. (eds.): *Impacts of Global Change of Tree Physiology and Forest Ecosystem*. Kluwer Academic Publisher, Dordrecht, The Netherlands, p. 255–261.
- Calvet, J. C., Noilhan, J., Roujean, J. L., Bessemoulin, P., Cabelguenne, M., Olioso, A. et al., 1998: An interactive vegetation SVAT model tested against data from six contrasting sites. *Agricultural and Forest Meteorology*, 92:73–95.
- Carrer, D., Roujean, J. L., Lafont, S., Calvet, J. C., Boone, A., Decharme, B. et al., 2013: A canopy radiative transfer scheme with explicit FAPAR for the interactive vegetation model ISBA-A-gs: impact on carbon fluxes. *Journal of Geophysical Research: Biogeosciences*, 118:888–903.
- Chen, C. W., 1993: The response of plants to interacting stresses: PGSM Version 1.3 Model Documentation. EPRI TR-101880. Electric Power Research Institute, Palo Alto, CA, USA, 128 p.
- Collatz, G. J., Ball, J. T., Grivet, C., Berry, J. A., 1991: Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology*, 54:107–136.
- Crowther, T. W., Todd-Brown, K. E. O., Rowe C. W., Wieder, W. R., Carey, J. C., Machmuller, M. B. et al., 2016: Quantifying global soil carbon losses in response to warming. *Nature*, 540:104–108.
- Davidson, R. L., 1969: Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Annals of Botany*, 33:561–569.
- Decharme, B., Boone, A., Delire, C., Noilhan, J., 2011: Local evaluation of the interaction between soil biosphere atmosphere soil multilayer diffusion scheme using four pedotransfer functions. *Journal of Geophysical Research: Biogeosciences*, 116:1984–2012.

- De Pury, D. G., Farquhar, G. D., 1997: Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environment*, 20:537–557.
- Dietze, M. C., Vargas, R., Richardson, A. D., Stoy, P. C., Barr, A. G., Anderson, R. S. et al., 2011: Characterizing the performance of ecosystem models across time scales: a spectral analysis of the North American Carbon Program site-level synthesis. *Journal of Geophysical Research: Biogeosciences*, 116: G04029.
- Dury, M., Hambuckers, A., Warnant, P., Henrot, A.-J., Favre, E., Ouberdous, M. et al., 2011: Response of the European forests to climate change: a modeling approach for the 21st century. *iForest – Biogeosciences and Forestry*, 4:82–99.
- Dyck, S., Peschke, G., 1995: *Grundlagen der Hydrologie*. Verlag für Bauwesen, Berlin, Germany, 536 p.
- Farquhar, G. D., von Caemmerer, S., Berry, J. A., 1980: A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, 149:78–90.
- Fischer, J. B., Huntzinger, D. N., Schwalm, C. R., Sitch, S., 2014: Modeling the terrestrial biosphere. *Annual Review of Environment and Resources*, 39:91–123.
- François, L. M., Delire, C., Warnant, P., Munhoven, G., 1998: Modelling the glacial–interglacial changes in the continental biosphere. *Global Planetary Change*, 16–17:37–52.
- François, L., Utescher, T., Favre, E., Henrot, A.-J., Warnant, P., Micheels, A. et al., 2011: Modelling late Miocene vegetation in Europe: results of the CARAIB model and comparison with palaeo-vegetation data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304:359–378.
- Franke, U., 1990: C- und N-Dynamik beim Umsatz organischer Substanz im Boden. *Akademie der Landwirtschaftswissenschaften der DDR, Dissertation 2*, Berlin, Germany, 140 p.
- Gérard, J. C., Nemry, B., François, L. M., Warnant, P., 1999. The interannual change of atmospheric CO₂: contribution of subtropical ecosystems? *Geophysical Research Letters*, 26:243–246.
- Gibelin, A. L., Calvet, J. C., Viovy, N., 2008: Modelling energy and CO₂ fluxes with an interactive vegetation land surface model, evaluation at high and middle latitudes. *Agricultural and Forest Meteorology*, 148:1611–1628.
- Glugla, G., 1969: Berechnungsverfahren zur Ermittlung des aktuellen Wassergehaltes und Gravitationswasserabflusses im Boden. *Albrecht-Thaer-Archiv*, 13:71–376.
- Golyandina, N., Zhigljavsky, A., 2013 (eds.): *Singular Spectrum Analysis for Time Series*. Springer Briefs in Statistics, Springer, Heidelberg, Germany, 119 p.
- Goudriaan, J., van Laar, H. H., van Keulen, H., Louwse, W., 1985: Photosynthesis, CO₂ and plant production. In: Day, W., Atkin, R. K. (eds.). *Wheat Growth and Modelling*. Plenum Press, New York, USA. NATO AS/ Series, Series A, 86:107–122.
- Goudriaan, J., 1986: A simple and fast numerical method for the computation of daily totals of crop photosynthesis. *Agricultural and Forest Meteorology*, 38:249–254.
- Grote, R., Suckow, F., Bellmann, K., 1998: Modelling of carbon-, nitrogen-, and water balances in pine stands under changing air pollution and deposition. In: Hüttel, R. F. and Bellmann, K. (eds.): *Changes of Atmospheric Chemistry and Effects on Forest Ecosystems. A Roof Experiment Without Roof*. Kluwer Publishers, Dordrecht, The Netherlands, p. 251–281.
- Haxeltine, A., Prentice I. C., 1996: A general model for the light-use efficiency of primary production. *Functional Ecology*, 10:551–561.
- Henrot, A.-J., Utescher, T., Erdei, B., Dury, M., Hamon, N., Ramstein, G. et al., 2017: Middle Miocene climate and vegetation models and their validation with proxy data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 467:95–119.
- Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L. et al., 2012: Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, 21:50–63.
- Hickler, T., Amming, A., Werner, C., 2015: Modelling CO₂ impacts on forest productivity. *Current Forestry Reports*, 1:69–80.
- Hollinger, D. Y., Richardson, A. D., 2005: Uncertainty in eddy covariance measurements and its application to physiological models. *Tree Physiology*, 25:873–885.
- Jacobs, C. M. J., 1994: Direct impact of atmospheric CO₂ enrichment on regional transpiration, PhD thesis, Agricultural University, Wageningen, The Netherlands, 192 p.
- Jansson P. - E., 1991: Simulation model for soil water and heat conditions. Description of the SOIL model (vol. 165). Swedish University of Agricultural Sciences, Department of Soil Sciences, Division of Agricultural Hydrotechnics, Uppsala, Sweden, 72 p.
- Joetzier, E., Delire, C., Douville, H., Ciais, P., Decharme, B., Carrer, D. et al., 2015: Improving the ISBA_{CC} land surface model simulation of water and carbon fluxes and stocks over the Amazon forest. *Geoscientific Model Development*, 8:1709–1727.
- Jorritsma, I. T. M., van Hees, A. F. M., Mohren G. M. J., 1999: Forest development in relation to ungulate grazing: A modeling approach. *Forest Ecology and Management*, 120:23–34.
- Kartschall, T., Döring, P., Suckow, F., 1989: Simulation of nitrogen, water and temperature dynamics in soil. *Systems Analysis Modelling Simulation Journal*, 6:117–123.
- Keane, R. E., Morgan, P., Running, S. W., 1996: FIRE-BGC – a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. *Research Paper INT-RP-484*, United States Department of Agriculture, Forest Service, Intermountain Research Station, Missoula, MT, USA, 122 p.

- Keenan, T. F., Baker, I., Barr, A., Ciais, P., Davis, K., Dietze, M. et al., 2012: Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO₂ exchange. *Global Change Biology*, 18:1971–1987.
- Koitzsch, R., 1977: Schätzung der Bodenfeuchte aus meteorologischen Daten, Boden- und Pflanzenparametern mit einem Mehrschichtmodell. *Zeitschrift für Meteorologie*, 27:302–306.
- Krause, P., Boyle, D. P., Base, F., 2005: Comparison of different efficiency criteria for hydrological model assessment. *Advances in Geosciences*, 5:89–97.
- Landsberg, J. J., Waring, R. H., 1997: A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, 95:209–228.
- Le Quéré, C., Andrew, M., Canadell, J. G., Sitch, S., Korsbakken, J. I., Peters, G. P. et al., 2016: Global carbon budget 2016. *Earth System Science Data*, 8:605–649.
- Larocque, G. R., Bhatti, J., Arsenaault, A., 2014: Integrated modelling software platform development for effective use of ecosystem models. *Ecological Modelling*, 288:195–202.
- Lasch, P., Badeck, F. - W., Suckow, F., 2005: Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). *Forest Ecology and Management*, 207:59–74.
- Lasch, P., Badeck, F. - W., Suckow, F., Lindner, M., Mohr, P., 2005: Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). *Forest Ecology and Management*, 207:59–74.
- Lasch-Born, P., Suckow, F., Gutsch, M., Reyer, C., Hauf, Y., Murawski, A. L. et al., 2015: Forests under climate change: potential risks and opportunities. *Meteorologische Zeitschrift*, 24:157–172.
- Lau, K. M., Wang, H. - Y., 1995: Climate signal detection using wavelet transform: How to make a time series sing? *Bulletin of the American Meteorological Society*, 76:2391–2402.
- Laurent, J. - M., François, L., Bar-Hen, A., Bel, L., Cheddadi, R., 2008: European bioclimatic affinity groups: data-model comparisons. *Global and Planetary Change*, 61:28–40.
- Law, B. E., Falge, E., Gu, L., Baldocchi, D. D., Bakwin, P., Berbigier, P. et al., 2002: Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, 113:97–120.
- Li, H., Zhang, F., Li, Y., Wang, J., Zhang, L., Zhao, L. et al., 2016: Seasonal and inter-annual variations in CO₂ fluxes over 10 years in an alpine shrubland on the Qinghai-Tibetan plateau, China. *Agricultural and Forest Meteorology*, 228–229:95–103.
- Li, X. R., Zhao, Z., 2006: Evaluation of estimation algorithms, part I: Incomprehensive measures of performances. *IEEE Transactions on Aerospace and Electronic Systems*, 42:1340–1358.
- Lloyd, J., Taylor, J. A., 1994: On the temperature dependence of soil respiration. *Functional Ecology*, 8:315–323
- Loehle, C., LeBlanc, D., 1996: Model-based assessments of climate change effects on forests: a critical review. *Ecological Modelling*, 90:1–31.
- Mahecha, M. D., Reichstein, M., Lange, H., Carvalhais, N., Bernhofer, C., Grünwald, T. et al., 2007: Characterizing ecosystem-atmosphere interactions from short to interannual time scales. *Biogeosciences*, 4:743–758.
- Mahecha, M. D., Reichstein, M., Jung, M., Seneviratne, S. I., Zaehle, S., Beer, C. et al., 2010: Comparing observations and process-based simulations of biosphere-atmosphere exchange on multiple time scales. *Journal of Geophysical Research: Atmospheres*, 115:7111–7125.
- Mäkelä, A., 1990: Modeling structural-functional relationships in whole-tree growth: resource allocation. In: Dixon, R. K., Meldahl, R. S., Ruark, G. A., Warren, W. G (eds.): *Process Modeling of Forest Growth Responses to Environmental Stress*. Timber Press, Portland, Oregon, 81–95.
- Masson, V., Le Moigne, P., Martin, E., Faroux, S., Alias, A., Alkama, R. et al., 2013: The SURFEXv7.2 land and ocean surface platform for coupled or offline simulation of Earth surface variables and fluxes. *Geoscientific Model Development*, 6:929–960.
- Medlyn, B. E., Robinson, A. P., Clement, R., McMurtrie, E., 2005: On the validation of models of forest CO₂ exchange using eddy covariance data: some perils and pitfalls. *Tree Physiology*, 25:839–857.
- Mintz, Y., Walker, G., 1993: Global fields of soil moisture and land surface evapotranspiration derived from observed precipitation and surface air temperature. *Journal of Applied Meteorology*, 32:1305–1334.
- Nash, J. E., Sutcliffe, J. V., 1970: River flow forecasting through conceptual models part I – A discussion of principles. *Journal of Hydrology*, 10:282–290.
- Nemry, B., François, L. M., Warnant, P., Robinet, F., Gérard, J. C., 1996: The seasonality of the CO₂ exchange between the atmosphere and the land biosphere: a study with a global mechanistic vegetation model. *Journal of Geophysical Research-Atmospheres*, 101:7111–7125.
- Noilhan, J., Planton, S., 1989: A simple parameterization of land surface processes for meteorological models. *Monthly Weather Review*, 117:536–549.
- Noilhan, J., Mahfouf, J. F., 1996: The ISBA land surface parameterization scheme. *Global and Planetary Change*, 13:145–159.
- Otto, D., Rasse, D., Kaplan, J., Warnant, P., François, L., 2002: Biospheric carbon stocks reconstructed and the Last Glacial Maximum: comparison between general circulation models using prescribed and computed sea surface temperature. *Global Planetary Change*, 33:117–138.

- Pan S., Tian, H., Dangal, S. R. S., Ouyang, Z., Tao, B., Ren, W. et al., 2014: Modeling and monitoring terrestrial primary production in a changing global environment: toward a multiscale synthesis of observation and simulation. *Advances in Meteorology*, 2014:1–17.
- Parton, W. J., Schimel, D. S., Cole, C. V., Ojima, D. S., 1987: Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, 51:1173–1179.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Valentini, R., Aubinet, M. et al., 2005: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, 11:1–16.
- Reyer, C., 2015: Forest productivity under environmental change – a review of stand-scale modeling studies. *Current Forestry Reports*, 1:53–68.
- Richardson, A. D., Mahecha, M. D., Falge, E., Kattge, J., Moffat, A. M., Papale, D. et al., 2008: Statistical properties of random CO₂ flux measurement uncertainty inferred from model residuals. *Agricultural and Forest Meteorology*, 148:38–50.
- Richardson, A. D., Anderson, R. S., Arian, M. A., Barr, A. G., Bohrer, G., Chen, G. et al., 2012: Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site synthesis. *Global Change Biology*, 18:566–584.
- Running, S. W., Gower, S. T., 1991: FOREST-BGC, A general model of forest ecosystem processes for regional applications II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*, 9:147–160.
- Saxton, K., Rawls, W. J., Romberger, J., Papendick, R., 1986: Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal*, 50:1031–1036.
- Schaber, J., Badeck, F. - W., 2003: Physiology based phenology models for forest tree species in Germany. *International Journal of Biometeorology*, 47:193–201.
- Schultz, M., Mudelsee, M., 2002: REDFIT: estimating red-noise spectra directly from unevenly spaced paleoclimatic time series. *Computers & Geosciences*, 28:421–426.
- Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964: A quantitative analysis of plant form – the pipe model theory. I. Basic analysis. *Japanese Journal of Ecology*, 14:97–105.
- Siqueira M. B., Katul, G. G., Sampson, D. A., Stoy, P. C., Juang, J. - Y., McCarthy, H. R. et al., 2006: Multiscale model intercomparisons of CO₂ and H₂O exchange rates in a maturing southeastern US pine forest. *Global Change Biology*, 12:1189–1207.
- Stoy, P. C., Katul, G. G., Siqueira, M. B., Juang, J. - Y., McCarthy, H. R., Kim, H. - S. et al., 2005: Variability in net ecosystem exchange from hourly to inter-annual time scales at adjacent pine and hardwood forests: a wavelet analysis. *Tree Physiology*, 25:887–902.
- Suckow, F., Badeck, F. - W. Lasch, P., Schaber, J., 2001: Nutzung von Level-II-Beobachtungen für Test und Anwendungen des Sukzessionsmodells FORESEE. *Beiträge für Forstwirtschaft und Landschaftsökologie*, 35:84–87.
- Sykes, M. T., Prentice, I. C., 1996: Carbon storage and climate change in Swedish forests: A comparison of static and dynamic modelling approaches. In: Apps, M. J., Price, D. T. (eds.). *Forest Ecosystems, Forest Management and the Global Carbon Cycle*. Springer-Verlag, Berlin, Germany, NATO ASI Series, 40:69–78.
- Torrence, C., Compo, G. P., 1998: A practical guide to wavelet analysis. *Bulletin of the American Meteorological Society*, 79:61–78.
- Trudinger, C. M., Raupach, M. R., Rayner, P. J., Kattge, J., Liu, Q., Pak, B. et al., 2007: OptIC project: An inter-comparison of optimization techniques for parameter estimation in terrestrial biogeochemical models. *Journal of Geophysical Research*, 112: G02027.
- Uppala, S. M., Kallberg, P. W., Simmons, A. J., Andrea, U., Da Costa Bechtold, V., Fiorino, M. et al., 2005: The ERA-40 re-analysis. *Quarterly Journal of the Royal Meteorological Society*, 131:2961–3012.
- Vinnichenko, N., 1970: The kinetic energy spectrum in the free atmosphere – 1 second to 5 years. *Tellus*, 22:158–166.
- Walker, W. E., Harremoes, P. J., Rotmans, J., Van Der Sluis, J. P., Van Asselt, M. B. A., Janssen, P. et al., 2003: Defining uncertainty: a conceptual basis for uncertainty management in model-based decision support. *Integrated Assessment*, 4:5–17.
- Wang, T., Brender, P., Ciais, P., Piao, S., Mahecha, M., Chevalier, F. et al., 2012: State-dependent errors in a land surface model across biomes inferred from eddy covariance observations on multiple timescales. *Ecological Modelling*, 246:11–25.
- Warnant, P., François, L. M., Strivay, D., Gérard, J.-C., 1994: CARAIB: a global model of terrestrial biological productivity. *Global Biogeochemical Cycles*, 8:255–270.
- Warnant, P., 1999: Modélisation du cycle du carbone dans la biosphère continentale à l'échelle globale. PhD thesis, Université de Liège, Liège, 276 p.
- Wythers, K. R., Reich, P. B., Tjoelker, M. G., Bolstad, P. B., 2005: Foliar respiration acclimation to temperature variable Q₁₀ alter ecosystem carbon balance. *Global Change Biology*, 11:435–449.

Appendix tables

Table A1. List of abbreviations and acronyms used in the text.

Abbreviation	Explanation
AR(1)	First order autoregressive function
bR ²	Slope of the regression times the coefficient of determination
CorrO	Correlation coefficient between the residuals and the observed NEE values
CorrE	Correlation coefficient between the residuals of the different models
D _{tr} ^c	Potential canopy transpiration demand of a cohort
DOY	Day of the year
DRI	Drought index
Dtr	Potential canopy transpiration demand
EC	Eddy covariance
E _{int}	Interception evaporation
EOF	Empirical orthogonal function
DGVM	Dynamic global vegetation model
GPP	Gross primary production
G _{max}	Maximum stomatal conductance
g _{tot}	Unstressed stomatal conductance
kurR	Kurtosis of the daily residual distribution
LAI	Leaf area index
ME	Mean error
NEE	Net ecosystem exchange
NMEE	Normalized median Euclidean error
NRMSE	Normalized root mean squared error
NSE	Nash-Sutcliffe efficiency
PFT	Plant functional type
PVM	Process-based vegetation model
RA	Residual analysis
RAD	Incoming solar radiation
R ²	Coefficient of determination
R _{eco}	Ecosystem respiration
Rescn	Residuals of the centered and normalized simulated and observed values
sdR	Standard deviation of the daily residual distribution
SEM	Statistical evaluation method
SSM	Scalar statistical measure
skR	Skewness of the daily residual distribution
SSA	Singular spectrum analysis
T	Air temperature
u	Wind velocity
VPD	Vapour pressure deficit
WA	Wavelet analysis

Table A2. Short description of the processes included in the CARAIB global dynamic vegetation model.

Plant functional types	Plant functional type or species level. In this study parameters for beech.
Spatial scale	Grid cell containing different PFTs or point scale.
Soil input initialisation	Sand fraction, clay fraction, rooting depth per PFT/species, soil color.
Forest structure and carbon pools initialisation	Grid cell with one layer of trees and one layer containing herbs and shrubs.
Climate input	CO ₂ , air temperature, amplitude of air temperature (Tday _{max} –Tday _{min}), precipitation, air relative humidity, short-wave incoming radiation, wind velocity. [Daily]
Spin-up	Yes, by using ERA-interim re-analysis (Uppala et al. 2005) [Daily] Light interception by big leaf approach with separation of sun and shaded leaves (De Pury & Farquhar 1997). Time step subdivided into sunny and non-sunny portions, depending on the percentage of sunshine hours. Photosynthesis thus calculated 3 times in each time step for each PFT/species: for sun and shaded leaves during the sunny portion and for all leaves during the non-sunny portion. Light use efficiency calculated by the model of Farquhar (1980), as simplified by Collatz (1991). Radiative transfer through the canopy according to Goudrian et al. (1985) with radiation attenuation by Beer's law. Gross primary production only calculated when air temperature >–10 °C and if LAI >0. [2-hourly]
Photosynthesis	Autotrophic respiration subdivided into growth respiration, as a fixed fraction of the carbon allocated to the growth of carbon pools, and maintenance respiration, as a Q ₁₀ function of temperature and proportional to the biomass and the C:N ratio of that pool (Warant et al. 1999) and decreasing with the average air temperature of the previous 2 months for leaves and the previous 4 years for wood/roots to mimic temperature acclimation process (Wythers et al. 2005). Heterotrophic respiration dependent on soil temperature and soil moisture (Nemry et al. 1996) [2-hourly]
Respiration	Photosynthetic products (GPP) are allocated to the metabolic (leaves and fine roots) and structural (wood and coarse roots) carbon reservoirs. The carbon partitioning between the two pools is species-specific and depends on environmental conditions (temperature and soil water) (Otto et al. 2002).
Allocation	
Carbon nitrogen balance	Constant C:N ratio prescribed at initialisation. Turnover of litter and organic matter vary with temperature and soil water. Three carbon reservoirs are considered: leaf litter, wood litter and humus. [Daily]
Soil water balance	Soil water budget modelled in the root zone. Soil hydraulic conductivity is calculated from soil texture, using the parameterization of Saxton et al. (1986). Soil water can vary from wilting point to saturation. [Daily]
Water interception storage	Parameterization from leaf bucket model run at very high temporal resolution (~1 minute), depending on precipitation, potential evapotranspiration and LAI. [Daily]
Evapotranspiration	Actual evapotranspiration calculated as the sum of snow sublimation, the evaporation of intercepted rain and the evaporation/transpiration from the soil-vegetation system. This sum cannot exceed the potential evapotranspiration calculated over the pixel from Penman's equation (e.g., Mintz & Walker 1993). Transpiration is considered as a supply function for the water transpired by the PFT/species growing on the pixel. [Daily]
Phenology	Regulated purely by evolution of LAI. LAI growth (resp. leaf fall) is initiated when the air temperature is above (resp. below) a prescribed species-dependent threshold. [Daily]
Regeneration/planting	Amount of seeds proportional to NPP. Seeds (here only beech) can colonize gaps in the canopy caused by mortality. [yearly]
Management	A prescribed fraction of biomass (leaf or wood) can be removed. [Daily] Not used in this study.
Mortality	Age dependent natural mortality and mortality caused by thermal and water deficit stress as well as by fire disturbance. [Daily]

Table A3. Short description of the processes included in the ISBA_{CC} global dynamic vegetation model.

Plant functional types	Several plant functional types in one gridcell possible, not interacting and each having their own soil. Here only temperate deciduous forest.
Spatial scale	Grid or point scale.
Soil input initialisation	Per layer: saturation, field capacity, permanent wilting point, sand fraction, clay fraction, carbon content, General: rooting depth, ground water depth.
Forest structure and carbon pools initialisation	Grid cell with one layer of trees.
Climate input	CO ₂ , air temperature, precipitation, air relative humidity, short-wave incoming radiation, long-wave incoming radiation, wind velocity. [Hourly]
Spin-up	Yes by cycling through the available meteorological data. [Hourly]
Photosynthesis	Semi-empirical parametrization of net carbon assimilation and mesophyll conductance following the photosynthesis model of Jacobs (1994) based on Goudriaan et al. (1985) and implemented by Calvet et al. (1998). 10-layer radiative transfer scheme taking into account direct and diffuse radiation and sunlit and shaded leaves to calculate photosynthesis in the canopy (Carrer et al. 2013). [Hourly]
Respiration	Maintenance respiration rates of twigs, sapwood and fine root carbon pools depending linearly on biomass of the pool and its temperature, calculated by the Arrhenius temperature function (Lloyd & Taylor, 1994; Joetzjer et al. 2015). Growth respiration proportional to the photosynthetic capacity of the leaves (Jacobs, 1994). Heterotrophic respiration based on the CENTURY model (Parton et al. 1987). [Hourly]
Allocation	Assimilated carbon directly allocated to leaves, twigs, aboveground and belowground wood and fine roots following the daily carbon balance of the leaves (Gibelin et al. 2006). [Daily]
Carbon nitrogen balance	Nitrogen not simulated.
Soil water balance	Multilayer (14 layers) solution of the Fourier law and the mixed-form of the Richards equation to calculate the soil energy and water budgets including freezing/thawing (Boone et al. 2000; Decharme et al. 2011). [Hourly]
Water interception storage	Depending on LAI, precipitation and a maximum interception pool. [Hourly]
Evapotranspiration	Sum of snow sublimation, evaporation of intercepted rain, transpiration and soil evaporation (Noilhan & Planton 1989). [Hourly]
Phenology	Directly resulting from the leaf carbon balance. A minimum LAI at all time (0.3 for deciduous trees). Leaves start to grow when the amount of assimilated carbon is larger than the amount of lost carbon through respiration and turnover. This depends on the incoming radiation, the temperature and is only possible when the soil moisture is not limiting. At the end of the growing season the inverse happens. [Daily]
Regeneration/planting	Not explicitly modelled, presence of a minimum LAI allowing plant functional types to grow when climatic conditions are favorable. [Daily]
Management	Not modelled
Mortality	Not explicitly modelled, except for leaves. Biomass decreases through turnover. [Daily]

Table A4. Short description of the processes included in the 4C forest model.

Plant functional types	No plant functional types. Fixed parameters available for 13 tree species, here beech.
Spatial scale	Stand-scale.
Soil input initialisation	Per layer: field capacity, permanent wilting point, soil density, pH, stone fraction, sand fraction, clay fraction, humus fraction, carbon and nitrogen content in the humus fraction, NH ₄ and NO ₃ content. General: rooting depth, ground water depth, evaporation depth, mineralization constant of humus in litter layer and in mineral soil, nitrification constant.
Forest structure and carbon pools initialisation	Per cohort: species, foliage biomass, fine root biomass, sapwood biomass, heartwood biomass, cross sectional area of heartwood at stem base, tree height, bole height, tree age, number of trees, diameter at crown base, diameter at breast height. Cohorts compete for light and for water and nutrients in the soil.
Climate input	CO ₂ , air temperature, precipitation, air relative humidity, net radiation, wind velocity. [Daily]
Spin-up	No.
Photosynthesis	Net photosynthesis as function of environmental drivers and physiological capacity depending on light use efficiency calculated according to Haxeltine & Prentice (1996) based on the mechanistic model of Farquhar (1980) as simplified by Collatz (1991) and limited by water and nitrogen availability and maximum nitrogen uptake per cohort. Net photosynthetic fraction per cohort proportional to its share in the absorbed photosynthetic active radiation, adapted when forest structure changes and with phenology (Lambert-Beer law). [Weekly, redistributed to daily values by a Q ₁₀ function of air temperature]
Respiration	Autotrophic respiration proportional to photosynthetic capacity (Landsberg & Waring, 1997). Heterotrophic respiration calculated by the carbon dynamics of the soil, dependent on soil temperature and soil moisture. [Weekly, redistributed to daily values by a Q ₁₀ function of air temperature]
Allocation	Theory of Mäkelä (1990), functional balance hypothesis (Davidson 1969), pipe model theory (Shinozaki, 1964) and mass-conservation law. Allometric relationships dynamically responding to water and nutrient limitations. [Yearly]
Carbon nitrogen balance	Decomposition of primary organic matter to humus described by first order reactions (Grote et al. 1998). Turnover from organic matter depending on water content, soil temperature and pH (Franko 1990; Kartschall 1989). Soil carbon/nitrogen depending on the percentage in the organic matter and their turnover rates (Running & Gower 1991). Outflow of nitrogen from the root zone by plant uptake and its transport by water. [Daily]
Soil water balance	Soil water balance per soil horizon by percolation model, bucket model, water leaching and conductivity parameter depending on soil texture (Glugla 1969; Koitzsch 1997). Link to vegetation is plant available water versus transpiration demand and limited when more than 10 percent difference from field capacity (Chen et al. 1993), divided per cohort depending on its share in fine root biomass. [Daily]
Water interception storage	Depending on precipitation and evapotranspiration (Jansson 1991) and proportional to LAI. [Daily]
Evapotranspiration	Potential evapotranspiration by equation of TURC if air temperature > 5 °C and by an equation of IVANOV if air temperature < 5 °C (Dyck & Peschke 1989). Calculation of potential transpiration takes into account the interception evaporation and partitioned to cohorts considering their relative conductance. [Daily]
Phenology	Interaction of growth-promoting and growth-inhibiting agents driven by temperature and photoperiod (Schaber & Badeck 2003). Leaves appearing and disappearing all together at one time point when the threshold is reached. [Yearly]
Regeneration/planting	Regeneration by seed supply (Rogers & Johnson 1998), seed germination (Jorritsma et al. 1999) Not used in this study. [Yearly]
Management	Thinning (from below or from above), harvest (clear cut, shelterwood) and planting strategies options (method, strength and timing; Lasch et al. 2005). Here used by thinning to target number of trees known during the study period. [Yearly]
Mortality	Intrinsic mortality depending on maximum life span (Botkin 1993) or carbon-based stress mortality, by drought stress or light shortage or by disturbances (Keane et al. 1996; Loehle & LeBlanc 1996; Sykes & Prentice 1996). Not used in this study. [Yearly]

Table A5. Scalar statistical measures (SSM) for simulated (S) versus observed (O) net ecosystem exchange (NEE), moments of the residual distribution (for abbreviations see Table A1) and correlation coefficients between the residuals and the observed values (CorrO) and the residuals of the other models (CorrE) for the three models run for the three sites.

SSM	Interpretation	Soroe			Vielsalm			Collelongo		
		4C	CARAIB	ISBA _{cc}	4C	CARAIB	ISBA _{cc}	4C	CARAIB	ISBA _{cc}
Scalar fit statistics: how well does S reproduce O?										
R ²	Fraction of the variance in O explained by linear relation between S and O; the closer to 1 the better	0.53	0.74	0.7	0.41	0.47	0.52	0.39	0.66	0.44
bR ²	Fraction of the variance in O explained by linear relation between S and O taking into account systematic error; the closer to 1 the better	0.44	0.44	0.59	0.35	0.25	0.34	0.23	0.22	0.15
NSE	S predicts better the O than the mean of O if NSE>0; the closer to 1 the better	0.22	0.7	0.67	0.17	0.11	0.27	0.3	0.37	0.29
Scalar error estimates: how large is the relative error of the models?										
NRMSE	Measure of the relative error between S and O; the closer to 0 the better	13.8	8.6	8.9	13.9	14.4	13	19.1	18.2	19.3
NMEE	Measure of the relative error between S and O; the closer to 0 the better	0.47	0.28	0.26	0.48	0.61	0.48	0.28	0.28	0.31
Moments of the distribution of the daily residuals: how are the model errors distributed?										
ME	Value far from 0 indicates a probable systematic bias or at least many more or more extreme errors in one direction	-1.42	-0.14	-0.05	-0.59	1.25	0.92	0.53	1.48	1.37
sdR	Expresses the variability in the model errors; high variability means high random error	2.69	1.66	1.74	0.41	0.33	0.52	0.55	0.61	0.54
skR	The more negative the heavier the tail of the negative errors; the more positive the more heavy the tail of the positive errors	-26.19	0.58	-0.34	-9.81	13.37	8.12	37.85	48.35	56.79
kurR	The more negative the less peaks in the distribution and the more the variance is dominated by many, but not very extreme errors. The more positive the more peaks; the more the variance is dominated by some rare extreme errors	232.7	36.22	46.46	92.3	81.09	58.45	390.7	300.0	405.7
Are model errors correlated with the observed NEE value and the errors of other models?										
CorrO	Correlation between the residuals and the observed values. The higher the more the error is dependent on the value of the observed flux	-0.65	-0.5	-0.8	-0.93	-0.81	-0.94	-0.84	-0.93	-0.93
CorrE	Correlation between the residuals and the residuals of the other models	4C	0.65	0.43		0.75	0.4		0.42	0.4
	The higher the more the errors between two models are correlated	CARAIB		0.35			0.17			0.75

Epigenetic memory effects in forest trees: a victory of “Michurinian biology”?

