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DENDROCLIMATIC STUDY OF A MIXED SPRUCE-FIR-BEECH FOREST IN THE CZECH REPUBLIC

DENDROKLIMATOLOŠKA ŠTUDIJA MEŠANEGA SMREKOVO-JELOVO-BUKOVEGA GOZDA V ČEŠKI REPUBLIKI

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Abstract / Izvleček

Abstract: *European forests are undergoing an important transition due to the current climate change, as monocultures are being gradually replaced by mixed forests. Understanding tree growth in mixed forests under a changing climate is challenging because of tree species' adaptation and long-term forest planning. In this study, we evaluate the long-term behaviour of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) from a low montane range at the Czech-Austrian border. Species-specific tree-ring width chronologies have revealed significantly decreasing growth trends since the 2000s. Temporally unstable climate–growth relationships showed an increasing negative effect of current growing season drought on spruce growth and a positive effect of dormant season temperature on fir and beech growth. Our results suggest that though species' response to climate change differs in the mixed forest, growth reduction in the last years has been proved for all species, likely due to frequent climate extremes.*

Keywords: Abies alba*,* Fagus sylvatica*,* Picea abies*, tree-ring width chronology, climate change, growth trends, mixed forest, Gratzen Mountains*

Izvleček: *Evropski gozdovi doživljajo pomembne spremembe zaradi trenutnih podnebnih dogajanj, ko monokulture postopoma nadomeščajo mešani gozdovi. Razumevanje, kako rastejo drevesa v mešanih gozdovih v spreminjajočem se podnebju, je izziv zaradi njihovih prilagoditev in dolgoročnega gozdnogospodarskega načrtovanja. V tej raziskavi smo ovrednotili dolgoročno obnašanje navadne smreke (*Picea abies*), bele jelke (*Abies alba*) in navadne bukve (*Fagus sylvatica*) iz nizkega montanskega pasu na češko-avstrijski meji. Kronologije širin branik za posamezne drevesne vrste od leta 2000 izkazujejo negativne trende rasti. Časovno nestabilne odvisnosti rasti od klime so pokazale naraščajoč negativni vpliv suše med tekočo rastno sezono na rast smreke in pozitiven učinek temperatur v obdobju mirovanja na rast jelke in bukve. Naši rezultati kažejo, da čeprav se odzivnost na podnebne spremembe razlikuje med posameznimi vrstami v mešanem gozdu, je bilo v zadnjih letih dokazano zmanjšanje rasti za vse vrste, najverjetneje zaradi pogostih izjemnih vremenskih dogodkov.*

Ključne besede: Abies alba*,* Fagus sylvatica*,* Picea abies*, kronologije širin branik, podnebne spremembe, trendi rasti, mešani gozd, Novohradské hory*

1 INTRODUCTION
1 UVOD

Norway spruce (*Picea abies* L. Karst) and European beech (*Fagus sylvatica* L.) are among the most widespread tree species in continental Europe (Euforgen, 2009). Although Norway spruce was less represented in Central European forests until the 18th century (Jansen et al., 2017), planting of its monocultures far beyond the limits of its natural range in the last two centuries has made this species very important socio-economically (Caudullo et al., 2016). Because of the intensification of human interventions in forests, manifested especially by the enforcement of spruce monocultures since

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the 19th century, the distribution of silver fir (*Abies alba* Mill.) markedly decreased in the Czech Republic (Kozáková et al., 2011). Currently, extensive spruce forest dieback due to increased pathogen and insect outbreaks (Marini et al., 2016) has led to the gradual conversion of conifer monocultures into more stable mixed forests with an abundant proportion of deciduous trees, especially European beech (Pretzsch et al., 2014). The historical changes described in forest management strategies caused that mixed spruce-fir-beech forests, which are typical of natural or extensively managed submontane forests, are nowadays relatively scarce (FMI, 2007). At present in the Czech Republic about 50% of the forest cover is represented by Norway spruce, 9% by European beech and only 1% by silver fir (RPFD, 2020). Spruce and beech, as the most widespread coniferous and broadleaved species with a wide range of utilization, are very important for wood technology and wood economy in the country.

Climatic fluctuations have a substantial impact on forest ecosystems (Hartl-Meier et al., 2014). The current climate change manifested by a significant temperature increase (Štěpánek et al., 2016) together with the decreasing soil moisture content (Trnka et al., 2015) can lead to a reduction in tree vitality and higher vulnerability of forest stands (Kölling & Zimmermann, 2007). Tree responses to climate change have been frequently studied in Central Europe for spruce (e.g. Koprowski, 2013; Rybníček et al., 2012), fir (e.g. Koprowski, 2013; Latreille et al., 2017), and beech (e.g. Bošeľa et al., 2018; Kolář et al., 2016). Most of these studies have presented the general conclusion that altitude is the leading factor controlling growth in temperate forests (Bošeľa et al., 2014), i.e. the growth of forest trees at high altitudes and latitudes is mainly limited by temperature (Leonelli et al., 2016), and of those at low elevations by precipitation and/or drought (Dobrovolný et al., 2016). Additionally, pure stands, especially even-aged conifer monocultures, are vulnerable to disturbances caused by climate change (Felton et al., 2017). By contrast, uneven-aged mixed stands seem to have better resilience (Lafond et al., 2014). Given that tree responses to a changing climate can significantly differ between pure and mixed stands (Nothdurft & Engel, 2020), it is important to study both kinds of stands in detail to support forest adaptation and mitigation strategies (Conte et al., 2018) and wood production.

