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Effects of environmental factors and management on dynamics of mixed calcareous forests under climate change in Central European lowlands

Abstract: Mixed lowland forests reserved for natural succession are sparse in the Czech Republic. However, their development provides essential insights into the natural processes of these forests and recommendations for forest management in a changing climate. The research describes the dynamics, productivity, structure, diversity, dead wood, and radial growth of hornbeam-oak groves and calcareous beech-dominated forests in the Karlštejn National Nature Reserve (Czechia) based on inventory in 2002, 2008, 2014 and 2020. The objective was to evaluate changes in differently managed stands (high forest, coppice with standards, and coppice) after leaving the stands to spontaneous development in 2004. The tree density increased by 2–10% from 2002 to 2014 and decreased by 6–18% in 2020. In the high forest, an increase in the stand volume was observed during the whole period, while in the coppice with standards and coppice, only until 2014. The stand volume ranged from 190 (coppice) to 630 (high forest) m^3 ha^{-1} in 2020 and increased by an average of 28% over 18 years. Overall diversity of tree layer showed an uneven structure in the high forest and a substantially diverse structure in the other variants. The deadwood volume has been steadily increasing (18–35 m^3 ha^{-1} in 2020), accumulating an average of 1 m^3 ha^{-1} yr^{-1}. A lack of precipitation and high temperatures from June to August were the main limiting factors of the radial growth of tree species, while the number of negative pointer years has increased in the last decade. European beech (*Fagus sylvatica* L.) was the most sensitive tree species to climate compared to the resilient European ash (*Fraxinus excelsior* L.). The lowest fluctuations in the diameter increment were recorded in Norway maple (*Acer platanoides* L.) and the highest in beech in the temperature cycles of 7–15 years. Over the last 20 years, sessile oak [*Quercus petraea* (Matt.) Liebl.] showed an increase in radial growth by 7%, while other tree species reported a decrease with a maximum in beech (by −38%). The forest stands managed as high forest, characterized by a higher production potential and lower diversity, had slower dynamics when compared to coppice with standards and coppice.

Keywords: hornbeam-oak groves, beech forests, stand structure, diversity, radial growth, Czech Republic

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Introduction

Over recent decades, forest management in Europe has increasingly moved towards the emulation of the structure and dynamics of natural forests (Heiri et al., 2009; Kuuluvainen et al., 2021). Lowland forests reserved for natural succession can be an important source of information for understanding the natural processes that drive the successional dynamics (Saniga et al., 2014; Vacek et al., 2019a). A partial substitute for primary forests, which are scarce and highly fragmented in Europe (Sabatini et al., 2018), lowland forests have not been sufficiently studied. Lowland forests of Central Europe are mainly composed of oak, lime, hornbeam, and chestnut species. These forests are predominantly located in the warmest and driest parts of the region, while higher altitudes are covered by beech, spruce and fir (Bohn & Neuhäusl, 2000; Bertrand et al., 2011). Their development reflects the local microclimatic and edaphic conditions (Heiri et al., 2009; Vacek et al., 2019b). Due to the long history of human settlement in the region and an intense use of forest resources, the forests in the area have been heavily altered by firewood logging (Suchomel et al., 2012; Pyttel et al., 2013), cattle grazing, or litter gathering as routine practices throughout the whole of Europe (Unrau et al., 2018). Being easily accessible, forests in the Czech Republic were also intensively affected in the past (Průša, 1985; Vacek et al., 2019a).

Countless anthropogenic and natural events historically influenced the structure of lowland forests. Traditional coppice management methods managed the thermophilic and hornbeam-oak groves in Central Europe for a long time, by which a disintegrated canopy closure of stands was maintained (Bradshaw et al., 2003; Birks, 2005). Fires contributed to reducing the canopy closure of oak stands (Kalis et al., 2003). Although small in area – due to the historical land use, forest management and competition from agriculture – the remaining unmanaged lowland forests are part of protected areas where conservation is often insufficient (Sabatini et al., 2018). Currently, we observe an increasing interest in them (Rohner et al., 2012; Svátek & Matula, 2015), especially in the context of the anticipated climatic changes (Kolström et al., 2011; Thom et al., 2017).

Throughout history, the forest management approach has also changed tree species composition and mixing (Heiri et al., 2009; Vacek et al., 2019b). Mixed forests have been in the spotlight since the early 1990s, when the fight against biodiversity reduction gained importance (Bieng et al., 2013; Suding et al., 2015). Compared to monocultures, mixed stands are far more advantageous regarding their ecological stability and resilience in the face of global climate change (Steckel et al., 2020; Jourdan et al., 2021). For example, mixing tree species generally reduces insect damage (Jactel & Brockerhoff, 2007). It has a positive impact on the provision of ecosystem services (Gamfeldt et al., 2013). Moreover, the mixed stands can mitigate the effects of future climate change on forest ecosystems (Bruckman et al., 2011; Bieng et al., 2013; Vacek et al., 2021a), explaining why the diversity of tree species and their representation in forest stands are used as biodiversity indicators (MCPFE, 2003).

Biodiversity can also be considerably affected by the type of forest management, as the coppice management, assuming high heterogeneity of resources, allows for plant species with different strategies of coexistence (light-demanding and shade-tolerant species), while plant species that prefer open habitats absent in high forests (Müllerová et al., 2014; Vacek et al., 2019b). As the traditional forest management methods are being abandoned, the canopy closure of previously open forests gradually increases, leading to taxonomic depletion and homogenization of forest ecosystems (Hobi et al., 2015). Management can also affect the occurrence of dead wood, of which quantity

represents between 2% in managed forests and 30% in unmanaged forests (Fridman & Walheim, 2000). The deadwood has an extensive ecological role in forests such as sustaining biodiversity (von Oheimb et al., 2007), regulation of nutrient cycles (Kuehne et al., 2008), providing a wide range of habitats for saproxylic and fungi organisms (Lassauce et al., 2011; Blaser et al., 2013), establishing of natural tree regeneration (Štícha et al., 2010) or carbon sequestration (Tavankar et al., 2022).

The significant impacts of forest management practices on forest ecosystems (Dieler et al., 2017) are particularly substantial in relation to global climate change (Thuiller et al., 2008; Allen et al., 2010). A decrease in precipitation results in more frequent and severe droughts, that will increase the risk for tree growth, ecological stability, and vitality of forest ecosystems during global climate change (Kolström et al., 2011; Alfaro-Sánchez et al., 2020; Gallo et al., 2020). In many places, both research and silviculture practice are currently focused on converting even-aged pure stands into uneven-aged mixed ones (Pretzsch & Schütze, 2009). The growth of trees can be positively affected by the mixing of species (Chamagne et al., 2017; Jactel et al., 2018; Pretzsch et al., 2020), although it does not always apply (Vitali et al., 2017). Similarly, climate change may not only negatively affect forest stands but can also contribute to increased forest stands production (Körner & Basier, 2010; Pretzsch et al., 2018).

This paper aims to evaluate the dynamics, structure, tree species biodiversity, dead wood, and radial growth of selected lowland forests (high forest, coppice with standards, and coppice; location Doutnáč in the Bohemian Karst Protected Landscape Area, Czechia) which have been intentionally reserved for natural succession since 2004 to allow researchers study natural processes. The studied location is unique in Czechia to pursue the following scientific issues:

– What changes have occurred in the stand structure (vertical, horizontal), tree species biodiversity, and deadwood occurrence over 18 years (2002–2020)?
– What are the stand production and biodiversity differences among individual forest types (high forest, coppice with standards, and coppice)?
– How does the radial growth (1960–2020) of the particular tree species differ regarding the effect of growth cycles, environmental factors, and climate change?

Material and Methods

Study area

The studied Doutnáč forest complex (the area of 67.64 ha), with six permanent research plots (PRPs), is located in Central Bohemia, in the Karlštejn National Nature Reserve (NNR), which is part of the Bohemian Karst Protected Landscape Area (PLA) – (Fig. 1). The first written data on forest management in the vicinity of the Karlštejn Castle comes from the first half of the 15th century (Černý, 1949). Until the mid-20th century, the studied Doutnáč forest
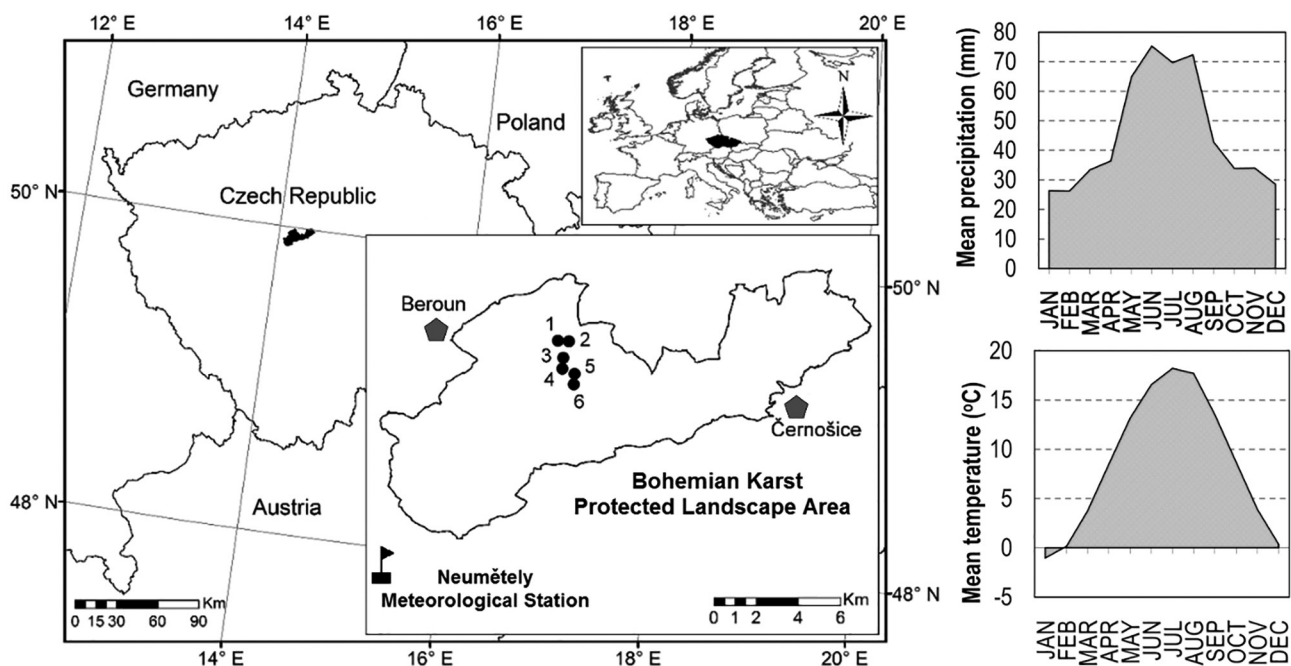