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Abstract

The study reviews trait inheritance, which is in contradiction with the rules of Mendelian genetics, and which was object of controversies among biologists (sometimes with grave political consequences) in the USSR and Soviet-controlled countries in the 1930s–1960s. “Carryover” or “memory” effects of the climate, to which maternal trees are exposed during seed development, on phenological behavior and other adaptively relevant traits of their offspring in conifers are mentioned; similar effects are associated with the germination and early growth environment. Molecular mechanisms underlying these effects include covalent modifications of DNA or DNA-associated proteins (cytosine methylation, various types of histone modifications), micro-RNAs and small interfering RNAs. Tools for the identification of these modifications are reviewed with a focus on cytosine methylation, along with an overview of the hitherto knowledge on the occurrence of DNA modifications in forest trees. The practical implications of epigenetic inheritance in forest trees are discussed with the focus on the adaptation to climate change and legislation on forest reproductive materials.

Key words: epigenetics; carryover effects; cytosine methylation; MSAP; climate change; Lysenko

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1. A bit of history

Although naturalists often suffer from the illusion that natural science is independent from external ideological and political influences, more than often this is just an illusion. The almost fifty-year period of so-called Michurinian biology in the Soviet Union and its eastern-European satellites (including Czechoslovakia) is a bitter reminder of detrimental, even fatal effects of political influence in science. This “science”, abusing the name of famous Russian and Soviet plant breeder I.V. Michurin, is associated with the name of T.D. Lysenko, a Stalin favourite and long-time director (1938–1962 with a short interruption) of VASKhNIL, the Lenin All-Union Academy of Agricultural Sciences. It was not only the abuse of political power for intimidation, professional and sometimes even physical disposal of scientific opponents, but also absurdity of theories and weakness of experimental fundamentals on which their dogmas were built, which characterized Lysenko’s era. Even though agricultural plants and animals were the primary focus of Soviet “agrobiologists”, the shadow of this pseudoscience did also encompass forestry, including Czechoslovak forestry in the 1950s

and early 1960s. In many cases, the theories of Michurinian biology can only be described as charlatan, such as those on the creation of living cells from mixtures of high-molecular organic substances, transformation of viruses into bacteria and back, or saltational changes of species identity under the influence of the environment (Soyfer 2011). Based on practical experience in agriculture and horticulture, Lysenko and his followers hypothesized “soft heredity” mediated by a plethora of organic substances in a cell (not nucleic acids), resulting in strong effects of environment on phenotype and transmission of such environment-induced phenotypic changes into the offspring generation (Flegr 2002).

Even though Lysenko’s influence started to decline already in late 1950s, he retained his position even during the Khrushchev era; it required an intervention of prominent Soviet scientists (mostly non-biologists) such as Sakharov and Kapitsa to have his theories proclaimed as pseudoscience, and he lost his position only after Khrushchev’s fall. Nevertheless, his effect on biology in the USSR was devastating and remained visible long after his dismissal.

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Now, the question is: was all the “Michurinian biology” a pure nonsense? And what does it have to do with forestry?

2. Uncommon trait inheritance in trees

In Scandinavia, conifer seed orchards or clonal collections used for seed production by mass controlled pollination were routinely moved to southern regions in order to obtain high yields of seed material in seed orchards, as the amount of seeds produced by the trees decreases and the intervals between mast years become longer towards the North due to the harshness of climate. However, the offspring of translocated seed orchards exhibited lower frost resistance compared to the original northern populations (Johnsen 1989; Dormling & Johnsen 1992). A poorer performance of such offspring in terms of frost hardiness was initially attributed to pollen contamination from the local (southern) pollen sources, which is typically high in Scandinavia. However, later investigations showed that progenies originated from controlled crosses behaved in the same manner. It appeared that the seeds produced in southern seed orchards ‘remember’ in some way the climate at the site of production, despite containing genes inherited from parents originating from the North (hence the designation ‘memory’ or ‘carryover’ effects). Similar observations were made on North-American conifers (Greenwood and Hutchison 1996; Stoehr et al. 1998; Webber et al. 2005).

Another line of evidence for heredity not obeying the rules of genetics comes from provenance transfer. In Scandinavia again, quite much Norway spruce originating from Central Europe (Germany, Austria, the Carpathians) was planted, and some plantations already reproduce. Offsprings from such plantations resemble the local indigenous plantations rather than the material translocated from identical Central-European source populations in terms of timing of budburst, budset, growth cessation and other adaptive traits, which means that in spite of unchanged genetic structures, the populations of Central-European origin changed their phenological behavior within a single generation (Skrøppa et al. 2010).

In later controlled-pollination experiments performed in climatic chambers, greenhouses and also under field conditions, it was found that the temperature during seed development of Norway spruce affects important phenological characteristics. Cold environment advanced autumn bud set, cold acclimation, spring dehardening and flushing. On the other hand, the conditions during the pre-zygotic stage and fertilization did not affect phenology (Johnsen et al. 2005a). The effect of temperature also interacts with the daylength effects, plants subjected to high temperature and long days and those subjected to low temperature and short days expressed characteristics similar to cold-subjected individuals from the

previously mentioned study: autumn bud set and spring flushing were earlier and they were more frost-hardy in the autumn (Johnsen et al. 2005b).

Environmental conditions during germination and early growth can affect phenology in a similar way. In a nursery experiment with Norway spruce and European larch, Gömöry et al. (2015) found that provenances sown in a warm nursery delayed budburst consistently compared to those grown in a cold nursery, wherever they were later transplanted.

In a certain way, such observations confirm Lysenko’s ideas of soft inheritance of traits, meaning that traits induced by environment during the ontogeny of an individual are transmitted to its offsprings. As this type of heredity is not associated with a change of the genetic information *sensu stricto*, it is called epigenetic. This term is used to describe heritable (not necessarily sexually, but at least during the cell division, mitosis) changes to gene expression not caused by changes of the DNA sequence itself.

3. Molecular mechanisms of epigenetic inheritance

Carryover effects and other epigenetic phenomena have important implications for biology, medicine, agriculture or forestry. Nevertheless, they do not contradict to the paradigms of genetics, and can be explained by mechanisms involved in the molecular basis of heredity. Phenotype of a tree does not depend exclusively on genotype (in the meaning of the composition of alleles constituting a genotype). It results from physiological processes depending on the activity of genes. Phenotypic traits from the subcellular level to the level of organism depend on the timing and location of gene expression. The basis of epigenetic inheritance needs to be looked for in molecular mechanisms regulating transcription and translation of genes, which are on one hand inducible by environmental signals, and on the other hand reproducible and transmittable across generations.

Mechanisms underlying epigenetic effects include histone modifications. Histones are proteins that pack the chromosomal DNA in eukaryotic cells into nucleosomes, molecular coils serving for the organization of huge DNA molecules and allowing the cell to manipulate with them during cell division. Each nucleosome consists of eight histone cores, around which approximately 147 bp (basepairs) of DNA are wound. In the nucleosome, each histone can be potentially modified by a number of covalent modifications, including acetylation, methylation, phosphorylation and ubiquitination, whereas the modification status decides whether the chromatin around nucleosomes and the associated genes will be transcriptionally active or inactive (Turner 2000).

Small interfering RNA (siRNA) and micro RNA (miRNA) molecules also play an important role in epi-

genetics. siRNAs are double-stranded RNA molecules with a length of 20 – 25 basepairs, while miRNAs are single-stranded with a length of about 22 nucleotides. Both types regulate gene expression by interfering with the translation of the information contained in the DNA to proteins, usually by cleaving the messenger RNA (mRNA), which is the carrier of information on protein primary structure, or otherwise speeding the degradation of mRNA.

Finally, gene expression is affected by methylation of DNA cytosines. Other DNA base modifications may occur as well (Vanyushin 2005). Adenine methylation was thought not to occur in eukaryotes, but has recently been reported in mouse embryonic stem cells (Wu et al. 2016). Methylated cytosines mostly occur in the context where cytosine is located next to guanine (CG). This configuration allows for symmetric methylation on both strands of DNA, as cytosine is complementary to guanine. In plants methylated cytosines often occur in other contexts as well (CHG and CHH sites; H = A, C or T), having their own maintenance mechanisms and function (Chan et al. 2005). Sometimes only one strand of DNA is methylated, which is called hemimethylation. The methylated CG sites often occur concentrated on the so-called methylated CG islands (Neumann & Barlow 1996). The function of DNA methylation also differs with its different position within the genes. While methylation towards the beginning of a gene (promoter or first exon) inhibits production of proteins, regions more downstream can behave differently (Suzuki & Bird 2008; Brenet et al. 2011). In the downstream regions of gene loci, DNA methylation has been shown to induce alternative splicing, i.e. the removal of introns from the primary transcript, creating different proteins from the same DNA template (Maunakea et al. 2013). There are several mechanisms how DNA cytosine methylation inhibits gene expression. First, DNA methylation seems to be linked with histone methylation and the formation of heterochromatin, a transcriptionally inactive (not protein-producing) state of chromatin (Soppe et al. 2002; Hashimoto et al. 2010). In a more direct manner, methylation interferes with binding of transcription factors, proteins that facilitate transcription of DNA into mRNA or, alternatively, may attract repressors of transcription (Bird 2002).

Epigenetic mechanisms play a role in a plenty of processes such as cellular differentiation (Hsieh & Gage 2005), inactivation of specific genes, transposons (DNA sequences that can change their position or multiply across the genome; Miura et al. 2001) and viral DNA/RNA (Raja et al. 2008).

4. Technical means for the study of DNA methylation

The technically easiest procedure for the identification and quantification of cytosine methylation in the genome

is the methylation-sensitive amplification polymorphism (MSAP) technique, which is a modification of the widely used amplified fragment length polymorphism (AFLP) method. AFLP is based on DNA cleaving with a pair of restriction endonucleases (enzymes searching DNA for a particular sequence motif and cleaving it where the motif is found), ligation of short oligonucleotides (adaptors) at the ends of the formed fragments and amplification of fragments by polymerase chain reaction (PCR). MSAP replaces frequent-cutter enzyme from AFLP with a pair of restriction enzymes with different sensitivity to cytosine methylation, HpaII and MspI both targeting identical recognition sequence (CCGG). Both of these enzymes can cut a non-methylated site, while only MspI is able to cut the DNA if the inner cytosine is methylated (C^mCCGG), either on both sides or one side of the double-stranded DNA whereas HpaII is able to cleave sites where the outer cytosine on only one strand is methylated (^mCCGG). Difference in the presence or absence of a particular fragment in samples treated by either endonuclease allows thus assessing the methylation status of the CCGG sequence on its end.

MSAP can be used on any species without prior knowledge of its genome, it covers the whole genome as the fragment positions are randomly distributed across the genome, and is relatively cost-effective. On the other hand, it screens anonymous loci, which cannot be associated with known genes or identify new genes, except when sequencing of fragments is performed *post hoc*. Moreover, some MSAP patterns are either questionable or cannot distinguish methylation change from a genetic mutation (Fulneček & Kovařík 2014). Also, MSAP is quite sensitive to technical imperfections and it is sometimes difficult to standardize the results.

There are several alternatives to detect DNA methylation. Bisulfite sequencing uses a series of chemical reactions to convert unmethylated cytosines to uracil, which is then replaced by thymine during the PCR reactions. Samples treated and untreated with bisulfite ions are then sequenced and compared to obtain the exact methylation information. This method requires DNA sequencing making it more complicated and expensive than MSAP; in spite of this, it has currently become a standard for epigenetic studies, especially in model organisms. Alternatively, the standard restriction enzymes used in MSAP can be replaced by MseI + Acc65I/KpnI (recognition sequence GGTACC) that has easier interpretation in regards to methylation than the HpaII/MspI pair used in MSAP (Chwedorzewska & Bednarek 2011). The methylation-sensitive restriction enzyme polymerase chain reaction (MSRE-PCR) and the methylation-dependent restriction enzyme PCR (MDRE-PCR) use restriction enzymes sensitive to or dependent on methylation (just like those used in MSAP) to cleave the DNA and subsequently attempt to amplify particular loci (for example candidate genes) with PCR, failing if the DNA between the primers has been cut, which in turn depends

on the methylation of the restriction site. MSRE-PCR can use a variety of available restriction enzymes, including HpaII, Hin6I, NotI or HhaI (Melnikov et al. 2005; Oakes et al. 2006). MDRE-PCR uses enzyme McrBC that cleaves R^mC(N₄₀₋₃₀₀₀)R^mC sites (R = G or A). The recognition site of McrBC is a bit more tricky, it requires two R^mC (i.e. G^mC or A^mC) half-sites separated by 40 to 3000 nucleotides (55 to 103 nucleotides are optimal). McrBC cuts the DNA near one of the half-sites, but it is not defined which one (Stewart et al. 2000), therefore it is important to have both half-sites located within the region that is to be amplified. MSRE-PCR and MDRE-PCR are also able to take advantage of the real-time PCR that further simplifies and speeds up the process of analysis (Oakes et al. 2006).

Direct sequencing of base modifications in single-molecule next-generation sequencers is expected to become common in the future. Currently only PacBio R instruments from Pacific Biosciences and nanopore instruments from Oxford Nanopore Technologies are useable in this way (Flusberg et al. 2010; Murray et al. 2012; Schreiber et al. 2013). However, such analysis will be hard to apply to trees, generally having large genomes.

5. Hitherto knowledge of epigenetic variation in trees

Epigenetics was suggested to be one of the mechanisms underlying phenotypic plasticity, i.e., the capability of a single genotype to be expressed in multiple phenotypes depending from the environment (Bossdorf et al. 2008; Jablonka and Raz 2009; Kramer et al. 2017). In forest trees as long-lived organisms with complex life cycles exposed to environmental fluctuations over their long lifetimes, plasticity is of utter importance for their survival and adaptation to rapidly changing climate conditions (Rehfeldt et al. 1999; Rohde and Junttila 2008).

The relation between epigenetics and phenotype in trees is an under-explored area, although first studies in this field exist. Bräutigam et al. (2013) provided an excellent review of various aspects of epigenetic in forest trees. Here we mention only those relevant in terms of responses of trees to environmental signals.

In the case of carryover effects associated with the climate and photoperiod during embryogenesis, a number of possible epigenetic mechanisms, including DNA methylation, were theorized to be responsible. Johnsen et al. (2005a) mentioned unpublished data suggesting that plants from warmer environment had higher levels of the overall DNA cytosine methylation. Yakovlev et al. (2010) found and sequenced 16 micro-RNAs that showed different transcription levels between cold-environment and warm-environment Norway spruce individuals. They also confirmed that these miRNAs indeed affect transcription levels of their predicted target genes.

In angiosperms, most evidence for epigenetic effects on phenotypic traits is available in poplars and eucalypts. In poplar cuttings of the same genotype obtained from different geographic locations, subsequently grown under common environmental conditions, and exposed to drought stress, Raj et al. (2011) observed differences in genome-wide DNA methylation levels and transcriptome composition related to climate conditions, in which parental trees were growing. Genotypic variation for both DNA methylation and yield-related traits and a relationship between them was observed in Euramerican black poplar hybrids (Gourcilleau et al. 2010). DNA methylation may be a mechanism of gene expression regulation in poplar in response to drought stress (Hamanishi & Campbell 2011). A functional link between an epigenetic mark and variation in cellulose content was discovered in eucalypts (Thumma et al. 2009). As for the other genera, Gugger et al. (2016) found an association between specific methylated sites and climatic variables in *Quercus lobata*.

There is also abundant evidence for the participation of DNA methylation or covalent modifications of histones in developmental processes and ontogeny (Fraga et al. 2002; Santamaria et al. 2009; Valledor et al. 2007); however, in this case the durability of epigenetic marking and its transferability across generations is questionable.

6. Implications for forestry practice?

The example of the translocation of conifer seed orchards in Norway clearly demonstrates that the current forestry practices and legislation largely ignore the issue of epigenetics. The current paradigm from which all practical measures are derived is that of classical quantitative genetics: tree phenotype results from the interaction between genotypic and environmental effects, where genotype and environment are independent. Genes remain the same wherever a tree naturally grows or is planted, and conversely, climate, soil, surrounding biota etc. are not affected by tree's genes. Consequently, the location of seed sources or nurseries does not matter, wherever basic materials are situated or wherever forest reproductive materials (FRM) are produced, their genetic structures remain unaffected. The problem of this view is that even though it has been traditionally and successfully applied in breeding, it is quite mechanistic. Indeed, environment cannot change nucleotide sequence in a gene (except for environment-induced mutations, but these are commonly rare in a typical forest environment, and are random, thus may be detrimental, neutral or beneficial). Therefore, neither the European legislation (Directive 1999/105/EC on the marketing of forest reproductive material) nor national legislations set any restrictions on the location of basic materials or growing plants. In fact, the EC directive prohibits setting such restrictions. Any forest company is allowed to estab-

lish a seed orchard or clonal collection at any place of their choice, any nursery is allowed to grow reproductive materials of any origin, and no state is authorized to set legal restrictions on marketing of such materials, provided it comes from approved sources. The underlying logic is that it is only the genes contained in the reproductive materials, which decide about its future behavior. The thing is, the way from the genetic information contained in a gene to the gene-controlled phenotypic trait is long and rarely simple. To become effective, the gene needs to be translated into a polypeptide, which needs then to fold and sometimes to be chemically modified to become a functional protein. For phenotypic expression, not only the quality of a gene product is important (although even here must be reminded that due to alternative splicing and posttranslational modifications a single gene may result in multiple functionally differing proteins). The when and where in the plant's body the protein is produced, and how much of it is produced, is also important. Environment can exert essential effects on timing, location and intensity of gene expression, and these effects can be persistent, even heritable. This is the basis of the epigenetic memory described above, and implies risks, which are not at all considered in the legislation on FRM. On a positive note, epigenetic phenomena may allow for a rapid adjustment of forest tree populations to environmental changes. We deliberately avoid using the term 'adaptation' in this context, as this term is commonly used for changes of allelic structures through natural selection in response to environmental pressures. The capacity of a population to adjust phenology (and potentially other adaptive traits) to local climate and photoperiod as described by Skrøppa et al. (2010) is relevant in the context of climate change: even when the adult trees will be damaged by climatic stress, the offspring generation may already be able to cope with the new climate. Close-to-nature forestry, leaving the broadest space for natural processes, may thus be a viable complementary strategy to assisted migration in mitigation of climate-change effects.

So, returning to the question in the title: does the discovery of epigenetics mean a victory for what was called "Michurinian biology"? Not at all. Even though the mainstream science is known to get the things wrong sometimes, the attitude of Lysenko and his followers was equivalent to that of the present-day climate-change skeptics: highlighting weak points in established theory is fully legitimate but ignoring scientific evidence and even denying everyday experience is not. Mendelian genetics and molecular biology proved their validity. On the other hand, Michurinian biology pointed out to several interesting phenomena (inheritance of environmentally induced traits is just one of them, cf. Flegr 2002), which are fully compatible with genetics and molecular biology but remained largely ignored by biologists and have been (still are) considered irrelevant in agricultural

and forestry sciences. The problems resulting from seed orchard translocation clearly demonstrate that dogmatic approaches to biological problems are detrimental whatever authority they rely on.

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References

- Bird, A., 2002: DNA methylation patterns and epigenetic memory. *Genes & Development*, 16:6–21.
- Bossdorf, O., Richards, C. L., Pigliucci, M., 2008: Epigenetics for ecologists. *Ecology Letters*, 11:106–115.
- Bräutigam, K., Vining, K. J., Lafon-Placette, C., Fossdal, C. G., Mirouze, M., Marcos, J. G. et al., 2013: Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecology and Evolution*, 3:399–415.
- Brenet, F., Moh, M., Funk, P., Feierstein, E., Viale, A. J., Socci, N. D. et al., 2011: DNA methylation of the first exon is tightly linked to transcriptional silencing. *PLoS ONE*: e14524
- Chan, S. W., Henderson, I. R., Jacobsen, S. E., 2005: Gardening the genome: DNA methylation in *Arabidopsis thaliana*. *Nature Reviews Genetics*, 6:351–360.
- Chwedorzewska, K. J., Bednarek, P. T., 2011: Genetic and epigenetic studies on populations of *Deschampsia antarctica* Desv. from contrasting environments on King George Island. *Polish Polar Research*, 32:15–26.
- Dormling, I., Johnsen, Ø., 1992: Effects of the parental environment on full-sib families of *Pinus sylvestris*. *Canadian Journal of Forest Research*, 22:88–100.
- Flegr, J., 2002: Was Lysenko (partly) right? Michurinist biology in the view of modern plant physiology and genetics. *Rivista di Biologia*, 95:258–72.
- Flusberg, B. A., Webster, D., Lee, J., Travers, K., Olivares, E., Clark, T. A. et al., 2010: Direct detection of DNA methylation during single-molecule real-time sequencing. *Nature Methods*, 7:461–465.
- Fraga, M. F., Rodriguez, R., Canal, M. J., 2002: Genomic DNA methylation-demethylation during aging and reinvigoration of *Pinus radiata*. *Tree Physiology*, 22:813–816.
- Fulneček, J., Kovařík, A., 2014: How to interpret Methylation Sensitive Amplified Polymorphism (MSAP) profiles? *BMC Genetics*, 15:2.
- Gömöry, D., Foffová, E., Longauer, R., Krajmerová, D., 2015: Memory effects associated with the early-growth environment in Norway spruce and European larch. *European Journal of Forest Research*, 134:89–97.

- Gourcilleau, D., Bogeat-Triboulot, M. B., Le Thiec, D., Lafon-Placette, C., Delaunay, A., El-Soud, W.A. et al., 2010: DNA methylation and histone acetylation: genotypic variations in hybrid poplars, impact of water deficit and relationships with productivity. *Annals of Forest Sciences*, 67:208.
- Greenwood, M. S., Hutchison, K. W., 1996: Genetic after effects of increased temperature in *Larix*. In: Hom, J., Birdsey, R., O'Brian, K. (eds.): Proceedings of the 1995 Meeting of the Northern Global Change Program, USDA Forest Service report, Radnor, p. 56–62.
- Gugger, P. F., Fitz-Gibbon, S., Pellegrini, M., Sork, V. L., 2016: Species-wide patterns of DNA methylation variation in *Quercus lobata* and their association with climate gradients. *Molecular Ecology*, 25:1665–1680.
- Hamanishi, E. T., Campbell, M. M., 2011: Genome-wide responses to drought in forest trees. *Forestry*, 84:273–283.
- Hashimoto, H., Vertino, P. M., Cheng, X., 2010: Molecular coupling of DNA methylation and histone methylation. *Epigenomics*, 2:657–669.
- Hsieh, J., Gage, F. H., 2005: Chromatin remodelling in neural development and plasticity. *Current Opinion in Cell Biology*, 17:664–671.
- Jablonka, E., Raz, G., 2009: Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *The Quarterly Review of Biology*, 84:131–176.
- Johnsen, Ø., 1989: Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard. I. Frost hardiness in a phytotron experiment. *Scandinavian Journal of Forest Research*, 4:317–330.
- Johnsen, Ø., Dæhlen, O. G., Østreg, G., Skråppa, T., 2005b: Daylength and temperature during seed production interactively affect adaptive performance of *Picea abies* progenies. *New Phytologist*, 168:589–596.
- Johnsen, Ø., Fossdal, C. G., Nagy, N., Mølmann, J., Dæhlen, O. G., Skråppa, T., 2005a: Climatic adaptation in *Picea abies* progenies is affected by the temperature during zygotic embryogenesis and seed maturation. *Plant, Cell and Environment*, 28:1090–1102.
- Kramer, K., Ducouso, A., Gömöry, D., Hansen, J.K., Ionita, L., Liesebach, M. et al., 2017: Chilling and forcing requirements for foliage bud burst of European beech (*Fagus sylvatica* L.) differ between provenances and are phenotypically plastic. *Agricultural and Forest Meteorology*, 234:172–181.
- Maunakea, A. K., Chepelev, I., Cui, K., Zhao, K., 2013: Intragenic DNA methylation modulates alternative splicing by recruiting MeCP2 to promote exon recognition. *Cell Research*, 23:1256–1269.
- Melnikov, A. A., Gartenhaus, R. B., Levenson, A. S., Motchoulskaia, N. A., Levenson, V. V., 2005: MSRE-PCR for analysis of gene-specific DNA methylation. *Nucleic Acid Research*, 33: e93
- Miura, A., Yonebayashi, S., Watanabe, K., Toyama, T., Shimada, H., Kakutani, T., 2001: Mobilization of transposons by a mutation abolishing full DNA methylation in *Arabidopsis*. *Nature*, 411:212–214.
- Murray, I. A., Clark, T. A., Morgan, R. D., Boitano, M., Anton, B. P., Luong, K. et al., 2012: The methylomes of six bacteria. *Nucleic Acids Research*, 2012:1–13.
- Neumann, B., Barlow, D. P., 1996: Multiple roles for DNA methylation in gametic imprinting. *Current Opinion in Genetics & Development*, 6:159–163.
- Oakes, C. C., La Salle, S., Robaire, B., Trasler, J. M., 2006: Evaluation of a quantitative DNA methylation analysis technique using methylation-sensitive/dependent restriction enzymes and real-time PCR. *Epigenetics*, 3:146–152.
- Raj, S., Bräutigam, K., Hamanishi, E. T., Wilkins, O., Schroeder, W., Mansfield, S. D. et al., 2011: Clone history shapes *Populus* drought responses. Proceedings of the National Academy of Sciences of the United States of America, 108:12521–12526.
- Raja, P., Sanville, B. C., Buchmann, C., Bisaro, D. M., 2008: Viral genome methylation as an epigenetic defense against geminiviruses. *Journal of Virology*, 82:8997–9007.
- Rehfeldt, G. E., Tchebakova, N. M., Parfenova, Y. I., Wykoff, W. R., Kuzmina, N. A., Milyutin, L. L., 2002: Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology*, 8:912–929.
- Rohde, A., Junntila, O., 2008: Remembrances of an embryo: long-term effects on phenology traits in spruce. *New Phytologist*, 177:2–5.
- Santamaria, M. E., Hasbun, R., Valera, M. J., 2009: Acetylated H4 histone and genomic DNA methylation patterns during bud set and bud burst in *Castanea sativa*. *Journal of Plant Physiology*, 166:1360–1369.
- Schreiber, J., Wescoe, Z. L., Abu-Shumays, R., Vivian, J. T., Baatar, B., Karplus, K. et al., 2013: Error rates for nanopore discrimination among cytosine, methylcytosine, and hydroxymethylcytosine along individual DNA strands. Proceedings of the National Academy of Sciences of the United States of America, 47:18910–18915.
- Skråppa, T., Tollefsrud, M., Sperisen, C., Johnsen, Ø., 2010: Rapid change in adaptive performance from one generation to the next in *Picea abies* – Central European trees in a Nordic environment. *Tree Genetics and Genomes*, 6:93–99.
- Soppe, W. J. J., Jasencakova, Z., Houben, A., Kakutani, T., Meister, A., Huang, M.S. et al., 2002: DNA methylation controls histone H3 lysine 9 methylation and heterochromatin assembly in *Arabidopsis*. *The EMBO Journal*, 23:6549–6559.
- Soyfer, V. N., 2011: Stalin and fighters against cellular theory. *Studies in the History of Biology*, 3:82–96.
- Stoehr, M. U., L'Hirondelle, S. J., Binder, W. D., Webber, J. E., 1998: Parental environment after effects on germination, growth, and adaptive traits in selected spruce families. *Canadian Journal of Forest Research*, 28:418–426.

- Suzuki, M. M., Bird, A., 2008: DNA methylation landscapes: provocative insights from epigenomics. *Nature Reviews Genetics*, 9:465–476.
- Thumma, B. R., Matheson, B. A., Zhang, D., Meeske, C., Meder, R., Downes, G. M. et al., 2009: Identification of a cis-acting regulatory polymorphism in a Eucalypt COBRALike gene affecting cellulose content. *Genetics*, 183:1153–1164.
- Turner, B. M., 2000: Histone acetylation and an epigenetic code. *Bioessays*, 22:836–845.
- Valledor, L., Hasbún, R., Meijón, M., 2007: Involvement of DNA methylation in tree development and micropropagation. *Plant Cell Tissue and Organ Culture*, 91:75–86.
- Vanyushin, B. F., 2005: Adenine methylation in eukaryotic DNA. *Molecular Biology*, 39:473–481.
- Webber, J., Ott, P., Owens, J., Binder, W., 2005: Elevated temperature during reproductive development affects cone traits and progeny performance in *Picea glauca* – *engelmannii* complex. *Tree Physiology*, 25:1219–1227.
- Wu, T. P., Wang, T., Seetin, M. G., Lai, Y. Q., Zhu, S. J., Lin, K. X. et al., 2016: DNA methylation on N6-adenine in mammalian embryonic stem cells. *Nature*, 532:329–333.
- Yakovlev, I. A., Fossdal, C. G., Johnsen, Ø., 2010: MicroRNAs, the epigenetic memory and climatic adaptation in Norway spruce. *New Phytologist*, 187:1154–1169.

Succession of ground beetle (Coleoptera: Carabidae) communities after windthrow disturbance in a montane Norway spruce forest in the Hrubý Jeseník Mts. (Czech Republic)

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Abstract

Wind disturbances are a key factor that is significantly involved in the life cycle of natural boreomontane coniferous forests. As most of these forests are currently intensively managed, we have limited knowledge on succession following natural disturbance. Succession in a Norway spruce stand after a windthrow event was studied using ground beetles as model bioindication taxa in the Hrubý Jeseník Mts. (Czech Republic). The study documented that the composition of ground beetle communities was significantly associated with stand age and its microclimatic parameters (particularly the minimal temperature and average and minimal humidity). Forest species including prey specialists, hygrophilous species, as well as habitat generalists were the most abundant in the mature stand, where the forest had the highest humidity and the least profound minimal temperatures. In contrast, open-habitat species, including euryoecious species and relict species of higher elevations, reached their highest abundances in clearing shortly after the windthrow. In clearing the humidity was lower and the temperature fluctuated significantly (the lowest minimal temperatures). Ground beetles, including forest species, were the least abundant in young stands (10 and 20 years after windthrow). We conclude that old stands are of particular importance because they harbour the highest abundance and diversity of ground beetles with various ecological requirements. Natural wind disturbances are important as well since they increase diversity by enabling the occurrence of many non-forest species. Hence, a mosaic of stands of different ages with a sufficient proportion of old stands should be maintained when managing montane coniferous forests.

Key words: forest stand development; microclimate; multivariate analysis, windstorm

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1. Introduction

Natural disturbances, such as windthrows, are key factors in the process of regeneration in continuity of coniferous temperate and boreal forests (Peterken 1996). As trees are broken or uprooted and open tree-fall gaps arise, the stable conditions of shady forest ecosystems are disrupted. Tree-fall gaps are characterised by bare patches of mineral soil, high amounts of dead wood, and increased sunlight reaching the forest floor. Thus, windthrows are followed by important changes in microclimate, ground structural heterogeneity and vegetation. These changes significantly affect the invertebrate fauna (Bouget & Duelli 2004).

Ground beetles (Carabidae) as a model bioindication group (Rainio & Niemelä 2003) are among the most studied invertebrates, and thus the succession of their

communities within the traditional forest management cycle from clear-cutting (i.e., artificial disturbance) to mature stands is also well studied (e.g., Butterfield 1997; Koivula et al. 2002; Magura et al. 2003; Purchart et al. 2013). In general, changes in ground beetle communities after natural disturbances (e.g., windthrows) are insufficiently studied (Skłodowski & Garbalińska 2007). However, some studies dealing with this topic have been conducted in the Alps (Duelli et al. 2002; Winter et al. 2015), northern Poland (Skłodowski & Garbalińska 2007), the Tatra Mountains (Urbanovičová et al. 2010; Šustek & Vido 2013) and North America (Gandhi et al. 2008). The results of these studies can be summarised into three main outcomes: i) windthrows are followed by decreased abundances of forest species, ii) tree-fall gaps are characterised by the occurrence of species specific to open habitats, and iii) changes in temperature

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and humidity are considered to be the most significant factors driving ground beetle community succession in these studies.

Although climatic factors (above all, temperature and humidity) are considered to substantially affect the succession of ground beetle communities after windthrows (see above), the exact relationships between changes in climatic factors and beetle succession were not addressed in the aforementioned studies. In addition, a majority of these studies were carried out in mountains, where climatic factors largely limit insect survival (Mani 1968). Therefore, the present study investigates the effects of selected forest stand characteristics and climatic factors on communities of ground beetles in a montane coniferous forest after windthrow. The following hypotheses were tested: i) ground beetle species composition and abundance are affected by forest disturbance by windthrow and its following regeneration and ii) ground beetle species composition and abundance are affected by habitat temperature and humidity. Both hypotheses were tested at the community, ecological guild and species levels. Based on our obtained results, we suggest implications for forestry management.

