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Sycamore maple (*Acer pseudoplatanus* L.) stands on former agricultural land in the Sudetes – evaluation of ecological value and production potential

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Abstract: Sycamore maple (*Acer pseudoplatanus* L.) is a fast-growing tree species that produces economically attractive timber, provides ecological services and has high site adaptability, but it is only a minor component of European forests. This paper describes production, structure and diversity of sycamore-dominated forest stands that originated by succession on former agricultural lands in the Orlické hory Mts., the Czech Republic. The partial objectives were to determine impact of climatic factors on the radial growth of sycamore maple and evaluate the effect of game on natural regeneration. The number of sycamore seeds on the ground was on average 9–34 seeds m⁻² and seedling mortality reached on average 89% caused by damage of hare and drought. Density of natural regeneration ranged from 1,532 to 4,244 recruits ha⁻¹, but growth dynamic was strongly influenced by ungulate browsing (69%) with the largest losses in sycamore (96%). Analyses of climatic effects showed a significantly close relationship with growth of sycamore in submontane areas, being especially sensitive to extremely dry and cold winters or very high summer temperatures. Radial growth was more significantly influenced by monthly temperatures compared to precipitation, but increasing sum of annual precipitation was main positive driver factor of diameter increment. Radial growth had the strongest relationship with weather conditions in July and October of previous year and March of the current year. Stand volume ranged from 378 to 545 m³ ha⁻¹ at age around 75 years, while sycamore accounted for 32–82%. The horizontal structure of the tree layer was mostly random to aggregated; resembling the clumped spatial pattern of natural regeneration. Besides their wood production, these stands fulfil many ecosystem functions that are associated with high ecological stability, high structural differentiation and medium to high species diversity.

Keywords: stand structure, growth dynamics, production, climate, tree-ring analysis, game damage, Central Europe

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Introduction

Sycamore maple (*Acer pseudoplatanus* L.) is a fast-growing broadleaved tree species of many European forests, especially typical for forests in central Europe (Úradníček et al., 2001). Despite its potential economic and ecological importance (Spiecker et al., 2009), the share of sycamore maple usually does not exceed 3% according to most national inventories in Europe (Hein, 2009). This lower stand volume is caused by the fact that sycamore rarely forms pure forest stands (Jones, 1945; Hein et al., 2009). Rather, it is found in mixture with European beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.), sessile oak (*Quercus petraea* [Matt.] Liebl.) and Norway maple (*Acer platanoides* L.); to a lesser extent it is associated with English oak (*Quercus robur* L.), field maple (*Acer campestre* L.), European hornbeam (*Carpinus betulus* L.) and wild cherry (*Prunus avium* L.; Ammer, 1996; Piovesan et al., 2005; Walentowski et al., 2006; Hein et al., 2009).

Sycamore is a tree that requires high levels of soil moisture and atmospheric humidity (Úradníček et al., 2001) and can be found in a variety of different habitat conditions (Piovesan et al., 2005). Generally, sycamore is a tree species of the moist mountain oceanic climate (Ellenberg, 1996). Typical mountain habitats of sycamore are characterized by high precipitation (900 – 1 400 mm yr⁻¹) or are located in areas where there is high atmospheric humidity, such as deep valleys and north-facing slopes (Piovesan et al., 2005). It grows most frequently on deep, humic moist soils with a high skeleton content but it does not tolerate water-logging with stagnant water. In limestone areas it occurs at the base of rocks on debris that is rich in humus deposits and sufficiently moist. The species has expanded throughout Europe, and it has been introduced into Asia, North America, South America, Australia, New Zealand and India (Röhrig & Ulrich, 1991; Rusanen & Myking, 2003; Kölling, 2007; Hein et al., 2009; Weidema & Buchwald, 2010).

The sycamore growth is highly influenced by environmental conditions (Skovsgaard & Jørgensen, 2004). Its growth is fast until 20–25 years of age, reaching about 20 m of height in suitable habitats and then its growth slows down (Claessens et al., 1999; Gill, 1992; Kupferschmid & Bugmann, 2008). In these habitats sycamore exceeds in productivity European beech and European ash (Henriksen & Bryndum, 1989; Schober, 1995; Lockow, 2004).

In most countries of Europe (Austria, Belgium, Denmark, Czech Republic, France, Germany, Lithuania, Netherlands, Poland, Sweden) sycamore has good natural regeneration (Dobrowolska, 1998; Tillisch, 2001; Rusanen & Myking, 2003; Ambrazevicius, 2016), producing seed every year starting

around the age of 25 to 30 years (Burschel & Huss, 1997). Individual trees can produce up to 170,000 seeds that are easily carried by wind, mostly within 200 m distance of the parent tree (Rusanen & Myking, 2003; Hérault et al., 2004; Thies et al., 2009). Seedlings are very vulnerable to competitive herbs (Diaci, 2002; Modrý et al., 2004; Vandenberghe et al., 2007). At young age, sycamore is very tolerant to shade; after it reaches a height of 2 to 3 m its requirements for light increase (Hölscher, 2004; Kazda et al., 2004). In maturity it can bear full illumination (Úradníček et al., 2001). In a number of European countries (Austria, Czech Republic, France, Germany, Switzerland, Slovakia) sycamore is heavily browsed by deer (Senn & Suter, 2003; Modrý, et al. 2004; Weidema & Buchwald, 2010; Vacek et al., 2014; Konôpka & Pajtk, 2015). Compared to its co-occurring species, its competitive advantage is its easy and abundant natural regeneration and fast growth in the first years. With sufficient light, it is capable to dominate European beech, whereas in low light conditions, its mortality is markedly higher than that of European beech (Petritan et al., 2007).

Sycamore produces very valuable wood with multiple uses (Soulères, 1997; Nunez-Regueira et al., 1997). Sycamore increases biodiversity and ecological stability of forest ecosystems (Binggeli, 1993; Pommerening, 1997; Bell, 2009) and it is an important soil-improving tree species that enhances humus formation and nutrient cycling (Weber et al., 1993; Heitz & Rehfuess, 1999). It has the potential to respond to projected future climate change (Kölling, 2007; Hein et al., 2009). For these reasons, especially in Central Europe, the species has value for both the forest sector and the wood processing industry (Spiecker et al., 2009; Thies et al., 2009).

In order to consider silvicultural practices in the face of projected global climate change and the increasing demand for ecosystem services (Spiecker et al., 2004; Puettmann & Ammer, 2007; Foster et al., 2010; Barbati et al., 2014), it is necessary to thoroughly understand the dynamics and adaptability of forest ecosystems (Lindenmayer et al., 2000; Baycheva et al., 2013). Only then is it possible to successfully adapt the methods of sustainable and near-natural management of forest ecosystems to future changing climate (Hein et al., 2009; Coote et al., 2012; Oxbrough et al., 2014). Most of the existing silvicultural practices applied to sycamore are based on operational experience in specific environmental conditions (Kerr & Evans, 1993; Joyce et al., 1998). Few of them are based on designed research and synthesis of acquired knowledge (Hein & Spiecker, 2009; Sjöstedt, 2012; Straigyte & Baliuckas, 2015). For these reasons the general objective of the present study was to describe structure and function of sycamore stands as basis for such knowledge-based

decision making. Particular goals were to: 1) evaluate stand production, structure, biodiversity and natural regeneration with emphasis on seeds characteristic of sycamore stands originated by succession on former agricultural lands; 2) assess the impact of climatic factors (temperature, precipitation) on the radial increment of sycamore and its dynamics and 3) determine the effect of game on growth and species composition of natural regeneration.

