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The increasing drought sensitivity of silver fir (*Abies alba* Mill.) is evident in the last two decades

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Abstract: Silver fir (*Abies alba* Mill.) is still counted among drought-tolerant tree species. However, its ability to cope with the recent extremely dry period has not yet been sufficiently studied. The objective of research was to analyse differences in the climate-growth response between silver fir, Norway spruce (*Picea abies* L. Karst.) and European larch (*Larix decidua* Mill.) growing in areas with large-scale disintegration of spruce stands. In 2019–2021, the increment cores were sampled at 16 sites along the altitudinal gradient of 340–775 m a.s.l. in different regions of the Czech Republic affected by bark beetle outbreak. The radial growth pattern of fir was compared with that of spruce or larch growing under the same site conditions. In fir, the missing rings were frequently recorded during the period of peak SO_2 pollution load in 1966–1985, but they were rarely identified in recent years. In spruce and larch, missing rings were less common and occurred mainly in the recent dry period after 2015. Fir was less sensitive to summer drought compared to larch and especially to spruce, which showed high sensitivity to summer drought regardless of the altitude. The significant positive response of fir to summer precipitation was recorded at sites up to 450 m a.s.l., however, its sensitivity to drought has increased in the last two decades. Hence, when considering the wider use of fir, it is necessary to respect its ecological requirements as much as possible in order to preserve its vitality and production potential in changing climatic conditions.

Keywords: Czech Republic; dendrochronology; European larch; growth; Norway spruce

Forest ecosystems have been under heavy pressure from environmental changes (Allen et al. 2010; Seidl et al. 2017). The rise in air temperatures, more frequent and intense periods of drought and heat waves affect forest trees significantly (Senf et al. 2020). Species that grow in limiting ecological conditions, whether it is at the xeric edge of their distribution range or outside their ecological niches, are prone to drought-induced dieback (Camarero et al. 2013; Gazol et al. 2015; Gazol, Camarero 2016). In addition, climate scenarios predict a continued significant rise in temperatures by 2050, negatively affecting tree performance (Buras, Menzel 2019). Therefore, the key issue for forest management is the resistance and resilience of individual tree species to drought.

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In Europe, silver fir is a key tree species for maintaining a high biodiversity of forest ecosystems thanks to its shade tolerance, plasticity to environmental conditions and ability to coexist with many tree species (Dobrowolska et al. 2017). In relation to the predicted climate changes, the higher resistance of fir to drought (Zang et al. 2014) and the ability to withstand low temperatures during the winter (Savill et al. 2016) are important. At the same time, however, it is necessary to take into account the higher sensitivity of fir to low air humidity (Guicherd 1994) and late frosts (Úradníček et al. 2009).

The vast decline of Norway spruce and Scots pine (*Pinus sylvestris* L.) has been observed in recent years in the Czech Republic and other Central European countries (Bošela et al. 2021; Haberstroh et al. 2022). The primary cause was recurrent droughts with subsequent activation of biotic pests and pathogens (Cienciala et al. 2017). In the regions of North Moravia and the Bohemian-Moravian Highlands, with intense spruce dieback, we observed survival of vital silver fir populations.

Previous dendroecological studies proved that silver fir is more drought tolerant than Norway spruce, European larch or European beech (*Fagus sylvatica* L.) (van der Maaten-Theunissen et al. 2012; George et al. 2019; Vitasse et al. 2019a) and similarly drought tolerant to Douglas fir (*Pseudotsuga menziesii* /Mirb./ Franco) (Vitali et al. 2017). However, the fir ability to cope with the recent dry period, which has been extreme in duration and intensity, has not yet been sufficiently studied.

Here, we analyse the growth pattern and spatiotemporal variation in the climate-growth response of Silver fir (Sf), Norway spruce (Ns) and/or European larch (El) growing in mixed stands distributed in different regions of the Czech Republic along the altitudinal gradient between 340 m a.s.l. and 775 m a.s.l., which corresponds with the altitudinal zone of intensive spruce dieback. The aim of the study was to confirm or refute differences between the studied tree species in terms of sensitivity to drought and to assess the temporal stability of the climate-growth relationship. We hypothesize that even fir trees have recently become more sensitive to rising temperatures and lack of precipitation due to chronic drought stress, which is gradually leading to the depletion of the tree internal reserves.

MATERIAL AND METHODS

Study sites. The study was carried out in the Czech Republic in five different regions (Table 1, Figure 1). The regions of Město Albrechtice and Černá Hora represent areas where large-scale disintegration of spruce stands has already occurred, while in Tábor, Rožmitál and Písek, the decline of spruce still has a patchy character. The original intention was to compare the growth dynamics of fir and spruce, but due to the high mortality of spruce in the Město Albrechtice region, it was necessary to include larch in the comparison, because spruce was no longer available at altitudes up to 500 m a.s.l.

In each region, 2–5 mature stands where fir occurred in a mixture with spruce or larch were chosen. A total of 16 sample sites were selected (Table 1, Figure 1) covering an altitude gradient of 340–775 m a.s.l. and representing nutrient-medium, nutrient-rich and moist sites according to forest ecosystem classification (Viewegh et al. 2003). According to the Köppen-Geiger climate classification, all sites are in the Dfb category, i.e. humid continental climate with warm summers (Beck et al. 2018). Most sites belong to the upper colline vegetation belt, sites MA5, ROZ2 and ROZ3 can be classified as submontane (Chytrý 2017). The sites, except MA5, are characterized by mean annual temperatures between 8.6 °C and 9.3 °C and total annual precipitation ranging between 588 mm and 705 mm. Site MA5 is cooler and wetter, with a mean annual temperature of 7.8 °C and annual precipitation of 859 mm (Figure 2). The climatic characteristics were calculated based on monthly temperature means and monthly precipitation sums obtained from Climatic Research Unit gridded Time Series (CRU TS) with 0.5° resolution (Harris et al. 2020) for the assessed period 1962–2018. Standard forest management is applied in all stands with the exception of MA5, which is located in a nature reserve. Most of the managed stands are single-layered, even-aged, 100–135 years old, established by artificial regeneration with regular thinning application. The two oldest stands, ROZ2 and MA4, probably originated from natural regeneration. Site MA4 was the only one recorded with an age difference between tree species, where fir was about 50 years older than larch and spruce.

