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Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective

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ABSTRACT

The study presents the results of long-term observations in seven old-growth beech-dominated forest reserves of the northwestern Carpathians. Investigated forests cover a variety of forest sites within the natural range of common beech (*Fagus sylvatica* L.) in Central Europe. The main goal of the research was exploring the magnitude and the character of the changes of basic stand characteristics over time.

Only those old-growth beech forests were included in the study, where the proportion of beech was higher than 90% according to the last measurement. In each investigated reserve, usually three rectangular plots of 0.5 ha were located and measured periodically every 10 years. Within each plot, we recorded all living and dead (standing and lying) trees. Basic stand characteristics (stem density, basal area, growing stock, volume, and proportion of deadwood) were calculated for each old-growth forest and measurement year. The temporal variability was quantified by the relative change (%) between subsequent decades. In addition, the differences of diameter distributions between particular reserves and measurement years were analysed.

The long-term average stem density ranged in the investigated old-growth forests from 226 to 401 ha^{-1} and the average growing stock from 452 to 744 $m^3\,ha^{-1}$. The highest temporal variability was recorded in stem density (mean relative change of 9–17%), whilst the changes of basal area and growing stock were significantly lower (less than 10%). The long-term average deadwood volume fluctuated amongst the reserves between 91 and 345 $m^3\,ha^{-1}$ and the deadwood proportion between 17% and 51%. The mean relative change of the deadwood volume reached 7–42%. The comparison of diameter distributions between the reserves showed a high variability of diameter structures, whereas no identical distributions were observed. In individual reserves, the diameter structure was relatively stable over time and it remained unchanged for at least three decades in most cases. The majority of analysed diameter distributions had a bimodal shape and the best fit was performed by a finite mixture of two Weibull functions. The results showed that old-growth beech forests of northwestern Carpathians can be considered very stable ecosystems and therefore the return of beech to the native sites can promote the overall stability of managed forests in Central Europe.

1. Introduction

During the last decades, close-to-nature forestry became a generally accepted way for ensuring the sustainable management of forests in Europe (Bradshaw et al., 1994; Emborg et al., 2000; Gamborg and Larsen, 2003; Johann, 2006; Meyer, 2005; Schütz, 1999, 2002a,b). One of its key issues is the emulation of natural processes that are considered a useful tool for optimising silvicultural interventions. An important principle the practice of close-to-nature forest management is based on, is the use of indigenous tree species that are best suited to the respective site conditions. In the region of Central Europe, common beech (*Fagus sylvatica* L.) is without doubt the most important broadleaved species. The share of beech in the potential natural vegetation in most countries of Central Europe exceeds the present area (Standovár and Kenderes, 2003). With the shift to continuous-cover forestry, the importance of beech is likely to increase in the future. Understanding of natural forest dynamics in beech-dominated forests is therefore a fundamental condition for a proper use of the close-to-nature principles in silvicultural practice.

Old-growth forest reserves represent study objects where natural processes undisturbed by man can be observed (Brang, 2005). Due to an intensive human activity, old-growth beech forests in the temperate zone of Europe are rare (Parviainen, 2005). Most of the old-growth beech and beech-dominated forest remnants are located in the Carpathians – in Slovakia (Korpeľ, 1995), Ukraine (Commarmot et al., 2005), Romania (Smejkal et al., 1995; Turcu and Stetca, 2006), and in the Dinaric Mountains – in Slovenia (Hartman, 1999), Albania (Meyer et al., 2003), and Bosnia and Herzegovina (Pintarić, 1999). In the Western Carpathians, beech dominates particularly in the intermediate and upper montane zones (Blattný and Šťastný, 1959) and it is considered the strongest

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competitor to other tree species like *Quercus petraea*, *Acer pseudoplatanus* or *Abies alba* (Körner, 2005). When growing under optimal conditions, beech is able to form single-species stands and retain a monospecific structure throughout the whole developmental cycle. According to Korpeľ (1987, 1989, 1995), primeval beech forests of eastern Slovakia belong to the best preserved primeval forest objects not only in Slovakia but also in entire Europe. They represent a unique example of undisturbed temperate forests and exhibit the most complete and comprehensive ecological patterns and processes of pure stands of European beech across a variety of environmental conditions. Therefore, selected primeval beech forests of Slovakia and Ukraine were inscribed on UNESCO World Heritage List in 2007 (Pichler et al., 2007).

In Central and Eastern Europe, the theory on the cyclic development of natural temperate forests became widely accepted during the second half of the last century. Leibundgut (1959) defined the development cycle of a natural forest by several phases. Korpeľ (1958, 1989, 1995) modified this concept and divided the development cycle into three stages – growth, optimum, and breakdown. Since the 1960s, he had established a network of permanent research plots in many forest reserves, covering the whole range of natural forest types present in the Western Carpathians. The aim was to study and quantify the changes of stand structure during the development cycle from a long-term view. In beech natural forests, a multi-layered height structure and a small-scale mosaic of development stages were observed as typical features. The duration of the development cycle (220–250 years) was found to be the shortest amongst all natural forest types in the Western Carpathians (Korpeľ, 1987, 1989, 1995). These findings were confirmed by the research results from beech natural forests in the Romanian part of the Carpathian Arc as well (Smejkal et al., 1995). The most recent study from beech-dominated natural forests of Central Europe (Král et al., 2010) focused on local variability in major stand structural features. The authors observed very high within-site variability which was determined mainly by the fine-scale mosaic of different developmental phases. Based on their results, the plot sizes between 0.01 and 0.09 ha were proposed as the most efficient for sampling in European beech-dominated natural forests.