In this study we used tree-ring width (TRW) series to analyse the radial growth of Norway spruce, silver fir and European beech growing at the same mixed forest stand since the 1960s. The study aims to investigate 1) the growth trends of these species in the last few decades when climate has been getting significantly warmer and drier, and 2) temporal climate-induced changes in the growth variability. We hypothesized that growth of *Picea abies* with a shallow root system is significantly more sensitive to unprecedented temperature increases accompanied by drier conditions than *Abies alba* and *Fagus sylvatica*, which have larger ecological niches and more differentiated root system stratifications.

2 MATERIALS AND METHODS
2 MATERIAL IN METODE

2.1 MATERIAL
2.1 MATERIAL

The Gratzen low mountain range along the Czech-Austrian border is a part of south and south-eastern foothills of the Bohemian Massif. The highest peak is the Viehberg on the Austrian side, reaching 1,112 metres a.s.l. The region consists of several old-growth forests and peat bogs. About

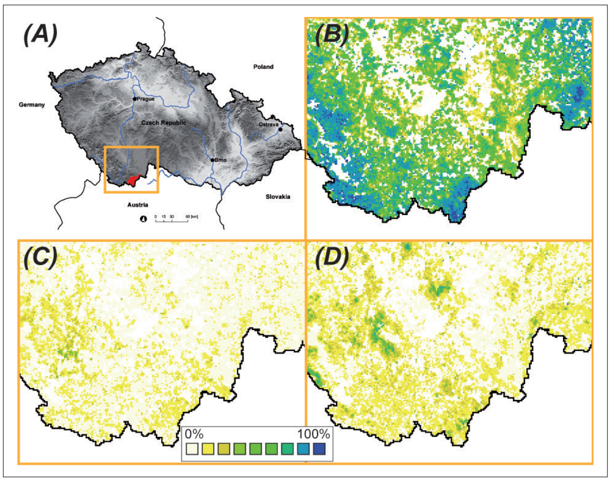

Figure 1. The Gratzen (Novohradské) Mountains at the Czech-Austrian border (A) and the current distribution of Picea abies *(B),* Abies alba *(C) and* Fagus sylvatica *(D) in the southwestern part of the Czech Republic.*
*Slika 1. Novohradské hory na češko-avstrijski meji (A) in trenutna razširjenost smreke (*Picea abies*) (B), bele jelke (*Abies alba*) (C) in navadne bukve (*Fagus sylvatica*) (D) na jugozahodnem delu Češke republike.*

three quarters of the region are covered by coniferous (approx. 90%) and deciduous forests, mostly represented by fir-beech and spruce-fir-beech forests. Currently, Norway spruce is the dominant species in the region (Fig. 1), cultivated mostly in monocultures, though originally European beech prevailed in the region (RPFD, 2020).

The study was performed in a spruce-fir-beech mixed forest stand (48.72481N, 14.73666E) located at 850 m a.s.l. in the north-eastern area of the Gratzen Mountains. During the focal period (1961–2017), the mean annual temperature was 6.2 °C. The lowest mean temperatures appear in January (-3.0 °C), the warmest months are June (15.2 °C) and August (14.9 °C). Annual precipitation totals vary from 660 to 1240 mm, with the highest totals in the summer months. During the April–August growing season the mean temperature ranged between 9.8 °C and 14.1 °C and precipitation totals between 340 and 700 mm. Increases in the annual mean temperature, evapotranspiration and precipitation totals were observed from 1961 to 2017. The relative soil water content (AWR) in the first 1.3 m of the soil profile slightly decreased in this period (Fig. 2).

2.2 TRW SAMPLING, CHRONOLOGY DEVELOPMENT AND VISUAL ASSESSMENT OF CROWN CONDITION

2.2 VZORČENJE LESA, SESTAVA KRONOLOGIJE IN VIZUALNA OCENA STANJA KROŠNJE

The sampling sites were selected in a mixed spruce-fir-beech forest. One core per tree was extracted (Kirdyanov et al., 2018) using a Pressler borer at breast height (1.3 m) along the contour line to avoid compression wood. Tree-ring width was measured on the cores using the VIAS TimeTable measuring system (©SCIEM, Austria) with 0.01-mm accuracy. The measuring and cross-dating of tree-ring width (TRW) series were performed using the PAST4 (©SCIEM, Austria) and COFECHA (Grissino-Mayer, 2001) programmes. The coherency among the individual TRW series was assessed using t-test Baillie and Pilcher (1973), t-test Hollstein (1980), Gleichläufigkeit (Eckstein & Bauch, 1969), and an optical comparison of the series. In order to remove non-climatic, age-related growth trends from the raw TRW series as well as other non-climatic factors (e.g. competition), cubic smoothing splines with a 50% frequency