Material and Methods

Description of the study area

The study was conducted in four forest stands with dominant sycamore maple that originated by succession on former agricultural lands in the Orlické hory Mts. Protected Landscape Area (PLA), the Czech Republic (Fig. 1). The predominant soil types are Cambisols. The average annual temperatures are between 4 and 7°C, and precipitation ranges from 800 to 1300 mm y⁻¹ (Vacek, 2003). The study territory belongs to humid continental climate characterised by hot and humid summers and cold to severely cold winters (Dfb) according to Köppen climate classification (Köppen, 1936), respectively by detailed region Quitt distribution (Quitt, 1971) to a cold climatic region and CH 7 subregion.

Historically, study forests were converted into pastures with only few scattered trees providing shade for cattle during the 16th century (Roček, 1970). During the WW II pasture intensity decreased and in many localities natural succession started (Vacek et al., 2009). Important prerequisite for the recolonization by woody species was the presence of scattered seed trees and very low game stocks. Later, all study forests were left for spontaneous development without any additional silvicultural treatments. Only

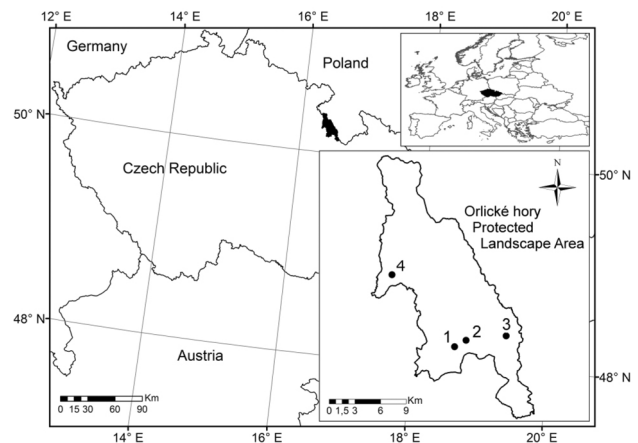


Fig. 1. Location of the permanent research plots with sycamore maple dominated forest stands in the Orlické hory Mts.

from 1992 to 1999 sanitary felling was performed. The permanent research plots (PRP) have had the same silvicultural treatment and origin according to available historical information and older forest management plans. The basic characteristics of PRP are shown in Tab. 1. A more detailed description of the area of interest can be found in Vacek et al. (2003, 2015, 2017).

In terms of phytocoenology these are mostly sub-alpine sycamore-beech forests, the association *Aceri-Fagetum* J. et M. Bartsch 1940 and partly on PRP 1 and 2 the association *Daphno mezerei-Aceretum pseudoplatani* Jeník et al. 1980. On PRP there were found 29–38 species of vascular plants and 11–16 species of bryophytes. Dominant species in tree layer are *Acer pseudoplatanus* and *Fagus sylvatica*; on all herbs there are relatively prominent levels of *Athyrium distentifolium*, *Athyrium filix-femina*, *Dryopteris filix-mas*, *Oxalis acetosella*, *Stellaria nemorum* and *Dryopteris carthusiana* or *Polytrichum formosum* and *Plagiothecium curvifolium* in moss layer.

Table 1. Summary of basic site characteristics of the permanent research plots

ID	Plot name	GPS coordinates	Altitude (m)	Grow. season (days)	Temp. in GS ¹ (°C)	Rainfall in GS ¹ (mm)	Geology	Soil type	Exposure	Slope (°)	Herbal cover (%)	Forest type ²	Species ³
1	Rokytnice 1	50°11'02"N 16°27'06"E	605	130	12.9	547	Schist	modal Cambisol	NW	15	70	5F (5A)	AP, FS, FE, AN, AI, SA, PA
2	Rokytnice 2	50°11'05"N 16°27'09"E	595	130	12.9	547	Schist	gleyed Cambisol	NW	16	75	5F (5A)	AP, FS, FE, AN, AI, BA, PA
3	Uhřínov	50°12'22"N 16°32'23"E	725	115	10.7	620	Gneiss	lithic Cambisol	NE	12	65	6A	AP, FS, SA, PA, AA
4	Vysoký kořen	50°16'05"N 16°20'37"E	645	120	11.3	596	Schist	modal Cambisol	NW	18	65	5A	AP, FS, FE, BA, SA, PA, UG, PR

Notes: GS¹ – growing season; ²Forest site type: 5F – *Abieto-Fagetum lapidosum mesotrophicum*, 5A – *Acereto-Fagetum lapidosum*, 6A – *Aceri-Piceeto-Fagetum lapidosum*; ³Species: AP – *Acer pseudoplatanus*, FS – *Fagus sylvatica*, FE – *Fraxinus excelsior*, AG – *Alnus glutinosa*, AI – *Alnus incana*, SA – *Sorbus aucuparia*, PA – *Picea abies*, BA – *Betula alba*, AA – *Abies alba*, UG – *Ulmus glabra*, PR – *Prunus avium*.

Data collection

The FieldMap technology (IFER-Monitoring and Mapping Solutions Ltd.) was used for the establishment of four PRP 50×50 m in size (0.25 ha) in 2015. Using this system, the position and crown projections at a minimum of four directions perpendicular to each other were measured in the tree layer with diameter at breast height (dbh) > 4 cm. In the tree layer dbh was measured with a metal calliper (accuracy 1 mm) and total height and height to crown base with a Vertex laser hypsometer (accuracy 0.1 m). In 30 dominant and co-dominant sycamore trees on each PRP the cores were sampled at dbh (130 cm) perpendicular to the trunk axis in a downslope and upslope direction.

For naturally regenerated saplings (height ≥ 50 cm, dbh < 4 cm) the position, height and crown width were measured on all plot in the same year. One-year-old and older seedlings were measured in 10×50 m transects. Height, height to crown base, position, crown width (accuracy 1 cm) and browse damage in seedlings 1 year and older were measured. Seedlings less than 1 year in age were tallied for quantity and mortality. The number of sycamore seeds that fell onto the soil surface was evaluated in September to November in 2014–2016, number of seedlings and their mortality in the growing season in 2015 and 2016 was evaluated at the centre of the above-mentioned transect (on an area of 1×50 m).

Data analysis

Growth parameters, production, biodiversity, horizontal and vertical structure were evaluated for all individuals in the tree layer on the PRP. Tree volume was estimated by using volume equations published by Petráš & Pajtik (1991). Height curves were constructed by using the Näslund height–diameter function (Näslund, 1936) with quality rating by coefficient of determination (R^2).

To evaluate various aspects of biodiversity, the following diversity indices were computed: Arten-profile

index (Pretzsch, 2006), index of diameter differentiation (Füldner, 1995), species heterogeneity index (Shannon, 1948), species evenness index (Pielou, 1975), species richness index (Margalef, 1958) and total stand diversity index (Jaehne & Dohrenbusch, 1997). Tab. 2 shows the criteria of structure indices.

To evaluate the spatial pattern of the stands Clark-Evans index (Clark & Evans, 1954) and Ripley L -function (Ripley, 1981) were calculated. The PointPro 2 programme (Zahradnik & Pus) was used to compute the characteristics that describe the horizontal distribution of individuals across a plot. The test of significance of deviations from the values expected for the random point pattern was performed by means of Monte Carlo simulations. The mean values were estimated as arithmetic means computed for 999 randomly generated point structures. Along with the measurements of horizontal structure on the PRP, stand density, crown projections area and crown closure were also calculated. Maps were made by using the ArcGIS programme (Esri).

Tree-ring increment series were individually cross-dated (removal of errors connected with the occurrence of missing tree rings) by using statistical tests in the PAST application (Hammer & Harper) and they were visually inspected according to Yamaguchi (1991). If a tree ring was found to be missing, a tree ring of 0.01 mm in width was inserted in its place. Particular curves from PRP were detrended and an average tree ring series was created from them in the ARSTAN programme (Laboratory of Tree-Ring Research). The 60-year spline was applied (Grissino-Mayer et al., 1992). Negative pointer years were analyzed according to Schweingruber et al. (1990). For each tree the pointer year was tested as an extremely thin tree ring that does not reach 40% of the average of increments from the preceding 4 years. The occurrence of a negative year was proved if such a strong reduction in increment occurred in at least 20% of the trees on the plot. Average tree ring series from PRP in the Orlické hory Mts. were correlated with annual and monthly climate data (temperature, precipitation). The DendroClim software

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

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

(DendroLab) was used to model diameter increment as dependent on climate-related variables. Temperature and precipitation data were collected at the meteorological station at Deštné v Orlických horách (656 m a.s.l.; GPS 50°18'24"N, 16°21'07"E). In order to analyse the effect of overall meteorological conditions on growth, Sielianinov hydrothermal coefficient (K) was used (Radzka & Rymuza, 2015).