Data collection. Increment cores were collected in 2019–2021 during the dormant season. At least

Table 1. Basic characteristics of sample sites

Region	Site	Coordinates		Altitude (m a.s.l.)	Forest type complex	Stand age (years)	Species sampled
		latitude	longitude				
Tábor	TB1	49.3703	14.6716	441	4H	98	Sf, Ns
	TB2	49.4047	14.5653	460	3S	135	
	TB3	49.4112	14.6362	410	4A	127	
Rožmitál	ROZ1	49.5546	13.8056	590	5O	116	Sf, Ns
	ROZ2	49.5665	13.7805	775	6S	195	
	ROZ3	49.5502	13.7672	705	5K	113	
Písek	PS1	49.2861	14.2886	430	3H	108	Sf, Ns
	PS2	49.2940	14.2919	410		108	
Černá Hora	CH1	49.5690	16.7636	610	5K	99	Sf, Ns
	CH2	49.5661	16.7951	540	4S	107	
	CH3	49.5644	16.7763	540	5U	120	
Město Albrechtice	MA1	50.2343	17.5768	340	4B	115	Sf, El
	MA2	50.1858	17.6181	450	4S	137	Sf, El
	MA3	50.2119	17.5306	540	4S	124	Sf, Ns, El
	MA4	50.1519	17.5068	640	4A	169	Sf, Ns, El
	MA5	50.1238	17.4044	710	5B	187	Sf, Ns

3H – loamy oak-beech; 3S – nutrient-medium oak-beech; 4A – stony-colluvial lime-beech; 4H – loamy beech; 4S – nutrient-medium beech; 4B – nutrient-rich beech; 5B –nutrient-rich fir-beech; 5K – acidic fir-beech; 5O – nutrient-medium beech-fir; 5U – moist ash-maple floodplain; 6S – nutrient-medium spruce-beech; Sf – silver fir; Ns – Norway spruce; El – European larch

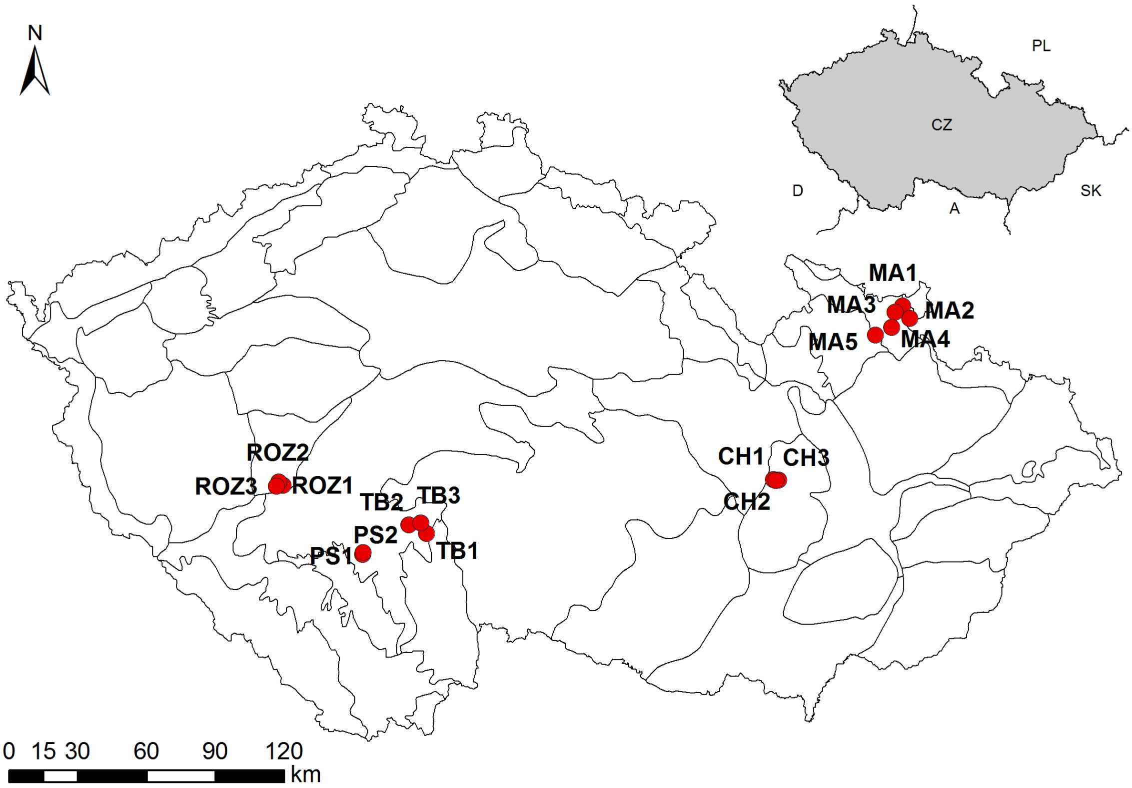

Figure 1. Localization of sample sites against the background of the forest nature areas of the Czech Republic

