



Intra- and interannual variability in diameter increment of *Fagus sylvatica* L. and *Picea abies* L. Karst. in relation to weather variables

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Abstract

We examined the effect of weather variables on radial growth of Norway spruce and European beech at the intra- and interannual level. We used database of regular growth measurements at 9 forest sites distributed along an altitudinal and spatial gradient within the Slovakia and Czech Republic. In the period of 2010–2017, we analysed data from 213 dendrometers with manual reading in monthly or biweekly interval. The mean daily and annual diameter increments were analysed in relation to air temperatures and precipitation observed during the respective growing seasons. The general intra-annual diameter increment was modelled using a log-normal function. Results of modelling suggest that precipitation was a better predicting factor of the increment in spruce, while air temperature enhanced predictions of increments in beech. The highest, eight-year-cumulative increment of spruce (31.1 mm) and beech (22.8 mm) was found in the mixed mountainous forest at Poľana site, where both species occur in their growth optimum. The inter-specific comparison of radial growth at this site revealed earlier culmination of increment in spruce compared to beech. The growth-limiting weather conditions for spruce occurred especially during the dry season 2015, while in beech sites the slight decrease of annual increment was observed in 2016. In the lowest altitudes of studied forest sites (beech 350 m a.s.l., spruce 440 m a.s.l.) the radial growth was reduced due to high summer temperatures. In the context of further predicted increase of air temperatures, these altitudinal limits for tree growth should be considered in the future forest management in Central Europe.

Key words: climate; beech; spruce; radial growth; dendrometers; Central Europe

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1. Introduction

Tree growth is one of the most significant ecological indicators of forest vitality and condition that reflect the influence of numerous mutually interacting environmental factors (Dobbertin et al. 2013). In the face of the predicted further increase of temperature, more frequent occurrence of heat waves and drought (Allen et al. 2015), it is especially important to study the impact of these changes on current and future forest production. The research focused on drought effects on growth and mortality of forest trees as well as on the possibilities of their adaptation to future climate has been ongoing for a number of years (Leuzinger et al. 2005; Bréda et al. 2006; Geßler et al. 2007; Cavin & Jump 2017). Recently, many studies have examined various aspects of the climate – forest growth interactions (Etzold et al. 2014; Kolář et al.

2017; Braun et al. 2017; Rötzer et al. 2017). According to the analysis of more than 315,000 radial increment cores obtained from 25,000 National Forest Inventory plots, climate warming was listed as a predominant driver of recent forest growth changes in Western Europe (Charru et al. 2017). In terms of used research data sources, we can recognise several bases for climate-growth investigations. Some findings are based on dendrochronological analyses determining tree-ring widths (Lebourgeois et al. 2005; Büntgen et al. 2007; Cienciala et al. 2016) or changes in basal area increment (Charru et al. 2017) in relation to environmental indicators. It was proved that advanced dendroecological techniques could clarify a complex of environmental factors affecting species-specific growth trends (Bošela et al. 2018). Other studies use databases of long-term periodical records of stem diameters or continual measurements of stem circumfer-

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ence (Dobbertin et al. 2013; Leca et al. 2015; Leštianska et al. 2015). Thanks to the increasing use of manual or digital dendrometers in forestry research, it is possible to obtain a number of records of tree growth dynamics at a finer temporal resolution of several minutes, hours or days (Herrmann et al. 2016). With these options, new methodological questions about the correct analysis and interpretation of the sub-annual growth data arise, as it is necessary to accurately distinguish the irreversible process of the actual wood production from hydrological shrinkage and swelling of stems (Merganičová et al. 2014). The water-induced processes in tree stems were well described e.g. in the study of Deslauriers et al. (2007) who pointed out how significant it is to analyse tree growth at fine-resolution scales. The proposal of McMahon & Parker (2015) how to fit general growth models to intra-annual measurements using standard optimisation functions made a methodological progress in processing seasonal data of radial growth. The authors demonstrated an extended approach to estimate the initial and final diameters in the growing season and pointed out at deviations from the fitted function that indicate breaks in growth due to weather.

In the forests of Central Europe, European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* L. Karst.) are both economically and ecologically the most relevant forest tree species. In Slovakia, European beech is the most abundant deciduous species, with the current proportion of 33.5% (Green report 2017a). On the contrary, the actual percentage of beech in the forests of the Czech Republic did not exceed the value of 8.3% (Green report 2017b). The current share of Norway spruce in the forests of Slovakia (SK) and the Czech Republic (CZ) is 23.1% and 50.5%, respectively.

Monitoring of forest health state has a long-term tradition in both countries, and it is still a part of the ICP Forests programme that commenced in 1985. Under the project titled *Further Development and Implementation of an EU-level Forest Monitoring System (FutMon)*, implemented in Europe in the period 2009–2011 and co-financed by the Life+, harmonisation and improvement of existing methods of forest state monitoring continued. Systematic continuous measurements of tree growth started in 2010 and since then growth survey in both countries has been performed according to the method described in the FutMon Field Protocol (Growth V2 270509, 2009). Permanent and continuous monitoring of stem diameter at breast height as an easy-to-measure variable is well-described in Dobbertin et al. (2013).

In this study, we assessed the radial increment of European beech and Norway spruce on the base of intensive monitoring data at selected SK and CZ forest sites within the period 2010–2017. The data set offers a possibility to study recent trends of forest growth as well as the response of two most relevant forest tree species to contrasting weather and various site conditions across the region of Central Europe.

We particularly aimed at (i) quantifying the seasonal growth of trees at selected SK and CZ forest sites between 2010 and 2017, (ii) identifying and evaluating weather factors that explain the intra-seasonal and inter-annual variability of stem increment at a forest stand level, and (iii) analysing the differences in growth responses of European beech and Norway spruce to contrasting and changing environmental (weather) conditions.

2. Material and methods

2.1. Study area

The study covers 9 forest sites distributed along an altitudinal and spatial gradient within the Czech Republic and Slovakia (Fig. 1, Table 1). In this study we used radial growth and weather data collected at selected permanent monitoring plots (PMP) in Slovakia and the Czech Republic belonging to the Level-II network of the ICP Forests programme (www.icp-forests.net) between 2010–2017. The altitudes of the forest sites vary in the range from 350 m a.s.l. to 1,010 m a.s.l.. Reference mean annual air temperature ranges from 8.2 °C at the Medlovce site located at the lowest altitude (350 m a.s.l.) to 4.2 °C in the highest locality of Železnô (1,010 m a.s.l.) situated in the Low Tatra Mts. in Slovakia. Mean annual precipitation total of the studied sites varies from 640 to 1,250 mm based on the new climatic normal 1981–2010 (Hlásny et al. 2017). In the context of the soil environment, various sub-types of cambisol occur at all selected forest sites except for the locality of Luisino údolí (LU) where Haplic podzol occurs (WRB 2006).

All studied forest stands have reached their maturity and are currently between 80 and 131 years old (Table 1). Forest stands are almost fully stocked with stem density expressed in a relative scale of stocking from 0.7 to 1.0. Mean heights of studied forests varied between 22.2–40.1 meters and mean diameters at breast height (dbh) reach values in the range from 25 cm to 54 cm (Table 1). Potential productivity of forest can be assessed using an absolute site index that represents mean height of a forest stand at an age of 100 years. The site index of studied forest stands varies in range from 20 to 38. The parameters of forest stand as an age, dbh, height, stocking and site index refer to year 2018.

