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Influence of weather and day length on intra-seasonal growth of Norway spruce (*Picea abies* L. (Karst.)) and European beech (*Fagus sylvatica* L.) in a natural montane forest.

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Abstract

Intra-seasonal growth responses of co-occurring European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* L. (Karst.)) to weather variability in montane forests can provide useful information on their future growth trends. To improve growth predictions, we aimed to identify: i) the main seasonal windows during which weather variability influences tree-ring growth; ii) species-specific differences in the response to weather fluctuations; and iii) teleconnections to remote sites in the Western Carpathians. We monitored intra-seasonal growth dynamics based on proxies extracted growth signals detected by high-resolution dendrometers in transition zone between beech and spruce altitudinal belt. Within 12 consecutive seasons in the natural montane forest (1350 m a.s.l.), the main part of spruce (68% to 10 July) and beech (95% to 26 August) annual increment was under the prevailing influence of temperature. After this, precipitation pattern (regarding spruce) and day length became the most influential variables during deceleration and cessation of growth. In addition, synchronous patterns with remote sites in the Western Carpathians were found. The results emphasize the importance of studying the influence of shorter-term weather fluctuations during the season. Our findings suggest that montane spruce tends to be less temperature-demanding and more drought-sensitive than beech, which may favor beech over the spruce under the future climate.

Keywords: European beech, Norway spruce, intra-seasonal growth, weather response, high altitude

Introduction

High altitude montane forests providing important ecosystem services are sensitive to the changing climate, which probably seriously influence their functioning (Lindner et al. 2010; Treml et al. 2012) also in Central Europe and Carpathians (Bosela et al. 2018, 2019; Hlásny et

al. 2016, 2017; Ponocná et al. 2016, 2018). In the Western Carpathians, beech and spruce represent the most abundant tree species, although natural beech representation has been reduced by forest management practices due to a preference for spruce in the past. Unlike spruce, beech is a species with high potential for different climates (Hofmann et al. 2015) and its plastic responses to changes in environmental conditions have been reported (Stojnic et al. 2013). In higher altitudes, beech naturally grows below the spruce altitudinal belt which forms the upper timberline. It often penetrates as an admixture into the spruce stands from the lower beech-dominated altitudinal belt. Growth of spruce and beech was found to significantly accelerate over the last decades in Central Europe (Pretzsch et al. 2014; Bosela et al. 2019), which is in contrast with other findings (Dittmar et al. 2003; Hartl-Meier et al. 2014). However, there are still gaps in our knowledge of future impacts of climate change on growth and productivity of co-occurring tree species.

Several dendrochronological studies have been already done in the Western Carpathians and surrounding area dealing with climatic response (e.g. Dittmar et al. 2003; Büntgen et al. 2007; Levanič et al. 2009; Rybníček et al. 2009, 2010; Kolář et al. 2017; Bosela et al. 2018, 2019; Čermák et al. 2019) or disturbance regimes (Čada et al. 2013; Holeksa et al. 2017; Schurman et al. 2019). While parameters of tree rings analyzed through conventional dendrochronology are useful to explain the inter-annual variability of tree-ring growth, they are not suitable for gaining information with intra-annual resolution (de Micco et al. 2012). Thus many studies deal with the intra-annual growth dynamic at cellular level (e.g. Gričar et al. 2007; Gryc et al. 2011; Giagli et al. 2015; Treml et al. 2015; Prislan et al. 2018) or with approximating intra-annual growth by means of dendrometers (Deslauriers et al. 2003; Ježík et al. 2016; Rötzer et al. 2017; Van Der Maaten et al. 2018; Klisz et al. 2019).

The link of intra-annual growth to weather variability, especially in transition zones between different species is still lacking. To help increase our knowledge base, we focused on the

intra-annual increment processes of co-occurring European beech and Norway spruce during 12 consecutive seasons in the selected mountain region of the Western Carpathians. We have turned our attention on three main research goals: to determine whether increment proxies extracted from dendrometers and further processed allow us to identify the main seasonal windows during which weather variability influences annual tree-ring growth (G1); to identify species-specific differences in the response to weather fluctuations (G2); and find out whether established inter- and intra-annual chronologies would confirm synchronicity with remote sites in the Western Carpathians (G3).