2. Methods

2.1. Study site

The study area is located in northern Moravia (the Czech Republic) in the Jeseníky Protected Landscape Area, and is 2 km east of Praděd Mt. (1492 m a. s. l.), near the Kamzičí chata cottage, at an elevation of 1200 – 1220 m a. s. l. (50.0820747N, 17.2619078E). The locality is situated in a seminatural montane spruce forest. The climate is cold, with a mean temperature of 1.9 °C, the long-term annual average rainfall is 1100 – 1200 mm, and snow cover lasts approximately 180 days, typically from November to early May (Quitt 1971).

We sampled four stands of different ages with areas ranging 2 – 5 ha, each stand representing a different stage of succession of spruce forest after windthrow of a mature stand: i) clearing 3 years after the event (hereafter “3”), ii) stand approximately 10 years after the event, young growth (“10”), iii) stand approximately 20 years after the event, young stand (“20”), iv) stand approximately 90 years old, mature stand (“90”). Following windthrow, the surviving trees (a few trees per ha) were kept in situ, but a majority of the dead wood caused by the windthrows or bark beetles was removed from the stands. As a result, a low amount of coarse dead wood was present in the studied stands. The studied stands were established by natural regeneration following the windstorm events, which was supported by artificial regeneration. The study stands were dominated by Norway spruce (*Picea abies* [L.] H. Karst.) (90%) with dispersed individuals of rowan (*Sorbus* sp.), European beech (*Fagus sylvatica* L.) and birch (*Betula pendula* Roth.).

2.2. Field sampling and variable measurement

Ground beetles were sampled using pitfall traps (8 cm in diameter, 15 cm deep, one-third filled with a 4% formaldehyde solution), a standard method used to sample epigeic invertebrates (Spence & Niemelä 1994). In each study stand, 8 traps were installed in a line at a spacing of 10 m. The trap lines were located in the centres of the study stands, and no trap was closer than 10 m from the stand edge. In total, 32 traps were used. The pitfall traps were exposed from 30. 5. to 16. 10. 2011 and were emptied at approximately three-week interval (21. 6., 9. 7., 27. 7., 14. 8., 1. 9., 19. 9. and 16. 10. 2011). Each sample was preserved in 95% ethanol. All ground beetles were identified to the species level using keys (Hůrka 1996). The used nomenclature follows de Jong (2012).

Additionally, one datalogger (Votcraft DL-120TH) was installed in the middle of each study stand and was active during the whole period of beetle trapping. Dataloggers were mounted 10 cm above the ground in a shaded location. The dataloggers recorded the following climatic characteristics: minimal daily temperature (hereafter “Tmin”), average daily temperature (“Tave”), maximal daily temperature (“Tmax”), minimal daily humidity (“Hmin”) and average daily humidity (“Have”).

2.3. Data analysis

Prior to data analysis, the number of individuals of each species per sample was converted to the number of individuals per sampling day (relative abundance) to remove possible bias caused by the slightly uneven lengths of the trap exposure intervals. For each interval of trap exposure, the mean values of the explanatory climatic variables (Tmin, Tave, Tmax, Hmin, Have) were calculated and coded as continuous variables.

To relate gradients in species composition and abundance to the studied predictors and to test the importance of these predictors, a canonical correspondence analysis (CCA) was used (ter Braak & Šmilauer 2002), which is appropriate for data with a larger gradient length (the gradient length was previously examined by detrended correspondence analysis (DCA)). The data were standardised and centred by sample, and a Monte Carlo permutation test was used (2000 permutations). All the explanatory variables (i.e., climatic variables and stand age) were treated as continuous variables. The four sampled stands (i.e., 3, 10, 20, 90) were treated as supplementary variables in the analysis. A forward selection procedure was used to test environmental variables. Since ground beetle communities are strongly affected by phenology (Rainio & Niemelä 2003), we treated the date of sample collection (coded as an ordinal week of the year) as a covariate.

Subsequently, we used generalised linear models (GLMs) with a Poisson distribution and log link function to separately assess the impact of selected single fac-

tors on particular species. The most significant factors according to the results of CCA were selected, which were stand age, Tmin and Have. Only species with at least 5 specimens recorded were tested by GLM. All these analyses were conducted using CANOCO, v. 4.5. (ter Braak & Šmilauer 2002).

Furthermore, we also studied differences in the abundance of particular ecological guilds of ground beetles among the various stages of forest succession. All species were divided into three guilds according to their habitat association: forest specialist, open-habitat specialist or habitat generalist (Hůrka 1996; Kašák et al. 2015). Since the resulting data on guild abundances did not exhibit a normal distribution (Shapiro-Wilk test), non-parametric Kruskal-Wallis (K–W) tests supplemented with box and whisker plots were used (Hollander & Wolfe 1999). These tests were performed in Statistica 10.0 (StatSoft 2013).

3. Results

In total, 2703 individuals of ground beetles belonging to 31 species were recorded. The most abundant species were *Carabus linnaei*, with 792 individuals, followed by *Carabus auronitens*, *C. sylvestris*, *C. violaceus*, *Pterostichus unctulatus* and *Trechus striatulus*, all with more than 100 specimens sampled. Among the others, several relict species, indicating naturally rich sites, were recorded: *Amara erratica*, *Cychrus attenuatus* and *Pterostichus rufitarsis cordatus*. The sampled ground beetle communities consisted of three different beetle guilds: a) forest species that predominated in the community (18 species represented by 1925 individuals), b) generalists (7 species represented by 455 individuals) and c) open-habitat species (6 species represented by 323 individuals). The numbers of species recorded in the different studied stands were similar, but the abundances of individuals differed remarkably: stand 90 – 1717 individuals/20 species; stand 20 – 228/19; stand 10 – 261/20; stand 3 – 497/23.

3.1 Community pattern of ground beetles

The CCA model revealed that the composition of ground beetle communities was significantly associated with stand age and climatic factors (Table 1, Fig. 1.). Among the tested factors, stand age exhibited the highest explanatory power (Table 1). The most important climatic factors were minimal temperature and average and minimal humidity (Tmin, Have and Hmin).

The longest gradient of species data in the CCA plot (Fig. 1) can be seen along the horizontal canonical axis and corresponds to the environmental changes from young stands to mature stands with a more stable microclimatic environment and higher minimal temperature and humidity. The forest species typical of mature stands

(*Calathus micropterus*, *Carabus auronitens*, *C. glabratus* and *C. linnaei*) predominated on the left side of the plot, whereas habitat generalists and open-habitat species (*Amara lunicollis*, *Carabus violaceus*, *Leistus ferrugineus*, *Notiophilus palustris*, etc.) were bound to the right side of the plot. Simultaneously, hygrophilous species (*Patrobus atrorufus*, *Trechus striatulus* and *T. splendens*) were associated with the left side of the plot, whereas euryoecious species tolerant of dry conditions (*Bembidion lampros*, *B. quadrimaculatum* and *Leistus ferrugineus*) were shown on the right side of the plot. Further, relict species from higher altitudes (*Amara erratica* and *Carabus sylvestris*) that are usually bound to nearby alpine habitats were also positioned on the right side of the plot.

Table 1 Results of canonical correspondence analysis. Effect of age of spruce stands and abiotic variables on communities of ground beetles.

Variable	F	Explained variability [%]
Age	11.21***	6.15
Tmin	2.06**	5.46
Have	2.25**	5.12
Hmin	2.98***	4.12
Tave	1.12 ^{ns}	4.09
Tmax	0.91 ^{ns}	2.56

^{ns}not significant; *** p < 0.001; ** p < 0.01; * p < 0.05

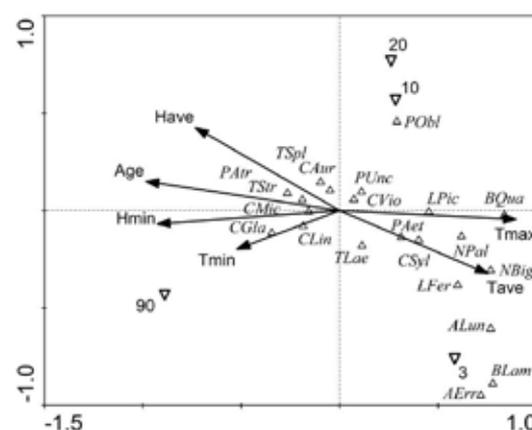


Fig. 1. Canonical correspondence analysis – triplot of associations between ground beetle occurrence in montane Norway spruce forest of Hrubý Jeseník Mts. and environmental variables (stand age and climatic variables), with supplementary environmental variables (the sampled 3-, 10-, 20- and 90-year-old stands) shown. Environmental variables are denoted as filled black arrows, supplementary (passive) variables are denoted as open downward pointing triangles. Only species with fit range > 2% are depicted in the ordination plot. The beetle species are denoted by open upward pointing triangles with corresponding abbreviations: *Amara erratica* (AErr), *Amara lunicollis* (ALun), *Bembidion lampros* (BLam), *Bembidion quadrimaculatum* (BQua), *Calathus micropterus* (CMic), *Carabus auronitens* (CAur), *Carabus glabratus* (CGLa), *Carabus linnaei* (CLin), *Carabus sylvestris* (CSyl), *Carabus violaceus* (CVio), *Leistus ferrugineus* (LFer), *Leistus piceus* (LPic), *Notiophilus biguttatus* (NBig), *Notiophilus palustris* (NPal), *Patrobus atrorufus* (PAtr), *Pterostichus aethiops* (PAet), *Pterostichus oblongopunctatus* (PObl), *Trechus splendens* (TSpl), *Trechus striatulus* (TStr), *Trichotichnus laevicollis* (TLae).

3.2. Responses of specific groups of ground beetles to stand age

The results of the K–W tests revealed that the abundance of ground beetle guilds differed significantly among stands of different ages (Fig. 2). The biggest differences were found in the occurrence of the guild of forest species, which reached its highest abundance by far in the mature 90-year-old stand. Open-habitat ground beetles were the most abundant in the youngest 3-year-old stand, less abundant in the mature 90-year-old stand and almost absent in the 10- and 20-year-old stands. Habitat generalists were the most abundant in the 90-year-old stand.

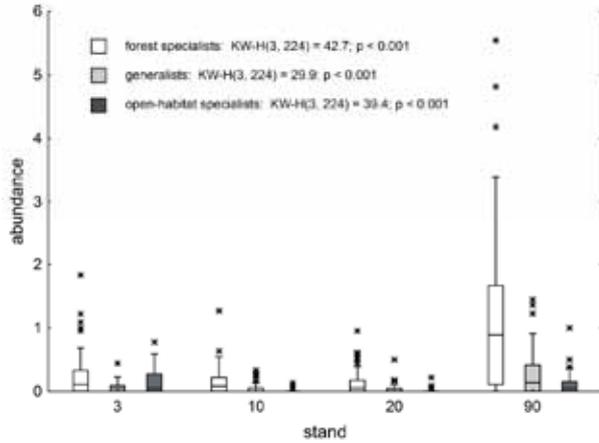


Fig. 2. Differences in abundance of three ecological guilds of ground beetles among stands in different stages of forest succession following windthrow in montane Norway spruce stand of Hrubý Jeseník Mts. On the x axis is age of stand in years. The box and whisker plots are composed of outliers (asterisks), non-outlier ranges (whiskers), lower and upper quartiles (boxes) and medians (middle lines). Results of Kruskal-Wallis tests are shown as well.

3.3. Responses of ground beetle species to stand characteristics

Using GLM analyses, the occurrences of 19 species of ground beetles were found to be significantly affected by at least one of the tested habitat factors (Table 2). Specifically, 18 species responded significantly to stand age (12 increased in abundance, 6 decreased), 12 were affected by the minimal temperature (all increased), and 12 varied in abundance according to the average humidity (9 increased, 3 decreased).

Thus, typical forest ground beetles increased in abundance in stands of higher age, which was particularly remarkable in the case of species of the genus *Carabus* and food specialists that prey on molluscs, such as *Cychrus caraboides* and *C. attenuates* (Table 2). In contrast, the abundance of open-habitat species (*Amara* spp. and *Carabus sylvestris*) and some euryoecious species (e.g., *Leistus ferrugineus* and *Notiophilus palustris*) that are associated with disturbed open habitats, such

Table 2. Results of generalised linear model analyses for beetles and their responses to different features of spruce stands.

Species	N	Age			Tmin			Have		
		Intercept	Slope	AIC	Intercept	Slope	AIC	Intercept	Slope	AIC
<i>Amara lunicollis</i>	6	-14	-0.06	1.45	1.12	0.14	2.43	-13.29	0.61	2.05
<i>Calathus micropterus</i>	90	1.8	1.05	11.55	2.96	0.86	13.96	9.96	0.82	14.51
<i>Carabus aurantiens</i>	123	1.3	1.69	15.91	4.09	1.01	16.87	10.72	1	18.16
<i>Carabus glabratus</i>	6	12.44	0.09	1.63	2.59	0.22	2.51	22.94	0.34	2.36
<i>Carabus linnaei</i>	792	1.94	5.18	76.12	5.17	2.74	96.42	10.02	2.45	109.24
<i>Carabus sylvestris</i>	312	-0.34	-0.87	35.46	1.46	1.26	33.98	-3.43	-0.94	35.41
<i>Carabus violaceus</i>	164	0.52	0.95	18.62	2.67	1.11	17.11	2.43	0.38	19.47
<i>Cychrus attenuatus</i>	7	12.66	0.09	1.75	19.77	0.44	2.26	7.44	0.19	2.81
<i>Cychrus caraboides</i>	15	1.41	0.63	3.78	5.96	0.39	3.8	15.63	0.43	3.96
<i>Leistus ferrugineus</i>	13	-2.17	-0.74	3.71	-0.91	-0.35	4.43	-14.3	-1	3.55
<i>Leistus piceus</i>	31	-0.98	-0.74	7.41	0.14	0.06	8.05	-5.65	-0.54	7.79
<i>Notiophilus biguttatus</i>	10	-13.48	-0.1	1.66	-0.17	-0.05	3.27	-12.68	-0.77	2.67
<i>Notiophilus palustris</i>	10	-1.68	-0.57	2.96	0.27	0.06	3.44	-8.72	-0.5	3.24
<i>Patriobis atrovirus</i>	17	3.52	0.75	3.07	6.57	0.41	4.84	16.87	0.49	5.07
<i>Pterostichus aethiops</i>	5	-0.48	-0.15	1.77	1.16	0.13	1.77	-6.12	-0.22	1.75
<i>Pterostichus diligens</i>	13	0.04	0.02	4.68	1.14	0.40 ^{ns}	4.56	6.8	0.23	4.59
<i>Pterostichus oblongopunctatus</i>	80	0.18 ^{ns}	0.15	13.57	0.64	1.81	13.43	5.27	0.49	13.29
<i>Pterostichus rufitarsis</i>	17	0.03 ^{ns}	0.05	4.72	0.26	0.07	4.71	-4.19	-0.27	4.64
<i>Pterostichus unctulatus</i>	615	0.73	2.39	60.34	2.29	2.04	59.41	4.97	1.28	64.86
<i>Trechus splendens</i>	91	1.53	1.58	15.11	2.79	0.85	17.28	14.6	1.02	17.13
<i>Trechus striatulus</i>	236	2.23	2.89	28.32	2.64	1.34	40.04	18.06	1.84	37.77
<i>Trichotichnus laevicollis</i>	37	0.35	0.3	8.38	2.29	0.52	7.95	-2.77	-0.26	8.35

^{ns} not significant; ** p < 0.01; *** p < 0.001; p-values in bold are significant at $\alpha \leq 0.05$; positive responses of species to the tested environmental variables are highlighted by a grey background.

as windthrow gaps, decreased in stands of higher age. Increasing humidity was associated with higher abundances of hygrophilous species of the genus *Trechus* and some forest species of the genus *Carabus*.

4. Discussion

Our results confirm that windstorm events in Norway spruce mountain forest and subsequent forest regeneration and succession are associated with dramatic changes in ground beetle communities. Among the tested factors, stand age (i.e., time elapsed after windthrow event), minimal temperature and average humidity affected ground beetles the most significantly (Table 1). In general, the abundance of forest species increased with an increase in the age of the stand. However, this increase is likely not linear but instead commences later in succession because the abundances of forest species were even slightly lower in 10- and 20-year-old stands (Fig. 2). Thus, forest ground beetles, as well as ground beetles in total, reached maximal abundances in the mature 90-year-old stand, which was characterised by the highest values of minimal temperature and average humidity. In contrast, open-habitat species and euryoecious species occurred most numerous in the clearing 3 years after windthrow. These results are in accordance with previous studies on carabid succession after wind disturbances (Šustek & Vido 2013; Winter et al. 2015) or during the standard forestry cycle (Magura et al. 2003).

A decrease in the abundance of forest ground beetles following windthrow or felling is explained mainly by dramatic changes in abiotic conditions (Koivula et al. 2002; Sklodowski & Garbalinska 2007). It is believed that forest ground beetles require a relatively stable microclimate (Thiele 1977). Such conditions are better maintained in mature (or undisturbed) forest stands, which protect the ground against direct sun and wind exposure due to the higher canopy closure (Sklodowski 2017). In contrast, the temperature fluctuates strongly in windthrow gaps or clear-cut areas (Chen et al. 1999), where high temperatures might be reached during a sunny day but temperatures decrease substantially at night or during a windy and cloudy day (Warren & Key 1991). In accordance, the highest minimal temperatures, reflecting the most stable microclimate, were maintained in the mature stands in the present study, where the highest abundance of forest ground beetles was also found (Fig. 1 and 2). Furthermore, our study documented the minimal temperature to be a more important climatic factor than average temperature (Table 1). Correspondingly, the survival and reproduction of animals are mostly affected by extreme values of habitat characteristics rather than by average values (Begon et al. 2006).

The aforementioned increased sun and wind exposure of the ground after windthrow or felling lead to lowered humidity (regardless of a higher total amount

of rainfall) (Ishizuka et al. 2002). Subsequently, as the canopy densifies during succession in a new forest stand, the humidity rises again, as was documented in the present study (Fig. 1), leading to increased abundances of hygrophilous forest ground beetles, such as *Trechus* spp., which were more numerous in the older stands (90 years old) in the present study (Fig. 1, Table 2). Similarly, in the present study, species of the genus *Cychrus* that feed upon molluscs (Hůrka 1996) also experienced an increase in abundance in older stands. The molluscs were previously reported to diminish after windthrow events due to lower humidity (Duelli et al. 2002). In the present study, the mature forest stand (90 years old), with the most stable climatic conditions (including a smaller range of extreme values), hosted the highest numbers of forest ground beetles as well as all ground beetles in total. Ground beetles may also prefer old stands because woody debris and litter provide shelter and preserve microhabitat conditions (Sklodowski 2016). Similar results were reported by Urbanovičová et al. (2010) in the Tatra Mts., showing the highest abundance of ground beetles in undisturbed forest stands.

Despite the substantial decrease in the abundance of forest ground beetles after windthrow, the abundance of forest ground beetles remained higher in the windthrow clearing (3 years after the event) than in slightly older (10- and 20-year-old) forest stands. This phenomenon has also been documented in other similar studies (Magura et al. 2003; Purchart et al. 2013; Sklodowski 2017), and it can be explained by the following: a) some ground beetle species (members of the genus *Carabus*) can survive several years in suboptimal habitats (Koivula et al. 2002) because their development takes several years (Hůrka 1996), and adults can live for a few years as well; b) a windthrow area might temporarily offer high numbers of prey because an open habitat with a substantial amount of freshly dead wood and an array of herbs is characterised by a high abundance of saproxylic and herbivorous invertebrates (Winter et al. 2015; Sklodowski 2017) c) temporarily increased amount of dead wood provides shelter for carabids (Sklodowski 2016; Sklodowski 2017).

Overall, the lowest abundances of forest ground beetles were recorded in 10- and 20-year-old stands in the present study (Fig. 2). Similarly, a decrease in abundance of forest ground beetles during the first half of the forest life cycle has been observed in several studies (Butterfield 1997; Magura et al. 2003; Purchart et al. 2013). This might be attributed to the fact that forest stands in this stage are usually very shady with a negligible amount of dead wood and a poorly developed herbaceous understorey (Purchart et al. 2013), so the supply of prey and shelters in such habitats is strongly limited (Taboada et al. 2008).

As expected, open-habitat ground beetle species reached their highest abundance in the clearing 3 years after windthrow, which corresponds to the results of other studies (Sklodowski & Garbalinska 2007; Gandhi

et al. 2008; Šustek & Vido 2013; Sklodowski 2017). The second highest abundance of open-habitat species was surprisingly found in the mature 90-year-old stand. This corresponds to the fact that mature montane spruce forests usually exhibit a partly open structure because their canopies are already disturbed by dieback or falling/felling of individual trees (Winter et al. 2015).

The clearing (3 years after windthrow) hosted the highest abundance of open-habitat species (*Amara* spp. and *Harpalus* spp.) and euryoecious ground beetles typical of disturbed habitats (*Bembidion lampros*, *B. quadrimaculatum*, *Leistus ferrugineus* and *Notiophilus palustris*). Several important bioindicator species, such as the boreomontane species *Amara erratica* and *Carabus sylvestris*, which are typically distributed in alpine meadows (Stanovský & Pulpán 2006), occurred in the clearing as well. Clearings after windthrows represent temporarily open habitats that can enable the reproduction of these species. Additionally, these species could easily colonise the clearing at our study site because of its proximity to alpine meadows in the Hrubý Jeseník Mts., where they are quite numerous (cf. Kašák et al. 2015).

5. Conclusion

Based on the results of the present, as well as several other studies (Magura et al. 2003; Niemelä et al. 2007), we can assume that the presence of old forest stands at a particular location is a fundamental prerequisite for the long-term survival of populations of specialised forest ground beetles. At the same time, newly regenerated forest stands after a windthrow event or felling do not become optimal for forest ground beetles until they are 60–90 years old. Therefore, montane forests should be managed to ensure that a sufficient area of mature forest stands is maintained near any clearing until the clearing becomes a middle-age-class stand. On the other hand, disturbed areas, such as windthrow clearings, support the occurrence of many non-forest species (e.g., open-habitat, euryoecious species) and thereby increase the overall diversity of ground beetles in these ecosystems. Hence, a fine mosaic of forest stands of various ages can enable the contemporary survival of many different ground beetle ecological groups and species.

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References

- Begon, M., Townsed, C. R., Harper, J. L., 2006: Ecology. From individuals to ecosystems. Blackwell Publishing, Oxford, 738 p.
- Bouget, Ch., Duelli P., 2004: The effects of windthrow on forest insect communities: a literature review. *Biological Conservation*, 118:281–299.
- Butterfield, J., 1997: Carabid community succession during the forestry cycle in conifer plantations. *Ecography*, 20:614–625.
- de Jong, Y. S. D. M. (ed.), 2012: Fauna Europaea version 2.6.
- Duelli, P., Obrist, M., Wermelinger, B., 2002: Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. *Forest Snow and Landscape Research*, 77:117–131.
- Gandhi, K. J. K., Gilmore, D. W., Katovich, S. A., Matson, W. J., Zasada, J. C., Seybold, S., 2008: Catastrophic windstorm and fuel-reduction treatments alter ground beetle (Coleoptera: Carabidae) assemblages in a North American sub-boreal forest. *Forest Ecology and Management*, 256:1104–1123.
- Hollander, M., Wolfe, D. A., 1999: Nonparametric statistical methods, 2nd edition. Wiley, New York, 816 p.
- Hůrka, 1996: Carabidae of the Czech and Slovak Republics—illustrated key. Kabourek, Zlín, 565 p.
- Hůrka, K., Veselý, P., Farkač, J., 1996: Využití střevlíkovitých (Coleoptera: Carabidae) k indikaci kvality prostředí. *Klapalekiana*, 32:15–26.
- Chen, J. Q., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosnoff, K. D., Mroz, G. D. et al., 1999: Microclimate in forest ecosystem and landscape ecology – Variation in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*, 49:288–297.
- Ishizuka, M., Ochiai, Y., Utsugi, H., 2002: Microenvironments and growth in gaps. In: Nakashizuka, M. (ed.): Diversity and interaction in a temperate forest community: Ogawa forest reserve of Japan. Springer, Tokyo, p. 229–244.
- Kašák, J., Mazalová, M., Šipoš, J., Kuras, T., 2015: Dwarf pine – invasive plant threatens biodiversity of alpine beetles. *Biodiversity and Conservation*, 10:2399–2415.
- Koivula, M., Kukkonen, Niemelä, J., 2002: Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation*, 11:1269–1288.
- Magura, T., Tóthmérész, B., Elek, Z., 2003: Diversity and composition of carabids during a forestry cycle. *Biodiversity and Conservation*, 12:73–85.
- Mani, M. S., 1968: Ecology and biogeography of high altitude insects. *Series Entomologica*, 4:1–528.
- Niemelä, J., Koivula, M., Kotze, D. J., 2007: The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *Journal of Insect Conservation*, 11:5–18.

- Peterken, G. F., 1996: Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, 540 p.
- Purchart, L., Tuf, I. H., Hula, V., Suchomel, J., 2013: Arthropod assemblages in Norway spruce monocultures during a forest cycle – A multi-taxa approach. *Forest Ecology and Management*, 306:42–51.
- Quitt, E., 1971: Klimatické oblasti Československa. Geografický ústav ČSAV, Brno, 73 p.
- Rainio, J., Niemelä, J., 2003: Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, 12:487–506.
- Sklodowski, J., Garbalińska, P., 2007: Ground beetle assemblages (Coleoptera, Carabidae) in the third year of regeneration after hurricane in the Puszcza Piska pine forests. *Baltic Journal of Coleopterologist*, 7:17–35.
- Sklodowski, J., 2016: Manual soil preparation and piles of branches can support ground beetles (Coleoptera, carabidae) better than four different mechanical soil treatments in clear-cut area of a closed-canopy pine forest in northern Poland. *Scandinavian Journal of Forest Research*, 32:123–133.
- Sklodowski, J., 2017: Three phases of changes in carabid assemblages during secondary succession in a pine forest disturbed by windthrow – results from first 10 years of observations. *Insect Conservation and Diversity*, doi: 10.1111/icad.12237
- Spence, J. R., Niemelä, J. K., 1994: Sampling ground beetle assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist*, 126:881–894.
- StatSoft Inc. 2013: Electronic statistics textbook. OK, Tulsa. [www document]. URL: <http://www.statsoft.com/textbook/>. (Site visited on 25 October 2016).
- Stanovský, J., Pulpán, J., 2006: Střevlíkovití brouci Slezska (severovýchodní Moravy). Muzeum Beskyd, Frýdek-Místek, 159 p.
- Šustek, Z., Vido, J., 2013: Vegetation state and extreme drought as factors determining differentiation and succession of Carabidae communities in forests damaged by a windstorm in the High Tatra Mts. *Biologia*, 68:1198–1210.
- Taboada, A., Kotze, D. J., Tarrega, J., Salgado, J. M., 2008: Carabids of differently aged reforested pine-woods and a natural pine forest in a historically modified landscape. *Basic and Applied Ecology*, 9:161–171.
- ter Braak, C. J. F., Šmilauer, P., 2002: CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA, 500 p.
- Thiele, H. U., 1977: Carabid beetles in their environments. Springer, Berlin, 366 p.
- Urbanovičová, V., Kováč, L., Miklisová, D., 2010: Epigeic arthropod communities of spruce forest stands in the High Tatra Mts. (Slovakia) with special reference to Collembola – first year after windthrow. *Acta Societatis Zoologicae Bohemicae*, 74:141–152.
- Warren, M. S., Key, R. S., 1991: Woodlands: past, present and potential for insects. In: Collins, N. M., Thomas, J. A. (eds.): *The conservation of insects and their habitats*. Academic Press, London, p. 144–212.
- Winter, M-B., Ammaer, Ch., Baier, R., Donato, D. C., Seibold, S., Müller, J., 2015: Multi-taxon alpha diversity following bark beetle disturbance: Evaluation multi-decade persistence of a diverse early-seral phase. *Forest Ecology and Management*, 338:32–45.

Appendix 1. Abundances of the ground beetles sampled in the Hrubý Jeseník Mts. and their ecological characteristics.

Species	H ^a	R ^b	Age of stand				Total
			3	10	20	90	
<i>Amara erratica</i> (Duftschmid, 1812)	O	R	2	0	0	0	2
<i>Amara lunicollis</i> Schiöde, 1837	O	A	6	0	0	0	6
<i>Bembidion lampros</i> (Herbst, 1784)	O	E	1	0	0	0	1
<i>Bembidion quadrimaculatum</i> (Linnaeus, 1761)	O	E	1	0	0	0	1
<i>Calathus micropterus</i> (Duftschmid, 1812)	F	A	10	4	1	75	90
<i>Carabus arvensis</i> (Herbst, 1784)	G	A	2	0	0	1	3
<i>Carabus auronitens</i> Fabricius, 1792	F	A	10	14	20	79	123
<i>Carabus glabratus</i> Paykull, 1790	F	A	0	0	0	6	6
<i>Carabus intricatus</i> Linnaeus, 1761	F	A	1	0	0	0	1
<i>Carabus linnaei</i> Panzer, 1810	F	A	89	5	17	681	792
<i>Carabus sylvestris</i> Panzer, 1793	O	A	157	16	19	120	312
<i>Carabus violaceus</i> Linnaeus, 1758	G	A	33	32	19	80	164
<i>Cychrus attenuatus</i> (Fabricius, 1792)	F	R	0	0	0	7	7
<i>Cychrus caraboides</i> (Linnaeus, 1758)	F	A	1	1	3	10	15
<i>Harpalus latus</i> (Linnaeus, 1758)	F	A	0	1	0	0	1
<i>Leistus ferrugineus</i> (Linnaeus, 1758)	G	E	11	0	1	1	13
<i>Leistus piceus</i> Frölich, 1799	F	A	18	6	1	6	31
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	F	A	10	0	0	0	10
<i>Notiophilus palustris</i> (Duftschmid, 1812)	G	E	6	3	1	0	10
<i>Patrobus atrorufus</i> (Stroem, 1768)	G	A	0	1	0	16	17
<i>Pseudoophonus rufipes</i> (De Geer, 1774)	O	E	0	1	0	0	1
<i>Pterostichus aethiops</i> (Panzer, 1797)	F	A	2	1	1	1	5
<i>Pterostichus diligens</i> (Sturm, 1824)	G	A	0	4	8	1	13
<i>Pterostichus niger</i> (Schaller, 1783)	F	E	0	1	1	0	2
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	F	A	8	21	39	12	80
<i>Pterostichus rufitarsis cordatus</i> Letzner, 1842	F	R	6	3	2	6	17
<i>Pterostichus unctulatus</i> (Duftschmid, 1812)	F	A	101	106	73	335	615
<i>Trechus pilisensis sudeticus</i> Pawlowski, 1975	F	A	0	0	2	0	2
<i>Trechus splendens</i> Gemminger et Harold, 1868	F	A	2	15	13	61	91
<i>Trechus striatulus</i> Putzeys, 1847	G	A	8	24	6	198	236
<i>Trichotichnus laevicollis</i> (Duftschmid, 1812)	F	A	13	2	1	21	37
Number of species			23	20	19	20	31
Number of individuals			498	261	228	1717	2704

Beetles were divided into three groups either ^a according to their habitat association: generalist (G), forest (F) and open-habitat (O) species, or ^b according to their ability to cope with environmental changes following Hürka et al. (1996) as either relicts (R), adaptive (A) or eurytopic (E).

Economic value production of trees as a criterion of their maturity in an uneven-aged forest

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Abstract

Tree maturity of the four main tree species that are most frequent in the uneven-aged forests of the Western Carpathians was analysed. The maturity was determined on the base of the economic value production in relation to tree diameter. We derived mean timber values of spruce, fir, pine, and beech trees (€ m^{-3}) depending on their diameters, quality and stem damage, and in the case of beech also depending on tree age. The assortment structure was calculated using the models of tree assortment tables that account for the stated tree parameters. The assortment prices were taken from the price list of logs in assortment and diameter classes of the Forests of the Slovak Republic, state enterprise, for the year 2016. Trees are mature when their mean timber monetary value is at maximum. Results show, that the highest mean value production of the majority of beech trees of average and above-average stem quality is $70 - 80 \text{ € m}^{-3}$ for trees with diameters between 45 and 55 cm. Monetary values of spruce and fir trees with diameters above 60 to 90 cm are $80 - 95 \text{ € m}^{-3}$, while the monetary values of pine trees with the same diameters are approximately $70 - 115 \text{ € m}^{-3}$. The value production of trees is reduced if the stems are of worse quality or damaged, but in the case of beech it also decreases with greater diameter or tree age.