2.2. Weather data measurements and processing

At all monitored localities, measurements of raw weather data were conducted using automatic weather stations manufactured by the Environmental Measuring Systems (EMS Brno, CZ). Digital meteorological stations have been installed in an open area nearby each study forest site and measurements have been performed

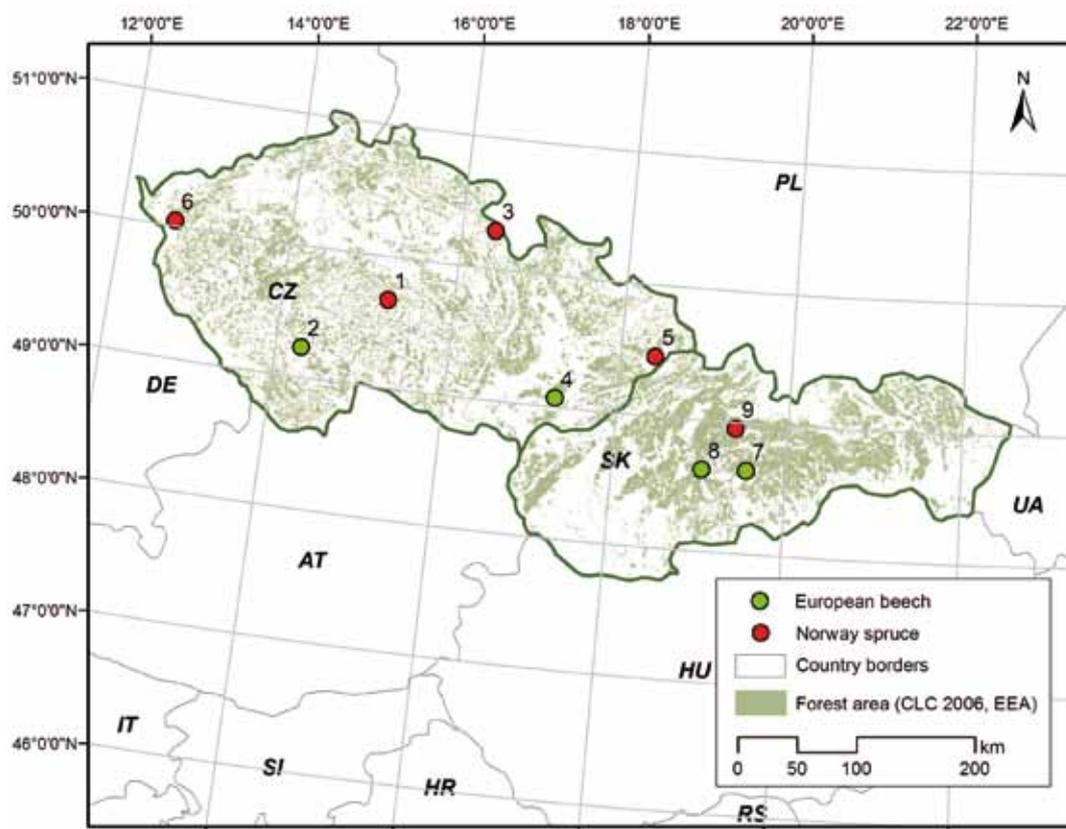


Fig. 1. Spatial distribution of selected 9 permanent monitoring plots (PMP) used in the study that belong to Level II network of ICP-Forests programme.

Table 1. Description of studied forest sites with radial growth measurements of Norway spruce and European beech trees with manual band dendrometers. Codes of the forest sites are identical to the numbers displayed in Fig. 1. Stand stocking is expressed in a relative scale from 0.0 to 1.0, where 1.0 refers to a fully stocked forest stand.

Forest site (PMP) [Code] Name	Altitude [m a.s.l.]	Stand age [yrs]	Tree species / Share in stand	Soil type [WRB 2006]	Site index	Mean diameter / Mean height		Stand stocking	Number of dendrometers
						[cm] / [m]			
[1] Želivka – ZE	440	116	<i>Picea abies</i> / 100	Entri-stagnic Cambisol	26	34.7 / 32.0		0.9	16
[2] Všetec – VS	615	124	<i>Fagus sylvatica</i> / 100	Epidystric cambisol	28	39.1 / 37.6		1.0	14
[3] Luisino údolí – LU	940	105	<i>Picea abies</i> / 100	Haplic podzol	20	36.8 / 22.2		0.9	15
[4] Medlovce – MED	350	118	<i>Fagus sylvatica</i> / 57	Endoeutri-stagnic cambisol	30	38.8 / 30.1		0.9	15
[5] Klepačka – KL	650	93	<i>Picea abies</i> / 96	Stagnic dystric cambisol	38	44.0 / 35.9		0.9	15
[6] Lazy – LZ	875	131	<i>Picea abies</i> / 100	Dystric cambisol	28	40.7 / 28.8		0.8	16
[7] Polána – PO	850	115	<i>Fagus sylvatica</i> / 70, <i>Picea abies</i> / 20	Haplic cambisol eutric	34	29.2 / 36.6		0.7	12
				Haplic cambisol humic, hypereutric, endoskeletal, siltic	38	53.8 / 40.1		0.7	10
[8] Turová – TU	575	80	<i>Fagus sylvatica</i> / 100	Haplic cambisol humic, hypereutric, endoskeletal, siltic	34	24.9 / 29		0.9	40
[9] Železnô – ZZ	1,010	90	<i>Picea abies</i> / 100	Haplic cambisol humic, dystric	30	32.8 / 28		0.8	20

in line with the standardised methodology of the ICP Forests programme (Manual for meteorological measurements, Part IX, available at www.icp-forests.net). Automatically measured data were stored into the battery operated datalogger (EdgeBox V8 or MiniCube VC, EMS Brno, CZ) of the meteorological station in 10 or 30-minute intervals. Air temperature was measured at a standard 2-metre height using integrated smart sensors (EMS33). Precipitation amount was measured in two different ways: 1) using an automatic rain-gauge with a dual-chambered tipping bucket design (Model MetOne

370, Oregon, USA), a collection area of 320 cm² and a resolution of 0.2 mm per pulse, and 2) with open rainfall samplers used for measurements of atmospheric deposition under the canopy (throughfall) and in an open area (bulk). Raw weather data were processed and aggregated to represent the periods between two readings of stem circumferences. Air temperatures were first processed to derive daily averages, minima and maxima, and in the next step we calculated average values representing the whole months at Czech forest sites and approximately two weeks at Slovak monitoring plots.

2.3. Dendrometric measurements and growth data processing

Data about stem diameter increment were obtained from 9 forest sites, while the Norway spruce (*Picea abies* L. Karst.) was the main species at 6 sites, and the European beech (*Fagus sylvatica* L.) dominated in the remaining 3 forest sites. In the mixed mountainous forest stand at permanent monitoring plot Pořana-Hukavský grůň (PO) we assessed radial growth data for both major tree species, i.e. beech as well as spruce (Table 1). The Turová (TU) research plot was included in the study only for the period 2010–2013 since the forest stand was substantially damaged and windthrown by the Žofia windstorm in May 2014.

For the analysis of the seasonal tree growth, the data from 213 dendrometers with manual reading were used (132 dendrometers installed on Norway spruce, and 81 on European beech trees). The measured trees were selected to represent all diameter classes of the given stand. Dendrometer increment sensors (model DB20, EMS Brno, CZ) consist of two parts – a measuring part with a scale and a spring, and a stainless tape that is non-invasively fixed on a stem at a height of 1.3 m above the ground. The values of stem circumferences are read at the nonius scale with 0.1 mm resolution. Manual reading is performed regularly at the end of a month (CZ sites) or approximately biweekly (SK sites) during the whole year. Each reading is identified with the tree number and exact date & time. In this study we evaluated data only for the period of the main growing activity usually occurring between April and September during the years 2010–2017.

As manual dendrometers measure stem circumferences of individual trees, the stem diameter increment at a forest stand level was calculated as an average of values of all measured trees at a sites (from 10 to 40 individuals, see Table 1). A number of the measured trees vary depending on thickness variability of stem diameters, which is individual for each studied forest stand. For the analysis, we used the increments calculated as the differences between the stem circumferences recorded at two consecutive dates during the growing season. The identification of the start and the end of the actual creation of wood (radial increment) was performed individually for each site and year, as these dates vary between the seasons depending on weather, tree species and site altitude. In order to unify the date terms between CZ and SK sites and to enable mutual comparison between localities we also calculated mean daily increments for each individual period during the all eight growing seasons.