Because of a lack of appropriate research objects and the necessarily long observation periods, the knowledge concerning long-term development of old-growth beech forests in Central Europe is very scarce. However, the understanding of temporal dynamics in natural beechwoods can be very helpful for correct modifications of forest ecosystem management in terms of close-to-nature silviculture. Therefore, the aim of this study was analysing the temporal dynamics on a series of old-growth beech-dominated forest reserves in the northwestern Carpathians over 40 years. In particular, we were interested in the following questions:

1. What is the local variability and the magnitude of temporal changes of basic stand characteristics (density, basal area, growing stock, and deadwood volume)?
2. What are the typical features of diameter structure and how its dynamics could be characterised?
3. What are the production abilities of beech forests stands as well as individual trees in its natural range in the northwestern Carpathians?
4. How could the results on temporal dynamics be interpreted with regard to disturbance regime?

2. Materials and methods

2.1. Study sites

Research objects of this study were old-growth beech-dominated forest remnants in the northwestern part of the Carpathian region. All study sites are located at the territory of the Slovak Republic (Fig. 1) and they have been under legal protection as National Nature Reserves (NNR) for at least half a century. Currently, there are no traces of direct human intervention in any of the investigated reserves. Moreover, the documentation (regional management plans) that mentions the reserves as forests without any management covers a long period before the beginning of legal protection. In the past, they served as hunting preserves or remained untouched due to their inaccessibility and therefore all studied reserves have a character of primeval forest.

This series of old-growth forest reserves covers the most common sites within the whole natural range of beech in the northwestern Carpathians (Table 1). Beech and fir-beech forests have the highest proportion amongst all forest communities that are native in the Carpathians (Korpeľ, 1995). Beech-dominated forests occur mainly in the submontane and montane zones, usually in the vertical range of 600 to 1200 m a.s.l. (Standovár and Kenderes, 2003). Geological conditions in the investigated reserves vary from

Fig. 1. Location of the investigated forest reserves.

Table 1
Characteristics of study sites.

	Forest reserve						
	Kyjov	Badín	Havešová	Stužica	Rožok	Raštún	Vtáčnik
Latitude [°N]	48°53′30″	48°41′19″	49°00′26″	49°04′23″	48°58′58″	48°27′36″	48°35′05″
Longitude [°E]	22°06′57″	19°03′31″	22°20′55″	22°32′25″	22°27′45″	17°16′32″	18°40′12″
Area of forest reserve [ha]	397.4	30.7	171.3	761.5	67.2	550	245.6
Number of plots	3	3	3	6	3	2	10
Plot size [ha]	0.5	0.5	0.5	0.5	0.5	0.5	0.5[a]
Years of measurement	1963, 1973, 1983, 1993, 2003	1970, 1977, 1986, 1996, 2007	1979, 1989, 1999, 2009	1971, 1981, 1991, 2001	1979, 1989, 1999, 2009	1973, 1983, 1993, 2003	2005
Altitude [m a.s.l]	750–780	700–850	575–600	650–900	650–700	650–720	1150–1180
Bedrock	Andesite	Andesite	Sandstone, claystone	Sandstone, claystone	Sandstone, claystone	Limestone	Andesite
Soil type	Dystric andosol	Eutric cambisol	Eutric cambisol	Eutric cambisol	Eutric cambisol	Rendzic leptosol	Dystric andosol
Mean temperature [°C]	5.2–5.7	5.3–5.8	6–6.5	4–5	6–7	7–8	4–5
Mean precipitation [mm]	950–1000	850–950	800–850	900–1250	800–900	700–750	1000–1050
Forest plant community	*Eu-fagenion* (Oberd. 1957)	*Eu-fagenion* (Oberd. 1957)	*Eu-fagenion* (Oberd. 1957)	*Eu-fagenion* (Oberd. 1957)	*Eu-fagenion* (Oberd. 1957)	*Eu-fagenion* (Oberd. 1957)	*Aceri-Fagion* (Ellenb.1963)

[a] One 5 ha plot subdivided into 10 subplots of 0.5 ha.

igneous (andesite) to sedimentary rocks (sandstone, limestone), on which diverse soil types have developed (cambisol, andosol, leptosol). Mean annual temperature ranges from 7–8 °C (NNR Raštún) to 4–5 °C (NNR Stužica, Vtáčnik). Annual precipitation reaches the lowest rate in the NNR Raštún (700–750 mm) and the highest rate in the NNRs Stužica and Vtáčnik (more than 1000 mm). Regarding the tree species composition, only those reserves were included in the study, where the admixture of the other tree species than European beech did not exceed 10% during the last decade.

2.2. Data collection and analysis

This study is based on data that have been collected for more than 40 years on a network of permanent research plots by the team of the Department of Silviculture at the Technical University in Zvolen, Slovakia. The series of research plots in old-growth forest reserves was established by Prof. Korpeľ during the 1960s and 1970s (Korpeľ, 1995). Since that time, repeated measurements have been conducted ordinarily every 10 years (Saniga, 1999, 2002, 2003; Saniga and Klimaš, 2004; Saniga and Veselý, 1998). Usually, a set of three rectangular plots with the size of 0.5 ha each was established in each reserve. Exceptions are the NNRs Stužica and Raštún with six and two research plots, respectively, and the NNR Vtáčnik with a single 5 ha plot established in 2005. On sample plots, all living trees, standing deadwood (snags) and lying deadwood (logs) were recorded. The lower size limit for standing stems was diameter at breast height (*dbh*) of 8 cm. Regarding the downed deadwood, we registered all logs or their parts with diameter of >8 cm. For each standing tree, we recorded species, *dbh*, height and status (living or dead). Tree species, small- and large-end diameter and total length were measured for the logs.