Key words: target diameters; stem quality; stem damage; assortment structure; selection management system

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1. Introduction

Tree and stand maturity are one of the most important indicators of efficient management in forest stands and are primarily based on their lifelong production. Forest stands are mature when the requirements on their target production are optimally fulfilled. In even-aged forests maturity is determined by the stand age, when the mean annual production is the highest, i.e. when the total mean stand increment culminates (Halaj et al. 1990). Target stand production can be represented by the highest volume production, high production of the most demanded or best-quality assortments, but above all by the highest economic value production quantified by the gross or net income expressed in monetary terms. Halaj et al. (1990) derived maturity ages for even-aged stands of spruce, fir, pine, oak and beech based on the culmination of the total average value increment. As a basis they used the models of yield tables (Halaj et al. 1981; Halaj & Petráš 1998) and assortment yield tables (Petráš et al. 1996). The ages were later updated using new timber prices and models of modal stocking of real stands (Petráš & Mecko 2013). Similarly, the maturity ages of poplar clone stands

of Robusta a I–214 were derived (Petráš et al. 2008a, b, 2015a).

In uneven-aged close-to-nature forests, and particularly in selection forests, which represent their ideal form, it is inefficient and practically impossible to determine a single maturity age for the whole stand or for each tree species. Maturity in selection forests must be related to individual trees, which shall optimally meet the requirements on the target production. The criteria of tree maturity should be as simple as possible, but at the same time they should integrate more factors. The physical age of trees cannot be used in these cases due to the varying dynamics of tree growth under the conditions of uneven-aged stands and particularly due to the difficulties in its assessment for this purpose. The physical age of a tree is usually replaced by the target diameter. Its application is practical because unlike other tree parameters, diameters can be determined easily and unambiguously. Maximum stem diameter retained after a selective cut is frequently used as an additional decision parameter in the optimisation of typical “inverse J” shaped diameter distributions of selection forests in European conditions (Pukkala et al. 2012). On the other hand, most yield regulation systems

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applied in uneven-aged tropical forests define trees to be harvested by minimum harvestable diameter, although other maturity condition criteria are also important and might be regarded (Seydack 1995).

Under the conditions of Central Europe, several authors have dealt with the economic value production and the target diameter, also called a dimension of the rotation type (Hanewinkel 2002; Hanewinkel et al. 2014; Doležal et al. 1969; Priesol & Polák 1991; Poleno 1999 and others). Saniga & Vencurik (2007) derived target diameters for mountainous fir-spruce forests of the Western Carpathians from the optimal curves of diameter frequencies for 3 groups of stands regardless of tree species. Reininger (1992, 1997) also presents only particular target diameters and their modification if stems are damaged by rot or are of worse quality. Due to this, he suggests that trees to-be-harvested should be selected not only on the base of the target diameter but also with regard to their quality. We can say that in the majority of national works the method of quantification of the impact of individual factors on the target diameter of trees is missing.

The aim of the presented paper is to analyse the value production of spruce, fir, beech, and pine trees, and to determine their target diameters as indicators of their optimal maturity. Tree species were selected on the base of their economic importance in the production of mixed and selection forests in the region.

2. Material and methods

The models of tree assortment tables (Petráš & Nociar 1990, 1991a, b) and the prices of raw timber assortments were taken as the basis for the calculation of tree value production. The models of assortment tables were derived from a large empirical material, which was collected during sorting of felled trees of the examined tree species in the main growth regions of Slovakia. The models produce the percentual proportions of assortments from the volume of the timber with the diameter greater than 7 cm inside bark assigned as $S\%$. The proportions were calculated using relationship (1) depending on tree diameter d , stem quality q , stem damage dmg , and tree age t .

$$S\% = f(d, q, dmg, t) \quad [1]$$

All tree parameters are significant only in the case of beech. In the case of fir and spruce, diameter, quality, and stem damage are significant, while in the case of pine, assortment structure is significantly affected only by tree diameter and stem quality. The models are non-linear for all tree species, and non-linearity is significant not only in relation to the single variables, but also for their combination. Generally can be stated, that trees with thicker stem with above-average quality and without significant stem damage have higher proportion of valuable assortments than thinner trees with below average stem quality

and stem damage. In the case of beech, the proportion of valuable assortments decreases significantly at the age higher than 120 years.

Assortments are represented by quality and diameter classes of logs. Assortment quality classes of logs I – VI are characterised as follows:

Class	Purpose of utilisation
I	Cross-cut veneer, special sport and technical equipment, with minimal diameter 40 cm for spruce, fir and beech, and 30 cm for pine.
II	Rotary-cut veneer, matches, sport equipment, with minimal diameter same as I.
III (A, B)	Saw timber (IIIA of higher quality, IIIB of lesser quality) and construction timber, with minimal diameter 16 cm.
V	Pulp wood, chemical and mechanical processing for the production of cellulose and agglomerated boards.
VI	Fuelwood.

In the model of tree assortment tables, the classes from I to IIIB are further divided into diameter classes 1 to 6+:

Class	Diameter [cm]	Class	Diameter [cm]
1	16 – 19	2	20 – 29
3	30 – 39	4	40 – 49
5	50 – 59	6+	60 and more.

It is natural that the proportion of higher diameter classes increases with increasing tree diameters.

Stem quality is evaluated according to the properties of its lower third as follows:

Class	Stem characteristics
A	Stems of the highest quality, straight, untwisted, centric, without shape distortions and knots, which can be used for veneer production.
B	Stems of average quality with minor technical defects, with sound and decayed knots not larger than 4 cm, which can be used as saw timber of better quality.
C	Stems of below-average quality with major technical defects, greater curvature, twisted growth up to 4%, sound knots without limitations, decayed knots in the conifers up to 6 cm and in deciduous tree species up to 8 cm, which can be used as saw timber of lesser quality or as pulpwood.
D	Stems of lower quality than in C class, with extensive rot, which can be used as fuelwood.

Percentual proportions of assortments were calculated using formula (1) separately for each tree species, for every stem quality A, B, C, and D in the case of beech, and for undamaged and damaged stems. The extent and the intensity of stem damage is not quantified, only its presence or absence is evaluated. The information about stem damage is important because it is related to the future or already existing presence of fungal infection and rots in stems. Its presence is evaluated not only in stems,

but also on stumps, root swellings and surface roots. Tree age is included only in the assortment models for beech, because adverse forms of false heart are frequent in older trees of this species. This was lately confirmed by Račko & Čunderlík (2011) and Trenčiansky et al. (2017). Due to this, the assortment structure of beech was calculated separately for the trees aged 100 and 140 years. These particular ages were selected as an example of the age influence on assortments structure and consequently on timber value in the case of beech. For the calculation of the assortment structure using relationship (1), we applied the mathematical form of the models of assortment tables (Petráš 1992).

The economic value production was quantified as an mean timber value of each tree $value [€ m^{-3}]$ calculated as a multiplication of the proportion of assortments (quality and diameter classes) $S\%$ and their prices:

$$value [€ m^{-3}] = \frac{S\%}{100} \cdot prices \quad [2]$$

The assortment prices were taken from the price list of logs in assortment and diameter classes for the first quarter of the year 2016 published by the Forests of the Slovak Republic, state enterprise.

3. Results

The economic value of trees was calculated using formula (2) and represents as an mean economic timber value of each tree. It depends on the structure of the assortments that can be potentially produced from every tree and their prices. Tree maturity was assessed on the base of the development of the mean value of the produced timber ($€ m^{-3}$) in relation to its diameter (Fig. 1 – 5). A tree is mature when it reaches the diameter when this value culminates. Timber values of all tree species grow faster when tree diameters exceed 16 cm, i.e. when better quality assortments I – III start to be more abundant in the assortment structure. The highest timber values are obtained for the best stems of A class regardless of tree species. In the case of spruce and fir (Fig. 1 and 2), the values continuously grow and reach $95 € m^{-3}$ at 90 cm tree diameter. The values of damaged stems are by about $5 € m^{-3}$ lower. In the case of average-quality stems (B class), the values of spruce timber culminate at tree diameters of 60 to 70 cm, when they reach the maximum of approximately $81 € m^{-3}$ or $75 € m^{-3}$ if a stem is damaged. The values of fir stems are by about $1 – 2 € m^{-3}$ higher. The timber values of spruce undamaged or damaged stems of below-average quality C culminate at diameters of 90 cm at a level of $78 – 70 € m^{-3}$, while in the case of fir, the maximum values of $76 – 67 € m^{-3}$ are obtained at diameter from 50 to 70 cm.

Pine timber values (Fig. 3) are significantly different from spruce and fir. Timber values of best-quality pine stems of class A continuously grow, and reach maximum

of $114 € m^{-3}$ at diameters of 90 cm. This is caused by the fact that the best-quality part of the stem becomes longer and goes up to the tree crown which is shorter than in the case of spruce or fir. In the case of pine, the pruned part of a stem makes approximately $2/3$ of stem volume, while in the case of spruce and fir it is only about $1/3$. The timber values of pine stems of average quality B culminate at diameters between 60 and 75 cm at a level of $72 € m^{-3}$. The timber values of stems of below-average quality C grow up to $60 € m^{-3}$ at tree diameters around 90 cm. The impact of stem damage on timber quality and value is very small in the case of pine, and thus, it is not taken into account.

The mean values of beech timber (Fig. 4 and 5) are significantly different from coniferous tree species, particularly in relation to tree diameters and stem damage. The timber values of stems of A and B classes culminate at diameters from 45 to 55 cm. As tree diameters grow, the timber values of such stems markedly decrease. For example, in the case of undamaged stems of class A, the timber value is reduced from $82 € m^{-3}$ to $72 € m^{-3}$. This trend is visible also in the case of stem damage, which is a much more significant factor in the case of beech than for spruce or fir. In addition, it is necessary to point out that in the case of beech the greatest stepwise increase of timber value is around tree diameters of 42 and 43 cm. This is caused by the fact that minimum top diameter of best-quality logs of class I is set to 40 cm. These logs have significantly highest price when compared with others beech cutouts. Due to the occurrence of false heartwood, the effect of tree age cannot be neglected. The frequency of adverse forms of false heartwood increases with tree age (Račko & Čunderlík 2011; Trenčiansky et al. 2017). Due to this, we calculated the model timber values for 100 and 140-year-old trees separately. At the culmination point of the timber values, the values of older trees are lower only by $2 – 4 € m^{-3}$. The lowest timber values are in the case of stems of below-average quality of class C or D, and vary approximately in the range from 51 to $46 € m^{-3}$. Their culmination is not obviously related to tree diameters, as it occurs within a wide span between 40 and 70 cm.

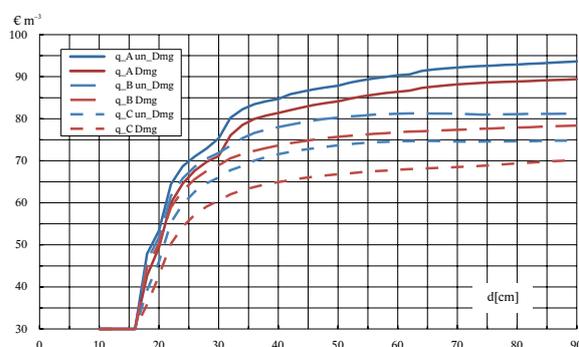


Fig. 1. Mean spruce timber value ($€ m^{-3}$) in relation to diameter d , quality q and stem damage (Dmg – damaged, un_Dmg – undamaged).

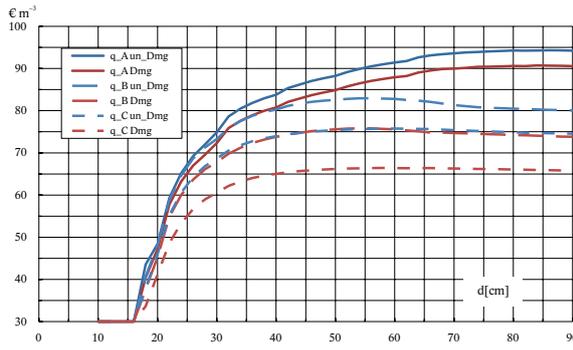


Fig. 2. Mean fir timber value (€ m^{-3}) in relation to diameter d , quality q and stem damage (Dmg – damaged, un_Dmg – undamaged).

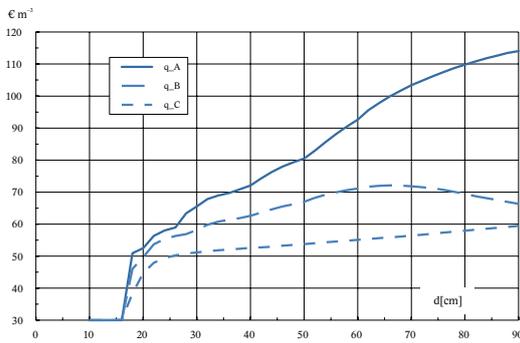


Fig. 3. Mean pine timber value (€ m^{-3}) in relation to diameter d and stem quality q .

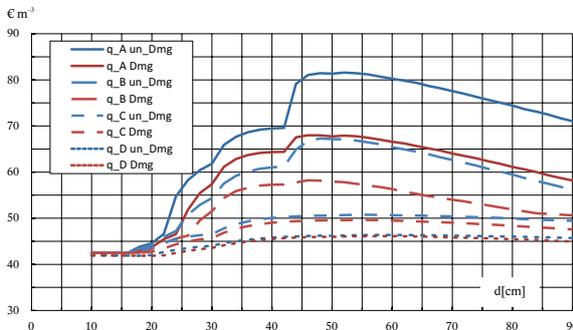


Fig. 4. Mean beech timber value (€ m^{-3}) in relation to diameter d , quality q and stem damage (Dmg – damaged, un_Dmg – undamaged) at the age of 100 years.

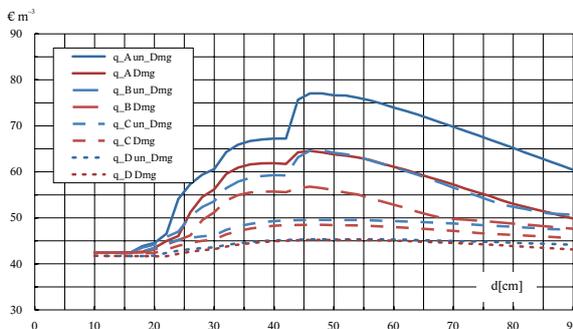


Fig. 5. Mean beech timber value (€ m^{-3}) in relation to diameter d , quality q and stem damage (Dmg – damaged, un_Dmg – undamaged) at the age of 140 years.

From the derived mean value production of timber we can unambiguously conclude that tree maturity depends not only on tree diameter, but also on stem quality and stem damage, and in the case of beech also on tree age. When summarising the obtained knowledge we can state that the timber values of best-quality stems of all three coniferous tree species culminate at a diameter around or above 90 cm. In the case of stems of average quality, the culmination shifts to lower diameters: 50 – 60 cm in the case of fir, 60 – 70 cm for spruce, and 60 – 75 cm in the case of pine. Timber values of stems of below-average quality slightly increase up to the largest diameters. The values of fir culminate at diameters of 50 – 70 cm. Timber values of spruce and fir culminate at the same tree diameter regardless of the stem damage. Only the value in € m^{-3} is significant. The values of damaged stems are lower by 5 € m^{-3} , 6 – 7 € m^{-3} and 8 – 9 € m^{-3} in the case of qualities A, B, and C, respectively.

Beech is significantly different from coniferous tree species. Its timber values culminate in the interval of diameters from 45 to 60 cm for all qualities and also in the case of stem damage. The culmination of trees with B stem quality and of older trees with A stem quality occurs within the smallest range of diameters from 45 to 50 cm. Younger trees reach their maturity at diameters by 5 cm greater than older trees. In addition, the timber values of younger trees with the same diameters are higher by 3 – 5 € m^{-3} than of older trees. Stem damage has a similar, though a more pronounced effect on beech maturity than in the case of spruce and fir. Tree diameter at which timber values culminate does not change with the damage. Only the timber values of damaged stems are reduced by 8 – 14 € m^{-3} . Beech timber values are generally lower than the values of coniferous tree species. This is also valid for diameters at which their timber values culminate.

4. Discussion

Tree maturity depends on tree value production, which integrates volume, quality and economic importance (price) of the produced timber. It is determined by tree diameter, at which the mean monetary timber value per 1 m^3 is the highest. This diameter can be considered as a target diameter for tree harvesting in a selection forest. According to our results, in the case of coniferous tree species it is mainly affected by stem quality. In the case of beech, damage and tree age also have significant effects apart from quality.

The presented results showed a different influence of tree parameters on the value of the produced timber. The influence is similar only in the case of spruce and fir. This results mainly from a similar stem shape and quality including the impact of stem damage on rot. As Petrás & Nociar (1991a) state, small differences between them are caused only by larger knots, and lower susceptibility of fir to wood rot than of spruce. The great similarity of the

use properties of both tree species causes that the prices of their assortments have been the same for a long time (Petráš et al. 2002). In the case of the slight differences in their prices, the value production has not changed significantly. It would become more pronounced if the price relations between the assortments changed more distinctively as stated by Poleno (1968) and Halaj et al. (1990). In such cases, the culmination of the mean timber values would change. The value production of spruce and fir is similar to the one of pine. The similarity is given by the stem shape. However, pine crown is situated higher than crowns of spruce and fir, and in the case of best-quality stems can the zone without knots reach the crown. The big advantage of pine is the low susceptibility of its timber to rot. A special feature of beech is its well-known great susceptibility to the formation of false heartwood. The frequency of its occurrence increases with higher age and greater diameter of trees, as well as with stem damage. Stem damage causes not only false heartwood but also rots. They are the main factors why beech values do not reach the values of the three coniferous tree species. This was also accounted for by Halaj et al. (1990) when deriving the economic maturity of beech stands. Similar causes of lower value production of beech in mixed stands with spruce and fir were mentioned by Petráš et al. (2015b).

When comparing our results with target diameters of trees published by other authors it is necessary to account for the methodology of their derivation. Saniga & Vencurik (2007) derived target diameters of trees from optimum curves of diameter frequencies without analysing the production value. They present target diameters for three groups of selection stands equal to 50, 70, and 74 cm regardless of tree species, but considering site production potential. Our results are derived from the assortment models for mean conditions in productive (management) forests of Slovakia, and are not comparable with the target diameter equal to 50 cm for the exposed sites of the protective character. The values of 70–74 cm correspond with our results for spruce and fir stems of average up to above-average quality, but underestimate pine and slightly overestimate beech.

Reininger (1992, 1997) states a lower target diameter of only 50 cm for undamaged stems of saw quality. When stems are damaged by rot are of worse quality, target diameter is significantly reduced. The author suggests the target diameter of approximately 60 cm for stems of best quality A. The given values of diameters are regardless of tree species.

Sterba (2004) applied a maximum dbh of 60 cm for spruce, fir, beech, pine and larch within the optimised treatment of mixed uneven-aged forests on productive sites in Austria targeted at a de Liocourt-equilibrium diameter distribution curve with a residual basal area of $40 \text{ m}^2 \text{ ha}^{-1}$.

Poleno et al. (2009) attempted to apply a time criterion in the assessment of target diameters of trees on the

base of their real diameters and annual diameter increments. At the same time they also indicated some doubts about their practical implementation. They stated that the culmination of the mean value increment of trees shifts to a higher age in comparison to diameter increment, particularly in the case of best-quality trees.

Recently, economic criteria based on the net present value regarding time factor through interest rate have been applied to address financial tree maturity, which depend mainly on tree value increment related to growing vigour, and on the stumpage value already achieved closely correlated to tree diameter (Knoke 2012). Vauhkonen & Pukkala (2016) simulated harvesting of trees with a value increment lower than the pre-defined threshold reflecting the interest rate (3, 5%). They proved that mainly large sized dominant trees were subjects to harvest, although in dense stands with high competition also thin trees were harvested. For the steady state economically optimised harvesting in a spruce continuous cover forest in Finland, Rämö & Tahvonen (2016) derived target harvest diameters from 20 cm in the case of 5% interest rate to 30 cm in the case of 1% interest rate.

The most complex approaches of harvesting optimisation in uneven-aged forests consider simultaneously both ecological and economic criteria. Roessiger et al. (2016) developed a matrix transition model that is density-dependent and sensitive to individual growth dynamics, which schedules optimal harvesting to maximise the net present value of cuttings and the remaining stand simultaneously to the long-term stand dynamics projection. Based on this model, the economic maturity of individual trees ranged from diameter 12 to 72 cm.

5. Conclusion

Our results indicate that the value production of trees culminates in a wide interval of diameters, hence it is not appropriate to define a single target diameter for a stand or a tree species. The level of value production depends not only on tree diameters but also on stem quality and is reduced by stem damage. In contrast to coniferous tree species, beech value decreases with increasing diameter and tree age.

At productive sites of the Western Carpathians, the highest mean value production of the majority of beech trees of average and above-average stem quality is $70 - 80 \text{ € m}^{-3}$ for trees with diameters between 45 and 55 cm. The highest mean monetary values of spruce and fir trees with diameters from 60 to 90 cm are $80 - 95 \text{ € m}^{-3}$, while the monetary values of pine with the same diameters are approximately $70 - 115 \text{ € m}^{-3}$. The given ranges of diameters can be considered as target values when managing uneven-aged forests under given conditions.

The culmination of the value production of coniferous tree species in relation to tree diameters is not distinct. In the case of best-quality stems the culmination does

not occur because the values gradually increase with the growing diameter. This allows to apply other criteria of maturity apart from the target diameter, for example, to modify stand density, structure, and tree species composition without significant impact on the value production of trees. As for beech, the situation differs, and from the point of the production value it is not appropriate to leave trees with diameters above 60 cm in a stand.

In general, the value production of a mixed uneven-aged forest in the Western Carpathians increases as the proportions of coniferous tree species and the proportion of high-quality, undamaged and well-growing trees increase.

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References

- Doležal, B., Korf, V., Priesol, A., 1969: *Hospodářská úprava lesů*. Praha, SZN, 403 p.
- Halaj, J., Bortel, J., Grék, J., Mecko, J., Midriak, R., Petráš et al., 1990: Rubná zrelosť drevín. Zvolen, Lesnícky výskumný ústav, Lesnícke štúdie, 48, 117 p.
- Halaj, J., Pánek, F., Petráš, R., 1981: Matematický model druhého vydania rastových tabuliek pre smrek, jedlu, dub a buk. *Lesnictví*, 27:867–878.
- Halaj, J., Petráš, R., 1998: *Rastové tabuľky hlavných drevín*. Bratislava, Slovak Academic Press, 325 p.
- Hanewinkel, M., 2002: Comparative economic investigations of even-aged and uneven-aged silvicultural systems: a critical analysis of different methods. *Forestry*, 75:473–481.
- Hanewinkel, M., Frutig, F., Lemm, R., 2014: Comparative economic investigations of even-aged and uneven-aged silvicultural systems: a critical analysis of different methods. *Forestry*, 87:49–60.
- Knoke, T., 2012: The economics of continuous cover forestry. In: Pukkala, T., Gadov, K. (eds.): *Managing Forest Ecosystems – Continuous Cover Forestry*. Springer, p. 167–193.
- Petráš, R., 1992: Mathematisches Modell der Sortimentstafeln für Hauptbaumarten. *Lesnícky časopis*, 38:323–332.
- Petráš, R., Halaj, J., Mecko, J., 1996: Sortimentálne rastové tabuľky drevín. Bratislava, SAP, 252 p.
- Petráš, R., Mecko, J., Bošela, M., 2015b: Kvalita dreva a jeho hodnota v zmiešaných verzus rovnorodých porastoch smreka, jedle a buka. In: Houšková, K., Černý, J. (ed.): *Proceedings of Central European silviculture*. Brno, Mendelova univerzita v Brně, p. 119–130.
- Petráš, R., Mecko, J., 2013: Rubná zrelosť porastov smreka, jedle a buka. In: Baláš, M., Podrázský, V., Kučerová, B. (ed.): *Proceedings of Central European Silviculture*. Kostelec nad Černými lesy, Česká zemědělská univerzita v Praze, p. 184–191.
- Petráš, R., Mecko, J., Nociar, V., 2008a: Models of assortment yield tables for poplar clones. *Journal of Forest Science*, 54:227–233.
- Petráš, R., Mecko, J., Nociar, V., 2008b: Value production of poplar clones. *Journal of Forest Science*, 54:237–244.
- Petráš, R., Mecko, J., Petrášová, V., 2002: Vývoj cien surového dreva hospodársky významných drevín Slovenska. *Lesnícky časopis - Forestry Journal*, 48:91–106.
- Petráš, R., Mecko, J., Petrášová, V., 2015a: Criteria for felling maturity of poplar clones grown for energy use. *Acta regionalia et environmentalica*, 12:43–45.
- Petráš, R., Nociar, V., 1990: Nové sortimentačné tabuľky hlavných listnatých drevín. *Lesnícky časopis*, 36:535–552.
- Petráš, R., Nociar, V., 1991a: Nové sortimentačné tabuľky hlavných ihličnatých drevín. *Lesnícky časopis*, 37:377–392.
- Petráš, R., Nociar, V., 1991b: Sortimentálne tabuľky hlavných drevín. Bratislava, Veda, 304 p.
- Poleno, Z., 1968: Dynamika cen surového dreva. *Lesnícká práca*, 47:271–276.
- Poleno, Z., 1999: Výběr jednotlivých stromů k obnově těžbě v pasečném lese. Kostelec nad Černými lesy, *Lesnícká práce*, 127 p.
- Poleno, Z., Vacek, S., Podrázský, N., Remeš, J., Štefančík, I., Mikeska, M. et al., 2009: Pěstování lesů III. Praktické postupy pěstování lesů. Kostelec nad Černými lesy, *Lesnícká práce*, 951 p.
- Priesol, A., Polák, L., 1991: *Hospodářská úprava lesov*. Bratislava, *Příroda*, 448 p.
- Pukkala, T., Lähde, E., Laiho, O., 2012: Continuous forestry in Finland – recent research results. In: Pukkala, T., Gadov, K. (eds.): *Managing Forest Ecosystems – Continuous Cover Forestry*. Springer, p. 85–128.
- Račko, V., Čunderlík, I., 2011: Vplyv veku stromu na frekvenciu výskytu a veľkosť nepravého jadra buka. *Acta facultatis xylogologiae Zvolen*, 53:5–14.
- Rämö, J., Tahvonen, O., 2016: Optimizing the Harvest Timing in Continuous Cover Forestry. *Environmental and Resource Economics*, Springer, p. 1–16.
- Reininger, H., 1992: Zielstärken-Nutzung oder die Plenterung des Altersklassenwaldes. Wien, *Österreichischer Agrarverlag*, fünfte Auflage, 163 p.
- Reininger, H., 1997: Hospodaření v lesích kláštera Schlägl. Těžba cílových tloušťek anebo výběr v lese věkových tříd. Praha, *Agrospoj*, 120 p.
- Roessiger, J., Ficko, A., Clasen, C., Griess, V.C., Knoke, T., 2016: Variability in growth of trees in uneven-aged stands displays the need for optimizing diversified harvest diameters. *European Journal Forest Research*, 135: 283–295.

- Saniga, M., Vencurik, J., 2007: Dynamika štruktúry a regeneračné procesy lesov v rôznej fáze prebudovy na výberkový les v LHC Korytnica. Zvolen, Technická univerzita vo Zvolene, 83 p.
- Seydack, A. H. W., 1995: An unconventional approach to timber yield regulation for multi-aged multispecies forests. I. Fundamental considerations. *Forest Ecology and Management*, 77:139–153.
- Sterba, H., 2004: Equilibrium Curves and Growth Models to Deal with Forests in Transition to Uneven-Aged Structure – Application in Two Sample Stands. *Silva Fennica*, 38:413–423.
- Trenčiansky, M., Lieskovský, M., Merganič, J., Šulek, R., 2017: Analysis and evaluation of the impact of stand age the occurrence and metamorphosis of red heartwood. *iForest* 10: 605-610. – doi: 10.3832/ofor2116-010 [online 2017-05-15]
- Vauhkonen, J., Pukkala, T., 2016: Selecting the trees to be harvested based on the relative value growth of the remaining trees. *European Journal Forest Research*, 135:581–592.

The impact of precision of tree position measurements and different plot designs on the estimates of tree level production and diversity parameters

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Abstract

Sample plots are basic units of statistical forest inventories. The choice of their shape and size, and sampling methods have changed over time due to economic constraints, efficiency and changes in human demands on data about forests. In the presented study we analysed the impact of three different sampling units: fixed-area plots, fixed-different-area plots, and nested concentric plots, on the estimates of tree level production and diversity parameters. These sampling units were measured during the regional inventory at the University Forest Enterprise of Technical University Zvolen, Slovakia, which was repeated four times (1986, 1992, 1998, 2012). Within each inventory plot, all positions of trees were repeatedly and independently measured three times (1986, 1998, 2012) by different operators using different tools. From these data we quantified the error of tree position resulting from human and technological factors and analysed its impact on the estimates of tree level diversity and production parameters. The selected parameters were: number of trees, stand basal area, standing volume per hectare, number of tree species and number of vertical tree layers. The results indicate that the plot design primarily affects ecological characteristics of forests. Fixed-area plots seem to be the most suitable sampling unit from the point of multi-criteria evaluation of forest status and forest change.

Key words: sample plot; forest inventory; monitoring; sampling simulation; sampling error

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1. Introduction

Forest inventory has a long tradition that dates several centuries back. The interest in inventory methods started in the late 18th century when the gaps in forest survey methods were identified (Fuchs 1993). In the 19th century, a complete census was usually performed (Kangas & Maltamo 2006). The development of statistical inventory methods started at the beginning of the twentieth century, when the first regional and national forest inventories were performed in Finland and Norway (Kangas & Maltamo 2006). About twenty years later, the progress in the development of forest inventory and monitoring methods was initiated in the USA (Stott 1947) followed by the works in Switzerland (Schmid 1963). While at the beginning, forest inventory was primarily aimed at gathering the information about the production parameters of stands (Rego et al. 2005), in the 80s of the last century their ecological functions started to become more important in the developed part of the world, due to which the

inventoried information spectrum has expanded (Söderberg & Fridman 1998). Hence, nowadays national forest inventories are becoming more comprehensive surveys of natural resources (Corona & Marchetti 2007). In addition, while originally the aim of forest inventories was to obtain the information about the actual state of the ecosystem, over time determining the net change of an ecosystem and explaining its development has become the main task (Scott 1998).

As the amount of information gathered during forest inventories increased, sampling designs have become more complex and sophisticated. While originally forest inventory was based solely on field data acquisition, recent trends are to combine field sampling with other data sources, particularly remote sensing methods (Tomppo et al. 2008), but also geographical information systems, digital elevation models, etc. (Wezyka et al. 2005). These data sources enable rapid data acquisition and reduce inventory costs (Katila 2004). Fieldwork itself has been enhanced by satellite positioning systems

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(GPS), automatic measuring devices, e.g. terrestrial laser scanner (Holopainen & Kalliovirta 2006), field computers and wireless data transfer (Holopainen et al. 2005). Due to this development, nowadays there are numerous approaches of forest inventory and monitoring applied at local, regional, and national scales (Kangas & Maltamo 2006).

The changes in acquisition methods often lead to the changes in the applied sampling or plot design (Tomppo et al. 2010). Such changes during successive inventories may affect the precision and the accuracy of the evaluation of temporal development of examined parameters. Subsequently, the accuracy of inventory data may have a significant impact on management decisions and planning (Islam et al. 2009) and models derived from these data (Lichstein et al. 2014).

Hence, the goal of the work was to analyse the effect of two kinds of sampling errors on tree level production and diversity parameters. From production parameters characterising a forest tree level we selected number of trees, stand basal area and stand volume. From diversity parameters we chose simple measures characterising tree species richness and stand vertical diversity that are easy to quantify and simple to interpret, since several studies have pointed at the shortages of explaining the values of commonly applied diversity indices (e.g. Jost 2006, Morris et al. 2014). Hence, as a tree species richness measure we selected the most commonly used number of tree species. Stand vertical diversity was quantified using the number of vertical tree layers, a frequently used measure of forest structure in national forest inventories (Winter et al. 2008), and the proportion of vertical layers calculated as a ratio between the number of trees representing one vertical layer and the total number of trees per plot. The first type of errors represents the random error of tree position measurements as a result of imprecise determination of distances inside inventory plots. The second type of errors occurs if the sampling design is changed in successive inventories. Our aim was to examine if these types of errors have a significant impact on the estimates of tree level production and diversity parameters.