2.4. Data analysis

The complex interplay of selected environmental (site & weather) factors and their role in the seasonal tree growth was analysed by a number of statistical methods using

Statistica software (Statistica Cz 12, StatSoft, Inc. 1984–2013) and R package cvequality (Version 0.1.3; Marwick & Krishnamoorthy 2018). The Tukey HSD post hoc test in ANOVA was used to verify the statistical significance of differences in mean annual increments between the individual sites regardless of tree species. This analysis enabled a comparison of the increment values between all selected forest sites and finally, contributed to meet the goals of study. The mean annual increments at individual sites were computed from eight years of measurements and four years of measurements for the TU site. To evaluate this locality, we used the Tukey's HSD test adjusted for non-equal samples size. Normality of distribution and homogeneity of variance, which are required if ANOVA is to be applied, were verified with Shapiro-Wilks and Levene's tests, respectively.

A similar analysis was used to test the differences in the tree growth between the individual years for the studied period. We analysed beech and spruce growing responses under the same site conditions and observed climatic situations. The PO monitoring plot was the only forest site with both tree species. The mean annual values of diameter increment measured on 10 trees of spruce and 12 trees of beech growing at the site were compared between the respective years. In the case of beech, the square root transformation of the increment data was necessary to remove the heteroscedasticity of variance.

For purposes of intra-annual radial growth analysis, we applied a log-normal function that was repeatedly applied in several previous studies (e.g. Canham et al. 2004; Bořela et al. 2013). A lognormal function considered as flexible and it is supported by both empirical evidence and theory (Canham et al. 2004). For modelling of the seasonal development of increment we used this function in shape of the base [1] and advanced [2] model:

$$SI_i = a \exp\left(-\frac{1}{2}\left(\frac{\ln(x_1/b)}{c}\right)^2\right) \quad [1]$$

$$SI_i = a \exp\left(-\frac{1}{2}\left(\frac{\ln(x_1/b)}{c}\right)^2 + dx_2\right) \quad [2]$$

Where: SI_i – seasonal increment; x_1 – factor of the day in the sequence of the particular year; a , b , c – estimated regression coefficients (a – maximum increment to which the model curve approximates; b – Julian day when the maximum increment occurs; c – band of the function). In case of advanced model [2] climate parameters were included into the function exponent as an another independent variable x_2 ; d – regression coefficient differentiating the course of the seasonal growth dependent on climatic condition.

The base and advanced models were parameterized for all eight years from altogether 48 monthly increment values for CZ sites (6 months of growing season \times 8 years of study) and 96 biweekly values of increment for SK sites (12 biweekly records \times 8 years). In the base model was only a day of the year (DOY) used as an independent variable. The base model was utilized to remove seasonal trend from mean daily increment data, in aim

to analyse an influence of climatic variables on residuals of radial increment. The advanced model was built up from the base model by a stepwise procedure of including observed climatic characteristics as independent variables. The model generalises the creation of the daily mean increment at a particular site over the selected six-months-long growing season (i.e. April to September) and during all eight years.

For further analysis, we chose the model that explained the greatest proportion of variance of increment creation during the growing season. That model was used to describe seasonal dynamics of tree growth for both tree species. Besides, the best advanced model was compared to the base model to assess the contribution of the included climatic variables to the explanation of increment variance.

Subsequently, for each forest site we calculated the residual deviations of the mean daily increments from the values predicted by the respective base model. By filtering the most significant residuals and their two-step ranking by months and years, we obtained information on specific time events within the examined eight years with the most frequent occurrence of significant positive and negative residuals of increments. Then we interpreted these findings in relation to the respective climatic variables of the identified periods. To filter significant residuals, we applied the rule that all deviations greater than mean ± 1.28 SD are considered significant. The selected threshold value of $z = 1.28$ for the one sided bounds within the normal distribution of values corresponds to approximately 10% of the most extreme values of positive and negative residuals.

Partial correlations were analysed between residuals as well as predicted values and climate variables (precipitation total and average temperature) at all forest sites. Based on correlation coefficients related to residuals, the influence of climate variables to intra-seasonal radial growth was interpreted. Reconnaissance of relation between climate variables and predicted values calculated from base model was utilized to reveal main climate drivers of radial increment seasonal trend.

3. Results

3.1. Analysis of weather data

For eight years (2010–2017), tree growth and various environmental factors were monitored at 9 forest sites across Czecho-Slovakia within the long-term and permanent monitoring of forests (Level II, ICP Forests). The studied period is interesting for the investigation of forest growth as it includes several climatologically contrasting years, during which many climatic and meteorological extremes were for several times exceeded.

The assessment of mean air temperatures and precipitation totals at individual sites during the growing seasons of 2010–2017 showed that their courses were synchronised with the highest temperatures in 2012 and 2015 and the lowest values in 2010 and 2013 (Fig. 2a). Every year, the highest seasonal precipitation totals were observed in mountainous research sites (ZZ, LU, KL and PO). The lowest precipitation total (on average 363 mm) was observed at almost all research localities during the growing season of 2015 (Fig. 2b).

From the aspect of between-site comparison (Fig. 3), the highest mean air temperatures (15.5 °C) together with the lowest precipitation total (358 mm) over the whole analysed period (2010–2017) were found in the MED beech stand situated at an altitude of 350 m a.s.l. followed by the ZE spruce forest site at 440 m a.s.l. (15 °C and 434 mm). The most significant differences between minimum and maximum precipitation totals during the growing seasons of examined eight years were recorded for LU, ZZ, KL forest sites. Relative average interception of spruce forest stands calculated for the growing seasons of years 2010–2017 varied between 18.3% from open field precipitation at ZZ site (Železnò) and 42.2% at ZE site (Želivka). The interception of pure beech forest stands was more balanced, as their values ranged from 32.6% at TU forest site to 37.5% at VS site (Všeteč). Mean seasonal interception of the mixed beech-spruce-fir forest stand at PO locality was 22.8% over the years 2010–2017. Data on interception were not directly included in the

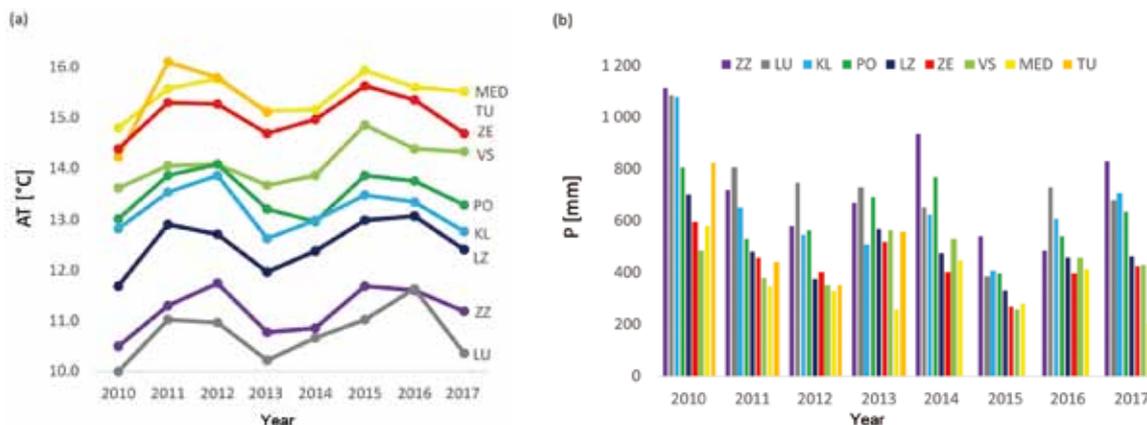


Fig. 2. Seasonal mean air temperature AT (a) and precipitation totals P (b) at individual forest sites and in years 2010–2017. Between-years and between-sites development of basic weather variables is presented.