Fig. 1. Localization of permanent research plots 1–6 in the Doutnáč locality, the Neumětely meteorological station – the data source used for dendrochronology analyses and the mean monthly climatic values (1960–2020)

Table 1. Overview of basic stand and site characteristics of permanent research plots 1–6 in the Doutnáč location (based on the Forest Management Plan, 2018; the age was updated for the year 2022)

PRP	WGS 84	Forest management	Tree species	Age (yr)	Height (m)	DBH (cm)	Stand volume (m³ ha⁻¹)	Altitude (m)	Exposure	Slope (°)	Forest site type
1	N 49°57'45"	High forest	*Fagus sylvatica*	90	27	32	167	412	NE	6	3W
2	E 14°09'17"		*Quercus petraea*		21	23	30				
			Carpinus betulus		16	16	18				
			Tilia cordata		23	26	29				
			Betula pendula		23	29	3				
			Sorbus torminalis		18	22	2				
			Total		21	25	249				
3	N 49°57'32"	Coppice with standards	*Quercus petraea*	108	17	22	58	433	NE	2	2A
4	E 14°09'11"		*Tilia cordata*		17	21	57				
			Carpinus betulus		15	16	18				
			Fagus sylvatica		20	24	22				
			Larix decidua		21	29	15				
			Betula pendula		19	23	2				
			Populus tremula		23	27	3				
			Total		19	23	175				
5	N 49°57'23"	Coppice	*Tilia cordata*	87	18	19	58	415	SE	17	2W
6	E 14°09'15"		*Carpinus betulus*		16	15	42				
			Quercus petraea		17	19	37				
			Acer platanoides		18	18	5				
			Fraxinus excelsior		18	18	3				
			Total		17	18	145				

Notes: 3W – limestone-calcareous oak-beech stand (*Querceto-Fagetum calcarium*), 2W – limestone-calcareous beech-oak stand (*Fageto-Quercetum calcarium*), 2A – stony-colluvial maple-beech-oak stand – (*Aceri-Fageto-Quercetum lapidosum*; Viewegh et al., 2003).

complex had been managed as coppice with standards with high intensity of logging in the stand, litter raking, and cattle grazing. This intensive use finished before World War II (Průša, 1985). After the proclamation of the Karlštejn National Nature Reserve in 1955, forest management was gradually reduced to support the natural spatial, species, and age composition of the forest (Ložek et al., 2005). Current local forests are mostly overmatured coppices, i.e., false high forests with isolated standards of seed origin (mostly oaks; Janík et al., 2008). The entire Doutnáč forest complex was officially reserved for natural succession in 2004. However, no forest management has been performed in the studied localities since 1986.

Doutnáč is an elongated, north-south oriented ridge, where the highest peak lies at an altitude of 433 m above sea level (Janík et al., 2008). The study territory has typically warm, dry summers and cool, dry winters with a narrow annual temperature range (climate type Cfb) according to Köppen climate classification (Tolasz, 2007). The mean annual temperature of the location has been 8.6 °C (14.6 °C in the growing season). The annual amount of precipitation has varied around 540 mm (360 mm in the growing season) in the period of 1960–2020 (Neumětely meteorological station). Maximum temperatures are reached in July (18.2 °C) and precipitation in June (75.3 mm), while the lowest in January (–1.0 °C) and in February (26.3 mm; Fig. 1). The average duration of the growing season is 165 days. In the climate change context, the average annual temperature has increased by 2.2 °C over the last 60 years (1960–2020), and the annual amount of precipitation has decreased by 16 mm, while fluctuations (standard deviation) of monthly climatic data during the year increased in both variables during the observed period.

The geological bedrock is predominantly formed by grey to red limestones. Predominating soils include the rendzinas, brown forest soils, and cambisols (Šamonil, 2007). It is a group of oak groves in the oak to oak-beech vegetation zone (Janík et al., 2008). In the lower altitudes, there are maple forests (*Tilio-Acerion* forests) with sycamore maple (*Acer pseudoplatanus* L.) and field maple (*Acer campestre* L.). Along the southern slope, the western and eastern slopes, they gradually change into mixed European hornbeam (*Carpinus betulus* L.) and sessile oak [*Quercus petraea* (Matt.) Liebl.] forests (*Melampyro Nemorosi-Carpinetum*). Towards the north, the representation of European beech (*Fagus sylvatica* L.) is increasing, and the calcareous beech forests (*Cephalanthero-fagetum*) dominate in the north. The forest-steppe on the southern slope is bordered by a downy oak forest (*Lathyro versicoloris-quercetum pubescentis*) – (Průša, 1985; Janík et al., 2008). An overview of primary data of PRPs 1–6 on the Doutnáč location is presented in Table 1.

Data collection

In 2002, six PRPs were established in size 50 × 50 m (0.25 ha) – two PRPs for each type of forest management: high forest (PRPs 1–2), coppice with standards (PRPs 3–4), and coppice (PRPs 5–6). The structure of the tree layer was measured using

a theodolite in 2002 and the FieldMap technology (IFER, CR) in 2008, 2014, and 2020. All measurements of the tree layer included the following parameters: the diameter at breast height (dbh) with an accuracy of 1 mm, the position of all individuals with dbh ≥ 4 cm measured by a Mapstar compass and laser range-finger ForestPro (Laser Technology), total height and the live crown base height using a Vertex laser hypsometer (Haglöf, Sweden) with an accuracy of 0.1 m, and tree-crown projection area at least in 4 cardinal directions. Deadwood (diameter ≥ 7 cm, length ≥ 1 m) was determined by position, parameters, tree species, and degree of decomposition [five degrees scale according to Spetich et al. (2002); 1 – stem undisturbed by decomposition, 5 – final disintegration phase]. For logs, the length and diameter of the butt, the small end and the middle section were measured, whereas dbh and the height for snags and the height and the diameter for stumps were measured. Only deadwood originating from the PRPs was evaluated (Vacek et al., 2015).

For a dendrochronological analysis of the samples, cores were taken using a Pressler auger (Haglöf Sweden) perpendicularly to the axis of the trunk at the height of 1.3 m above the ground. One core sample was taken from each selected tree in direction up-down the slope in November 2020. Healthy predominant and dominant trees were randomly (RNG function, Excel) chosen on PRPs as the significant growth response to environmental factors and management (compared to intermediate and suppressed trees; Remeš et al., 2015). Thirty core samples were extracted from the following five major tree species in all PRPs: European beech, sessile oak, small-leaved lime (*Tilia cordata* Mill.), Norway maple, and European ash (*Fraxinus excelsior* L.). Only up to 15 core samples were taken from admixed European hornbeam, European larch (*Larix decidua* Mill.), and wild service tree [*Sorbus torminalis* (L.) Grantz] due to insufficient numbers of trees. The increment cores were measured using an Olympus microscope with a LINTAB measuring table (Rinntech, Heidelberg, Germany). The measurement was performed with an accuracy of 0.01 mm. TSAP-Win software (Rinntech, Heidelberg, Germany) was employed to record the increment cores.

Data analysis

The stand volume was calculated according to Petráš & Pajtík (1991). Deadwood volume was estimated according to the methodology of Harmon et al. (1986). Newton's formula was used for logs, whereas for dead standing trees, volume tables of Lesprojekt Ltd. where the volume of snags and stumps is calculated from the dbh or diameter and height (Vacek et al., 2015). The relative stand density index (SDI; Reineke, 1933), the crown closure (CC; Crookston & Stage, 1999), and the crown projection area (CPA) were assessed for each plot.

Species diversity was evaluated by species richness (Margalef, 1958), species heterogeneity (Shannon, 1948) and species evenness (Pielou, 1975). In terms of structure, horizontal structure (Clark & Evans, 1954), vertical structure (Pretzsch, 2006) and diameter and height differentiation were calculated (Füldner, 1995). Moreover, total stand diversity was determined based on tree species diversity, vertical structure, spatial tree distribution, and crown differentiation (Jaehne & Dohrenbusch, 1997). Detailed information about the used indices is listed in Table 2.

