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Coping with Central European climate – xylem adjustment in seven non-native conifer tree species

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Abstract: The introduction of tree species raises the question of whether they find suitable conditions in their secondary range and whether they can successfully adapt to the new conditions in the context of an unstable climate. Stem secondary growth of trees and the changes in xylem cell structure make it possible to trace the adaptation process to the new climate on an inter- and intra-seasonal scale. The objective of this study was to determine whether the seven non-native conifer species in Central Europe differ in climate sensitivity and to what extent late frost and spring-summer drought can influence xylem changes.


In our study, we investigated the growth pattern and xylem cell structure modifications of seven introduced conifer species *Pseudotsuga menziesii*, *Pinus strobus*, *Tsuga canadensis*, *Abies grandis*, *Pinus banksiana*, *Pinus rigida*, *Pinus nigra*, growing under uniform conditions in Poland. To determine species-specific temporal variations in climate sensitivity, we used stationary and non-stationary correlations of ring width with daily climate variables: mean, minimum, and maximum temperatures, precipitation sum, and SPEI, supported by a pointer-year analysis. Changes in xylem structure (frost rings and intra-annual density fluctuations) were analyzed using light and fluorescence microscopy.


Warming of the winter-spring period benefits both southern European and North American introduced conifers, as reflected in the extended responsiveness period. However, as the growing season warms and the risk of late frosts increases, the potential for acclimatization of non-native species decreases, especially with respect to their juvenile growth phase. Negative precipitation and evapotranspiration balance at spring-summer period can lead to reduced growth and anomalies in earlywood xylem structure, commonly referred to as intra annual density fluctuations. *P. strobus*, the species that loses both frost-induced cambium damage and drought-induced xylem anomalies in summer is the fastest growing non-native species, along with *P. menziesii*.


Although the results presented here show the potential and the limitations in the acclimatization of coniferous species, the obvious limitations related to local environmental conditions and the different ages of the trees make us cautious in generalizing the conclusions. Therefore, we call for the creation of a pan-European dendro-network of sites of non-native coniferous species.




Keywords: introduced tree species, wood anatomy, IADF, frost ring, late frost, drought

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Introduction

Reliable knowledge of the occurrence, radial growth and acclimatization of non-native conifer species in European forests varies by species and region. Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (PSME), one of the most important non-native conifer species in Europe, has been extensively studied (e.g. Thurm et al., 2016; Castaldi et al., 2020; Miller et al., 2022), whereas much less information is available on grand fir, *Abies grandis* (Douglas ex D.Don) Lindl. (ABGR), eastern white pine, *Pinus strobus* L. (PIST), and black pine, *Pinus nigra* Mill. (PINI) (Leal et al., 2008; Bijak, 2013; Wilczyński & Kulej, 2019; Läänelaid & Helama, 2020). In contrast, studies on the climate-growth relationships of pitch pine, *Pinus rigida* J.F.Arnold (PIRI), jack pine, *Pinus banksiana* Lamb. (PIBA), and eastern hemlock, *Tsuga canadensis* (L.) Carrière (TSCA) in Europe are hardly available (Cedro et al., 2013; Song et al., 2021). Thus, an objective comparison of conifers alien in Europe is difficult to find, while existing studies mainly refer to common garden experiments (George et al., 2019; Schueler et al., 2021; Song et al., 2021), where the analyzed growth period is limited by the age of the genetic experiment, usually not exceeding 40 years. Therefore, forest stands where multiple non-native species are planted for production purposes offer a unique opportunity to assess growth performance and acclimatization of non-native species under comparable soil and climatic conditions.