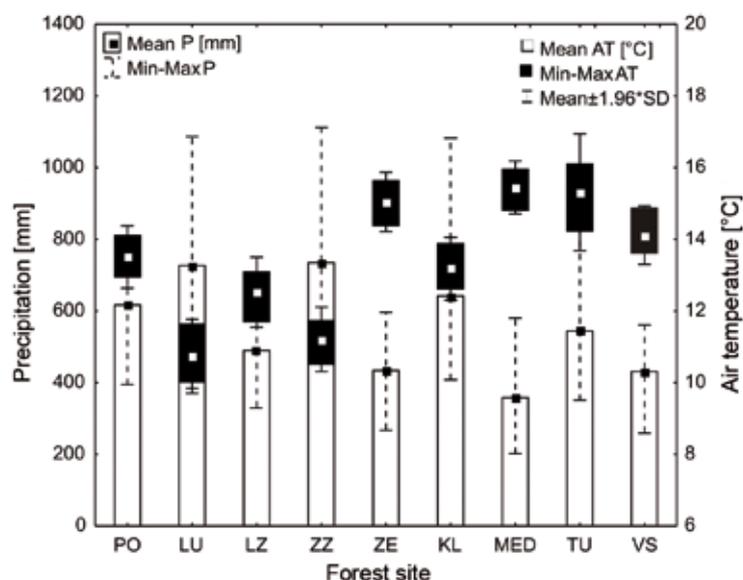


Fig. 3. Comparison of seasonal precipitation totals and air temperatures between studied forest sites. The mean, minimum and maximum values over the analysed period 2010–2017 are displayed.

growth analyzes, but usefully supplement the information on how the individual forest stands transformed the infiltration of atmospheric precipitation via canopy and provide a more detailed picture of the stand structure.

3.2. Analysis of radial growth

Over the whole studied period, the highest mean annual increment of spruce (3.9 ± 0.50 mm) as well as of beech (2.8 ± 0.59 mm) was found at PO forest site (with 95% confidence) (Table 2). At this locality, the total eight-year-cumulative increment of spruce and beech reached the values of 31.1 mm and 22.8 mm, respectively. This result corresponds with the highest site quality and productivity of the PO stand from all evaluated forest sites (Table 1). On the other hand, the lowest mean annual increment (1.9 ± 0.38 mm) as well as the lowest eight-year-cumulative increment (15.3 mm) was observed in the artificially planted spruce forest at Klepačka site (KL) despite the same site index as in the case of PO (site index for spruce equal to 38, Table 1).

While the lowest inter-annual variability in the annual increment was found in the ZZ spruce forest site (coeff. var. $s_x\% = 14.2\%$), the highest between-year fluctuations of mean annual increment values were observed in the beech forests at VS ($s_x\% = 40.4\%$) and MED ($s_x\% = 31.6\%$). Generally, the coefficient of variation was higher in beech stands than in spruce stands (Table 2), which may indicate greater sensitivity of beech to inter-annual changes of climate. However, the differences between the coefficients of variation from multiple samples (Marwick & Krishnamoorthy 2018) of beech and spruce stands were not significant ($p = 0.05$), probably due to a small sample size (8 years).

The test of the differences in the mean annual increments between the forest sites (Fig. 4) showed that the spruce increment at PO site was significantly greater than the increment of spruce at LZ site. Moreover, mean annual increments of spruce at these two sites and LU site as well as beech increment at PO were significantly different from the values at ZZ, ZE, and KL sites.

Table 2. Descriptive statistics of annual diameter increments at studied forest sites during the period 2010–2017. Explanation of used abbreviations: CI – confidence interval; StdDev – standard deviation, $s_x\%$ – coefficient of variation.

Forest site	Tree species	N	Annual increment [mm]					StdDev	$s_x\%$	
			Mean	CI -95%	CI +95%	Sum	Min			Max
PO	spruce	8	3.9	3.4	4.4	31.1	2.9	4.6	0.60	15.5
LU	spruce	8	3.2	2.7	3.7	25.6	2.3	3.9	0.60	18.6
LZ	spruce	8	3.0	2.6	3.3	23.6	2.3	3.8	0.47	15.9
ZZ	spruce	8	2.0	1.8	2.3	16.2	1.4	2.3	0.29	14.2
ZE	spruce	8	2.0	1.7	2.3	16.1	1.5	2.6	0.40	20.0
KL	spruce	8	1.9	1.5	2.3	15.3	1.3	2.7	0.45	23.6
PO	beech	8	2.8	2.3	3.4	22.8	1.8	3.6	0.70	24.6
MED	beech	8	2.1	1.5	2.6	16.6	1.5	3.5	0.66	31.6
TU	beech	4	2.0	1.2	2.8	7.8	1.3	2.5	0.50	25.6
VS	beech	8	1.9	1.3	2.6	15.5	1.1	3.1	0.78	40.4

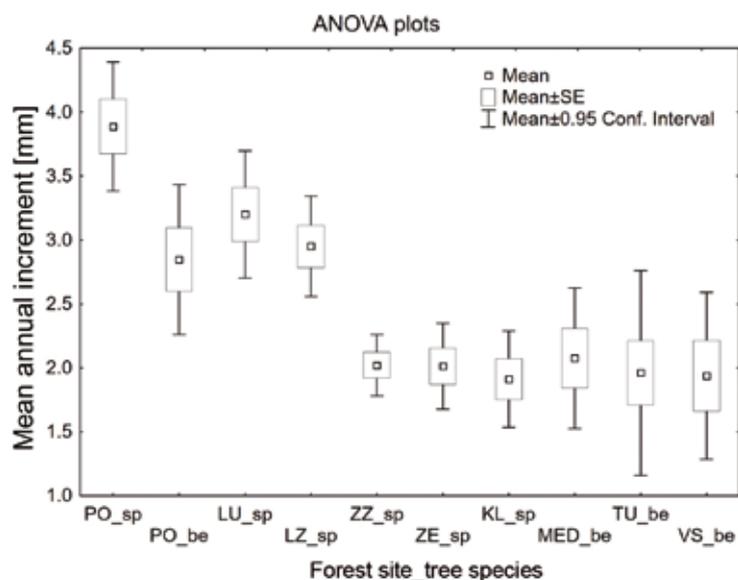


Fig. 4. Between-site comparison of mean annual increments in 2010–2017 (ANOVA, Tukey HSD post hoc test).

The temporal courses of spruce annual increments at most forest sites were similar with the most significant decline in 2015 (Fig. 5a). The only forest site with a different pattern and a higher annual increment in the year 2015 in comparison to the years 2014 and 2016 was LZ monitoring plot. The annual increment of beech did not show a synchronised inter-annual temporal pattern of individual forest sites. The common, although weak decline of annual increments was found only in the years 2016 and 2011 (Fig. 5b).

The analysis of variance and the inter-annual comparison of seasonal increments of beech and spruce in the mountainous mixed stand at Pořana site revealed that the spruce increments in the years 2015 and 2017 were significantly different from the increments in 2010, 2012, and 2014 (Fig. 6a). The result corresponds with the pattern of precipitation totals in the growing seasons of the given years (Fig. 2b), since in the year 2015 the lowest precipitation total was recorded at Pořana (395 mm), while in the year 2010 the precipitation total (807 mm) was the highest from all analysed years. The

annual increment of beech growing at the same site in the year 2013 was significantly different from those in the years 2012 and 2014, and the increment in 2014 differed from 2016, while the increment in 2016 differed from the one in 2012 (Fig. 6b). The link between beech increments and meteorological characteristics of the particular year is not as clear and easily detectable as in the case of spruce.

3.3. Modelling of seasonal diameter increment

The general intra-annual radial growth pattern was expressed using a log-normal function. Depending on the locality, the base model explained from 14% to 58% of the variability in mean daily increments of spruce and up to 58–72% of the variability in beech increments (Table 3). In general, the proportion of the explained variability by base models was higher for beech than for spruce sites. For the studied spruce stands, the percentage of

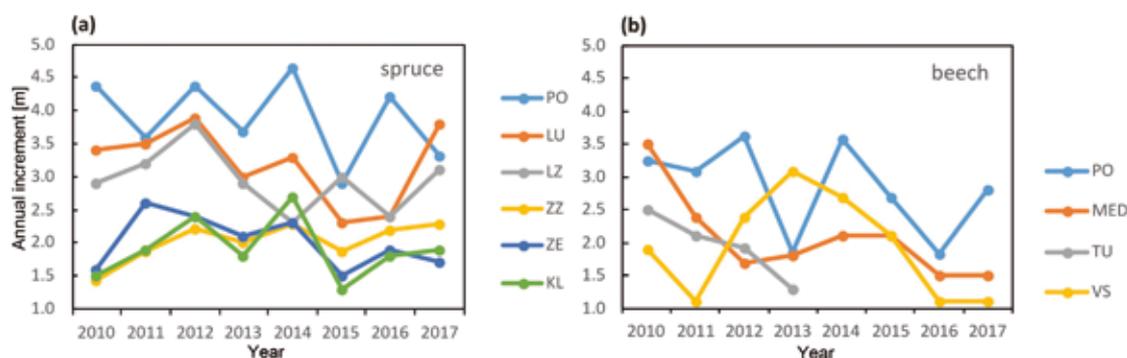


Fig. 5. Development of annual increments of Norway spruce (a) and European beech (b) during the years 2010–2017.

