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Dynamics of mixed lowland forests in Central Bohemia over a 20-year period

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Abstract: The paper deals with the effect of environmental factors and management on various mixed lowland forests in the Medník National Natural Monument, Czech Republic, over a 20-year period. The objectives were to evaluate the structure, production, dynamics and radial growth in relation to climatic conditions in the mixed hornbeam-oak, herb-rich beech and spruce forest stands. The tree density decreased by 8.5% (to 120–1,364 trees·ha^{-1}), while stand volume increased by 28.0% (to 244–767 m^3·ha^{-1}) from 1998 to 2018. Large-leaved lime (*Tilia platyphyllos* Scop.) and Norway spruce (*Picea abies* /L./ Karst.) showed high variability and sensitivity to climatic factors in radial growth compared to stability and resistance in sessile oak (*Quercus petraea* /Matt./ Liebl.) and European beech (*Fagus sylvatica* L.). April, June and July were determined as the most significant months in relation to diameter increment. The synergism of precipitation deficit and high air temperature was a limiting factor of growth in the studied lowland area. The frequency of negative pointer years with extremely low radial growth has been increasing recently. Generally, hornbeam-oak stands are characterized by rich structure, high density and lower productivity, herb-rich beech stands represent rich structured productive forests and spruce forests are very productive stands but with low ecological stability.

Keywords: protected area; stand structure; tree-ring dating; climate change; Czech Republic

The natural forest as an original biocoenosis is the top of a natural ecosystem, the components of which are in very long-term interaction (Průša 1985). This type of forest represents the most advanced and complex climax community of the study area of Central Bohemian Uplands, which can arise here and keep up spontaneously in long term (Vacek et al. 2018). However, it does not put an end to forest dynamics, but it represents its lasting continuation based on internal and external influences leading to the general regularity (Korpeľ 1995).

The principle of self-regulation is the basis of the original forest development (Veblen 1992). The original autochthonous and natural forests are suitable model objects from this point of view (Král et al. 2015; Bílek et al. 2016). Natural forest communities as complex living organisms at the highest hierarchical level have a prominent tendency to homeostasis (Mayer, Ott 1991; Vacek 2003). This capability relatively promptly responds to disturbance by creating specific conditions, characters and other elements ensuring the existence of the original natural forest or continually following with

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structure and ecosystem dynamics (Slanař et al. 2017; Vacek et al. 2017a). However, the forest ecosystems are influenced by climate change at present (Pretzsch et al. 2014; Ponocná et al. 2018) and there are still many uncertainties related to the effects of these changes on forests. It concerns both the regional and the continental level. This is mainly due to the absence of long-term studies using similar methodologies (Peters et al. 2015; Bosela et al. 2016; Sharma et al. 2016, 2017). Nevertheless, it is perceptible that climate change has an increased impact on forests and poses a threat to the provision of basic functions of forest ecosystems (Vacek et al. 2016, 2017b; Conte et al. 2018). Climate change has a great influence on forest ecosystems in the short term (Anderegg et al. 2016) and at the same time on their long-term dynamics (Millar, Stephenson 2015). The negative influence of climate changes on forest ecosystems (Bréda et al. 2006; Hanewinkel et al. 2013) should be understood as a certain trend which it will be necessary to adapt to in the future (Beniston 2004; Kunz et al. 2018).

Climate change gravity has been on the rise in recent years and forestry in Central Europe is facing several unprecedented events (Čater, Diaci 2017; Nagel et al. 2017). Of course, the tree growth of European forests is limited by low temperatures in northern areas and at higher altitudes and low availability of water and drought in warmer lower regions and southern areas (Babst et al. 2013; Primicia et al. 2015). Some of the most important European tree species have already shown great sensitivity to climate change (Cukor et al. 2019a; Vacek et al. 2019a; Mikulenka et al. 2020). That concerns particularly the Norway spruce (*Picea abies* /L./ Karst.) because of its great vulnerability to drought, which already distinctly threatens it at present and even more negative effects are pronounced for the future (Hanewinkel et al. 2013; Zang et al. 2014; Cukor et al. 2019b). Consequential drought may also lead to significant changes in the structure and species composition of forest stands (Fonti et al. 2006; Choat et al. 2012), changes in competitive relations (Bittner et al. 2010), stability (Lloret et al. 2012), carbon sequestration (Adams et al. 2009; Cukor et al. 2017a) and negative economic impacts on forestry in general (Kunz et al. 2018). On the other hand, the rising temperature and the reduction in rainfall are preconditions for increasing the range of other tree species (Urli et al. 2015). In addition, global warming is conductive to an earlier start of the growing season and change in the tree species distribution range (Matisons et al. 2013; Netsvetov et al. 2017). Therefore a reliable assessment of forest ecosystem productivity, including climate change impacts and other severe effects as determining factors is increasingly considered as crucial for forest management planning and as a means for climate change mitigation (Hanewinkel et al. 2013; Hlásny et al. 2017). Thanks to this fact the decision making on differentiated management methods in specially protected areas on ecological approach, to ensure their ecological stability and biodiversity is a very difficult task. Any decision must always be based on a detailed study and assessment of specific site and forest stand conditions, in particular as regards the structure and development of model forests on natural and close-to-nature areas (Bílek et al. 2014; Vacek 2017).