Materials and methods

Study area

The major part of the study was conducted at an elevation of 1350 m a.s.l. (48°37'47" N; 19°27'43" E; Fig. 1). The experimental research plot, Predná Poľana, was established in the natural montane spruce forest located on the flat plateau of the eroded caldera of the extinct tertiary stratovolcano Poľana Mt. (1458 m a.s.l.). The mountain range is located in the southern part of the Western Carpathian Arc, where the warm Pannonian climate intersects with the Carpathian mountain climate. In these highest parts of the mountain range, old-growth primeval montane Norway spruce forests can be found at their southernmost distribution range in the Western Carpathians (WC, Sedmáková et al. 2019). Here, European beech represents an admixture species (together with European rowan (*Sorbus aucuparia* L.)), reaching its upper altitudinal distribution limit in WC. These stands are unmanaged, fully protected, and comprise part of the national natural reserve. The parent rock material is volcanic, and the soil type has been classified as a Dystric Cambisol. The area is characterized by a cold mountain climate with a mean annual temperature of 3.2 °C and annual precipitation of 1044 mm. Temperature and precipitation long-term average for

the period 1961–1990 were calculated from the nearest meteo-stations of the Slovak hydrometeorological institute in the area Víglaš-Pstruša (48.543735°N, 19.320141°E, 366 m a.s.l.) and Lom nad Rimavicou ((48.643878°N, 19.649233°E, 1019 m a.s.l.) based on vertical gradients.

The mosaic stand structure is highly differentiated in the density, height, and integrity of the main spruce canopy layer (with the stocking value about 0.6). Beech is present mostly in parts where the spruce stand and its canopy layer are more open. In these conditions, spruce form long crowns with branches often reaching the ground (typical mountain form), which also occurs with beech. For long-term monitoring of seasonal circumference variations, three beech trees representing common mean individuals were selected at the site (Table 1). Also, three spruce individuals were selected for measurement, belonging to the group of younger spruce trees where a high increment was expected. Their diameter, height, and age matched more selected beech trees than mean spruce trees that were much larger, but they were co-dominant regarding micro-sites of the area of younger trees. They were characterized by still young, smooth bark. During the years 2015–2016 another two beech individuals were measured, and during 2018 another four large dominant spruce trees.

Circumference variation and increment proxy extraction

Changes in stem circumference were monitored continuously during the 2007–2018 seasons. We used high-resolution band DRL26 dendrometers with embedded data loggers (resolution 1 µm; EMS Brno, Czech Republic), which were noninvasively fixed to the sample trees at a height of 2.5 m. The hourly mean values were derived from measurements taken at 30 min intervals. From the diurnal stem cycle (Fig. 2b), we calculated the curve of the daily stem circumference increase (proxy for stem growth; Ježík et al. 2016) as the degree to which the 6 a.m. (Central European Time) value circumference exceeded the previous 6 a.m. maximum

on the curve of the seasonal stem circumference. Seasonal daily increment (SCI) chronologies were derived as differences between consecutive days (Fig. 2c, d). We used relative values for intra-seasonal chronology construction. The chronologies of daily SCI (Fig. 2d) were divided by the whole sum of growth during 2007–2018 for each individual and computed as a percent (the whole process is presented on absolute values in Fig. 2, but we used these relative ones after the step on Fig. 2d). In order to enhance variance with approximate wavelengths of more than a week, chronologies were further processed by 13-day-long Hamming filters (low-pass filter) to obtain seasonal low-frequency SCI chronologies (Fig. 2e). There are gaps in the datasets for spruce after 15 July 2011 (for all three individuals) and after 30 July 2014 (for spruce 01). All these gaps, where we were not able to calculate mean values based on all three trees were omitted from the calculations for spruce. As we will see later, these gaps occurred during periods when most seasonal growth was already formed.

To demonstrate wider teleconnection of spruce with more remote sites in the Western Carpathians, we used available data from Tatranská Lomnica in the High Tatras. The data came from an experimental site (49°10'55" N; 20°14'30" E; Fig. 1) situated under the upper timberline (1380–1480 m a.s.l.); on top of this area (cca 1480–1490) montane spruce forest (dbh age 150 and more) reaches the timberline and changes into *Pinus mugo* stands. A total of 30 trees were measured on this site, but only nine of them (with sufficient growth trends) were selected (mean diameter = 34 cm, mean height = 22 m) for comparison due to old age (weak growth trends) and relatively large dimensions.

Tree ring data and dendrochronology measurements

To explore wider teleconnections of beech, the Poľana beech chronology (PZP) was compared with more remote sites in the Western Carpathians. The data from seven additional high-altitude beech chronologies were used (see Fig. 1). All cores were air-dried, glued onto

5.2 mm wooden bars, and sanded by grain paper (400–600 grain). TRW (tree ring width) was measured to the nearest 0.01 mm with a DAS digital positiometer (Sedmáková et al. 2019) or WinDENDRO (Density 2014c), after being scanned in 2400 dpi (EPSON Expression 11000 XL) and processed by standard methods. We compared mean CDendro (Cybis Elektronik & Data AB) heavily detrended chronologies (default parameters, divided by the mean of a frame of length 15 years - minimum 10 years, depreciation factor start value 0.9, and stepwise reduction factor 0.9) of these sites from 1900 to 2012 (technical note in Supplementary material).

