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Temporal dynamics in old-growth spruce dominated forests in the Western Carpathians, Slovakia

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Abstract

In the conditions of ongoing climate change, the old-growth forest remnants of the Western Carpathians provide a unique possibility to study the structural changes in forests undisturbed by human activity. In four subalpine primary spruce forests in Slovakia, we analysed the temporal variability of basic stand characteristics, the dynamics of diameter structures and the development of tree species composition. The study was conducted in a series of 10 permanent research plots with the size of 0.5 ha. Within each plot, we recorded all living trees (dbh > 8 cm) as well as the recruitment individuals (dbh 0.1–8.0 cm). Old-growth spruce forests Babia hora, Kotlový žľab and Pilsko showed continuous reduction of stem density, basal area and growing stock during the investigated period. In the last two decades, the negative interdecadal changes of basal area and stand volume even exceeded the rate 35% as a consequence of severe disturbances caused by the windstorms and bark-beetles. Breakdown of these stands affected also their diameter structure and the unimodal distributions were replaced by the more differentiated structures of rotated sigmoid shape. Such significant change was followed by a massive increase in stem density of spruce and rowan recruitment. Stable bimodal diameter structure was observed only in old-growth forest Zadná Poľana, that was characterized by the small-scale gap dynamics. The results documented the intense breakdown of natural spruce stands with unimodal structure and the key role of the existing seedlings and saplings bank of spruce and rowan for their regeneration after the disturbance events.

Key words: basic structural characteristics; diameter structure; ingrowth; largest trees; *Picea abies* [L.] H. Karst.

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1. Introduction

In the past, the traditional approach to the research of old-growth forests in Europe focused mainly on the monitoring and description of basic production characteristics such as stem density, basal area and growing stock (Leibundgut 1982; Korpeľ 1989). The research on extent and character of temporal variability of these structural features is getting more important also in present, as confirmed by several studies published in recent years from beech-fir forests in the Dinaric mountains (Diaci et al. 2010, 2011) and from beech forests in the Carpathians (Vrška et al. 2009; Kucbel et al. 2012) and in Jura Mountains (Heiri et al. 2009). For the interpretation of the structural dynamics of old-growth forests, the mentioned basic production parameters become important when they are integrated with other characteristics, especially with diameter distributions. The analysis of temporal and spatial changes in diameter distributions is important from several viewpoints. Changes in diameter structures help to identify historical disturbances, understand processes of regeneration, growth and mortality, estimate future stand development and assess competitive relationships between tree species (Aldrich et al. 2005; Woods et al. 2021).

Several types of diameter distributions are used to characterize the diameter structure of old-growth forests in an equilibrium state (Goff & West 1975; Lorimer 1980; Leak 1996; Westphal et al. 2006): negative exponential type, negative power type, type with an increasing quotient and rotated sigmoid type. The biological rationale for these distribution shapes is related to changes in the reduction quotient (i.e. the ratio between the stem density in adjacent diameter classes) with increasing diameter.

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The reduction quotient can be constant (negative exponential distribution type), decreasing (negative power distribution type), increasing (increasing quotient type), or variable (rotated sigmoid distribution type). With regard to historical disturbances, the rotated sigmoid type and the increasing quotient type are considered to be the result of development under the influence of weak to moderate disturbances (Leak 1996). Unimodal diameter distributions usually indicate the occurrence of strong disturbances, often associated with subsequent successional development (Aldrich et al. 2005; Kucbel 2014; Holeksa et al. 2017). Due to the existence of possible other factors that influence the development and changes of the diameter distributions, the diameter structure should always be interpreted in connection with other structural parameters (Goodburn & Lorimer 1999).

Basic structural characteristics are subject to constant periodic changes in old-growth forests. A typical feature of the development dynamics of spruce subalpine forests is the tendency to create single-layer stands with a horizontal canopy, even in the case of significantly uneven-aged structure (Korpeľ 1989; Mayer & Ott 1991; Schmidt-Vogt 1991; Leibundgut 1993). This period of the life cycle represents the so-called optimum stage (sensu Korpeľ 1989) and its long duration (80–100 years) is a consequence of the combination of the high physical age of spruce (350–400 years) and its ability to live 150–200 years longer than its height growth lasts (Schmidt-Vogt 1991; Begović et al. 2023). In spruce old-growth forests, even with considerable age differentiation, the forming of a significantly differentiated structure of a selection forest usually does not occur in any phase of their natural development. Structurally homogeneous spruce old-growth forests, especially on slopes with only weakly changing site conditions, are highly susceptible to the so-called catastrophic breakdown, which is often associated with succession development through pioneer and intermediate forest (Korpeľ 1989). More stable and differentiated structures can be maintained for a longer period only in places where site conditions (soil environment, climate) limit the formation of a typical optimum stage (Mayer & Ott 1991; Schmidt-Vogt 1991; Ott et al. 1997). At the upper forest limit of their distribution range, the stability of spruce forests is increased by their horizontal differentiation and the creation of cluster structures, which are one of the strategies for adapting to the extreme conditions of the upper tree limit (Schönenberger 1986).

Main driving forces of primary dynamics in old-growth Norway spruce forests are natural disturbances. Disturbances of various frequency, severity and size shape the tree species composition of forest stands as well as horizontal and vertical distribution of trees. They generate also new environments for the emergence and growth of natural regeneration (Janda et al. 2014; Čada et al. 2016; Spinu et al. 2020; Cerioni et al. 2024). In spruce forests of the Carpathians, the most important natural disturbance agents are windstorms and bark beetles (Mezei et al. 2014; Svoboda et al. 2014; Trotsiuk et al. 2014; Primicia et al. 2015). Disturbances caused by these agents repeat here usually in relatively short intervals and are spatially limited, nevertheless they significantly affect the structure of spruce stands (Synek et al. 2020). Large-scale disturbances induced by heavy windstorms appear only rarely (on average once in 100 years), however their consequences are massive removal of overstory trees on areas with the size of several dozens of hectares (Svoboda et al. 2014; Trotsiuk et al. 2014; Čada et al. 2016; Holeksa et al. 2017; Janda et al. 2017; Schurman et al. 2018). The windstorm disturbance is usually followed by the bark-beetle outbreaks that enlarge total extent of the original disturbance (Mezei et al. 2014; Janda et al. 2019). Crucial role of severe, less frequent large-scale disturbances on the developmental dynamics of spruce natural forests was confirmed by several studies (Svoboda et al. 2010; Zielonka et al. 2010; Svoboda et al. 2012; Čada et al. 2013, 2016; Červenka et al. 2016; Holeksa et al. 2016, 2017; Spinu et al. 2020).

Presence of large trees and the related dominant diameter of the stand represents one of the key features distinguishing the old-growth forest structure from the forests affected by the human interventions (Bauhus et al. 2009; Di Filippo et al. 2017). Even if the amount of large old trees is significantly limited, they play important role in the functioning of forest ecosystems. In ecosystem processes they influence the hydrological regimes, carbon storage and nutrient cycling as well as micro- and meso-climatic conditions. Large old trees provide suitable habitats for a variety of plant and animal species and contribute to the regeneration of forest stands by their reproductive ability, making them one of the keystone structures of forest ecosystems (Lindenmayer 2017; Lindenmayer & Laurance 2017). Global climate changes and related disturbances (Seidl et al. 2017), however, accelerate the reduction of their numbers in primary forests (Svobodová et al. 2019; Begović et al. 2023).