Dendrochronological data were analyzed in R software (R Core Team, USA) using the packages "dplR" (Zang et al., 2020) and "pointRes" (van der Maaten-Theunissen et al., 2021). Age detrending of each measured sample was carried out by negative exponential detrending with a spline of 1/3 of the age of each tree using "dplR" instructions. The expressed population signal (EPS) was calculated for the detrended data series. The comparison limit for using the dendrochronological data series related to the climatic data was a significant EPS threshold to be EPS > 0.85. The signal to noise ratio (SNR), the inter-series correlations (R-bar) and the first-order autocorrelation (Ar1) were calculated for

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

Criterion	Quantifiers	Label	Reference	Evaluation
Species diversity	Richness	D (Mi)	Margalef (1958)	minimum $D = 0$, higher D = higher values
	Heterogeneity	H' (Si)	Shannon (1948)	minimum $H´ = 0$, higher $H´$ = higher values
	Evenness	E (Pii)	Pielou (1975)	range 0–1; minimum $E = 0$, maximum $E = 1$
Horizontal structure	Aggregation index	R (C&Ei)	Clark & Evans (1954)	mean value $R = 1$; aggregation $R < 1$; regularity $R > 1$
Vertical structure	Arten-profile index	A (Pri)	Pretzsch (2006)	range 0–1; balanced vertical structure $A < 0.3$; selection forest $A > 0.9$
Structure differentiation	Diameter dif.	TM_d (Fi)	Füldner (1995)	range 0–1; low $TM < 0.3$; very high differentiation $TM > 0.7$
	Height dif.	TM_h (Fi)		
Complex diversity	Stand diversity	B (J&Di)	Jaehne & Dohrenbusch (1997)	monotonous structure $B < 4$; uneven structure $B = 6$–8; very diverse structure $B > 9$

dendrochronological data series (Fritts, 1976). The EPS, SNR, R-bar, Ar1 were calculated by the instructions to "dplR" based on standard dendrochronological models (Fritts, 1976).

The analysis of pointer years through relative growth change was carried out (Schweingruber et al., 1990) to determine changes in tree-rings. A pointer year is created by normalizing the tree-ring series in a moving window with each year placed as a central point. Pointer years reflect the number of standard deviations from the local mean of the average ring width of the previous four years. Pointer years identify event years where a pointer year > 0.75 standard deviations of the previous four years. The threshold on the percentage of trees in a negative or positive event year was used for better clarity (Neuwirth et al., 2007).

Spectral analyses for the detrended radial increment of each studied tree species were performed with Statistica 13 software (TIBCO, USA). The calculation was performed with the "Single Furier (Spectral) Analysis" function, using the output "Periodogram plot by Period". In this software, dendrochronological data series of individual tree species were correlated with monthly precipitation and air temperature data from April of the previous year to September of the current year. The average tree-ring series for main tree species were correlated with climatic data (monthly precipitation, temperatures in 1960–2020) from the nearby Czech Hydrometeorological Institute Neumětely station (322 m a.s.l., GPS 49°51'14"N, 14°2'15"E).

Unconstrained principal component analysis (PCA) in Canoco 5 (Šmilauer & Lepš, 2014) was used to analyse the relationships between dynamics, structure, production, diversity and management of studied forest stands. Data were log-transformed, centred and standardized before the analysis. The situation map was created in ArcGIS 10.8 software (Esri, USA).

Results

Stand structure, production, and dynamics

We observed the highest values for mean diameter in the high-forest plots (32.6–37.7 cm; Table 3). With 14.0–16.7 cm in coppice and 19.1–21.5 cm in coppice with standards, these values were considerably lower in the other stands. We noted a similar trend for mean height. The lowest number of trees was on the PRPs 1–2 (high forest), while it was 4.8 times higher on the PRPs 5–6 (coppice). The number of living trees increased from 360–1992 trees ha^{-1} in 2002 to 368–2160 trees ha^{-1} (by 2–10.3%) in 2014, and subsequently, tree numbers decreased to 348–1672 trees ha^{-1} (by 5.5–17.9%) in 2020 on individual PRPs (not variants). Similar dynamics were recorded in the case of the density indices (SDI, CPA, and CC). The stand density index ranged from 0.54 to 0.78 in 2002. It showed an increase (0.61–0.97) until 2014 to be followed by a decrease (0.68–0.95), except for the high forest (PRPs 1 and 2).

The average stand basal area in the observed period increased on all plots. In contrast, it was the highest in the high forest (41.4 m^2 ha^{-1}) and the lowest in the coppice with standards in 2020 (33.5 m^2 ha^{-1}; Table 3). During the 12-year study, the stand volume changed from 456 to 590 m^3 ha^{-1} (+ 29%), from 218 to 258 m^3 ha^{-1} (+18%), from 153 to 210 m^3 ha^{-1} (+37%) in the high forest (PRPs 1–2), the coppice with standards (PRPs 3–4) and the coppice (PRPs

Table 3. Overview of stand characteristics in high forest (PRPs 1–2), coppice with standards (PRPs 3–4), and coppice (PRPs 5–6) in the Doutnáč location in 2002, 2008, 2014, and 2020; the table shows the average values for the two plots; an increase in the values during dynamics is highlighted in grey

PRP	Year	Age (yr)	dbh (cm)	h (m)	h$_{95}$ (m)	v (m³)	BA (m² ha⁻¹)	V (m³ ha⁻¹)	N (trees ha⁻¹)	HDR	MAI (m³ ha⁻¹ yr⁻¹)	CPA (ha ha⁻¹)	CC	SDI
1–2	2002	84	32.6	27.1	32.6	1.160	32.7	456	394	83.1	5.47	2.55	0.92	0.57
	2008	90	33.6	27.2	32.8	1.255	35.1	500	398	81.1	5.60	2.80	0.93	0.61
	2014	95	35.0	27.5	33.6	1.385	38.7	558	404	78.5	5.88	3.17	0.96	0.66
	2020	99	37.7	27.9	35.6	1.585	41.4	590	372	74.2	5.96	3.13	0.96	0.68
3–4	2002	86	19.1	14.8	22.0	0.230	27.8	218	990	77.8	2.53	3.30	0.96	0.59
	2008	92	19.5	14.7	23.0	0.240	30.0	239	1,027	75.8	2.60	3.74	0.97	0.64
	2014	97	20.1	14.7	24.0	0.265	33.7	276	1,082	73.4	2.84	4.34	0.98	0.71
	2020	100	21.5	13.8	22.4	0.280	33.5	258	930	63.0	2.58	4.26	0.99	0.69
5–6	2002	71	14.0	11.6	16.0	0.080	28.7	153	1,870	82.8	2.15	4.07	0.97	0.73
	2008	77	14.7	11.6	16.5	0.090	32.8	175	1,944	79.2	2.27	4.61	0.97	0.81
	2014	81	15.6	11.7	17.0	0.110	38.4	217	2,024	75.4	2.68	5.29	0.98	0.92
	2020	89	16.7	11.2	17.9	0.115	35.6	210	1,766	66.7	2.36	5.93	0.99	0.89