Statistical analyses were processed in the Statistica 12 software (StatSoft, Tulsa). Data were log-transformed to acquire normal distribution (tested by Shapiro-Wilk test). Differences in mean height of natural regeneration recruits and height of recruits not damaged and damaged by browsing were separately tested by one-way analysis of variance (ANOVA). To determine the combined effect of average annual temperature and annual sum of precipitation on diameter increment of sycamore, correlation quadratic model was used. Variances are shown by standard deviation (\pm SD).

Results

Growth parameters of tree layer

The number of living trees ranged from 376 to 696 trees ha^{-1} (with sycamore at 244–496 trees ha^{-1}) and a stand density index of 0.56–0.86 (Tab. 3). The stand volume ranged between 378–545 $\text{m}^3 \text{ha}^{-1}$, while sycamore accounted for 175–392 $\text{m}^3 \text{ha}^{-1}$, and admixed tree species (*Fagus sylvatica*, *Fraxinus excelsior*, *Alnus glutinosa*, *Alnus incana*, *Sorbus aucuparia*, *Picea abies*, *Betula pendula*, *Abies alba*, *Ulmus glabra*, *Prunus avium*) accounting for the rest. The highest total stand volume (545 $\text{m}^3 \text{ha}^{-1}$) was found on PRP 1, and the lowest (378 $\text{m}^3 \text{ha}^{-1}$) on PRP 2. The highest stand volume for sycamore (82.0%; 392 $\text{m}^3 \text{ha}^{-1}$) was on PRP 4 and the lowest (32.1%; 175 $\text{m}^3 \text{ha}^{-1}$) on PRP 1. Periodic annual increment of stand currently fluctuated in the

range of 8.7–9.8 $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$ (in sycamore 4.0–7.4 $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$) and mean annual increment was 6.1–7.4 $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$ (in sycamore 2.8–5.0 $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$). The total stand basal area ranged between 33.0 and 48.3 $\text{m}^2 \text{ha}^{-1}$ and 15.6–32.4 $\text{m}^2 \text{ha}^{-1}$ for sycamore. Crown closure was in the range of 91.2–96.8 % and crown projection areas ranged from 2.43 to 3.43 ha.

Diameter and height structure of tree layer

The stands were mostly composed of two or three storeys with varied differentiation of the vertical canopy. Average dbh on all PRP ranged from 29.3 to 35.2 cm for all trees and from 26.7 to 33.1 cm for sycamore (Fig. 2). On PRP the largest range of diameter classes was found for the range of 28–44 cm (the representation of the diameter class of small wood 4–8 cm was the highest on PRP 4), in sycamore it was 24–44 cm. Fig. 3 illustrates the relationship between dbh and tree height on the PRP ($R^2 = 0.85\text{--}0.88$).

The tallest sycamore trees on the PRP reached 28–32 m. The maximum height for admixed Norway spruce (*Picea abies* [L.] Karst.) was 32–41 m and for European beech 30–33 m. The height of the crown base of sycamore varied considerably. In the tree understorey it was mostly in the range of 2–8 m and in the overstorey 9–17 m. The slenderness ratio decreases with dbh in all studied tree species while a more pronounced decrease, with the least variability, was observed in the thinnest trees of sycamore when the variance of values was minimum.

Radial growth

In the sycamore study sites of the Orlické hory Mts. region, the average tree-ring width in the 50-year period was lowest on PRP 4 2.6 mm (\pm 0.4 SD), on PRP 3 3.2 mm (\pm 0.4 SD), on PRP 2 3.2 mm (\pm

Table 3. Basic stand characteristics of the permanent research plots 1–4

PRP	t (y)	dbh (cm)	h (m)	f	v (m^3)	N (trees ha^{-1})	G ($\text{m}^2 \text{ha}^{-1}$)	V ($\text{m}^3 \text{ha}^{-1}$)	HDR	PAI ($\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$)	MAI ($\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$)	CC (%)	CPA (ha)	SDI
Sycamore maple														
1	63	26.7	20.36	0.547	0.624	280	15.6	175	76.3	4.0	2.78	76.8	1.46	0.30
2	64	33.1	23.03	0.525	1.041	244	21.0	254	69.6	6.3	3.97	84.0	1.83	0.36
3	75	28.7	23.32	0.501	0.756	496	32.1	375	81.3	6.5	5.00	88.4	2.15	0.59
4	79	31.5	20.42	0.593	0.943	416	32.4	392	64.8	7.4	4.96	91.3	2.44	0.57
All tree layer														
1	83	35.2	22.78	0.549	1.216	448	43.5	545	64.7	9.0	6.57	91.2	2.43	0.67
2	61	33.5	22.06	0.518	1.007	376	33.0	378	65.9	9.1	6.20	94.3	2.87	0.56
3	77	29.7	22.47	0.527	0.820	696	48.3	571	75.7	9.8	7.40	96.8	3.43	0.86
4	79	29.3	17.86	0.662	0.797	600	40.3	478	61.0	8.7	6.05	96.4	3.33	0.72

Notes: t – average stand age, dbh – mean quadratic breast height diameter, h – mean height, f – form factor, v – mean tree volume, N – number of trees, G – basal area, V – stand volume, HDR – slenderness ratio, PAI – periodic annual increment, MAI – mean annual increment, CC – canopy closure, CPA – crown projection area, SDI – stand density index.

