https://doi.org/10.17221/82/2019-JFS

Growth response of mixed beech forests to climate change, various management and game pressure in Central Europe

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Citation: Vacek S., Prokůpková A., Vacek Z., Bulušek D., Šimůnek V., Králíček I., Prausová R., Hájek V. (2019): Growth response of mixed beech forests to climate change, various management and game pressure in Central Europe. Journal of Forest Science, 65: 331–345.

Abstract: The growth, structure and production of mixed beech (*Fagus sylvatica* L.) forests were analysed in the Broumovsko Protected Landscape Area, Czech Republic. The objective of the paper was to evaluate stand structure, timber production and dynamics of forests with historically different silvicultural practices in relation to climate conditions, management and game damage. The results indicate that scree forests (coppices and coppices with standards) were stands with high-rich species diversity and structure compared to herb-rich beech forests (high forests) with higher timber production. The Norway spruce (*Picea abies* [L.] Karst.) was the most sensitive tree species compared to low growth variability in European beech. The climate factors had the highest effect on radial growth from June to August. Natural regeneration showed great density potential (13,880–186,462 recruits·ha^{-1}), especially in expansion of maples and European ash (*Fraxinus excelsior* L.). However, recruits were seriously limiting by damage caused by hoofed game, especially in silver fir (*Abies alba* Mill.; 53% browsing damage), wych elm (*Ulmus glabra* Hudson; 51%) and rowan (*Sorbus aucuparia* L.; 50%).

Keywords: stand structure; forest dynamics; radial growth; silviculture; game damage

European forest ecosystems play a very important role as providers of ecosystem functions (Stenger et al. 2009; Conte et al. 2018) when global changes pose a threat to forest ecosystems and their functions (Anderegg et al. 2016; Sicard et al. 2016). This is the reason why the knowledge of dynamics and structure of close-to-nature forests with regard to global changes is of great importance for their protection and management (Leuschner, Ellenberg 2017). In this context, the objectives of many papers have been structural and growth parameters (Bolte et al. 2010; Vacek et al. 2016; Dulamsuren et al. 2017). The growth of forests has been well documented in many studies in the last decades as an increasing parameter (Cole et al. 2010; Pretzsch et al. 2014a). However, there are many studies that documented trends of growth decrease in several areas by several factors (Bontemps et al. 2010; Rabasa et al. 2013). Basic effects include particularly climate changes (Bošeľa et al. 2016; Kunz et al. 2018), increased CO_2 concentration in the atmosphere (Cole et al. 2010), increased nitrogen depositions (Braun et al. 2010; Landuyt et al. 2018), increased con-

Supported by the Internal Grant Agency (IGA No. A02/19), Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague.

https://doi.org/10.17221/82/2019-JFS

centrations of tropospheric ozone (Matyssek et al. 2010) and light availability that is also important for the stand dynamics (Lambers et al. 2008; Pretzsch, Schütze 2009). Subsequent physiological responses of tree species to these abiotic effects determine their survival, distribution and growth (Annighöfer 2018).

It is well-known that various species can show different growth responses in relation to the availability of resources (Petritan et al. 2009; Poorter et al. 2012). It is to note that responses within one species can also be variable (Rijkers et al. 2000). The effect of climate factors on the vitality of particular species of trees is usually more demonstrative at the edge of their geographic or ecological range (Hampe, Petit 2005). Ultimate consequences of climate changes can lead to variations in ecological and geographic ranges of various species of trees, species composition (Bolte et al. 2010; Rigling et al. 2013), stand structure (Wang et al. 2012), mutual competition between tree species (Tylianakis et al. 2008) or forest stand stability (Ives, Carpenter 2007; Lloret et al. 2012).

In case of European beech (*Fagus sylvatica* L.) an initial decrease in productivity was observed at the edge localities using production indicators (Jump et al. 2006; Peñuelas et al. 2008). Ongoing changes can be expected in future when the weights and frequency of hot and dry years continue increasing (Bindoff et al. 2013), which can have relatively serious consequences for beech forests of Central Europe (Gessler et al. 2007; Dulamsuren et al. 2017), such as in mixed beech forests with oak, lime, maple and hornbeam the increment (Cavin et al. 2013; Zimmermann et al. 2015). Recurrent droughts have a still more negative impact on tree vitality (Lévesque et al. 2016).

Taking into account the above-mentioned facts, with regard to the higher resistance of stands to climate changes, mixed forest stands should be supported that are considered as more resistant to disturbances as well as to extreme events (e.g. droughts, frosts, windstorms, air pollution load) in comparison with unmixed stands (Pretzsch et al. 2013a; Yurtseven et al. 2018; Vacek et al. 2019). Moreover, mixed forest can provide better ecosystem functions (Brassard et al. 2013) and higher productivity due to the more comprehensive use of the site (Morin et al. 2011; Forrester, Albrecht 2014). Therefore, some studies have suggested that in future forest production will probably depend on forest composition and structure (Coomes et al. 2014; Vacek et al. 2014a). In line with this trend, at many localities in Europe spruce monocultures are transformed to more stable mixed uneven-aged stands with a high proportion of beech (Knoke et al. 2008; Pretzsch et al. 2014a), which currently provides a high reproductive and productive potential in Central European areas affected by spruce decline, with relatively wide ecological valence (Ammer et al. 2008; Kolář et al. 2017). On the other hand, mixed forests are more endangered by game damage, especially attractive tree species (Ammer 1996; Vacek 2014b). Increasing ungulate population nowadays reached the highest densities and significantly negatively influences growth of natural regeneration by browsing loses (Konôpka et al. 2015; Vacek 2017).