Notes: Age – average stand age, dbh – mean quadratic diameter at breast height, h – mean height, h95 – top 95% height, v – average tree volume, BA – basal area, V – stand volume, N – number of trees per hectare, HDR – slenderness ratio, MAI – mean annual increment, CPA – crown projection area, CC – canopy closure, SDI – stand density index.
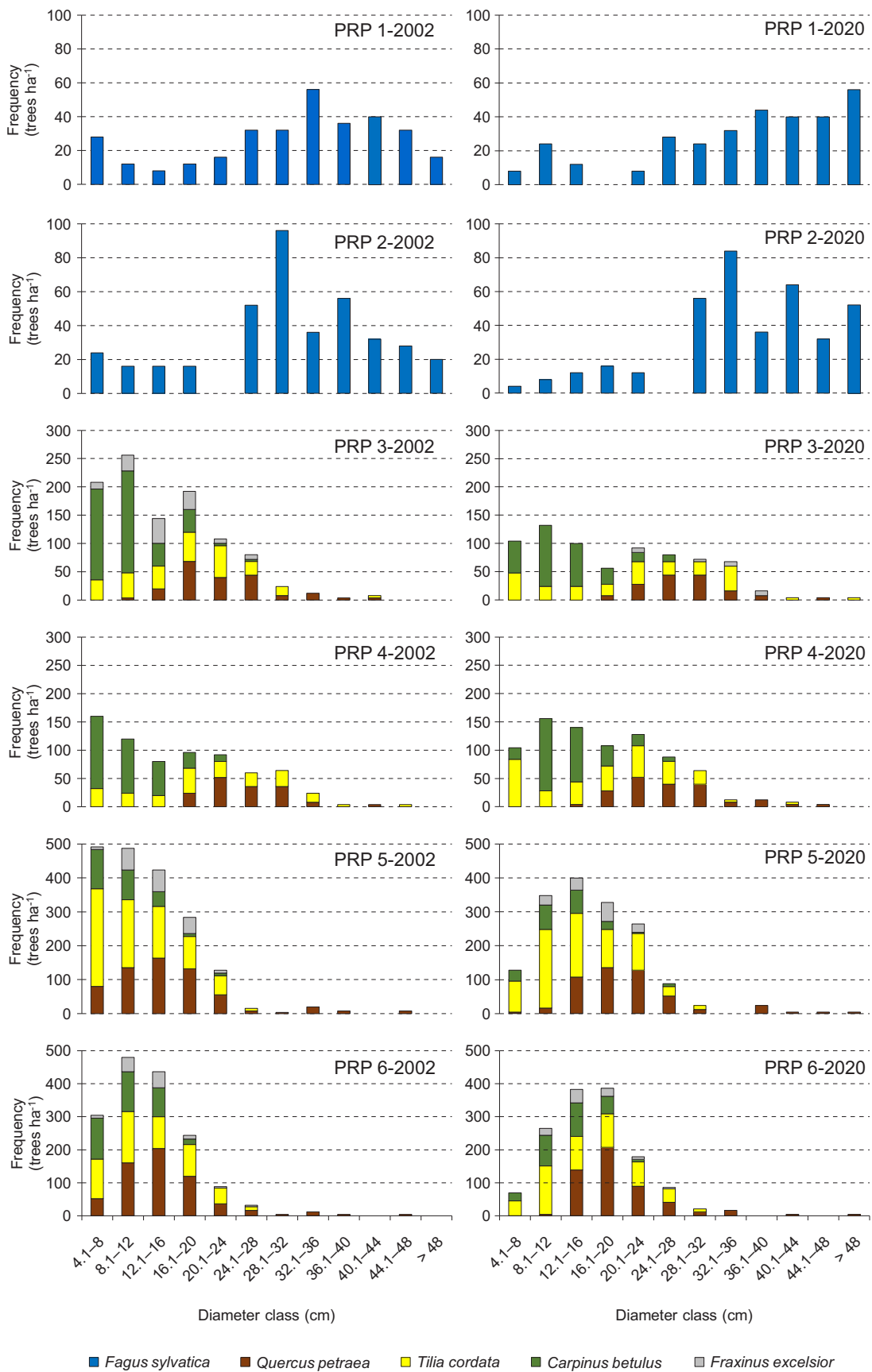
Fig. 2. Histogram of the diameter structure of the tree layer in high forest (PRPs 1–2), coppice with standards (PRPs 3–4), and coppice (PRPs 5–6) in the Doutnáč location differentiated by the main tree species in 2002 (left) and 2020 (right); only tree species with share ≥ 5% are shown

5–6), respectively. While an overall increase of the stand volume occurred in the high forest over the entire period, it increased in the coppice with standards and coppice until 2014, and then it decreased. On PRP 1–2, 95% of the volume represented beech. On PRPs 3–4, small-leaved lime (29–31%) and sessile oak (26–30%) were the dominant tree species. Similarly, sessile oak (42–44%) and small-leaved lime (34–37%) reached the largest volumes on PRPs 4–5. The mean annual increment (MAI) reached 5.96 m³ ha⁻¹ yr⁻¹ in 2020 in the high forest, while MAI was lower by 56% and 60% in the coppice with standards and coppice, respectively.

The diameter frequencies of the tree layer in 2002 and 2020 showed different structures and dynamics (Fig. 2). On PRPs 1–2, two layers were distinguished, in these beech dominated with the most frequency diameter classes from 28 to 36 cm in 2002, while the diameter structure was right-sided in 2020. On PRPs 3–4, the stands had the overall character of the selection structure. At the same time, hornbeam was the dominant tree species in the lower storey and lime with oak in the upper storey of the coppice with standards plots. PRPs 5–6 also showed features of the selection structure based on diameter structure. However, lime was the dominant tree species in the coppice. During the monitored 18 years, the number of trees in the thinnest diameter class (4–8 cm) decreased by 20, 56–84, and 236–364 trees ha⁻¹ on PRPs 1–2, PRPs 3–4, and PRP 5–6, respectively.

Stand biodiversity

In terms of species diversity, the species richness of the tree layer was medium from 2002 to 2020 in the high forest (PRPs 1–2), high in the coppice (PRPs 5–6) and very high in the coppice with standards (PRPs 3–4; Table 4). Until 2020, there was a slight increase in species richness on all PRPs except for high forest. The species heterogeneity of the tree layer and species evenness were low in 2002–2020 on PRPs 1–2, medium on PRPs 5–6, high on PRPs 3–4. The diversity was relatively stable in all the variants during the observed period.

On the one hand, the horizontal structure was random with a tendency to regular distribution in the case of high forest during the monitored years. On the other hand, the spatial pattern of trees was significantly aggregated on other PRPs, especially in the coppice. The vertical structure within the PRPs (not variants) was relatively variable (A=0.189–0.700), ranging from a low (PRPs 1–2 in 2002) to medium (in 2020) to fairly diversified vertical diversity, which consists of several (3–4) storeys on PRPs 3–6. It slightly increased on all plots except the coppice during the monitored years, where it decreased more significantly between 2014 and 2020.

The height and diameter differentiation of stands was predominantly medium except for the low differentiation in the case of the coppice. At the end of the study period, the diameter differentiation increased in the coppice with standards and decreased in the high forest. Height differentiation increased on all PRPs. In terms of total diversity, an uneven structure (B = 6.545–6.742) was observed on PRPs 1–2 and a very diverse structure (B=9.228–10.623) on PRPs 3–6. Stand variability slightly increased during the study period on all PRPs except PRP 2, where a slight decrease in the second half of the study period occurred (Table 4).

Table 4. Indices describing the diversity of the tree layer in high forest (PRPs 1–2), coppice with standards (PRPs 3–4), and coppice (PRPs 5–6) in the Doutnáč location in 2002, 2008, 2014, and 2020; the table shows the average values for the two plots; an increase in the values during dynamics is highlighted in grey

PRP	Year	Species richness	Species heterogeneity	Species evenness	Horizontal structure	Vertical structure	Diameter differentiation	Height differentiation	Total diversity
1–2	2002	0.503	0.105	0.175	1.137	0.209	0.424	0.254	6.628
	2008	0.502	0.105	0.176	1.134	0.214	0.417	0.263	6.738
	2014	0.501	0.106	0.177	1.132	0.223	0.407	0.275	6.755
	2020	0.340	0.091	0.194	1.052	0.444	0.347	0.274	6.652
3–4	2002	1.162	0.737	0.772	0.960	0.676	0.393	0.281	10.186
	2008	1.153	0.737	0.772	0.922*	0.674	0.396	0.304	10.285
	2014	1.147	0.738	0.773	0.894*	0.670	0.403	0.331	10.403
	2020	1.318	0.734	0.734	0.881*	0.692	0.417	0.357	10.463
5–6	2002	0.864	0.577	0.660	0.716*	0.649	0.323	0.233	9.465
	2008	0.860	0.580	0.664	0.716*	0.658	0.321	0.253	9.393
	2014	0.855	0.585	0.669	0.720*	0.670	0.318	0.277	9.310
	2020	0.937	0.588	0.651	0.736*	0.557	0.320	0.288	9.729

Notes: Species richness – Margalef D index, Species heterogeneity – Shannon H' index, Species evenness – Pielou E index, Horizontal structure – Clark-Evans aggregation R index, Vertical structure – Arten-profile A index, – Diameter differentiation – Füldner TMd index, Height differentiation – Füldner TMh index, Total diversity – Jaehne-Dohrenbusch B index; * statistically significant (p < 0.05) aggregated horizontal structure.

Structure and dynamics of deadwood

The deadwood volume ranged from 1.7 (PRP 1) to 16.2 m^3 ha^{-1} (PRP 6) and reached 0.2–9.8% of the total stand volume in 2002. The proportion of lying deadwood prevailed over the standing by 22% at the beginning of the monitoring (Table 5). Until 2014, the proportion of deadwood increased only imperceptibly. A significant increase in deadwood occurred only between 2014 and 2020. In 2020, the proportion of deadwood in the total stand volume ranged from 4.1% (high forest) to 14.3% (coppice). Specifically, the lowest deadwood proportion was on PRP 4 (18.3 m^3 ha^{-1}) in 2020, i.e., 6.2% of the stand volume compared to the highest proportion on PRP 6 (35.4 m^3 ha^{-1}), i.e., 15.6% of stand volume. In 2020, the proportion of standing deadwood prevailed by 40% over logs.

Regarding the representation of tree species in standing dead wood, dominating oak (43.4%) is followed by spruce (15.3%), lime (13.4%), and hornbeam (10.3%). In terms of the degree of decomposition of standing deadwood, the 1st and 2nd degree (55.5 and 29.4%) were the most represented, less the 3rd degree (17.6%) and the least was the 4th degree (2.4%; Table 5). In terms of the degree of decomposition of lying deadwood, the 3rd and 2nd degrees (60.0 and 20.0%) were the most occurred, the 4th degree was less represented (10.9%), and the least belonged to the 1st degree (9.1%). The horizontal structure of standing and lying deadwood was mainly random, and it was clustered only for lime in 2014 and 2020.