In subalpine spruce forests, the conditions for natural regeneration of trees are spatially and temporally limited, what negatively impacts the dynamics of regeneration processes and makes the regeneration of stands in these altitudes very problematic (Kucbel 2014). To the ecological factors, which cause the difficulties with natural regeneration belong above all the low temperatures, limited water-holding capacity of soil surface, interception, low competitive ability against the ground vegetation, fungi infestations and less frequent seed years (Ott et al. 1997). The problems with regeneration are partly compensated by natural longevity of subalpine forest. On the one hand, it promotes the forming of mono-layered spruce stands, however on the other hand it provides the stands with sufficiently long timespan for the gradual regeneration. Suitable conditions for emergence of scattered natural regeneration in subalpine spruce stands are provided mostly in larger canopy gaps with the size of at least several hundreds of square meters. Here, he majority of young spruces can be found on lying deadwood in advanced decomposition degree. Small, suppressed individuals usually wait in sapling bank on the release after the canopy gap enlarges (Kucbel 2014; Holeksa et al. 2021). A special case is the large-scale regeneration of spruce stands after severe disturbances. Rapid mortality of mature trees in the large extent during such events leads to open, early seral systems with significant changes in site conditions (higher intensity of solar radiation, development of ground vegetation, more extreme temperatures, accelerated nutrient cycle in soil etc.). After the breakdown of upper tree layer, the height increment of suppressed regeneration accelerates as a consequence of increased light level (Nováková & Edwards-Jonášová 2015; Červenka et al. 2016). A rich recruitment layer which is formed then mitigates the effect of sudden change of light conditions by its shading and thus limits the development of ground vegetation (Havira et al. 2017). Natural regeneration after disturbances represents one of the crucial elements of the resilience in subalpine spruce ecosystems (Winter et al. 2015).

Knowledge about the long-term development of spruce old-growth forests is very rare in Central Europe due to the relatively small number of suitable research objects where the databases covering a period of several decades are available. At the same time, understanding the temporal dynamics of natural spruce ecosystems can be helpful in the development of such concepts for effective management of subalpine spruce forests that are based primarily on maintenance of the protective function and the stability of stands, without the need for artificial regeneration (Wasser & Frehner 1996; Kräuchi et al. 2000; Janda et al. 2017).

The aim of this study was to analyse the temporal variability of the structures of four subalpine old-growth spruce forests of the Western Carpathians. Attention was paid in particular to the following research questions:

What is the magnitude of temporal changes of basic structural characteristics (stem density, basal area and growing stock) in old-growth spruce forests?

What are the typical features of their diameter structure and how can its changes over time be characterized?

How do the various disturbance regimes influence the development of recruitment?

2. Material and methods

2.1. Study sites

The assessment of temporal dynamics and variability of structural characteristics was carried out in four subalpine primary spruce forests: Babia hora, Kotlový žľab, Pilsko and Zadná Poľana (Fig. 1). Investigated old-growth forest localities represent the best-preserved remnants of spruce primary forests in northwestern part of the Carpathian Arch (Mikoláš et al. 2019), which are under strict protection for a long time (Babia hora and Kotlový žľab since 1926, Zadná Poľana since 1953 and Pilsko since 1967). They cover the natural range of subalpine spruce forests in this region, from the southernmost occurrence in Poľana massif to the northernmost occurrence in the Oravské Beskydy Mts., in the altitudes ranging approximately from 1,200 to 1,500 m a.s.l.

In the investigated reserves, the bedrock consists of andesite and flysch and dominant soil types are andosols, cambisols and podsols (Table 1). The average annual temperature ranges from 1.9 °C (Kotlový žľab) to 3.8 °C (Zadná Poľana) and the average annual precipitation totals from 1050 mm (Zadná Poľana) to 1,650 mm (Kotlový žľab). From a typological point of view, the most represented groups of forest types are *Sorbeto-Piceetum*, *Acereto-Piceetum* and *Fagetum abietino-piceosum* (Zlatník 1976). Forest communities consist almost exclusively of Norway spruce (*Picea abies* [L.] H. Karst.). Besides spruce, rowan (*Sorbus aucuparia* L.) occurs here as the most important accompanying tree species and European beech (*Fagus sylvatica* L. – old-growth forests Zadná Poľana and Pilsko), silver fir (*Abies alba* Mill. – old-growth forest Zadná Poľana) and sycamore maple (*Acer pseudoplatanus* L. – old-growth forest Zadná Poľana) are present as a single admixture.

2.2. Data collection and analysis

Data on trees for the purposes of this study were obtained from a network of permanent research plots (PRPs), which were established in the investigated forest sites in the 1960s, 1970s and 1980s (Table 1). Since the establishment of the PRPs, repeated measurements have been carried out regularly, usually at intervals of 10 years. Research plots have a rectangular shape and the size of 0.5 ha. For more detailed measurements, a 10 m wide transect was established within each research plot (Korpeľ 1989). In all PRPs we registered tree species and diameter at breast height (dbh) for all living trees with dbh > 8 cm. On the transects, tree species and dbh of recruitment individuals (dbh 0.1–8.0 cm) were also recorded as well as heights of all living trees, with the total of 998 measured tree heights.

For each old-growth forest locality, the dominant dbh ($d_{10\%}$) was calculated as the average dbh of 10% of the largest stems (Šmelko 2000).

Stand height curves for particular old-growth forests were calculated using Prodan's formula (Prodan 1951):

$$h = 1.3 + \frac{d^2}{a + bd + cd^2} \qquad [1]$$

where h is the tree height and d is the tree diameter at breast height.