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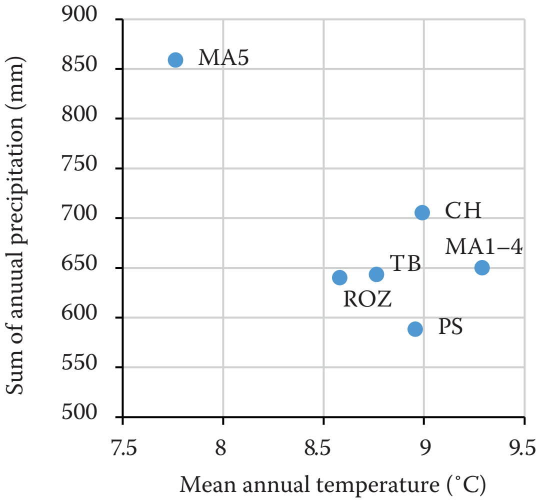

Figure 2. Climograph showing mean annual temperatures and total annual precipitation for individual regions/sites

20 dominant or codominant trees per tree species were selected in each stand; thus, we obtained two or three tree sets for each site. Two cores per tree were taken at breast height (1.3 m above ground) using a Haglöf increment borer (Haglöf, Sweden). To avoid compression wood, core sampling was performed along the contour line. Tree-ring widths (*TRW*) were measured to the nearest 0.01 mm, using the TimeTable measuring stage (VIAS, Austria).

Data processing and chronology development. Ring-width series were visually crossdated and statistically verified using the PAST 4 (Knibbe 2004) and COFECHA programme (Grissino-Mayer 2001). Successfully crossdated series were included in the final dataset. Anomalies in tree-ring formation, such as partly and completely missing rings (Bräuning et al. 2016), were detected during this stage. The occurrence of missing rings and growth decline were used as indicators of stress periods. Basic statistics of raw tree-ring measurements are shown in Table 2.

In order to remove both age-related trends in *TRW* and other non-climatic noise, we performed individual-based detrending using a cubic smoothing spline with a 64% variability cut-off at the mean segment length of a given tree set. The remaining autocorrelation was eliminated by autoregressive modelling in ARSTAN software (Cook, Krusic 2005). The resulting residual chronologies were aggregated in site-species-level chronologies by calculating the biweight robust means. For each chronology mean sensitivity and expressed population signal (*EPS*) were calculated (Table 2). *EPS* quantifies how well a chronology based on a finite number of trees represents a theoretical infinite population. For all chronologies in the common period 1962–2018, the *EPS* reached a value higher than 0.85, which means that the chronologies represent the population signal with sufficient quality (Wigley et al. 1984).

Principal component analysis (PCA) was used to detect similarities in growth patterns of different tree species growing in different regions. PCA was carried out based on the covariance matrix of the residual tree-ring chronologies. The number of significant principal components was selected based on those with eigenvalues greater than 1 (Kaiser rule).

Climate-growth relationship. The gridded monthly climatic data from the CRU TS dataset with 0.5° resolution (Harris et al. 2020) were used for the growth-climate response analysis. The selected climate series corresponded to the closest grid point to each sample site. In addition to average monthly temperatures and monthly precipitation totals, climatic variables related to drought stress such as the Standardized Precipitation Evapotranspiration Index – *SPEI* (Vicente-Serrano et al. 2010) and self-calibrating Palmer Drought Severity Index – *scPDSI* (Wells et al. 2004) were derived from the CRU TS dataset.

Long-term growth-climate relationships were evaluated for each tree set using a simple correlation analysis (Pearson's correlation coefficient) for the period 1962–2018. Monthly climatic variables entered the analysis in sequence from April of the previous year to August of the current year, i.e. the observation year for growth parameters. In addition to the monthly data, we also calculated the seasonal average for the summer months (June–August) to determine correlations with *TRW* indices.

To assess the temporal stability of the climate-growth relationship, we computed moving correlations. The method is based on progressively shifting the period of a fixed number of years across time to compute the correlation coefficients. In this study, we chose a window of 20 years starting with the period 1962–1981. Standardized *TRW*s were gradually correlated with seasonal climatic values related to drought stress, such as the mean temperatures, the sum of precipitation, *SPEI* and *scPDSI* during the peak growing season (June–August).

All statistical analyses were performed in OriginPro software (Version 9.9, 2022).

Table 2. Basic characteristics of raw tree-ring measurements and residual tree-ring chronologies