Radial growth and climate effect

Beech (1.98 mm) and larch (1.98 mm) showed the highest mean radial growth compared to the lowest, rowan (0.92 mm) and ash (1.00 mm; Table 6). Autocorrelation AR1 showed similarity of all tree species (0.45–0.66). Results of EPS were significant (EPS > 0.85) in the case of beech (EPS=0.95), oak (EPS=0.96), Norway maple (EPS=0.88), and ash

Table 5. The volume of standing, lying, and total deadwood based on the degrees of decomposition in high forest (PRPs 1–2), coppice with standards (PRPs 3–4), and coppice (PRPs 5–6) in the Doutnáč location in 2002, 2008, 2014, and 2020; the table shows the average values for the two plots; an increase in the values during dynamics is highlighted in grey

PRP	Year	Dead wood (m^3 ha^{-1})										Total (m^3 ha^{-1})	Proportion in the total stand volume (%)
		Standing (stumps)					Lying (logs)						
		Decomposition degree											
		1.	2.	3.	4.	(%)	1.	2.	3.	4.	(%)		
1–2	2002	0.5	0.5	0.0	0.0	40.5	0.2	1.1	0.0	0.0	59.5	2.2	0.4
	2008	0.2	1.7	0.0	0.0	51.0	0.1	1.1	0.2	0.0	49.0	3.2	0.7
	2014	0.1	2.8	0.0	0.0	87.0	0.0	0.9	0.0	0.0	13.0	3.8	0.7
	2020	17.0	5.0	0.5	0.0	93.5	0.6	0.5	0.4	0.1	6.5	23.9	4.1
3–4	2002	0.7	1.4	0.6	0.0	29.5	1.3	1.8	1.8	0.1	70.5	7.6	3.7
	2008	1.2	2.4	1.2	0.0	36.5	0.9	0.9	3.9	0.6	63.5	12.9	5.4
	2014	1.6	3.2	1.7	0.0	45.0	0.6	0.3	6.3	0.8	55.0	14.6	5.4
	2020	11.7	3.9	1.4	0.1	73.5	1.0	0.6	4.5	1.2	26.5	22.8	9.2
5–6	2002	2.2	1.8	2.0	0.3	47.0	1.0	2.8	2.8	0.2	53.0	13.1	8.5
	2008	1.8	2.2	3.5	0.5	49.5	0.5	1.4	5.5	0.5	50.5	15.7	8.8
	2014	1.3	2.7	4.5	0.7	47.5	0.0	0.4	8.0	0.7	52.5	18.2	8.3
	2020	14.0	3.1	3.1	0.4	68.0	0.3	0.9	5.8	2.7	32.0	30.1	14.3

Table 6. Characteristics of standardized tree-ring chronologies of tree species in 1960–2020

Species	No. cores (pcs)	Mean RW (mm)	Min–max RW (mm)	Min–max age (yr)	SD	AR1	R-bar	ESP	SNR
Fagus sylvatica	30	1.98	1.27–3.33	55–107	0.87	0.61	0.42	**0.95**	20.68
Quercus petrea	30	1.13	0.77–1.94	57–171	0.53	0.61	0.35	**0.96**	21.77
Carpinus betulus	14	1.24	0.91–1.83	50–111	0.58	0.41	0.04	0.35	0.55
Tilia cordata	28	1.32	0.68–2.00	56–111	0.71	0.49	0.07	0.68	2.14
Acer platanoides	30	1.20	0.47–3.60	52–115	0.67	0.45	0.17	**0.88**	10.08
Larix decidua	5	1.98	1.24–2.97	89–98	1.27	0.66	0.30	0.68	2.13
Sorbus torminalis	2	0.92	0.70–1.15	65–88	0.44	0.53	0.19	0.07	0.08
Fraxinus excelsior	27	1.00	0.58–1.92	74–118	0.48	0.56	0.34	**0.94**	14.37

Notes: No. cores – number of cores used for analyses, RW – tree ring width, SD – standard deviation, AR1 – first-order autocorrelation, R-bar – inter-series correlation, EPS – expressed population signal (significant numbers EPS > 0.85 are in bold), SNR – signal-to-noise ratio.

(EPS=0.94). The values of EPS in hornbeam, lime, larch, and wild service tree were < 0.85, and they were not included for other climate analyses. Values of SNR were the highest in oak (SNR=21.77), followed by beech (SNR=20.68). Over the last 20 years (compared to the preceding 20 years), the radial growth has increased in oak by 7.0%, while the highest decrease was observed in beech (–37.9%).

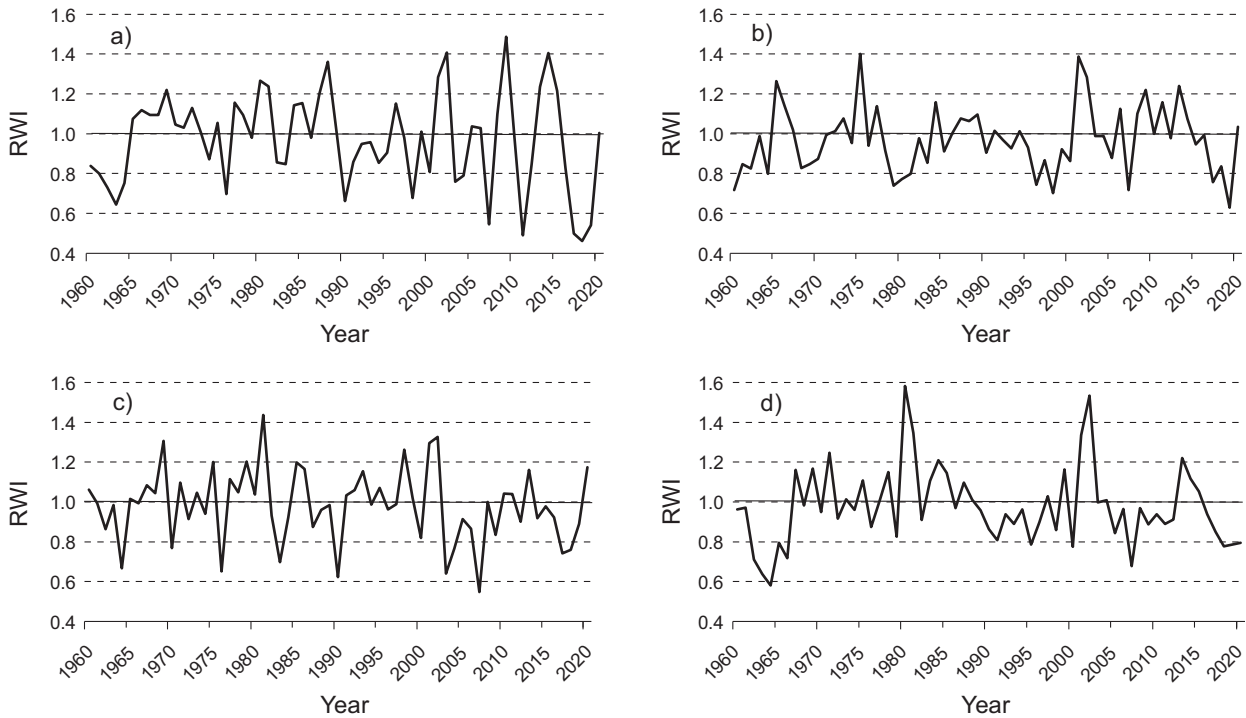In the case of comparable sampling depth (beech, oak, lime, maple and ash), the highest mean growth

Fig. 3. Standardized ring width chronologies of European beech (a), sessile oak (b), Norway maple (c), and European ash (d) in 1960–2020; RWI – ring width index
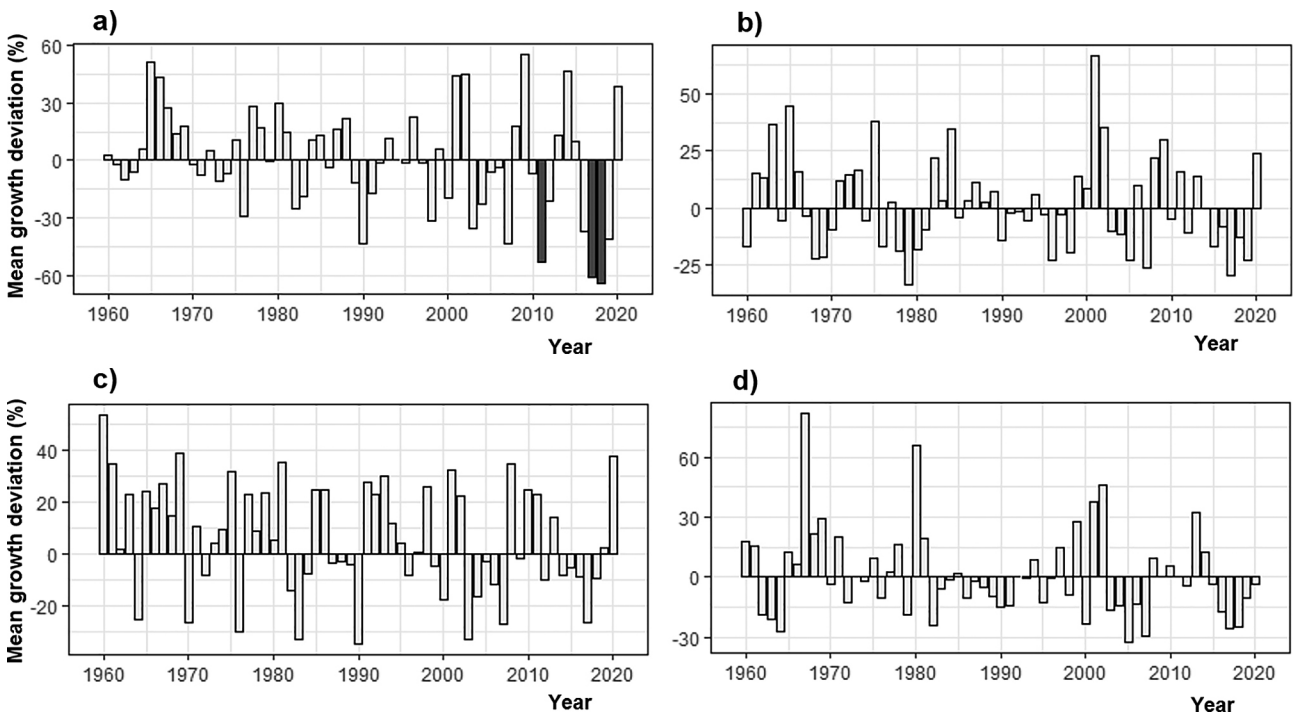
Fig. 4. Pointer years (relative growth change) of European beech (a), sessile oak (b), Norway maple (c), and European ash (d) in 1960–2020; light grey bars – mean growth deviation, dark grey bars – signify significant pointer years with deficient radial growth