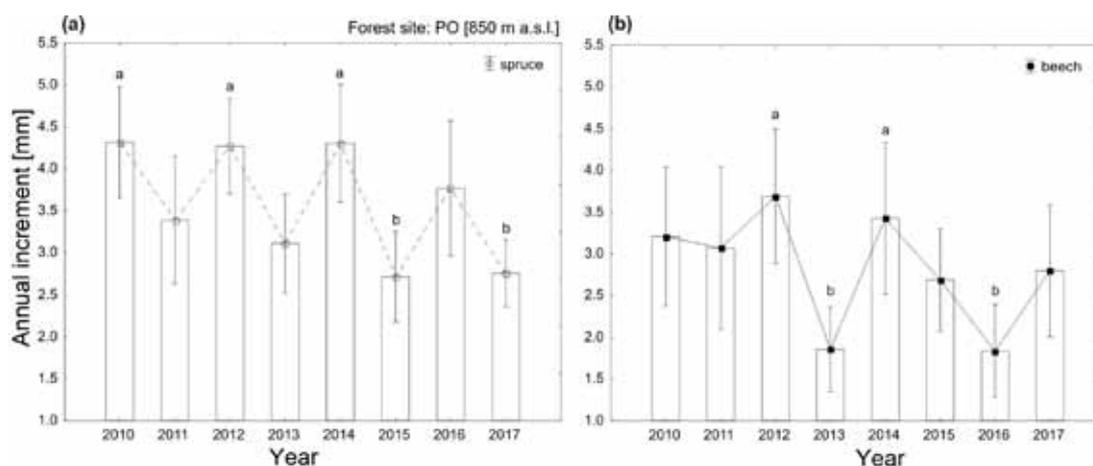


Fig. 6. Inter-annual comparison of annual increments of spruce (a) and beech (b) at Poľana (PO) forest site using ANOVA. Differences were tested by Tukey's HSD post-hoc test below significance level $p < 0.05$.

Table 3. Parameters of base and advanced log-normal models of daily mean increments (mm) of beech and spruce. In this function the parameter a represents the maximum daily increment to which the model curve approximates, the parameter b indicates the day of the year (DOY) when the daily increment culminates, and the parameter c indicates the band of the function. The parameter d is the regression coefficient that differentiates the course of the seasonal growth dependent on the climate variable (Canham et al. 2004).

Norway spruce							
Site/model	a	b	c	d	R^2	DF	RMSE
PO/Base	0.0417	165.4	0.2189	0.0110	0.34	94	0.0183
PO/Precip	0.0258	165.8	0.2301		0.53	93	0.0155
LU/Base	0.0472	170.1	0.1553		0.58	45	0.0147
LU/Precip	0.0343	169.0	0.1511	0.0027	0.62	44	0.0139
LZ/Base	0.0370	169.2	0.1892		0.52	45	0.0123
LZ/Precip	0.0261	169.5	0.1930	0.0045	0.59	44	0.0114
KL/Base	0.0270	167.0	0.1699	0.0033	0.45	45	0.0087
KL/Precip	0.0205	167.5	0.1392		0.57	44	0.0078
ZZ/Base	0.0251	169.0	0.1637	0.0082	0.14	94	0.0163
ZZ/Precip	0.0147	166.2	0.1669		0.28	93	0.0149
ZE/Base	0.0270	155.7	0.1922	0.0088	0.54	45	0.0087
ZE/Precip	0.0126	157.6	0.1907		0.71	44	0.0069
European beech							
Site / model	a	b	c	d	R^2	DF	RMSE
PO/Base	0.0384	172.0	0.1656	0.0466	0.72	94	0.0083
PO/ATmin	0.0226	169.2	0.1703		0.74	93	0.0081
MED/Base	0.0269	153.8	0.1837		0.64	44	0.0068
MED/ATmin	0.1086	165.8	0.1577	-0.1237	0.69	43	0.0064
TU/Base	0.0258	154.7	0.1879	0.0904	0.64	46	0.0062
TU/ATmin	0.0098	147.7	0.1783		0.69	45	0.0057
VS/Base	0.0227	156.5	0.2058	0.0034	0.58	44	0.0069
VS/Precip	0.0157	154.1	0.2144		0.63	43	0.0064

the explained variability increased by 4% to 19% when precipitation was included in the model. The R square of advanced models was higher than of the base models, as it fluctuated between 0.28 and 0.71 depending on the spruce forest site. On the contrary, air temperature was the most significant factor affecting the seasonal increment dynamics in beech forest stands (an increase by 2–5% in comparison to the base model), except for the Všetec (VS) forest site, where the advanced model with precipitation explained seasonal variations of the increment better than the one with temperature ($R^2=0.63$ in advanced model).

The greatest differences in the proportion of the explained variability between the base and advanced models were found in the case of spruce at Poľana forest site, and the least improvement rate of the model was observed in the case of beech at the same site. Examples

of models fitted to daily mean increments of spruce and beech at the mentioned locality are demonstrated in Fig. 7a–d.

The value of the b parameter in the function indicates the day of the year (Julian day DOY), when the daily mean increment culminated, i.e. when it reached its maximum (Table 3). Spruce increment culminated first at the lowest site Želivka (June 7th) and last at Lazy (June 19th). Beech daily mean increment reached its maximum from 28th May at Turová (TU) to 18th June at Poľana (PO). The data from the mixed stand at PO, where both species occur at the same site, revealed that in the 8-year-long studied period the radial increment of spruce culminated three days before beech (June 15th versus June 18th).

The predicted values of spruce and beech increments significantly positively ($p < 0.05$) correlated with air temperature ($r=0.51–0.56$), with the exception of the lowest

Table 4. Partial correlation coefficients between predicted respective residual values of daily mean increment and air temperature (AT) and precipitation (P) in beech and spruce forest stands. Values significant at $p=0.05$ are highlighted in italics.

Species	Norway spruce					European beech				
Forest site	ZE	KL	PO	LZ	LU	ZZ	MED	TU	VS	PO
Altitude [m asl]	440	650	850	875	960	1,010	350	575	615	850
Predict vs. AT [°C]	0.19	<i>0.53*</i>	<i>0.51*</i>	<i>0.51*</i>	<i>0.51*</i>	<i>0.52*</i>	<i>-0.72*</i>	0.23	0.25	<i>0.56*</i>
Predict vs. P [mm]	0.21	0.10	<i>0.23*</i>	0.23	0.05	0.12	0.09	<i>0.42*</i>	0.16	<i>0.21*</i>
Resid vs. AT [°C]	-0.23	-0.29	<i>-0.27*</i>	-0.06	-0.01	<i>-0.33*</i>	0.05	0.07	-0.04	0.01
Resid vs. P [mm]	<i>0.68*</i>	<i>0.43*</i>	<i>0.59*</i>	<i>0.38*</i>	<i>0.44*</i>	<i>0.53*</i>	0.25	<i>0.29*</i>	0.26	0.08