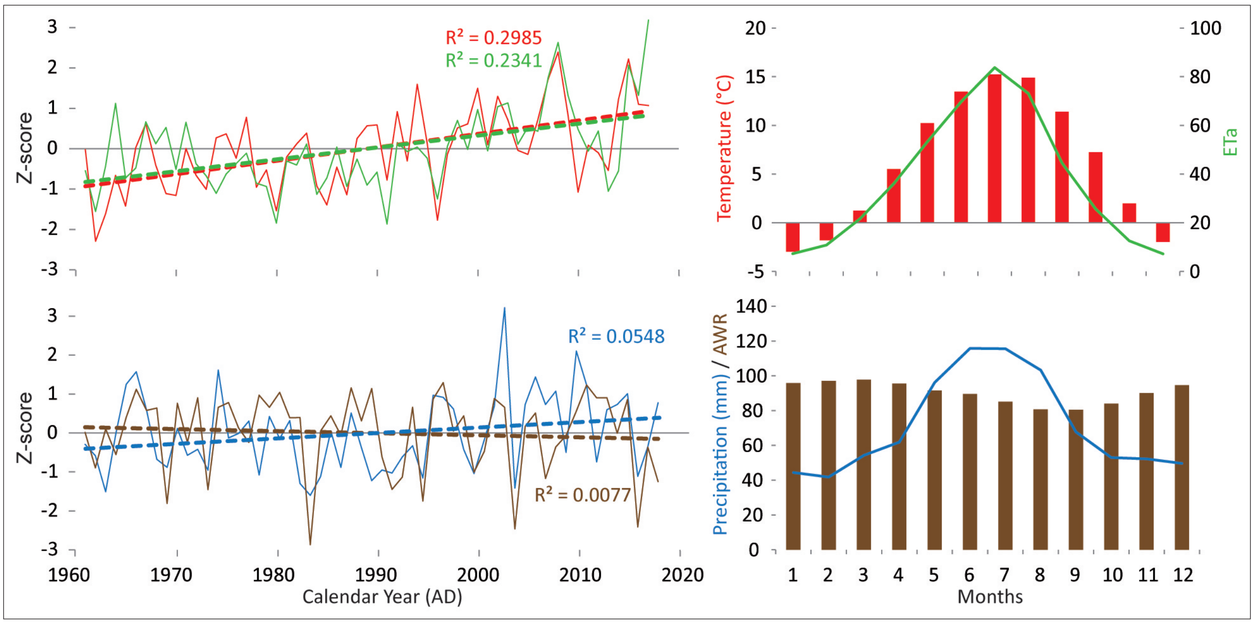

Figure 2. Annual standardized values with coefficients of determination (left) and climate diagram (right) of mean temperature, precipitation totals, evapotranspiration (Eta) and soil moisture content (AWR; depth 0–1.30 m) for the study site from 1961 to 2017.

Slika 2. Letne standardizirane vrednosti z determinacijskimi koeficienti (R^2) (levo) in klimograma (desno) za povprečne mesečne temperature, vsote padavin, evapotranspiracijo (Eta) in vsebnosti vlage v tleh (AWR; globina 0–1,30 m) za raziskovalno ploskev od leta 1961 do 2017.

cut-off at 100 years were applied (Cook & Peters, 1981) using the ARSTAN software (Cook & Krusic, 2005). This standardization method was chosen due to its flexibility, as each raw TRW chronology revealed a different growth trend (Fig. 3), and because of its ability to preserve inter-annual to multi-decadal growth variations. TRW indices (TRWi) were calculated as residuals after the appropriate power transformation of the raw data to minimize end-effect problems (Cook & Peters, 1997). Mean TRW species-specific chronologies were calculated using bi-weight robust means, and their signal strength was assessed using the inter-series correlation (Rbar) and the Expressed Population Signal (EPS) (Wigley et al., 1984).

Concurrently, we visually evaluated crown condition of the same trees using binoculars (Cudlín et al., 2001; Eichhorn et al., 2010). We assessed the following parameters in summer (July): total defoliation, proportion of secondary shoots (both in intervals of 5%), stem foliation, discolouration, i.e. yellowing and browning (unspecific damage symptoms), and fruiting, with the number of trees having these features being recorded. Defoliation was defined as needle/leaf loss in the assessable crown compared to a local reference tree (Eichhorn et al., 2010), and was observed regardless of the cause of lost foliage.