variability was observed in beech (SD=0.87), while a relatively stable growth was confirmed in ash (SD=0.48; Table 6, Fig. 3). In beech and maple, their reduced increment in 1990 was negatively affected by an extreme lack of precipitation (394 mm, with the mean of 544 mm in 1960–2020). In 2007 and 2011, low radial growth in beech was caused by a late frost and European oak leafroller (*Tortrix viridana*) feeding in 2007. In 2016–2019, a significant growth depression was elicited by extremely high temperatures and long-term drought, evenly for other tree species. The reduced increment of sessile oak was caused by tracheomycosis in the 1995–2000 period and European oak leafroller feeding in 2007, as in the case of maple. On the other hand, the radial growth increased after thinning in 1970 and 1981. In maple, growth depressions were caused by a high occurrence of tar spot (*Rhytisma acerinum*) in 1990 and 2004. In the case of ash, the growth depression was elicited by a late frost in 1964 (temperature in March was –2.1 °C, the mean is 3.7 °C), such as in 2007. Conversely, a growth increase noted in 2002 was positively affected by the synergism of a high annual sum of precipitation (713 mm, mean 544 mm) and an above-average temperature (9.4 °C, mean 8.6 °C).

A negative pointer year was observed only for beech in the second part of the studied period, namely 2011, 2018, and 2019 (Fig. 4). The year 2018 was the historically warmest year (10.5 °C, mean 8.6 °C). Similarly, a hot growing season was typical of 2019, primarily June (21.5 °C, mean 16.3 °C). On the other hand, no positive pointer year was observed in oak, maple, and ash. The lowest mean annual growth deviation and the possibility of pointer years were confirmed in the case of maple.

The monthly climatic characteristics (temperatures and precipitation sum) had a significant effect ($p < 0.05$) on the radial growth of the four tree species studied (Fig. 5). The radial growth was affected by climate primarily in the growing season, especially in July of the current year. The temperature (13 significant months) was the key driving factor for the growth compared to the low effect of precipitation (7 months). Generally, the precipitation had a positive and the temperature negative effect on the diameter increment in the studied lowland area. According to tree species, beech was the most sensitive tree species to climate factors (7 months), followed by maple. In comparison, ash (3 months) and oak (4 months) were the most resistant.
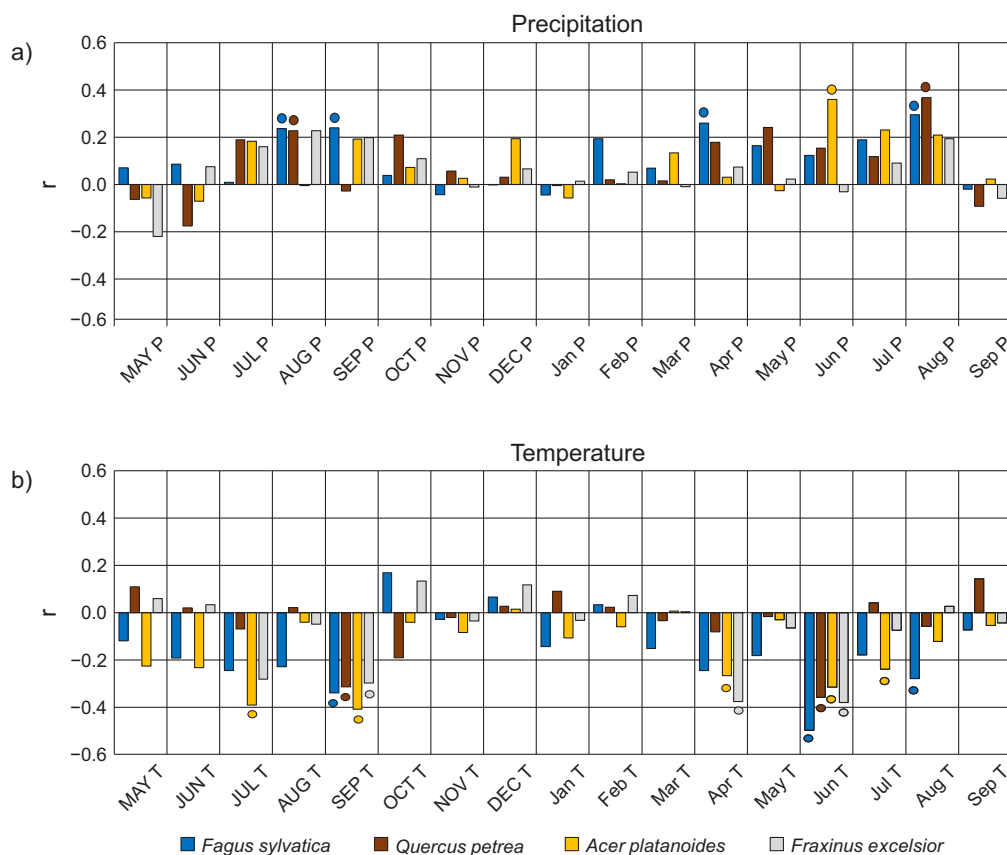

Fig. 5. Coefficients of correlation in the regional residual index tree-ring chronology of European beech, sessile oak, Norway maple, and European ash with the sum of precipitation (P) and monthly average air temperature (T) from May of the previous year (uppercase letters) to September of the current year (lowercase letters) in 1960–2020; statistically significant ($p < 0.05$) values are marked with a circle
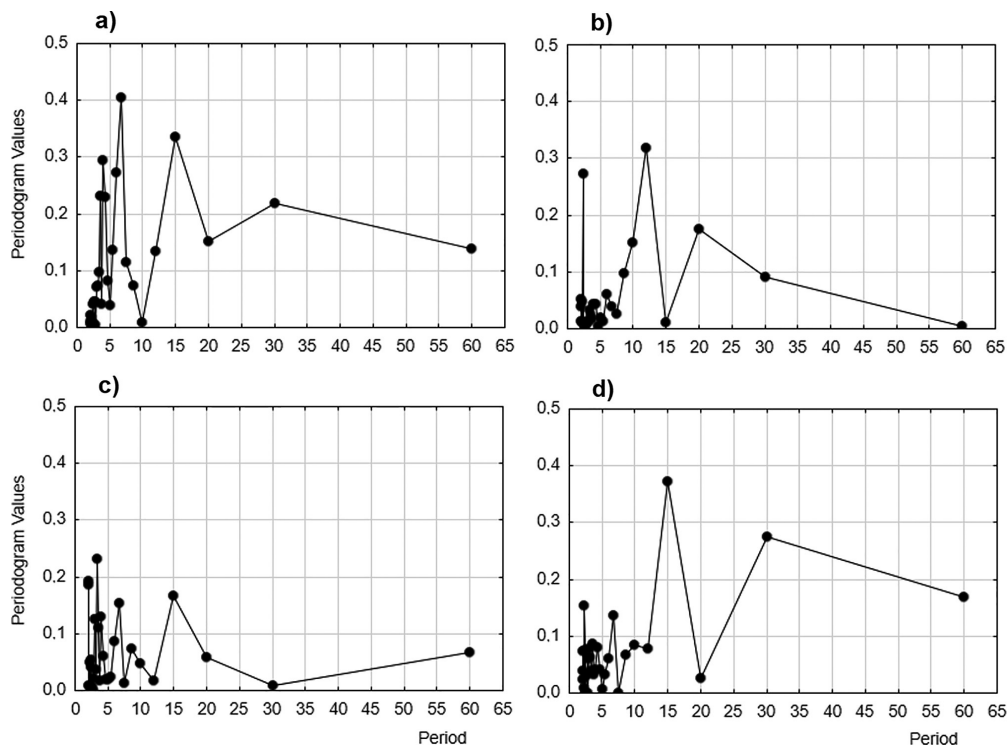
Fig. 6. Single spectral analysis of the indexed ring-width chronology of European beech (a), sessile oak (b), Norway maple (c), and European ash (d) in the Doutnáč location for the 1960–2020 period

Based on cyclic fluctuations in the radial growth of the RWI of the studied tree species using spectral analysis, the most considerable fluctuations in the radial growth were recorded in beech, which is reflected in the highest values periodogram values (Fig. 6). Conversely, the lowest cyclical fluctuations were recorded for maple. Beech and maple recorded 4 to 7 and 15-year cycles in radial growth. Ash recorded 15 and 30-year cycles and oak 12 and 20-year cycles. Overall, the most frequently recorded radial growth cycles were 2 to 7 years and 15 years.