Climatic data and meteorological measurements

An automatic meteorological station with an EMS33 sensor to measure air temperature and relative humidity (EMS Brno, Czech Republic) was established at an open patch close to the research stand (approximately 650 m, 1260 m a.s.l.). Meteorological variables were measured every 1 min and stored in 10 min intervals (2 m above ground). Precipitation was measured 1 m above the ground, using the tipping bucket rain gauge with a collecting area of 320 cm² (Met One 370, USA). The measured data were stored in an edgeBox V12 data logger (EMS Brno, Czech Republic) powered by a 12 V solar-charged battery.

Soil water potential (Ψ_{soil} , MPa) was continuously monitored under the forest canopy by a standard measuring set consisting of three calibrated gypsum blocs (Delmhorst Inc., USA) and a MicroLog SP3 data logger (EMS Brno, Czech Republic). The soil water potential values were in the range of 0 up to –1.5 MPa, which were at the lower measurable limit of the equipment. The measurements were conducted at three soil depths (15, 30, and 50 cm) during 2010–2018 (only one block at 30 cm during 2007–2009) and stored at 60 min intervals. In this work, we used the mean values of the 3 depths. Since the measurements were carried out only

on one point, this provided us with only a little information about Ψ_{soil} (occurrence of mosaic drought or pre-drought).

To calculate the average daily values of meteo variables used in intra-seasonal SCI response analysis, the hourly meteo and Ψ_{soil} values were shifted 18 hours forward to correspond to the time of circumference extraction. Therefore, for example, we calculated the temperature for 1 May as the average temperature in the 24 h preceding 6 a.m. on 1 May. The obtained data were processed using Mini32 software (EMS Brno, CZ). Chronologies of weather variables were further processed by low-pass filtering (Fig. 2e) using 13-day-long Hamming filters, for the purpose of using correlation analysis with appropriate low-frequency SCI chronologies.

Statistical analysis

Statistical analysis was performed using Statistica® statistical software (Statsoft, Tulsa, OK, USA) and Excel (MS Office). Simple Pearson's correlation coefficients (and R^2 based on them) were used for chronology comparison together with principal component analysis (variance obtained by the first eigenvector) as simple methods for chronology quality assessment and teleconnection analyses. Common signals in chronologies were further tested by expressed population signal (EPS; Wigley et al. 1984):

$$EPS = \frac{n\bar{r}_{BT}}{n\bar{r}_{BT} + (1 - n\bar{r}_{BT})}$$

where $\bar{r}_{BT}$ is average correlation between all pairs of trees, and n is number of trees in the calculation.

To model intra-seasonal increment processes, for spruce we calculated the Gompertz function:

$$y = Ae^{-be^{-cx}}$$

where A is the upper asymptote and b sets the curve displacement along the x axis, c determines the growth rate and x is time in DOY (day of the year).

For beech we calculated the Weibull function:

$$y = a \left(1 - e^{-\left(\frac{x}{b}\right)^c} \right)$$

where a is the upper asymptote, b and c are shape parameters and x is time in DOY. Functions were parametrised in their cumulative form based on cumulative SCI values, from which values of increment form were derived by simple differentiation.

To analyze the main factors controlling circumference growth and changes and their effects during the season, we used an intra-seasonal moving correlation function. From the chronologies of circumference increments (e.g., Fig. 5), time windows of 30 days (e.g., first from 1 April to 30 April) were selected from each year and joined chronologically across years (30 days from 2007 + 30 days from 2008 + ... + 30 days from 2018) for both species ($n = 12 \times 30 = 360$) and were shifted by one day towards the end of seasons (second window: 2 April to 1 May 2007 + 2 April to 1 May 2008 + ... + 2 April to 1 May 2018). In some windows the number of increments available for correlation was lowered, specifically for spruce after 9 July ($n = 330$, due to missing low frequency SCI data after this day in 2011) and after 24 July ($n = 300$, missing data after this day in 2014).

Results

Meteorological conditions and weather variability

The mean air temperature values were well above the long-term mean (1961–1990) across the whole 2007–2018 period (Fig. 3a). For the April–August period it represented +2.9 °C, and for the summer months (June–August) it was +3.0 °C above the long-term mean. From April to August, long-term mean was exceeded from 2.2 °C in May to 3.5 °C in August. Overall, we can characterize 2007–2018 vegetation periods (April–August/September) as very warm with varying precipitation amounts.

Regarding yearly deviations, we registered many marked anomalies for both temperature and precipitation (Fig. 3c, d). All months from April to August were at least normal during 2007–2018 and were frequently markedly warmer (more than 1° C), including extremes such as April 2009 and 2018 (+5.9 °C and 6.5 °C, respectively), May 2018 (+4.9 °C), June 2017 (+4.0 °C), July 2015 (+4.2 °C), August 2015 (+5.6 °C, with 17.3 °C being the hottest during observation) and 2018 (+5.2 °C). The period from April to August was the coldest in 2014 (+2.1 °C) and the warmest in 2018 (+4.6 °C), while summer months (June–August) were the coldest in 2014 (+1.9 °C) and the warmest in 2015 (+4.1 °C). Regarding precipitation, the most significant positive anomalies were registered in May (2010, 2013, 2015), July (2008, 2011, 2012, 2014, 2016), and then September and October. The highest negative deviations were in May (2009, 2012), June (2014, 2015, 2017), July (2013), August (2012).