2.4 CLIMATE DATA
2.4 KLIMATSKI PODATKI

Climate data were derived from the 500-m-resolution gridded daily dataset for the location (48.72481N, 14.73666E, 850 m a. s.l.) based on the interpolation from a set of nearby weather stations by applying the local weighted regression and accounting for the effect of the altitude. The original station series were subjected to quality control and homogenization using ProClimDB (Štěpánek, 2007). All observations of the weather variables were tested for outliers and breaks using a detailed homogenization sequence, and the gaps of missing data were filled. All weather elements could be interpolated using the high-density network for the sampling site (Štěpánek et al., 2011). The database for the research area included daily data on the maximum and minimum temperatures, precipitation and global radiation totals and the daily mean wind speed and water vapour pressure. Using the AgriClim (Trnka et al., 2012) and SoilClim (Hlavinka et al., 2011) software packages, the daily soil moisture content (expressed as relative water availability – AWR; depth 0–1.3 m) was calculated. The AWR is estimated for a daily time step accounting not only for the balance among evapotranspiration, precipitation and the antecedent AWR, but also for the snow presence/absence, aspect and slope of the site, critical soil water holding properties, and the phenological stage of the canopy. This routine was based on the approach proposed by Allen et al. (1998) and described in detail by Hlavinka et al. (2011) and Trnka et al. (2015).

2.3 ANALYSIS OF GROWTH TRENDS AND GROWTH-CLIMATE RELATIONSHIPS
2.3 ANALIZA RASTNIH TRENDOV IN ZVEZE MED RASTJO IN KLIMO

Growth trends of the species-specific TRWi chronologies were explored during three delineated periods to find the species' response to the effects of environmental factors during the study period (1961–2017). The delineated periods were established based on the main and previously studied environmental changes. The first period (1961–1980) was characterized by increasing air pollution in Central Europe (Smith et al., 2011), the second (1980–2000) by gradual pollution control and concurrent temperature increase (Kolář et al., 2015), and the most recent period (2000–2017) by an unprecedented rise in temperature (Neukom et al., 2019). Simple linear regressions were calculated in the R package to show growth trends during the delineated periods.

The residual TRWi chronologies were used to calculate the correlation with the climatic variables in the treeclim R package (Zang & Biondi, 2015) for the period 1961–2017. Given that monthly correlations were generally low and mostly insignificant (not presented), correlation coefficients in 20-year moving windows for the previous growing season (previous April–previous August), dormant season (previous September–March) and growing season (April–August) of the year of tree-ring formation (referred to as the "current year") were calculated.

3 RESULTS AND DISCUSSION
3 REZULTATI IN RAZPRAVA

3.1 CHARACTERISTICS OF THE SPECIES-SPECIFIC CHRONOLOGIES
3.1 ZNAČILNOSTI KRONOLOGIJ POSAMEZNIH VRST

The species-specific TRW chronologies representing one mixed forest stand cover the common period of 1890–2017. These raw TRW chronologies, each replicated by seventeen trees, showed various growth characteristics (Tab. 1). The influence of juvenile wood on TRW was confirmed by the relationship between the mean segment lengths and the average growth rate, because the shortest beech series correspond to their widest TRW. Fir and beech showed a considerably higher growth variability (expressed by standard deviation) compared to spruce, especially in the most recent period (Fig. 3), even if the fir chronology was represented by very old trees. By contrast, the high growth variability of beech resulted from its highest age diversity. The high first-order autocorrelation of the fir raw TRW chronology indicates a greater temporal memory than in beech and spruce. These characteristics were also reflected in different growth trends of raw TRW chronologies. The increasing growth trend of fir mainly from 1980 to 2000 is in contradiction to the gradual growth decrease of spruce since the 1980s. However, beech showed an apparent decline of TRW in the first 60 cambial years followed by an unexpected rising growth trend, peaking in the 1930s, and a substantial growth reduction since the 1990s. The visual assessment of crown conditions showed the most damaged crowns in the case of spruce trees, where defoliation was more than double in comparison to fir and beech. The relatively high portion of secondary shoots in spruce and stem foliation in fir point to crown regeneration processes during the last ten years. However, while fir crown condition was improved thanks to the foliation, the current spruce crown condition is noticeably worse, which was indicated by marked defoliation or even the secondary shoots.

Table 1. Basic characteristics of the tree-ring width chronologies and tree habitus of Picea abies, Abies alba *and* Fagus sylvatica*.*

Preglednica 1. Osnovni podatki o kronologijah širin branik in habitusih dreves za vrste Picea abies, Abies alba *in* Fagus sylvatica*.*

Species	Tree number	Tree-ring width chronology / Kronologija širin branik									Tree habitus / Habitus drevesa				
		MSL	AGR	SD	Rbar	EPS	AC1	Start	End	Length	TD	SS	SF	Dis	Fr
Vrsta	Število dreves	MSL	AGR	SD	Rbar	EPS	AC1	Začetek	Konec	Dolžina	TD	SS	SF	Dis	Fr
Picea	17	108	1.92	0.67	0.44	0.84	0.70	1890	2017	128	40.3	44.7	–	1	17
Abies	17	147	1.63	0.94	0.24	0.83	0.83	1831	2017	187	17.3	–	11	12	16
Fagus	17	80	2.61	1.09	0.33	0.87	0.76	1849	2017	169	18.2	–	0	2	11

MSL, mean segment length; AGR, average growth rate (mm); SD, standard deviation; Rbar, inter-series correlation; EPS, expressed population signal (minimum EPS in the studied period); AC1, first autocorrelation; TD, total defoliation (%); SS, secondary shoots (%); SF, stem foliation (no. of trees); Dis, Discoloration (no. of trees); Fr, Fruiting (no. of trees with beech masts / spruce and fir cones).