2. Materials and Methods

2.1. Inventory Area

The presented study is based on the data from four successive regional forest inventories performed at the University Forest Enterprise (UFE) of Technical University Zvolen in the years 1986, 1992, 1998, and 2012. Currently, the enterprise covers 9,937 ha. The largest part of the forests (80%) belongs to a category of forests for special purposes, primarily for education and research activities. Elevation of the enterprise ranges from 250 to 1,050 m above sea level.

Mixed spruce–fir–beech, pure beech and mixed oak–beech stands are most common forest stands in the area.

Overall, deciduous species dominate (mainly common beech (*Fagus sylvatica* L.), oak (*Quercus spp.*) and hornbeam (*Carpinus betulus* L.)) over coniferous ones, represented mainly by Norway spruce (*Picea abies* Karst.), silver fir (*Abies alba* Mill.) and Scots pine (*Pinus sylvestris* L.).

2.2. Inventory Design

The inventories were performed at tracts laid in a square (2×2 km) lattice over the whole area of the forest enterprise (Fig. 1). Each tract is 100×200 m large, and is composed of maximum six sample plots with 100 m distance between the neighbouring plots in the tract (Fig. 1). Hence, it is a systematic cluster sampling design, where tracts represent clusters of sample plots. In 1986, the tracts and sample plots were permanently established if situated on forest land. In total, 27 tracts and 121 sample plots were established at the time of the first inventory of UFE. The tracts or plots which were located outside the forest land were not established.

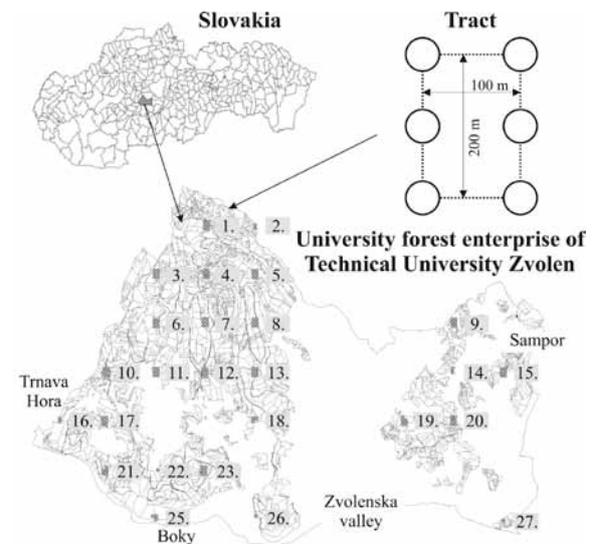


Fig. 1. Location of the University Forest Enterprise of Technical University Zvolen and the distribution of sample plots over the area.

All inventories were carried out on circular plots, but the plot design changed in time. During the first and second inventories in 1986 and 1992, sampling at each sample plot was performed on circular plots of different size from 200 to 500 m² (hereafter as fixed-different-area plots) depending on the stand density and stand growth stage. The radius of each sample plot was determined in the field to include in the measurements approximately 20 trees with diameters at breast height equal to or greater than 7 cm over bark (Batcheler & Craib 1985; Šmelko 1986). During the third inventory performed in 1998, five nested concentric sample plots (hereafter as concentric plots) were used. On each plot, a group of trees with a predefined size was measured as defined below (Šmelko 2000): (i) trees with tree height <1.3 m on

1 m² square; (ii) trees with tree height >1.3 m and diameter at breast height (dbh) <8 cm on circular plots with radius $r = 2.52$ m (i.e. area 20 m²); (iii) trees with dbh from 8.1 to 16.0 cm on circular plots with radius $r = 5.64$ m (100 m²); (iv) trees with dbh from 16.1 to 28.0 cm on circular plots with radius $r = 7.98$ m (200 m²); (v) trees with dbh above 28.1 cm on circular plots with radius $r = 12.62$ m (500 m²).

The last inventory in 2011/2012 was performed on circular plots with a fixed radius of $r = 12.62$ m (hereafter as fixed-area plots). Within this inventory all trees with dbh equal to or greater than 7 cm over bark were measured on the plots.

2.3. Real Data of Tree Positions

Tree positions, i.e. the distance and the bearing to a tree from the plot centre, were repeatedly and independently measured during three inventories in 1986, 1998 and 2011/2012 by different operators. The measurements of positions were performed only for the trees with dbh exceeding a certain threshold (7 cm in 1986 and 2011/2012, and 8 cm in 1998). In 1992, only the positions of ingrowth trees, i.e. trees with dbh below 7 cm at the first inventory but greater than 7 cm at the time of the second inventory, were measured, while the positions of other trees were taken over from the first inventory in 1986. In the first inventory, tree distances from the plot centre were measured using a measuring tape. In the last two inventories in 1998 and 2011/2012, hypsometers Vertex I and III were used for measuring the distances of trees from the plot centre with 1% accuracy of distance measurements, respectively. The bearings to trees from the plot centre were measured using a survey compass Keuffel & Esser Co New York with a precision of 1°.

2.4. Simulated Data

To quantify the effect of sampling design and the error of tree positions on the selected tree level diversity and production parameters, we generated forest stands, each 1.44 ha large, using STRUGEN structural generator (Pretzsch 1993) implemented in SIBYLA growth simulator (Fabrika 2005). For the generation of the stands, we used basic stand parameters, i.e. mean stand diameter, mean stand height, stand age taken from yield tables of Halaj & Petráš (1998). First, individual tree diameters were generated using Weibull function. This was followed by the generation of tree heights from modelled height curves. Then, tree crown parameters were generated on the base of tree diameters and heights. At the end, tree positions were generated within the modelled area of 1.44 ha. The size of the generated stand was set to 1.44 ha to enable systematic sampling without autocorrelation effects between the plots.

In total we generated 99 stands that represented 3 categories of stand vertical diversity (low, moderate and high), 3 categories of tree species richness and 11 decennial age classes starting from 40 to 140 years. The categories of stand vertical diversity were derived from the variability of tree diameters, because of the high correlation between tree diameter and height, defined by the coefficient of variation with the values for low, medium and high variability equal to 15%, 35%, and 50%, respectively. This approach is implemented in the structural generator used for generating stand structure. Tree species richness categories were defined as low, moderate and high if stands consisted of 3, 6, and 9 tree species, respectively, following the work of Merganič & Šmelko (2004). Age categories can be taken as a surrogate of stand density following the premise that the number of trees per hectare as a measure of stand density decreases with the increasing age.

The stand structure of each modelled stand was randomly generated 15 times using the same initial stand characteristics (i.e. mean diameter, mean height, stand volume of individual species). In each modelled stand, 9 inventory plots were systematically distributed over the whole area of the stand. The distance between the neighbouring plots was set to 45 m, which is greater than the minimum grid spacing of 20 m required for excluding the autocorrelation effects between the plots (Motz et al. 2010). It means that each combination of categories (richness × vertical diversity × age) was represented by 135 plots (i.e. 9 plots × 15 generations). At each simulated inventory plot, we applied the above-defined three plot designs that had been used in the regional forest inventories of the University Forest Enterprise, i.e. fixed-different-area plots, concentric plots, and fixed-area circular plots. For each inventory plot and the applied plot design, we calculated the selected tree level production and diversity parameters: number of trees per hectare, stand basal area and standing volume per hectare, tree species richness measure defined as a number of tree species per plot, and two vertical diversity measures defined as a number of vertical layers per plot and a proportion of vertical layers calculated as a ratio between the number of trees representing one vertical layer and the total number of trees per plot. The borders between the vertical layers were defined using the ratios of the maximum tree height in the stand: 90%, 80%, 60%, and 30%, i.e. each forest stand was divided into five vertical layers (0 – 30%, 30 – 60%, 60 – 80%, 80 – 90%, 90 – 100%). The values of the parameters were used for the subsequent analyses described in Methods.

2.5. Methods

2.5.1 Errors of Tree Position Measurements

Due to the repeated measurements of tree positions in successive inventories, it was possible to analyse the error of tree positions resulting from human and technological factors and the random error. The analysis was performed only for the trees with the measured positions from the plot centre, i.e. the trees with diameter at breast height equal to or greater than 7 cm over bark. The trees smaller than 7 cm were excluded from the analysis.

The analysis of tree positions was performed in Mathcad (PTC 2011) and GIS software called SAGA (Bock et al. 2008) as follows. Each inventory was represented by one layer of the vector data of tree positions. The trees measured in the first inventory in 1986 were assigned tree numbers starting from 1. The trees in successive inventories were assigned tree numbers using an algorithm programmed in Mathcad that checked if the following conditions were met: (1) the difference in their position between the particular inventory and the preceding inventory within the plot was less than 0.5 m, (2) the tree species was the same in both inventories, (3) the diameter at breast height determined in the successive inventory was equal to or greater than the diameter measured in the preceding inventory. Each tree that was linked to the tree from the previous inventory was assigned the same tree number. If the tree did not meet the above-mentioned criteria, it was assigned a new tree number that did not occur in the preceding inventory. In the next step, the inventory layers were overlapped in SAGA environment and the assigned tree numbers were visually checked and harmonised. This harmonisation was driven and controlled by an operator with regard to the inventory plot design, assigned tree species and diameters at breast height in individual inventories.

Afterwards, the differences in tree positions of the same tree between the individual inventory years were calculated. In total, we analysed 2,932 pairs of tree positions. From the individual differences we calculated the average difference as an arithmetical mean of all differences, which represented the systematic error of the measurements, i.e. bias, and their standard deviation (SD), which represented the variability of the differences, and hence the random error of tree position measurements. Afterwards, we divided the values of differences into twenty-six 0.5 m wide distance classes, and for each distance class we calculated its standard deviation. In the next step, we calculated relative standard deviations (RD) as a ratio between the standard deviation of the particular distance class and the distance from the plot centre (DIST). Subsequently, the regression analysis was applied to describe the relationship between RD and DIST. Thus, we obtained a function $RD_m = f(DIST)$, where RD_m is a modelled relative standard deviation, which was used to calculate a modelled standard deviation $SD_m = RD_m \times DIST$. The values of SD_m were used

in the subsequent analyses as they specify the uncertainty belt around the plot border.

2.5.2 Impact of Random Error (SD_m) of Plot Radius on Tree Level Production and Diversity Parameters

In the case of the trees located within the uncertainty belt around the plot boundary defined by the random error of tree position measurements (i.e. plot radius $\pm SD_m$) it may happen that the trees that are already outside the plot are measured as if they were inside the plot, or vice versa the trees that are situated inside the plot near the plot border are excluded from measurements. Due to this, the plot values of tree level diversity and production measures may be under- or overestimated. Hence, the impact of the random error of tree position measurements calculated from the successive inventories of UFE on the values of tree level production and diversity parameters was examined using the simulated forest stands. The analysis was performed at a plot level, i.e. at each inventory plot inside the generated forest stands we compared the “precise” values of the examined parameters with the values obtained when the random error of the plot border was included.

The impact of the random error of tree position measurements on the tree level diversity and production parameters was examined within individual tree species richness categories, vertical categories, and age classes with multivariate analysis of variance (MANOVA) using Statistica software (StatSoft 2011). This analysis allowed us to examine also their mutual interactions between the individual factors and their interactions with the applied plot design.

2.5.3. Impact of Plot Design on the Estimates of Tree Level Production and Diversity Parameters

The sampling was analysed from the point of the impact of the applied plot design and the stand structure on the values of the selected tree level production and diversity parameters.

The effect of the inventory plot design was analysed by taking fixed-area circular plots as a basis and comparing the other two samplings with fixed-area circular plots. First we calculated the differences between the values of a particular parameter obtained from fixed-different-area plots or concentric plots and the values obtained at fixed-area circular plots. Negative differences represented underestimation of a particular parameter, while positive differences indicated their overestimation using a specific plot design in comparison to fixed-area circular plots. From these differences, average differences and their confidence intervals were calculated and tested if they were significantly different from zero.

3. Results

3.1. Errors of Tree Position Measurements

The calculated average bias from 2,932 analysed tree pair positions was equal to 6 cm. This value means that the positions of the same tree measured at two inventories differed by 6cm on average. The random error of tree position measurements represented by standard deviation (SD) of average difference was ± 28 cm. This error is the measure of precision of individual tree position measurements. The analysis of the standard deviations at different distances from the centre of the inventory plot (at 0.5m wide classes of distances) revealed the increasing trend of standard deviation towards the plot border. The values of relative standard deviation (RD) decreased with the increasing distance from the plot centre following a non-linear trend. The derived model $RDM = f(DIST)$ had the following form:

$$RDM = 1 - e^{(-0.1085 * 0.8849^{DIST})} \quad [1]$$

and $R^2 = 0.76$. This equation was used to calculate the modelled standard deviations SDm for the specific plot radii. The impact of this error was analysed in the next step using the simulated data.

3.2. Impact of Random Error of Plot Radius ($\pm SDm$) on Bias of Tree Level Diversity and Production Parameters

The analysis revealed that the random error of the plot border did not significantly affect the estimates of tree level diversity if fixed-area and concentric plots were used. MANOVA results showed that the interaction of the plot design and the categories of vertical diversity had a significant impact on the tree species richness measure at 95% significance level ($F = 2.67, p = 0.03$). The results indicated that when fixed-different-area plots were used for sampling, there was a tendency to overestimate the tree species richness measure in the stands with low vertical diversity, while in the stands with moderate vertical diversity we observed a tendency to its underestimation.

In the case of the number of vertical layers, the error of the plot radius did not significantly influence its estimates obtained from the fixed-area plots. MANOVA results revealed that the number of vertical layers was not significantly affected by the main factors separately, but by their interactions, namely: (i) the interaction of plot design and categories of vertical diversity ($F = 3.37, p = 0.009$), (ii) the interaction of age categories, vertical diversity categories and plot design ($F = 1.65, p = 0.006$), (iii) the interaction of age categories, tree species richness categories and vertical diversity categories ($F = 1.45, p = 0.03$). According to the results, there was a tendency to underestimate the number of vertical layers in the stands with moderate vertical diversity if concentric plots were

used for sampling, and in the stands with high vertical diversity if fixed-different-area plots were applied.

Similarly, the error of plot radius did not significantly influence the estimates of the proportion of vertical layers if sampling was performed on fixed-area plots. However, if concentric and fixed-different-area plots were used, significant overestimation of the proportion of vertical layers was found. The overestimation was most pronounced in most frequent vertical layers. MANOVA results showed that the three main factors: age category, vertical layer and plot design significantly affected the estimates of the proportion of vertical layers. The impact of the vertical layers and plot design was significant at 99% significance level ($F = 22.15$ and $F = 20.16$, respectively with $p = 0.000$).

In the case of the tree level production parameters, the error of plot radius did not cause a bias in the estimates obtained from fixed-area plots, but caused their significant overestimation in the case of concentric and fixed-different-area plots. However, according to MANOVA analysis, no factors had a significant impact on the estimates of the selected production parameters.

3.3. Impact of Random Error of Plot Radius ($\pm SDm$) on Variation of Tree Level Diversity and Production Parameters

The precision of tree species richness was not found to be affected by the random error of the plot radius, but the relative change of the precision of the vertical diversity measure and production parameters fluctuated between -69% and $+266\%$ depending on the examined parameter (Table 1) and other factors. The precision of tree species richness was primarily affected by vertical diversity, while the precision of the vertical diversity measure was mainly affected by age category and the occurrence frequency of height layers. The precision of the production parameters was mainly affected by the plot design and age class.

3.4. Impact of Plot Design on the Estimates of Tree Level Diversity and Production Parameters

As shown in Fig. 2, plot design significantly affected the estimates of tree species richness characterised by the

Table 1. Effect of the random error of plot radius ($\pm SDm = f(DIST, RDM)$) on the precision of examined parameters.

Group of parameters	Parameter	Relative change of parameter precision [%]	
		Min	Max
Species diversity	Number of tree species	-3	+3
	Proportion of a vertical layer	-5	+69
Vertical diversity	Number of vertical layers	-18	+15
	Number of trees per hectare	-69	+15
Production	Basal area per hectare	-68	+266
	Standing volume per hectare	-69	+264

of tree species. Both concentric and fixed-different-area plots significantly underestimated the measure of tree species richness in all categories of vertical diversity, all categories of species richness, and almost all age classes. The underestimation of the number of tree species was greatest in young stands with high level of species richness. With the increasing age, the underestimation was significantly reduced, and in the stands older than 110 years the estimates of tree species richness became unbiased if concentric plots were applied. The estimates of the number of tree species from concentric plots were slightly better than the estimates obtained from fixed-different-area plots. The maximum differences were equal to -3 and -4 tree species, for concentric and fixed-different-area plots, respectively, indicating that the tree species richness measure estimated from sampling based on concentric or fixed-different-area plots was only 66% or 55% of the number of tree species on the site, respectively.

Similar effects of the plot design were shown in the case of vertical diversity characterised by the average number of vertical layers (Fig. 2). Both concentric and fixed-different-area plots significantly underestimated this vertical diversity measure in all categories of vertical diversity, all categories of species richness, and almost all age classes. In the case of fixed-different-area plots, the underestimation was greatest in young stands and decreased with the increasing stand age (Fig. 2). When sampling was performed at concentric plots, the best estimates of the number of vertical layers were in middle-aged stands. Similarly to tree species richness, the estimates of the number of tree layers from concentric plots were better than those from fixed-different-area plots.

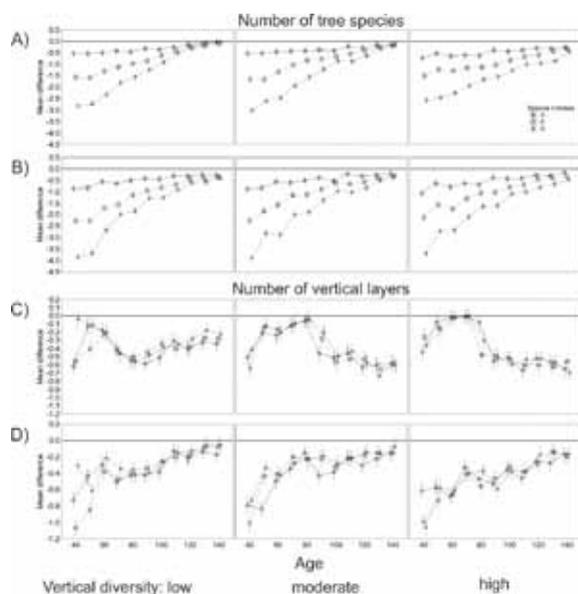


Fig. 2. Differences between the estimates of the number of tree species (A, B) and the number of vertical layers (C, D) at concentric (A, C) or fixed-different-area (B, D) sample plots and the estimates at fixed-area sample plots in categories of species richness (three lines), vertical diversity and age classes.

The analysis of the impact of the applied plot design on the proportion of vertical layers showed that the estimates obtained from concentric and fixed-different-area plots were significantly different from the values quantified at fixed-area plots in the 2nd and 4th vertical layers. The proportions of the other three vertical layers were not influenced by the applied plot design. Similarly, the estimates of the production parameters were not significantly affected by the applied plot design, although sampling at concentric plots had a tendency towards an overestimation of all examined parameters, while sampling at fixed-different-area plots tended to slightly underestimate the parameters.

4. Discussion

In repeated inventories, the position of trees is usually measured only once when the tree is measured for the first time. During the successive inventories, the tree is identified on the base of its polar coordinates, i.e. its bearing and the distance from the plot centre measured before, and only the values of tree parameters are updated. Such an approach ensures that the same trees are identified during every inventory and only ingrowth is added to the list. However, tree position measurement may also be affected by errors resulting from human and/or technological factors, such as imprecise identification of the plot centre, experience with the applied technology, but also from environmental conditions, e.g. slope of the terrain, undergrowth disrupting the laser beam, etc. The data used in the presented study allowed us to analyse such errors because a non-standard approach of re-measuring the polar coordinates of trees was applied in three repeated inventories of the University Forest Enterprise. The results revealed that the overall average bias of tree position measurements between the two independent inventories was 6 cm. This value is not relevant from the practical point of view, and can be neglected.

The random error of tree position measurements fluctuated from 2 to 5% depending on the tree distance from the plot centre. This error may cause problems mainly around the plot border, where it may happen that the trees that are already outside the plot are included in the plot measurements, or vice versa the trees that are situated at the plot border inside the plot are not measured. In the case of circular plots, the problems which trees are inside and which are outside the plot border can also result from the fact that the plot boundary is curved (West 2009). Nevertheless, the analysis of the impact of this random error on the plot values of diversity and production parameters revealed that it does not significantly affect the examined parameters if fixed-area plots are used for sampling. If concentric or fixed-different-area plots are applied, significant bias of production parameters and diversity measures was found. However, the magnitudes of the detected bias were small, and can be from the practical point of view neglected. Although the

random error of the plot radius did not have a profound impact on the absolute values of the examined parameters, it influenced their precision (Table 1). Particularly, the precision of the quantified production parameters was significantly affected by the random error of the plot radius, which can lead to incorrect interpretation of inventory and monitoring results.

The analysis of the applied plot design on the production and diversity parameters revealed that the plot design did not have a significant impact on the estimation of production parameters. This corresponds with the previous findings of the works comparing different plot designs (Schreuder et al. 1992). However, from the biodiversity point of view, the results showed that the plot design significantly affected the estimates of both tree species richness and vertical diversity. Concentric and fixed-different-area plots significantly underestimated the number of tree species per plot (Fig. 2). This is caused by the fact that both concentric and fixed-different-area plots cover a smaller number of individuals and/or a smaller plot area in comparison to fixed-area plots. The number of species is known to have a strong positive relationship to the size of the sampled area (Cam et al. 2002). According to Brose et al. (2003), observed species richness is always smaller than true species richness, while the difference between them depends on the sampling intensity and the evenness in species' abundances.

Motz et al. (2010) compared the estimates of different diversity indices from fixed area sample plots and angle count methods and concluded that fixed area plots are more suitable for consistent estimation of tree diversity. Our results showed that fixed area sample plots are also superior to concentric and variable-size plots (Fig. 2), particularly if biodiversity quantification is one of the main inventory aims.

Permanent fixed-area plots should also be preferred if the main focus of monitoring is on the change of an ecosystem rather than its state (Scott 1998), because such a plot design allows to identify all components of change (Poso 2006). In addition, the impact of possible underlying mechanisms causing the change can be deduced from the information obtained from repeated observations of the same sample (Nusser et al. 1998). From the practical point of view, circular fixed-area plots are easy to establish (West 2009), and simple to measure (Poso 2006). Although their time costs are double the costs of angle count methods and by 12–30% greater than the costs of concentric or fixed-different-area plots (Šmelko 2013), fixed-area plots are more efficient for estimating increments of e.g. basal area (Poso & Waite 1995), because calculation problems of concentric or angle count plots related to the compatibility of the successive measurements are excluded (Poso 2006).

On the base of the presented results we can state that the plot design may significantly influence the evaluation of ecological characteristics, which can negatively affect the assessment of their temporal development using the

continuous monitoring data. Fixed-area plots seem to be the most suitable sampling units from the point of multi-criteria evaluation of forest status and forest change.

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References

- Batcheler, C. L., Craib, D. G., 1985: A variable area plot method of assessment of forest condition and trend. *New Zealand Journal of Ecology*, 8:83–95.
- Bock, M., Bohner, J., Conrad, O., Kothe, R., Ringeler, A., 2008: Saga: System for the automated geoscientific analysis. Dept. Phys. Geogr. Hamburg, Ger. URL <http://www.saga-gis.org/en/index.html/> (last Verif. 19 April 2009).
- Brose, U., Martinez, N. D., Williams, R. J., 2003: Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*, 84:2364–2377.
- Cam, E., Nichols, J. D., Hines, J. E., Sauer, J. R., Alpijar-Jara, R., Flather, C. H., 2002: Disentangling sampling and ecological explanations underlying species–area relationships. *Ecology*, 83:1118–1130.
- Corona, P., Marchetti, M., 2007: Outlining multi-purpose forest inventories to assess the ecosystem approach in forestry. *Plant Biosystems*, 141:243–251.
- Fabrika, M., 2005: Simulátor biodynamiky lesa SIBYLA, koncepcia, konštrukcia a programové riešenie. Zvolen, Technical university in Zvolen, 238 p.
- Fuchs, A., 1993: Wiederholungsaufnahme und Auswertung einer permanenten Betriebsinventur im Bayerischen Forstamt Ebrach, 157 p.
- Halaj, J., Petráš, R., 1998: Rastové tabuľky hlavných drevín. Bratislava, SAP, 325 p.
- Holopainen, M., Kalliovirta, M. S. J., 2006: Modern data acquisition for forest inventories. *Forest Inventory*. Springer, p. 343–362.
- Holopainen, M., Talvitie, M., Leino, O., 2005: Forest biodiversity inventory by means of digital aerial photographs and laser scanner data. *Schriften aus der Forstl. Fak. der Univ. Göttingen und der Niedersächsischen Forstl. Versuchsanstalt*, 138:340–348.
- Islam, M. N., Kurtila, M., Mehtätalo, L., Haara, A., 2009: Analyzing the effects of inventory errors on holding-level forest plans: the case of measurement error in the basal area of the dominated tree species. *Silva Fennica*, 43:71–85.

- Jost, L., 2006: Entropy and diversity. *Oikos*, 113:363–375.
- Kangas, A., Maltamo, M., 2006: Forest inventory: methodology and applications. Springer Science & Business Media, p. 5–11.
- Katila, M., 2004: Controlling the estimation errors in the Finnish multisource National Forest Inventory. Finnish Forest Research Institute, Vantaa Research Centre, Research Papers 910
- Lichstein, J. W., Golaz, N.-Z., Malyshev, S., Shevliakova, E., Zhang, T., Sheffield, J. et al., 2014: Confronting terrestrial biosphere models with forest inventory data. *Ecological Applications*, 24: 699–715.
- Merganič, J., Šmelko, Š., 2004: Quantification of tree species diversity in forest stands – model BIODIVERSS. *European Journal of Forest Research*, 123:157–165.
- Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S. et al., 2014: Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, 4:3514–3524.
- Motz, K., Sterba, H., Pommerening, A., 2010: Sampling measures of tree diversity. *Forest Ecology and Management*, 260:1985–1996.
- Nusser, S. M., Breidt, F. J., Fuller, W. A., 1998: Design and estimation for investigating the dynamics of natural resources. *Ecological Applications*, 8:234–245.
- Poso, S., 2006: Change monitoring with permanent sample plots. *Forest Inventory*, Springer, p. 65–84.
- Poso, S., Waite, M., 1995: Calculation and comparison of different permanent sample plot types, 29:159–169.
- Pretzsch, H., 1993: Analyse und Reproduktion räumlicher Bestandesstrukturen: Versuche mit dem Strukturgenerator STRUGEN. Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt. J.D. Sauerländer's Verlag, Frankfurt am Main. No. 114.
- PTC, 2011: Mathcad - Parametric Technology Corporation and/or Its Subsidiary Companies.
- Rego, F., Godinho-Ferreira, P., Uva, J. S., Cunha, J., Marchetti, M., 2005: Combination of structural and compositional factors for describing forest types using national forest inventory data. *Monitoring and Indicators of Forest Biodiversity in Europe—From Ideas to Operationality*, 51:153–162.
- Scott, C., 1998: Sampling methods for estimating change in forest resources. *Ecological Applications*, 8:228–233.
- Schmid, P., 1963: Vergleich von Vollkluppierung und Stichprobenaufnahme. *Schweiz Zeitschrift Für Forstwesen*, p. 412–425.
- Schreuder, H. T., Rennie, J. C., Williams, M., 1992: Comparison of three sampling schemes for estimating frequency and D 2 H by diameter class—a simulation study. *Forest ecology and management*, 50:117–131.
- Söderberg, U., Fridman, J., 1998: Monitoring of forest biodiversity from forest resource inventory data. *Assessment of Biodiversity for Improved Forest Planning*, Springer, p. 233–239.
- StatSoft, I., 2011: STATISTICA, ver. 10. Tulsa, OK.
- Stott, C., 1947: Permanent growth and mortality plots in half the time. *Journal of Forestry*, 45:669–673.
- Šmelko, Š., 2013: New view of properties and applicability of the circular and relascope sample plots for the inventory and monitoring of the forest ecosystems. *Lesnícky časopis*, 59:1–19.
- Šmelko, Š., 2000: Nové varianty terestrickej inventarizácie a monitoringu stavu a produkcie lesa, Záverečná správa etapy vedecko-výskumného projektu VEGA 1/4030/97-02.
- Šmelko, Š., 1985: Nové smery v metodike a technike inventarizácie lesa. *Vedecké a pedagogické aktuality 6. zVOLEN*, Vysoká škola lesnícka a drevárska, 122 p.
- Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R. E., Gabler, K., Schadauer, K. et al., 2010: National forest inventories. Pathways for Common Reporting. *European Science Foundation*, p. 541–553.
- Tomppo, E., Haakana, M., Katila, M., Peräsaari, J., 2008: Multi-source national forest inventory: Methods and applications. Springer Science & Business Media.
- West, P., 2009: *Tree and forest measurement*. Springer, 191 p.
- Wezyka, P., Traczb, W., Guzikc, M., 2005: Evaluation of landscape structure changes in Tatra mountains (Poland) based on the 4D GIS analysis. *Environment*, 138:224–232.
- Winter, S., Chirici, G., McRoberts, R. E., Hauk, E., Tomppo, E., 2008: Possibilities for harmonising national forest inventory data for use in forest biodiversity assessments. *Forestry*, 81:33–44.

Reconstructing past forest status using inventory and tree ring data to support uneven-aged forest management

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Abstract

The decision to change forest management system from the traditional even-aged to the selection one based on statistical inventory is often limited by a missing previous inventory. To avoid this issue, we used available forest inventory data from ca 2 000 ha of mixed uneven-aged beech-fir-spruce-pine forest and tree ring data from 831 trees to reconstruct forest status from one decade ago. For this purpose, we have created three sets of species-specific models: 1) diameter-stump models to reconstruct the diameter of missing trees, 2) diameter-increment models based on tree ring data to estimate past diameters, and 3) height-diameter models to estimate past tree heights. This approach has allowed us to completely reconstruct the state of the forest as it was ten years ago and use the results as a substitution for a previously missing inventory.

Key words: stump-diameter models; height-diameter models; diameter increment models; forest inventory; selection forest management

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1. Introduction

Selection management systems are used only rarely in Central and Eastern Europe. Contrary to that, the importance of uneven-aged and/or close-to-nature forest management as defined by Möller (1922) and as newly summarized e.g. by Bauhus et al. (2014) is expected to increase in the future. Uneven-aged forests are considered to better fulfil the requirements for multipurpose forest use and the provision of ecosystem services than even-aged forests (Pukkala 2016). The main reason for their limited use, in extreme cases even for disallowing of selective logging, is a lack of adequate inventory and planning tools (Dvorak 2000), more easier to apply and cheaper than traditional methods developed already in 19th century.

Control methods (Biolley 1887) used for planning in uneven-aged forests and selective logging management are based on periodical forest inventories using the same method. Other relatively simple methods for modelling and management planning, particularly in uneven-aged forests, are matrix transition models. These models are derived from population growth models (Leslie 1945; Buongiorno & Michie 1980; Pukkala et al. 2009; Roessiger et al. 2016) which are also based on a regular inventory cycle. At present, a lot of attention is given to single

tree-based growth simulators (as summarized e.g. by Hasenauer 2006) able predict forest development after one inventory. Nevertheless, their application is not very widespread due to the complexity of their inputs and knowledge of their application in selection forests is largely unknown.

There are two main non-destructive sources of data on tree growth. The first one is based on a regular inventory cycle whilst the second uses tree ring chronologies (Biondi 1999). Tree rings provide valuable information on individual tree growth, stand history and dynamics, and even past climate (e.g. Fritts 1976; Schweingruber et al. 1978). If a decision is made to change a management system in forests from even-aged based on stand mensuration to uneven-aged using an initial statistical inventory, previous inventory data crucial for the calibration of control method based planning models are missing. In such a case, the combination of forest inventory data with tree ring data is needed, often deemed essential (Biondi 1999; Lindbladh et al. 2007).

The aim of the study is to design procedure based on the existing inventory and tree ring data for statistical reconstruction of past forest status in the absence of previous forest inventory.