Most studies on the secondary growth adjustment to current climatic conditions focused on the annual xylem tissue production rather than on anomalies in xylem cell structure caused by adverse weather events (e.g., Huang et al., 2017; Wilczyński & Kulej, 2019). This is all the more surprising given that the increasing frequency of climatic anomalies, such as late frosts and summer droughts, appears to be an important factor limiting the ability of trees to adapt to the novel climate (Ruosteenoja et al., 2018; Liu et al., 2018; Ma et al., 2019). While annual growth reductions caused by spring frosts and summer droughts have been studied under European conditions (Puchalka et al., 2016; Song et al., 2021), the effects of these weather phenomena on anomalies in xylem structure and thus disruptions in the function

of this tissue are rare and mainly focused on native species (Gazol et al., 2019; Matisons et al., 2020).

Formation of frost rings at subzero temperatures during the period of cambium cell activation results in death of xylem mother cells. Although the cambial initials remain alive, their development is disturbed, resulting in the formation of irregular tracheids that do not perform their main ecophysiological functions, e.g. water transport and mechanical support (Glerum & Farrar, 1966). Finally, when the cambial initials become fully functional again, the newly formed earlywood tracheids are restored, the trees regain their hydraulic conductivity, but xylem cavitation resistance remains reduced (Dai et al., 2020). Thus, even if damage to cambium cells and deformation of earlywood tracheids does not entail a reduction in annual growth, the functionality of xylem tissue may be impaired as a result of climatic anomalies in early spring. Increased susceptibility to damage of cambium tissue and deformation of xylem cells by frost is observed in trees transferred to new climatic conditions, both within and outside their natural range (Montwé et al., 2018; Sebastian-Azcona et al., 2020). Therefore, frost rings appear to be a good indicator of acclimation of species in their secondary distribution (Sanders et al., 2019).

Disruption of xylem tissue formation conditions in conifers can lead to intra-annual variability in the anatomical structure of earlywood tracheids, resulting in disruption of water transport and structural support (Björklund et al., 2017). This abnormal earlywood cell structure is commonly referred to as intra-annual density fluctuations (IADF) and is determined macroscopically by analyzing microdensity profiles or profiles of anatomical parameters (e.g., lumen diameter, cell wall thickness) (Battipaglia et al., 2016). Changes in the structure of the xylem tissue, manifested in the formation of the IADF structure, leads to disturbances in the functioning of this tissue (de Micco et al., 2016). The response of trees to abnormal climatic conditions expressed in the adjustment of the xylem structure, supports the process of adaptation of trees to climate change (Klisz et al., 2019; Hevia et al., 2020). Thus, if we assume that the development of IADF structure in trees under adverse conditions is aimed at a plastic growth response, we can conclude that this predisposition

is a good indicator of the acclimatization of non-native trees to new climatic conditions (George et al., 2015). Although IADF formation is species-specific, intraspecific variation in this structural response is also observed (George et al., 2015a; Klisz et al., 2016; 2019; Hevia et al., 2020; Versace et al., 2021). Unfortunately, knowledge of the origin of non-native tree species introduced into Europe is still incomplete, so it is hardly possible to consider intraspecific variability when assessing the acclimatization of these species (Isaac-Renton et al., 2014; Hintsteiner et al., 2018).

For a better understanding of the growth performance of non-native tree species in their secondary distribution area, the climate transfer effect may be helpful (Schueler et al., 2021). However, this requires knowledge of the exact origin of the introduced populations (Isaac-Renton et al., 2014). Such knowledge is available only for a few non-native species that are important for European forestry. Therefore, the only way to determine the climatic tolerance range of an introduced species is often to characterize the climatic conditions of its secondary distribution (Box, 1981). Such a solution is very inaccurate for obvious reasons. Since the exact origin of the introduced populations is not known, the full range of variation

in native climatic conditions can be compared with the climate of the place of introduction to determine climatic suitability. A limitation of this approach, however, is that it generalizes climatic conditions and thus neglects the climatic extremes that play an important role in acclimatization to the climatic conditions of introduction (Bolte et al., 2009).

To compare the growth performance of seven non-native conifer species in Central Europe, we used a unique set of mature forest stands under uniform conditions of a temperate climate. We aimed to understand (a) whether these species differ in their sensitivity to climate, (b) temporal variation in climate sensitivity exist among these species, and (c) to what extent late frost and drought may determine their growth response.