				Raw measurements					Residual chronology	
Region	Site	Species	No. of trees/ series	Mean *TRW* (mm)	Proportion of missing rings (%)	Series intercorrel. vs. mean	Mean sensitivity	1st order autocorrel.	Mean sensitivity	*EPS*
Tábor	TB1	Sf	19/35	1.88	0.92	0.618	0.305	0.68	0.237	0.96
		Ns	20/32	2.14	0.24	0.625	0.279	0.68	0.236	0.96
	TB2	Sf	19/32	1.85	1.96	0.706	0.313	0.77	0.289	0.97
		Ns	18/32	1.81	0.76	0.667	0.326	0.65	0.258	0.96
	TB3	Sf	16/30	1.65	3.72	0.681	0.298	0.78	0.254	0.96
		Ns	16/27	2.09	0.40	0.683	0.322	0.62	0.267	0.95
Rožmitál	ROZ1	Sf	20/37	2.02	2.42	0.601	0.261	0.83	0.214	0.96
		Ns	25/48	2.21	0.23	0.513	0.215	0.78	0.164	0.94
	ROZ2	Sf	13/23	1.63	1.05	0.636	0.279	0.79	0.244	0.94
		Ns	19/36	1.47	0.10	0.610	0.249	0.79	0.187	0.95
	ROZ3	Sf	22/43	1.81	0.97	0.602	0.255	0.81	0.188	0.95
		Ns	19/36	1.93	0.08	0.621	0.208	0.73	0.153	0.95
Písek	PS1	Sf	16/30	1.88	0.00	0.713	0.261	0.73	0.260	0.96
		Ns	15/29	2.82	0.00	0.688	0.327	0.60	0.266	0.94
	PS2	Sf	19/34	2.29	0.00	0.636	0.321	0.68	0.259	0.96
		Ns	15/29	2.82	0.00	0.592	0.327	0.60	0.266	0.94
Černá Hora	CH1	Sf	15/27	1.83	2.28	0.592	0.320	0.76	0.241	0.93
		Ns	14/27	2.03	0.00	0.632	0.238	0.57	0.197	0.95
	CH2	Sf	18/32	2.03	0.25	0.604	0.262	0.74	0.192	0.93
		Ns	10/20	2.48	0.00	0.705	0.259	0.73	0.247	0.94
	CH3	Sf	11/21	1.80	1.67	0.614	0.267	0.83	0.227	0.90
		Ns	9/15	2.23	0.00	0.615	0.218	0.69	0.168	0.90
Město Albrechtice	MA1	Sf	14/26	2.04	2.32	0.624	0.311	0.79	0.252	0.94
		El	15/30	1.78	0.82	0.668	0.339	0.75	0.321	0.95
	MA2	Sf	19/37	1.32	1.76	0.652	0.324	0.71	0.294	0.97
		El	16/30	1.22	0.51	0.608	0.330	0.61	0.269	0.94
	MA3	Sf	21/39	1.49	1.41	0.687	0.267	0.83	0.250	0.97
		Ns	19/34	1.93	0.27	0.633	0.264	0.73	0.231	0.96
		El	19/35	1.85	0.17	0.663	0.269	0.68	0.232	0.96
	MA4	Sf	18/33	1.09	2.77	0.672	0.277	0.80	0.246	0.96
		Ns	18/33	1.65	0.05	0.576	0.239	0.74	0.189	0.94
		El	16/30	1.14	0.96	0.654	0.276	0.78	0.231	0.96
	MA5	Sf	11/21	1.80	2.29	0.648	0.275	0.82	0.245	0.93
		Ns	13/21	1.82	0.71	0.560	0.263	0.85	0.214	0.91

TRW – tree-ring width; *EPS* – expressed population signal; Sf – silver fir; Ns – Norway spruce; El – European larch

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RESULTS

Growth dynamics. Ring-width chronologies of fir and spruce show synchronous year-to-year fluctuations within the given region as well as between different regions. Mean ring-width series for individual tree species calculated based on a pooled dataset from all sample sites illustrate the major differences in growth dynamics between tree species (Figure 3). Series of fir and spruce have a synchronous course until the end of the 1950s. Later, from the 1960s to the 1980s, fir experienced a deep growth depression, followed by a period of intensive regeneration in the 1990s. The increase in fir growth was interrupted by a drought in 2003, after which growth stagnated or decreased. Spruce showed its first growth reduction in the period 1992–1995 and then a steep growth decline after 2003 with an increasing occurrence of missing rings. Inter-annual ring-width variations in larch differ from those of both fir and spruce. However, similarly like in spruce, there was also a growth decline after 2003 in larch, but it had a lower intensity.

Missing rings are most common in fir (Figure 4, Table 2). The anomalies in tree-ring formation were recorded with a similar frequency in all re-

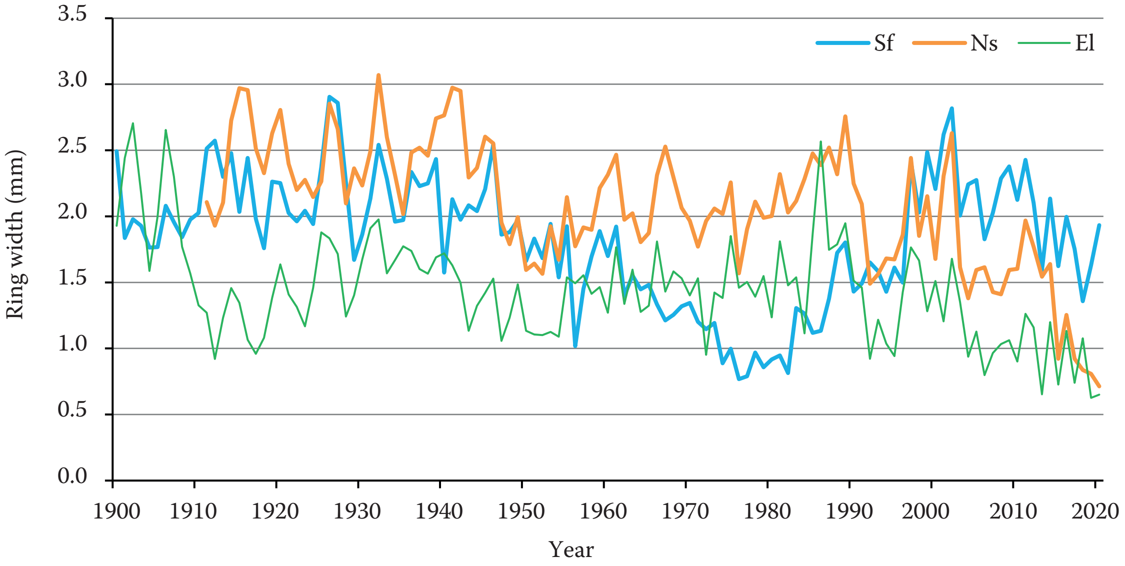

Figure 3. Mean ring-width series for silver fir (Sf), Norway spruce (Ns) and European larch (El)