The long-term objective of forest management in specially protected areas is to maintain their significant proportion under spontaneous development (Götmark 2007; Králíček et al. 2017). Subsequently, more diversified stands could be created which are more resilient (Pretzsch et al. 2013; Seidl et al. 2016) and which can provide a wide range of ecosystem services (Gamfeldt et al. 2013; Mina et al. 2018). Differences between various species in tolerance to shadow, crown phenology, canopy density and structure, depth of root system or diverse rhizomorph organisms may be associated with increased productivity of these stands (Brassard et al. 2013; Toïgo et al. 2015). Moreover, mixed and rich structured forests are more stable in terms of environmental changes and they better resist to disturbances (Vacek et al. 2019b, 2019c). The most protected areas apply the specific management oriented on the main theme. It is nature conservation, which is maintaining and strengthening the most northern population of *Erythronium-dens canis* in Europe at this locality.

The objective of this paper is to assess the structure, production and dynamics of mixed hornbeam-oak, herb-rich beech and spruce forests at the Medník National Natural Monument (NNM) between 1998 and 2018 under the influence of climate change and contribute to one of the greatest challenges of current forestry, which is preservation of stable, economically and environmentally sustainable forest ecosystems. The basic hypothesis was that hornbeam, oak and herb-rich beech for-

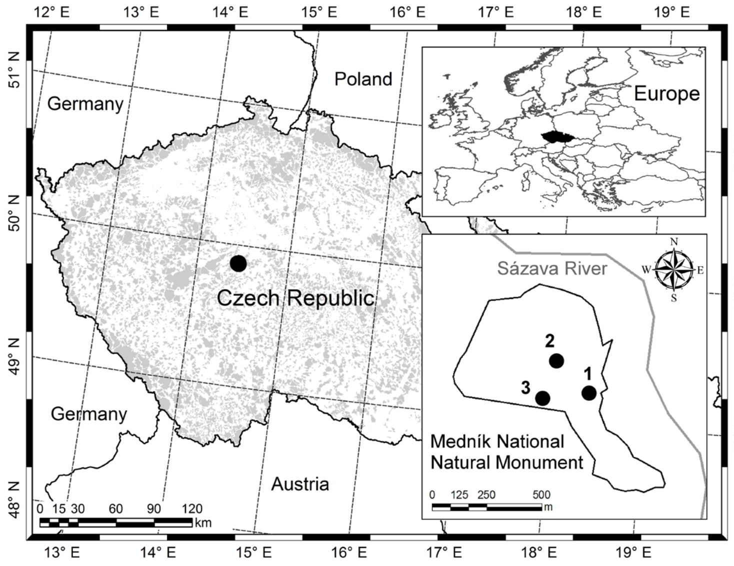

Figure 1. Localization of a series of permanent research plots 1 (PRP 1A-B), 2 (2A-2D) and 3 (3A- 3B) in the Medník National Natural Monument

ests are significantly more stable than secondary spruce stands forests and thus they can better resist to climate change.

MATERIAL AND METHODS

Study area. The Medník NNM is located on the left bank of the Sázava River valley midway between Pikovice and Luka settlements, on the north and northeast slopes of Malý Medník at the altitude of 220–398 m a.s.l. (Figure 1). A reason for the protection of this territory since the 1930s has been the conservation and expansion of *Erythronium-dens canis*, a critically endangered species in the Czech Republic (Holub, Procházka 2000) in this isolated locality, the northernmost one of its European occurrences. A further motive was the conservation of natural colluvial forests with a number of protected and endangered flora and fauna species on the area of 43.67 ha. The average annual temperature at this locality is 8–9°C and annual precipitation varies around 550–600 mm (Tolasz et al. 2007). Metabasics prevail in the bedrock with the occurrence of granodiorites. The prevailing soil type is represented by mesotrophic Cambisols and Ranker Cambisols up to Rankers on steep slopes.

A lime-oak-hornbeam forest dominates in the NNM, accounting for 63%. This is a coppice forest dominated by European hornbeam (*Carpinus betulus* L.) with admixed large-leaved lime (*Tilia platyphyllos* Scop.), sessile oak (*Quercus petraea* /Matt./ Liebl.) and European beech (*Fagus sylvatica* L.) and the following interspersed species: sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), field maple (*Acer campestre* L.), Scots elm (*Ulmus glabra* Huds.) and wild service tree (*Sorbus torminalis* /L./ Crantz). These are communities (phytocoenoses) of the *Carpinion* alliance Issler 1931 and Melampyro nemorosi-Carpinetum plant association Passarge 1962 and Stellario-Tilietum Moravec 1964. The herb-rich beech stands are represented abundantly (30%) with domination of beech and with admixed hornbeam in the lower tree layer. Oak and silver birch (*Betula pendula* Roth.) are interspersed scarcely. They represent the *Eu-Fagenion* suballiance Oberdorfer 1957 and *Dentario enneaphylli-Fagetum* association Oberdorfer ex W. et. A. Matuszkiewicz 1960. Relict spruce stands of the Sázava ecotype of Norway spruce (*Picea abies* /L./ Karst.) belong to the *Piceion abietis alliance* Pawłowski et al. 1928 and with admixed birch they are represented by 6%. Summary of the PRP basic data is given in Table 1.