Intra-seasonal dynamics of stem circumference increment and link to weather conditions

Low frequencies represent mainly increment and growth processes (Fig. 2f–i), while high frequencies are coupled with reversible variations, associated mainly with precipitation and abrupt weather changes. High values of the first eigenvector and EPS (Table 2) suggest a very high proportion of common variability in low frequencies for both species, which enabled us to use mean values for further analysis. The low-frequency variation forms a larger part of the variability for beech than for spruce and the increment function better fits the course of low frequency SCI extracted during individual years.

Figure 4 illustrates yearly increments obtained by dendrometers. Beech reached the lowest increment in 2011 and spruce in 2013. Intra-seasonal courses of the low frequency SCI (Fig. 5) and results of intra-seasonal moving correlation function (Fig. 6) clearly show similarities and differences between responses of both species. This is also reflected in the mean 2007–2018 trends calculated from all seasons (Fig. 7). At the beginning of a season, the main factor

influencing SCI variability seems to be accumulation of temperatures above 5 °C from the beginning of April (Fig. 6). This influence was the greatest on spruce until 9 June, after which the influence of average daily temperature (during the day of SCI formation or preceding days) was the prevailing factor up to 10 July, with a short comeback between 25 and 27 July. From the end of May to the end of the season, there was an increased difference between the day of SCI formation and preceding days, with the temperature of the preceding 4–5 days having the most influence. The strongest influence of precipitation among weather variables (mainly during day of SCI formation) was recorded from 14 July to the end of the season. As for beech, the highest impact of temperature accumulation lasted until 28 June, followed by a dominating influence of daily temperature until 26 August and subsequently by daylength to October. In contrast with spruce, there were not such big differences in the influence of temperature between days of SCI formation and preceding days until mid-August, with temperatures of the preceding 2–3 days having the most and the preceding 5 days the least influence. The influence of precipitation started to increase from the end of August and became dominant from 7 October. The above results summarize the impact of main factors over 12 studied seasons. Spruce (Fig. 7) tends to start and accelerate its increment earlier at the beginning of the season than beech (exceeding the threshold value of 0.025 on 20 May (2.4% of seasonal SCI) vs. 1 June for beech (2.1%)). It also culminates earlier (18 June vs. 8 July, according to increment functions) and continuously decelerate SCI earlier in the season (exceeding the threshold value of 0.025 until 3 August (86.6%) vs. 27 August for beech (95.3%)). Unlike the individual seasons, we found a somewhat higher fit of the increment function to smoothed curves for spruce than beech, which culmination is flatter (forming a high plateau) than that approximated by the Weibull function. The impact of main factors over 12 studied seasons sometimes differed distinctly during the individual seasons following different weather courses (Fig. 5, Fig. S1). By studying monthly

increments (Fig. S2a, b) we can conclude that June was the most important month for the annual SCI formation of spruce. It was followed by July and May (in 2007 and especially 2018) during years with a warm or hot spring (2018) and/or the end of May. Thus, the low frequency SCI (Fig. 5) of spruce started at the beginning of May during 2018 or accelerated rapidly in the second half of May (2007). Low SCI during June and especially July was the main cause leading to the lowest annual SCI of spruce during 2013. By studying monthly SCI of beech, it is obvious that the most important month for annual SCI formation was July, followed by June and/or August (Fig. S2c, d). During the remaining months SCI of beech was negligible. High SCI in June was connected most probably to either high temperature accumulation (2007, 2018; Fig. 3) and/or the hot June itself (2007, 2008, 2017, 2018). Low SCI during July and August was the main cause of the lowest annual SCI of beech during 2011.

Teleconnections to remote sites in the Western Carpathians

The course of previously analyzed intra-seasonal spruce chronology (three individuals) is highly synchronous with the course of huge dominant trees (Table 1) from the same area as well as with nine mature trees growing at a remote high-altitude site (just under the timberline) in Tatranská Lomnica (TL; Fig. S3a, Table S1). Their characteristics and mutual fit (Table S1) as well as principal component analysis (Fig. 8a) point to a surprisingly higher common synchronicity between Predná Poľana (three younger long-term studied individuals) and the remote site of TL than between trees coming from the same site. This occurred particularly at the end of the season, which was connected to the occurrence of late seasonal drought, the compensation after rain events (Fig. S1), and may be linked to some differences in dendrometer installation.