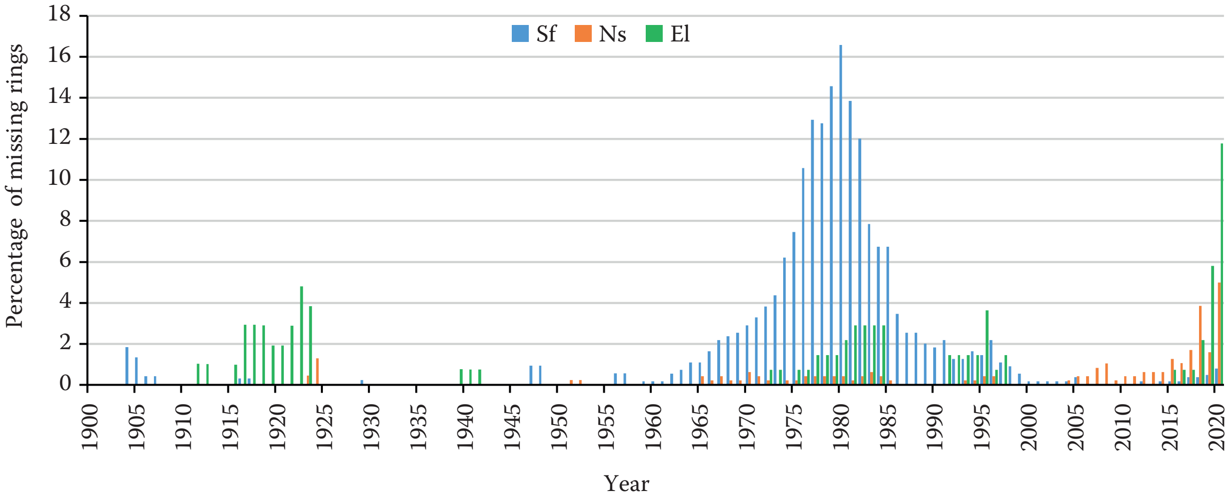

Figure 4. Occurrence of missing rings in individual years for silver fir (Sf), Norway spruce (Ns) and European larch (El)

gions with the exception of Písek, where no missing rings were determined. Here, fir has also shown almost no growth decline since 1960. In other regions, missing rings in fir mostly occurred in the period 1966–1985 but they were rarely identified in recent years (Figure 4). Missing rings were much less common in spruce and larch than in fir. In spruce, they occurred mainly in the last dry period after 2003, with a steep increase after a dry year in 2015. For larch, missing rings occurred in several periods: 1915–1923, 1976–1984, 1991–1996 and after 2015, with the most missing rings recorded in 2019 and 2020.

The PCA revealed that ring-width chronologies were relatively similar. The first principal component (PC1) retained 43.5% of the total variance and represented the tree-ring width variability common to all species growing in different regions, since it was strongly related to all tree sets (Figure 5A). The signal captured in PC1 indicates a high common variance in tree growth driven by climatic factors. PC2 (14.5%) divided chronologies into groups according to the tree species and was positively related to larch and spruce and negatively to fir chronologies. It points to a higher similarity in the growth pattern of spruce and larch and to the dissimilarity of fir. PCA loadings on PC3 were differentiated mainly by region (Figure 5B), separating the eastern Moravian regions from the western Bohemian regions. However, PC3 retains only 9.9% of the overall variance. This means that regional affiliation explains only a small part of the common variability in tree growth.

Climate-growth relationship

The correlation analysis showed a significant ($P < 0.05$) positive effect of higher temperatures during the winter and early spring on the growth of fir in sites at an altitude above 700 m a.s.l. and in a moist site CH3 located in a cool valley position. Summer temperatures had no effect on fir growth in any of the sample sites (Figure 6A). Similarly, for larch, there was no significant effect of summer temperatures on most sites. However, a negative effect of high spring temperatures in the previous year was obvious for larch trees. On the other hand, spruce growth was negatively affected mainly by high temperatures during the summer of the current year and in September of the previous year in lower sites up to 550 m a.s.l.

The growth of all three species was positively related to precipitation totals in the summer months of the current year (Figure 6B). They clearly had a significant ($P < 0.05$) positive effect on the growth of spruce at all sample sites across the altitude gradient studied and then also on the growth of larch, with the exception of the highest site, MA4. By contrast, for fir, a significant ($P < 0.05$) relationship with summer precipitation was observed only at two sites in lower locations.

The relationship of growth to the *SPEI* index followed the same pattern as the relationship of growth to precipitation and confirms the higher sensitivity to summer drought in spruce and larch compared to fir (Figure 6C).