Data collection. A theodolite and FieldMap technology (IFER) were used for the establishment of 8 permanent research plots (PRP) of 50 × 50 m in size for determining the stand structure in 1998 and 2008. Two PRPs (1A-1B) were situated in hornbeam-oak stands, four PRPs (2A-2D) in herb-rich beech stands and two PRPs (3A-3B) in secondary spruce stands. The position of all individuals of the tree layer with breast height diameter (DBH) ≥ 4 cm was measured. The height of the live crown base and the crown diameter were also measured in the tree layer, at least in 4 directions perpendicular to each other. Diameters of the tree layer were

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Table 1. Overview of basic characteristics of permanent research plots

ID	GPS	Altitude (m)	Exposition	Slope (°)	Association	Species	Age	Diameter (cm)	Height (m)	Volume ($m^3 \cdot ha^{-1}$)
1A-1B	49.8704725N 14.4503036E	300	NE	28	*Carpinion*	Cb, Tp, Qp, Ap, Apl, Ac, Fs, Ug	75	18.6	15.5	246
2A-2D	49.8713714N 14.4520417E	330	N	5	*Fagion*	Fs, Cb, Qp, Bp	116	44.8	29.5	346
3A-3B	49.8703203N 14.4495311E	380	NE	8	*Piceion abietis*	Pa, Bp, Cb, Ps, Ld	98	37.7	31.9	458

Cb – *Carpinus betulus*, Tp – *Tilia platyplhyllos*, Qp – *Quercus petraea*, Ap – *Acer pseudoplatanus*, Apl – *Acer platanoides*, Ac – *Acer campestre*, Fs – *Fagus sylvatica*, Ug – *Ulmus glabra*, Bp – *Betula pendula*, Pa – *Picea abies*, Ps – *Pinus sylvestris*, Ld – *Larich decidua*

measured with a Mantax Blue metal calliper (Haglöf, Sweden) to the nearest 1 mm and heights were measured using a Vertex laser hypsometer (Haglöf, Sweden) to the nearest 0.1 m.

Increment cores were randomly (RNG function in Excel) taken from 20–25 dominant and co-dominant trees (with DBH ≥ 25 cm) of all main tree species (beech, lime, spruce and oak) on each PRP series in spring 2018 using the Pressler auger at breast height (130 cm) at right angles to the axis of the stem, both uphill and downhill. Annual ring widths were measured to the nearest 0.01 mm under an Olympus binocular microscope on the LINTAB measuring table and recorded with TsapWin software (Rinntech).

Data analysis. The basic structure and production characteristics of the tree layer were evaluated by the SIBYLA 5 forest growth simulator (Fabrika, Ďurský 2005). The tree volume was calculated according to the volume equations published by Petráš, Pajtík (1991). Horizontal structure of stands was evaluated according to the *L*-function (Ripley 1981) in PointPro 2 software (CULS). The relative stand density index (SDI), the crown closure (CC) and the crown projection area (CPA) were observed for each plot.

Annual ring series were individually crossdated using statistical tests in the PAST application (Knibbe 2007) and subsequently subjected to visual inspection according to Yamaguchi (1991). If the missing ring was found, there was a ring with 0.01 mm width put in its place. Age detrending was done in ARSTAN software. The 30-year spline was applied (Grissino-Mayer et al. 1992). Analysis of significant negative pointer years was carried out according to Schweingruber (1990). For each tree the pointer year was tested as an extremely narrow tree-ring that does not reach 40% of the increment average from the four preceding years. The occurrence of the negative year was proved if such a strong reduction in increment occurred at least in 20% of trees on the PRP. Average annual ring series of PRP were correlated with climate data (precipitation and temperature) of the Neumětely Station (322 m a.s.l.) of the Czech Hydrometeorological Institute in the period 1960–2017. The DendroClim software (Biondi, Waikul 2004) was used for the modelling of radial increment dependence on the climatic characteristics.