Material and methods

Species selection and study site

The study was located in a lowland area in Central Europe (N 52.00–52.15, E 20.85–21.10, 171 m a.s.l.), where the State Forests National Forest

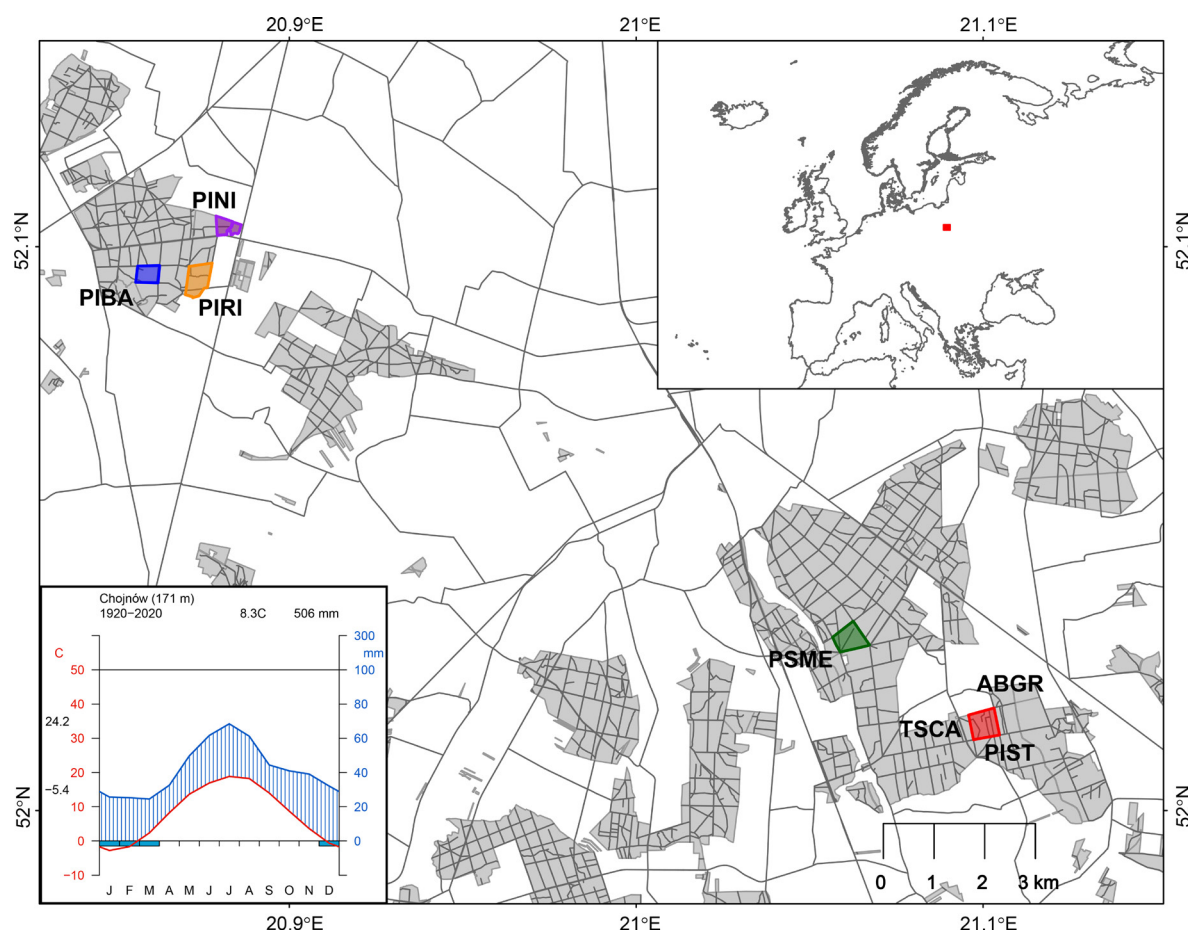


Fig. 1. Location of the study sites (data source: State Forests Information System). Panel in lower left corner: Walter and Lieth climate diagram for the study area (data source: E-OBS, version 24.0e). For species IDs see data Table 1