In this study due to mentioned reasons, we would like to increase the knowledge of mixed forests with dominant European beech in relation to changing environmental conditions in protected areas on long-term research plots as the most valuable objects for monitoring in forest ecosystems (Bakker et al. 1996; Vacek et al. 2017). One of the urgent challenges of current forestry under pressure of a probable decrease in the representation of the most important commercial tree species (Hanewinkel et al. 2013) is to find suitable ecological and economic sustainable methods of management (Fürst et al. 2007; Bolte et al. 2009; Vitali et al. 2017). Such strategies should support the adaptive capacity of forests to climate changes (Linder et al. 2000; De Dios et al. 2007) and to create more resistant forest ecosystems (Biggs et al. 2012), that will show higher resistance to external influences in combination with a faster return to the original pre-disturbance state (Rammer, Seidl 2015).

The objective of the paper was to evaluate structure and production of scree forests and herb-rich beech forests influenced by global changes (warming, climatic extreme events, high population of game, insect disturbances, etc.), where different management methods were used in the past (high forest, coppice with standards and coppice) in Broumovsko Protected Landscape Area (PLA). The aims were to (1) determine and compare production and structure of study mixed high forest, coppice with standards and coppice forest stands, (2) evaluate dynamics of radial growth and describe the effect of climate, silviculture and ex-

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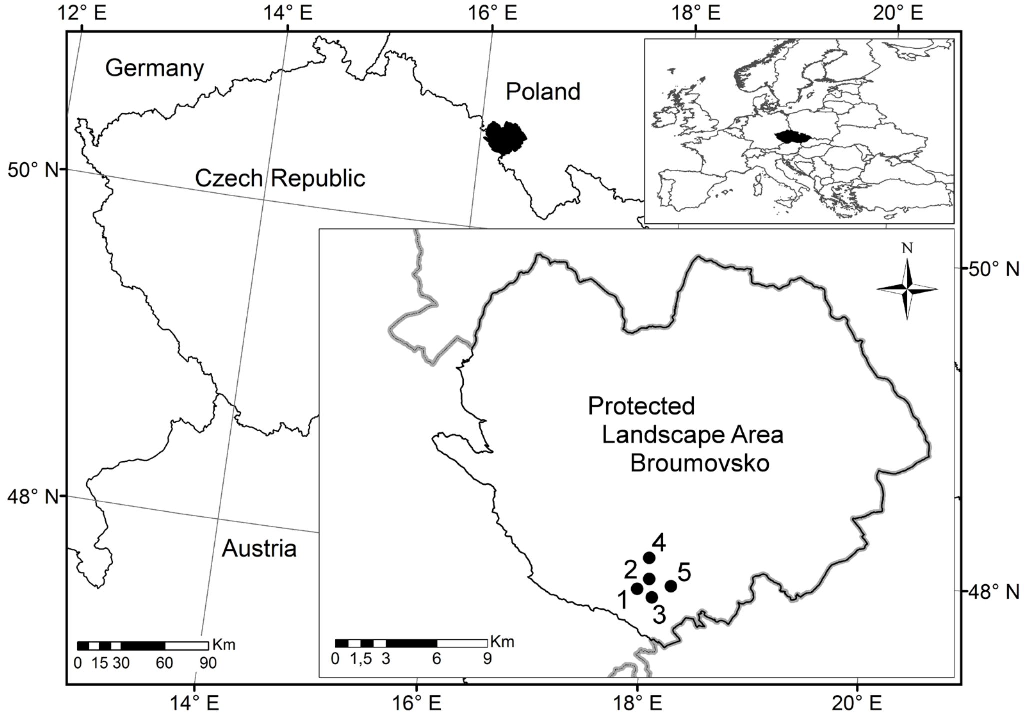

Fig. 1. Localization of permanent research plots 1–5 at the Kozínek Site of Community Importance, Protected Landscape Area Broumovsko

treme events on individual tree species and (3) quantify the influence of ungulates on growth of natural regeneration differentiated by tree species.

MATERIAL AND METHOD

Study site

The area of interest Kozínek Site of Community Importance (SCI; CZ 0520507) is one type of protected areas within the NATURA 2000 network in Broumovsko PLA, Czech Republic. It was established in 2004 for the protection of sites of Community importance and species of Community interest on an area of 84.08 ha (AOPK 2004). The locality is interesting for a frequent occurrence of the priority biotope of scree and slope forests (biotope code L4) along with biotopes of calcareous rocky slopes (S1.1) and for a large area of herb-rich beech forests (L5.1; Guth, Kučera 2005). The altitude of the locality is 378–504 m a.s.l. The bedrock is composed of Cretaceous sediments of middle and lower Turonian or upper Cenomanian, and fluvial and fluvio-deluvial Quaternary sediments are also represented. Prevailing soil types are Pararendzinas and Cambisols. Climatically the Kozínek locality belongs to humid continental climate characterized by hot and humid summers and cold to severely cold winters (region Cfb; Köppen 1936) according to Köppen climate classification, respectively by detailed region Quitt distribution to moderately warm region (region MT7; Quitt 1971). The average annual air temperature was 7.2°C and annual sum of precipitation reached 742 mm (with maximum in July – 17.1°C and 82 mm; Tolasz et al. 2007). The length of the growing season ranged from 140 to 155 days with mean sum of precipitation 390 mm and air temperature around 13.5°C. The length of snowing period was 60 days with maximum average snow height between 20–30 cm.