RESULTS

Dynamics and production of tree layer

In hornbeam-oak stands (PRP 1A-1B), the tree density ranged from 1,268 to 1,512 trees·ha^{-1} in 1998 (Table 2). During 20 years of study, the total numbers decreased by 9%, while SDI increased by 15% to 0.74. The average basal area was 27.6 m^2·ha^{-1} in 1998 and this area increased by 21% during 20 years. The stand volume ranged between 171 and 178 m^3·ha^{-1} in 1998, of which 50–61% was hornbeam, 18–20% lime and 17–31% oak. During 20 years, the stand volume increased by 43–51%. The mean annual increment increased from 2.7 (1998) to 3.2 m^3·ha^{-1}·y^{-1} (2018). Of all PRPs the highest number of trees with canopy and the lowest stand volume with increment were observed on PRP 1A and 1B.

In herb-rich beech stands (PRP 2A-2D), the number of trees decreased during 20 years by 2.4 to 11.7% to 120–164 trees·ha^{-1} in 2018 (Table 2). SDI slightly changed from 0.42 in 1998 to 0.43 in 2018. The average basal area was 26.4–31.1 m^2·ha^{-1} in 1998 and the area average increased by 7% during 20 years. The stand volume ranged between 419 and

Table 2. Basic stand characteristics on permanent research plots (PRP) in 1998 and 2018

PRP	Year	Age (y)	DBH (cm)	*H* (m)	*N* (trees·ha^{-1})	BA (m^2·ha^{-1})	*V* (m^3·ha^{-1})	HDR	PAI (m^3·ha^{-1}·y^{-1})	MAI (m^3·ha^{-1}·y^{-1})	CC (%)	CPA (ha)	SDI
1A	1998	64	15.6	13.74	1,512	29.0	178	88.1	4.8	2.78	99.4	5.14	0.68
	2018	84	18.2	15.74	1,364	35.4	268	86.5	5.4	3.31	99.5	5.28	0.79
1B	1998	64	16.2	14.39	1,268	26.1	171	88.8	4.1	2.66	99.1	4.70	0.60
	2018	84	18.4	16.06	1,160	31.0	244	87.3	4.7	3.04	99.2	4.81	0.68
2A	1998	106	52.5	31.57	144	31.1	545	60.1	6.6	5.14	82.6	1.75	0.44
	2018	126	57.3	33.46	120	30.9	569	58.4	6.3	5.33	80.2	1.62	0.42
2B	1998	106	46.7	26.80	164	27.9	467	57.4	6.4	4.41	82.9	1.77	0.42
	2018	125	50.4	28.41	148	29.4	524	56.4	5.5	4.71	81.3	1.68	0.43
2C	1998	104	44.9	27.19	168	26.4	419	60.6	6.5	4.03	80.6	1.64	0.39
	2018	124	49.5	29.08	164	31.3	519	58.7	6.2	4.41	83.8	1.82	0.45
2D	1998	104	44.8	29.05	172	27.1	436	64.8	6.7	4.14	84.8	1.88	0.40
	2018	124	49.1	30.98	152	28.7	498	63.1	6.2	4.55	81.8	1.70	0.41
3A	1998	88	34.2	30.22	484	44.6	571	88.4	11.5	6.48	69.2	1.18	0.66
	2018	108	40.5	32.03	452	58.3	767	79.1	11.2	7.37	76.0	1.43	0.81
3B	1998	87	32.4	28.44	476	39.1	494	87.8	10.4	5.68	70.5	1.22	0.61
	2018	107	38.4	30.19	464	53.8	699	78.6	10.7	6.60	78.5	1.54	0.78

Age – average stand age, DBH – mean quadratic breast height diameter, *H* – mean height, *N* – number of trees per hectare, BA – basal area, *V* – stand volume, HDR – height-to-diameter ratio (slenderness quotient), PAI – periodic annual increment; MAI – mean annual increment, CC – canopy closure, CPA – crown projection area, SDI – stand density index

545 m^3·ha^{-1} in 1998, of which 79–97% was beech and 3–15% hornbeam. During 20 years, the stand volume increased by 4–24%. The mean annual increment increased by 7.5% to 4.8 m^3·ha^{-1}·y^{-1} in 2018. Of all PRPs the lowest number of trees on PRP 2A and/or the lowest height-to-diameter ratio (HDR) on PRP 2B were recorded.

In secondary spruce stands (PRP 3A-3B), the number of trees decreased by 2.6–6.6% to 452 to 464 trees·ha^{-1} and SDI by 23–28% to 0.78–0.81 during 20 years (Table 2). The average basal area was 39.1–44.6 m^2·ha^{-1} in 1998 and this area increased by 31–38% in 2018. The stand volume ranged between 494 and 571 m^3·ha^{-1} in 1998, of which 83 to 97% was spruce. During 20 years, the stand volume increased by 34–41%. The mean annual increment increased from 6.1 (1998) to 7.0 m^3·ha^{-1}·y^{-1} (2018). Overall, of all PRPs the highest stand volume (767 m^3·ha^{-1}) as well as MAI (7.4 m^3·ha^{-1}·y^{-1}) were observed in 2018 on PRP 3A.