MSL, srednja dolžina segmenta; AGR, povprečna stopnja rasti (mm); SD, standardni odklon; Rbar, medsektorska korelacija; EPS, izražen populacijski signal (minimalni EPS v proučevanem obdobju); AC1, avtokorelacija prve stopnje; TD, skupna defoliacija (%); SS, sekundarni poganjki (%); SF, olistanost (št. dreves); Dis, diskoloracija (št. dreves); Fr, semenenje (št. dreves z bukovim žirom / smrekovimi in jelovimi storži).

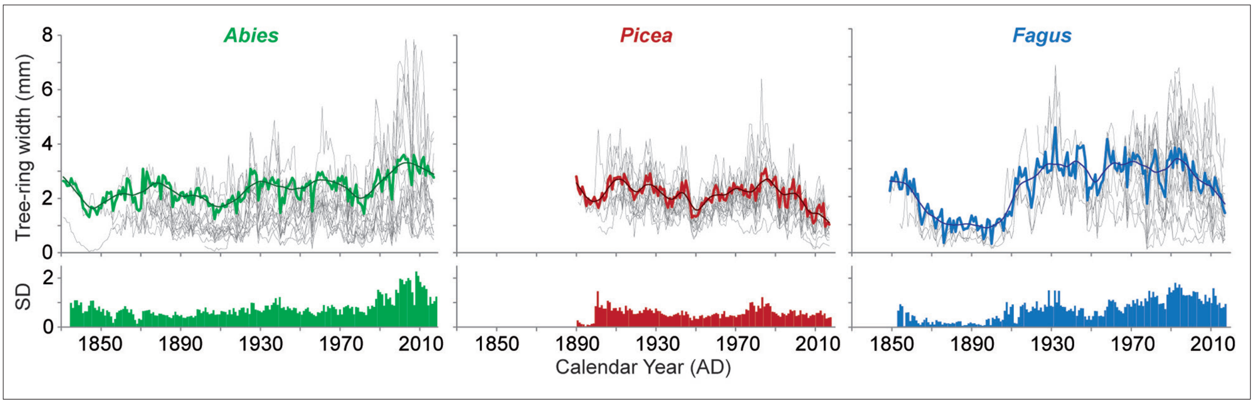

Figure 3. Tree-ring width chronologies (up) and standard deviation (down) of Abies alba*,* Picea abies *and* Fagus sylvatica *smoothed by the LOWESS (Locally Weighted Scatterplot Smoothing) curves. Individual TRW measurements are in grey.*

Slika 3. Kronologije širin branik (zgoraj) in standardni odklon (spodaj) za vrste Abies alba*,* Picea abies *in* Fagus sylvatica*, zglajene po metodi LOWESS. Posamezna zaporedja širin branik so prikazana v sivi barvi (zgoraj).*

3.2 ANALYSIS OF GROWTH TRENDS
3.2 ANALIZA RASTNIH TRENDOV

Growth trends of the standardized TRWi chronologies as evaluated by linear regression in the three delineated periods showed a wide variation of growth among species (Fig. 4). In the first period, beech and fir growth significantly declined, whereas spruce growth was stable. This period was characterized by a relatively stable climate (Fig. 2), but ended in the extremely cold and harsh winter of 1978/1979. An intensive cold front hit the Czech lands on 31 December 1978 and 1 January 1979. The meteorological stations recorded a sudden drop in temperature (approximately 25 °C in 24 h) from approximately +10 °C at the New Year's Eve night of 1978/1979 (Rein & Štekl, 1981). Beech and fir radial growth is very sensitive to climate changes and especially very cold winters (Koprowski, 2013; Šimůnek et al., 2019), which are more pronounced at higher altitudes. Short-term growth disturbances and growth depressions at the end of the 1970s were observed in tree ring series of beech trees growing on higher altitude sites in Central Europe, leading to the assumption that increased tropospheric ozone concentrations are involved in the process of changed beech sensitivity and resistance (Dittmar et al., 2003).

Additionally, air pollution could play an important role in the growth decline of silver fir because of its high vulnerability to emissions, as was recorded at the Czech–Polish–German border (Łuszczyńska et al., 2018), where extensive forest dieback occurred and hardly any fir stands in this region have been preserved until today. The SO_2 and NO_x emissions increased strongly after approximately 1950 (Smil, 1990), and peaked at the beginning of the 1980s (Kopáček & Veselý, 2005). Although our study site is quite far from the main foci of air pollution in the Black Triangle (Grübler, 2002), the whole territory of Czechoslovakia was markedly influenced and a significant effect on fir was also observed in Southern Germany (Elling et al., 2009). Therefore, air pollution together with the harsh winter of 1978/1979 most likely caused the substantial growth trend decline of silver fir, which is more susceptible to air pollution and sudden winter frosts than Norway spruce (Mikulenka et al., 2020).