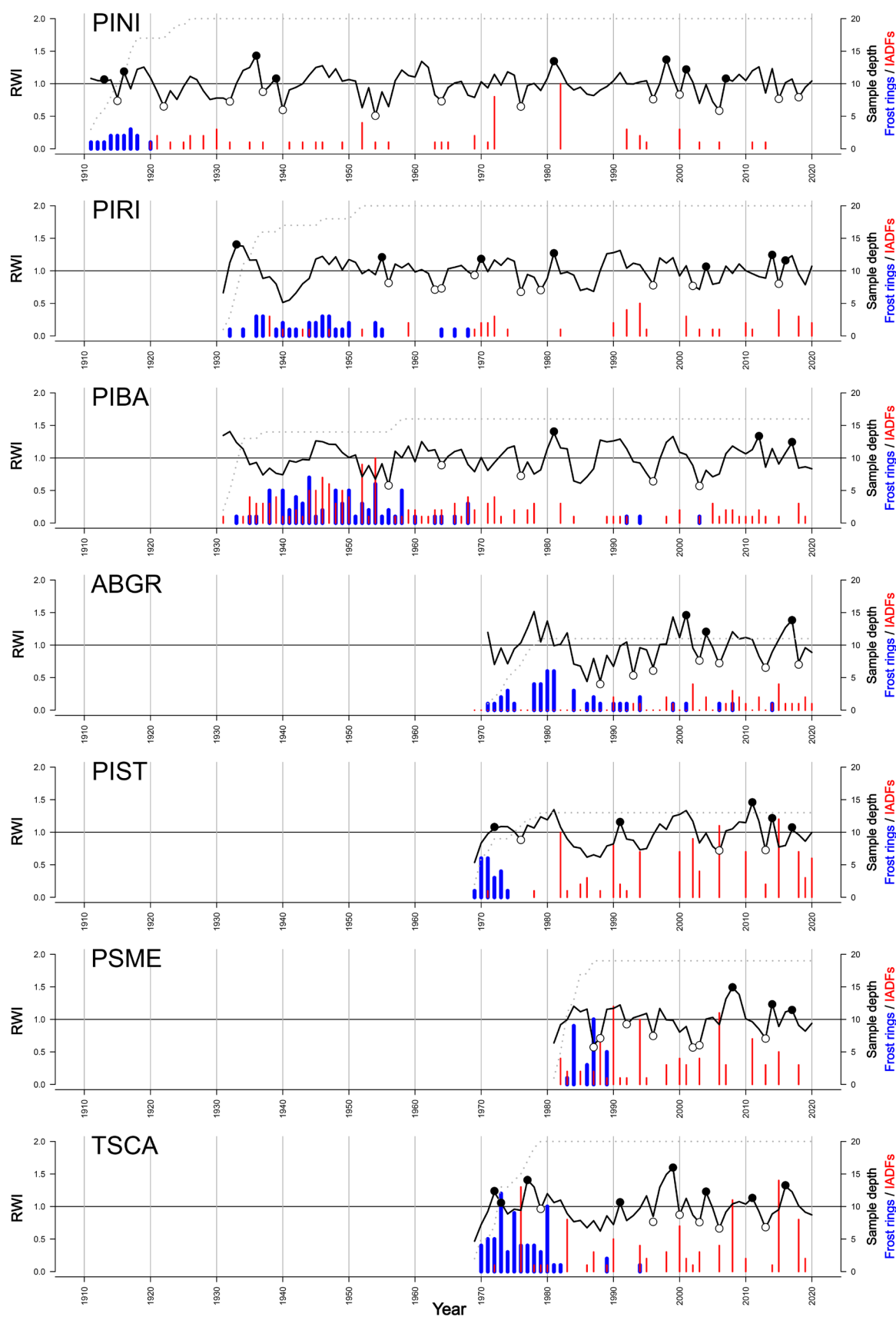


Fig. 2. Residual site chronologies for study species (black line), identified pointer years (black dots – positive, white dots – negative), IADF and frost ring frequency. RWI – ring width index, Sample depth – sample replication. For species IDs see data Table 1