Structure of tree layer

The diameter frequency on PRP 1A and 1B shows statistically visible left-skewed distribution, where oak and lime dominated in overstorey and hornbeam and rowan in understorey with other interspersed tree species (Norway maple, sycamore, field maple, beech, Scots elm). The diameter class 8–16 cm was the most commonly represented one on PRP 1 (Figure 2). The diameter distribution of herb-rich beech forest (PRP 2A–2D) was relatively diverse. Beech and hornbeam dominated in the largest diameter classes in the upper storey and in the lower storey it was hornbeam and sparsely interspersed oak and birch. The highest representation was found out in the diameter class 64+ cm (Figure 2). The secondary spruce forest on PRP 3A and 3B showed the Gaussian distribution of diameter classes. Spruce dominated in the largest diameter classes and in the top tree layer while hornbeam, oak, Scots pine, European larch and birch were interspersed in understorey. The greatest representation was revealed in the diameter classes 28–36 cm on PRP 3 (Figure 2). In the course of the studied 20 years, a shift to larger diameter classes occurred (Figure 3). On the other hand, a shift in the lowest diameter class was sporadic (except for PRP 3) due to game damage to natural regeneration.

In relation to horizontal structure, the tree layer of hornbeam-oak stand (PRP 1A-2B) showed cluster distribution of individual trees according to their distance (spacing) up to 5–6 meters as shown

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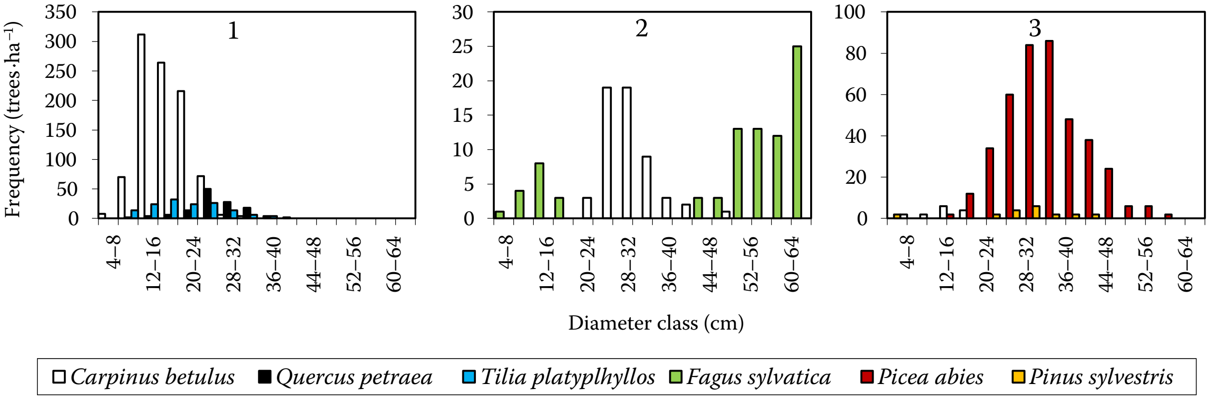

Figure 2. Histogram of tree layer diameter structure on permanent research plots 1 (PRP 1A-1B), 2 (2A-2D) and 3 (3A-3B) differentiated according to main tree species in 2018

by Ripley's *L*-function. In the case of larger spacing the trees were distributed randomly. Mostly random distribution of the tree layer was found on PRP 2A–2D, only on PRP 2B with the spacing up to 3 m cluster aggregated horizontal structure was analysed. Similarly, mostly random arrangement of trees in spruce stands was on PRP 3A–3B. Trees were distributed regularly only in the case of spacing up to 4 m on PRP 3A and up to 3 m on PRP 3B. A shift towards regular structure was observed on all PRPs during 20 years.

Radial growth and effect of climate

The average tree-ring width was lowest in oak (1.37 mm) and in spruce (1.54 mm), while the highest increment was in lime (1.75 mm) and beech (1.62 mm; Table 3). The highest variability in growth was observed in lime (0.87 SD), while the highest stability in increment was in oak (0.42 SD). Similarly, the most resistant tree species in relation to significantly negative pointer years with extreme radial growth were oak (1 year) and beech (2 years). Conversely, the most sensitive tree species in relation to extreme climatic events were lime (6 years) and spruce (5 years). Moreover, the frequency of significant negative pointer years was increasing in 1960 to 2017. In the first part of the period, only 3 years were observed, while it was 6 years in the second part.

The dynamics of radial growth showed a significant decrease in all tree species in 2007 (Figure 4), when the warmest year (9.4 °C, mean 7.8 °C) and especially the warmest winter 2006/2007 (3.4 °C, mean –0.9 °C) were observed in the studied period. The significantly negative pointer year 2000 (for spruce and lime) was characterized by extremely high annual temperature (9.2 °C) and extremely hot June and July (18.5 °C, mean 16.4 °C) were characteristic of the year 2017. In lime, significantly extremely low radial growth was observed in the two driest years 1982 (361 mm, mean 590 mm) and 1976 (418 mm) in connection with late frost. Similarly, the year 1990 with the historically driest June and July (39 mm, mean 153 mm) caused a significant decrease in radial growth of lime.