Scree forests consist of the plant associations *Aceri-Carpinetum*, *Mercuriali-Fraxinetum* and of *Lunario-Aceretum* to a lesser extent, herb-rich beech forests are composed of *Aceri-Fagetum, Asperulo-Fagetum* and *Dentario enneaphylli-Fagetum* and of the association *Tilio cordatae-Fagetum,* which is a transition between beech forests and scree forests. The prevailing part of forests in the area of interest was historically established as coppice forests. On PRP 2 and 3 the forest stands have been converted to high forest; on PRP 1 and 4

https://doi.org/10.17221/82/2019-JFS

Table 1. Overview of the basic characteristics of permanent research plots 1–5 (stand parameters according to Forest Management Plan)

ID	GPS	Age (y)	Mean height (m)	Mean DBH (cm)	Stand volume ($m^3 \cdot ha^{-1}$)	Altitude (m)	Exposure	Gradient (°)	Site type	Forest type	Soil type
1	50°30'05''N 16°11'58''E	140	19	32	540	425	SE	45	3J	coppice with standards	leptosols modal
2	50°30'11''N 16°12'23''E	158	22	39	550	435	S	29	3A	high forest	cambisols leptosolic
3	50° 29'57''N 16°12'17''E	104	24	30	520	420	NE	36	3A	high forest	cambisols leptosolic
4	50°30'50''N 16°12'49''E	142	18	32	560	440	W	40	3J	coppice with standards	rendzic leptosols
5	50°30'10''N 16°12'45''E	61	17	23	280	430	W	28	3J	coppice	rendzic leptosols

DBH – quadratic mean diameter; 3J – lime-maple forest (*Tilio-Aceretum saxatile*), 3A – stony-colluvial lime-oak-beech forest (*Tilii-Querceto-Fagetum acerosum lapidosum*)

the stands have been converted to coppice with standards (20% and 8% of trees are from sprouts); on PRP 5 the stands were left as a coppice with prolonged period. Although forest management practices were completely terminated in 2004, forest management was extensive even before. The last officially executed management practice (moderate qualitative selection) was carried out on all PRP in 1963, 1974, 1985 and 1994 (except PRP 5 in 1963). Thinning was focused on supporting original tree species composition, quality trees originated from seeds and to remove sprouts on PRP 1–4 and support high-quality stump sprouts on PRP 5. The first research activities on PRP 1–5 focused on phytocoenological relevés were recorded in 1961. The localization of PRP 1–5 is represented in Fig. 1 and basic characteristics of PRP are shown in Table. 1.

Data collection

To determine the tree layer structure of forest stands on 5 PRP of 50×50 m in size (0.25 ha) the FieldMap technology (IFER-Monitoring and Mapping Solutions Ltd.) was used in 2014. This technology was used to localize the position of all tree layer individuals of diameter at breast height (DBH) ≥ 4 cm and the tree-crown projection area was measured minimally at 4 directions perpendicular to each other. In the tree layer tree heights and heights to the live crown base were measured with a Vertex laser hypsometer (accuracy 0.1 m; Haglöf) and DBH were measured with a Mantax Blue metal calliper (accuracy 1 mm; Haglöf).

Natural regeneration on particular PRP was measured on transects 10 × 50 m in size that were representative of regeneration. These characteristics were measured: position of all recruits, height, height to the live crown base, crown width with a height pole (accuracy 1 cm) and damage by game browsing (terminal shoot).

As for 10 dominant trees for European beech, Norway spruce (*Picea abies* [L.] Karst.), Sycamore maple (*Acer pseudoplatanus* L.), wych elm (*Ulmus glabra* Hudson), sessile oak (*Quercus petraea* L.) and small-leaved lime (*Tilia cordata* Mill.) on each PRP (in the case of occurrence) increment cores were taken at breast height (130 cm) with the Pressler borer perpendicularly to the trunk axis up- and downslope in 2016. Annual ring widths were measured with an accuracy of 0.01 mm by an Olympus binocular microscope on the LINT-AB measuring table (Rinntech) and recorded with TsapWin software (Registograph).

Data analysis

Stand volume was calculated using volume equations published by Petráš and Pajtík (1991). Stand density index (SDI), crown closure (CC) and crown projection area (CPA) were derived. Situational map was created in the ArcGIS program (ESRI).

Tree-ring increment series were individually crossdated (removal of errors caused by missing tree

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rings) using statistical tests in the PAST application (Knibbe 2007) and subsequently subjected to visual inspection according to Yamaguchi (1991). If a missing tree ring was revealed, a tree ring of 0.01 mm in width was inserted in its place. Particular curves from PRP were age detrended in a standard way and an average tree-ring series was created in the ARSTAN program (Tree-Ring Laboratory). The analysis of negative pointer years was done 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 average of increments from preceding 4 years. The negative year was proved if such a strong increment reduction occurred at least in 20% of trees on the plot. Average tree-ring series from PRP in the SCI Kozínek were correlated with climate data (air temperatures, precipitation) according to particular years provided by the Meteorological station Úpice – Czech Hydrometeorological Institute (413 m a.s.l.). To simulate diameter increment in relation to climate characteristics the DendroClim 2002 software was used (Biondi, Waikul 2004). In this program, residual chronology was correlated with monthly average air temperatures and sum of precipitation, from it was found out when the statistically significant correlations occurred ($\alpha = 0.05$).

RESULTS

Tree layer structure

The number of living trees ranged from 240 (high forest) to 720 (coppice) trees·ha^{-1} with SDI 0.55–0.79 (Table 2). The average basal area was in range 36.7–47.0 m^2·ha^{-1}. The stand volume reached between 340 (coppice) and 699 (high forest) m^3·ha^{-1}. The highest stand volume in European beech was on PRP 1 (45%), on PRP 2 (98%), on PRP 3 (60%) and PRP 4 (83%). On PRP 5 the highest volume was revealed in sycamore maple (42%). Crown closure was the highest on PRP 1 (coppice with standards), while the lowest canopy was observed on PRP 2 (high forest).