The relationship of growth to the *scPDSI* corroborated strong limitation of spruce growth by the

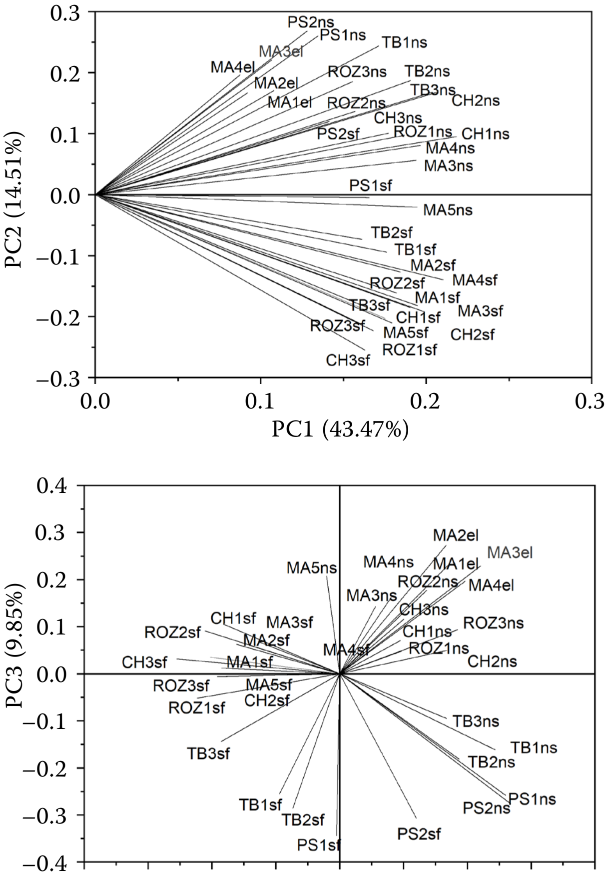

Figure 5. PCA loading plots of residual tree-ring chronologies for the common period 1962–2018; (A) PC1 against PC2; (B) PC2 against PC3; percentage indicates the proportion of the variance explained by a given principal component, the vector name consists of the site name (e.g. MA4) and tree species code (sf – Silver fir, ns – Norway spruce, el – European larch)

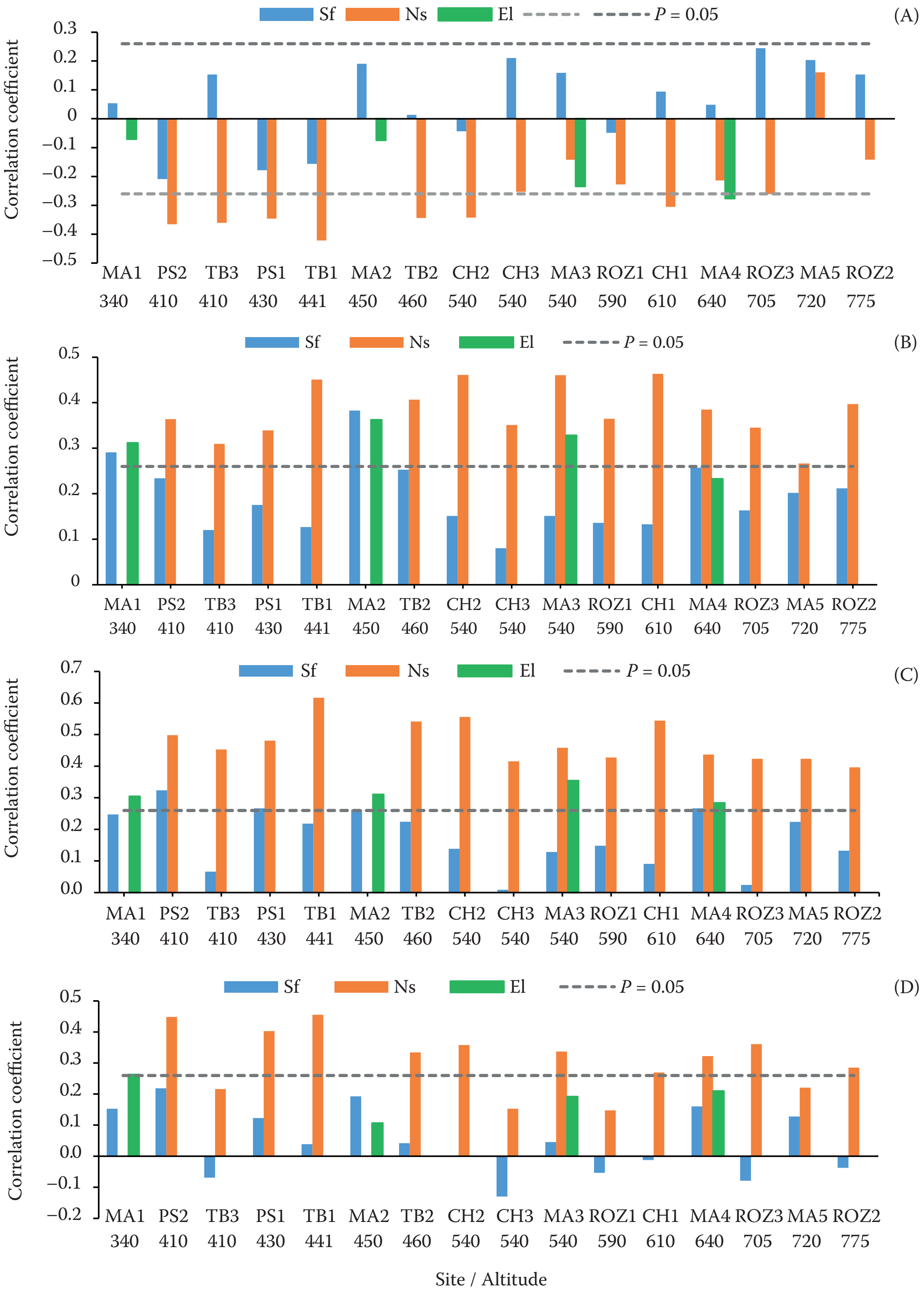

Figure 6. Correlation of silver fir (Sf), Norway spruce (Ns) and European larch (El) growth with summer (A) temperatures, (B) precipitation totals, (C) Standardised Precipitation Evapotranspiration Index (*SPEI*) and (D) self-calibrated Palmer Drought Severity Index (*scPDSI*) for the common period 1962–2018; the dashed line indicates the limit for statistically significant values ($P = 0.05$)