Regarding beech, intra-seasonal chronologies follow the same synchronous pattern when we also include additional individuals during 2015 and 2016 (Table 1, Fig. S4). We can also confirm wider teleconnections (Fig. 8b) of beech chronology with more remote sites (Fig 1, Table S2). Focusing on the 2007–2018 period (Fig. S3b), we registered that chronologies from sites in the south-central part (PZP, VLR, and VTK) on volcanic parent rocks reached the lowest RWI in 2011.

Discussion

Intra- and inter-seasonal dynamics of stem increment, their connection, link to climate and weather conditions, teleconnections to remote sites

Seasonal growth of stem tissues (phloem and mainly xylem) due to new cell production and expansion is linked to environmental factors, including photoperiod, temperature, and drought stress (Deslauriers et al. 2003; Rossi et al. 2006; Köcher et al. 2012; Takahashi and Koike 2014; Chan et al. 2016) through functional processes involving also source-sink relationships and hormonal controls (Savidge 2001; Rathgeber et al. 2011). Sedmáková et al. (2019) stated that based on a gradient study in the area, recent warming had a significant impact on the growth of two main species, European beech and Norway spruce. The growth of spruce and beech was released in the montane and high-montane belts and suppressed in sub-montane conditions in 1991–2012. In relation to this, in natural montane forest, spruce responded positively to April–July temperatures as well as July precipitation, while beech responded mostly to summer (June–August) temperatures, when the influence of temperature in July and August was the most pronounced (Fig. S5). These results are more or less in accordance with further dendrochronological studies on spruce (Büntgen et al. 2007; Levanič et al. 2009; Treml et al. 2012; Van Der Maaten-Theunissen et al. 2013; Sidor et al. 2015; Ponocná et al. 2018; Čermák et al. 2019), beech (Dittmar et al. 2003; Piovesan et al. 2005; Bosela et al.

2018), or both species (Hartl-Meier et al. 2014; Kolář et al. 2017; Bosela et al. 2019). Many studies have also examined the intra-annual growth dynamics of these two species (Ježík et al. 2016; Van Der Maaten et al. 2018; Rötzer et al. 2017; Klisz et al. 2019), but few included montane sites at high altitudes (Leca et al. 2015; Carrer et al. 2017; Prislan et al. 2018). Detected responses to weather variability differed for the two species between different altitudes and site conditions. Whereas at lower altitude sites mostly the positive influence of spring temperatures and the negative impact of high summer temperatures and precipitation shortages were revealed (Gričar et al. 2014; Giagli et al. 2015; Ježík et al. 2016; Rötzer et al. 2017; Klisz et al. 2019), at higher altitudes the positive response to summer temperature tended to predominate (Rossi et al. 2007, 2008; Treml et al. 2015). In accordance with the presented findings, spruce inclined to be less temperature-demanding and more drought-sensitive than beech. For both species, intra-annual increment formation started and culminated earlier at lower-altitude sites and cessation was prompted many times by the occurrence of drought.

The low frequency signal of increment proxies was correlated against the low frequency signal of weather variables via intra-seasonal moving window across all twelve seasons. This enabled us to identify main factors influencing the intra-seasonal increment dynamics. The examination of "pointer years" 2011 and 2013 for beech and spruce shows the main causes leading to low SCI formation (narrow rings). By exploring average intra-seasonal trends (Fig. 7) during 12 seasons (Fig. 5) and their response to weather (Fig. 6), we noticed similarities and specific differences in their seasonal biorhythm and links to weather variations. The formation of the smallest increments in 2011 and 2013 was linked to these differences. It seems that for both species the most important factor was the occurrence of repeated negative weather conditions, such as extreme cooling during the period of onset of increment formation, then around culmination, when there was a predisposition for a high level of

increment and the highest proportion of seasonal increment was created on average. Also cooling in the period after usual culmination may have led to early cessation of growth (probably in interaction with the photoperiod). These facts were obvious during 2011, when the coolest July occurred, which is the month with the highest impact on beech increment. Beech produced greater increment during August 2010 and 2014 than in 2011 (Fig. S2c), despite lower August temperatures (-1.3 °C and -2.4 °C, respectively, Fig. 3c) due to more continuous favorable temperature conditions following July (Fig. 5). Substantial cooling occurred towards the end of May and at the beginning of June 2013. The occurrence of the morning frost on 27 May, may have caused shock to an already reactivated cambial zone of spruce (Begum et al. 2013). Rossi et al. (2008) stated that air temperatures for the onset and ending of xylogenesis were around 4–5, 5–9, and 13–14 °C for daily minimum, mean, and maximum, respectively. Rossi et al. (2007) cited 5.6–8.5 °C for mean daily temperature, and noted similar thresholds among *Larix decidua*, *Pinus cembra*, and *Picea abies* supposed to limit growth at the treeline. Cambial activity occurred from May to July/August and cell differentiation from May/June to September/October. Giagli et al. (2015) reported following values for 130 resp. 45 years old beech stands: 5.0, 8.0 and 11.2 °C, resp. 5.4, 8.5 and 11.8 °C for daily minimum, mean, and maximum temperatures. No significant differences were found between different ages of stands. Treml et al. (2015) stated 8.3 and 11.3 °C for air temperatures, resp. 1.6 and 4.6 °C of soil temperatures for the onset and “significant increase” in cambial activity. In this context Rossi et al. (2013) point out the linear relationships between different cambial phenological phases, when shifts of one phenological phase are associated with synchronous and comparable shifts of the successive phases. However, relationships between phenological timings and cell production were distinctly non-linear and involved an exponential pattern.