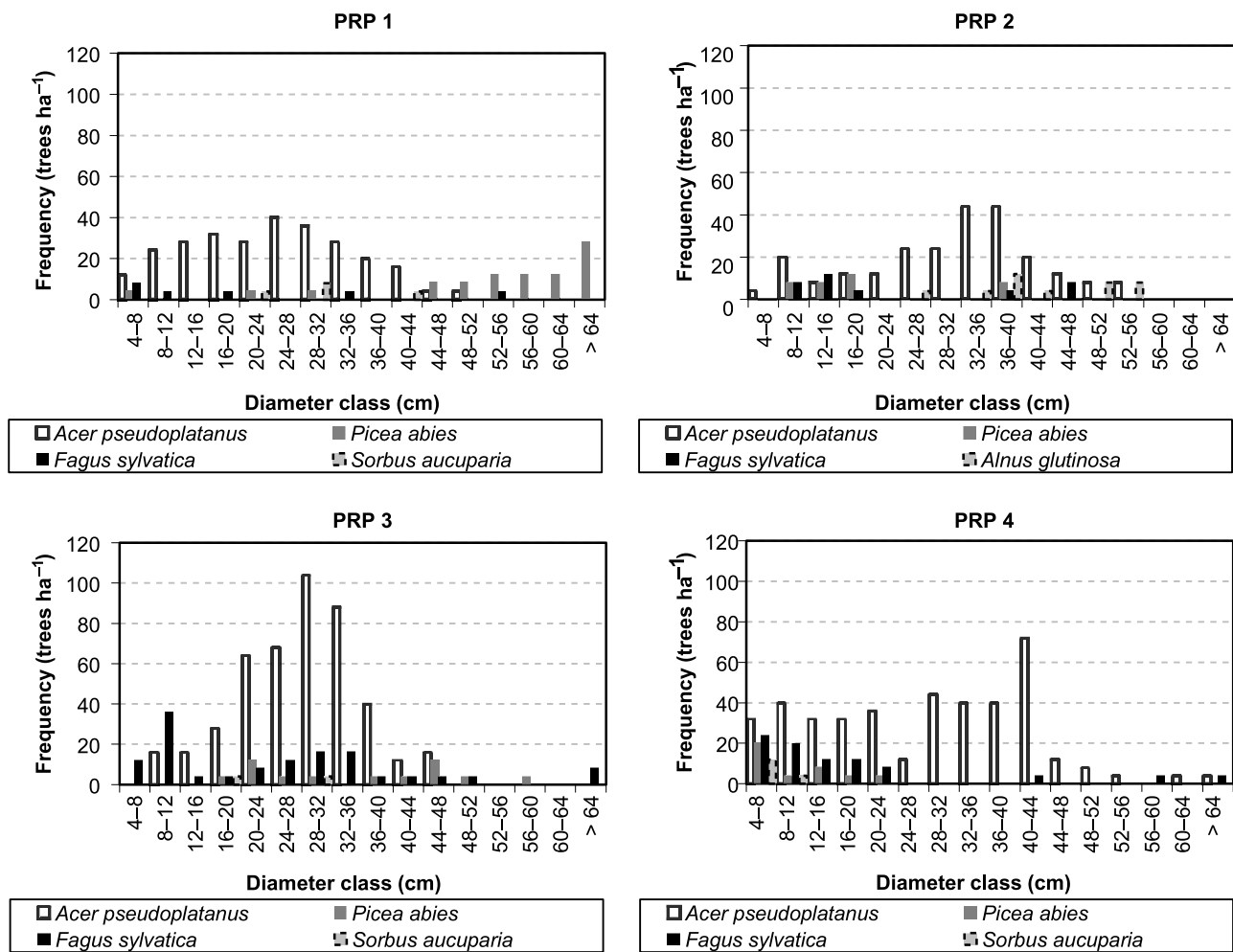


Fig. 2. Histogram of diameter classes indicated by tree species on the permanent research plots

0.8 SD) and the highest increment on PRP 1 3.3 mm (± 0.6 SD).

We observed three distinct patterns of tree growth. From 1960 to 1963, an increase of radial increment was observed, subsequently a relatively

balanced growth followed during the years 1963 to 1975 and declining growth was found from 1976 to 2014 (Fig. 4). The low radial increment that occurred during 1952, 1996 and 2007 confirmed them as negative pointer years. The period from January through April 1996 (in January only 9 mm; long-term mean 96 mm), the driest period from January to April in 1961–2014, and extremely frosty winter (-4.2°C , long-term mean -2.3°C) caused decrease in radial increment by 42 %. In 2007, the summer temperatures were extremely hot (the hottest June 16.3°C in 1961–2014, long-term mean 13.4°C), a typical characteristic of these negative pointer years.

A comparison of average tree-ring curves of sycamore indicated their high mutual correspondence when the t-test ≥ 3.4 showed the reliability of synchronization. Therefore, it was possible to construct the regional standardized ring-width chronology for sycamore in the Orlické hory Mts. (Fig. 5).

Comparisons of diameter increment with climatic factors found significant relationships. In the Orlické hory Mts. region diameter increment in 1961–2014 was significantly positively correlated ($\alpha = 0.05$) with temperature in September of the previous year

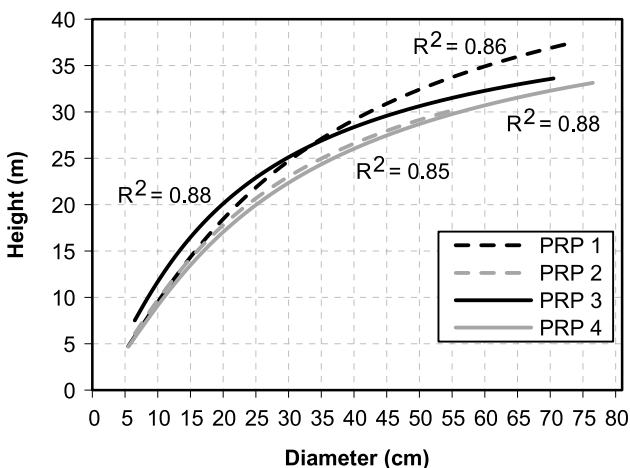


Fig. 3. The relationship between diameter and tree height with coefficient of determination (R^2) on the permanent research plots 1–4

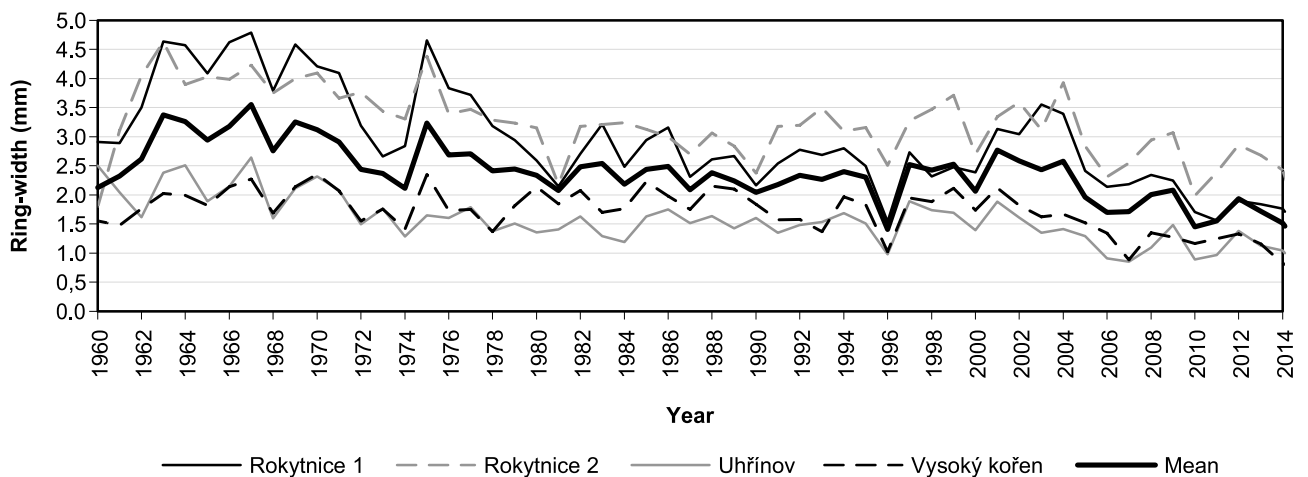


Fig. 4. Annual ring-width chronologies for the permanent research plots 1–4 and the entire study area of Orlické hory Mts.

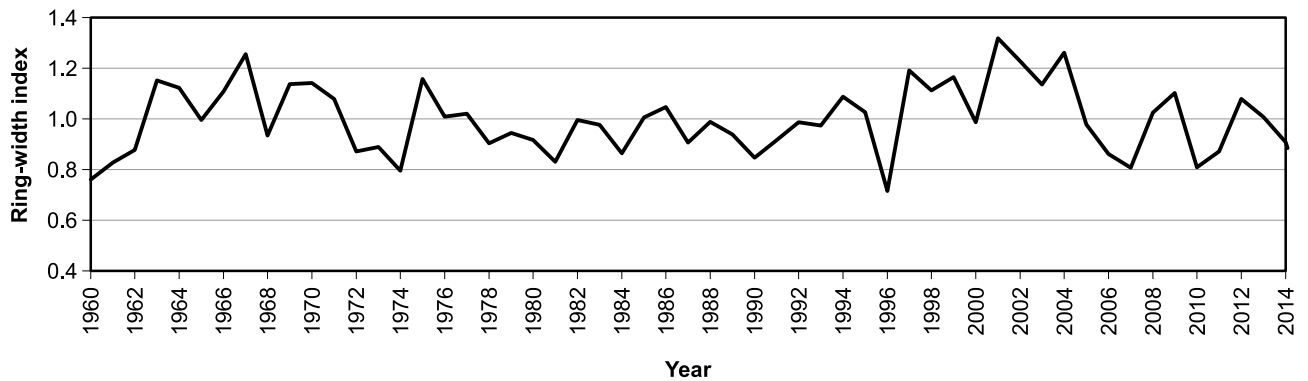


Fig. 5. Average annual ring increment in the entire study area of the Orlické hory Mts. after removing the age trend