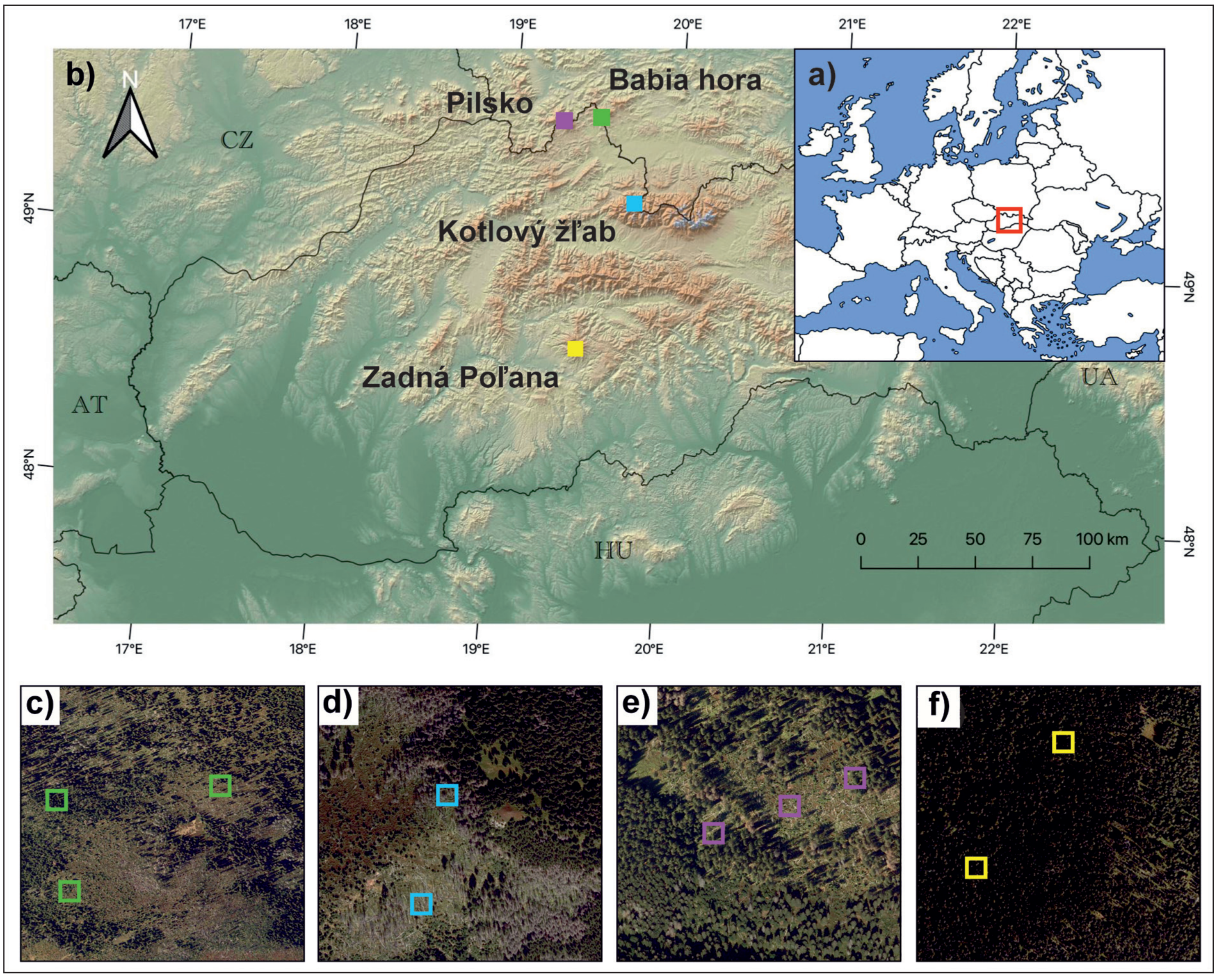

Fig. 1. Map of the investigated old-growth forest sites a) location of northwestern part of the Carpathian Arch in Europe, b) research stands location in the Western Carpathians. Location of permanent research plots in primary spruce forests c) Babia hora, d) Kotlový žľab, e) Pilsko, f) Zadná Poľana.

Table 1. Characteristics of study sites.

	Babia hora	Kotlový žľab	Pilsko	Zadná Poľana
Latitude	49°33'40"	49°14'20"	49°31'20"	48°38'20"
Longitude	19°31'00"	19°45'16"	19°18'20"	19°28'50"
Altitude (m a.s.l.)	1,270–1,430	1,480–1,500	1,210–1,370	1,330–1,370
Bedrock	Sandstones, claystones	Orthoquartzite, granite	Sandstones, claystones	Andesite
Soil type	Cambisols, podsols	Podsols	Podsols	Andosols
Mean temperature (°C)	2.3	1.9	2.3	3.8
Mean precipitation (mm)	1,585	1,650	1,585	1,050
Forest plant community (Zlatník 1976)	*Sorbeto-Piceetum*	*Sorbeto-Piceetum*, *Acereto-Piceetum*	*Fagetum abietino-piceosum*, *Sorbeto-Piceetum*	*Acereto-Piceetum*, *Sorbeto-Piceetum*
Number of plots	3	2	3	2
Plot size (m)	83.3 × 60.0	71.4 × 70.0	90.0 × 55.5	90.0 × 55.5 71.4 × 70.0
Years of measurement	1980, 1987, 1995, 2005, 2023	1968, 1978, 1988, 1998, 2019	1977, 1988, 1997, 2007, 2015	1974, 1984, 1994, 2004, 2013, 2022

Note: Values of mean temperature and mean precipitation for study sites were calculated by the gradient method (Škvarenina et al. 2009; Lukasová et al. 2021).

The stem volume of individual trees was calculated according to the two-parameter (dbh, height) equations published in the study by Petráš & Pajtík (1991).

The values of the basic stand characteristics (stem density, basal area and growing stock) were calculated for individual old-growth forests and measurement years as an average from the research plots of the given locality. Changes in basic stand characteristics over time were analyzed using the relative decadal changes between pairs of consecutive measurement years:

$$\textit{relative change}\ [\%] = \frac{\textit{present value} - \textit{previous value}}{\textit{previous value}} \cdot 100 \quad [2]$$

If the interval between measurements was different than 10 years, the relative change was converted to standard interval of 10 years by dividing its value by the interval (in years) and multiplying it by 10.

To determine the types of diameter structures, two models were fitted to the empirical diameter distributions from each measurement year and locality (21 distributions): single Weibull function (three-parameter form) and a finite mixture of two Weibull functions (seven-parameter form; Zhang et al. 2001; Westphal et al. 2006). The goodness of fit was examined by the likelihood-ratio χ^2 test. All calculations were performed using the „*mixdist*“ R package (Macdonald with contributions from Du 2010, R Development Core Team 2010).

3. Results

In the investigated old-growth forests, the stem density within the monitored period ranged from 49 ha^{-1} to 710 ha^{-1}, basal area from 1.7 $m^2\ ha^{-1}$ to 62.4 $m^2\ ha^{-1}$ and growing stock from 14 $m^3\ ha^{-1}$ to 630 $m^3\ ha^{-1}$ (Fig. 2). The long-term lowest average values of basal area and growing stock were reached in old-growth forest Babia hora (33.7 ±5.5 $m^2\ ha^{-1}$ and 292 ±48 $m^3\ ha^{-1}$) and on the contrary the highest ones in old-growth forest Zadná Poľana (46.1 ±1.2 $m^2\ ha^{-1}$ and 468 ±16 $m^3\ ha^{-1}$).

Regarding the development of stand characteristics over time, we observed no oscillation around the average value, but typical for particular locality was the persistence of an increasing or decreasing trend. A permanent decrease in stem number was recorded in all investigated objects. Similar trend was observed also for basal area and growing stock, with the only exception of old-growth forest Zadná Poľana, where on the contrary the values of both stand characteristics were increasing.

Majority of the changes in stand characteristics during the investigated period did not exceed 20% (Fig. 3), with the dominance of negative changes, i.e. the reduction of stem density, basal area and growing stock. Especially significant negative changes of basal area and growing stock were recorded in the last two decades in old-growth forests Babia hora (−35% and −36%), Kotlový žľab (−46% and −46%) and Pilsko (−59% and −64%). Only in old-growth forest Zadná Poľana the changes of basal area and growing stock were positive, but did not exceed the threshold of 12%.