For each reserve, the dominant height ($h_{10\%}$) was computed as the mean height of the 10% thickest trees and the dominant diameter ($d_{10\%}$) as the mean *dbh* of the 10% thickest trees (Šmelko, 2000). Stand height curves for particular old-growth forests were calculated using Prodan's formula (Prodan, 1951):

$$h = 1.3 + \frac{d^2}{a + bd + cd^2} \quad (1)$$

where d is the tree diameter and h is the height. For the calculation of $h_{10\%}$, $d_{10\%}$ and stand height curves we pooled the data on live trees without broken or deformed tops from all investigated plots in respective reserve.

Volume of individual trees was calculated according to the two-parameter (*dbh* and height) equations derived by Petráš and Pajtík (1991). Details of the formula can be found in the Appendix. For the determination of the volume of broken standing deadwood Huber's formula was used (Šmelko, 2000):

$$v = \frac{\pi}{4} d_{1/2}^2 h_B \quad (2)$$

where $d_{1/2}$ is the mid-height diameter and h_B is the height of broken snag. The mid-height diameter was calculated by linear interpolation using the snag *dbh* and respective tree height from the stand height curve.

Downed deadwood volume was computed by Smalian's formula (Šmelko, 2000):

$$v = \frac{\pi}{4} \frac{d_S^2 + d_L^2}{2} l \quad (3)$$

where d_S is the small-end diameter, d_L the large-end diameter, and l is the log length. In order to achieve results comparable with other studies, we adjusted the deadwood volume to a standard minimum diameter of 5 cm using the equation proposed in the study of Christensen et al. (2005).

The values of basic stand characteristics (stem density, basal area, growing stock, volume and proportion of deadwood) for a particular reserve and measurement year were calculated as the mean of usually three (2–6) sample plots of 0.5 ha (the exception was the NNR Vtáčnik with only one measurement and one 5 ha plot that was subdivided into 10 subplots of 0.5 ha). Changes of basic stand characteristics over time were analysed using the relative change between subsequent measurement years (inventory campaigns):

$$\text{relative change } [\%] = \frac{\text{present value} - \text{previous value}}{\text{previous value}} \times 100 \quad (4)$$

As the relative changes were positive as well as negative, the mean relative change for the respective study site was calculated from absolute values.

Diameter structures of investigated reserves were compared in two ways. Firstly, we examined the differences between diameter distributions from the latest measurement across individual old-growth forests using the two-sample Kolmogorov–Smirnov test. Afterwards, the differences between diameter distributions of particular measurement years in the respective reserve were analysed by the exact Wilcoxon rank sum test. Subsequently, following three models were fitted to the empirical diameter distributions of each measurement year and reserve (27 data sets in total): negative exponential function, single Weibull function (three-parameter form), and a finite mixture of two Weibull functions (seven-parameter form). Detailed information to the functions can be found in Westphal et al. (2006) and Zhang et al. (2001). The goodness of fit was examined by the likelihood-ratio χ^2 test. All calculations were performed using the "*mixdist*" package of R software (Macdonald with contributions from Du, 2010; R Development Core Team, 2010).

3. Results

3.1. Local and temporal variability of stand characteristics

Stem density in investigated old-growth beech forests ranged from 196 ha^{-1} to 479 ha^{-1}, with the overall mean of 303 ± 80 ha^{-1} (mean ± SD). When comparing individual old-growth reserves, the highest stem density was observed in Kyjov (401 ± 51 ha^{-1}) and the lowest in Raštún (226 ± 13 ha^{-1}). The mean basal area reached 37.4 ± 3.9 m^2 ha^{-1}, with the maximum of 46.9 m^2 ha^{-1} and the minimum of 29.8 m^2 ha^{-1}. The growing stock lay in the range of 405–805 m^3 ha^{-1}, whereas the overall mean value amounted to 598 ± 112 m^3 ha^{-1}. The highest growing stock level in the long term was observed in the old-growth forest Rožok (744 ± 47 m^3 ha^{-1}) and the lowest in the Kyjov reserve (452 ± 32 m^3 ha^{-1}, Table 2).

Regarding the changes over time, the most variable stand characteristic was stem density with the interdecadal mean relative change of 9–17% depending from the reserve. The temporal variability of basal area and growing stock was significantly lower and its mean value did not exceed 10% in any reserve (4–9% for basal area and 3–10% for growing stock, respectively). The highest observed interdecadal change reached +39% for stem density,+15% for basal area and + 18% for growing stock. The number of negative and positive changes (i.e. increase or decrease in following decade) was nearly balanced for all basic characteristics, with a slight prevalence of negative changes (Fig. 2).