Climatic analyses in relation to radial growth showed several significant ($\alpha = 0.05\%$; $r = -0.42$ to

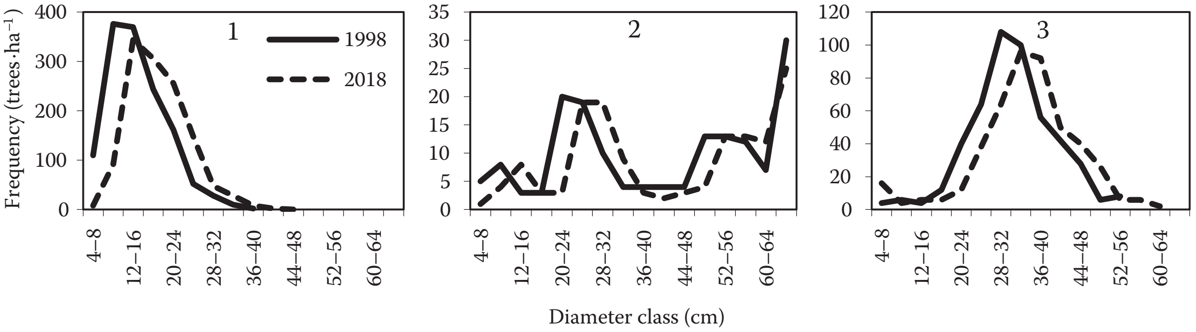

Figure 3. Dynamics of diameter structure of the tree layer on permanent research plots 1 (PRP 1A-1B), 2 (2A-2D) and 3 (3A-3B) in 1998 and 2018

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Table 3. Characteristics of tree-ring chronologies of main tree species and negative pointer years characterizing extremely low radial growth in 1960–2017

Tree species	Number of samples	Mean(mm)	SD	Negative pointer years
Quercus petraea	20	1.37	0.42	2007
Fagus sylvatica	25	1.62	0.63	1998, 2007
Picea abies	24	1.54	0.70	1976, 2000, 2005, 2007, 2017
Tilia platyplhyllos	19	1.75	0.87	1982, 1989, 1990, 2000, 2007, 2017

0.33) months in 1960–2017 (Figure 5). The most sensitive tree species lime (8 significant months) was followed by spruce and beech (5 months), while the lowest effect of climate was observed in oak (4 months). Generally, the air temperature had a higher effect on radial growth compared to precipitation. The effect of air temperature was mostly negative in all tree species (except for October of the previous year), while the effect of precipitation was positive in all cases in the studied lowland area. April and June were the most significant months with respect to climate sensitivity of radial growth as well as July and September of the previous year.

DISCUSSION

Tree density decreases by 8.5% to 120 to 1,364 trees·ha^{-1} on studied PRPs during the period 1998–2018. The highest tree density was observed in hornbeam-oak stands. These coppice forests showed especially an increase of stocking, similarly like in other localities in comparable conditions (Paillet et al. 2010; Müllerová et al. 2015). Basal area also showed a distinct increase during the 20 years – on average by 5.8 m^2·ha^{-1}. The canopy reaching 99% on the studied PRPs is usually in the range of 85–87% on the average forest sites (Paillet et al. 2010; Pretzsch, Schütze 2014), and it is usually higher in mixed forests. In the course of 20 years stand volume increased to 244–699 m^3·ha^{-1}. The lower stand volume was documented by Vacek et al. (2018) in the Czech Karst (145–183 m^3·ha^{-1}) and Szymura et al. (2014) in the Polish coppice forests (65–370 m^3·ha^{-1}). The stand volume difference is affected by past management that can persist even more than 100 years (Paillet et al. 2010; Müllerová et al. 2015).

In herb-rich beech stands the tree density was lowest on all PRPs (146 trees·ha^{-1}), which is given by the specific site of the locality, which is intent on a maximum size *of Erythronium dens-canis* population in the most northern site of the European distribution (Sádlo 2009). *Erythronium dens-canis* needs enough light for successful development (Guitián et al. 2002). Vacek et al. (2014) reported higher tree density in beech forests in Eastern Bohemia (188–656 trees·ha^{-1}). The beech is the strongest species in this locality from the competition