In the studied localities, we analysed the diameter structure according to the type of diameter distribution and its development in time (Fig. 4a, b). A stable diameter structure was confirmed in old-growth forest Zadná Poľana, where the distribution had a bimodal character modelled by a finite mixture of two Weibull functions and no significant change of the distribution type was registered during the investigated period. In old-growth forests Babia hora, Kotlový žľab and Pilsko, we recorded

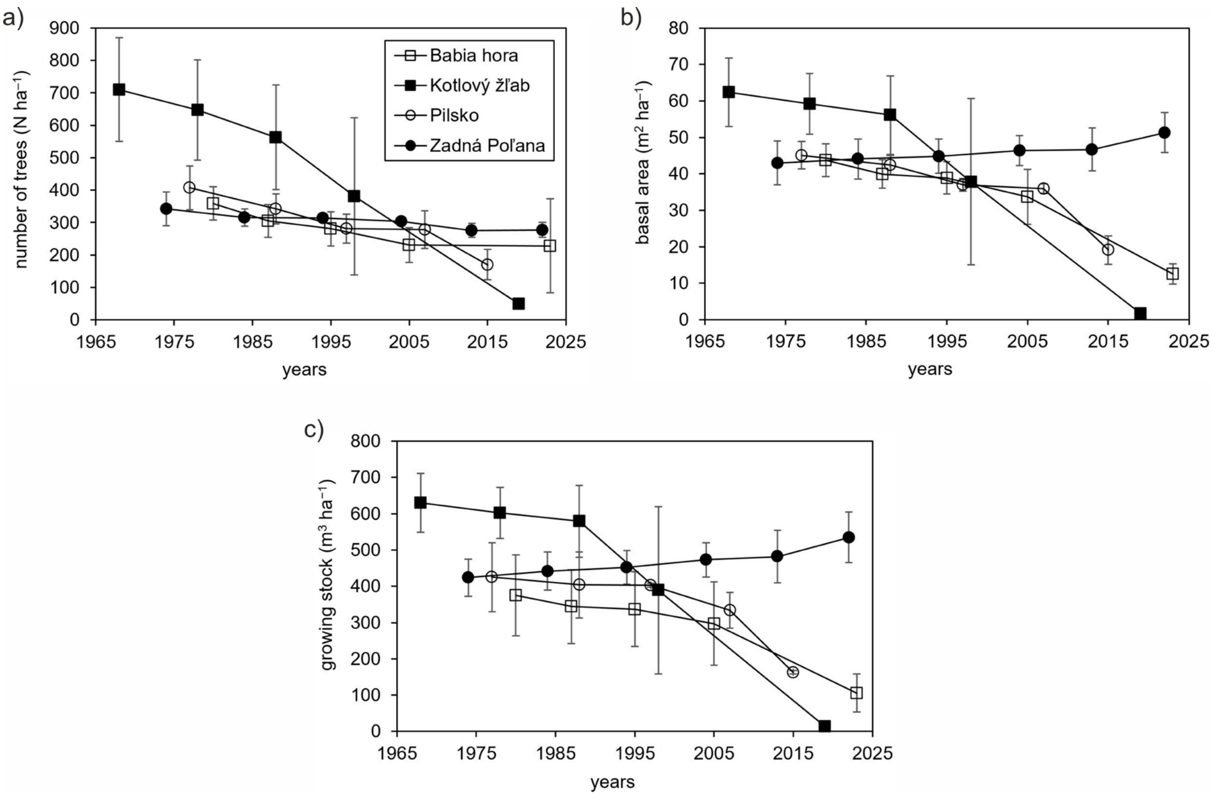

Fig. 2. Temporal changes of basic stand characteristics (living trees of dbh > 8 cm) in the investigated forest reserves (mean ±SE).

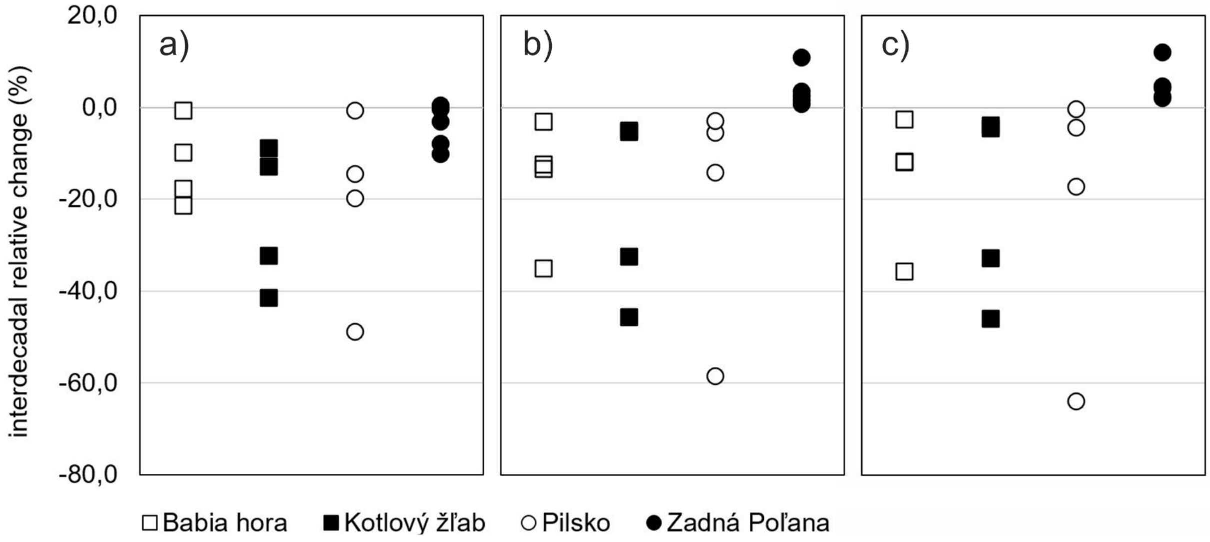

Fig. 3. Interdecadal relative changes of stand characteristics (a – stem density, b – basal area, c – growing stock) in the investigated forest reserves for the period 1974–2023.

a typical unimodal diameter structure modelled by single Weibull function. In the last measurement year (in Pilsko in the last two measurements), we observed the shift from homogenous to differentiated structure, expressed by the replacement of unimodal distribution by the rotated sigmoid distribution modelled by a finite mixture of two Weibull functions.

The tree species composition in analysed stands was distinctively dominated by Norway spruce. Its proportion calculated from stem density in single localities ranged from 87% (Zadná Poľana, year 2013) to 100% (Kotlový žľab, years 1968−1998) during the investigated period. The proportion of spruce calculated from basal area and growing stock did not decrease in any case under 95%. Besides Norway spruce, rowan was present in all surveyed sites (Fig. 5), with more or less stable share (between less than 1% in Kotlový žľab and 8% in Zadná Poľana). The proportions of beech (Pilsko and Zadná Poľana), maple and fir (Zadná Poľana) did not exceed 4%. A moderately increasing trend of beech proportion has been observed in Pilsko and Zadná Poľana since the 1990s.

In Zadná Poľana, the average density of the large trees with dbh above 60 cm did not decrease under 50 ha^{-1} (Table 2). More than a two-fold lower proportion of large stems was registered in the stands of the other old-growth forests (Babia hora, Kotlový žľab and Pilsko), with the only exception of PRP 3 in Babia hora, where the density of stems larger than 60 cm reached the long-term average 51 ha^{-1}. Even more significant differences between investigated reserves were observed in the densities of stems with dbh above 70 cm and 80 cm.