($r = -0.23$) and in April of current year ($r = -0.24$). Annual increment was significantly negatively correlated with mean temperature in months during the dormant season (December, January and March $r = -0.23$ – 0.33 ; Fig. 6). Significant positive correlations were also found between the amount of precipitation in July and October of the previous year ($r = 0.27$ to 0.32) and March of the current year ($r = 0.23$; Fig. 6). Moreover, soil moisture had effect on radial growth of sycamore on PRP. Mean temperature

had the highest effect on radial growth on the water-logged PRP 2 (4 significant months), while there was almost no effect of precipitation (only positive effect in October of the previous year). Conversely on PRP 3 with the lowest soil moisture, there was observed the highest positive effect of precipitation on increment (4 significant months; moreover, June of the previous year).

The main positive factor influencing the diameter increment of sycamore in study area was identified

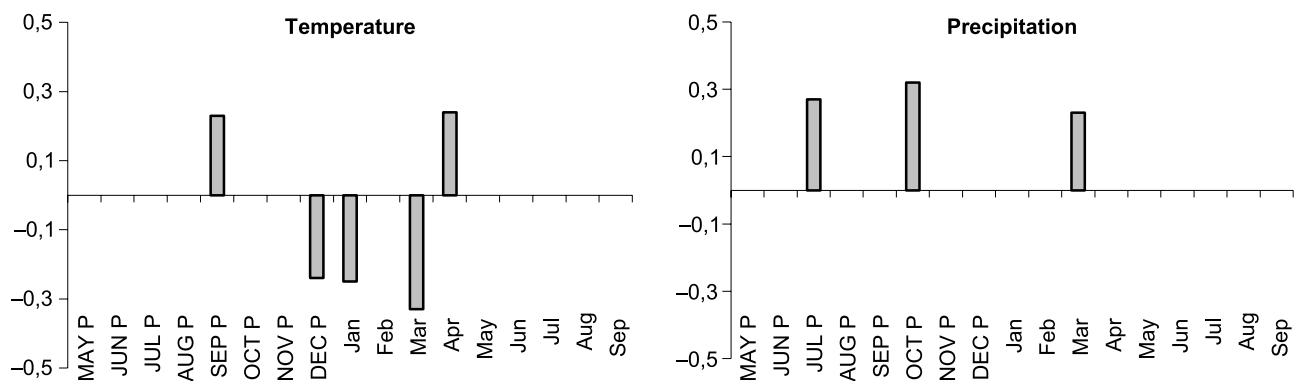


Fig. 6. The values of correlation coefficients of the regional residual index tree-ring chronology with the monthly temperature (left) and precipitation (right) from May of the previous year (P) to September of the current year for the period 1961–2014; correlation coefficients with significant values ($\alpha = 0.05$) are shown

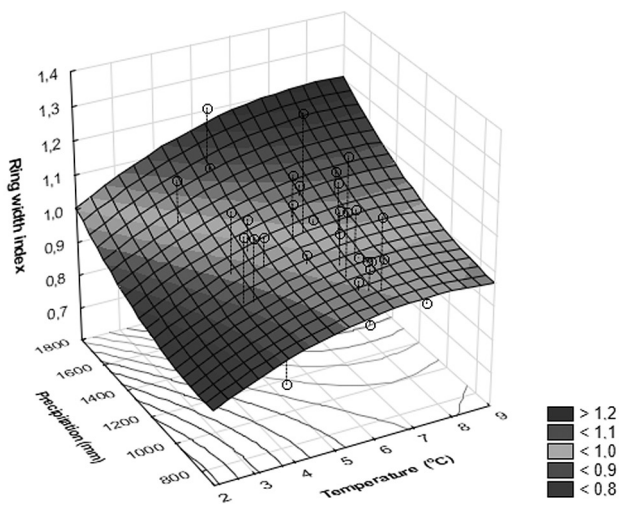


Fig. 7. Response of ring width index of sycamore maple to annual sum of precipitation and annual mean temperature (correlation quadratic model, years 1961–2014)

the precipitation (Fig. 7). Annual sum of precipitation had higher effect ($r=0.21$, $p=0.15$) on radial growth compared to annual average temperature ($r=0.09$, $p=0.49$). Diameter increment increased with increasing precipitation, while optimal growth was observed in annual temperature range from 7.5 to 8.5°C. According to hydrothermal index K , climate (combination of temperature and precipitation) had the significant positive impact on radial growth in July ($r=0.37$, $p < 0.01$) and October of the previous year ($r=0.33$, $p < 0.05$).

Tree layer biodiversity

Vertical structure according to A index was moderately to strongly-varied ($A = 0.45$ – 0.63 ; Tab. 4). Diameter differentiation was medium ($TM_d = 0.36$ – 0.50). Species biodiversity H' was found to be at a medium level ($H' = 0.33$ – 0.46). Species evenness ranged from medium to high ($E = 0.36$ – 0.65) diversity. Total stand diversity B suggested an uneven structure on PRP 2 and 3 ($B = 7.74$ – 0.78) and a more diverse structure on PRP 1 and 4 ($B = 8.48$ – 8.80).

Horizontal structure of all tree species was mostly random (Tab. 4, Fig. 8). The exception was PRP 3,

Table 4. Indices of the tree layer biodiversity on the permanent research plots 1–4

PRP	A (Pri)	TM_d (Fi)	H' (Si)	E (Pii)	D (Mai)	R (C&Ei)	B (J&Di)
1	0.454	0.494	0.463	0.595	0.819	1.081	8.795
2	0.631	0.391	0.452	0.647	0.675	1.073	7.737
3	0.601	0.358	0.403	0.577	0.611	0.883	7.822
4	0.465	0.427	0.329	0.364	1.094	1.028	8.480

Notes: A – Arten-profile index, TM_d – diameter differentiation index, H' – species heterogeneity index (entropy), E – species evenness index, D – species richness index, R – aggregation index, B – total diversity index.

where according to the R index, the distribution of tree layer individuals was significantly aggregated ($\alpha = 0.05$). The sycamores of the tree layer were randomly distributed on PRP 1 and 4. On PRP 2 and 3 the spatial pattern of trees was significantly aggregated according R index. The mostly random distribution of tree layer individuals according to their distance followed from Ripley's L -function, only on PRP 3 the spatial pattern was aggregated at distance shorter than 3 m. On the other hand, the random spatial pattern of sycamore in the tree layer occurred on PRP 4, on PRP 1 only at distance shorter than 5 m and on PRP 2 shorter than 6.5 m. In the other cases it was an aggregated distribution, being the most pronounced on PRP 3 (Fig. 9).

Natural regeneration

The number of maple seeds that fell on the PRP was highly variable during 2015, considered a seed-medium to rich year. Seed fall within the transect on PRP 1 was 16–144 seeds (36 seeds on average), on PRP 2 it was 4–76 seeds m^{-2} (30 seeds), on PRP 3 0–54 seeds m^{-2} (18 seeds) and on PRP 4 18–126 seeds m^{-2} (52 seeds). Across all four PRP, the average was 34 seeds m^{-2} . The weaker seed year 2016 was also variable. Number of seeds was on transect on PRP 1 in the interval 6–68 seeds m^{-2} (24 seeds), on PRP 2 it was 2–52 seeds (16 seeds), on the PRP 3 0–36 seeds (14 seeds) and on PRP 4 it was 4–90 seeds (26 seeds). The whole average of all four PRP was 20 seeds m^{-2} .