We can again speculate on whether spruce would have been able to produce higher SCI during July 2013 if the temperature course had been the opposite, reaching the same monthly average. The positive impact of precipitation on spruce SCI was registered in July (when the influence of temperature gradually decreased), and more markedly in August. This points out the sensitivity of spruce to a lack of precipitation and summer heat waves even at such high-altitude environments. We also registered a much smaller fit of the Gompertz function (Table 2) to the unusual course of intra-seasonal SCI chronology of spruce than during other years (Fig. 5). A lack of precipitation and subsequent Ψ_{soil} decrease might have slightly also influenced beech during August 2013 (Fig. S2). This was probably more pronounced on remote sites at some lower altitudes (Fig. S3b). Low RWI values in 2016 on remote sites SHS and PRE are likely associated with masting (personal observation on VLR site cored in 2015), which plays an important role in the inter-annual growth variation (Hacket-Pain et al. 2017). Spruce growth was found to be much more sensitive to drought than beech growth, most probably the consequence of their different water conservation strategies (isohydric vs. anisohydric; Rötzer et al. 2017). Cabon et al. (2020) found that cambial activity of larch and spruce was strongly constrained by both temperature and water potential at all elevations up to treeline along a 900 m elevational gradient in the Swiss Alps. Sedmáková et al. (2019) reported also about the influence of July temperature on spruce growth (Fig. S5). This seemed to be disappearing during recent extreme hot years. Generally, we can state that most of the annual SCI of both species was under the rule of temperature (either alone or together with accumulated temperatures in spring); regarding spruce, about 68% was produced during this time (to 10 July), and for beech about 95% (to 26 August). After this time, day length (more pronounced for beech) and precipitation pattern (more pronounced for spruce) were ruling variables during deceleration and cessation of SCI formation. Although the influence of day length was not so clear from the statistical analysis

for spruce, spruce culmination occurred around the summer solstice (Table 2, Fig. 7). This is in accordance with Rossi et al. (2006) that conifers in cold environments synchronize their maximum rate of tree-ring formation with day length. Whereas beech culmination was shifted toward the temperature culmination and the following cessation was associated with day length. In addition, spruce formed most of its increment until the end of July, while for beech, August SCI formation was very important. In the context of global warming and in agreement with Lenoir et al. (2008) and Sedmáková et al. (2019), we may expect that the enhanced competitive ability of beech in the high-montane zones provides the potential for a shift of beech distribution from the lower beech-dominated altitudinal belt into higher altitudes dominated by spruce in East-Central Europe.

Stem size variations, SCI (increment proxy) extraction, and processing

Stem size variations recorded by dendrometers are primarily attributed to two components: (a) irreversible seasonal growth of stem tissues discussed above; and (b) reversible variations connected to water potential expressing water balance of stem tissues. These are linked with depletion and recovery of tree water storage reservoirs, buffering an imbalance in transpiration, transportation, and water uptake by roots (e.g., Betsch et al. 2011; Köcher et al. 2012) or partially seasonal changes in osmotic concentration (Mencuccini et al. 2013). To minimize signals linked with reversible changes we used SCI extraction (Fig. 2b). A daily increase of morning (6 a.m.) circumference compared to the previous maximum on the seasonal curve was considered as a proxy for daily increment. This procedure minimizes inter-morning as well as more long-term shrinkage and recovery swelling occurring during periods of drought, heat waves, and precipitation deficits, leading also to decreased tree water status or deficit (Sánchez-Costa et al. 2015). Nevertheless, studying similarly derived daily or even hourly increment proxies (Deslauriers et al. 2003; Wang et al. 2016) still reflects the