The overall mean deadwood volume in the studied beech-dominated reserves reached 169 ± 95 m^3 ha^{-1} and fluctuated from 76 m^3 ha^{-1} to 414 m^3 ha^{-1}. The reserve with the long-term highest deadwood volume was Badín (345 ± 51 m^3 ha^{-1}). The deadwood volume in this old-growth forest differed distinctively from the others and was more than twice as high as in the other reserves, whose long-term means did not exceed 155 m^3 ha^{-1} (Table 3). The values of the dead to live wood ratio ranged from 14.4% to 59.8%, with the overall mean of 28.3 ± 14.4%. Comparing individual reserves, the mean deadwood proportion exceeded 21% only in two old-growth forests (Kyjov, Badín).

Analysis of the temporal variability showed relatively high fluctuation of deadwood amount, whereas the interdecadal mean relative change ranged from 7% to 42% according to the reserve. The highest interdecadal change was observed in old-growth forest Rožok (+84%). Unlike the basic stand characteristics (stem density, basal area, growing stock), positive changes of the deadwood volume were more than twice as numerous as negative (Fig. 2).

3.2. Diameter structure

The comparison of the empirical diameter distributions between the investigated reserves revealed a considerable diversity of diameter structures, whereas no identical distributions were found ($p < 0.01$). Considering the variability in individual old-growth forests over time, two different diameter structures were detected in most of the reserves during the investigated period (Table 4). If changes of diameter distributions occurred, they were usually abrupt and took place within one decade. Gradual transitions from one to another diameter structure were quite rare. After forming a new diameter structure, this was retained for at least three decades in most cases. The most stable diameter structure was found in the old-growth forests Rožok and Raštún, where no

Table 2
Changes of basic stand characteristics (living trees of *dbh* > 8 cm) in the investigated forest reserves (the data refer to measurement years reported in Table 1).

Stand characteristics	Forest reserve						
	Kyjov	Badín	Havešová	Stužica	Rožok	Raštún	Vtáčnik
Stem density [N ha^{-1}]							
1961–1970	**479**[a]	311	n/a	n/a	n/a	n/a	n/a
1971–1980	437	249	313[a]	465[a]	305[a]	230	n/a
1981–1990	359	228[b]	225	409	254[b]	237[a]	n/a
1991–2000	341[b]	233	225	321[b]	268	204[b]	n/a
2001–2010	389	324[a]	**196**[b]	336	254[b]	232	352
Mean ± SD	401 ± 50.7	269 ± 40.4	240 ± 43.8	383 ± 58.0	270 ± 20.8	226 ± 12.8	352
Basal area [m^2 ha^{-1}]							
1961–1970	34.6	40.2	n/a	n/a	n/a	n/a	n/a
1971–1980	36.7[a]	39.1	35.3[a]	43.5[a]	38.5	41.4[a]	n/a
1981–1990	32.8	35.9	34.5	42.1	37.1[b]	38.9	n/a
1991–2000	**29.8**[b]	35.2[b]	35.1	38.4	40.6	36.7	n/a
2001–2010	32.9	40.5[a]	31.9[b]	38.2[b]	41.8[a]	32.5[b]	**46.9**
Mean ± SD	33.4 ± 2.3	38.2 ± 2.2.	34.2 ± 1.3	40.5 ± 2.3	39.5 ± 1.8	37.4 ± 3.3	46.9
Growing stock [m^3 ha^{-1}]							
1961–1970	458	666	n/a	n/a	n/a	n/a	n/a
1971–1980	503[a]	686	666	619[a]	703	526[a]	n/a
1981–1990	449	646[b]	674	600	694[b]	491	n/a
1991–2000	**405**[b]	646[b]	690[a]	563	773	466	n/a
2001–2010	443	760[a]	627[b]	560[b]	**805**[a]	411[b]	613
Mean ± SD	452 ± 31.6	681 ± 42.1	664 ± 22.9	585 ± 25.1	744 ± 46.6	473 ± 41.9	613

Overall maximum and minimum in bold.
[a] Maximum value in particular reserve.
[b] Minimum value in particular reserve.

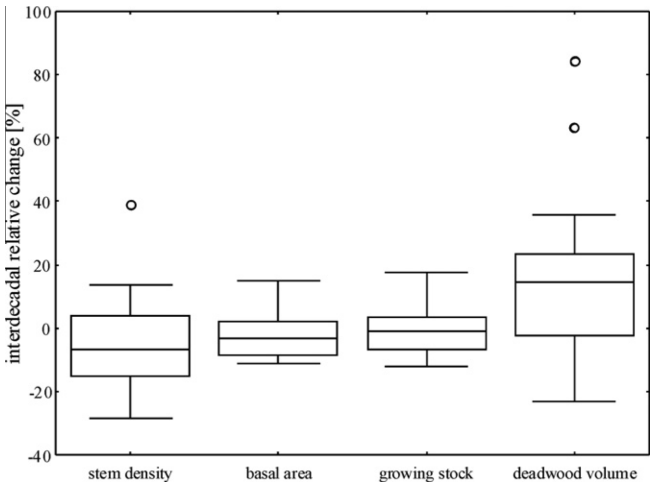

Fig. 2. Distribution of interdecadal relative changes of stand characteristics in the investigated forest reserves for the period 1961–2010 (horizontal line – median value, box – interquartile range, whiskers – non-outlier range, circles – outliers).

significant difference between diameter distributions was observed during the whole investigated period.

The most suitable function for modelling the empirical diameter distributions was proved to be the finite mixture of two Weibull functions that gave the best fit for all 27 data sets but one (old-growth forest Raštún, measurement 1973). Exponential and single Weibull functions were able to describe the empirical distributions in only three and four cases, respectively, mostly in the old-growth forest Havešová. Empirical diameter distributions together with the respective fitted functions referring to the first and the latest measurement in each reserve are shown in Fig. 3.