Holding experimentally planted non-native coniferous species to assess their acclimatization to Polish climatic conditions in the first and second half of the 20th century (Fig. 1). For this study, we selected seven conifer tree species: PSME, PIST, TSCA, ABGR, PIBA, PIRI and PINI, of which six are alien in Europe and PINI non-native in Poland. Experiments with non-native species were established as single species or mixed stands with *Pinus sylvestris*, dominated by a non-native species (PSME, PIST, TSCA, ABGR and PINI, PIBA, PIRI, respectively). Study sites were represented by seven isolated, age-differentiated stands, with the oldest PINI stand 110 years old and the youngest PSME stand 40 years old (Fig. 1 and 2). The study area is characterized by advantageous climatic conditions (temperate climate) for tree growth with moderate annual precipitation sums and a mild annual temperature average (506 mm and 8.3 °C for the period 1920–2020, Fig. 1) (E-OBS 0.1° × 0.1° gridded climate data, version 24.0e: Haylock et al., 2008). Seven bioclimatic parameters for the period 1979–2013 from the Chelsa database with a spatial resolution of 30 arc seconds were used to characterize climatic conditions at the study sites relative to climatic conditions in the natural range of each NNT: bio2 – mean diurnal range of temperatures averaged over 1 year [°C], bio3 – ratio of diurnal variation to annual variation in temperatures, bio4 – standard deviation of the monthly mean temperatures, bio10 – mean air temperature of the warmest quarter [°C], bio11 – mean air temperature of the coldest quarter [°C], bio18 – mean monthly precipitation amount of the warmest quarter [kg m⁻²], bio19 – mean monthly precipitation amount of the coldest quarter [kg m⁻²] (Karger et al., 2017). We then calculated the absolute value of the difference from the study sites for each site from the natural range of NNTs and standardized them with the $n7$ – quotient transformation method (x/range) method using the `data.Normalization()` function from the ‘clusterSim’ package (Walesiak & Dudek, 2020). Finally, we obtained for each bioclimatic variable, values falling within the range of 0 – 1 where a value of 0 corresponds to full compliance with study site conditions. The bioclimatic conditions of study sites represented different parts of the natural species’ distribution in North America or southern Europe (in the case of PINI, Fig. S1). Forest soil type was homogeneous, rusty soils developed on loose sand. Due to homogeneity of climate and soil conditions, the studied tree species were considered to grow under comparable environmental conditions.

Radial growth data

For each target species, 12 to 20 sample trees were selected following their biosocial status (dominant or co-dominant trees), health status and location

within a closed stand (avoiding trees at the edge of gaps and stand edges). Two increment cores were extracted from each sample tree at a height of 1.3 m. Increment cores were extracted from two perpendicular directions with 5-mm-diameter Pressler borers. Then, to enhance identification the annual rings, dry cores were treated with a series of progressively finer grades of sandpaper (grain size up to 1000). Finally, wood samples with clear radial growth ring patterns were scanned at 2400 dpi (Epson Expression XL12000). Annual ring-widths were measured to an accuracy of 0.01 mm and cross-dated using ‘CooRecorder’ and ‘CDendro’ software (Cybis Electronic & Data, 2017). Once the samples have been cross-dated, each sample was examined under a binocular (258× magnification ZEISS Axiozoom.V16) for the occurrence of low temperature-induced xylem disfunctions (so-called frost rings, name hereafter FR) and high temperature-induced intra-annual density fluctuations in earlywood (so-called false rings, name hereafter IADF). To verify the identification of FR and IADF, fluorescence green light (wavelength 488 nm) was used in addition to bright light (Billinton & Knight, 2001). Additionally, the rotary microtome (Leica HistoCore BIOCUT) was used to produce the 12–14 µm-thick cross-sections from samples with identified FR or IADF (Fig. S4, S5). The cut sections were stained with Safranin and Astra blue solutions, dehydrated, and covered by Eukitt. An automatic slide scanner (200× magnification ZEISS AxioScanZ1) was then used to obtain the final microscope images. As a result, FRs and IADFs have been assigned to calendar years to established time series of FR and IADF frequencies. These traits reflect the adverse climatic conditions for the growth leading to the formation of anomalies in the xylem structure and were therefore used to assess the course of species-specific acclimatization (Wimmer et al., 2000). To test the potential effect of tree age on vulnerability to low temperatures and water deficit, principal component analysis was applied to the FR and IADF frequency time series. Partitioning Around Medoids clustering algorithm (Kaufman & Rousseeuw, 1987) was applied to distinguish groups of species differing in FR and IADF frequency.