In 2016 there was found on average 17 seedlings m^{-2} (PRP 1 on average 20 seedlings, PRP 2 15 seedlings, PRP 3 9 seedlings and PRP 4 24 seedlings). The year 2014 was seed-poor productive compared to year 2015, averaging only 9 seedlings m^{-2} across all PRP. The minimum number was observed on PRP 3 0–12 seedlings m^{-2} (on average 3 seedlings), while maximum density was reached on PRP 4 2–46 seedlings m^{-2} (14 seedlings). As of 30th November 2015, the mortality of seedlings was very high due to herbivory by brown hare (*Lepus europaeus* Pallas) and also by drought, when mortality ranged from 84 to 93% (on average 89%), which corresponds to 0.2–1.4 seedlings m^{-2} . The total number of natural regeneration ranged in 2015 from 1,532 (PRP 3) to 4,244 (PRP 4) recruits ha^{-1} (Tab. 5). On average, European beech accounts for 47% of the total, sycamore 23%, European rowan (*Sorbus aucuparia* L.) 9%, and black alder (*Alnus glutinosa* [L.] Gaertn) 8%. The percentages of the remaining tree species were below 4%.

Species richness of natural regeneration was very high on PRP 1 and 4, and high on PRP 2 and 3 (Tab. 5). Species heterogeneity of natural regeneration was very high. Species evenness (index E) was very high on PRP 1–3 and high on PRP 4 (Tab. 5). The spatial

pattern of recruits on all plots was significantly aggregated ($R = 0.52-0.77$) with the highest tendency to aggregation on PRP 1 (Fig. 8).

Height and diameter differentiation of the natural regeneration of the PRP was limited by browsing

pressure mainly from roe deer. The height structure of natural regeneration was left-skewed while the highest number of recruits belongs to height classes below 100 cm (78.2–97.9%; Fig. 10). The percentage of recruits higher than 50 cm was low (15.2–17.6%

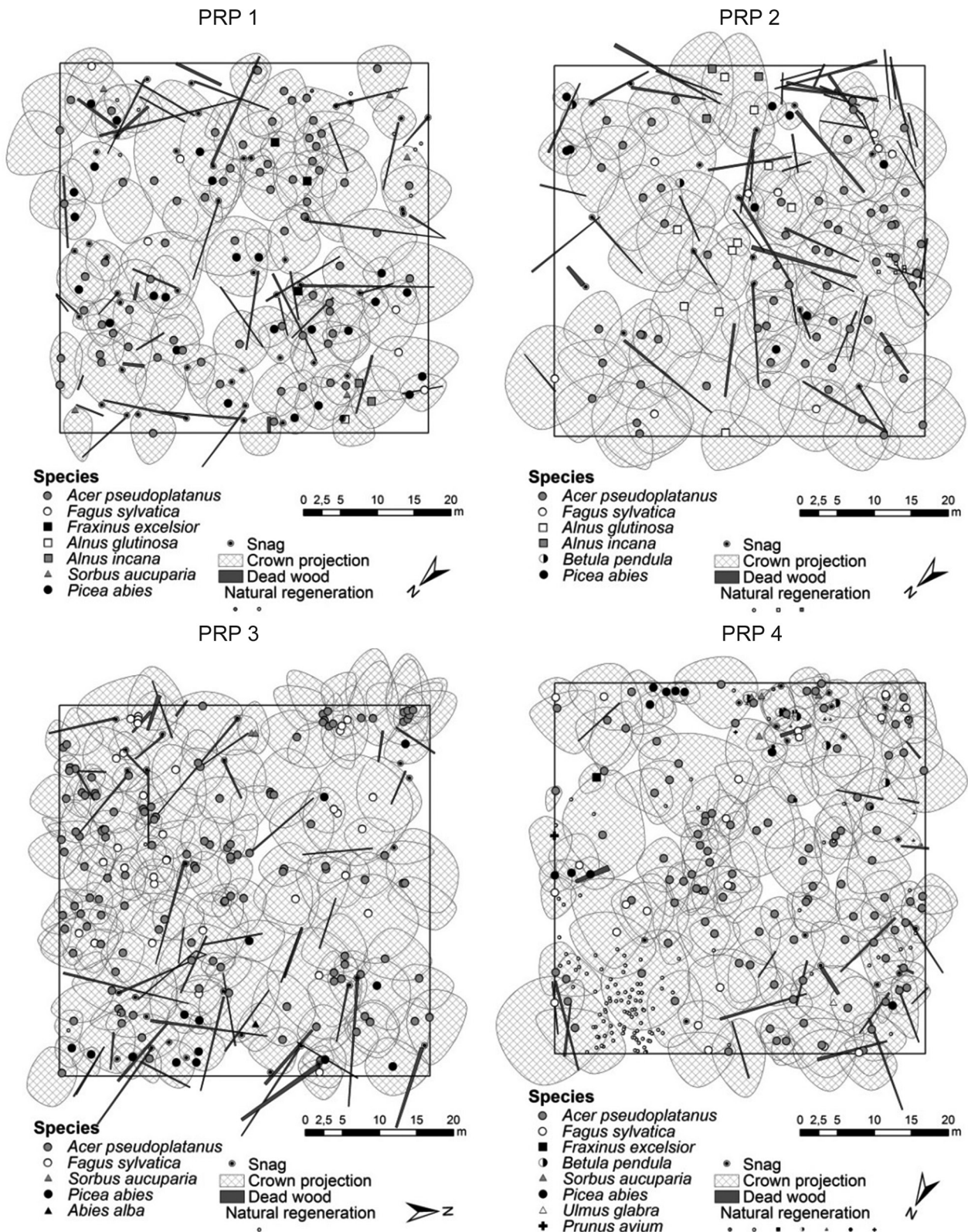


Fig. 8. Horizontal structure of the tree layer and natural regeneration on the permanent research plots 1–4

Table 5. Indices of the species diversity and per-hectare numbers (share) of natural regeneration specified according to main tree species on the permanent research plots

PRP	D	H'	E	<i>Acer pseudoplatanus</i>	<i>Fagus sylvatica</i>	<i>Alnus glutinosa</i>	<i>Sorbus aucuparia</i>	Other tree species	Total density
	(Mai)	(Shi)	(Pii)	%	%	%	%	%	recruits ha ⁻¹
1	0.778	1.482	0.761	27.4	42.9	13.1	10.3	6.3	2 240
2	0.665	1.565	0.873	26.0	38.5	21.7	2.3	11.5	1 852
3	0.545	1.170	0.727	31.6	55.7	0.4	9.6	2.7	1 532
4	0.958	1.310	0.596	12.4	60.5	0.5	15.8	10.8	4 244

Notes: D – species richness index, H' – species heterogeneity index (entropy), E – species evenness index.

on PRP 1–3 and 39.8% on PRP 4). No more than 0.5% of the sycamore seedlings with primary leaves survived in 2015 due to browsing by brown hares. Natural regeneration had the largest height differentiation and age-range structure on PRP 4 (Fig. 10). The average height of recruits was distinctly taller ($F_{(3, 489)} = 21.3$, $P < 0.001$) on PRP 4 ($67.0 \text{ cm} \pm 4.3 \text{ SD}$) than on PRP 3 ($28.8 \pm 3.0 \text{ SD}$) and PRP 1 ($27.9 \pm 2.5 \text{ SD}$); the smallest height was on PRP 2 ($27.7 \pm 2.1 \text{ SD}$).

A comparison of average heights of natural regeneration without damage and individuals reduced by browsing showed that ungulates had a significant influence on the growth of natural regeneration ($F_{(1, 491)} = 134.7$, $P < 0.001$). The highest losses due to browsing of terminal shoots occurred in sycamore (96%), European rowan (92%), silver fir (*Abies alba* Mill.; 90%), wild cherry (85%), Scots elm (*Ulmus glabra* Huds.; 82%), while the relatively lowest losses are incurred in Norway spruce and alders (*Alnus* sp.