Table 2. Dominant diameter and the characteristics of large living trees in individual reserves.

Forest reserve	$d_{10\%}$[a]	Stem density			Largest spruce tree[b]		
		>60 cm	>70 cm	>80 cm	DBH	Height	Stem volume
	(cm)	(N ha^{-1})	(N ha^{-1})	(N ha^{-1})	(cm)	(m)	(m^3)
Babia hora							
PRP 1	53.4	2	1	0	71.2	17.1	2.2
PRP 2	55.4	10	2	0	77.0	23.2	3.7
PRP 3	75.1	51	18	2	92.5	37.7	9.0
PRP 1−3	61.3	21	7	1	92.5	37.7	9.0
Kotlový žľab							
PRP 1	51.0	8	1	0	81.1	33.9	6.2
PRP 2	47.2	2	1	0	71.6	33.1	4.8
PRP 1−2	49.1	5	1	0	81.1	33.9	6.2
Pilsko							
PRP 1	67.2	26	4	1	98.6	38.4	10.3
PRP 2	60.0	8	2	1	74.3	28.9	4.4
PRP 3	51.3	3	2	0	74.5	18.5	2.7
PRP 1−3	59.5	12	3	1	98.6	38.4	10.3
Zadná Poľana							
PRP 1	75.7	52	25	6	96.2	33.8	8.5
PRP 2	73.3	50	18	7	95.3	33.7	8.3
PRP 1−2	74.5	51	22	7	96.2	33.8	8.5

Note: [a] Mean value during the whole observation period, [b] largest spruce found during the whole observation period.

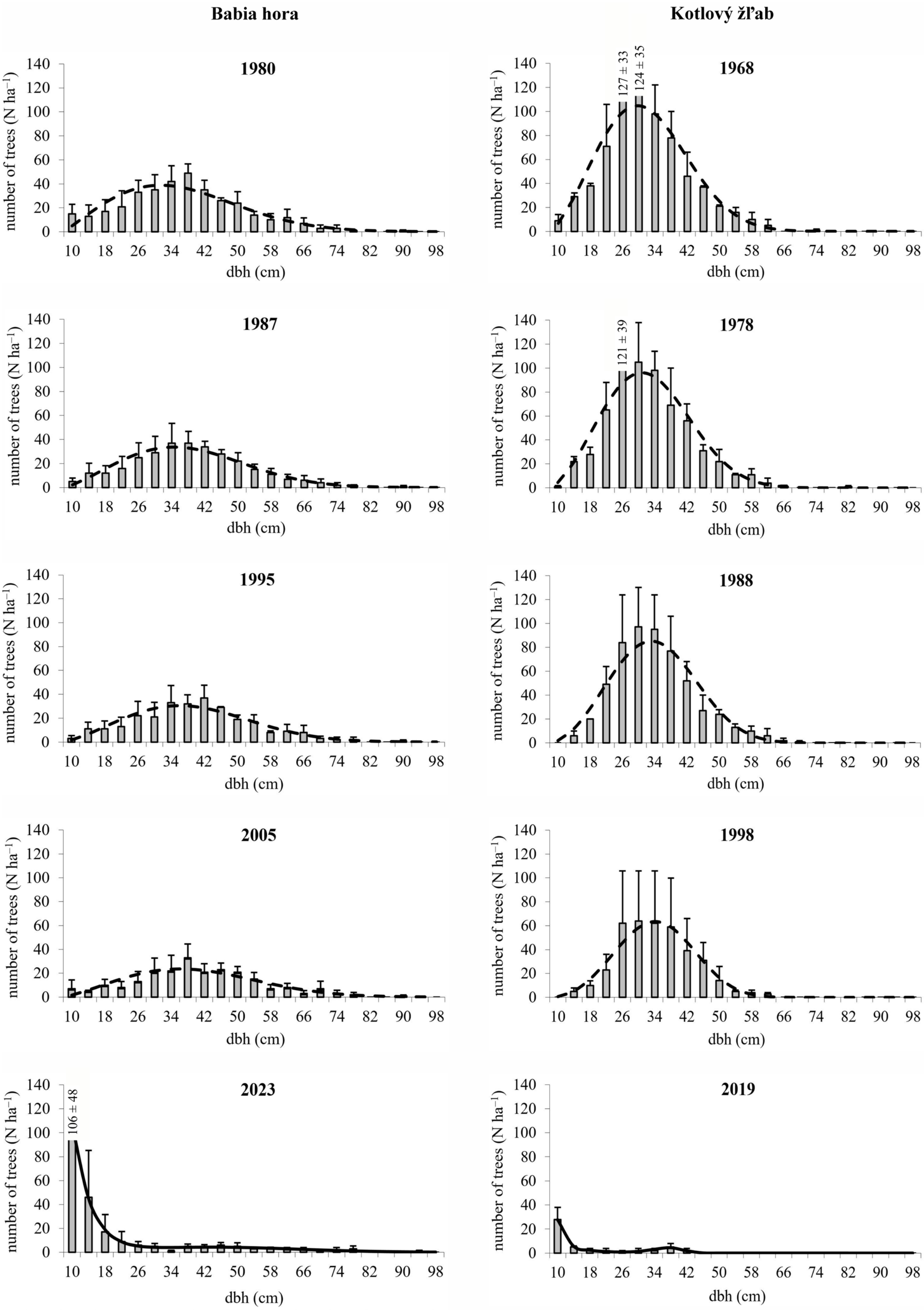

Fig. 4a. The empirical (mean ±SE) and fitted diameter distributions in old-growth spruce forests Babia hora and Kotlový žľab (dashed line – distribution predicted by single Weibull function, solid line – distribution predicted by finite mixture of two Weibull functions).