Dendrochronological analysis

The two growth series per tree were averaged into individual tree-ring series. Individual growth series were cross-dated both visually and statistically with the CDendro program. Finally, only those growth series that achieved a minimum correlation coefficient value of 0.2 were detrended using a cubic smoothing spline with a cut-off of 50% of the frequency at a wavelength of 30 years (Cook & Peters, 1981; Speer, 2012). To remove the remaining

temporal autocorrelation and highlight the high-frequency signal (year-to-year variability) of growth, they were preweighted using the first-order autoregressive model (Cook & Kairiukstis, 1990). We used a biweight robust mean to develop residual chronologies for the species. To characterize and qualify the site chronologies, the Gleichläufigkeit (glk, i.e. the coherence coefficient; Eckstein & Bauch, 1969; Buras & Wilmking, 2015), and mean inter-series correlation in the 10-year moving window (mean rbar, an indicator of the strength of the common signal in the growth series of individual trees within a stand; Wigley et al., 1984; Cook & Kairiukstis, 1990) were calculated. To test the representativeness of the developed site chronologies, the expressed population signal (SSS; a measure of the strength of a common growth signal within a population; Wigley et al., 1984; Buras, 2017) and first-order autocorrelation (AR1, indicator of the effects of previous year conditions on current year growth) were calculated from the index series (RWI, standardised ring-width time series delivering dimensionless ring-width indices). These measures were calculated using the dplR R package (Bunn, 2008) for the common period from 1985 to 2020 and used to assess the quality and characteristics of the chronologies.

Climate sensitivity

To study the effect of key climatic drivers on radial growth reaction, we applied the daily response function from the dendroTools R package (Jevšenak & Levanič, 2018; Jevšenak, 2020), which slides a moving window through daily climate data (E-OBS $0.1^\circ \times 0.1^\circ$ gridded climate data, version 24.0e; Haylock et al., 2008) and aggregates it into seasonal values, and simultaneously calculates the correlations with tree-ring parameter. We considered all seasons spanning from 14 to 60 days, from the current and previous year. These correlations were calculated for aggregated mean daily temperatures (T_{mean}), precipitation sum, and standardized precipitation evapotranspiration index (SPEI), which considers actual precipitation and potential evapotranspiration (PET) to determine drought (Begueria & Vicente-Serrano, 2017). PET was calculated using the Hargreaves-Samani method (Hargreaves & Samani, 1985) using the Eq. 1, where T_{mean} , T_{min} and T_{max} depict mean, minimum and maximum daily temperatures, respectively, while R_a is daily net radiation at the surface in MJ/m^2 . Next, the climatic water deficit was calculated as the difference between the daily precipitation sum and daily PET. Finally, the accumulated drought effects were calculated by aggregating climatic water deficits into a log-logistic probability distribution to obtain SPEI series of considered seasons (Jevšenak, 2020). The R script that was used to

calculate day-wise aggregated correlations for SPEI is given as the Appendix 1.