Interaction among stand dynamics, structure, production, diversity, and management

The results of PCA are presented in an ordination diagram showing relationships among forest dynamics, stand structure, biodiversity, timber production, and management (Fig. 7). The first ordination axis explains 64.8% of the data variability, the first two axes together demonstrate 82.2%, and the first four axes even 96.9%. The x-axis illustrates the tree volume height and MAI, and the y-axis represents diameter differentiation and HDR. The basal area was the lowest explanatory variable in the ordination diagram. Stand and tree volume, height, dbh, and MAI were positively correlated to each other while negatively correlated to the stand density, canopy, vertical, and total diversity. Diameter differentiation

was increasing with the stand age. Height differentiation was negatively correlated with HDR. The high forest was characterized by increased production
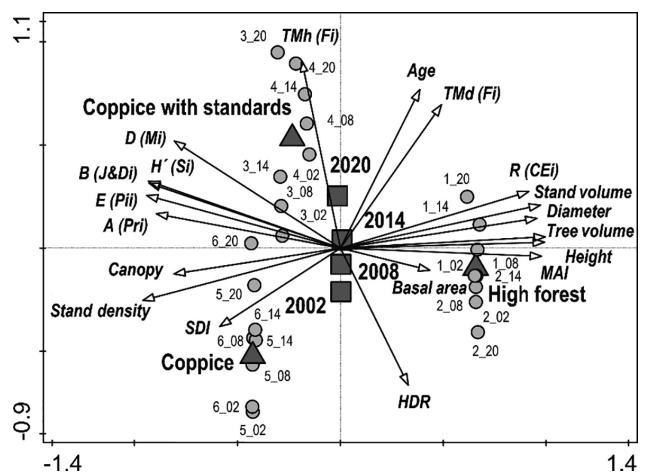

Fig. 7. Ordination diagram showing results of the principal component analysis of relationships between stand structure (stand density, canopy – crown closure, diameter at breast height, height, tree volume, stand volume, age of the stand, SDI – stand density index, HDR – slenderness ratio, MAI – mean annual increment), diversity (D – species richness, H' – species heterogeneity, E – species evenness, R – horizontal structure, A – vertical structure, TM_d – diameter differentiation, TM_h – height differentiation, B – total diversity), management (high forest, coppice with standards, coppice) and time (2002, 2008, 2014, 2020); ■ indicate years of investigation, ▲ signify a type of forest and ● are plots with years

parameters, the coppice by high SDI, canopy, and stand density, while the coppice with standards by high diversity parameters, particularly height differentiation. The highest forest dynamic was observed in the last period (2014–2020). Over the monitored period, the lowest dynamics was noted in the high forest.

Discussion

Stand structure, production, and dynamics

In 2002–2014, the production parameters increased on all PRPs, and they decreased in the 2014–2020 period due to increased tree mortality, except the high forest. In this management variant, the volume increment replaced the loss caused by mortality. The tree mortality ranged from 7% in the high forest to 14 % in the coppice with standards. The higher mortality in the coppice was caused by substantially greater number of younger individuals, higher tree density and faster dynamics of sprouts compared to the high forest. The most considerable changes in the stand structure occurred in the coppice and coppice with standards, concurring with previous studies (Pailett et al., 2010; Müllerová et al., 2015).

The increase in the stand density from 394–1870 to 404–2024 trees per ha in 2002–2014 affected the stand characteristics. In particular, the crown closure was above 92% in our study, whereas it ranges between 64–83% and 85–87% in pure and mixed stands, respectively, in average forest habitats (Pretzsch, 2013). However, the crown projection area is several times larger than the stand area in the case of a combination of light-demanding and shade-tolerant tree species (Pretzsch, 2013). It was identical in our case for the crown projection area, reaching almost six times the stand area in the coppice plot. At the same time, the crown shape changes and the crown efficiency increases due to asymmetric competition (Grams & Andersen, 2007; Štefančík, 2017). High-density stands tend to adapt to the effective trunk and crown ratio, reducing the crown projection area and increasing radiation use efficiency, mainly in mountainous regions with lower mean air temperatures (Bulušek et al., 2016; Černý et al., 2020). In 2014–2020, the number of trees decreased from 404–2024 to 372–1766 per ha, being the highest in the coppice forest.

The stand volume reached the highest values in the coppice and coppice with standards in 2014 (217–276 m³ ha⁻¹), while the maximum in the high forest was attained in 2020 (590 m³ ha⁻¹), again indicating a considerable variability of plots, similarly to the study of Szymura et al. (2014). These results are comparable with studies evaluating close-to-nature oak-beech forests in Romania at a similar altitude (350–620 m), where the average stand volume was 577 m³ ha⁻¹ and 675 m³ ha⁻¹ in mixed oak forests and pure beech stands, respectively. Even a higher stand volume (635–875 m³ ha⁻¹) was documented in the oak-dominated forests in the same Runcu Grosi Natural Reserve in Romania (Petritan et al., 2014). Contrarily, similar results to our research occurred in Polish forests (Szymura et al., 2014), with a stand volume of 65–370 m³ ha⁻¹. In our case, the high stand volume is primarily related to the previous management because these plots have been transformed into a high forest in the last 50 years. Nevertheless, some authors state that such transformation and impact of the original management may last more than 100 years (Paillet et al., 2010; Müllerová et al., 2015).

For individual management variants, the mean annual increment ranged between 2.15–5.47 m³ ha⁻¹ (in 2002) and 2.36–5.96 m³ ha⁻¹ (in 2020), favouring the high forest. However, it was the highest in 2014 in the coppice and coppice with standards. These results show a more pronounced dynamics of changes after allowing spontaneous development in a former coppice than in the stands converted to a high forest. Similarly, the highest MAI was documented in herb-rich beech high forest (4.7 m³ ha⁻¹) compared to a scree coppice (3.9 m³ ha⁻¹) and coppice with standards (3.7 m³ ha⁻¹) in Broumovsko in eastern Czechia (Vacek et al., 2014). The volume stabilization was supposed to occur in the high forest at the age of 70 (Bruckman et al., 2011). However, the volume may still increase at this age in the case of coppices because the share of the trunk in the stand biomass is different in the high and coppice forests (Suchomel et al., 2012).

In relation to profitability, economic efficiency of dominant oak coppice could be greater compared to high forest or over-mature coppice in study area of central Bohemia (Březina et al., 2020). Moreover, young coppices seem as one of the promising adaptable forest management alternatives, with a better adaptive strategy on extreme sites under water limiting conditions compared to stands established from seeds (Stojanović et al., 2016). On the other hand, this advantage of coppice gradually decreases as coppice sprouts transpire significantly higher (Stojanović et al., 2017). This can be reflected in the overall demand for water in soil, which may be scarce in times of climate change and increasing drought periods (Anderegg et al., 2020).

Stand biodiversity

The results of our study indicate that only minor changes in the stand diversity in the Doutnáč forest complex occurred during the observed 18-year period. In Białowieża National Park forests, most

structural attributes revealed also high stability over last 80 years, but noticeable changes in the tree species composition took place related to declining occurrence of many tree species (Brzeziecki et al., 2018). In our case, more pronounced changes in forest diversity dynamics were only observed in the last period (2014–2020). This trend is probably caused by the short research period, during which the dynamics of the tree layer was not sufficiently reflected, as according to Kucbel et al. (2012). In addition, as reported by Dieler et al. (2017), the knowledge on the impact of management on biodiversity, in general, is often partial, while the key aspects are not fully understood yet. Biber et al. (2015) state that a higher diversity at the forest landscape level is not necessarily associated with less intensive management.

The species composition in our case indicates that mixed stands (hornbeam-oaks) with dominating oak and lime, complementing each other, show a higher tree species diversity than beech-dominated high forests. Compared to the original tree species composition, oak-hornbeam forests naturally occur in lowland habitats. In contrast, acidophilous oak forests typify mid-altitudes and beech forests for submontane and montane areas of Czechia (Chytrý, 2012). Similarly, the highest total diversity was observed in the coppice with standards and coppice compared to low diversity in the high forest. From a long-term point of view, oak absents in the younger classes. On the contrary, it is more significantly replaced by a hornbeam. Similarly, oak together with other tree species (aspen, birch, ash, maple) exhibited large decreases in density, while a hornbeam and lime have increased in importance across a wide range of initial compositional types in Białowieża National Park (Brzeziecki et al., 2016, 2020). We witness a similar situation when coppicing is abandoned, followed by a gradual increase in the canopy cover (Plue et al., 2013; Müllerová et al., 2015). It can be achieved by increasing the proportion of beech and hornbeam, usually leading to more significant shading of the soil surface and worsening the conditions for the herb layer and natural regeneration (Plue et al., 2013).