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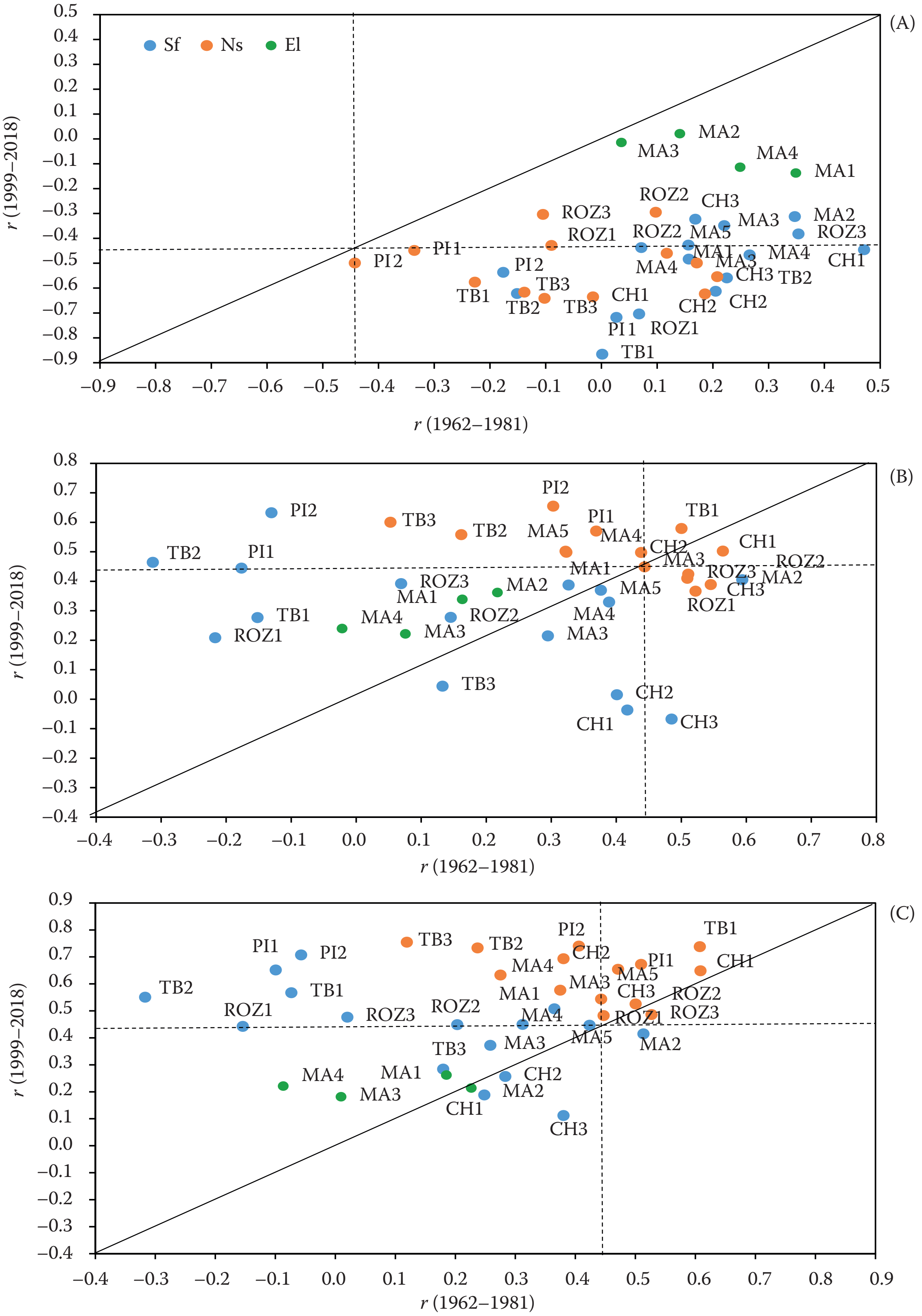

Figure 7. Overall stability of the individual climate-growth relationships expressed by correlation values for summer (A) temperatures, (B) precipitation and (C) Standardised Precipitation Evapotranspiration Index (*SPEI*) for the 1999–2018 (on the y-axis) and previous 20-year period 1962–1981 (on the x-axis), vertical and horizontal dashed lines indicate significance levels ($P = 0.05$), and the solid diagonal line represents a perfect stationary response

dry summer period, while larch and fir were less responsive (Figure 6D).

The temporal stability of the climate-growth relationship was studied using moving correlations. We focused on seasonal climatic values related to drought stress. The overall individual stability at the site- and tree-species levels can be seen in Figure 7, which illustrates the shift in the climate-growth relationship between the two 20-year periods 1962–1981 and 1999–2018. Scattering of the correlation values around the diagonal line represents the theoretical perfect stationary response. The growth response to summer temperatures was unstable at both the individual and the global level, resulting in an asymmetrical displacement of the cloud of points (Figure 7A). While in the period 1962–1981 the relationship of growth to summer temperatures was insignificant for all tree species and sites, and the values of correlation coefficients reached positive values, in the period 1999–2018, spruce and fir showed a statistically significant ($P < 0.05$) negative relationship with temperatures at most sites. The growth response of larch did not change significantly.

The response to summer precipitation was individually unstable but overall stable with the individual responses symmetrically divided by the diagonal line (Figure 7B). Spruce growth was significantly ($P < 0.05$) positively related to precipitation in both periods at most sites, whereas for larch and most fir populations the correlations were insignificant in both time windows. However, a distinct shift in the growth response of fir was obvious for the *SPEI* index (Figure 7C). The fir became more sensitive to drought in the recent 20-year period.