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2. Material and Methods

2.1. Study area

The study area represents the “Pro Silva” model forest unit Smolnícka Osada covering 2,132 hectares of forest in the Volovské Mountains in the Central West Carpathians (48°44' N, 20°46' E). The selection management system has been applied in the mixed beech-fir-spruce forests with admixed pine for more than 50 years during which uneven-aged forest structures have formed (Fig. 1). The geological bedrock is build mainly by phyllites with a dominant representation of dystric and typical cambisols. The altitude ranges from 440 to 1,150 m above sea level, within which the 4th (beech) and 5th (fir-beech) altitudinal vegetation zones are most prevalent with minor presence of 6th (beech-fir-spruce) zone. Despite the dominance of complex uneven-aged stand structures, traditional forest mensuration based on yield tables is still used for forest planning in a ten year cycle.

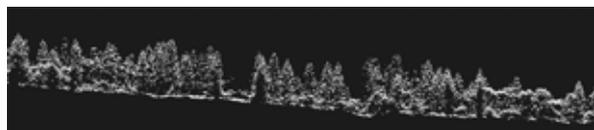


Fig. 1. A typical profile of Smolnícka Osada model forest derived from airborne laser scanning data.

2.2. Extended forest inventory

To support transition to management methods more suitable for uneven-aged forests, the first statistical inventory was completed in 2014. Inventory data were collected from 344 inventory plots (IP) established in a 250 × 250 m grid, each of which comprised a minimum of 20 trees with variable plot radii between 7.5 and 20 m. Data on diameter at breast height (*dbh*), tree height, crown length, crown quality (A – big/dense, B – medium, C – small/sparse), stem quality (A – high, B – medium, C – low) and stem damage (0 – undamaged, 1 – damaged) were collected for each tree with *dbh* > 8 cm. The position of each tree was ascertained by polar coordinates. Additionally, position and diameter measurements from all stumps of trees harvested in the last decade were taken. For this purpose, a catalogue of visual parameters, mechanical properties and signs of biotic colonisation of stumps from all targeted species and different post-felling periods was compiled using forest management records from the model area. According to species specific scales, three age categories of stump age were estimated (A – 1 to 3, mean 2 years; B – 4 to 7, mean 5 years; C – 8 to 10, mean 9 years after cutting). Finally, on the subset of 87 IP in the 500 × 500 m grid, tree cores were taken for tree ring analysis in a pattern which reflected variations in tree sizes, altitude and stand conditions representing independent variables of the models described in next text. The data was processed by standard MS Office tools and models were derived using R–package (R core team, 2016) and STATISTICA.12 (StatSoft, 2013).

2.3. Diameter-stump models

Diameter-stump models based on the data obtained from tree stumps are necessary for the reconstruction of missing trees cut during the last decade. For this purpose, National Forest Inventory data (NFI 2015) from 496 NFI plots located only on productive sites in the 4th–6th altitudinal vegetation zones were used to calculate simple one factor linear models. Data was sourced from 1,375 beeches, 1,537 spruces, 327 firs and 88 pines with simultaneously measured diameter at breast (1.30 m) and stump (0.25 m as mean) height.

2.4. Diameter increment models

An extensive dendrochronological material including cores from 334 beech, 280 fir, 144 spruce and 63 pine trees from 75 model area inventory plots in a 500 × 500 grid was used for diameter increment modelling. One core was taken from each pre-selected tree at breast height in a direction perpendicular to the slope. Due to high unexplained variability of absolute increments obtained from cores (tree ring widths), diameter increment models were constructed for relative diameter increment (*rdi*). Dependent variable *rdi* was calculated as a ratio of double mean tree ring width from the past ten year period to tree *dbh*. Since *rdi* has shown an exponentially decreasing relationship with *dbh*, power and exponential functions have been chosen for modelling. The following factors have been tested as independent variables: diameter at breast height (*dbh*), relative crown proportion to the tree height (*cp*), crown quality assessed through crown vitality and density to three categories A, B and C (*cq*), mean stand diameter (*dg*), stand timber volume per hectare (*vha*), species specific site index (*si*) and basal area proportion competition index (*CIg*). *CIg* have been assessed as highly relevant in relation to diameter increment by Bošela et al. (2015), calculated according to Formula 1:

$$CIg = \sum_{j=0}^n \frac{g_j}{g_i} \quad [1]$$

Where: *CIg* is basal area proportion index, g_i is basal area of *i*th target tree, g_j is basal area of a *j*th neighbour. All trees on IP were considered as neighbours. Variable IP radius resulting to approximately the same number of trees on plots was assumed to ensure comparable results.

2.5. Height-diameter models

Data from a 500 × 500 grid was used for the computation of local height curves. Only trees with no crown and/or stem abnormalities such as broken top, tilted stem etc. were included in the analysis. Except for *dbh* as a main predictor, the following factors were tested for their influence on the model: mean stand diameter (*dg*), stand tim-

ber volume per hectare (*vha*), species specific site index (*si*) and basal area proportion competition index (*CIg*). For all species, universal three-parameter exponential function with inflexion point well-fulfilling biological assumptions has been computed.

2.6. Reconstruction of past forest status

Finally, forest status from ten years ago has been statistically derived in three steps. Firstly, *dbh* of each individual tree felled during the past decade was reconstructed using a diameter-stump model (Formula 2 in the Results section). Secondly, *dbh* of all trees was re-calculated for the tenth year before the present inventory (2004) using diameter increment models (Formula 3 – 6 in the Results section). Thirdly, the height of trees in the same time point was calculated using height-diameter models (Formula 7 in the Results section). In the case of felled trees with *dbh* reconstructed by diameter-stump models, the felling year estimated within stump inventory was regarded to consider increment before tree was cut. Missing model parameters of felled trees (*cp*, *cq*) were replaced by mean values, while stand parameters (*dg*, *vha*, *si*) generally were taken from inventory 2014. This way, we were able to statistically reconstruct the missing previous inventory 2004. Its data was compared with an existing completed inventory 2014, and information about forest dynamics during last decade can be derived.

3. Results

3.1. Diameter-stump models

One factor linear diameter-stump model appeared to be sufficient for tree diameter (*dbh*) estimation from stump diameter (Formula 2).

$$dbh = a + b \times ds \tag{2}$$

Where: *dbh* is diameter at breast height (mm), *ds* is stump diameter (mm), and *a*, *b* are species specific coefficients (Table 1).

Table 1. Coefficients and statistics of diameter-stump models based on NFI data (Formula 2).

Species	Parameter estimates				
	a	b	n	R ²	RMSE
European beech	0.152 ⁿ	0.810 ¹	1375	0.95	28.0
Silver fir	22.228 ¹	0.765 ¹	327	0.97	24.2
Norway spruce	26.811 ¹	0.706 ¹	1537	0.96	27.2
Scots pine	-2.010 ⁿ	0.843 ¹	88	0.97	19.5

R² – coefficient of determination, RMSE – root mean square error, significance codes: ¹< 0.001, ⁰0.001–0.01, ³0.01–0.05, ²> 0.05.

Figure 2 shows clear linear relationship between *dbh* and *ds*. If the different tree species have the same stump diameter value *ds*, then the smallest *dbh* is expected for Norway spruce and largest *dbh* for Scots pine. The reasons are probably related to species specific differences in root swelling formation.

3.2. Diameter-increment models

A multiple power model with a different set of statistically significant variables was selected for a relative diameter increment estimation of beech, fir and spruce (Formula 3 – 5). An exception was pine, where exponential function appeared to be more suitable (Formula 6).

$$\text{European beech: } rdi = a \times dbh^b \times cp^c \times cq^d \times vha^e \tag{3}$$

$$\text{Silver fir: } rdi = a \times dbh^b \times cp^c \times cq^d \times dg^e \tag{4}$$

$$\text{Norway spruce: } rdi = a \times dbh^b \times cp^c \times vha^d \tag{5}$$

$$\text{Scots pine: } rdi = a \times e^{(-b \times dg + c \times si)} \tag{6}$$

Where: *rdi* is relative diameter increment (%), *dbh* is diameter at breast height (mm), *cp* is relative crown proportion (%), *cq* is crown quality, *dg* is mean stand diameter (mm), *vha* is stand timber volume per hectare (m³), *si* is species specific site index (m), and *a*, *b*, *c*, *d*, *e* are species specific coefficients (Table 2).

Table 2. Coefficients and statistics of local diameter increment models (Formula 3 – 6).

Species	Parameter estimates					n	R ²	RMSE
	a	b	c	d	e			
Beech	6.12 ²	-0.827 ¹	0.619 ¹	-0.420 ¹	-0.275 ¹	319	0.57	0.006
Fir	13.73 ²	-0.676 ¹	1.322 ¹	-0.547 ¹	-0.487 ¹	283	0.69	0.004
Spruce	732.8 ⁿ	-1.299 ¹	1.838 ¹	-0.733 ¹	—	111	0.74	0.005
Pine	0.004 ⁿ	0.006 ¹	0.052 ³	—	—	64	0.34	0.002

R² – coefficient of determination, RMSE – root mean square error, significance codes: ¹< 0.001, ⁰0.001–0.01, ³0.01–0.05, ²> 0.05.

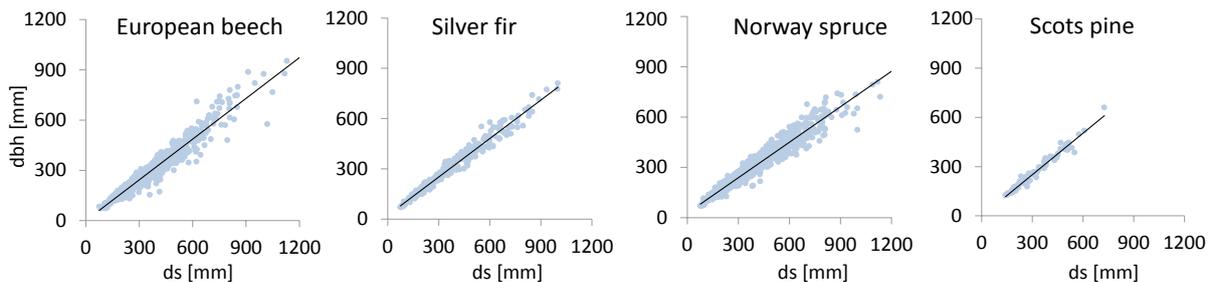


Fig. 2. NFI data shows high species specific correlation between *dbh* and *ds*.

From the tested factors, only basal area proportion index (*CIg*) failed to be a significant *rdi* predictor for any of the species. Its influence was overshadowed by single tree crown parameters *cp*, *cq*, simultaneously with one of the stand density or maturity indicators *vha* and/or *dg*. Fir showed locally the highest diameter increment in the last decade, followed by beech (Fig. 3). For both species *rdi* dynamics are well described by 4-parameter power function with a similar set of predictors. Spruce *rdi* was comparable in the lowest *dbh*, but with increasing *dbh* began to fall dramatically. In contrast to the previous models, *cq* parameter was missing in the spruce *rdi* model. Partial relation of current *cq* status to the spruce *rdi* together with strong *rdi* decrease with increasing *dbh* can be explained by acute spruce decline of older trees caused by biotic agents common in the model area over the last two decades. Pine was generally the lowest with the weakest relationship to the tested predictors. Pine *rdi* model with only two stand related predictors differing from other species explained a lower proportion of *rdi* variability.

3.3. Height-diameter models

Height curves of all species are naturally dependent on *dbh*. In addition, they appeared to be significantly influenced by mean stand diameter (*dg*), what is biologically well proven. Height-diameter curves are shifting upwards during stand development and the stand development

(known as growth stages) is well approximated by the mean stand diameter. A general model for all species was defined by Formula 7.

$$h = 1.3 + a \times e^{(-b/dbh + c/dg)} \quad [7]$$

Where: *h* is tree height (m), *dbh* is diameter at breast height (mm), *dg* is mean stand diameter (mm), and *a*, *b*, *c* are species specific coefficients (Table 3).

Table 3. Coefficients and statistics of local height-diameter models (Formula 7).

Species	Parameter estimates				R ²	RMSE
	a	b	c	n		
European beech	46.998 ¹	170.308 ¹	-33.090 ³	214	0.79	3.94
Silver fir	61.268 ¹	238.712 ¹	-56.790 ¹	175	0.87	3.64
Norway spruce	55.016 ¹	194.602 ¹	-49.755 ¹	74	0.85	2.91
Scots pine	51.098 ¹	117.219 ¹	-83.941 ¹	64	0.59	2.77

R² – coefficient of determination, RMSE – root mean square error, significance codes: ¹< 0.001, ²0.001–0.01, ³0.01–0.05, ⁴> 0.05.

Fir showed the highest height-growth potential, followed by spruce, pine and beech (Fig. 4). As expected, the shape of height curves differs between tree species. While at the middle stand diameter (*dg* = 36 cm) and *dbh* = 20 cm pine was the tallest (23 m), followed by spruce (20 m), beech (19.5 m) and fir (17 m), at *dbh* = 50 cm fir was the tallest (34 m), followed by spruce and pine (33.5), and finally beech (32 m). Also at higher *dbh* the fir curve remained steep, whilst for other species, pine in particular, the curves became flatter. The pine height-diameter model was the most (beech the least) affected by stand growth stage expressed by *dg*.

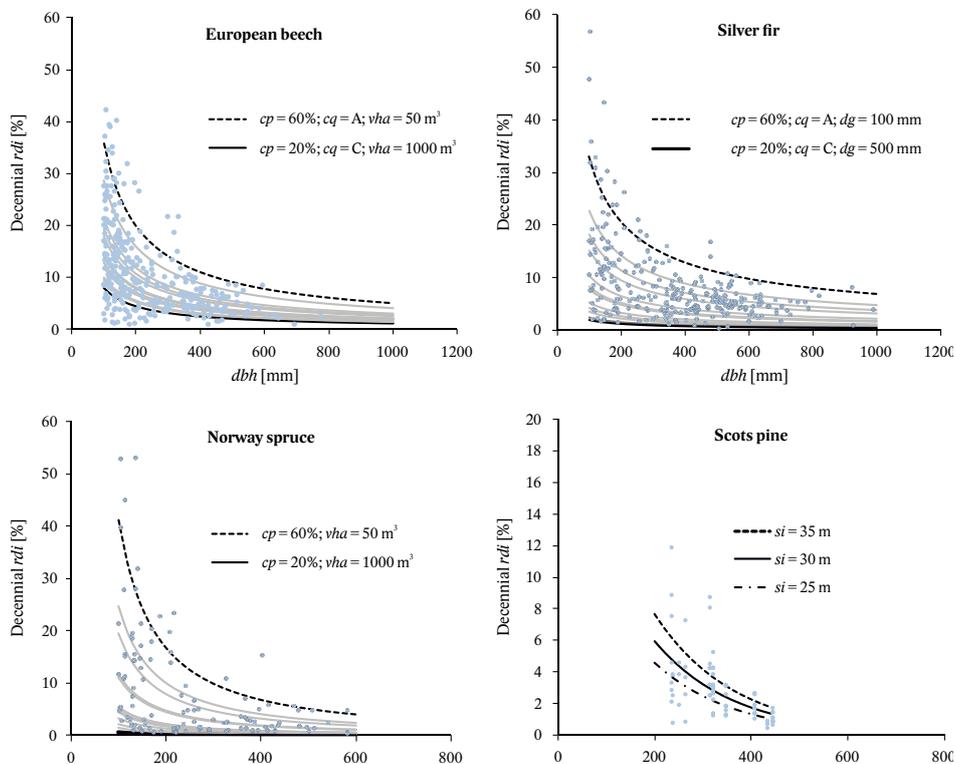


Fig. 3. Species specific diameter increment model characteristics at different levels of significant variables against the original data background.

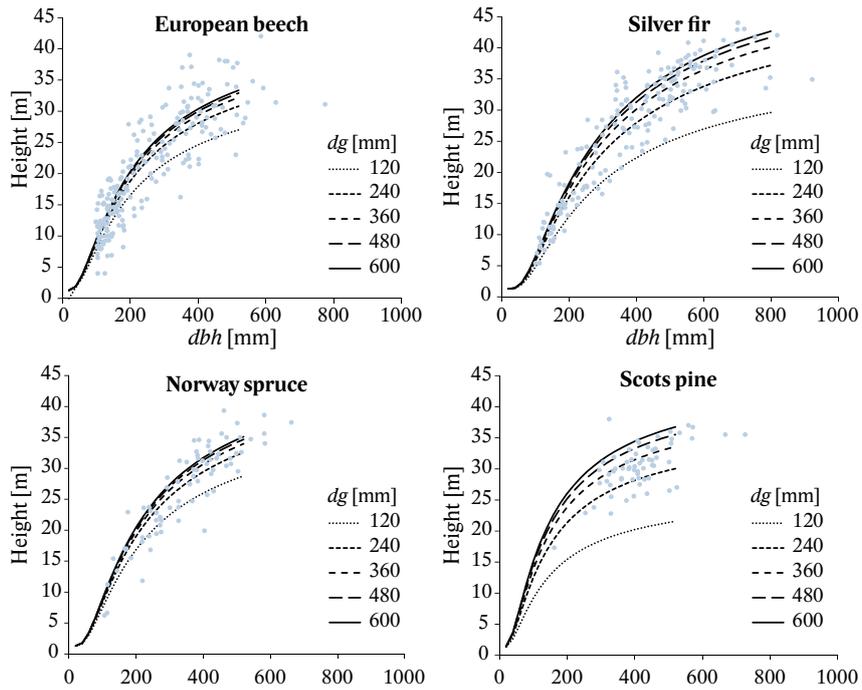


Fig. 4. Species specific height-diameter model characteristics at different mean stand diameter (dg) against the original data background.

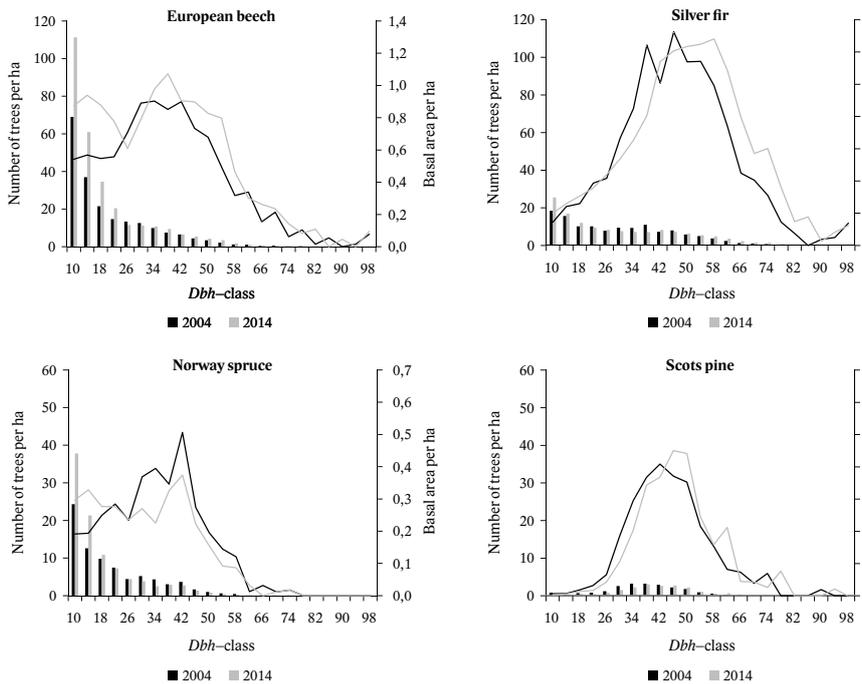


Fig. 5. Changes in species specific dbh (columns) and basal area (lines) distribution by 4-cm dbh classes between statistically reconstructed inventory in 2004 and real inventory in 2014.

3.4. Statistically reconstructed past forest status

Figure 5 illustrates forest status in 2004 estimated statistically using the set of models described above against the results of inventory in 2014. Shade tolerant species such as fir, beech and spruce showed expo-

nentially decreasing dbh distribution and accelerated ingrowth in the last decade in contrast to pine, which is not able to regenerate in shade and therefore also survive prospectively in such a forest structure. Distribution of the basal area (ba) of all species except spruce shifted more or less to the higher dbh classes, what caused an

increase of total standing timber volume, while *ba* of the beech is higher almost for all *dbh* classes suggesting that mainly beech gradually replace the declining spruce. A general decrease of spruce *ba* due to mortality caused by bark beetles was compensated by the increment of other species. There might be more causes behind vigorous regeneration and ingrowth processes of shade tolerant species in the understorey observed in the last decade. Fairly intensive felling in the 1994–2004 period (72 m³/ha according to FMP) was probably the main cause combined with larger canopy openings following felling of declining spruce trees, and a general shift of residual stock to higher *dbh* classes enabling understorey regeneration as described e.g. by Olivier & Larson (1996).

Table 4 summarizes fundamental parameters of the model forest: growing stock, felling and increment, as well as its dynamics during the period of interest. Increment was calculated simply as a difference of growing stock volume between 2014 and 2004 regarding total felling in the period (Formula 8). All trees with measured (2014) or reconstructed (2004) *dbh* higher than 8.0 cm were involved in stock, hence increment includes also ingrowth of new trees.

$$\text{Increment} = \text{Stock}_{2014} - \text{Stock}_{2004} + \text{Felling} \quad [8]$$

Table 4. Development of Smolnicka Osada model forest based on the real and statistic inventory reconstructed by the models.

	Year	Stock	Harvest	Increment
		m ³ /ha (±se 95%)		
Reconstructed inventory	2004	343±21	57±8	100±19
Real inventory	2014	386±23		

4. Discussion

4.1. Diameter-stump models

Several authors have reported that using simple linear regression is fully justified for modelling the *dbh*–stump diameter relationship (e.g. Myers 1963; Hann 1976; Bylin 1982; Corral-Rivas et al. 2007; Özçelik et al. 2010). However, models incorporating stump height as a predictor variable can be superior. This is mostly correct for trees cut at different stump heights. In cases where stump height is not included in the model and there is a high variability of stump heights, the predictive ability of the model is low (Chhetri & Fowler 1996; Pond et al. 2014). In our study, we have calculated a simple linear regression model to predict diameter at breast height from the stump diameter outside bark. The stump height was not considered as a predictor variable given the assumption that all trees were cut at the height where stem started to be regular, i.e. not much deformed by root swells. Our species-specific models indicated the total *dbh* variance of 95% for beech, 96% for spruce, and 97% for fir and pine. Myers (1963) and Hann (1976) developed a linear model for Ponderosa pine and White fir with correlation of determination values of 0.99 and 0.98, respectively. We

have recorded higher values of beech *dbh* estimates than those reported by Bylin (1982) whose model explained only 71% of the total *dbh* variance due to a small sample size (n = 15). Wharton's (1984) model explained slightly lower percentage (93%) of the total *dbh* variance for beech. Conversely, Ercanli et al. (2015) used mixed effect models for predicting *dbh* from the stump diameter of Oriental beech with a coefficient of determination of 0.99. Thorpe et al. (2010) developed a linear model for black spruce explaining 97% of the total *dbh* variance.

4.2. Diameter-increment models

Our models have shown that except for *dbh*, crown proportion (*cp*) and crown quality (*cq*) variables are of higher importance than the other tree and stand variables. Furthermore, our study has confirmed that crown parameters might outweigh the influence of basal area proportion index *CIg* which was selected for this study as the best of five tested competition indices based on the study from similar mixed mature forests (Bošela et al. 2015). Thus they can be referred to as competition indices related to the radial growth. Crown parameters are more stable over time, thus providing information on past competition of trees in forest stands. As reported by Biging & Dobbertin (1992), trees with large crowns are stronger competitors compared to trees with small crowns.

The best results of model fitting were obtained for spruce where the model incorporating only *dbh*, crown ratio and total growing stock per hectare explained 74% of variance in radial growth. Crown quality variable for spruce fell outside the set of predictors due to short term changes of foliage density caused by a sudden bark beetle attack. For fir, *dbh*, crown proportion, crown quality and stand mean diameter explained 69% of the radial increment variation. For beech, mean diameter was replaced by total growing stock per hectare and the model accounted for 57% of the total variation in radial growth. Only 34% of the total variance in radial increment was explained by quadratic mean diameter and site index for pine. This apparent lack of correlation can be partly attributed to shade intolerance of the species and a small sample size (n = 64). It may be assumed that emergent pines occupying dominant positions in the canopy have never been exposed to intense competition. This fact confirms previous findings in the literature (e.g. Stadt et al. 2007). Similarly to our results, Monserud and Sterba (1996) demonstrated that most of the variance in basal area increment was attributed to *dbh* and crown ratio.

4.3. Height-diameter models

We applied the modified Michailoff's function (Michailoff 1943) to describe the tree height-diameter relationship for four targeted tree species. In addition, both *dbh* and mean diameter of the stand (*dg*) were considered

as predictor variables. The inclusion of mean diameter into Michailoff's function has proved to be valid and has increased the accuracy of the tree height-diameter model. Temesgen and Gadow (2004) found that including BAL (basal area of large trees) as a predictor variable besides *dbh* increases the accuracy of the height-diameter model for complex forest stands. Alternatively, Sharma & Zhang (2004) included the basal area, number of trees per hectare and *dbh* to improve their model's accuracy. Based on our evaluation statistics, we can conclude that our models performed satisfactorily. When comparing the model root mean squared errors (RMSE), we have found relatively small RMSEs for pine and spruce compared to two other tree species. Although the highest coefficient of determination was obtained for fir (0.87), the RMSE was the second highest (3.64 m). The model for beech had the lowest prediction accuracy with RMSE of 3.94 m. This poor performance was not surprising. In fact, to accurately measure tree height is much more challenging for broadleaved trees than for conifers due to their differences in apical dominance and greater variability in the estimation of broadleaved tree heights (Garman et al. 1995). Using long-term experimental plot data from mixed forest stands of spruce, fir and beech in the Western Carpathians, Petráš et al. (2014) created height-diameter models employing Michailoff's and Korf's function. Their data showed that the best model performance was obtained for fir with the coefficient of determination 0.94 – 0.95 and RMSE 1.94 – 1.97 m. Better results than those ours are conditioned by long term data series and more or less even-aged stand structure. Recent studies suggest using general mixed effect height-diameter models rather than general ordinary least square models because of their higher prediction accuracy (Adamec 2015; Mehtätalo et al. 2015; Sharma et al. 2016). This could also improve modelling of height-diameter relation in markedly uneven-aged forests. As noted by Crecente-Campo et al. (2014), species-specific models should be used for capturing at least the variation between tree species.

4.4. Forest dynamics derived from real and reconstructed inventory

Using real and statistically reconstructed previous inventory we recorded annual increment of 10 cubic meters per hectare, realistic in favourable growth conditions and stand structures in the study area. Our results are consistent with Saniga & Szanyi (1998), who estimated a potential increment of 9 – 12 and 8 – 10 cubic meters per hectare, respectively, based on the results from two long-term research plots established within the study area. Slovak mean increment derived from mensuration data is 6.3 cubic meters per hectare (Moravčík et al. 2016) which also includes low production forests.

Suggested procedure based on a real and a statistically reconstructed past inventory seems to be more accu-

rate and correct than simplified methods recommended by some authors for rough estimates of increment using yield tables and/or management records for the transition period when first inventory is missing (e.g. Záhradníček 2010). Furthermore, it provides a complete data set for calibration of relevant models for the appropriate management of uneven-aged forests, such as, matrix models, or traditional control methods.

5. Conclusions

In our study, we have proposed and verified an approach of using a set of three species specific models to reconstruct past forest status. Developed diameter-stump model, diameter increment model, and height-diameter model are simple and can easily be locally calibrated using standard inventory data combined with tree ring data.

Our results have shown that biometric relations and growth dynamics in mixed uneven-aged forests are strictly species specific. A high radial increment was related to trees with higher crown length and better crown quality, growing on fertile sites in younger growth stages. We are aware that results of our study are of only local validity, and models can be used for prediction only at a regional level and in specific uneven-aged mixed forest stands. Conversely, suggested procedure can be considered universal and applicable for any forest at the time of change from stand-based to plot-based inventories, related to a change from traditional even-aged to uneven-aged forest management based on control methods and/or population models.

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References

- Adamec, Z., 2015: Comparison of linear mixed effects model and generalized model of the tree height-diameter relationship. *Journal of Forest Science*, 61:439–447.
- Bauhus, J., Puettmann, K. J., Kühne, Ch., 2014: Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems? In: Messier, Ch., Puettmann, K. J., Coates, K. D. (eds.): *Managing Forests as Complex Adaptive Systems*. Routledge London and New York, p. 187–213.
- Biging, G. S., Dobbertin, M., 1992: A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science*, 38:695–720.

- Biolley, H., 1887: Quelques réflexions sur le jardinage à propos des publications de M. Gurnaud. Schweizerische Zeitschrift für Forstwesen, 38:189–192.
- Bošela, M., Tobin, B., Šebeň, V., Petráš, R., Larocque, G. R., 2015: Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. Canadian Journal of Forest Research, 45:1577–1586.
- Buongiorno, J., Michie, B. R., 1980: A matrix model of uneven-aged forest management. Forest Science, 26: 609–625.
- Bylin, C. V., 1982: Estimating dbh from stump diameter for 15 southern species. Res. Note SO-286. New Orleans, LA: US Department of Agriculture, Forest Service, Southern Forest Experiment Station 3, 286 p.
- Chhetri, D. B. K., Fowler, G. W., 1996: Estimating diameter at breast height and basal diameter of trees from stump measurements in Nepal's lower temperate broad-leaved forests. Forest Ecology and Management, 81:75–84.
- Corral-Rivas, J. J., Barrio-Anta, M., Aguirre-Calderón, O. A., Diéguez-Aranda, U., 2007: Use of stump diameter to estimate diameter at breast height and tree volume for major pine species in El Salto, Durango (Mexico). Forestry, 80:29–40.
- Crecente-Campo, F., Corral-Rivas, J. J., Vargas-Larreta, B., Wehenkel, C., 2014: Can random components explain differences in the height–diameter relationship in mixed uneven-aged stands? Annals of forest science, 71:51–70.
- Dvorak, L., 2000: Kontrollstichproben im Plenterwald. Dissertation ETH Nr. 13 799. Eidgenössische Technische Hochschule Zürich.
- Ercanli, I., Gunlu, A., Başkent, E. Z., 2015: Mixed effect models for predicting breast height diameter from stump diameter of Oriental beech in Göldağ. Scientia Agricola, 72:245–251.
- Garman, S. L., Acker, S. A., Ohmann, J. L., Spies, T. A., 1995: Asymptotic height-diameter equations for twenty-four tree species in Western Oregon, Research Contribution 10, Forest Research Laboratory, Oregon State University, Corvallis, 22 p.
- Hann, D. W., 1976: Relationship of stump diameter to diameter at breast height for seven tree species in Arizona and New Mexico. Dept. of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
- Hasenauer, H. (ed.), 2006: Sustainable Forest Management – Growth models for Europe. Springer, 398 p.
- Leslie, P. H., 1945: The use of matrices in certain population mathematics. Biometrika, 33:183–212.
- Mehtätalo, L., de-Miguel, S., Gregoire, T. G., 2015: Modeling height-diameter curves for prediction. Canadian Journal of Forest Research, 45:826–837.
- Michailoff I., 1943: Zahlenmässiges Verfahren für die Ausführung der Bestandeshöhenkurven. Forstwissenschaftliches Centralblatt – Tharandter Forstliches Jahrbuch, 6:273–279.
- Möller, A., 1922: Der Dauerwaldgedanke – Sein Sinn und Seine Bedeutung. Springer-Verlag Berlin, 136 p.
- Monserud, R. A., Sterba, H., 1996: A basal area increment model for individual trees growing in even and uneven-aged forest stands in Austria. Forest ecology and management, 80:57–80.
- Moravčík, M. et al., 2016: Green report on the Slovak forestry 2015. Ministry of Agriculture of the Slovak Republic and National Forest Centre, 76 p.
- Myers, C. A., 1963: Estimating volumes and diameters at breast height from stump diameters, southwestern ponderosa pine (Vol. 9). Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture.
- Olivier, C. D., Larson, B. C., 1996: Forest stands dynamics. John Wiley, New York, 520 p.
- Özçelik, R., Brooks, J. R., Diamantopoulou, M. J., Wiant Jr, H. V., 2010: Estimating breast height diameter and volume from stump diameter for three economically important species in Turkey. Scandinavian Journal of Forest Research, 25:32–45.
- Petráš, R., Bošela, M., Mecko, J., Oszlányi, J., Popa, I., 2014: Height-diameter models for mixed-species forests consisting of spruce, fir, and beech. Folia Forestalia Polonica, 56:93–104.
- Pond, N. C., Froese, R. E., 2014: Evaluating published approaches for modelling diameter at breast height from stump dimensions. Forestry, 87:683–696.
- Pukkala, T., 2016: Which type of forest management provides most ecosystem services? Forest Ecosystems, p. 2–16.
- Pukkala, T., Lähde, E., Laiho, O., 2009: Growth and yield models for uneven-sized stands in Finland. Forest Ecology and Management, 258:207–216.
- Roessiger, J., Ficko, A., Clasen, C., Griess, V. C., Knoke, T., 2016: Variability in growth of trees in uneven-aged stands displays the need for optimizing diversified harvest diameters. European Journal Forest Research, 135:283–295.
- Saniga, M., Szanyi, O., 1998: Modely výberkových porastov vo vybraných lesných typoch a geografických celkoch Slovenska. Vedecké štúdie 4/1998/A. TU Zvolen, 50 p.
- Sharma, M., Zhang, S. Y., 2004: Height-diameter models using stand characteristics for *Pinus banksiana* and *Picea mariana*. Scandinavian Journal of Forest Research, 19:442–451.
- Stadt, K. J., Huston, C., Coates, K. D., Feng, Z., Dale, M. R., Lieffers, V. J., 2007: Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Annals of Forest Science, 64:477–490.
- Temesgen, H., Gadow, K. V., 2004: Generalized height-diameter models – an application for major tree species in complex stands of interior British Columbia. European Journal of Forest Research, 123:45–51.