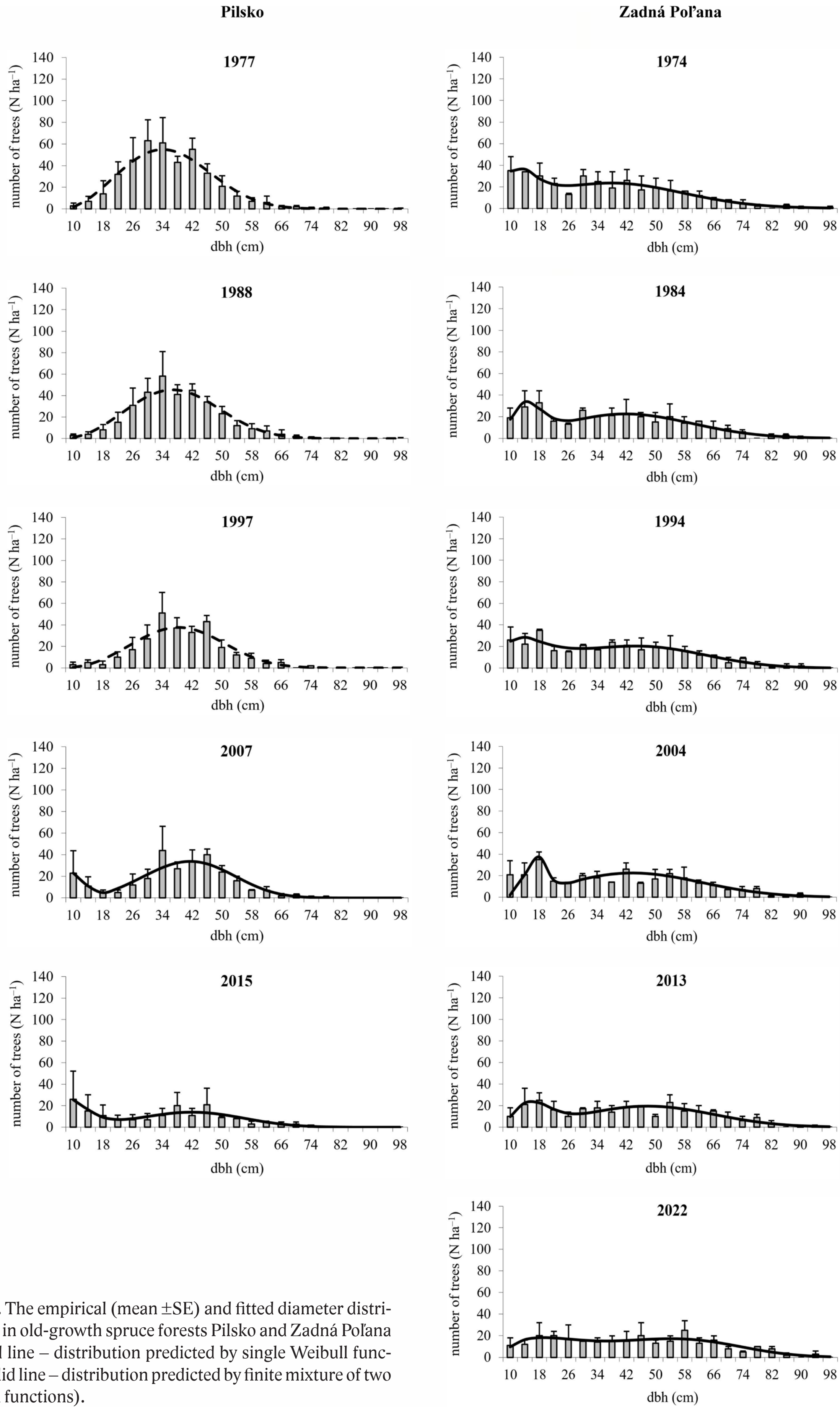

Fig. 4b. The empirical (mean ±SE) and fitted diameter distributions in old-growth spruce forests Pilsko and Zadná Poľana (dashed line – distribution predicted by single Weibull function, solid line – distribution predicted by finite mixture of two Weibull functions).

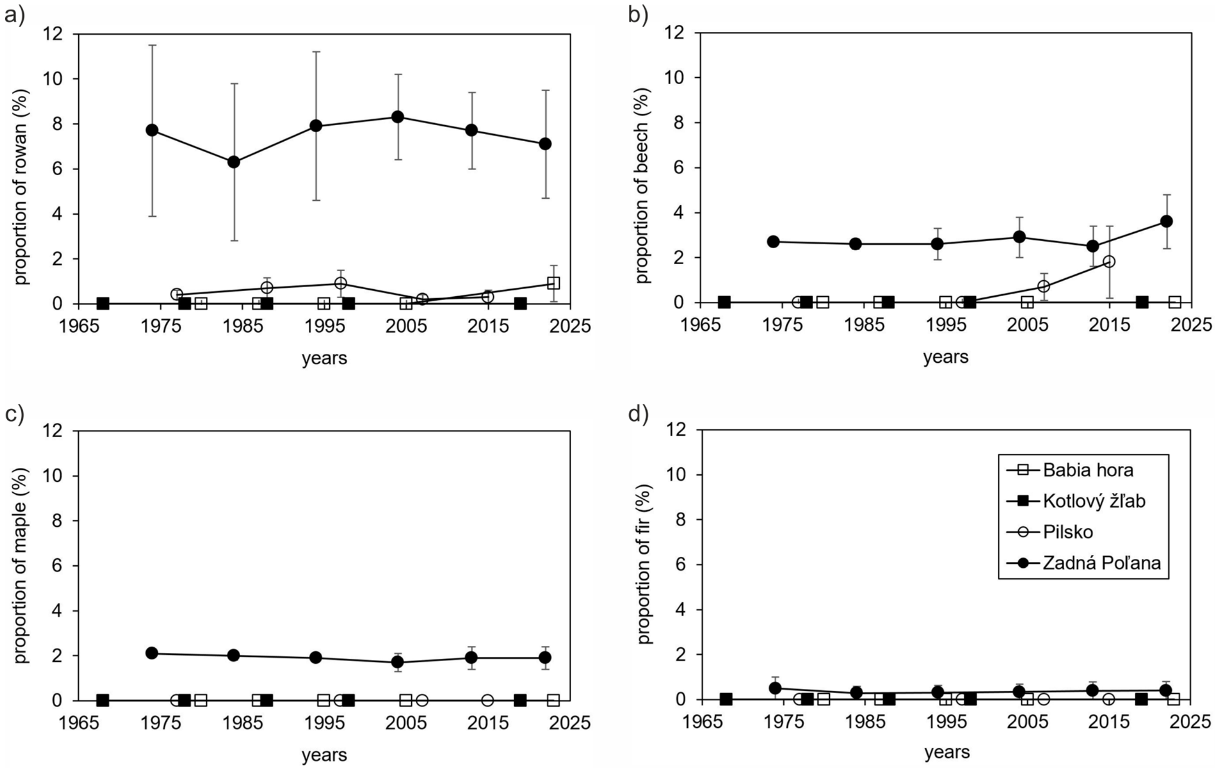

Fig. 5. Proportion of rowan (a), beech (b), maple (c) and fir (d) calculated from the stem density of trees with dbh above 8 cm in investigated old-growth spruce forests (mean ±SE).

The long-term average value of the dominant dbh ($d_{10\%}$) in Zadná Poľana reached approximately 75 cm. A similar value was registered only in PRP 3 in Babia hora. However, in general the dominant dbh ($d_{10\%}$) in Babia hora, Kotlový žľab and Pilsko was between 10 and 25 cm lower than that in Zadná Poľana.

The volume of the largest spruce trees with dbh of 92.5 cm (Babia hora), 98.6 cm (Pilsko) and 96.2 cm (Zadná Poľana) did not exceed the threshold of 11 m^3.

The recruitment (trees with dbh 0.1–8.0 cm) in investigated sites consisted mainly of spruce and rowan in variable proportions; in Pilsko and Zadná Poľana also beech recruitment was present (Fig. 6). Significant increase of recruitment density was observed in the last two decades in Babia hora (from 48 ±33 ha^{-1} in 2005 to 641 ±238 ha^{-1} in 2023), Kotlový žľab (from 0 ha^{-1} in 1998 to 1,666 ±928 ha^{-1} in 2019) and Pilsko (from 99 ±44 ha^{-1} in 1997 to 557 ±351 ha^{-1} in 2015). On the contrary, a relatively stable density of recruitment during the investigated period (from 31 ±11 ha^{-1} in 2013 to 112 ±60 ha^{-1} in 1974) was registered in Zadná Poľana.