3.3. Growth conditions and the largest trees

Analysis of the diameter-height relationships in individual old-growth forests showed that two quite distinctively separated groups exist (Fig. 4). The trees of the same diameter, especially those with the *dbh* > 60 cm, are considerably taller in the reserves Havešová, Rožok and Badín, than in the other four reserves. This difference was confirmed also by the dominant heights. Their values did not sink below 41 m in the first group, whilst in the second one they did not exceed 34 m. The long-term mean values of the dominant *dbh* ($d_{10\%}$) in Havešová, Rožok and Badín reached 86 cm, being at least 10 cm more than in the rest of the investigated old-growth forests (Table 5). The same situation was observed for the average density of large trees above 80 cm (100 cm), which was higher than 14 ha^{-1} and 3 ha^{-1}, respectively, in Havešová, Rožok and Badín. Beech stems with the largest diameter were found in the reserves Badín and Kyjov (121 cm), whereas the highest volume of more than 25 m^3 reached a beech tree in Badín.

4. Discussion

In last two decades, much attention was paid to the research on European beech and many studies on beech-dominated natural forests were published (Christensen et al., 2005; Commarmot et al., 2005; Drössler and Lüpke, 2005, 2007; Emborg et al., 2000; Standovár and Kenderes, 2003; Tabaku and Meyer, 1999; Zeibig et al., 2005). Most of them focused on the analysis of stand structure and basic structural elements, regeneration processes, forest cycle and disturbance patterns. However, less is known about the magnitude and character of temporal variability of stand structures and their characteristics. This is caused by a scarcity of the beech old-growth forest remnants in Europe and a lack of long-term observation data. Some of the few exceptions represent the

Table 3
Changes of deadwood amount (snags and logs) and its proportion from growing stock in the investigated forest reserves (the data refer to measurement years reported in Table 1).

	Forest reserve						
	Kyjov	Badín	Havešová	Stužica	Rožok	Raštún	Vtáčnik
Deadwood volume [m^3 ha^{-1}]							
1961–1970	87[b]	293	n/a	n/a	n/a	n/a	n/a
1971–1980	105	284[b]	127	93[b]	114[b]	**76**[b]	n/a
1981–1990	136	387	125[b]	101	210[a]	87	n/a
1991–2000	222	350	130	117	161	111[a]	n/a
2001–2010	223[a]	**414**[a]	150[a]	133[a]	133	92	101
Mean ± SD	155 ± 57.6	345 ± 50.8	133 ± 9.7	111 ± 15.3	154 ± 36.1	91 ± 12.5	101
Deadwood proportion [%]							
1961–1970	19.1[b]	44.0	n/a	n/a	n/a	n/a	n/a
1971–1980	20.9	41.5[b]	19.1	15.0[b]	16.2[b]	**14.4**[b]	n/a
1981–1990	30.3	**59.8**[a]	18.6[b]	16.9	30.2[a]	17.8	n/a
1991–2000	54.9[a]	54.1	18.8	20.8	20.9	23.7[a]	n/a
2001–2010	50.4	54.5	23.8[a]	23.7[a]	16.5	22.3	16.5
Mean ± SD	35.1 ± 14.9	50.8 ± 6.9	20.1 ± 2.2	19.1 ± 3.4	20.9 ± 5.7	19.6 ± 3.7	16.5

Overall maximum and minimum in bold.
[a] Maximum value in particular reserve
[b] Minimum value in particular reserve.

Table 4
Changes of *dbh* distributions over time (different letters denote significantly different *dbh* distributions according to the exact Wilcoxon rank sum test, $p < 0.05$).

Decade	Forest reserve										
	Kyjov		Badín		Havešová		Stužica		Rožok		Raštún
1961–1970	a	b	a								
1971–1980	a		a	b	a		a		a		a
1981–1990		b		b	a	b	a		a		a
1991–2000	a	b		b	a			b	a		a
2001–2010	a	b	a	b		b		b	a		a