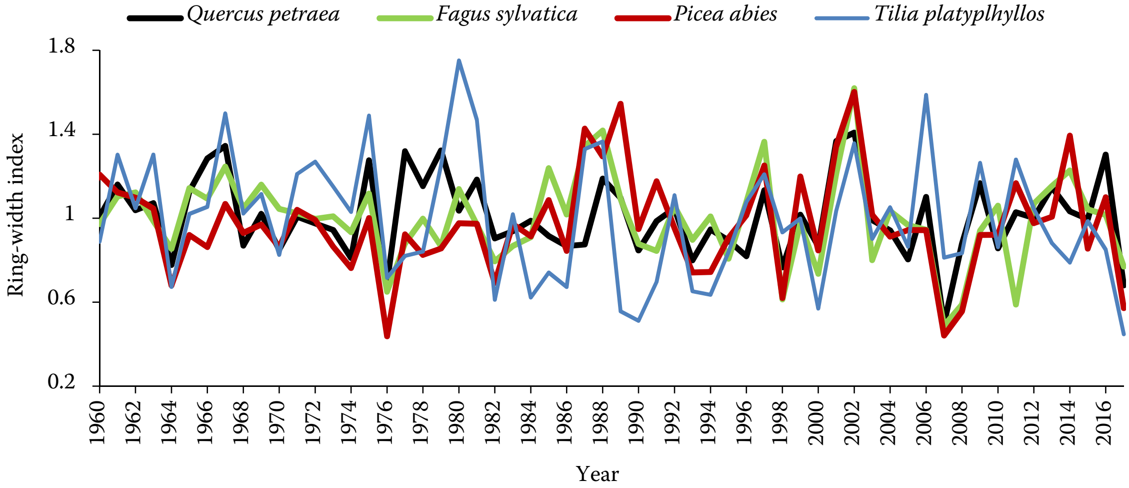

Figure 4. Standardized ring-width chronologies of main tree species on permanent research plots after age detrending in 1960–2017

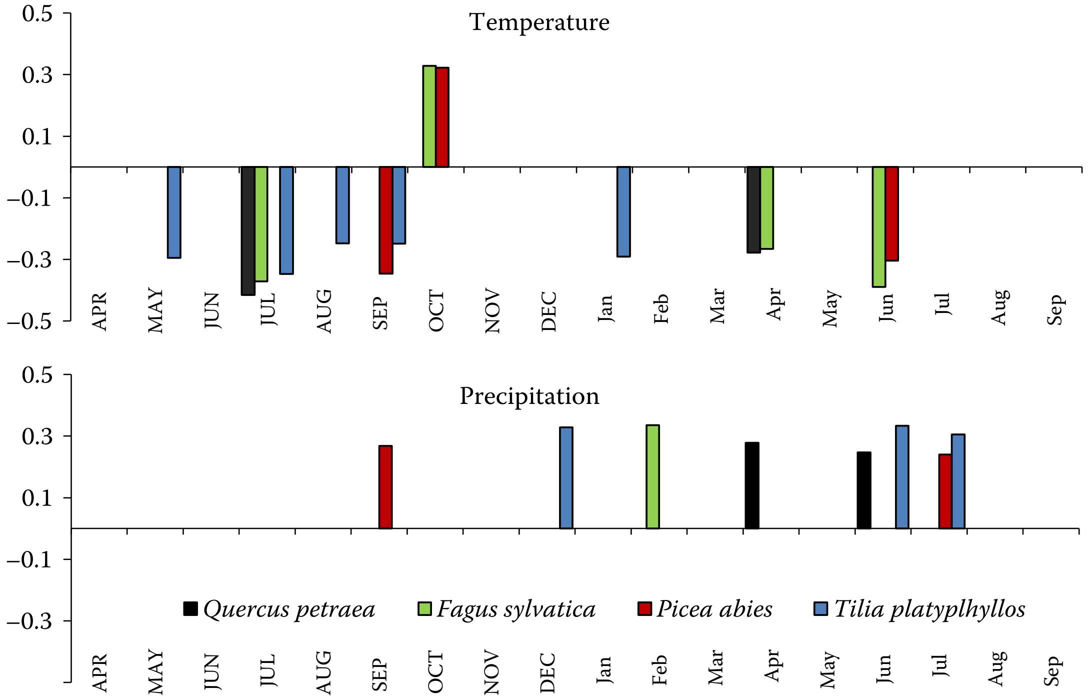

Figure 5. The values of correlation coefficients of the standardized tree-ring chronology with monthly temperatures (upper part) and precipitation (lower part) from April of the previous year (capital letters) to September of the current year (small letters) for the period 1960–2017 for main tree species on permanent research plots; correlation coefficients with statistically significant values (α = 0.05) are displayed

point of view, which corresponds to its ecological characteristics (Bosela et al. 2016). The dynamics of basal area has dropped slightly to 28.7–31.3 $m^2 \cdot ha^{-1}$, which are slightly lower values compared to Vacek et al. (2014) (30.1–44.8 $m^2 \cdot ha^{-1}$). Stand volume in the studied beech stand increased from 419 to 545 $m^3 \cdot ha^{-1}$ to 498–569 $m^3 \cdot ha^{-1}$ during the 20 years. Similar results from comparable sites and stand conditions (491–601 $m^3 \cdot ha^{-1}$) were obtained by Vacek et al. (2014).