From the early 1980s, radial growth of beech and fir suddenly started to improve (Fig. 4) together with growth variability among TRW series (Fig. 3) as a consequence of the previous apparent growth depression. Rapid growth recovery was probably caused by a complex of several factors, such as release after the harsh winter accompanied by a gradual temperature increase (Štěpánek et al., 2016), as well as pollution control, especially in the case of pollution-sensitive fir. Given that common growth variability can be interpreted as a similar response to climatic conditions, similarities among TRW series should increase under harsh climatic conditions when the same response of all trees is expected. Therefore, this sudden growth release and more favourable conditions (also evident from moving correlations getting near to zero; Figs. 5B and 5C) led to the high common inter-series growth variability of fir and beech. On the other hand, spruce growth, not impacted by the previous reduction, was slightly decreasing in this delineated period, which could be caused by the warming climate, in particular during the current growing season (see climate-growth relationship). Additionally, the still slightly decreasing spruce growth variability suggests that the warmer and drier climate has become more and more limiting to its growth.

At the beginning of the 21st century, the unprecedented growth improvement of conifers at higher elevations, mainly silver fir, was related to global warming (e.g. Büntgen et al., 2014; Bošeľa et al., 2018). However, all three species at the site in the Gratzen Mountains revealed statistically significant decreases (Fig. 4) despite, or likely due to, the continuing temperature increase. Although precipitation totals also increased slightly and available water in the soil moisture demonstrated no trend, evapotranspiration, owing to higher temperatures, showed a substantial increase (Fig. 2). Additionally, the period since 2000 is characterized by severe summer heat waves and drought spells, particularly in 2003 (Luterbacher et al., 2004) and 2015 (Ionita et al., 2017), with significant impacts on silviculture, agriculture, and viniculture (e.g. Možný et al., 2016; Brázdil et al., 2015; Štěpánek et al., 2016). Such phenomena can lead to the severe tree growth reduction of fir (Bošeľa et al., 2018), beech (Kolář et al., 2016), and especially spruce (Čermák et al., 2019), which is characterized by high transpiration demands and a shallow root system already threatened by short droughts. The drying of the upper soil could be intensified by a decreasing stand density (sanitary felling). These may also be the reasons why Norway spruce TRWi already decreased in the 1981–2000 period.

3.3 GROWTH–CLIMATE RELATIONSHIP
3.3 ZVEZA MED RASTJO IN KLIMO

The results of growth trends were reflected in the moving correlation coefficients between species-specific TRWi chronologies and climate parameters that have not been stable over time (Fig. 5). The radial growth of Norway spruce had been significantly negatively affected by evapotranspiration during the previous April–August, but the influence disappeared in the last twenty years. By contrast, an increasing positive effect of soil moisture content (to significant values) and precipitation together with a sharply increasing negative effect of temperature during current April–August emerged at the end of the study period (Fig. 5A). Water deficits during the growing season lead to the reduction of stomatal conductance, carbon uptake and tree growth (Lévesque et al., 2013). These relationships

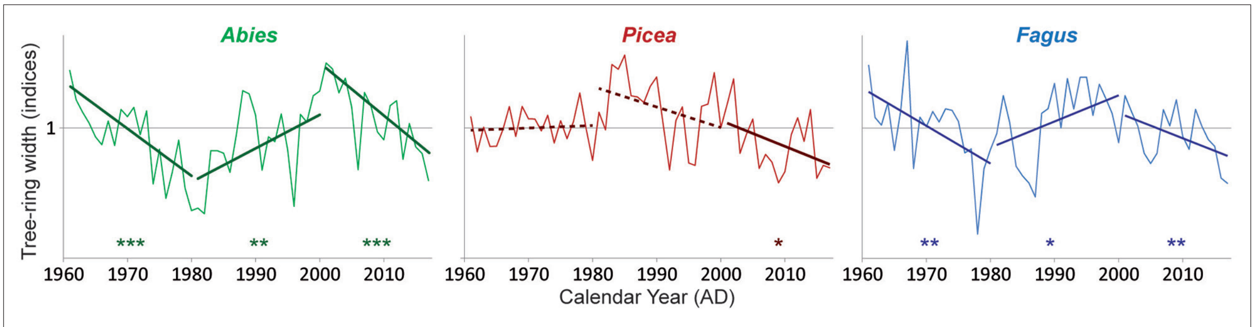

*Figure 4. Standardized TRW chronologies for the period (1961–2017) with linear regression fitted to standardized data in three intervals (1961–1980, 1981–2000 and 2001–present). Full lines show a significant regression trend, dashed lines non-significant trends. Stars indicate the significance level of regression at: *** - < 0.01, ** - < 0.05, and * - < 0.1.*

*Slika 4. Standardizirane kronologije širin branik za obdobje (1961–2017) z linearno regresijo, prilagojeno standardiziranim podatkom v treh intervalih (1961–1980, 1981–2000 in 2001-danes). Polne črte kažejo statistično značilen regresijski trend, črtkane črte pa neznačilnega. Zvezdice kažejo stopnjo statistične značilnosti regresije pri: *** - <0,01, ** - <0,05 in * - <0,1.*

indicate increasingly unfavourable climate conditions for Norway spruce growth, as previously reported for many areas of Central Europe, including its southern regions (e.g. Hartl-Meier et al., 2014; Lévesque et al., 2016; Kolář et al., 2017; Martinez del Castillo et al., 2018; Čermák et al., 2019).