4. Discussion

In the investigated old-growth spruce forests, with respect to the basic stand characteristics, no significant differences from other subalpine spruce forests in Central and Southeastern Europe were confirmed regarding the basic stand characteristics. Authors who studied old-growth spruce forests (Leibundgut 1993; Holeksa 2001; Zielonka 2006; Svoboda & Pouska 2008; Lamedica et al. 2011; Svoboda et al. 2014; Svobodová et al. 2019) reported average values of growing stock ranging from 270 m^3 ha^{-1} to 550 m^3 ha^{-1} and basal area from 35 m^2 ha^{-1} to 55 m^2 ha^{-1}. As the values observed in our research objects corresponded to this range, it can be assumed that the growing stock of 550 m^3 ha^{-1} and basal area 55 m^2 ha^{-1} represent threshold values that the old-growth spruce forests of Central and Southeastern Europe exceed only exceptionally. The example can be old-growth forest Kotlový žľab, where the values of basal area ranged from 56.1 to 62.4 m^2 ha^{-1} and those of growing stock from 579 to 630 m^3 ha^{-1} in the period 1965–1985.

Interdecadal changes of stand characteristics (stem density, basal area and growing stock) in analysed old-growth forests usually did not exceed the threshold 20%. Nevertheless, in the last two/three decades we observed a significant reduction of basal area and growing stock in the reserves Babia hora, Kotlový žľab and Pilsko. In Babia hora and Pilsko, the breakdown of forest stands was triggered by the uprooting of several groups of trees by the wind in the first decade of 21st century. Subsequently, the bark-beetle outbreak followed as main disturbance agent. Slightly different situation was recorded in Kotlový žľab, where the bark-beetle has been spreading since the beginning of the 1990s and now nearly the entire reserve (about

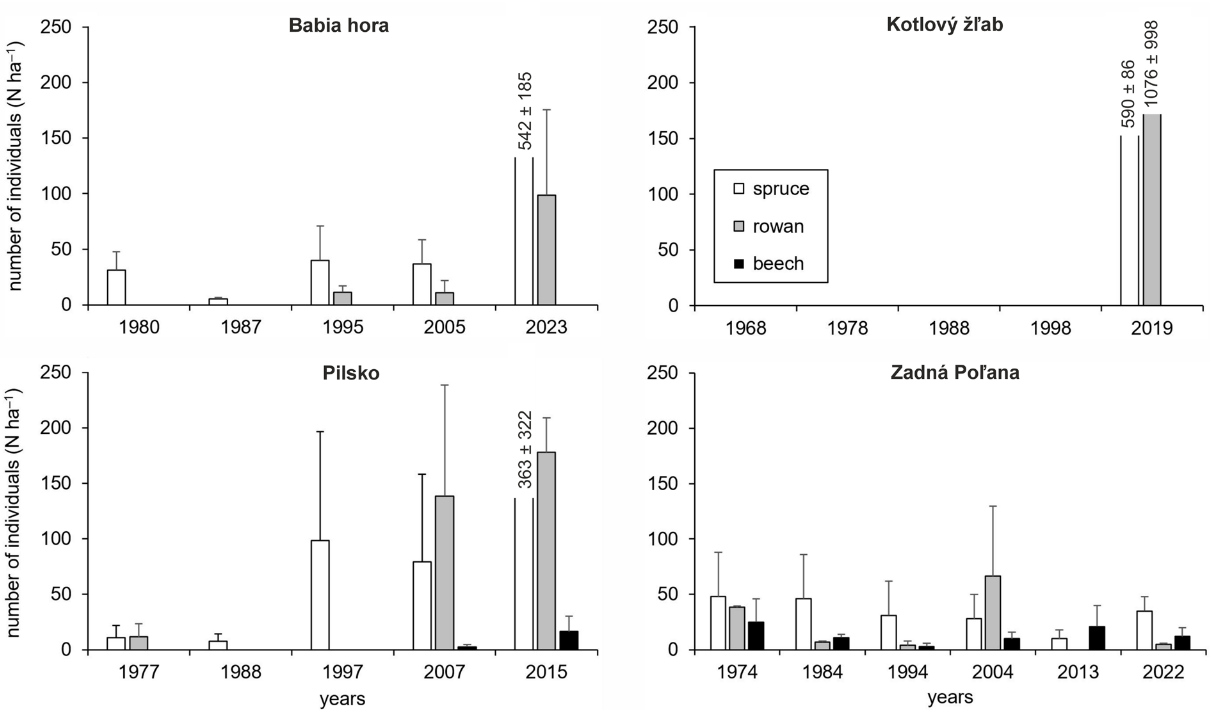

Fig. 6. Number and tree species composition of recruitment (dbh 0.1–8.0 cm) during the investigated period (mean ±SE).

70 ha) is affected by the stand breakdown. The reduction of growing stock by more than one third indicates a relatively severe disturbance. We assume, that the homogenous stand structure expressed by the unimodal diameter distribution contributed to a large extent to the disintegration of the upper tree layer, as such less resistant and resilient structures are usually the object of severe and large-scale natural disturbances (so-called "catastrophic breakdown" sensu Korpeľ 1989). It is obvious, that the disturbances in spruce forests caused by natural agents are closely related to their age and stand structure. In general, spruce forests growing in less suitable conditions and consisting of stems with smaller dimensions are less susceptible to the damage by wind and bark-beetles than mature stands or stands growing in more favourable sites. For example, the drought stress can contribute to the gradation of bark-beetle population, however, if the stem density and tree dimensions are low, the risk of the outbreak remains relatively low as well (Schurman et al. 2018). Temporally synchronised disturbances in the past led to the uniformity of tree dimensions and age structure in old-growth spruce forests. If a severe disturbance occurred, it was usually followed by a period without any stronger events (Čada et al. 2016). Especially the lack of more severe disturbances in the past could have predisposed the analysed old-growth forests to the stronger breakdown (Lausch et al. 2013; Havira et al. 2017; Janda et al. 2017, 2019). The extensive dieback of spruce stands can be nevertheless observed in the entire western part of the Carpathians during the recent decades (Mezei et al. 2014; Janda et al. 2019). Another significant factor is the climate change, that contributes to the higher frequency of windstorms and suitable conditions for the development of bark-beetles, especially due to the increasing temperatures and the drought-induced vitality decline of spruce stands (Marini et al. 2012; Holeksa et al. 2017; Schurman et al. 2018).

The most frequent diameter distributions in natural subalpine spruce forests are unimodal or bimodal distributions (Holeksa et al. 2007, 2016, 2017), what was confirmed also by our results. It is very likely, that unimodal structures in old-growth forests Babia hora, Kotlový žľab and Pilsko were the result of severe disturbances affecting the stands in the past. Nevertheless, due to the longevity of developmental cycle and natural tendency to form single-layered structures in spruce forests, the homogenous stands can originate also from other disturbance regimes as gap dynamics or disturbances of moderate severity (Holeksa et al. 2017; Janda et al. 2017).