A loss of diversity in deciduous forests was observed in the previous studies (Bartha et al., 2006; Hédl et al., 2010). A decrease in the abundance of downy oak (*Quercus pubescens* Willd.) and wild service tree has been recorded in Doutnáč since the 1950s, as it was the case with the light-demanding species of the herb layer (Průša, 1985). In the evaluated years 2002–2020, the trend of increasing the overall diversity of the tree layer prevailed. However, it subsided after 2014, followed by stagnation and finally by a slight decrease due to increased mortality. As in Doutnáč, Hédl et al. (2010) reported analogous phases of stand development of similar forests in Milovice in Central Bohemia. After abandoning the

traditional management, this trend was also demonstrated in oak forests in Denmark (Strandberg et al., 2005) and the Netherlands (Haveman & Schaminée, 2005). However, Heiri et al. (2009) suggest that environmental factors determine the tree species composition at larger scales compared to historical management strategies that are obviously adapted well to the species autecological requirements.

In terms of spatial pattern, the difference between the high forest (with dominant beech and a reasonably regular tree distribution) and the aggregated horizontal structure in mixed hornbeam-oak groves is evident. For these areas, the previous coppice with standards and coppice management led to a more significantly aggregated horizontal structure of the tree layer. Forest management and silvicultural treatments significantly affect the spatial pattern of trees (Vacek et al., 2018; Hájek et al., 2020). In the upper storey, the distribution is rather random (Petritan et al., 2014), while a tendency of increasing clumping with decreasing storeys, or the formation of groups from light-demanding tree species, is evident (Suchomel et al., 2012; Bulušek et al., 2016). In fact, this also applies to our study because individuals on all PRPs were clustered in the lower storey. Generally, close-to-nature management of mixed stands with the high tree species diversity, uneven-aged and spatially irregular forests are the best options to prepare for future uncertainty in time of global climate change (Rößiger et al., 2019; Vacek et al., 2020b).

Structure and dynamics of deadwood

In forest development, the mortality of individual trees is crucial, as it causes changes in diversity (Debeljak, 2006; Burrascano et al., 2008). In addition, the volume and density of deadwood are considered a useful structural indicator of both the diversity of forest ecosystems and naturalness (Bartha et al., 2006; Bölöni et al., 2017). In our case, deadwood volume was lower (on average 14 m^3 ha^{-1}) than 241 m^3 ha^{-1} in close-to-nature beech-oak forests in Romania (Petritan et al., 2014), not exceeding 35 m^3 ha^{-1} during our study period. Comparable results were presented by Burrascano et al. (2008), who reported 12 m^3 ha^{-1} and 45 m^3 ha^{-1} in managed and primaeval forests, respectively, in Italy. A higher deadwood volume (median 53 m^3 ha^{-1}) is also documented in beech-dominated and oak lowland forests in North-Western and Central Europe with an annual accumulation rate from 0.1 to 19 m^3 ha^{-1} yr^{-1} (Vandekerkhove et al., 2009). In our case, the mean annual deadwood accumulation was accelerated during the observed period, reaching 1 m^3 ha^{-1} yr^{-1}. Similar accumulation rates were observed in 545 research plots in beech-dominated forests in North-Western Germany (Meyer & Schmidt, 2011).

The shares of standing and lying deadwood on the plots were variable. The standing deadwood volume on the plots was 55.7% on average. This proportion was significantly higher on the plots with dominated beech in the tree layer (68:32), corresponding to stands in the optimum stage (Debeljak, 2006). The balanced share of the standing to lying deadwood reflects the fact that these stands are relatively young (approximately one hundred years), where competition between individuals still plays a role, and there is no breakdown of the tree layer within the natural development cycle. Higher amount of deadwood and its highest share simultaneously due to the stand volume can be found on the plots with an aggregated structure, higher species variability, and higher competition between trees (Vacek et al., 2015).

The standing deadwood volume was dominated by oak, which may be substantiated by an increased canopy, followed by spruce and lime. In the lying deadwood, oak, hornbeam, beech, and lime were abundant. In terms of decomposition degrees, the 1st and 2nd degrees were the most represented in standing deadwood and the 2nd and 3rd degrees in lying one, indicating the short time since the plots were reserved for natural succession (Debeljak, 2006). Since leaving the forest for natural development, the deadwood volume has shown only a slight increase. Changes in the tree species composition are related to oak (+5%), spruce (+2%), lime (−3.2%), and hornbeam (−2%). The horizontal deadwood distribution is primarily random, corresponding to the results of other authors (Král et al., 2015; Vacek et al., 2015).

In relation to climate change, dead wood plays an important role in carbon flux (Tavankar et al., 2022). Warmer climates indicate faster decomposition and carbon release compared to cooler climates (Russell et al., 2015). In addition, with higher volume of dead wood and richer stand structure (coppice), there is a higher risk of fires. Especially in Mediterranean countries, the consequences of climate change on the fire regime have direct and significant impact on forest ecosystems, due to likely increases in area burnt and in fire intensity and severity (Moriondo et al., 2006).

Radial growth and the climate effect

The individual tree species radial growth in the studied locality showed higher differentiation in beech and lime than oak and ash with lower growth variability. In addition, climatic sensitivity of beech was confirmed by the most increased occurrence of negative pointer years in the last 10 years during ongoing climate change. In the previous 20 years, the radial growth has increased by 7.0% in oak, while it decreased in all of the other studied species, particularly in beech (−37.9%). However, that differentiation of radial growth closely correlates with habitat, altitude, and stand conditions (Rozas et al., 2015; Šimůnek et al., 2021). To a large extent, radial growth, and the associated production potential, are influenced by the tree species mixing (Pretzsch et al., 2020, 2021; Vacek et al., 2021a), air pollution load (Král et al., 2015; Putalová et al., 2019), drought (Steckel et al., 2020), game damage (Cukor et al., 2019a, 2019b; Vacek et al., 2020a), fertilization (Cukor et al., 2017; Gallo et al., 2021) or historical land use (Cukor et al., 2020; Vacek et al., 2021b).

Climatic and growth conditions are generally considered to be principal factors affecting radial growth (Schweingruber et al., 1990; Šimůnek et al., 2019). The radial growth of tree species in the Doutnáč location was negatively affected by the temperature and positively by precipitation, particularly from July to August. The work of Alfaro-Sánchez et al. (2020) found a negative effect on oak growth in connection with the water deficit in the soil from June to July of the current year. Besides that, Andersson et al. (2011) showed that precipitation had a higher effect on oak growth than temperature.

Anyway, the current impact of climate change on growth may not always be well understood, as the growth is influenced by several different factors that play many different roles (Urli et al., 2015). In addition, global warming accelerates the onset of springs, extending the growing season length (Menzel et al., 2006), leading to changes in the growth-climate relationship (Rozas et al., 2015; Netsvetov, 2017). In our case, tracheomycosis in oak and *Rhytisma acerinum* in maple can also be held responsible for harming the growth. The *Tortrix viridana* feeding also negatively affected radial growth. Strong late frosts also reduced radial growth, especially in beech, maple and ash (Gallo et al., 2017; Šimůnek et al., 2019). However, increased competition, which could be eliminated by silvicultural treatments, is also one of the crucial factors influencing growth (Scharnweber et al., 2011).

Beech showed the most considerable fluctuations in radial growth. Generally, beech is more vulnerable than oak to drought and high temperatures in lowlands (Vacek et al., 2019). It can be expected that the beech stands will gradually spread to upper altitude areas and to the north while declining in the south and lower altitudes in relation to climate change (Kramer et al., 2010; Dulamsuren et al., 2017), such as other three species. Contrastingly, the under-represented Norway maple showed the lowest fluctuations in radial growth. It was confirmed by a study from the Krkonoše Mountains, where closely related sycamore maple (*Acer pseudoplatanus* L.) also achieved the lowest cyclic fluctuations in RWI (Hájek et al., 2021). Cyclically, the most pronounced factor influencing the radial growth of all tree species is air temperature, of which 7-year cycles were recorded in the

Czech Republic (Šimůnek et al., 2020, 2021). There are variations of 7 and 15-year periods in our results, which we attribute to the influence of temperatures. Oak showed 12 and 20-year cycles in radial growth, markedly similar to the solar cycles recorded for beech in the Czech Republic (Šimůnek et al., 2020, 2021).

Conclusion

The study provides significant evidence and examples of how the differently managed forest ecosystems altered their successional dynamics after being reserved for natural succession without human interventions since 2004. The data gathered and evaluated within this research will help us better understand natural processes in the studied forest stands. It brings valuable knowledge for future forest management practice, considering climate change and its impact on forests. The limiting factor of radial growth was the lack of precipitation and high temperature in the growing season in terms of climate. The most climate-sensitive tree species was beech, which belongs to submontane regions by native area of distribution, compared to the resilience of ash and a positive growth increase in oak. For the landscape mosaic, it is recommended to use various silvicultural systems for hornbeam-oak groves and calcareous beech forests: under the current climatic conditions, silviculture utilizing coppice with standards and the backup of admixed tree species to support forest diversity and faster dynamics, and contrarily, the high forest system for the highest production potential.

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Conflicts of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: K.V., Z.V. and S.V.; methodology: K.V., Z.V., and S.V.; software and analysis: Z.V., V.Š. and V.H.; investigation: K.V., M.Š., Z.V., A.P., and I.K.; resources: V.S.; data curation: S.V., Z.V., and V.Š.; writing – original draft preparation: K.V., M.Š., Z.V., S.V., J.G., V.P., I.Š., and I.K.; supervision: S.V. and Z.V.; funding acquisition: M.Š.

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