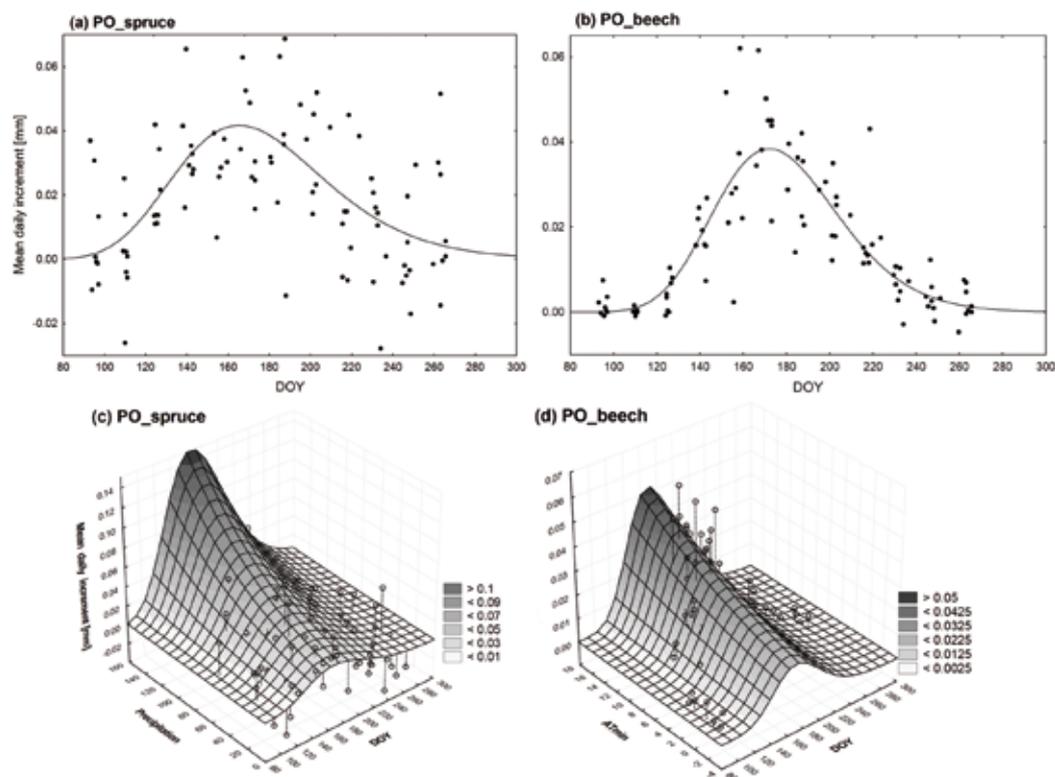


Fig. 7. Base (a, b) and advanced (c, d) models for daily mean increments of spruce (a, c) and beech (b, d) for forest site Polana (PO). Advanced models include the best explaining climatic variable for each tree species (c, d).

sites (ZE, TU, VS), where temperature was obviously not the significant limiting factor of growth (Table 4). At Medlovice site (350 m a.s.l.), air temperature negatively correlated with the predicted beech increment, which indicates that at elevations, where beech is at its rear edge of natural distribution, air temperature increase reduces radial increments (Fig. 8). In addition, it is also clear that the increment residuals of the base model are positively correlated with precipitation totals at all spruce forest sites (Table 4). At the beech sites influence of climate variables is not unilateral, excluding TU site, where significant influence of precipitation totals appears ($r=0.29$).

In the further step of the analysis, we identified the events with the most significant residuals of daily mean increments at all spruce forest stands (Fig. 9). Negative percentage presents the frequency of negative residuals and positive percentage expresses the frequency of positive residuals occurred in individual months and years. For example, in the year 2012 the highest percentage of positive differences of increments from the model was

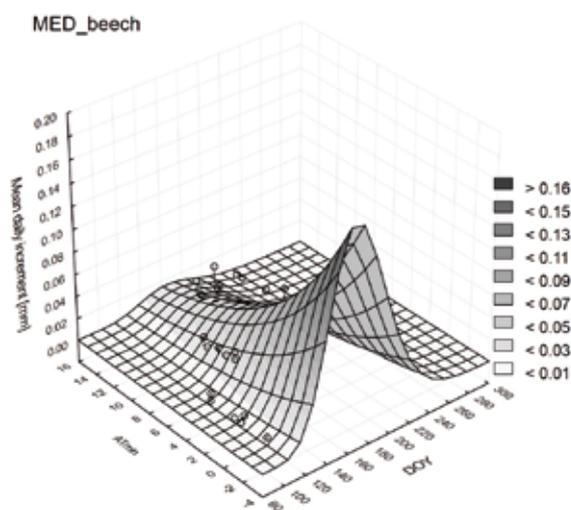


Fig. 8. An advanced model of the daily mean increment of beech at Medlovice (MED) forest site during the growing season (DOY) shows the negative correlation of increment with minimum air temperature.

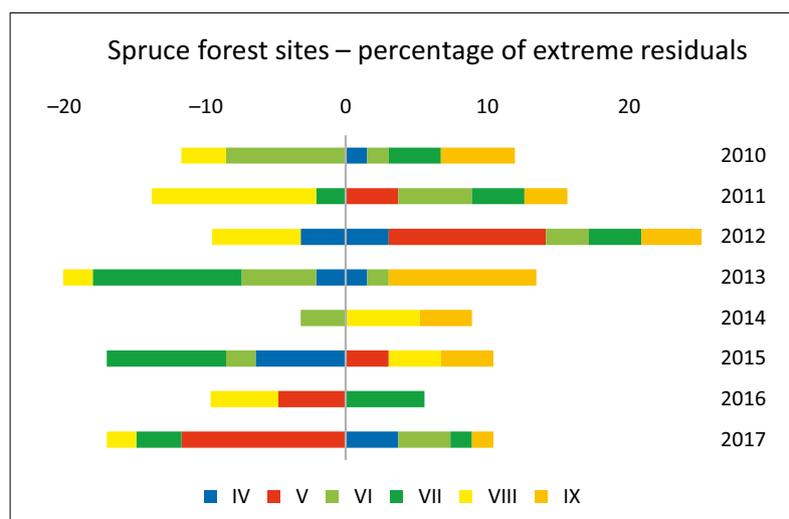


Fig. 9. Relative frequency of the most significant residuals of daily mean increments at all spruce forest sites used in the study.

identified, which means that in 2012 (especially in May) extreme values of daily mean increments were observed at most forest sites. On the contrary, the highest number of negative residuals were identified in 2013, 2015 and 2017, mainly in July and May 2017.

To demonstrate the development of residual increments with regard to the identified significant climatic events we selected four spruce stands along an altitudinal gradient from 440 m a.s.l. to 1,010 m a.s.l. (Fig. 10a–d). The periods with significantly high (green) and low (red) residual values in the years 2012, 2013, 2015 and 2017, in which most residuals occurred, are highlighted. Mean monthly air temperatures as well as the mean temperature calculated for the whole 8-year-long analysed period (AT avg_10–17) are presented. Two significantly negative periods with almost zero precipitation totals at Poľana site are highlighted with red triangles.

From the climatological point of view, precipitation in May 2012 was substantially below-normal, e.g. at the Sliac station (313 m a.s.l.) located in the region of the Zvolenská valley monthly precipitation total was only 21% of the long-term 1961–1990 normal (Bochniček & Ondruška 2012). This information is relevant from the point of spruce increments at nearby forest site Poľana, where low precipitation total was observed in the second half of May, when the increment residuals fluctuated around zero, but the recorded increment was not extremely low (Fig. 10c). Slightly lower temperatures in that period in comparison to the calculated 8-year mean (represented by a grey line parallel to x axis in Fig. 10) can be one of the explanations of this inconsistency. As precipitation increased in June 2012 (green bars of precipitation totals), significant increase of increment was observed at both forest sites located at higher altitudes (Fig. 10c, d). On the contrary, precipitation deficit in August and September 2012 resulted in significantly low increments at these sites (red bars of precipitation totals, or red triangles).

In July 2013, we found significantly low increments at all sites except for Poľana forest site. This is the result of below-normal precipitation and higher air temperatures observed in this month within the altitudinal transect of spruce sites (Fig. 10a–d). At all sites except for the Želivka forest site situated at the lowest altitude, increments of spruce positively reacted to increased precipitation total in September 2013.

A similar growth reaction in the opposite direction was observed at a majority of sites in July 2015 and 2017, when significantly lower increments and lower precipitation totals were recorded. The only exception was the lowest spruce site of Želivka (440 m a.s.l.), where slightly above-average temperatures measured in June and July most probably reduced growth in spite of sufficient precipitation totals. This site is characterised by the highest absolute temperatures due to its lower altitude, which may lead to future reduced growth of spruce at such altitudes even under sufficient precipitation.