In relation to diameter frequencies, on PRP 1 the tree layer was created by three storeys where beech was dominant (24%; Fig. 2). Diameter structure was relatively even distribution of diameter classes. In the upper storey only beech, sycamore and elm were present. On PRP 2 in the three-storeyed stand beech was a clearly dominant tree species (77%). Distribution of diameter classes in the tree layer was relatively pronounced right-skewed. On PRP 3 there were also three storeys in the tree layer where beech was also dominant (49%). Distribution of diameter classes was relatively uneven of the Gaussian curve type. In the lower and middle storeys all tree species were represented and in the upper storey only beech, lime and sycamore were present. On PRP 4 the tree layer consisted of three storeys. The tree layer was dominated by beech (64%), such as in the upper layer. Due to the cumulative tree class 60+ cm diameter class distribution was the U-shaped type. On PRP 5 there were also three storeys in the tree layer in which sycamore was dominant (40%). Overall, it was a relatively uneven distribution of diameter classes of the Gaussian curve type.

Tree-ring analyses

The regional standardized ring-width chronology of European beech on PRP 1–5 in 1955–2015 indicated a relatively uneven radial increment (RWI ± 0.14 SD; Fig. 3). According to individual PRP, the lowest variability was on PRP 5 with the lowest share of beech in tree species composition. Depressions of radial growth in 1980, 1996, 1997, 2006 and particularly in 2011 were caused by severe late frost damage to the assimilating organs while in 1985 it was caused by a heavy attack of the beech scale insect (*Cryptococcus fagi*). In 2014 and 2015 a decrease in radial increment was due to drought. Years 1958, 1980, 1985, 1994, 2011 and 2015 were negative pointer years with low radial increment of European beech. This tree species had a minimum average annual radial increment of beech on PRP 2, while maximum value was reached by beech on PRP 4.

The regional standardized ring-width chronology of sycamore maple on PRP 1, 4 and 5 showed a relatively uneven radial increment (RWI ± 0.14 SD; Fig. 3). The minimum value of diameter increment was determined on PRP 4, maximum value on PRP 5. Highly decreased radial increment in 1967, 1973, 1979, 1997 was caused by the pathogen *Rhytisma acerinum* in combination with drought. Years 1957, 1964, 1973, 1984, 1985, 1996, 1997, 2008 were the negative pointer years. In term of small-leaved lime (RWI ± 0.17 SD), the negative pointer years were 1957, 1959, 1974, 1980, 1992, 1995, 1996, 1998,

https://doi.org/10.17221/82/2019-JFS

Table 2. Stand characteristics on permanent research plots 1–5 according to main tree species

PRP	Species	DBH (cm)	*h* (m)	*v* (m^3)	*N* (trees ha^{-1})	BA ($m^2 \cdot ha^{-1}$)	*V* ($m^3 \cdot ha^{-1}$)	CC (%)	CPA ($ha \cdot ha^{-1}$)	SDI
1	beech	47.9	26.2	2.630	104	18.6	274	71.4	1.25	0.28
	s. maple	55.0	27.8	3.379	32	7.5	108	29.0	0.34	0.11
	hornbeam	33.3	20.6	0.907	88	7.6	80	56.5	0.83	0.13
	N. maple	28.4	20.6	0.763	56	3.5	43	27.2	0.32	0.07
	elm	28.5	17.8	0.603	68	4.3	41	31.4	0.38	0.09
	ash	31.7	23.3	0.789	36	2.8	28	15.8	0.17	0.05
	spruce	41.7	31.8	1.696	8	1.1	14	3.0	0.03	0.01
	lime	16.4	14.6	0.167	36	0.7	6	14.0	0.15	0.02
	total	37.1	22.0	1.386	428	46.1	593	96.9	3.48	0.76
2	beech	49.5	28.91	3.164	184	35.4	582	87.3	2.06	0.52
	hornbeam	30.9	15.8	0.534	8	0.6	4	5.9	0.06	0.01
	lime	30.9	18.5	0.640	4	0.3	3	3.8	0.04	0.01
	s. maple	13.0	9.1	0.065	24	0.3	2	6.0	0.06	0.01
	total	44.2	24.6	2.463	240	36.7	591	89.9	2.28	0.55
3	beech	38.1	28.7	1.738	240	27.3	417	85.8	1.95	0.45
	lime	34.8	27.4	1.399	176	16.7	246	62.9	0.99	0.28
	s. maple	27.8	23.7	0.759	36	2.1	27	13.2	0.14	0.04
	N. maple	18.0	15.3	0.237	24	0.6	6	9.6	0.10	0.01
	spruce	23.5	27.0	0.510	4	0.2	2	0.8	0.01	0.00
	total	35.0	26.8	1.432	488	47.0	699	96.0	3.21	0.79
4	beech	38.0	16.8	1.684	300	33.9	505	90.7	2.38	0.56
	spruce	43.2	27.4	1.567	44	6.4	69	16.8	0.18	0.09
	fir	47.9	31.3	2.360	12	2.1	28	6.2	0.06	0.03
	s. maple	12.9	11.5	0.080	72	0.9	6	16.7	0.18	0.02
	lime	12.6	10.4	0.091	28	0.3	3	7.2	0.08	0.01
	total	34.5	16.8	1.296	472	43.9	612	94.7	2.93	0.71
5	s. maple	25.7	18.7	0.493	288	14.9	142	56.3	0.83	0.29
	beech	32.4	18.1	0.828	64	5.2	53	36.0	0.45	0.09
	oak	32.0	19.2	0.712	64	5.1	46	26.6	0.31	0.10
	birch	23.2	17.5	0.302	88	3.7	27	19.6	0.22	0.07
	fir	31.7	22.1	0.849	20	1.5	17	6.4	0.07	0.03
	ash	32.9	21.9	0.764	20	1.7	15	11.4	0.12	0.03
	lime	44.9	21.3	1.601	8	1.3	13	7.7	0.08	0.02
	hornbeam	27.0	17.3	0.490	24	1.4	12	19.4	0.22	0.03
	aspen	20.6	17.2	0.215	40	1.3	9	9.9	0.10	0.03
	spruce	16.7	13.3	0.132	44	1.0	6	8.0	0.08	0.02
	total	25.8	17.5	0.472	720	37.6	340	92.8	2.63	0.71