DISCUSSION

In this study, we focused on spatiotemporal changes in the growth response to climate depending on tree species and regional affiliation. Analyses were restricted to trees > 100 years old to avoid the age-related effect on the climate-growth relationship (Carrer, Urbinati 2004), and the stands were selected at sites well supplied with nutrients to eliminate the effect of site quality.

For spruce at site CH1, the resulting chronology reached less than 60 years, although the age of the stand was around 100 years. This was due to the frequent occurrence of stem rot in spruce trees at this lower site. Therefore, we analysed the growth pattern for the period 1962–2018, which was common to all sites and tree species.

The observed deep growth depression in fir from the early 1960s to the late 1980s corresponds to the findings of other studies from different parts of Europe (Becker et al. 1989; Elling et al. 2009; Gazol et al. 2015; Vitali et al. 2017; Bošela et al. 2018). The growth decline was probably the result of exposure to atmospheric pollution, in particular to sulphur dioxide, to which fir is sensitive (Elling et al. 2009; Mikulenka et al. 2020). With 3 150 kilotons in 1985, SO_2 emissions in the Czech Republic were the highest in Europe (Hůnová 2020). Pollution had a clear effect on the growth pattern of fir during this period and may have modified the growth response to climatic factors (Rydval, Wilson 2012; Kolář et al. 2015).

The vitality of silver fir has increased since the end of 1980s in many stands in Central and Western Europe (Büntgen et al. 2014; Gazol et al. 2015; Bošela et al. 2018) due to a decrease in SO_2 emissions, air warming with constant precipitation and an increase in nitrogen deposition (Elling et al. 2009; Büntgen et al. 2014). Our study shows that the increase in fir growth was interrupted by a drought in 2003 (Ciais et al. 2005), after which growth stagnated or decreased.

Spruce growth failed during the hot and dry periods in the first half of the 1990s (Brázdil et al. 2009). After an extreme drought in 2003, followed by several dry years with further extremes in 2015 (Ionita et al. 2017) and 2018 (Salomón et al. 2022), there was a rapid decline in spruce growth in most locations with an increasing occurrence of failures in tree-ring formation, which indicates severe drought stress (Bräuning et al. 2016). The correlation analysis also clearly indicated high sensitivity of spruce to drought across the altitude gradient. Also, van der Maaten-Theunissen et al. (2012) and Vitali et al. (2017) detected higher sensitivity of spruce to summer droughts compared to that of co-occurring silver fir, regardless of the elevation.

Silver fir is generally more resistant to drought than Norway spruce, larch and European beech (reviewed in Vitasse et al. 2019b). However, Cailleret and Davi (2011) reported higher sensitivity of silver fir to summer water stress compared to beech under mountain conditions in the Mediterranean area. Our study confirmed higher drought tolerance in fir compared with larch and particularly spruce. The fir tree has a deep taproot system (Úradníček et el. 2009) that allows it to use water from deeper soil layers. In addition, this species controls its transpiration efficiently via the rapid closure of its stomata in response to a vapour-pressure deficit (VPD) increase (Nourtier et al. 2014). Both functional traits allow fir to cope with dry periods.

In the entire period 1962–2018, fir showed lower sensitivity to summer drought, however, in the most recent 20-year period, the susceptibility of fir to summer temperatures and *SPEI* values has increased. In 1999–2018, the highest positive correlation with *SPEI* was recorded in the Písek region. Here, we observed the mortality of fir trees after the drought in 2018. This means that even the relatively drought-resistant fir may currently experience local decline due to drought stress in Central European conditions. So far, the decline of silver fir triggered by drought has been reported mainly from southwestern Europe, where fir populations grow at their xeric distribution limit (Macias et al. 2006; Linares, Camarero 2012). However, drought-induced tree decline and mortality are complex phenomena. Trees weakened by drought are susceptible to secondary stressors, including pests and pathogens (Mattson, Haack 1987; Gaylord et al. 2013). Also, nutritional imbalances may accelerate the decline and death of climatically stressed trees (Hevia et al. 2019; Gonzáles de Andrés et al. 2022). Silver fir shows humus forms with lower surface humus accumulation, but with soil chemistry very comparable with that of Norway spruce (Podrázský et al. 2018). The importance of impaired nutrition may increase in the future, as the concentration of nutrients in foliage is decreasing in the long term on a European scale (Jonard et al. 2015).

CONCLUSION

Fir is a vital tree species that showed a remarkable ability to recover from a decline period in the 1970s and 1980s when air pollution peaked. In recent years, the strongest abiotic stressor has been climate change manifested by periods of drought and an increased frequency of extreme events. Compared to European larch and Norway spruce, silver fir is more resistant to a lack of precipitation, however, its sensitivity to drought has increased in the last two decades, and in some sites at a lower elevation, fir is currently showing symptoms of decline, even in the central part of its distribution range.

Due to the intense dieback of spruce and pine stands, fir appears to be a promising coniferous tree species that certainly has a high potential for use in mixed temperate forests in Central European conditions. However, it is necessary to apply cautious forest management with respect to the ecological requirements of this tree species.

The selected sites do not represent the entire ecological amplitude of the investigated tree species, which can be considered a weak point of the study. The selection was restricted to the altitudinal zone up to 800 m a.s.l., i.e. the zone with large-scale disintegration of spruce stands. Future research should focus also on sites in the montane zone, as changes in the growth-climate relationship can be expected even there. In this study, larch was studied only at a limited number of sites. More attention should be paid to this tree species in subsequent studies as it is expected to be more widely used in mixed forests of the temperate zone.

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