In spite of the absence of a visible altitudinal trend in the correlation coefficients of residuals vs. precipitation (Table 4), the examination of significant residuals of spruce forest sites (Fig. 10a–d) allowed us to identify climatic events characteristic for different altitudes.

Significantly lower increments at lower altitudes occurred only in July, when the temperatures reached the highest average values due to the natural seasonal pattern of temperatures and the precipitation totals were lower. Significant reduction of increments in the lowest stand was also recorded in July 2013 and 2017 (Fig. 10a), when precipitation totals were relatively higher, which indicates that high temperatures had a negative impact on spruce growth at lower sites. Significantly positive residuals in the selected years occurred only when greater precipitation totals were recorded at sites located at both lower and higher altitudes.

In the seasons with summer precipitation deficit we observed significant increase of increment residuals at

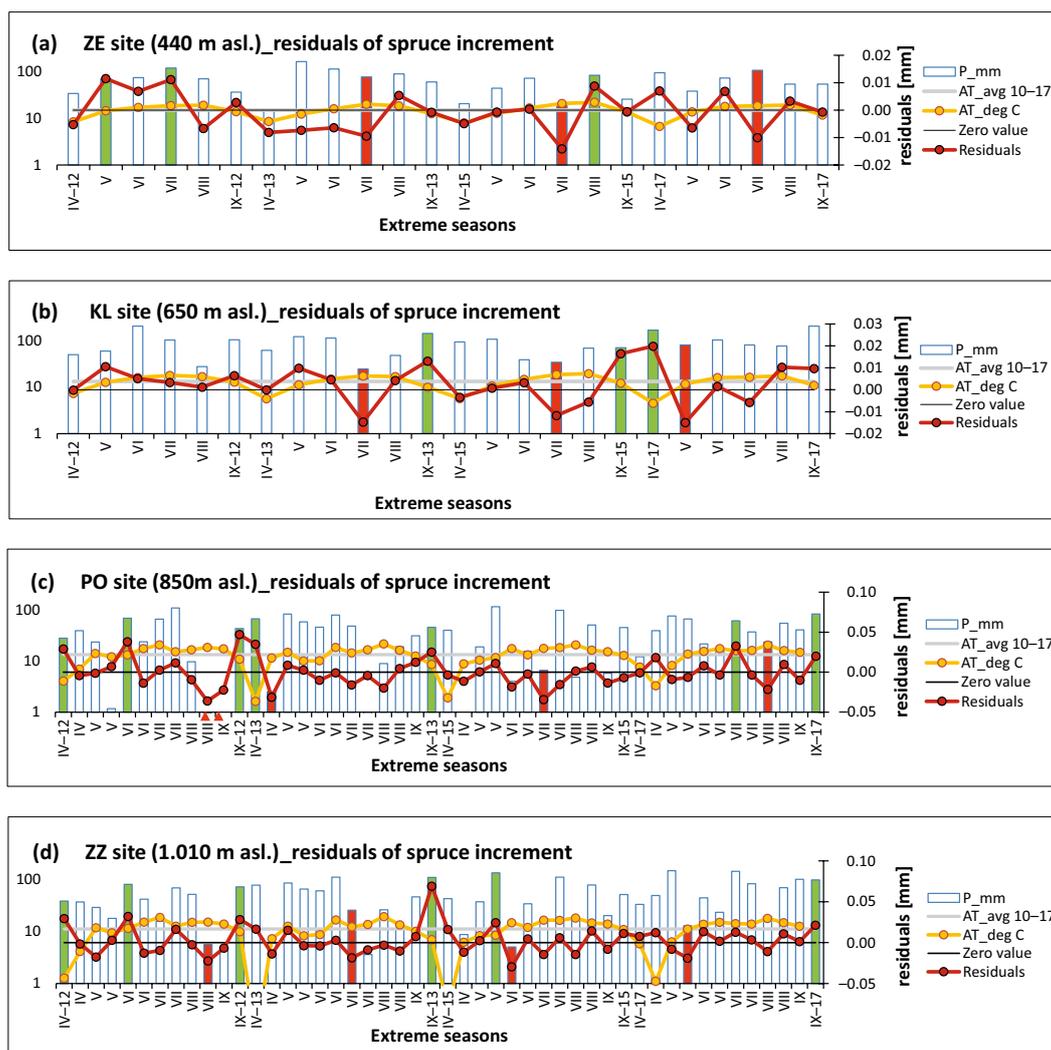


Fig. 10. Development of residuals of mean daily increment in selected spruce forests at ZE site situated at the lowest altitude (a), at KL site (b) and PO site (c) located at medium altitudes, and at ZZ site (d) from the highest altitude, during the periods identified as extreme growing seasons.

higher altitudes in September, which was linked with the improved precipitation balance of the growing season. Significantly lower residual values of increments at higher altitudes were always coupled with low precipitation totals (Fig. 10c, d), while these were not restricted to the months with the highest mean temperatures as it was at lower spruce stands.

4. Discussion

From the climatological point of view, the studied period 2010–2017 provided an exceptionally interesting base for the assessment of growth responses of the most relevant forest tree species to contrasting weather and various site conditions across the region of Central Europe. This is well-supported by the fact that the last decade 2008–2017 was marked as the warmest period in Europe on record ever (WMO 2018). Since the year 2000, several extreme heat waves have occurred, mainly

in 2003, 2006, 2007, 2010, 2014, 2015 and 2017. Based on the recent statement on global climate, the years 2015, 2016 and 2017 were the world's three warmest years on record (WMO 2018). On the base of our meteorological measurements at the investigated forest sites we can confirm that especially the summers of 2012, 2015 and 2017 were extraordinary hot, sunny and dry. In contrast, despite the above-normal air temperatures, the growing seasons of the years 2010, 2014 and 2016 were humid with the sufficient supply of rainfall.

During the observed 8-year period, the highest annual mean and cumulative increments of both investigated species were found at the PO permanent monitoring plot (850 m a.s.l.). This typical Carpathian mountainous forest composed of beech, spruce, and fir grows at a high-quality site (Table 1). On the other hand, the lowest mean increment of spruce (a half of the increment at PO) was found at the KL forest site with the same site index (Table 1). Since the climatic conditions of both

sites during the growing seasons 2010–2017 were comparable (Fig. 2), we suppose that the reason for the lower radial growth of the younger spruce stand at KL locality could be explained by the higher forest stocking (Table 1). Almost full stand stocking at this site could lead to lower available space for the growth of individual trees which tend to invest more into height growth than to the radial growth.

High mean annual increments of spruce were found also at other mountainous sites, namely LZ (875 m a.s.l.) and LU (940 m a.s.l.), which benefited from higher summer temperatures and longer growing seasons in recent years (Kolářová et al. 2014), but were not stressed by drought. This was confirmed by the analysis of the drought risk in forest stands in the extreme year 2015, when the region of Slavkovský les (LZ site) and Orlické hory (LU site) was not affected by moisture deficit (Šrámek & Neudertová-Hellebrandová 2016). According to the values of soil water potential (SWP) in the upper soil layers measured at LZ forest site, drought started at the beginning of August, and reached its maximum on 14th and 15th August 2015. The reduction of soil water was compensated after a short but an intense rainy period in the second half of August 2015. Hence, the period of soil drought at LZ site was very short in the year 2015 (Šrámek et al. 2016). In addition, high mean annual increment of spruce at LU site, could be stimulated by nitrogen deposition, which has been increasing in that region since the year 2000 (Vacek et al. 2015). The sensitivity of spruce growth to N-deposition was repeatedly proved by many studies also in other regions of Europe (Etzold et al. 2014; Cienciala et al. 2016; Braun et al. 2017). In the study of Kolář et al. (2017) was found that the growth–temperature relationships of Norway spruce was reduced due to the influence of acid deposition in the well-known air-polluted “Black Triangle” area.