$$\text{PET} = 0.0023(T_{mean} + 17.8)\sqrt{T_{max} - T_{min}}R_a \quad (\text{Eq. 1})$$

To perform the climate sensitivity analyses, we used E-OBS $0.1^\circ \times 0.1^\circ$ gridded climate data containing daily precipitation sums as well as daily mean, minimum, and maximum temperatures for the common observation period between 1985 and 2021 (Haylock et al., 2008; version 24.0e). The common period was defined for 1985–2020, omitting the four years represented in the shortest chronology (PSME) to exclude the years with the lowest sample replication. To determine the period of the previous and current year when key climatic factors determine growth reaction, we calculate daily response correlations with a moving window of 14 to 60 days (Jevšenak & Levanič, 2018). To test the temporal variation in climate sensitivity, the 10-years window moving with 1-yr offset has been calculated for studied chronologies using daily temperature, precipitation and SPEI datasets. These analyses were performed for the common period from 1985 to 2021. To test the effect of extreme climatic events on radial growth reactions a pointer-year analysis was applied (Schweingruber et al., 1990). The “Cropper” method, a window size of 5 years, and a series threshold of 60% were used as criteria for negative and positive pointer years (Cropper, 1979). Years in which at least four of the seven NNTs indicated a pointer year at the specific site were defined as common pointer years (CPY, Klisz et al., 2019a). To assess a secondary growth response to extreme drought events, a superposed epoch analysis (SEA, Chree, 1913) with 1,000-fold bootstrapped resamples and 3-year lags before and after drought events was applied. The standardized precipitation evapotranspiration indices (SPEI) accounted below -2 was used to define years of severe drought events (McKee et al., 1993; Paulo et al., 2012) separately at 3- and 6-month accumulation scales. The calculation was based on the detrended and prewhitened residual chronologies, and the statistical significance ($p < 0.05$) of the response was determined using a nonparametric bootstrap resampling.

All dendroclimatic analyses were computed in R (R Development Core Team, 2022). Detrending, chronology building, SEA, and calculation of the chronology statistics were performed using the ‘dplR’ package 1.7.2 (Bunn, 2010). Pointer-year analysis was done by the “pointRes” 2.0.0 package (van der Maaten-Theunissen et al., 2015). Standardized precipitation evapotranspiration indices were calculated using the customised R script. Stationary and nonstationary daily response correlations were performed using ‘dendroTools’ 1.2.0 package (Jevšenak & Levanič, 2018).

Results

Species-specific chronologies

The PSME and PIST chronologies had the highest value of r_{bar} (share of common radial growth signal), while the PINI and PIBA chronologies had the lowest values of r_{bar} (0.583, 0.546 and 0.415, 0.433 respectively) (Table 1). This pattern was also observed for the Gleichläufigkeit value (the coherence coefficient), while the opposite pattern was confirmed for the first-order autocorrelation value (AR1). Among the species chronologies, ABGR and PIBA had weaker environmental signal ($SNR < 12$), while the TSCA, PIRI and PSME had the strongest ($SNR > 20$).

Anomalies in radial growth

Frost rings predominated in the first cambial years (Fig. 2), with the frequency of FRs in the second, third, and fourth cambial years distinguishing species in terms of the sensitivity of their secondary tissue to low temperatures (Fig. 3A). PIST and TSCA had a significantly higher FR frequency than the other species (Fig. 3B). The relationship between the frequency of anomalies in xylem structure and cambial age was not confirmed for IADFs (Fig. 3C). In the case of IADFs, high frequency in the first cambial years was found only in PIBA, PSME, and TSCA, although it was highest in these years only in PIBA (Fig. 2). Grouping of cambial years based on Partitioning Around Medoids clustering algorithm revealed significantly higher frequency of IADF in growth rings formed at the mature stage (Fig. 3D).