All climate parameters of the previous growing season seem to be less important for silver fir growth than the winter dormant period and current growing season (Fig. 5B). While the significance of negative correlations with the current April–August precipitation totals and positive correlations with April–August evapotranspiration disappeared, the September–March temperature started to be statistically significant with values exceeding 0.6 (Fig. 5B). The strong positive impact of winter temperature has confirmed the high sensitivity of fir to extreme winter frosts (van der Maaten-Theunissen et al., 2013) as well as late winter/early spring temperature (Koprowski, 2013). The effect of late winter temperature is related to the relatively high temperature which is needed to start the photosynthetic activity (Guehl, 1985).

The results of beech growth-climate relationship showed a generally negative impact of drought during the previous growing season, which was recorded not only in Central Europe (e.g. Scharnweber et al. 2011) but mainly in the southern regions of the Mediterranean (e.g. Čufar et al., 2008; Tegel et al., 2014; Martinez del Castillo et al., 2018). By contrast, the dormant season temperature had a positive impact on TRW (Fig. 5) which is related to late frost sensitivity of European beech (e.g. Menzel et al., 2015; Kolář et al., 2016). The current growing season soil moisture content and precipitation totals reduced while tem-

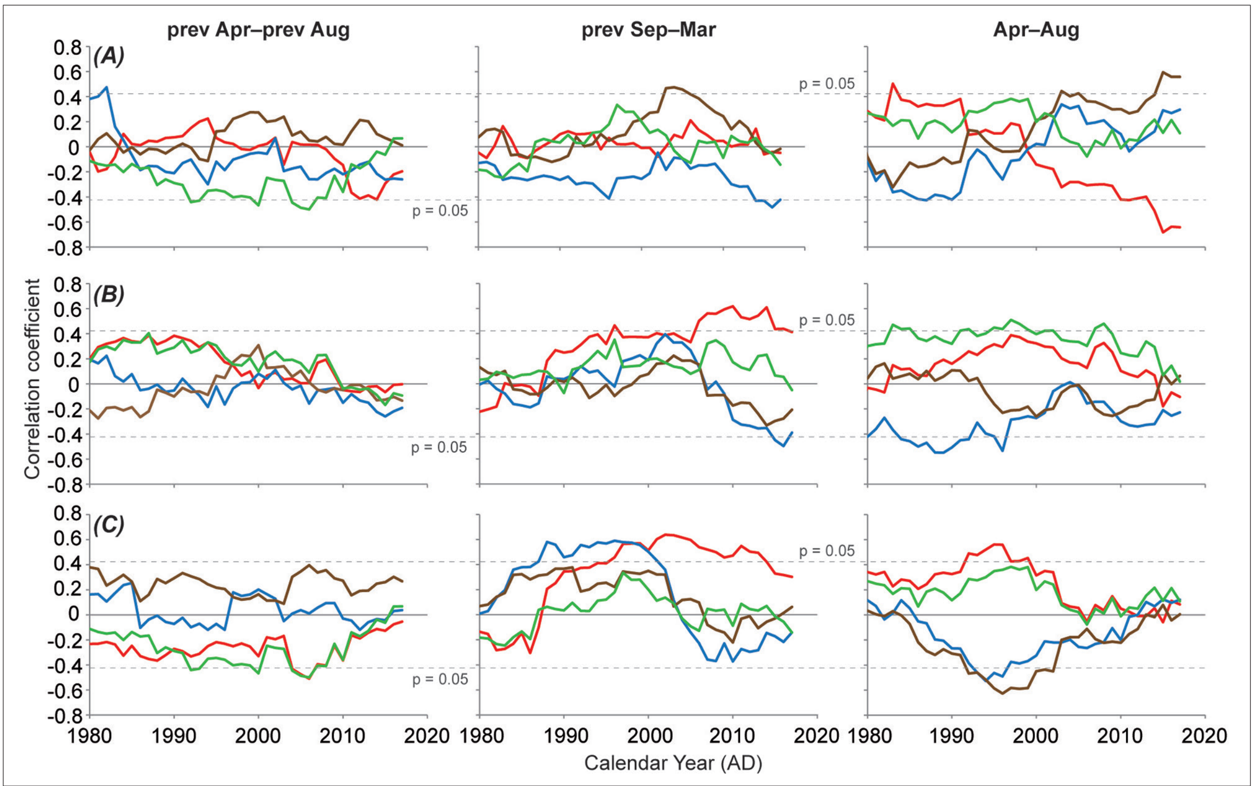

Figure 5. Twenty-year moving backward Pearson's correlation coefficients between residual TRW index chronologies of Norway spruce (A), silver fir (B) and European beech (C) and mean temperature (red), precipitation (blue), soil moisture content (brown) and evapotranspiration (green) for the previous growing season (left column), dormant season (middle column) and current growing season (right column).