In the case of beech forest sites, the difference between their mean annual increments was not significant (Table 2), although the highest increment of beech was at PO site, where beech grows together with other tree species (spruce, fir, maple, ash) and where it occurs in its production optimum. Mean heights of dominant and co-dominant beech individuals in the PO stand reached values of about 38 m and mean diameter was 41 cm (unpublished data measured in 2017). Such high growth is in line with the findings from Central Europe, where beech exhibited accelerated growth dynamics during the last 140 years (Pretzsch et al. 2014; Bošela et al. 2018).

In general, inter-annual variability of beech increments was greater than that of spruce increments (Table 2), although this difference could not be confirmed statistically due to the short examined period (8 years). The finding is opposed to the results presented in the study of Bošela et al. (2013), who found a contrariwise lower variability in beech increments compared to spruce.

In the context of the inter-annual comparison of the study sites, we observed relatively synchronised devel-

opments of spruce annual increments, while no unifying pattern was found for beech localities. The spruce increment values copied the particular climatic characteristic of individual years with regard to its demands on climate. The lack of precipitation reduced spruce radial growth especially in the dry year of 2015. In the “rainfall-exclusion” study from the southern Germany, diameter increment of spruce reached high values in the humid year 2014 whereas in 2015 its growth was significantly reduced due to heavy drought. This is a typical response of isohydric species to water deficit (Rötzer et al. 2017).

Temporal patterns of annual increments in beech forest sites could not be easily related to climate conditions in (actual) appropriate periods. It is probable that beech is more sensitive to climate and reacts to the climate of preceding periods with a time lag, which was repeatedly justified in dendroclimatological studies (e.g. Dittmar et al. 2003; Budeanu et al. 2016). The amount of winter precipitation, temperatures in May and water availability in summer were identified as major drivers of beech radial growth (Lebourgeois et al. 2005). Our analysis of data revealed that beech did not reduce its annual increment in the dry year 2015, but in the subsequent year 2016, which was from the climatological point of view above-average wet in Europe (WMO 2018). A very similar result was achieved under the experiment presented in Rötzer et al. (2017), within which the extremely dry conditions in 2015 did not reduce stem growth of beech at all. This revealed the species-specific response to limited water availability and differences in water management between isohydric (spruce) and anisohydric (beech) species (Klein 2014).

The modelling of the seasonal growth revealed that the percentage of variance of daily mean increments explained by the base model ranged in intervals 14–58% and 58–72% for spruce and beech, respectively. Including climatic variables in the advanced model showed that seasonal precipitation was a significantly better predicting factor of the increment creation in Norway spruce, while air temperature enhanced predictions of beech daily increments. The results fully correspond with the previous research conducted in a young mixed beech and spruce stand, where it was proved that including precipitation in the advanced model explained 10% of the variability of spruce stem growth, while air temperature improved the model by 3% from the point of beech diameter increment variability (Bošela et al. 2013). Lesser improvement rate of explained variability by the advanced model in the case of beech (by 2–5%) is related to the fact that the base model for beech already explained a higher proportion of variability in radial increments than the model of seasonal dynamics derived for spruce. In contrast, including a climatic characteristic in the advanced model for spruce increased the explained variability by 4 to 19%.

The analysis of the values of correlation coefficients (Table 4) showed that the base model of intra-annual increment development coincided with the development

of temperatures to a high degree, i.e. the modelled curve of the intra-annual increment creation significantly correlated with the seasonal temperature development at all plots except for ZE and TU. It is obvious that beech increment is more sensitive to temperature than spruce, which can be directly linked to the known relationship between the intra-annual development of temperature, beech phenology, and increment creation (Jochner et al. 2016; Delpierre et al. 2017).

An interesting finding was obtained from the advanced model for the lowest beech stand (MED), which revealed that the intra-annual radial beech growth dynamics was significantly negatively affected by temperature ($R=-0.72$). The reduction of minimum mean temperatures resulted in the increased daily mean increments of beech. In the context of recent and projected climate change, it points out at the altitudinal limits of beech distribution (Czúcz et al. 2011) at low elevations of already 350 m a.s.l. This fact should be taken into account in the future management of forest ecosystems in Central Europe.

The analysis of the correlation coefficients showed that the predicted values are closely related to air temperature, while the residuals are related to precipitation (Table 4). Possible interpretation is that air temperature is the primary factor determining the dynamics of intra-annual tree growth, while precipitation significantly modified increment values. At three spruce forest sites (KL, PO, ZZ), slight negative correlations (correlation coefficients varying from -0.21 to -0.28) were found between temperature and residual deviations. Negative coefficients indicate that higher air temperatures slightly reduced daily mean increments of spruce. Such a relationship was not revealed at any of the examined beech sites. All sample correlation coefficients for spruce exceeded correlation coefficients of beech, which indicates a closer link of spruce growth processes with precipitation during a year. Significant positive correlation between precipitation and tree-ring growth of spruce was identified also in south-eastern Norway (Čermák et al. 2017).

Modelling of intra-annual growth at study sites revealed that spruce increment culminated from June 7th (at ZE site situated at 440 m a.s.l.) to June 19th (LZ site at 875 m a.s.l.) depending not only on the altitude but also on other site-specific attributes. Similar timing of culmination of the radial stem growth of spruce (from June 2nd to June 11th) was observed in the northern part of Slovakia (500 m a.s.l.) between 2008–2012 (Leštianska et al. 2015). Maximum daily increment of beech at our plots was recorded from May 28th (TU site) to June 18th (PO site). In the mountainous stand at Poľana, where both tree species occur at the same site, thanks to which we could perform the inter-specific comparison of radial growth, we found earlier culmination of increment in spruce (June 15th) compared to beech (June 18th). The identical result was obtained in the 30-years-old mixed beech-spruce forest stand located in the same orographic

unit Poľana in Slovakia between the years 2009–2012 (Bošela et al. 2013).

At all spruce forest sites, the most significant positive residuals from the generalised daily mean increments of spruce were found in the year 2012 and in September 2013 (Fig. 9). Most significant declines of increments were recorded in July 2013, 2015 and in May 2017. By analysing significant residuals at selected spruce sites we identified climatic periods characteristic for different altitudes (Fig. 10). Negative impact of high summer temperatures on spruce growth was confirmed for the sites located at lower altitudes. Significantly positive residuals occurred exclusively in periods with high precipitation totals, while significantly lower residual values of spruce increments at higher altitudes were always in periods with low precipitation totals. An increasing sensitivity of *Picea abies* to precipitation and summer temperatures was also identified in the Tatra Mountain region (Büntgen et al. 2007). Recent changes in climate, especially the increase in temperature during the last decades, have been associated with drought stress in Norway spruce stands (Solberg 2004; Čermák et al. 2017). A large-scale evaluation of climate-growth effects showed that the productivity of spruce was more sensitive to climate compared to beech (Hlásny et al. 2017).

5. Conclusions

Knowledge on tree-growth responses to changing environmental conditions may help to detect shifts in forest development and may contribute to optimising future adaptive forest management. On the base of the regional case study in area of the Czech Republic and Slovakia, we assessed the effects of weather variables on intra-annual and annual diameter increments of the two most relevant forest tree species in the region. We conclude that in the time interval of weeks to years, data from manual dendrometers can contribute to understanding the changes in intra- and inter-annual radial growth and forest productivity. The evaluation of 8-year-long time series from regular dendrometric measurements pointed out at the different strategy of intra-annual radial growth of beech and spruce with regards to their reaction to water supply from precipitation and air temperature. Thus, at the studied measurement level (breast height), the performance of diameter growth of beech and spruce and its response to climate variables was obviously species-specific. However, recent findings point to the fact that the analysis of radial growth only at breast height may underestimate the influence of climatic conditions or/and disturbances on tree productivity (Rubio-Cuadrado et al. 2018).

At the lower altitudinal end of beech growth optimum, its annual increment was significantly reduced as the temperature increased. Similarly, negative impact of high summer air temperatures on spruce growth was confirmed at lower sites. Considering the climate sce-

narios that predict further increase of air temperature and reduced soil water availability in Europe (Jacob et al. 2014; Hlásny et al. 2017), this information can be taken as a signal that at lower altitudes beech and spruce productivity will be most probably limited by climate. This is a message for future forest management that should consider not only possible ecological risk but also economic efficiency.

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