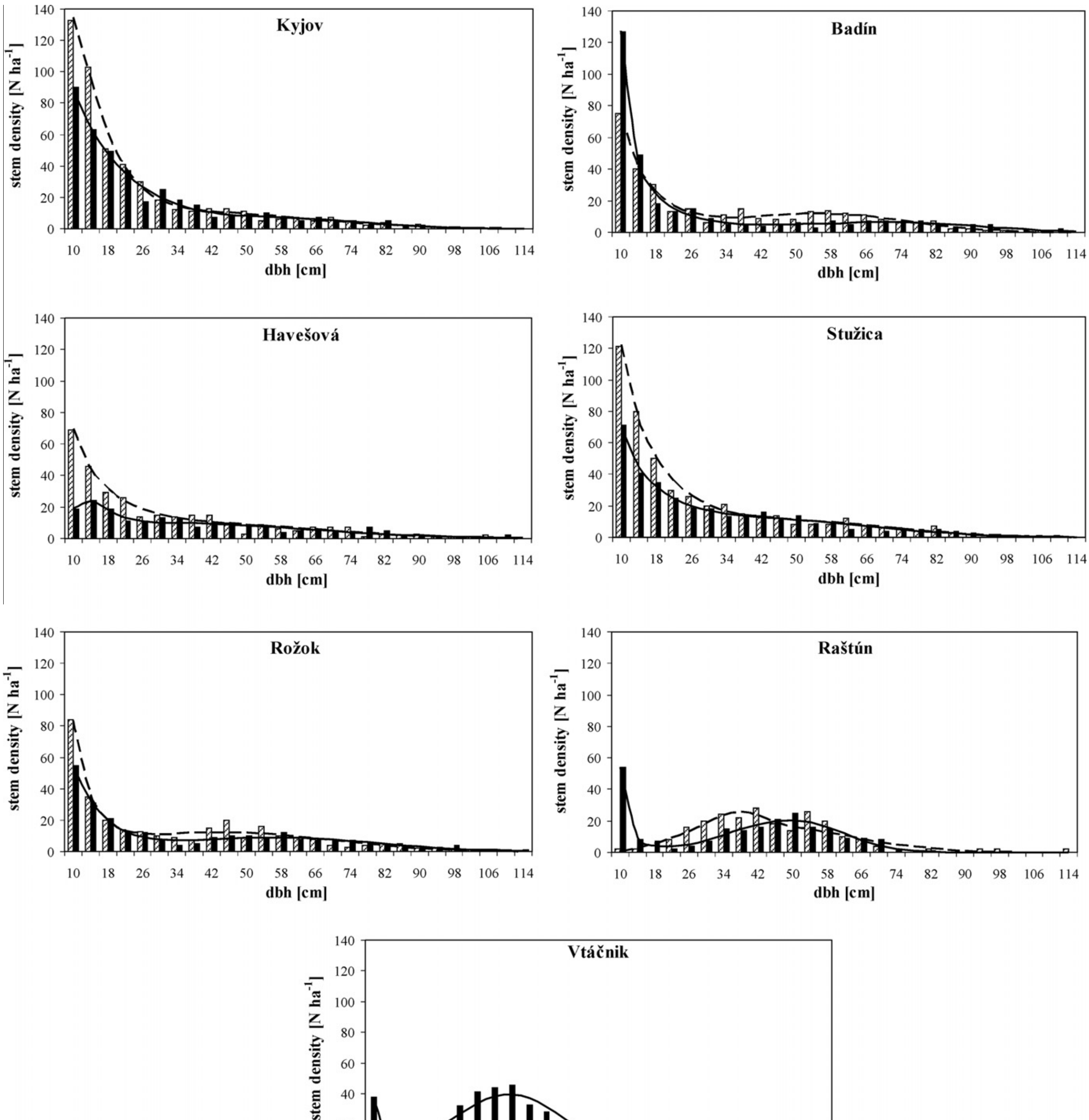

Fig. 3. The empirical and fitted diameter distributions of the investigated old-growth beech forests (hatched bars – empirical distribution of the first measurement, black bars – empirical distribution of the last measurement, dashed line – distribution predicted by finite mixture of two Weibull functions for the first measurement, solid line – distribution predicted by finite mixture of two Weibull functions for the last measurement).

recently published studies of beech-fir forests in the Dinaric Mountains (Diaci et al., 2007, 2010) or beech-dominated forests in the Carpathians (Vrška et al., 2009) and in Switzerland (Heiri et al., 2009), respectively.

Regarding the basic stand characteristics, the situation in the reserves presented in our study do not differ significantly from the values reported from the other beech-dominated old-growth forests in Europe (Christensen et al., 2005; Commarmot et al., 2005; Meyer et al., 2003). The so far largest database on beech natural forests in Europe was published by Christensen et al. (2005) and covers 86 beech reserves. Although focused on deadwood, it provides also valuable information about the growing stock for the majority of investigated localities. Within the reported range of 201–876 $m^3\,ha^{-1}$, Carpathian beech forests included in our study represent the more productive ones. Especially the reserves Rožok, Havešová and Badín belong to the beech-dominated forests

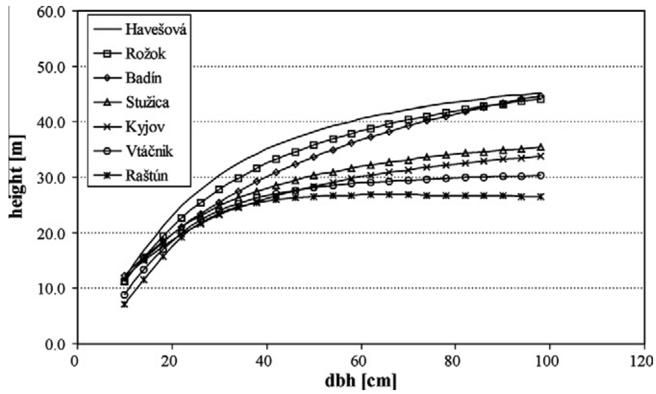

Fig. 4. Stand height curves of individual old-growth forest reserves (calculated according to Prodan (1951) from the pooled data from usually three (2–6) plots of 0.5 ha per reserve, data refer to the last measurement in each reserve).

Table 5
Dominant diameter and the characteristics of large living trees in individual reserves.