In secondary spruce stands the number of trees decreased by 4.6% to 458 $trees \cdot ha^{-1}$ during the 20 years. On the other hand, the increase in stand volume and in canopy was up to 41%. Conversely in many parts of Europe, spruce stands are currently very vulnerable to climate change, especially by increasing temperatures, more frequent droughts (Lévesque et al. 2013; Zang et al. 2014) and subsequently by bark beetle outbreaks (Hlásny, Turčáni 2013; Kolb et al. 2016), as well as sensitivity to other types of biotic factors increased (Marini et al. 2017; Mezei et al. 2017). Despite all the climate change threats the studied stands have not yet been significantly affected mainly due to specific microclimate conditions with the availability of water in those localities. Vacek et al. (2014, 2015a, 2015b) or Kolář et al. (2015) presented similar results from certain Sudetes sites.

In relation to the spatial pattern, the tree layer of hornbeam-oak stands showed aggregated o random distribution of trees. Mostly random horizontal structure of the tree layer was found in herb-rich beech forest stands. Mostly random distribution of trees with tendency to the regular one was observed in spruce stands. In general, the random distribution of trees is characteristic of the high forest of optimum stage (Zahradník et al. 2010; Ambrož et al. 2015) and, on the contrary, the aggregated pattern is typical of stands in extreme localities (Bulušek et al. 2016) or of coppices (Vacek et al. 2018).

The growth of trees is affected by many environmental factors, especially by silvicultural practices (Remeš et al. 2015; Švec et al. 2015; Bílek et al. 2018; Štefančík et al. 2018), fertilization (Vacek et al. 2006; Cukor et al. 2017a, b; Vacek et al. 2019d) and climatic factors (Krejčí et al. 2013; Vacek et al. 2016; 2017c). Large-leaved lime showed the highest vulnerability to climatic factors in growth compared to high resistance in sessile oak. Similarly, the oak with beech showed low growth variability and small climate effect in scree forests in the Broumov region (Vacek et al. 2019b). The lime was negatively affected especially by droughts and high air temperature, while the negative effect of tracheomycosis was observed in oak. Colder and wetter weather at the beginning of the growing season is appropriate for an optimal radial increment of oak in Central Europe (Kern et al. 2013; Čufar et al. 2014). In addition, Urli et al. (2015) reported, as regards the oak and climate change, that a suitable change of precipitation and temperature increase may be the driving force in the distribution of this species. In beech, growth depressions have been recorded in recent years that were caused by *Cryptococcus fagi*, by late frost, and by drought like in previous cases. Králíček et al. (2017) and Šimůnek et al. (2019) proved, in relation to beech growth, the significant negative effect due to the damage of crowns by icing and *Cryptococcus fagi*.

In secondary spruce stands a significant negative effect of drought and high temperatures was also observed, however the ecotype of Sázava spruce maintains good production and is relatively resistant to dry summer periods compared to allochthonous populations. Spruce was the most vulnerable tree species in Kozínek site (430 m a.s.l.) in relation to climate (Vacek et al. 2019b). A considerable negative effect of drought on spruce radial increment was confirmed by Bolte et al. (2010) and Cukor et al. (2020), who observed a decrease of spruce growth in the Orlické hory Mts. Mäkinen et al. (2001) similarly documented that a pronounced decrease of spruce growth was due to the negative correlation of summer temperatures. The negative effect of temperature decreases with increasing altitude where the effect of precipitation is diminished (Andreassen et al. 2006; Hauck et al. 2012).

Generally, the precipitation had a positive effect while the air temperature had a negative effect on growth in the studied lowland area. Growing season, especially July and September of the previous year and April and June of the current year, were the most significant months in relation to the effect of climate on radial growth like in other studies (Mäkinen et al. 2001; Putalová et al. 2019). Currently, particularly a significant negative impact of droughts and warming in recent years is evident related to ongoing climate change, which represents a crucial issue in European forest ecosystems (Čater, Diaci 2017; Vitali et al. 2018).

CONCLUSION

Forests of hornbeam-oak stands, herb-rich beech stands and secondary spruce stands in the Medník NNM have been specifically managed since 1930 for the occurrence of the protected and critically endangered *Erythronium dens-canis* population. The forest management applied for a long time has largely influenced the structure and diversity of stands, when these impacts were largest in hornbeam-oak stands and smallest in spruce stands. There is no need to engage in forest regeneration in the next decades because of enough stump sprouts in the hornbeam-oak coppice. On the other hand, it will be necessary to initiate the process of their gradual controlled natural regeneration in herb-rich beech stands and spruce stands in small game-proof fences because of complete damage by hoofed game browsing. In relation to climatic factors, large-leaved lime showed the highest vulnerability to climatic factors in growth compared to high resistance in sessile oak and European beech. Also, the local population of Sázava Norway spruce showed good adaptability to climate extremes compared to allochthonous spruce populations. The synergism of precipitation deficit and high air temperature was a limiting factor of growth together with extreme droughts, high air temperature and late frost in the studied NNM. The frequency of negative pointer years with extremely low radial growth has been increasing during the time. Close-to-nature small-scale silviculture together with support of resistant tree species in mixed forests represents necessary management measures for adaptation to climate change and conservation of these valuable forest ecosystems.

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