DBH – mean diameter at breast height, *h* – mean height, *v* – average tree volume, *N* – number of trees, BA – basal area, *V* – stand volume, CC – canopy closure, CPA – crown projection area, SDI – stand density index

2004, 2009. The regional standardized ring-width chronology of wych elm on PRP 1 revealed an uneven diameter increment (RWI ± 0.30 SD). After thinnings in 1963 and 1992 released trees had a substantially increased radial increment. Years 1975, 1988, 1989, 1990, 1992 and 2015 were the negative pointer years. The standardized ring-width chronology of sessile oak showed a relatively steady radial

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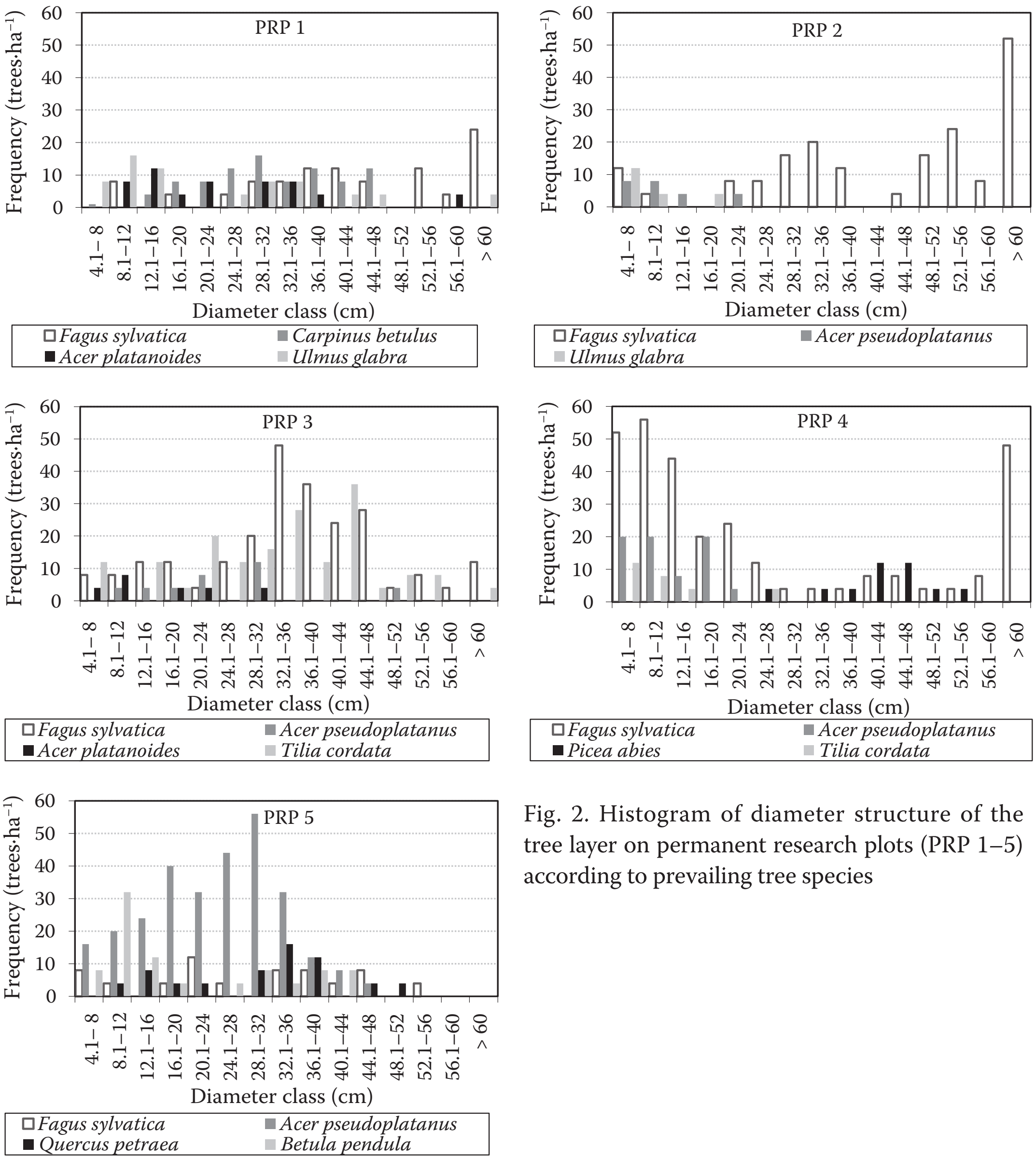

Fig. 2. Histogram of diameter structure of the tree layer on permanent research plots (PRP 1–5) according to prevailing tree species

increment (RWI ± 0.23 SD). An extraordinary depression of radial increment in negative years 2014 and 2015 was conditioned by drought. An extremely unsteady radial increment was observed in Norway spruce (RWI ± 0.35 SD). The tree-ring curve had a downward trend by 1985 and since that year an unsteadily upward trend. In 1980-1988 the decreased radial increment of spruce was caused by SO_2 air pollution load. The radial growth considerably increased there after a silvicultural treatment in 1994. A depression of radial growth in 2015 was mainly due to drought. Years 1964, 1965, 1966, 1971, 1972, 1979, 1980, 1981, 1982, 1984, 1985, 1992, 2005 were negative pointer years (Fig. 3).

Correlations of diameter increment of main tree species with average monthly air temperatures showed some statistically significant values (Fig. 4.). Beech diameter increment showed a significant ($P < 0.05$) positive correlation with air temperature in three months, while negative effect of precipitation on radial growth was prevailing. Sycamore radial growth showed only positive correlations with climatic factors, especially in the growing season of the current year. Air temperature had significant prevailing effect on radial growth of lime, while increment of elm was influenced mainly by precipitation. The lowest effect of climatic factors was determined in oak. On the other hand, spruce was the most climate sensitive tree species with nine significant months. Main limiting factor of spruce growth was low precipitation and high air temperature.