The presence of rotated sigmoid diameter structures in old-growth spruce forests represents probably only a transitional state during their developmental cycle. Their formation is usually linked to the occurrence of weak disturbances, which mainly affect the upper layer of forest stands. Combination of varying intensity of mortality depending on the stem diameter, i.e. higher mortality in the understory and among the oldest and thickest stems, and lower mortality among vital canopy trees of medium diameter classes is, according to several authors (Goff & West 1975; Westphal et al. 2006), a biological reason for the occurrence of this diameter structure type. The largest stems are usually affected by wind and bark-beetles, while the understory trees die due to the light shortage resulting from the competition of the higher neighbours. The opening of the canopy supports the more or less continuous natural regeneration and subsequent ingrowth of trees into the higher stand layers (Holeksa et al. 2017; Vencurik et al. 2020). However, as a result of height transitions to the middle and upper layer, the crown space is gradually getting denser. The lower tolerance of spruce to shading causes the stagnation of regeneration processes and the diameter structure progressively changes to a unimodal one, as observed in old-growth forest Zadná Poľana. The structures recorded in Babia hora and Kotlový žľab that originate from severe exogenous disturbances can be regarded as threshold cases of bimodal structures, that approximate by their shape the rotated sigmoid distribution.

In subalpine forests, the proportion of rowan usually does not exceed 5% of the stem number and 1% of the basal area or growing stock (Holeksa et al. 2017). Such threshold values were surpassed only in Zadná Poľana (6–8% of the stem number, 2–3% of the growing stock), where the small-scale gap dynamics made possible the continuous ingrowth of rowan saplings into the higher stand layers. The other tree species as maple, fir and beech occurred in analysed old-growth forests only rarely, that is characteristic for these forest communities (Čada et al. 2016; Janda et al. 2019; Begović et al. 2023). Moderately increasing proportion of beech in reserves Pilsko and Zadná Poľana could be a short-term episode, which is related to the ongoing structural changes. On the other hand, it could signify the gradual shift in tree species composition of the stands triggered by the changing climate. Physiological constraints, especially the susceptibility of beech to low temperatures prevent this tree species from reaching higher size classes in high altitudes. With the ongoing global warming, however, this situation can gradually change. As a consequence, the investigated subalpine, monospecific spruce forests can become increasingly mixed (Weigel et al. 2018; Schurman et al. 2024).

The presence of large trees and related dominant diameter of the stand is one of the basic features distinguishing the structure of old-growth forests from forests impacted by human management interventions (Bauhus et al. 2009). In old-growth forest Zadná Poľana, the dominant dbh ($d_{10\%}$) in the long-term average oscillated around 75 cm, and the mean density of stems with dbh $\geq$ 60 cm exceeded 50 ha^{-1}. Significantly lower values of these characteristics were observed in Babia hora (except PRP 3), Kotlový žľab and Pilsko, which were affected by severe exogenous disturbances during the recent decades. The disturbance events caused the mortality of the majority of large trees and formed the structures, which will be dominated by thin trees of the following generation for a relatively long period (Korpeľ 1989; Čada et al. 2016). For the old-growth forests of Central Europe, the authors indicate the density of trees with dbh $\geq$ 80 cm reaching 10–17 ha^{-1}, on the other hand, in boreal forests they found only a rare presence of trees with diameter above 70 cm. In boreal spruce forests, a decisive influence of disturbances on the large trees density was observed, which was confirmed as a significant factor affecting their presence also in the studied subalpine spruce forests of the Western Carpathians. Relevant data on the density of large trees from subalpine spruce trees growing in comparable conditions was provided also by Svoboda & Pouska (2008) from the locality Trojmezná in the Bohemian Forest, where the stems with dbh $\geq$ 70 cm reached the average density of 13 ha^{-1}. Our results exceeded this threshold only in sites, which were not affected by severe disturbances in the near past, i.e. Zadná Poľana and part of Babia hora. The largest spruce stems reached in most of the investigated old-growth forests the dbh 90–100 cm and the volume between 9 and 11 m^3. These values can be regarded as the limit for spruce in subalpine conditions of the Western Carpathians (Kucbel 2014; Janda et al. 2017).

Spruce and rowan in initial phases of regeneration are able to tolerate the shading relatively good and survive under the canopy of mature stand even for decades. During this period, a rich bank of seedlings and saplings is gradually formed. With increasing size (age) of the regeneration, the light requirements of spruce and especially of rowan are rapidly growing (Holeksa et al. 2017). In the case of subalpine spruce forests with dominant small-scale gap dynamics, the rare occurrence of recruitment of both tree species is therefore concentrated to the irregularly scattered canopy gaps. Such gradual progress of regeneration processes was registered during the entire investigated period only in old-growth forest Zadná Poľana. On the contrary, in the reserves Babia hora, Kotlový žľab and Pilsko, where the canopy was suddenly destroyed by the severe disturbances during the recent decades, the regeneration of spruce and rowan grew vigorously and formed dense recruitment stands. Spruce saplings usually react to enhanced light conditions after the windthrow or bark-beetle disturbances by the intense diameter and height growth. Good growth potential of spruce in sites with high radiation is, besides the morphological plasticity of needle tissues, also the consequence of the ability to increase the nitrogen allocation to photosynthetic enzymes and thus enhance the photosynthetic capacity per unit mass (Orman et al. 2023). It is reasonable to assume, that besides spruce, also rowan will be able to thrive in such conditions for several decades. Nevertheless, it will be gradually outcompeted by the competitive stronger spruce, which will form here more or less homogenous stands (Żywiec & Ledwoń 2008; Żywiec & Holeksa 2012; Żywiec et al. 2013; Holeksa et al. 2017).

5. Conclusion

This study presents the results based on one of the longest regular measurements on permanent research plots in old-growth spruce forest reserves in Europe. Nevertheless, 50-years long observations still cover only a fraction of the entire life cycle in old-growth spruce forest, that has to be considered during the formulation of any general conclusions. Despite the aforementioned limitations, it seems very likely that the developmental cycle in subalpine spruce forests proceeds stable and without significant fluctuations only rarely and for a rather short period. The presence of relatively stable, rotated sigmoid structures does not represent a permanent state and is usually limited to the period of a few decades. An unstable development interrupted by stronger disturbances is much more common, usually resulting in less stable, unimodal structures. Such structures have the tendency to an intense breakdown and in the case of a severe disturbance, the climax forest returns by means of succession from pioneer and intermediary forest. In this process, the existing seedlings and saplings bank of spruce and rowan plays the crucial role, enables the regeneration of forest stands after disturbances and thus increases their resilience.

The knowledge of natural processes that drive the natural forests not impacted by human activity can be applied also in the management of subalpine spruce stands outside the strictly protected reserves, where the society demands the protection of neighbouring infrastructure against the natural hazards. By the maintenance of subalpine spruce forests in more stable and resilient structures, the effects of severe disturbances can be significantly limited. One of the ways is the application of silvicultural interventions, which imitate the impact of moderate, but more frequent disturbance events. Such low-severity interventions should continuously reduce the stem density of upper tree layer and counteract the tendency to homogenization of stand structures. At the same time, the consequence of the interventions should be the initiation and support of natural regeneration, in optimal situation also the forming and maintenance of differentiated stand structures (rotated sigmoid type).

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