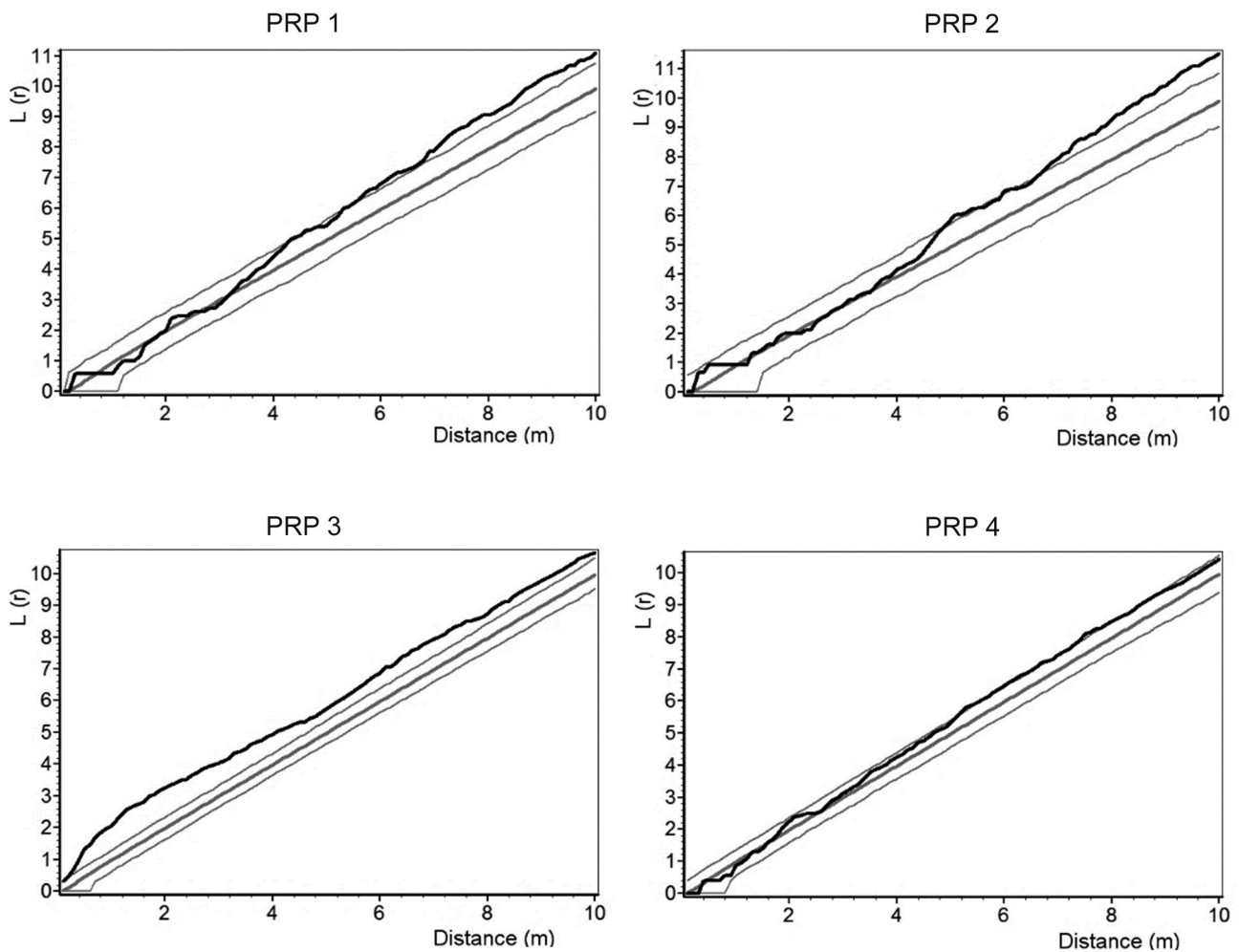


Fig. 9. Horizontal structure of sycamore maple on the permanent research plots expressed by the L -function; the black line represents the L -function for real distances of trees; the bold gray line represents the mean course for random spatial distribution of trees and the two thinner central curves represent 95% interval of reliability; when the black line of tree distribution on the PRP is below (above) this interval, it indicates a tendency of trees toward regular distribution (aggregation)

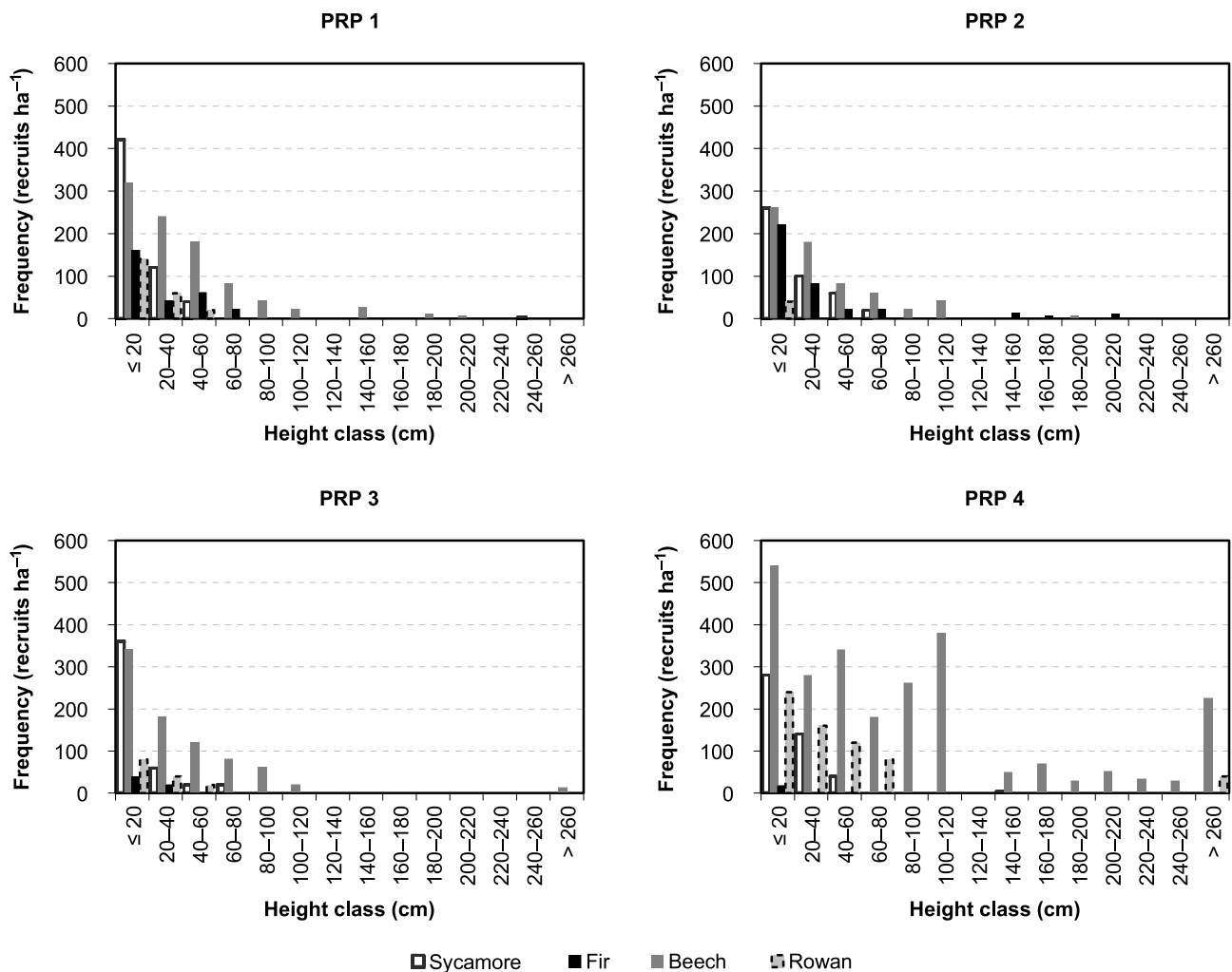


Fig. 10. Histogram of the height classes of natural regeneration of main tree species on the permanent research plots 1–4

< 50 %). Natural regeneration of European beech was substantially eliminated due to the beechnut caching by wildlife (in the range of 64–91% on PRP in 2015). In terms of phytocoenology, the lowest damages were observed on PRP 2 with the largest herbal and moss cover.