Slika 5. Dvajsetletni Pearsonovi drseči korelacijski koeficienti med residualnimi kronologijami indeksov širin branik smreke (A), jelke (B) in bukve (C) ter povprečne temperature (rdeča), vsote padavin (modra), vsebnosti vlage v tleh (rjava) in evapotranspiracija (zelena) za predhodno rastno sezono (levi stolpec), obdobje mirovanja (srednji stolpec) in tekočo rastno sezono (desni stolpec).

perature enhanced beech radial growth (above all during the 1990s; Fig. 4, 5C), as already found for other areas, e.g. in the Western Carpathians and Southern Alps (Bošeľa et al., 2018). However, the correlation coefficients with all climate parameters in the current growing season have fallen near to zero since 2000.

The changes in fir and beech growth-climate relationships described above, especially for the current growing season, are probably connected to the growth decline after 2000 (Fig. 4). It seems that both species have stopped benefiting from the increasing temperature, which most likely initiated radial growth increases in the 1990s (Büntgen et al., 2014). It is assumed that the climatic extremes such as tropical days or a decreasing number of wet days during spring and summer (Štěpánek et al., 2016; Beranová & Kyselý, 2017) started to limit radial growth and disturb the relationships between monthly climate parameters and TRW.

4 CONCLUSIONS
4 ZAKLJUČKI

Our study showed that even if Norway spruce, silver fir and European beech grow in a mixed forest stand under the same conditions, each species displays different growth patterns and climate responses. While spruce has responded negatively to the recent warmer and drier climate, fir and beech have been proved to be more tolerant to drought and actually benefited from a temperature increase, especially during winter, due to the lower danger of extreme frosts. These patterns were reflected in growth trends as well as the visual assessment of the crown. Whereas fir and beech most likely profited from the significant rise in temperature of 1981–2000, spruce already exhibited a decreasing growth trend in that period. Although the growth trends of all species have significantly decreased since 2000, suggesting that more frequent climatic extremes limit the radial growth of all species, spruce seems to be the most vulnerable under such conditions, even in a mixed forest at quite a high elevation of 850 m a.s.l. This was also proved by the high total defoliation and the number of secondary shoots. Therefore, the projected scenarios of climate change, including recurrent climate extremes, should mainly be the cause of serious concern with regard to the spruce.

5 SUMMARY
5 POVZETEK

Evropski gozdni ekosistemi doživljajo pomembne spremembe zaradi trenutnih podnebnih sprememb, ko prej razširjene monokulture postopoma nadomeščajo mešani gozdovi. Razumevanje rasti dreves v mešanih gozdovih v spreminjajočem se podnebju je svojevrsten izziv zaradi prilagoditve drevesnih vrst in dolgoročnega gospodarjenja z gozdovi. V tej raziskavi smo proučili dolgoročno obnašanje navadne smreke (*Picea abies*), bele jelke (*Abies alba*) in navadne bukve (*Fagus sylvatica*) iz nizkega montanskega pasu v pogorju Novohradské hory na češko-avstrijski meji. Vzorce lesa za dendrokronološke raziskave smo pridobili iz odraslih dreves s pomočjo prirastoslovnega svedra. Sledila je priprava vzorcev, merjenje širin branik, sinhroniziranje, sestavljanje kronologij širin branik in analiza zveze med rastjo in klimo vzorcev rastnega in podnebnega odziva, pri čemer smo uporabili standardne dendrokronološke metode. Analize širin branik smreke, jelke in bukve, ki rastejo na 850 m n. m. v., so najprej omogočile sestavo treh kronologij širin branik, dolgih 128, 187 in 169 let, pri čemer je vsaka odražala prirastne značilnosti posamezne vrste. Raziskave so pokazale, da čeprav smreka, jelka in bukev rastejo v mešanem gozdu v enakih razmerah, vsaka vrsta kaže drugačen vzorec rasti in različen odziv na klimo. Medtem ko se je rast smreke negativno odzvala na nedavno toplejše in bolj suho podnebje, se je za jelko in bukev izkazalo, da bolje prenašata sušo in naraščanje temperatur, kar ima zlasti pozimi pozitiven vpliv predvsem zaradi manjše nevarnosti hudih zmrzali. Omenjeni vzorci so se odražali tudi v rastnih trendih in vizualnih ocenah krošenj. Medtem ko sta se jelka in bukev pozitivno odzvali na dvig temperatur v obdobju 1981–2000, je smreka že v tem obdobju kazala trend upada širin branik. Čeprav se trendi rasti vseh vrst znatno zmanjšujejo od leta 2000, kar kaže na to, da pogostejše vremenske skrajnosti omejujejo radialno rast vseh treh drevesnih vrst, se zdi, da je smreka v razmerah podnebnih sprememb najbolj ranljiva tudi v mešanem gozdu na precej visoki nadmorski višini 850 m. Slednje se je odražalo tudi v propadanju krošnje, ki ga spremlja izguba iglic in sekundarnih poganjkov. Glede na predstavljene ugotovitve bi morali biti napovedani scenariji podnebnih sprememb, vključno s ponavljajočimi se vremenskimi skrajnostmi, vzrok za resne skrbi predvsem za uspevanje in preživetje smreke.

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