- Thorpe, H. C., Vanderwel, M. C., Fuller, M. M., Thomas, S. C., Caspersen, J. P., 2010: Modelling stand development after partial harvests: an empirically based, spatially explicit analysis for lowland black spruce. *Ecological Modelling*, 221:256–267.
- Wharton, E. H., 1984: Predicting diameter at breast height from stump diameters for northeastern tree species (Vol. 322). US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.
- Záhradníček, J., 2010: Metodika hospodářské úpravy nepasečných hospodářských lesů. Ministerstvo životního prostředí České republiky, 59 p.

Long-term transformation of submontane spruce-beech forests in the Jizerské hory Mts.: dynamics of natural regeneration

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Abstract

The paper deals with development of the natural regeneration of even-aged spruce-beech forests during their transformation to uneven-aged stands with diversified structure at the Jedlový důl area in the Protected Landscape Area Jizerské hory Mts., Czech Republic. Shelterwood management system and free felling policy based on selection principles has been applied there since 1979 with the support of admixed tree species of the natural species composition, especially silver fir (*Abies alba* Mill.). The research was focuses on structure and development of natural regeneration with the emphasis on ungulate damage and interaction with tree layer from 1979 to 2015. In the course of 36 years, the regeneration structure was diversified towards the close-to-nature tree species composition, spatial and age structure. The number of regeneration recruits increased in average from 941 to 41,669 ind ha⁻¹. During this period share of European beech (*Fagus sylvatica* L.) significantly ($p < 0.01$) increased (by 53.6%), while the share of Norway spruce (*Picea abies* [L.] Karst.) decreased (by 51.5%), such as damage caused by ungulate (by 61.4%) with the highest loses on sycamore maple (*Acer pseudoplatanus* L.), rowan (*Sorbus aucuparia* L.) and silver fir. Moreover, the parent trees had a significant negative influence on natural regeneration at smaller spacing (within a 1 – 5 m radius from the stem). Both, regeneration potential and effective role of the tree layer during the forest transformation has been confirmed as important prerequisites for ongoing forest transformation.

Key words: regeneration development; forest transformation; shelterwood system; stand structure; browsing damage

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1. Introduction

Currently, many studies are devoted to sustainable forest management and conservation of biological diversity (Fürst et al. 2007; Pretzsch et al. 2008; Pimm et al. 2014; Schulze et al. 2016; Correia et al. 2017). Most national forest strategies have been formulated in support of this trend e.g. 2016–2025 Strategy of Conserving Biological Diversity of the Czech Republic (Mach et al. 2016). There is also a strong emphasis on the transformations of forest stands that were degraded in the past (Stanturf et al. 2014) or have undergone significant changes in the last 70 years. This happened mainly in the former socialist countries of Eastern and Central Europe, where nationalization of forest estates, vast plantations of conifers and subsequent restitutions in the 90s of the 20th century took place (Bouriaud et al. 2015; Podrázský et al. 2014; Schulze et al. 2014). In addition, anthropogenic changes in global ecosystems (Kareiva et al. 2007; Ellis

et al. 2013) and assumed impacts of climate change still enhance the need of forest stand transformation (Steffen et al. 2007; Zalasiewicz et al. 2010; Kulla & Sitková 2012). Transformations become part of a broader strategy of climate change mitigation, and other urgent environmental problems of this time such as loss of biological diversity (Thomas et al. 2014; Spiecker et al. 2004). One of the crucial factors influencing the success of performed forest transformations is the existence of natural regeneration that is more productive and resistant to external environmental impacts in comparison with artificial regeneration (Hasanov et al. 2016). At the same time it also is an indicator of forest vitality and stability (Šticha et al. 2010). Natural regeneration is an inherent element of natural forest dynamics and belongs to the general concept of forest adaptation on the basis of forest dynamics and its management including active and passive strategies of forest ecosystem management (Millar et al. 2007).

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Taking into account vast forest areas that are suitable for stand transformations, approaches accentuating the ecosystem functionality can be more beneficial contrary to conventional approaches aimed at predetermined species composition at small area units (Lamb et al. 2012; Oliver 2014). A determinant trait of functional transformations is orientation to sustainability in multifunctional ecosystem processes including hydrological cycles and ecosystem productivity (Stanturf et al. 2014).

In the past there were forest ecosystem transformations with limited success only or that failed completely (Wuethrich 2007). This is the reason why it is important that current and future projects, which usually demand great efforts and many times considerable investments, will be performed in a sustainable and relatively flexible way. In this context Wagner (2004) presented adaptive forest management aimed at maintenance and development of forest functionality as a precondition to meet future needs of forest ecosystems. Such management is defined as a dynamic approach, where the consequences of interventions and particular decisions are monitored and evaluated all the time. This approach continually affects future management steps for the purpose of optimum fulfilment of management objectives (Bolte et al. 2009). Mostly, reasons for forest transformation failure are genetically inconvenient reproductive material not sufficiently adapted to conditions of the given environment and unsuitable silvicultural methods and techniques (Godefroid et al. 2011; Wenying et al. 2013). The reproductive material is very important for transformation because it influences transformation success from both short-term and long-term aspects (Thomas et al. 2014). Genetic suitability positively influences not only individual tree populations (Breed et al. 2012) but also the general ecosystem function and resistance (Thompson et al. 2010; Kettenring et al. 2014).

In the framework of transformations of spruce-beech stands and ongoing climate changes it is to take into account that long-term temperature increase is considered as a reason for higher competitiveness of beech in comparison to spruce (Grundmann et al. 2011). It is to note that spruce is more vulnerable to heat and drought events because of its shallow root system (Schmid 2002; Bolte et al. 2014) and its adaptation to cold and humid climate (Latołowa & van der Knaap 2006). Therefore an increasing proportion of beech is to expect in future at many sites in the Central European region (Menšík et al. 2009).

The objective of the present study is to evaluate natural regeneration in relation to the tree layer within forest stand transformation from 1979 to 2015. The study should answer the following questions:

- which changes have occurred in the species composition of natural regeneration,
- which changes have occurred in the maturity and spatial pattern of regeneration,
- which changes have occurred in the biodiversity of regeneration,

- how ungulates have affected the height structure and species composition of regeneration,
- what is the relation between natural regeneration and tree layer.

The basic hypothesis is that forest stands with this silvicultural strategy have higher ecological stability and biodiversity compared to evenaged spruce-dominated stands.

2. Material and methods

2.1. Study site

The territory of interest in the area of Jedlový důl in the Jizerské hory Mts. is RC1265 Josefodol I Regional Biocentre, which encompass the Josefův důl Gene Resources. At the same time, this territory is part of the Jizerské hory Protected Landscape Area (PLA) and Jizerské hory Bird Conservation Area CZ0511008.

In terms of the CR geomorphological classification according to Demek et al. (1987) the territory of interest belongs to the Krkonoše-Jeseníky range system (province), Krkonoše Mts. subsystem (subprovince), Jizerské hory Mts. area and Jizerská hornatina subarea. The bedrock is composed of porphyritic medium-grained granite or granodiorite of the Krkonoše-Jizerské hory granite pluton (Chaloupský 1989). Cambisols and Cryptopodzols are prevailing soil types. The climate of the area is suboceanic, which is related to the distinctly windward position of the Jizerské hory Mts. Average annual temperature is in the range of 5.2–6.5 °C relative to the altitude. Annual precipitation amounts are 1 200–1 300 mm. The study territory belongs to humid continental climate characterised by hot and humid summers and cold to severely cold winters (Dfb) with the transition to subarctic climate (Dfc) according to Köppen climate classification (Köppen 1936), respectively by detailed region Quitt distribution (Quitt 1971) to a cold climatic region and CH 7 subregion.

The studied territory is covered by foothills spruce-beech forests of more or less natural type. These are mostly highly structured stands of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst.), interspersed sycamore maple (*Acer pseudoplatanus* L.), silver fir (*Abies alba* Mill.), rowan (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth.) with ongoing natural regeneration of all above-mentioned species. The fir was introduced into these stands in the 80s and 90s of the 20th century through group underplantings (combined regeneration). In terms of phytocoenology these are mostly acidophilous foothills beech forests (the association *Luzulo luzuloidis*–*Fagetum sylvaticae* Meusel 1937, *Calamagrostio villosae*–*Fagetum* Mikyška 1972) and partly impoverished forms of herb-rich beech forests (the association *Dentario enneaphylli*–*Fagetum* Oberdorfer ex W. et A. Matuszkiewicz 1960).

Figure 1 shows the location of permanent research plots (PRP) while basic data on PRP are documented in Table 1. On all PRP the growing season length is about 131 days, average temperature in the growing season is around 10.7 °C and rainfall amount in the growing season is 646 mm on average. The bedrock of all PRP is built of porphyritic, medium-grained granite. Soil type is predominantly modal Cambisol.

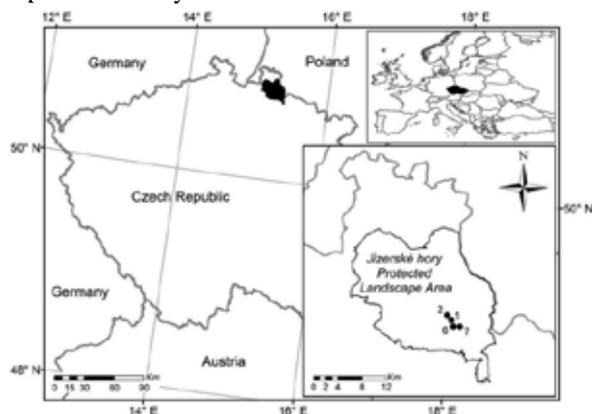


Fig. 1. Localization of spruce-beech forests on permanent research plots 1, 2, 6 and 7 in the Jizerské hory Mts.

2.2. Data collection

To determine the tree layer and regeneration structure of forest ecosystems 4 PRP of 50 × 50 m in size (0.25 ha) were established in 1979 by prof. S. Vacek and Ing. Z. Cipra in cooperation with Forest Research Station at Opočno and PLA Administration Jizerské hory Mts. using theodolite (Vacek & Cipra 1979). In 2015 the FieldMap technology (IFER–Monitoring and Mapping Solutions Ltd.) was used for the re-measurement.

For the individuals of regeneration with breast-height diameter (dbh) < 4 cm and height ≥ 150 cm these characteristics were measured on the whole plot: position, height, distance of live crown base to the ground level, crown width (with a height measuring pole to the nearest cm), root collar diameter and the species was identified. The same parameters were measured for recruits in height range 5 – 150 cm, only on representative subplots 10 × 50 m in size on each PRP. Browsing by ungulate on leading shoots (0 = no browsing, 1 = the first browsing of leading shoot, 2 = repeated browsing of leading shoot) was monitored in all recruits as specified according to the tree species lateral browsing was studied in the same way.

2.3. Data analysis

Structural and growth parameters, abundance, vertical structure, spatial pattern and species diversity were evaluated for all individuals of regeneration on each plot. For evaluation of species diversity of natural regeneration following indices were used: species richness indices D_1 (Margalef 1958) and D_2 (Menhinick 1964), species heterogeneity indices H' (Shannon 1948) and λ (Simpson 1949) and species evenness indices E_1 (Pielou 1975) and E_2 (Hill 1973). The height structure was evaluated by the Gini index G using individual recruit data (Gini 1921). The Gini coefficient was calculated using equation according to Glasser (1962). Criteria for the assessment of these biodiversity indices are shown in Table 2.

For the spatial pattern of regeneration these indices were computed: Hopkins-Skellam index A (Hopkins & Skellam 1954), Pielou-Mountford index α (Pielou 1959; Mountford 1961), Clark-Evans index R (Clark & Evans 1954) and Ripley's K -function (Ripley 1981). Among dis-

Table 1. Basic site and stands characteristics of permanent research plots.

PRP	GPS coordinates	Altitude [m]	Exposition	Slope [°]	Forest site type ¹	Tree species ²	Felling (1979–2015) [m ² ha ⁻¹]	Year of record	Age of tree layers (y)	Stand volume [m ³ ha ⁻¹]	Number of trees [trees ha ⁻¹]
1	50°47'26" N 15°15'02" E	750	SE	9	6S	FS, PA, AA, SA	63	1979	153/22	559	408
								2015	117	604	1032
2	50°47'28" N 15°14'59" E	730	SE	8	6S	FS, PA, AA, AP	150	1979	153/26	604	420
								2015	117	536	1464
6	50°47'24" N 15°15'04" E	765	SE	7	6S	FS, PA, AA, SA, BP	67	1979	153/26	489	380
								2015	117	530	1464
7	50°47'25" N 15°15'11" E	725	SE	11	6S	FS, PA, AA, AP	82	1979	153/22	400	444
								2015	117	497	1424

Explanatory notes: ¹6S – *Piceo-Fagetum oligomesotrophicum*, *Calamagrostio villosae-Fagetum* Mikyška 1972; Species²: FS – *Fagus sylvatica*, PA – *Picea abies*, AA – *Abies alba*, SA – *Sorbus aucuparia*, AP – *Acer pseudoplatanus*, BP – *Betula pendula*.

Table 2. Overview of the indices describing regeneration diversity and their interpretation.

Criterion	Quantifiers	Label	Reference	Evaluation
Species diversity	Heterogeneity	H' (Shi)	Shannon (1948)	minimum H' (λ) = 0, higher H' (λ) = higher values
		λ (Sii)	Simpson (1949)	
	Evenness	E_1 (Pi)	Pielou (1975)	range 0 – 1; minimum $E = 0$, maximum $E = 1$
		E_2 (Hi)	Hill (1973)	
Richness		D_1 (Mai)	Margalef (1958)	minimum $D = 0$, higher D = higher values
		D_2 (Mei)	Menhinick (1964)	
Horizontal structure	Index of non-randomness	α (P&Mi)	Pielou (1959); Mountford (1961)	mean value $\alpha = 1$, aggregation $\alpha > 1$, regularity $\alpha < 1$ mean value $A = 0.5$, aggregation $A > 0.5$, regularity $A < 0.5$ mean value $R = 1$, aggregation $R < 1$, regularity $R > 1$ mean value $CS = 0$, aggregation $CS < 0$, regularity $CS > 0$
		A (H&Si)	Hopkins & Skellam (1954)	
		R (C&Ei)	Clark & Evans (1954)	
	Index of cluster size	CS (D&Mi)	David & Moore (1954)	
Vertical structure	Gini index	G (Gi)	Gini (1921); Glasser (1962)	range 0 – 1; low $G < 0.3$, very high differentiation $G > 0.7$

tribution indices based on the tree frequency in particular quadrats the David-Moore index *CS* (David & Moore 1954) was used. The chosen size of quadrats on PRP was 10 × 10 m (25 quadrats). To compute these characteristics describing the horizontal structure of individuals on the plot the PointPro 2 programme (© 2010 CULS, Zahradnik & Pus, Prague) was used. The test of significance of deviations from the values expected for the random pattern of points was done by Monte Carlo simulations (95% confidence interval). The mean values of the *K*-function were estimated as arithmetical means of the *K*-functions computed for 1999 randomly generated point structures. The spatial relations of natural regeneration and tree layer were evaluated by the cross-type pair correlation function *g(r)* – (Stoyan & Stoyan 1992).

Statistical analyses were processed in Statistica 13 (© 2016 Del Inc., Tulsa). Differences in tree species composition, game damage and diversity indices of natural regeneration recruits in course of time and among PRP were tested by one-way analysis of variance (ANOVA) and significant differences were consequently tested by post-hoc comparison Tukey’s HSD tests. Significance of statistics was noted as follows: $p > 0.05$, $p < 0.05$, $p < 0.01$ and $p < 0.001$. Unconstrained principal component analysis (PCA) in the CANOCO for Windows 5 program (© 2013 Biometris, ter Braak & Smilauer, Wageningen) was used to analyse relationships among natural regeneration parameters, characteristic of tree layer, tree species, time and similarity of 4 PRP. Data were centred and standardized during the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram.

3. Results

3.1. Species composition and density

The number of natural regeneration on PRP in 1979 was from 680 (PRP 7) to 1,152 (PRP 6) recruits ha⁻¹. The proportion of beech on PRP at that time was 13 – 26%, spruce 67 – 83%, fir 0 – 1%, rowan 0 – 2%, birch 0 – 5%

and sycamore maple 0 – 4%. The number of recruits (in fir also partly of individuals of combined regeneration – fir underplanting from denser natural seeding in the given stands was performed in 1980–1984) in 2015 ranged from 24,964 (PRP 1) to 77,036 (PRP 6) recruits ha⁻¹. The proportion of beech on PRP was 43 – 84%, spruce 15 – 52%, fir 0 – 6%, rowan 0 – 3% and the proportions of sycamore and birch were negligible (Table 3).

In the course of 36 years, the total number of natural regeneration significantly increased (44 times; $F_{(1,6)} = 11.7$, $p < 0.01$), respectively density of all main tree species ($F_{(1,30)} = 6.9$, $p < 0.01$). Specifically, significant increase ($p < 0.05$) were observed in spruce, beech and fir. In the study period, share of beech significantly increased ($F_{(1,6)} = 28.9$, $p < 0.01$) by 53.6%, while the share of spruce significantly decreased ($F_{(1,6)} = 30.0$, $p < 0.01$) by 51.5%. There were no significant differences in density dynamics of fir ($F_{(1,6)} = 1.6$, $p > 0.05$; increase by 1.6%) and rowan ($F_{(1,6)} = 0.8$, $p > 0.05$; decrease by 0.9%).

3.2. Diversity

Table 4 shows the indices describing species diversity of natural regeneration on PRP. Species richness evaluated by the index of the relative measure of species diversity *D*₁ was medium on all PRP while it was low according to the *D*₂ index. According to the λ index the species diversity was medium on all PRP and by the entropy *H'* index it was medium on PRP 2 and 6, high on PRP 1 and low on PRP 7. The species evenness of natural regeneration according to the Pielou index of was low to medium and according to Hill index it was medium to high. Comparing individual PRP, there were observed similarity ($F_{(3,24)} = 0.2$, $p > 0.05$) in diversity (except aggregation indices).

The spatial pattern of natural regeneration on all plots in 2015 was significantly aggregated ($A = 0.708 - 0.851$, $\alpha = 1.997 - 3.796$, $R = 0.714 - 0.832$, $CS = 5.516 - 8.477$) with the highest trend of clumpiness on PRP 7 (Table

Table 3. Per-hectare numbers (share) of natural regeneration (height ≥ 5 cm, dbh < 4 cm) specified according to tree species in 1979 and 2015.

PRP	Year	<i>Fagus sylvatica</i>		<i>Picea abies</i>		<i>Abies alba</i>		<i>Sorbus aucuparia</i>		<i>Betula pendula</i>		<i>Acer pseudoplatanus</i>		Total density recruits
		recruits	%	recruits	%	recruits	%	recruits	%	recruits	%	recruits	%	
1	1979	248	26.1	640	67.2	4	0.4	12	1.2	48	5.1	0	0	952
	2015	19,804	79.3	3,852	15.4	644	2.6	660	2.6	4	0	0	0	24,964
2	1979	136	13.9	816	83.3	8	0.8	4	0.4	16	1.6	0	0	980
	2015	13,888	42.5	16,968	51.9	1,816	5.6	4	0	0	0	0	0	32,676
6	1979	168	14.6	932	80.9	4	0.3	48	4.2	0	0	0	0	1,152
	2015	58,372	75.8	16,824	21.8	496	0.6	1,340	1.8	0	0	4	0	77,036
7	1979	88	12.9	540	79.4	8	1.2	16	2.4	0	0	28	4.1	680
	2015	26,896	84.1	5,036	15.7	64	0.2	4	0	0	0	0	0	32,000

Table 4. The indices describing the diversity of regeneration on permanent research plots 1, 2, 6 and 7 in 2015.

PRP	<i>D</i> ₁ (Mai)	<i>D</i> ₂ (Mei)	λ (Sii)	<i>H'</i> (Shi)	<i>E</i> ₁ (Pi)	<i>E</i> ₂ (Hi)	α (P&Mi)	<i>A</i> (H&Si)	<i>R</i> (C&Ei)	<i>CS</i> (D&Mi)	<i>G</i> (Gi)
1	0.466	0.068	0.454	0.856	0.532	0.615	0.795*	2.886*	0.791*	5.809*	0.399
2	0.349	0.054	0.354	0.631	0.455	0.624	0.815*	3.715*	0.832*	5.516*	0.459
6	0.433	0.049	0.306	0.562	0.349	0.583	0.708*	1.997*	0.819*	8.477*	0.499
7	0.365	0.066	0.524	0.307	0.221	0.958	0.851*	3.796*	0.714*	5.926*	0.518

Explanatory notes: *D*₁ and *D*₂ – indices of species richness, λ and *H'* – indices of species heterogeneity, *E*₁ and *E*₂ – indices of species evenness; α , *A*, *R* and *CS* – aggregation indices (* statistically significant at level $\alpha = 0.05$); *G* – index of vertical structure.

4). The aggregation of recruits smaller than 1.5 m was higher on all PRP than that of all recruits. The aggregated pattern of recruits according to their distance (spacing) is indicated by Ripley's K-function (Fig. 2). The most distinct clumpiness was on PRP 7. Higher clumpiness was demonstrated in beech than in spruce. The vertical structure reached medium (PRP 1, 2) to high (PRP 6, 7) differentiation.

3.3. Height development

In 1979 natural regeneration on PRP was mostly unestablished (96% of recruits were smaller than 50 cm), while substantial development and differentiation of natural regeneration occurred until 2015, in fir partly of the combined established regeneration. The height structure of recruits in 2015 was mostly left-skewed. Most recruits belong by their height to classes in the range of 30 to 120 cm (67.7–82.6%), in beech it was 46.1–81.5% and in spruce 51.9–85.6% (Fig. 3). Established regeneration (above the height of 50 cm) was dominant on all PRP. The proportion of unestablished regeneration (lower than 50 cm of height) on PRP ranged of 23.2–38.7%, in beech it was 14.4–26.3%, in spruce 20.8–58.9% and in fir 0–62.1%.

The mean height of recruits was comparable on all plots, ranging from 97 to 169 cm, in beech it was 105–149 cm, in spruce 68–120 cm, in fir 92–227 cm, in sycamore maple 150 cm, in rowan 104–255 cm and in birch 38–330 cm. In recruits smaller than 150 cm the range was 69–82 cm, in beech 77–88 cm, in spruce 58–86 cm, in fir 53–70 cm, in rowan 68–72 cm and in birch 38 cm. In recruits taller than 150 cm the height range was 238–266 cm, in beech 285–314 cm, in spruce 222–232 cm, in fir 204–232 cm, in sycamore maple 150 cm and in rowan 190–391 cm. On the particular PRP the natural regeneration development specified according to tree species was of similar character.

3.4. Damage by wildlife

In 1979 natural regeneration was severely and repeatedly damaged by ungulate game, especially by red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.). The greatest damage was caused by browsing of the leading shoot to sycamore maple, rowan and fir (100%), 93% in beech, 69% in spruce and 66% of leading shoots were damaged in birch. Browsing of lateral shoots in sycamore maple amounted to 100% on average, 94% in rowan, 90% in fir, 82% in beech, 48% in spruce and 45% in birch.

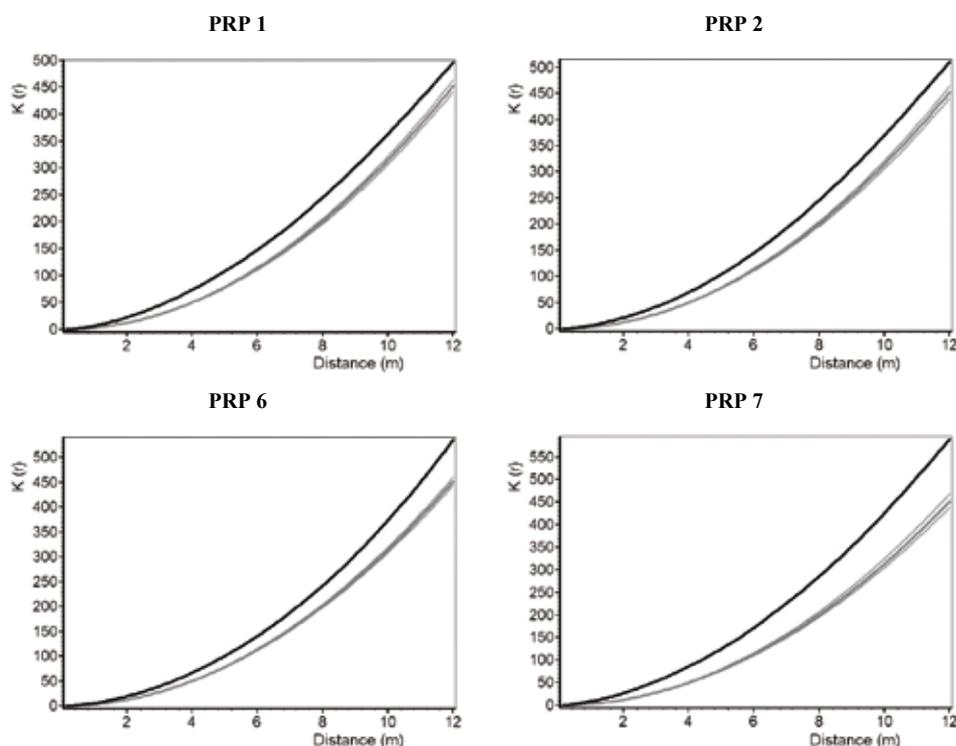


Fig. 2. Horizontal structure of natural regeneration on particular permanent research plots in 2015; the black line represents the K -function for real distances of recruits on PRP, the thick grey line illustrates the random spatial distribution of recruits and two thinner central curves represent a 95% confidence interval; when the black line of recruits distribution on PRP is below this interval, it indicates a tendency of individuals toward regular distribution, and if it is above this interval, it shows a tendency toward aggregation.

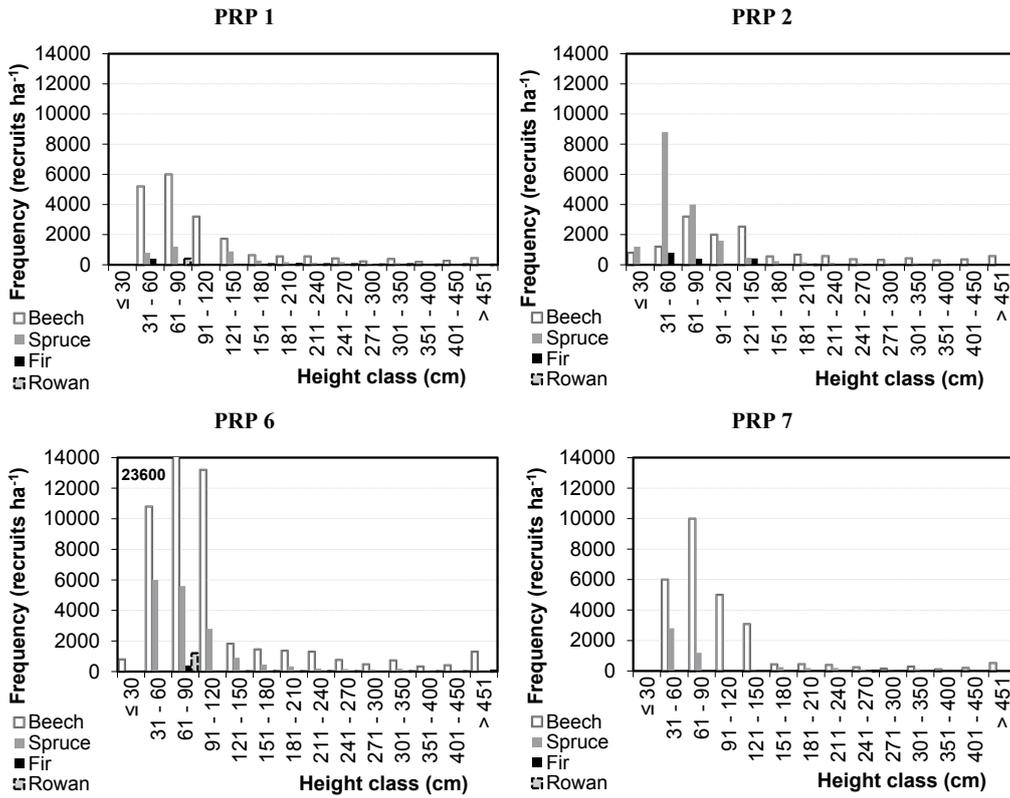


Fig. 3. Histogram of the height structure of recruits specified according to dominant tree species on permanent research plots 1, 2, 6 and 7 in 2015.

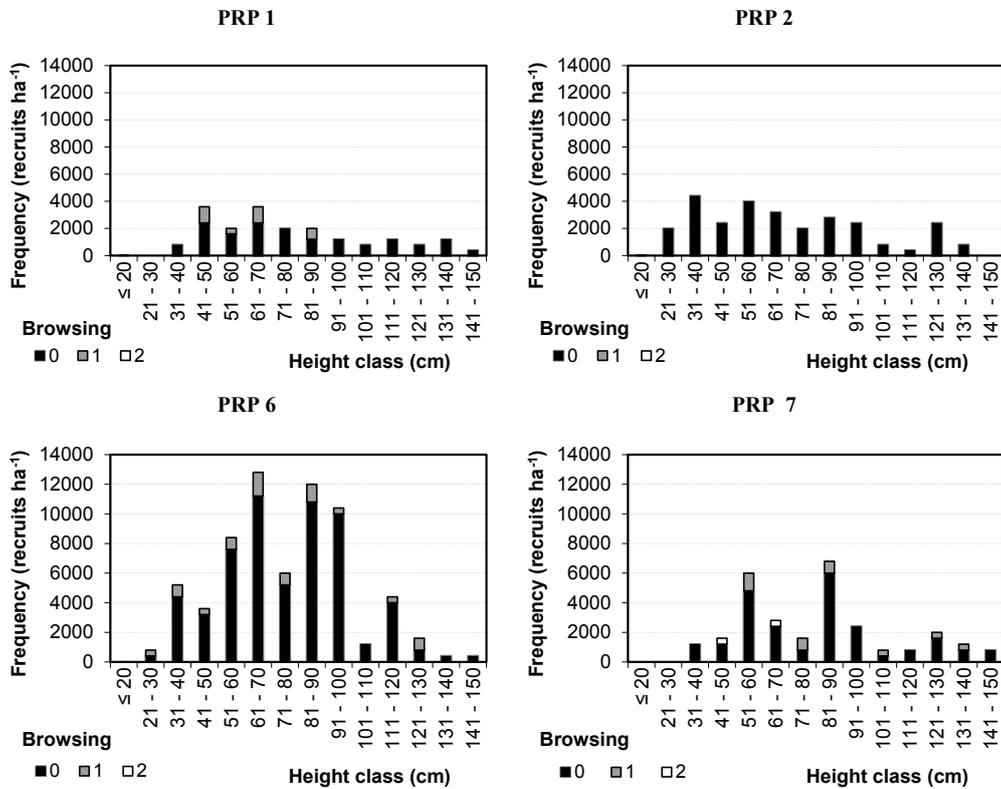


Fig. 4. Distribution of browsing of leading shoots in height classes of regeneration on permanent research plots in 2015; 0 = no browsing, 1 = the first browsing of leading shoot, 2 = repeated browsing of leading shoot.