Forest reserve	$d_{10\%}$[a]	Stem density >80 cm (>100 cm)[a]	Largest beech tree[b]	
			dbh	Volume
	[cm]	[N ha^{-1}]	[cm]	[m^3]
Kyjov	71.8	9 (1)	121.0	19.5
Badín	86.3	15 (3)	121.0	25.7
Havešová	86.0	14 (4)	117.3	24.2
Stužica	76.3	12 (0)	110.0	17.2
Rožok	86.1	18 (3)	115.5	23.2
Raštún	72.1	2 (0)	92.2	9.2
Vtáčnik	64.2	1 (0)	81.5	8.1

[a] Mean value during the whole observation period.
[b] Largest beech found during the whole observation period.

with the highest growing stock, not only in the northwestern Carpathians but also in the entire beech natural range in Europe. With a long-term mean living wood volume of 744 m^3 ha^{-1}, the reserve Rožok seems to approach the upper production limit of European old-growth beech forests. In the review by Christensen et al. (2005), more reserves with the living wood volume >750 m^3 ha^{-1} are listed, however most of them are mixed forests with an admixture of conifers or even forests with the beech proportion <50%. In pure beech old-growth forests with the admixture of other tree species less than 10%, a higher growing stock than that of reserve Rožok was reported from the Uholka reserve (mean value of 770 m^3 ha^{-1} calculated from 40 sample plots of 0.25 ha) in northeastern Carpathians (Commarmot et al., 2005) and from the reserves Puka and Rajca (mean value of 780–800 m^3 ha^{-1} calculated from 14 and 24 plots of 0.25 ha, respectively) in Albania (Meyer et al., 2003). Therefore, the growing stock of a European beech old-growth forest in equilibrium probably does not exceed 750–800 m^3 ha^{-1} in the long term.

At the establishment of research plot network presented in this study in 1960s and 1970s, individual plots were placed having in mind covering various developmental stages. Therefore, the values of basic stand characteristics are to a certain extent influenced by the location of the sample plots and the respective stand structure. Despite this fact, our results on growing stock and deadwood volume in the reserves Kyjov and Havešová correspond very well with the data acquired by Drössler and Lüpke (2007) from a series of 20 regularly distributed sample plots of 0.39 ha in both old-growth forests. Nevertheless, far more interesting than a mere inventory of data was the possibility to follow and quantify their changes over time within a 40-year period. As expected, the highest temporal variability was observed in stem density; the variation range of this stand property was twice as high as that of basal area and growing stock. Majority of the changes in stem density is due to an intense dynamics, i.e. competition and subsequent mortality in the understory. This is clearly confirmed also by the inspection of diameter distributions, where the highest variability of stem numbers is observable in the lower tree layer (*dbh* classes 10 and 14 cm). Growing stock proved to be relatively stable in all studied forests and the single interdecadal difference does not exceed 12%. The only exception was the last decade in the Badín reserve, where the growing stock increased by 17.5%, which was confirmed also by the data based on full callipering of the entire 30.6-ha large reserve (unpublished data by M. Saniga). The results of a previous study from the old-growth forest Badín (Kucbel et al., 2010) revealed a very low proportion of fresh dead trees in the 1st decay class. The combination of low mortality and high number of large stems >80 cm (23 ha^{-1} in 2007) might be the most likely reason for the high growing stock increase in this reserve during the last decade.

Deadwood represents an important feature of the old-growth forest structure. The deadwood volume as well as the dead to live wood ratio in the surveyed forest reserves reached values close to the mean (130 m^3 ha^{-1} and 22%, respectively) of the range reported by Christensen et al. (2005). The only outlier was the old-growth forest Badín whose volume was more than twice as high as in the other reserves. The likely reason of a high deadwood volume and proportion in this reserve was the intensive mortality of silver fir (decrease from 25% in 1970 to 7% in 2007), which was ongoing since the 1950s (Korpeľ, 1995) and has eventually stopped in last decade. This, together with a relatively long decomposition time (50–60 years, according to unpublished data by Š. Korpeľ) resulted in the observed deadwood accumulation. Nevertheless, our results as well as the results of previous studies confirm that the deadwood proportion lies usually near 20–25% in European natural beechwoods and the deadwood volume exceeds 200 m^3 ha^{-1} quite rarely. The highest deadwood volumes and deadwood proportions were observed in the reserves with the best developed old-growth structures (Kyjov, Badín, Rožok). In natural forests, the deadwood amount fluctuates temporally and spatially (Müller-Using and Bartsch, 2003; Rademacher and Winter, 2003; Saniga and Schütz, 2001, 2002). Regarding temporal changes, the deadwood volume proved to be the most variable stand characteristics and its interdecadal relative change exceeded 10% in most cases. Mean value in the investigated Carpathian beech reserves reached 21%, and was two times higher than that of the montane beech forests calculated by Christensen et al. (2005).

Diameter structure in old-growth forests was traditionally described by the reverse J-shaped (negative exponential) curve (Meyer, 1952; Leibundgut, 1993). In North America, Goff and West (1975) noted a rather bimodal form of diameter distributions in old-growth forest stands, with a second peak in the mid-sized diameter classes. Therefore, they suggested biologically more reasonable rotated-sigmoid form of the diameter structure for the old-growth forests in equilibrium. First attempts to fit the bimodal diameter distribution with a mixture of two Weibull functions were done by Liu et al. (2002) and Zhang et al. (2001). Westphal et al. (2006) used this approach for the analysis of the diameter distributions of virgin beech forests in south-eastern Europe, where a trend towards a rotated sigmoid distribution was observed in all nine investigated stands. The same trend was reported by Diaci et al. (2007) from five old-growth fir-beech forests in the Dinaric Mountains. In our study, the finite mixture of two Weibull functions produced the best fit for the vast majority of analysed distributions. Concerning the results of all mentioned studies, the rotated sigmoid form seems to be more appropriate for describing diameter distributions than monotonically descending curves and it could be considered a typical feature of old-growth beech forests.