impact of precipitation and stem water balance on increment, also at sites with no drought occurrence and relatively low atmospheric evaporative demands. This suggests the presence of reversible variation and/or the importance of water balance related to turgor pressures inevitable for cell enlargement. Therefore, these problems cannot be solved without models that include these phenomena (Chan et al. 2016; Coussement et al. 2018). Consequently, to further minimize problems with reversible variation, we used the low-frequency part of the daily SCI spectrum, which is linked to daily increment patterns and seasonal growth (Fig. 2f, h). Whereas the high-frequency spectrum (reversible variation; Fig. 2g, i) is strongly associated with precipitation and abrupt changes in humidity and atmospheric evaporative demands. Moreover, spruce trees monitored over the long term were younger than the main canopy layer of mature spruce trees in the area, with still relatively high increment. By comparing small younger and large older spruce trees, we can simply register the differences at the end of the season during the presence of drought (Fig. S11, S3a), which also emphasizes the importance of outer bark removal. Younger individuals measured permanently during 2007–2018 on PP were characterized by still smooth bark, which was easily further smoothed by a hard plastic brush. Regarding the older trees, this procedure was only enough to clean the thin outer part of the rough grooved bark, because we worked in a strictly protected area and did not want to leave bigger visible signs on the trees (the dendrometers used were non-invasive). In TL, on the other hand, the outer bark of the trees was almost completely removed before installation. European beech, with its smooth thin bark and harder wood, seems to be an ideal species for dendrometer measurements related to growth processes, which also suggests a higher proportion of low-frequency variability (Table 2). Beech with the smallest yearly increment and highest proportion of high-frequency variation during the period of cessation of continuous growth was selected for demonstration in Fig. 2.

Conclusions

The major part of the study was done in the central part of the Western Carpathians, representing sites where beech penetrates from lower altitudes into natural montane spruce forests. Also, wider teleconnections to similar, more remote sites in the Western Carpathians were found.

Response of the low-frequency part of the spectrum of daily stem circumference increase (SCI, as a proxy for increment) to the corresponding part of the spectrum of weather variables was identified using an intra-seasonal moving correlation window across all twelve seasons. This enabled us to recognize the main factors and changes in their influence during the seasons. The main part of annual SCI formation was under the prevailing influence of temperature for both spruce and beech, but with different time windows during the season. Both species responded positively to temperature (and its accumulation) from the beginning of the season to around mid-July, and regarding beech, this influence (which was also stronger) lasted until the end of the main growth period (end of August to beginning of September). In the case of spruce, the main part of seasonal increment was created until the end of July, during which precipitation gradually became the main factor influencing SCI, while August SCI formation was very important for beech. The results bring new insights into the field of dendrochronology emphasizing the importance of studying the influence of shorter-term weather fluctuations, which are not sufficiently reflected in analyses based on monthly averages and totals.

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Fig. 1. (a) Location of the Western Carpathians arc in Europe. (b) Locations of study sites: Pol'ana Mt. (E, dashed white rectangle), high altitude beech chronologies sites (A-H, Table S2), high altitude near spruce timberline site in Tatranská Lomnica (white dot). (c) Detail of extinct tertiary stratovolcano Pol'ana, with part 1 (Predná Pol'ana, white dot indicate place of dendrometers instalation) and part 2 (Zadná Pol'ana), white lines delineate altitude range of

721 1280-1300 m a.s.l., where beech forests reach their upper distribution limit in the Western
722 Carpathians. Above this line montane spruce forests predominate sparsely admixed with beech.
723 (The map was created using Esri ArcMap 10.1., Base maps: (a) GTOPO30 (30 Arc Seconds)
724 – USGS, ESRI Data & Maps 2004 DVD (ESRI, Redlands, CA, www.esri.com), (b, c) SRTM
725 90m Digital Elevation Database (Jarvis et al. 2008))

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Fig. 2. The method of daily SCI (a-d) and principles of the low- and high frequency spectrum extraction (d-i). Daily increment proxies (SCI) were calculated from 1-hour averages at 6 am (which was approximately the peak from the part of stem expansion phase) as the part to which the stem circumference exceeded the previous morning maximum on the cumulative

curve of circumference changes (b, c). The data were further processed (along with weather variables) by low-pass filtering (e) to obtain low-frequency SCI (f) as a proxy for daily increment, which is associated with growth (h, cumulative growth form), while high frequencies (g) represent reversible changes (i, cumulative form). (Note: the example on the figure is in absolute values, but we used relative ones (obtained values were standardized as a proportion (in %) from the whole 2007–2018 SCI) for each tree after step on d)

Fig. 3. (a) The average 2007–2018 monthly temperature (green line) and the long term average (red dashes), (b) the average 2007–2018 monthly precipitation totals (blue bars) and the long term average (red dashes), (c) monthly temperature and (d) precipitation totals during 2007–2018 and the long term average (black dashes). Capital letters on x-axis refer to months within the season.

Fig. 4. The annual 2007–2018 increments for spruce (blue) and beech (green). Vertical lines represent 95% confidence intervals. All values were indexed against 2007–2018 mean. * mark 2011 and 2014, when there were gaps in datasets and real increment of spruce should be slightly higher. SCI – stem circumference increment index.

Fig. 5. The mean intra-seasonal daily SCI low-frequency chronologies of spruce (blue line) and beech (green line) and low-frequency daily mean temperature (dotted red line) during

2007–2018 (a-l). The first derivation of Gompertz function for low frequency chronologies of spruce (dashed grey line) and Weibull function for beech (dashed black line).