In 2015 the proportion of recruits damaged by browsing of the leading shoot was from 0 to 23%. 22.5% of recruits on PRP 1 were damaged by the first browsing of the terminal shoot, while it was 0% on PRP 2, 12.8% on PRP 6 and 17.2% of recruits on PRP 7. On PRP 7 0.7% of recruits suffered damage by repeated browsing of the terminal shoot. The highest losses due to browsing were observed in sycamore maple (100%), followed by rowan (57%), fir (36%), beech (12%) and the lowest loss was incurred in spruce (3%). Fig. 4 shows browsing distribution in height classes of regeneration. The greatest damage by ungulate game was caused to recruits of 40 – 90 cm in height and with the root collar diameter of 6 – 12 mm. Sycamore seedlings were almost totally eliminated by hares (*Lepus europaeus* Pallas) there and rowan seedlings to a large extent. Browsing of lateral shoots on PRP accounted for 1 – 18%. The first browsing of lateral shoots damaged 18.2% of recruits on PRP 1, 0% on PRP 2, 8.8% on PRP 6 and 14.4% of recruits on PRP 7. 0.4% of individuals were damaged by repeated browsing of lateral shoots on PRP 7. In the course of 36 years, damage by browsing significantly decreased ($F_{(1,34)} = 35.0, p < 0.01$) across all tree species due to high

density of natural regeneration. Comparing individual tree species, there were observed significant differences ($F_{(4,31)} = 3.6, p < 0.05$) in the size of damage by browsing. The significantly highest ungulate damage was observed in maple, while the significantly lowest damage was in spruce ($p < 0.05$).

3.5. Relations of regeneration and tree layer

On all PRP the spatial pattern of recruits in relation to the tree layer was evaluated as random at distances longer than 5 – 7 m, only on PRP 1 from a distance of 1 m (Fig. 5). The regular pattern was observed at shorter distances, while especially within 1 m it was a distinctly regular distribution, significant on all plots. This pattern reflects a negative influence of the tree layer on natural regeneration at small distances.

Relationships among natural regeneration parameters, characteristic of tree layer, tree species and time are presented in the form of the ordination diagram (PCA) in Fig. 6. The first ordination axis explains 49.1%, the first two axes together 84.2% and the first four axes

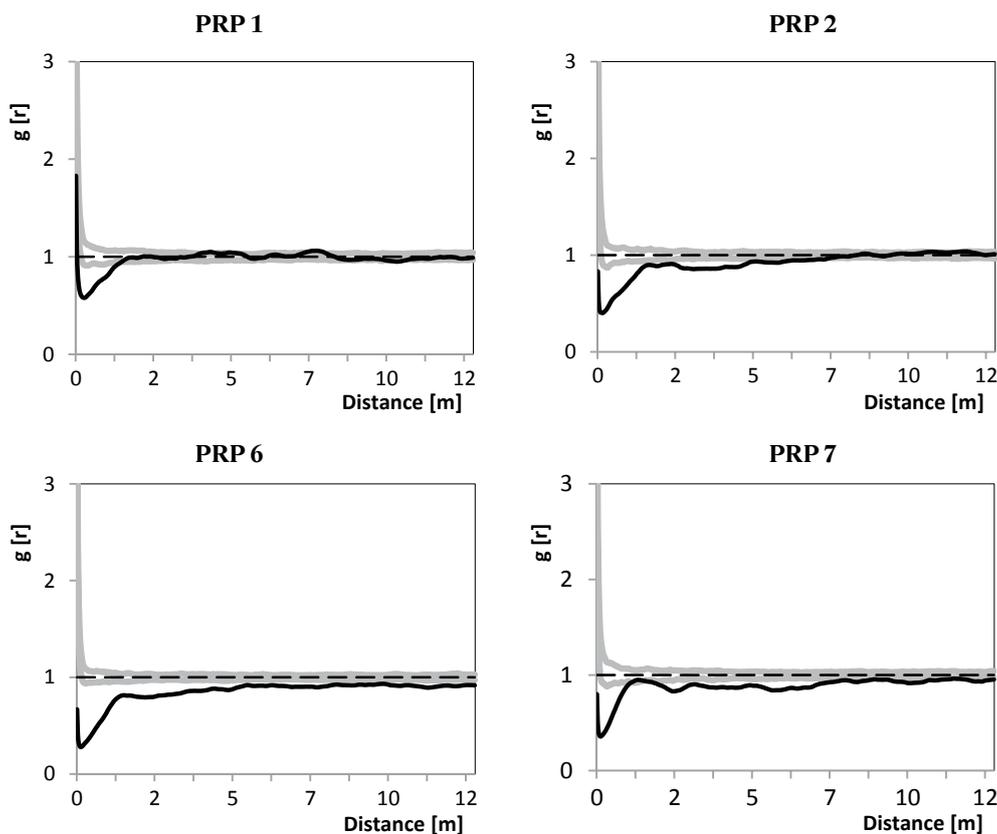


Fig. 5. The relation between natural regeneration and the tree layer of all tree species in a mixed stand on particular permanent research plots; the bold black line represents the cross-type pair correlation function for real distances of individuals; the dashed black line on the level of $g(r) = 1$ represents the mean course for random spatial distribution of trees and the two grey curves 95% confidence interval; when the observed value exceeds the upper limit of the simulation interval, it indicates significant aggregation – positive relationship between two tested groups, and if it is under this interval, it shows inhibition – negative relationship.

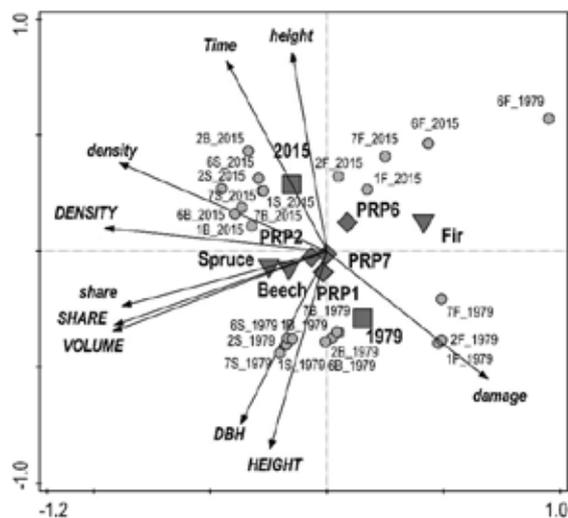


Fig. 6. Ordination diagram showing results of PCA analysis of relationships among natural regeneration parameters (*density* – number of recruits, *height*, *share* of tree species, *damage* – browsing by game), characteristic of tree layer (*DENSITY* – number of trees, *HEIGHT*, *DBH* – diameter at breast height, *SHARE* of tree species, stand *VOLUME*) and time (*Time*); large codes: ▼ indicate tree species (*Fir*, *Beech*, *Spruce*), ■ year of measurement (1979, 2015), ◆ PRP (1, 2, 6, 7); small codes: ● indicate PRP with tree species and year of measurement.

together explain 96.2% variability of the data. The first axis X represented density of tree layer. The second axis Y represented mean height of tree layer and natural regeneration. Regeneration species composition was positively correlated with species composition of tree layer. In course time, the mean height of regeneration was increasing, while DBH and height of tree layer and damage on regeneration caused by game were decreasing over 36 years. Particular PRP showed relatively similarity (instead of PRP6) compared to great differences between years of measurement and tree species. Differences of species were remarkable for fir as marks of each record were relatively distant from one another whereas marks for spruce and beech were fairly close together in the diagram. Fir with the highest browsing damage occupied the right part of the diagram, while higher stand volume, share and density were typical for beech and spruce (left part).

4. Discussion

Modern silvicultural approaches are based on continuous improvement and gradual management of forest ecosystems in order to reduce risks and uncertainties related to climate change and other environmental factors (Schelhaas et al. 2010). According to Schelhaas et al. (2015) two methods are applicable for these approaches. The one consists in shortening the rotation period and

the other in the adjustment of species composition in favour of tree species in which their better adaptability to changing climatic conditions is expected. In our study we focused especially on natural regeneration during forest transformation whose long-term development is continually associated with a change in species composition.

The results of our study explicitly document a significant increase in the proportion of beech (by 53.6%) recruits in natural regeneration over 36 years, mainly at the cost of spruce (decrease by 51.5%). This trend is in agreement with the results of some long-term studies that confirmed beech expansion at many locations in Europe (Emborg et al. 2000; Rohner et al. 2012). Poljanec et al. (2010) expected that along with climate changes the beech representation would be increasing also in future. Similar conclusions were drawn by Dakskobler (2008), who predicted beech expansion particularly into older spruce stands and pioneer forests but did not assume beech expansion into locations not so favourable for beech like frost pockets, water-logged, very steep, rocky or too dry sites. The representation of other tree species occurring as admixed ones at these localities showed quite few changes in their proportions during the studied period when the increased proportion of fir was a result of artificial regeneration – underplantings of this species in forest stands.

The total number of recruits on PRP in the studied period significantly increased from 941 to 41,669 ind ha⁻¹. Similar numbers like those were reported by others researches in the Czech Republic from spruce-beech near-natural forest in the Orlické hory Mts. – 37,230 recruits ha⁻¹ (Vacek et al. 2014; Králíček et al. 2017), while higher regeneration density were observed in the Voděradý Beechwoods – 60,859 recruits ha⁻¹ (Bílek et al. 2014), in Krkonoše Mts. – 75,395 recruits ha⁻¹ (Vacek et al. 2015a) or in old-growth forest in Slovenia – 62,000 recruits ha⁻¹ (Dusan et al. 2007). The number of recruits differs on the particular plots in relation to vegetation cover of the herb layer, topography (Štícha et al. 2010; Vacek et al. 2015b) and canopy cover of mature forest (Madsen & Hahn 2008; Sefidi et al. 2011). Light availability strongly affects the survival, growth rate and form of recruits (Grassi et al. 2004; Mountford et al. 2006). Taking into account an increasing beech proportion and generally relatively high numbers of recruits it is to state that the stand transformation currently develops well and should result in more stable forest stands better adapted to climate change in future. According to Bolte et al. (2010), in conditions of climate changes the beech shows an increased resistance to abiotic and biotic factors in comparison with spruce.

The ongoing development and related changes at the studied localities are in fact in line with the conclusions of Alexander et al. (2011), who stated that one of the proposed objectives of ecological transformations from the aspect of the Society for Ecological Restoration is the reintroduction of autogenic ecological processes. Subsequently, these processes should lead to the arrangement

of tree species into a functional and resistant ecosystem that will adapt itself to changing conditions of the environment and at the same time will provide crucial ecosystem functions (Thomas et al. 2014). Relative to the arrangement of forest ecosystems we focused on stand diversity within particular PRP. Generally, mainly lower to medium diversity was indicated in studied stands. Nevertheless, we expect its further increase with ongoing forest transformation. Knoke et al. (2008) reported that the relatively structurally complex close-to-nature mixed stands have, compared to the relatively structurally simple monospecific forests, higher stability and resistance to disturbances. The horizontal pattern of natural regeneration on all PRP was significantly aggregated, which is in agreement with many studies on natural regeneration (Nagel et al. 2006; Paluch 2007; Ambrož et al. 2015; Vacek et al. 2015a). Particularly in beech as a shade-tolerant tree species, the tendency to clumpiness in our study was more significant than in spruce. The pronounced clumpiness is due to the occurrence of recruits in small gaps in the canopy (Szwagrzyk et al. 2001; Grassi et al. 2004). But the relationships between natural regeneration and canopy density can be quite variable depending on local conditions (Collet & Le Moguedec 2007) and damage caused by the wildlife (Ficko et al. 2011; Vacek et al. 2014; Mattila & Kjellander 2017).

Monitoring of game damage on the studied PRP has revealed a generally high pressure on natural regeneration during the whole period of study. Nevertheless, there was a marked significant decrease (by 61.4%) in damage in the studied period because of 44 times higher regeneration density. However, we repeatedly observed total elimination of sycamore maple (100%) and a great part of rowan (57%) and fir (36%) were also damaged. On the contrary the lowest damage was caused to spruce (3%). These results are consistent with Vacek et al. (2014), who presented a marked suppression or even disposal of natural regeneration of fir, sycamore and rowan recruits, while the lowest damage was also reported for spruce. The attractiveness of sycamore and rowan for game was also confirmed by studies from the Italian Alps (Motta 2003), from Krkonoše Mts. (Čermák & Grundmann 2006) and from Slovakia (Konôpka & Pajtkík 2015). A high pressure on fir and factually the disposal of its natural regeneration by game browsing were described by Bottero et al. (2011) in Bosna and Herzegovina, by Jaworski et al. (2002) in the Western Carpathians or by Klopčič et al. (2010) in Slovenia; the latter authors reported about unfenced fir-beech stands, where great damage to fir recruits or even the total disposal of fir regeneration by browsing was observed. In relation to the high game pressure Vrška et al. (2001) concluded that selected forest stands should be fenced to provide natural spontaneous development of the regeneration of spruce-fir-beech forests. In our case the reducing of still increasing ungulate popula-

tions (Konôpka et al. 2015; Vacek 2017) and mechanical or repellents protection with focusing on support of fir, sycamore maple and other species largely suffering from browsing seems to be necessary (Olesen & Madsen 2008; Häslér & Senn 2012).

In terms of spatial relations between regeneration and tree layer, the spatial pattern of recruits relative to the tree layer was evaluated as random at distances over 1 – 5 m. At shorter distances the individuals of the tree layer had negative influence on natural regeneration, which was mostly revealed in Sudetes Mts. (Bulušek et al. 2016; Králíček et al. 2017). On the other hand, in those studies a positive relationship of recruits and tree layer in beech was confirmed on plots with extreme site conditions due to natural layering. In these conditions the tree layer creates better microsite conditions for regeneration (Vacek & Hejcman 2012).

5. Conclusion

A shelterwood system with the application of selection principles has become the main objective of close-to-nature silvicultural management in the forest sector in the Czech Republic, where natural regeneration plays a crucial role. One of these examples are studied forest stands in the Jizerské hory Mts. at more advanced phase of transformation as a result of the combination of spontaneous development and intentional silvicultural practices emerging structurally diversified forest stands. Currently, site and growth conditions in the area are, unlike those at the time of the air-pollution disaster culminating in the 1980s, more favourable for close-to-nature stand structures, which is manifested by a decreased share of spruce in natural regeneration mainly in favour of beech. In the stand transformation process the maximum utilization of natural regeneration should further continue for a relatively long time when particularly natural regeneration of fir, which suffers very much from damage by game, should be supported. In a limited period certain economic risks can be expected relative to the loss of timber value mainly in beech (false heart) caused by its relatively high age. These trees will have to be left in forest stands many times in order to maintain the relevant stand structure. On the other hand, it is to expect in future a pronounced reduction in the costs of regeneration and tending. Moreover structurally diversified stands normally show higher ecological stability and biodiversity.

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References

- Alexander, S., Aronson, J., Clewell, A., Keenleyside, K., Higgs, E., Martinez, D. et al., 2011: Re-establishing an ecologically healthy relationship between nature and culture: the mission and vision of the society for ecological transformation. In: Grenkin, J., Mulongoy, (eds.): Contribution of Ecosystem Transformation to the Objectives of the CBD and a Healthy Planet for All People. Abstracts of Posters Presented at the 15th Meeting of the Subsidiary Body on Scientific, Technical and Technological Advice of the Convention on Biological Diversity. Montreal, Secretariat of the Convention on Biological Diversity, p. 7–11.
- Ambrož, R., Vacek, S., Vacek, Z., Král, J., Štefančík, I., 2015: Current and simulated structure, growth parameters and regeneration of beech forests with different game management in the Lány Game Enclosure. *Lesnícky časopis - Forestry Journal*, 61:78–88.
- Bílek, L., Remeš, J., Podrázský, V., Rozenbergar, D., Diaci, J., Zahradník, D., 2014: Gap regeneration in near-natural European beech forest stands in Central Bohemia – the role of heterogeneity and microhabitat factors. *Dendrobiology*, 71:59–71.
- Bolte, A., Hilbrig, L., Grundmann, B. M., Roloff, A., 2014: Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study. *Annals of Forest Science*, 71:139–147.
- Bolte, A., Hilbrig, L., Grundmann, B., Kampf, F., Brunet, J., Roloff, A., 2010: Climate change impacts on stand structure and competitive interactions in a Southern Swedish spruce–beech forest. *European Journal of Forest Research*, 129:261–276.
- Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G. J., Schall, P. et al., 2009: Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. *Scandinavian Journal of Forest Research*, 24:473–482.
- Bottero, A., Garbarino, M., Dukic, V., Govedar, Z., Lingua, E., Nagel, T. A. et al., 2011: Gap phase dynamics in the old-growth forest of Lom, Bosnia and Herzegovina. *Silva Fennica*, 45:875–887.
- Bouriaud, L., Bouriaud, O., Elkin, C., Temperli, C., Reyser, C., Duduman, G. et al., 2015: Age-class disequilibrium as an opportunity for adaptive forest management in the Carpathian Mountains, Romania. *Regional Environmental Change*, 15:1557–1568.
- Breed, M. F., Gardner, M. G., Ottewell, K. M., Navarro, C. M., Lowe, A. J., 2012: Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany. *Ecology Letters*, 15:444–452.
- Bulušek, D., Vacek, Z., Vacek, S., Král, J., Bílek, L., Králíček, I., 2016: Spatial pattern of relict beech (*Fagus sylvatica* L.) forests in the Sudetes of the Czech Republic and Poland. *Journal of Forest Science*, 62:293–305.
- Čermák, P., Grundmann, P., 2006: Effects of browsing on the condition and development of regeneration of trees in the region of Rýchory (KRNAP). *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, 54:7–14.
- Clark, P. J., Evans, F. C., 1954: Distance to nearest neighbour as a measure of spatial relationship in populations. *Ecology*, 35:445–453.
- Collet, C., Le Moguedec, G., 2007: Individual seedling mortality as a function of size, growth and competition in naturally regenerated beech seedlings. *Forestry*, 80:359–370.
- Correia, D. L. P., Raulier, F., Filotas, É., Bouchard, M., 2017: Stand height and cover type complement forest age structure as a biodiversity indicator in boreal and northern temperate forest management. *Ecological Indicators*, 72:288–296.
- Dakskobler, I., 2008: Pregled bukovih rastisc v Sloveniji. Research Reports Forestry and Wood Science and Technology, 87:3–14.
- David, F. N., Moore, P. G., 1954: Notes on contagious distributions in plant populations. *Annals of Botany of London*, 18:47–53.
- Demek, J., 1987: Zeměpisný lexikon ČSR. Hory a nížiny. Praha, Academia, 584 p.
- Dusan, R., Stjepan, M., Igor, A., Jurij, D., 2007: Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech–fir forest reserves in South East Europe. *Forestry*, 80:431–443.
- Ellis, E. C., Kaplan, J. O., Fuller, D. Q., Vavrus, S., Klein Goldewijk, K. et al., 2013: Used planet: A global history. *Proceedings of the National Academy of Sciences*, 110:7978–7985.
- Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000: The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, 126:173–189.
- Ficko, A., Poljanec, A., Boncina, A., 2011: Do changes in spatial distribution, structure and abundance of silver fir (*Abies alba* Mill.) indicate its decline? *Forest Ecology and Management*, 261:844–854.
- Fürst, C., Vacik, H., Lorz, C., Makeschin, F., Podrázský, V., Janeček, V., 2007: Meeting the challenges of process-oriented forest management, *Forest Ecology and Management*, 248:1–5.
- Gini, C., 1921: Measurement of inequality on income. *Economic Journal*, 31:22–43.
- Glasser, G. J., 1962: Variance formulas for the mean difference and coefficient of concentration. *Journal of the American Statistical Association*, 57:648–654.
- Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R. et al., 2011. How successful are plant species reintroductions? *Biological Conservation*, 144:672–682.
- Grassi, G., Minotta, G., Tonon, G., Bagnaresi, U., 2004: Dynamics of Norway spruce and silver fir natural regeneration in a mixed stand under uneven-aged management. *Canadian Journal of Forest Research*, 34:141–149.

- Grundmann, B. M., Bolte, A., Bonn, S., Roloff, A., 2011: Impact of climatic variation on growth of *Fagus sylvatica* and *Picea abies* in southern Sweden. *Scandinavian Journal of Forest Research*, 26:64–71.
- Hasanov, Z. M., Ibrahimov, Z. A., Nabiyev, V. R., 2016: Beech forests of Azerbaijan: The modern condition, age structure and regeneration. *Annals of Agrarian Science*, 14:1–5.
- Häsler, H., Senn, J., 2012: Ungulate browsing on European silver fir *Abies alba*: the role of occasions, food shortage and diet preferences. *Wildlife Biology*, 18:67–74.
- Hill, M. O., 1973: Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54:427–432.
- Hopkins, B., Skellam, J. G., 1954: A new method for determining the type of distribution of plant individuals. *Ann Bot-London* 18:213–227.
- Chaloupský, J., 1989: *Geologie Krkonoš a Jizerských hor*. Praha, Ústřední ústav geologický, 288 p.
- Jaworski, A., Kolodziej, Z. B., Porada, K., 2002: Structure and dynamics of stands of primeval character in selected areas of the Bieszczady National Park. *Journal of Forest Science*, 48:185–201.
- Kareiva, P., Watts, S., McDonald, R., Boucher, T., 2007: Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, 316:1866–1869.
- Kettenring, K. M., Mercer, K. L., Reinhardt, A. C., Hines, J., 2014: Application of genetic diversity – ecosystem function research to ecological transformation. *Journal of Applied Ecology*, 51:339–348.
- Klopčič, M., Jerina, K., Bončina, A., 2010: Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: Are red deer an important factor? *European Journal of Forest Research*, 129:277–288.
- Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008: Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research*, 127:89–101.
- Konôpka, B., Pajčík, J., 2015: Why was browsing by red deer more frequent but represented less consumed mass in young maple than in ash trees?! *Journal of Forest Science*, 61:431–438.
- Konôpka, J., Kaštner, P., Konôpka, B., 2015: Teoretické východiská a praktické opatrenia na harmonizáciu záujmov lesného hospodárstva a poľovníctva na Slovensku. *Lesnícky časopis - Forestry Journal*, 61:114–123.
- Köppen, W., 1936: *Das Geographische System der Klimate*, Handbuch der Klimatologie. Gebrüder Borntraeger, Berlin.
- Králíček, I., Vacek, Z., Vacek, S., Remeš, J., Bulušek, D., Král, J. et al., 2017: Dynamics and structure of mountain autochthonous spruce-beech forests: impact of hilltop phenomenon, air pollutants and climate. *Dendrobiology*, 77:121–139.
- Kulla, L., Sitková, Z. (eds.). 2012: *Rekonštrukcie nepôvodných smrekových lesov: poznatky, skúsenosti, odporúčania*. Zvolen, NLC-LVÚ, 208 p.
- Lamb, D., Stanturf, J., Madsen, P., 2012: What is forest landscape transformation? In: Stanturf J., Lamb D., Madsen P. (eds.): *Forest Landscape Transformation*. Dordrecht, Springer, p. 3–23.
- Latałowa, M., van der Knaap, W. O., 2006: Late Quaternary expansion of Norway spruce *Picea abies* (L.) Karst. in Europe according to pollen data. *Quaternary Science Reviews*, 25:2780–2805.
- Mach, J., Pojer, F., Plesník, J., Hošek, M., Dušek, J., Trubačiková, R., 2016: *Strategie ochrany biologické rozmanitosti České republiky 2016–2025*. Praha, MŽP, 136 p.
- Madsen, P., Hahn, K., 2008: Natural regeneration in a beech-dominated forest managed by close-to-nature principles – a gap cutting based experiment. *Canadian Journal of Forest Research*, 38:1716–1729.
- Malik, K., Remeš, J., Vacek, S., Štícha, V., 2014: Development and dynamics of mountain spruce (*Picea abies* [L.] Karsten) stand regeneration. *Journal of Forest Science*, 60:61–69.
- Margalef, D. R., 1958: Information theory in ecology. *International Journal of General Systems*, 3:36–71.
- Mattila, M., Kjellander, P., 2017: The tree species matrix, influence on the level of herbivore browsing in mixed forest stands in southwest Sweden. *Scandinavian Journal of Forest Research*, 32:1–5.
- Menhinick, E. F., 1964: A Comparison of Some Species-Individuals Diversity Indices Applied to Samples of Field Insects. *Ecology*, 45:859–861.
- Menšík, L., Fabiánek, T., Tesař, V., Kulhavý, J., 2009: Humus conditions and stand characteristics of artificially established young stands in the process of the transformation of spruce monocultures. *Journal of Forest Science*, 55:215–223.
- Millar, C. I., Stephenson, N. L., Stephens, S. L., 2007: Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*, 17:2145–2151.
- Motta, R., 2003: Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. *Forest Ecology and Management*, 181:139–150.
- Mountford, M. D., 1961: On E. C. Pielou's index of non-randomness. *Journal of Ecology*, 49:271–275.
- Mountford, E. P., Savill, P. S., Bebb, D. P., 2006: Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. *Forestry*, 79:389–408.
- Nagel, T. A., Svoboda, M., Diaci, J., 2006: Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. *Forest Ecology and Management*, 226:268–278.
- Oliver, C. D., 2014: Functional transformation of social-forestry systems across spatial and temporal scales. *Journal of Sustainable Forestry*, 33:123–148.

- Olesen, C. O., Madsen, P., 2008: The impact of roe deer (*Capreolus capreolus*), seedbed, light and seed fall on natural beech (*Fagus sylvatica*) regeneration. *Forest Ecology and Management*, 255:3962–3972.
- Paluch, J. G., 2007: The spatial pattern of a natural European beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forest: A patch-mosaic perspective. *Forest Ecology and Management*, 253:161–170.
- Pielou, E. C., 1959: The use of point-to-plant distances in the study of the pattern of plant populations. *Journal of Ecology*, 47:607–613.
- Pielou, E. C., 1975: *Ecological Diversity*. New York, Wiley, 165 p.
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N. et al., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, DOI: 10.1126/science.1246752.
- Podrázský, V., Zahradník, D., Remeš, J., 2014: Potential consequences of tree species and age structure changes of forests in the Czech Republic – Review of forest inventory data. *Wood Research*, 59:483–490.
- Poljanec, A., Ficko, A., Boncina, A., 2010: Spatiotemporal dynamic of European beech (*Fagus sylvatica* L.) in Slovenia, 1970–2005. *Forest Ecology and Management*, 259:2183–2190.
- Pretzsch, H., Grote, R., Reineking, B., Rötzer, T. H., 2008: Models for forest ecosystem management: a European perspective. *Annals of Botany*, 101:1065–1087.
- Quitt, E., 1974: *Klimatické oblasti Československa*. Brno, ČAV – GÚ, 73 p.
- Ripley, B. D., 1981: *Spatial Statistics*. New York, John Wiley & Sons, 252 p.
- Rohner, B., Bigler, C., Wunder, J., Brang, P., Bugmann, H., 2012: Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. *Journal of Vegetation Science*, 23:892–905.
- Sefidi, K., Mohadjer, M. R. M., Mosandl, R., Copenhaver, C. A., 2011: Canopy gaps and regeneration in old-growth Oriental beech (*Fagus orientalis* Lipsky) stands, northern Iran. *Forest Ecology and Management*, 262:1094–1099.
- Shannon, C. E., 1948: A mathematical theory of communications. *Bell System Technical Journal*, 27:379–423.
- Schelhaas, M. J., Hengeveld, G., Moriondo, M., Reinds, G. J., Kundzewicz, Z. W., ter Maat, H., Bindi, M., 2010: Assessing risk and adaptation options to fires and windstorms in European forestry. *Mitigation and Adaptation Strategies for Global Change*, 15:681–701.
- Schelhaas, M. J., Nabuurs, G. J., Hengeveld, G., Reyer, C., Hanewinkel, M., Zimmermann, N. E. et al., 2015: Alternative forest management strategies to account for climate change-induced productivity and species suitability changes in Europe. *Regional Environmental Change*, 15:1581–1594.
- Schmid, I., 2002: The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. *Basic and Applied Ecology*, 3:339–355.
- Schulze, E. D., Bouriaud, L., Bussler, H., Gossner, M., Walentowski, H., Hessenmöller, D. et al., 2014: Opinion paper: forest management and biodiversity. *Web Ecology*, 14:3–10.
- Schulze, E. D., Aas, G., Grimm, G. W., Gossner, M. M., Walentowski, H., Ammer, C. et al., 2016: A review on plant diversity and forest management of European beech forests. *European Journal of Forest Research*, 135:51–67.
- Simpson, H., 1949: Measurement of diversity. *Nature*, 163:688.
- Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J. P., Sterba, H., von Teuffel, K. (eds.), 2004: *Norway spruce conversion: options and consequences*. Leiden, Brill, 320 p.
- Stanturf, J. A., Palik, B. J., Dumroese, R. K., 2014: Contemporary forest transformation: a review emphasizing function. *Forest Ecology and Management*, 331:292–323.
- Steffen, W., Crutzen, P. J., McNeill, J. R., 2007: The Anthropocene: are humans now overwhelming the great forces of nature. *AMBIO: A Journal of the Human Environment*, 36:614–621.
- Stoyan, D., Stoyan, H., 1992: *Fraktale Formen und Punktfelder: Methoden der Geometrie-Statistik*. Berlin, Akademie verlag GmbH, 395 p.
- Szwagrzyk, J., Szewczyk, J., Bodziarczyk, J., 2001: Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. *Forest Ecology and Management*, 141:237–250.
- Štícha, V., Kupka, I., Zahradník, D., Vacek, S., 2010: Influence of micro-relief and weed competition on natural regeneration of mountain forests in the Šumava Mountains. *Journal of Forest Science*, 56:218–224.
- Thomas, E., Jalonen, R., Loo, J., Boshier, D., Gallo, L., Cavers, S. et al., 2014: Genetic considerations in ecosystem transformation using native tree species. *Forest Ecology and Management*, 333:66–75.
- Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2010: A synthesis on the biodiversity-resilience relationships in forest ecosystems. In: Koizumi, T., Okabe, K., Thompson, I., Sugimura, K., Toma, T., Fujita, K. (eds.): *The Role of Forest Biodiversity in the Sustainable Use of Ecosystem Goods and Services in Agro-Forestry, Fisheries, and Forestry*. Ibaraki, Japan, Forestry and Forest Products Research Institute, p. 9–19.
- Vacek, S., Cipra, Z., 1979: *Struktura porostů v biocentru Jedlový důl. Zpráva pro CHKO Jizerské hory. VS Opočno a SCHKO Jizerské hory*, 18 p.

- Vacek, S., Hejcman, M., 2012: Natural layering, foliation, fertility and plant species composition of a *Fagus sylvatica* stand above the alpine timberline in the Giant (Krkonoše) Mts., Czech Republic. *European Journal of Forest Research*, 131:799–810.
- Vacek, S., Bulušek, D., Vacek, Z., Bílek, L., Schwarz, O., Simon, J. et al., 2015a: The role of shelterwood cutting and protection against game browsing for the regeneration of silver fir. *Austrian Journal of Forest Science*, 1:81–102.
- Vacek, Z., Vacek, S., Bílek, L., Král, J., Remeš, J., Bulušek, D. et al., 2014: Ungulate impact on natural regeneration in spruce-beech-fir stands in Černý důl nature reserve in the Orlické Hory mountains, case study from central Sudetes. *Forests*, 5:2929–2946.
- Vacek, Z., Vacek, S., Podrázský, V., Bílek, L., Štefančík, I., Moser, W. K. et al., 2015b: Effect of tree layer and microsite on the variability of natural regeneration in autochthonous beech forests. *Polish Journal of Ecology*, 63:233–246.
- Vacek, Z., 2017: Structure and dynamics of spruce-beech-fir forests in Nature Reserves of the Orlické hory Mts. in relation to ungulate game. *Central European Forestry Journal*, 63:23–34.
- Vrška, T., Hort, L., Odehnalová, P., Horal, D., Adam, D., 2001: The Boubín virgin forest after 24 years (1972–1996) – development of tree layer. *Journal of Forest Science*, 47:439–459.
- Wagner, S., 2004: Möglichkeiten und Beschränkungen eines funktionsorientierten Waldbaus. *Forst und Holz*, 59:105–111.
- Wenying, J., Yufen, C., Xiaoxiao, Y., Shiling, Y., 2013: Chinese Loess Plateau vegetation since the Last Glacial Maximum and its implications for vegetation transformation. *Journal of Applied Ecology*, 50:440–448.
- Wuethrich, B., 2007: Biodiversity. Reconstructing Brazil's Atlantic rainforest. *Science*, 315:1070–1072.
- Zalasiewicz, J., Williams, M., Steffen, W., Crutzen, P., 2010: The new world of the Anthropocene. *Environmental Science & Technology*, 44:2228–2231.