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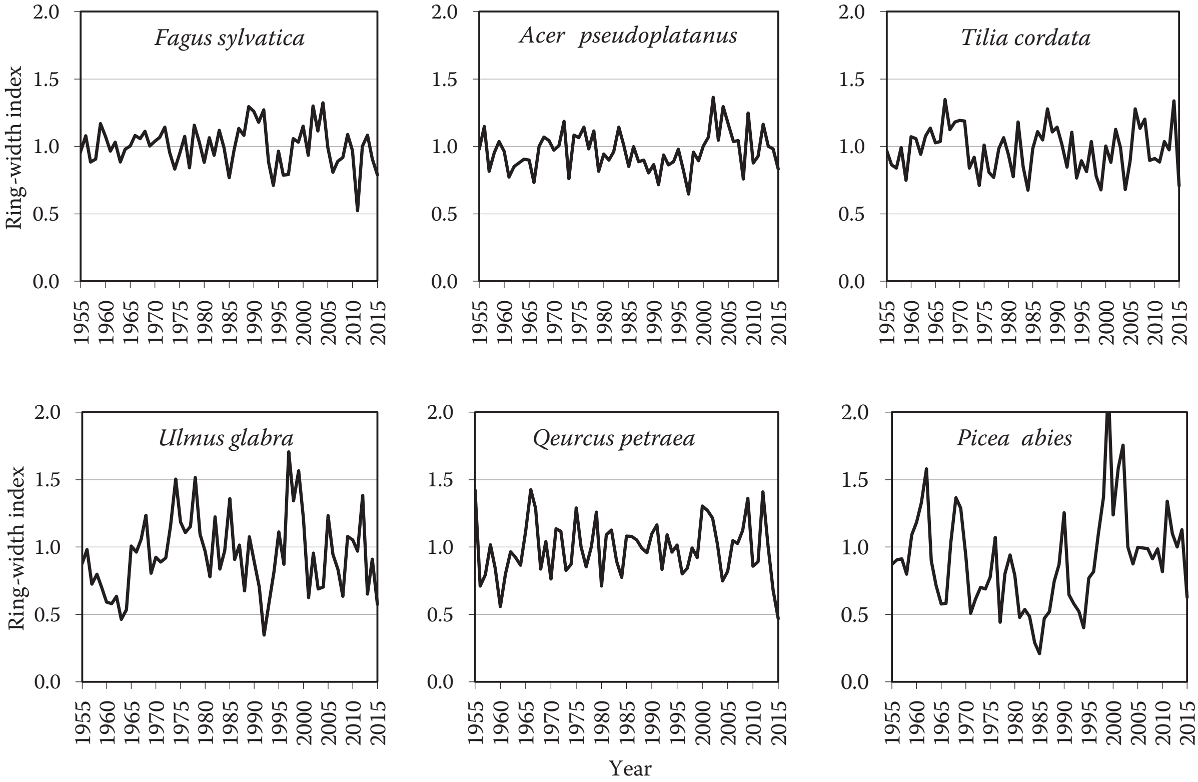

Fig. 3. Standardized ring-width chronologies of main tree species after age detrending