Discussion

In our study the stand volume of mixed-species forests with dominant sycamore varied from 378 to 571 m³ ha⁻¹ while the sycamore share amounted to 175–392 m³ ha⁻¹. In southern Sweden, comparable results were obtained in stands with dominant sycamore maple at 60 years of age where the sycamore volume was 198 to 361 m³ ha⁻¹ (Sjöstedt, 2012). However, in that study, the basal area of sycamore individuals was slightly larger and its range was also larger (22–45 m² ha⁻¹) than on our PRP (16–32 m² ha⁻¹). The average height of sycamore was 2–5 m less in the case of Swedish sites. On PRP in the Orlické hory Mts. the average height of sycamore individuals

was from 20.4 to 23.3 m. These values correspond to site class 3 and 2 according to Danish yield tables (Kjølby, 1958).

The number of sycamore trees on plots in southern Sweden was significantly higher (340–800 trees ha⁻¹; Sjöstedt, 2012) than on our PRP in the Orlické hory Mts. (244–496 trees ha⁻¹), while stand volume was comparable on both localities. However, in most studies the stand volume with sycamore was derived from growth tables (cf. Hein et al., 2009), which resulted in its wide range according to site and stand conditions [e.g. in Sweden 32–407 m³ ha⁻¹ according to Sjöstedt (2012) and in Denmark 274–766 m³ ha⁻¹ according to Kjølby (1958)]. Schrober (1995) reported that the stand volume production of sycamore in the best yield class in Germany was around 1050 m³ ha⁻¹ and was much higher than in beech, (546 m³ ha⁻¹ at 80 years of age) or ash (555 m³ ha⁻¹). Lockow (2004) from Germany stated that sycamore of 30 m in height exceeded the ash volume by 180 m³ ha⁻¹ while beech had a larger volume than sycamore only at a height above 30 m. If the stand volumes of sycamore and beech stands from similar site conditions of the Orlické hory Mts. were

compared, the obtained values were similar (175–392 m³ ha⁻¹ in sycamore and 194–484 m³ ha⁻¹ in beech; Králíček et al., 2017). Dynamics of diameter increment is in close correlation with volume increment. In sycamore, similarly like in the other tree species, diameter increment and natural formation of crowns apparently depend on site and stand conditions that are influenced by silvicultural practices (Hemery et al., 2005; Hein & Spiecker, 2009; Hein et al., 2009). From this aspect Thill (1975) and Hein (2004) compared crown width development with diameter increment development in sycamore maple. Kerr & Evans (1993) considered the sycamore radial increment of 4–5 mm with the rotation period of 60–75 years as optimum for most of Europe. These values correspond with radial increment on PRP in the Orlické hory Mts. that was 3.0–6.4 mm (4.8 mm on average) at around 60 years of age.

In terms of increment, interaction between climate and radial growth of sycamore showed close relation in submontane areas. Sycamore was very sensitive on extreme weather conditions, such as very cold winters without snow or hot summers. Correlation between radial increment and temperature was stronger than precipitation, but precipitation had higher positive effect on radial growth (prevailing negative effect of winter precipitation). The climate in July and October of previous year and March of the current year had the highest effect on diameter increment. Conversely in lowlands of the Czech Republic, diameter increment of sycamore was influenced by precipitation more significantly. In the locality Klapý on former agricultural land (190 m a.s.l.) hot temperatures was limiting factor for growth, especially in April and June (Vacek et al., unpublished).

Rusanen & Myking (2003) stated that individual trees can produce up to 170,000 seeds. On the PRP study sites, trees with the largest crowns could reach these numbers in 2015, nevertheless the number of seeds per m² was 18–52 (34 on average) in this rich-seed year compared to 2014 and 2016. Considering the seed dispersal, Neyrinck et al. (2000) concluded that there were significant differences between the soil environment of sycamore seedlings and that of European beech seedlings. Better physical and chemical properties in sycamore regeneration compared to beech were also demonstrated by Podrázský et al. (2010), because sycamore has higher-quality leaf litter fall with faster decomposition.

Although it has been reported in many studies that sycamore seedlings and saplings are very vulnerable to the competition of ground vegetation (Diaci, 2002; Modrý et al., 2004; Vendenbergh et al., 2007), on the studied PRP sycamore regeneration has survived and is prospering only in localities with ground vegetation and dead wood because on the other (open) plots it is almost completely eliminated by game.

Sycamore is an attractive tree species to hoofed game, mainly to red deer, roe deer, fallow deer and sika deer that are browsing on leaves, buds and young shoots (Gill, 1992). The browsing of juvenile sycamore individuals decreases their height growth (Kupferschmid & Bugmann, 2008) and often results in the increased occurrence of stem forking (Harmer, 2001; Modrý et al., 2004). On study PRP sycamore regeneration was heavily damaged (89%) by roe deer, and partly by red deer, such as in others locality in the Orlické hory Mts. (Vacek et al., 2014; Slanař et al., 2017). Great losses were caused also by brown hare there (Vacek, 2017). Schulze et al. (2014) reported that sycamore regeneration is damaged by red and roe deer to a greater extent than European beech regeneration. Similar findings were observed from stands under conversion or from stands with dominant Norway spruce where the number of juvenile sycamore individuals was low (Diaci, 2002; Nagel et al., 2015). In these cases, Mosandl & El Kateb (1988) and Ammer (1996) recommended the control and regulation of game stocks in order to provide for sufficient density of regeneration and its prosperity. Modrý et al. (2004) stated that the high pressure of game on sycamore regeneration leads to beech dominance, which is evident also on the study area.

On the studied plots the spatial pattern of individuals of the sycamore tree layer was mostly aggregated, there was occasionally a random pattern to a distance of 15 m. Janík et al. (2016) reported the prevailing aggregated distribution of sycamore groups in the tree layer in the Žofínský virgin forest while the regular pattern occurred there only occasionally and at distances greater than 12 m. A distinctly positive spatial correlation at distances of 9–11 m and 18–19 m was found between individuals of the tree layer and sycamore regeneration whereas the negative correlation was not determined on any of the plots. Next these authors also stated that sycamore natural regeneration did not depend on larger stand gaps. But other studies (Marinšek & Diaci, 2004; Nagel et al., 2010) found to the contrary.

Generally, the studied stands showed high production potential and considerable ecological value. The latter mainly with respect to structural diversity and tree species composition, where mainly Sycamore leaf litter fall contributes to the formation of high-quality humus with the good nutrient cycle (Heitz & Rehfuess, 1999), which contributes to ecological stability and biodiversity of these ecosystems (Bell, 2009).

Conclusion

In Sudetes range system, as in most of Europe, sycamore maple is a very important tree species. Yet, the species has not been studied extensively until

now because of its lower representation in forest stands. Our study stands originated naturally by succession, especially on abandoned agricultural lands. Those mixed stands with an abundant proportion of sycamore are characterized by their considerable production and economic value, although they received minimum silvicultural treatments in the past. However, browsing by game is a limiting factor of sycamore regeneration. Growth analyses show higher relationship with temperature, especially high sensitive to extremely cold dry winters and high summer temperatures, while precipitation is more crucial factor for growth in these submontane areas. Our results demonstrate that sycamore is a tree species with high wood production capable to spontaneously create forest stands with high ecological stability and considerable biodiversity.

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