Fig. 6. Intra-seasonal moving correlations (30-day moving window for the each season) between low frequency SCI of spruce (a, b, c) and beech (d, e, f) and daylength (a, d, dotted red line), low frequency of: sum of temperatures above 5 °C from April 1 (a,d, solid red line), daily mean temperature (b, e, from current day (red line) up to 5 days preceding (dashed violet line)), daily precipitation totals (c, f, from current day (red line) up to 5 days preceding

(dashed violet line)). Correlations are dated towards the last day of 30-day window. Strips on the bottom mean the highest response of SCI to: daylength (a, d, yellow), and among weather variables (excluding daylength) to sum of temperatures above 5 °C from April 1 (a, d, orange), daily mean temperature (b, e, red), daily precipitation totals (c, f, blue). Dashed horizontal lines represent 95% significance level (Note: the critical values of correlation coefficients were calculated as approximations by simplified approach ignoring existence of autocorrelation in time series of correlated variables).

Fig. 7. The average 2007–2018 intra-seasonal low-frequency chronologies (red line, vertical grey represents 95% confidence intervals) smoothed by 21-day Hamming filter (blue line) of spruce (a) and beech (b). Gompertz and Weibull functions calculated to smoothed lines with their fit (R^2). Relative growth curves (green lines) calculated from smoothed (blue) curves. Strips on the upper part means the highest response of SCI to: daylength (yellow lower strip), and among weather variables (excluding daylength) to sum of temperatures above 5 °C from April 1 (orange), daily mean temperature (red), daily precipitation totals (blue).

Fig. 8. (a) Principal component analysis of spruce intra-seasonal chronologies during 2018 in Predná Poľana (blue, younger trees, $n=3$), red (old trees, $n=4$) and Tatranská Lomnica (green, $n=9$). (b) Principal component analysis of beech CDendro heavy detrended chronologies for time interval 1901–2012 (sites on volcanic parent rock with the lowest RWI in 2011 during 2007–2018 are red). PC1–2 – principal component 1–2.

Table 1. Basic characteristics of trees monitored on Predná Poľana.

Tree_no.	dbh [cm]	height [m]	period of measurement	Social status (Kraft)
Beech 01	30.9	15.0	2007-2018	subdominant
Beech 02	37.2	16.0	2007-2018	co-dominant
Beech 03	30.9	13.5	2007-2018	co-dominant
Beech 04	37.2	14.0	2015-2016	dominant
Beech 05	22.6	12.0	2015-2016	subdominant
Spruce 01	48.1	24.5	2007-2018	co-dominant
Spruce 02	31.2	21.0	2007-2018	co-dominant
Spruce 03	34.1	19.0	2007-2018	co-dominant
Spruce 04	72.6	28.0	2018	dominant
Spruce 05	69.1	25.0	2018	dominant
Spruce 06	68.4	27.5	2018	dominant
Spruce 07	70.3	28.0	2018	dominant

Note: Social status classes (crown canopy classes) after Kraft: (1 = dominant, 2 = codominant, 3 = subdominant, 4 = suppressed, 5 = dying)

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Table 2. Basic characteristics of studied intra-seasonal chronologies during 2007-18.

year	spruce				beech			
	LF [%]	PC1 [%]	EPS	Gompertz function fit (R ²) [%], culmination	LF [%]	PC1 [%]	EPS	Weibull function fit (R ²) [%], culmination
2007	59.5	98.7	0.994	69.7, (June 10)	65.4	98.5	0.992	85.8, (June 28)
2008	36.6	98.3	0.992	83.6, (June 21)	55.3	98.0	0.990	88.9, (July 4)
2009	44.1	98.4	0.992	69.4, (June 19)	57.0	99.1	0.996	90.1, (July 14)
2010	56.6	98.1	0.990	60.5, (June 25)	62.9	97.8	0.989	90.3, (July 15)
2011*	60.6	99.6	0.998	66.2, (June 9)	63.7	97.5	0.987	73.7, (July 3)
2012	49.3	98.5	0.993	83.6, (June 11)	69.0	99.1	0.995	91.5, (July 6)
2013	56.8	97.9	0.989	26.5, (June 28)	77.6	97.4	0.987	76.0, (July 15)
2014*	42.9	97.3	0.986	70.3, (June 26)	65.0	98.1	0.990	83.3, (July 12)
2015	54.4	96.9	0.984	54.2, (June 21)	66.9	96.2	0.980	76.4, (July 7)
2016	45.9	96.6	0.982	74.9, (June 24)	65.0	98.8	0.994	85.2, (July 9)
2017	43.2	94.3	0.970	72.7, (June 23)	65.8	97.8	0.988	76.7, (July 7)
2018	46.5	98.0	0.989	79.6, (June 2)	62.2	91.1	0.951	66.8, (July 1)

Notes: * There are missing data in low-frequency chronologies of spruce after July 9, 2011 and after July 24, 2014