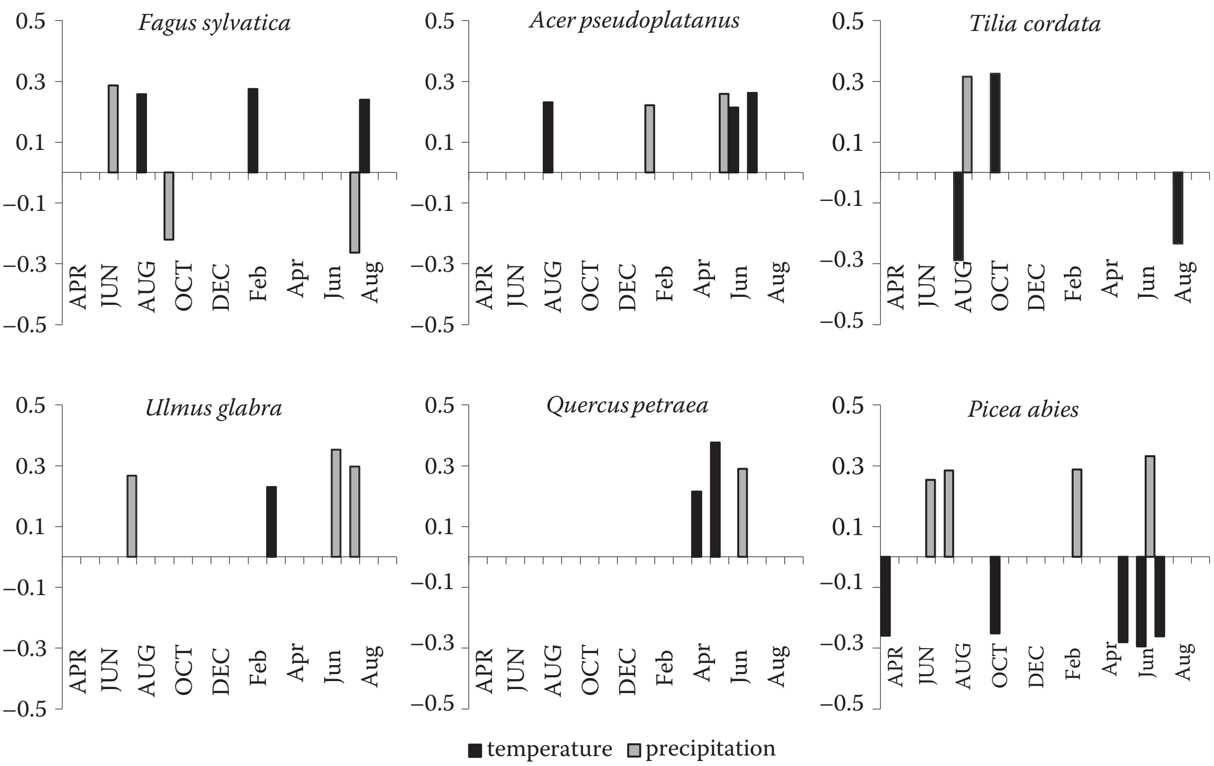

Fig. 4. The coefficients of correlation of the standardized ring-width chronology of main tree species with monthly air temperatures (black) and precipitation (grey) from April of the preceding year (capital letters) to September of the current year (small letters) for the period 1963–2015 only correlation coefficients with statistically significant values (α = 0.05) are displayed

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Table 3. Numbers of recruits and browsing damage caused by game according to main tree species on permanent research plots 1–5

Species	PRP 1		PRP 2		PRP 3		PRP 4		PRP 5	
	density (pcs·ha^{-1})	damage (%)	density (pcs·ha^{-1})	damage (%)	density (pcs·ha^{-1})	damage (%)	density (pcs·ha^{-1})	damage (%)	density (pcs·ha^{-1})	damage (%)
beech	4,440	18.0	72,414	10.4	46,960	8.0	5,000	8.0	1,640	56.0
oak	0	–	1,134	6.8	40	0.0	40	0.0	800	25.0
hornbeam	440	27.3	12,798	14.5	1,560	0.0	160	0.0	2,320	74.1
elm	360	55.6	0	–	400	0.0	160	0.0	2,480	96.8
ash	24,440	16.5	7,290	18.4	160	13.3	600	13.3	20,520	20.0
N. maple	9,040	42.9	20,736	32.5	26,440	5.7	2,800	5.7	400	50.0
s. maple	3,600	17.8	69,660	28.8	6,160	12.9	3,720	12.9	280	57.1
fir	0	–	0	–	40	3.8	1,040	3.8	360	55.6
rowan	0	–	162	36.5	160	100.0	40	100.0	1,800	62.2
lime	0	–	648	42.6	3,960	0.0	0	–	240	–
spruce	0	–	0	–	80	0.0	0	–	80	50.0
Total	42,640	27.6	186,462	20.4	85,960	17.9	13,880	17.9	31,240	51.5

Natural regeneration structure and game damage

On PRP 1–5 the numbers of natural regeneration ranged from 13,880 (PRP 4) to 186,462 (PRP 2) recruits·ha^{-1} (Table 3). High structure of natural regeneration on PRP 1–5 was relatively little grown-up while individuals of maximally 30 cm in height prevail. On the overall average on PRP 1–5 European beech accounts for 36.2%, sycamore maple for 23.3%, Norway maple (*Acer platanoides* L.) for 16.4%, European ash (*Fraxinus excelsior* L.) for 14.7%, European hornbeam (*Carpinus betulus* L.) for 4.8% and the other tree species are only scarcely interspersed (maximally 1.5%). Maples and European ash showed significant increase in share of tree species composition of natural regeneration compared to tree layer. Crown closure of natural regeneration reached 0.16–0.62 and crown projection area was 0.18–1.69.

Table 3 shows the proportion of recruits with terminal shoots damaged by browsing on PRP 1–5 separately according to tree species. In general, the damage to terminal shoots of natural regeneration on PRP was great (17.9–51.5 %), on average amounting to around 30%. The highest losses were observed in silver fir (*Abies alba* Mill.; 53%) followed by wych elm (*Ulmus glabra* Hudson; 51%), rowan (*Sorbus aucuparia* L.; 50%), Norway maple (41%), sycamore maple (34%), European hornbeam (26%), Norway spruce (25%), European beech and European ash (23%), small-leaved lime (20%) and sessile oak (8%). Individuals from a height of 15 cm were damaged to the highest extent.

DISCUSSION

Results of the basic stand characteristics in detail document structural and production differences between high forest, coppice with standards and coppice forests on the studied locality where beech was a dominant tree species except on PRP 5. In this context Bošeľa et al. (2016) suggested that beech would have a crucial role in European forest ecosystems also in future while the knowledge of the impact of climate change is not quite definite and unambiguous yet. As for production, the stand volume was 340–699 m^3·ha^{-1}, when the highest standing volume was on PRP 3 and the lowest on PRP 5. In our study, although stand volume was influenced by a number of factors (age, microsite, tree species composition, management), such a large range was given by different types of forest because there was a coppice on PRP 5. The other plots (high forest, coppice with standards) had much higher stand volume than the latter plot. In connection with stand volume and climate change some authors supported an assumption that mixed multi-species stands can provide higher production (Del Río et

https://doi.org/10.17221/82/2019-JFS

al. 2013) and they can also be even more resistant to severe droughts (Pretzsch et al. 2013b) which have however had negative impacts in the last years in spite of the relatively high species diversity of the studied localities. This trend was confirmed in Europe by many studies (e.g. Bontemps et al. 2010; Rabasa et al. 2013). For example, comparing production of high forests in our study, the higher stand volume (699 $m^3 \cdot ha^{-1}$) was observed on mixed PRP 3 with beech share of 72% compared to PRP 2 (beech share 98%, volume 591 $m^3 \cdot ha^{-1}$). Moreover, the lowest variability in growth of beech in relation to environmental factors was observed on PRP 5 where beech was only admixed tree species (16%). A comparison of stand characteristics with similar localities in Central Europe basically reveals very similar production characteristics from many different sites (Bulušek et al. 2016; Králíček et al. 2017). The timber production can be influenced not only by the mix of forest but also by the type of mix (Ngo Being et al. 2013).