The analysis of temporal variability of diameter distributions in individual old-growth forests confirmed that the diameter structure remained quite stable over time. Even if a change of diameter distribution occurred, the bimodal character of the diameter structure was preserved. Comparing the investigated old-growth forests, most of the stands followed slightly sigmoid rotated shape (according to the classification by Podlaski, 2010). Only two forest reserves (Raštún, Vtáčnik) differed from this pattern and their diameter structure had a distinctively sigmoid rotated form. These stands have obviously been undergoing the process of return to equilibrium after some large-scale natural disturbance in the past and the typical fine-scale mosaic of developmental stages is still developing. Natural dynamics similar to that of reserves Raštún and Vtáčnik was observed by von Oheimb et al. (2005) in a near-natural beech forest in north-east Germany being in the phase of recovery from a past forest devastation.

The presence of large living trees is considered one of the important features of old-growth forest structure. Density of living trees with *dbh* > 70 cm reaching 10–20 per hectare was proposed by Nilsson et al. (2002) as a reference value for the virgin forests in Central Europe and southern Scandinavia. Regarding the beech-dominated forests of Central Europe, the authors report the densities of living trees with *dbh* > 80 cm between 10 and 17 per hectare, what was confirmed by other surveys as well (Meyer et al., 2003; von Oheimb et al. 2005). The long-term average density of large trees in the old-growth forests from our study is quite balanced and higher than 9 per hectare, but it can reach distinctively higher values in particular cases (e.g. 23 per hectare in the reserve Badín in 2007). Large trees are rather rare only in the reserves Raštún and Vtáčnik, which are still developing towards a typical old-growth structure. In the stands investigated in our study, the height of individual beech trees did not exceed 50 m. Similar results were confirmed in other beechwoods of Central and south-eastern Europe (Commarmot et al., 2005; Holeksa et al., 2009; Turcu and Stetca, 2006). Although Drössler and Lüpke (2007) reported one beech of 56 m from old-growth forest Havešová, beech trees higher than 50 m are to be considered as an exception in the old-growth forests of Central Europe. Regarding the basic environmental characteristics of reserves with the best diameter-height curves (Havešová, Rožok, Badín), it seems that the combination of eutric cambisol, mean temparature of 5.5–7 °C and annual precipitation of 800–950 mm represents the most suitable site conditions for beech in Central Europe.

Traditionally, small-scale gap processes caused by the mortality of individual trees were considered to be the most important type of disturbance in temperate beech-dominated old-growth forests of Europe (Korpeľ, 1995; Leibundgut, 1978). However, some recent studies (Drössler and Lüpke, 2005; Nagel and Diaci, 2006; Nagel and Svoboda, 2008) demonstrated also the role of intermediate disturbances in the developmental dynamics of these forests. Results of our study, especially the analysis of deadwood dynamics, allow some indirect conclusions regarding the disturbance regime of the investigated forests. Within the 40-year period of observation, the mortality rate (i.e. the proportion of fresh deadwood volume from the growing stock within a decade) higher than 10% was detected in only three cases, whilst in none of them the value exceeded 18%. Moreover, the decades with a more distinctive increase of deadwood volume were not necessarily associated with a significant change of diameter structure at studied plots. An intermediate disturbance, once it occurs, represents certainly a significant factor, which influences the subsequent forest development, but the results of our study suggest that the events of this kind are very rare in time. This is supported also by the fact that the only documented severe disturbance reported from the investigated old-growth forest reserves was a 6.1-ha large windthrow in Badín in 1947 (Korpeľ, 1995). Although the reserves included in the study cover a wide range of beech forests growing under various natural conditions, the results show very similar patterns regarding their temporal variability. Regardless of site features, old-growth beech-dominated forests are characterised by a relatively high stability and it is very likely that the more distinctive changes are associated with a significant proportion of intermixed species, especially with fir and its past mortality.

The presented data-sets represent one of the longest regular investigations of this type in Europe. However, the results of 40-years observations still cover only a fraction of the beech forest life cycle and therefore do not allow reliable generalizations. Nevertheless, according to the acquired results, beech forests of the northwestern Carpathians seem to be very stable ecosystems that underlie relatively moderate changes of structure elements. Regarding the basic features of its natural dynamics, beech-dominated forests can be considered one of the most appropriate forest types for maintaining the sustainable management of forests in Central Europe. The at least partial return of the beech to its native sites can contribute to the stability of managed forest stands and thus to support one of the crucial conditions for the continuous-cover forestry.

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Appendix A

Formula for individual tree volume of European beech by Petráš and Pajtík (1991)

$$v = \frac{\pi d^2 h}{40000}\left(a + \frac{b}{d} + \frac{c}{d^2} + \frac{e}{d^3} + fh + gdh + kd^2h + ld^3h\right)$$

where v is volume (m^3), d is tree diameter (cm), h is tree height (m), and a, b, c, e, f, g, k and l are species-specific parameters.

Values of parameters for European beech:

a	0.54201
b	−3.11830
c	44.32746
e	−235.97272
f	-1.07177×10^{-3}
g	-1.86004×10^{-5}
k	8.80628×10^{-7}
l	-5.99567×10^{-9}

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