The structure of diameter class distribution was very much differentiated on PRP, which can be explained by different silvicultural practices (type of thinning, transformation of coppice to coppice with standards and high forest) in the past. Heterogeneity of results can also be related with the size of the studied plots (Paluch 2007). At the studied localities Gaussian distribution, relatively even distribution and clearly left-skewed as well as right-skewed distribution can be found. According to Král et al. (2010) the Gaussian distribution is typical of the stage of the optimum on a larger spatial scale. Left-skewed distribution is typical of old-growth close-to-nature beech stands (Korpeľ 1995; Schütz et al. 2001) that usually reflect the regime of small-plot disturbances (Zeibig et al. 2005) and are at the growing-up stage or at the initial stage of disintegration (Podlaski 2006; Zenner et al. 2015).

In the framework of a wider study of diameter of individual trees on PRP we focused on a long-term radial growth in the period 1955–2015. In connection with the relative diversity of species structure the studied diameter increment was influenced by a number of various factors (drought, late frosts, pests, etc.) while in beech as a dominant tree species at all localities except PRP 5 an increment reduction has been observed in the last years particularly due to drought similarly like in spruce on PRP 4, in the other tree species this trend has not been so obvious. A comparison of this situation with some European localities showed that the beech mainly at the southern edge of its natural range suffers from an increment reduction (Jump et al. 2006; Bontemps et al. 2010) even though regional differences may be large (Tegel et al. 2014). Szymura et al. (2013) stated that an amount of available water is a key factor for beech distribution because at water deficit the beech is less competitive than other tree species occurring at these localities, e.g. oak. An increment reduction at European localities was also reported by Dittmar et al. (2003). On the contrary, other studies from Europe confirmed an increment increase in beech between 1950 and 1980 (Hlásny et al. 2011; Pretzsch et al. 2014b). Bošeľa et al. (2018) suggested a positive effect of increasing summer air temperatures at higher latitudes or altitudes above sea level and at the same time they predicted an increase in beech increment at the northern edge of its range. Comparing other tree species, Norway spruce was the most sensitive to negative years with extreme low radial growth, such as in other studies (Vacek et al. 2019), while growth of European beech, sycamore maple, sessile oak, and small-leaved lime was relative stable. Moreover, higher diameter increment and resistance are reached in mixed forests compared to monocultures (Pretzsch et al. 2014a). The future development of increment will basically depend on regional climate and locality productivity to a great extent (Aertsen et al. 2014). These local factors largely influence the generalization of results for a wider spectrum of forest stands and underlie different results of many studies.

Natural regeneration is an important component of close-to-nature forests (Petritan et al. 2007; Vacek et al. 2017). Our study showed the relatively high population density (13,880–186,462 $recruits \cdot ha^{-1}$) and increasing proportion in maples and ash. In comparison with other locality in PLA Broumovsko, lower density of regeneration was observed in range of 1,472–44,888 $recruits \cdot ha^{-1}$ (Vacek et al. 2015). Beech was a dominant tree species in natural regeneration although its proportion far from its representation in Bílek et al. (2014) in the Voděradské bučiny National Nature Reserve or from the highly dominant proportion of beech in Nature Reserve Broumovské stěny reported by Vacek et al. (2015). At the studied localities there was much higher diversity of species composition that appears unique by its richness in comparison with other studies from Central Europe (e.g. von

https://doi.org/10.17221/82/2019-JFS

Oheimb et al. 2005; Králíček et al. 2017) when the papers presenting so rich natural regeneration were very scarce. Even though natural regeneration consisted of a high number of recruits and species, it did not avoid the considerable pressure of wildlife that caused great losses of recruits by browsing of terminal shoots. The individuals of fir, elm and rowan suffered the greatest damage, but almost all tree species in natural regeneration were more or less damaged. In the Czech Republic a great pressure of wildlife was reported from many localities (Vacek 2017; Cukor et al. 2019a, b), when some authors confirmed increasing food attractiveness with a decreasing proportion of tree species in natural regeneration (Ammer 1996; Čermák et al. 2009). In this context Vacek et al. (2015) stated that it is practically impossible to grow some tree species without fencing at some localities because the wildlife causes losses not only by browsing but also by fraying and bark stripping. Bark stripping done mainly by red deer can threaten also older stands that have grown up enough to avoid browsing (Vacek et al. 2012). If we want to conserve rich species composition in the studied stands also in future, it will be necessary to reducing of still increasing ungulate population densities to an environmentally acceptable limit and protect threatened tree species by individual or group fencing.

CONCLUSION

The structure of scree forests and herb-rich beech forests at the Kozínek Site of Community Importance was influenced by a number of factors. The main factor influencing the specific site and stand conditions of scree forests and herb-rich beech forests was a change in silvicultural practices, specifically the transformation of coppice to high forest while small-scale management methods were maintained. Studied coppice stands confirmed higher structural differentiation and diversity, while higher stand volume was observed in high forests. Moreover, global climate change also had an impact on these stands. It was evident mainly from the trends of radial increment of main tree species. European beech and sycamore maple showed the lowest variability in radial growth, while the lowest significant effect of climatic factors was observed in sessile oak. On the contrary, the most endangered tree species from the point of climate change was sensitive Norway spruce. Particularly the pronounced growth minima caused by both abiotic and biotic factors documented the high vulnerability of these ecosystems, especially of shallow-rooted tree species in scree forests. Development of natural regeneration has played an important role in the last years. It is to note that damage caused by hoofed game to natural regeneration was great, considerably constraining its further dynamics. The obtained results will be used for the definition of close-to-nature management with emphasis on original tree species composition, spatial and age differentiation in similar site conditions, where it is necessary to realize the transformation of forest stands to stands with a higher degree of naturalness.

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Received for publication July 14, 2019
Accepted after corrections September 17, 2019