Climate–growth relationships

Analysis of common pointer years (CPY, where at least four out of seven species chronologies shared the same growth response) showed one positive and four negative CPY (2017 and 1996, 2003, 2006 and 2013, respectively; Fig. 2). Uniform climatic conditions (Fig. 1) determined the growing conditions of the study sites, as reflected in the main climatic

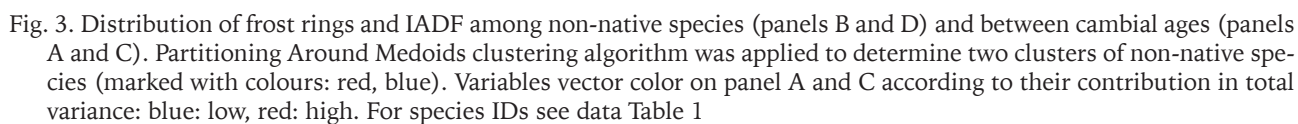
drivers common to all species (Fig. 4). Precipitations in June and July and mean, minimum and maximum daily temperature from February to April positively correlated with the ring width of all studied non-native species (Fig. 4 and S3). However, species-specific growth responses differed with respect to the optimal periods of responsiveness. In the case of July precipitation, the length of the response was shortest for PIBA and PINI and twice as long for the other species, while in the case of February and March mean, minimum and maximum daily temperature length of the response was shortest for: PIRI and PSME; PIBA, ABGR and PIST; PIBA, PIST and PSME, respectively. The interspecific variation in growth response was most evident in the climatic factors characterizing the previous year's conditions, namely December precipitation and October and November mean temperature (Fig. 4). Precipitation in the previous December correlated positively with the growth of PINI, PIRI, PSME and TSCA and negatively with PIBA, ABGR and PIST. In turn, mean temperature in October and November of the previous year correlated positively with the growth of ABGR and PIST, but negatively with PIRI, PIBA, PSME and TSCA.

Climate-growth temporal stability correlation analysis for mean daily temperature and a daily sum of precipitation showed a relatively similar pattern of temporal variation in climate sensitivity (Fig. 5). For all species, winter and early spring mean daily temperatures positively correlated with the ring width throughout the period analyzed. In contrast, the mean temperatures of the previous summer negatively correlated with the growth in the following year. However, this pattern weakened towards the end of the period studied and remained pronounced only for PSME. Spring and summer precipitation positively correlated with the ring width for most species except PSME. This pattern has strengthened in recent years for PIST and PINI and weakened for TSCA, ABGR and PIRI.

On the other hand, summer precipitation significantly correlated with ring width in recent years, positively for ABGR and TSCA but negatively for PIST. Moving window correlation (10-year window)

Table 1. Characteristics of tree-ring width chronologies of the seven study species: growth period represented in chronologies (period considered), number of trees used to build the chronology (NTree), the average stem diameter at breast height (DBH), mean tree-ring width (TRW), Gleichläufigkeit (glk), signal-to-noise ratio (SNR), correlation between trees (r_{bar}), expressed population signal (SSS), and first order autocorrelation (AR1)

Species	Species ID	Period considered	NTree	DBH (cm)	TRW	glk	SNR	r_{bar}	SSS	AR1
<i>Pinus nigra</i>	PINI	1911–2020	20	22.6	1.27	0.67	13.509	0.415	0.931	0.741
<i>Pinus rigida</i>	PIRI	1931–2020	16	22.7	1.70	0.69	22.362	0.544	0.957	0.622
<i>Pinus banksiana</i>	PIBA	1931–2020	20	15.0	1.55	0.68	11.510	0.433	0.920	0.798
<i>Abies grandis</i>	ABGR	1971–2020	12	11.9	1.42	0.71	8.207	0.448	0.891	0.765
<i>Pinus strobus</i>	PIST	1969–2020	13	22.9	3.02	0.69	14.612	0.546	0.936	0.733
<i>Pseudotsuga menziesii</i>	PSME	1981–2020	19	27.1	4.05	0.73	24.786	0.583	0.961	0.542
<i>Tsuga canadensis</i>	TSCA	1969–2020	20	14.1	1.76	0.73	20.680	0.531	0.954	0.632



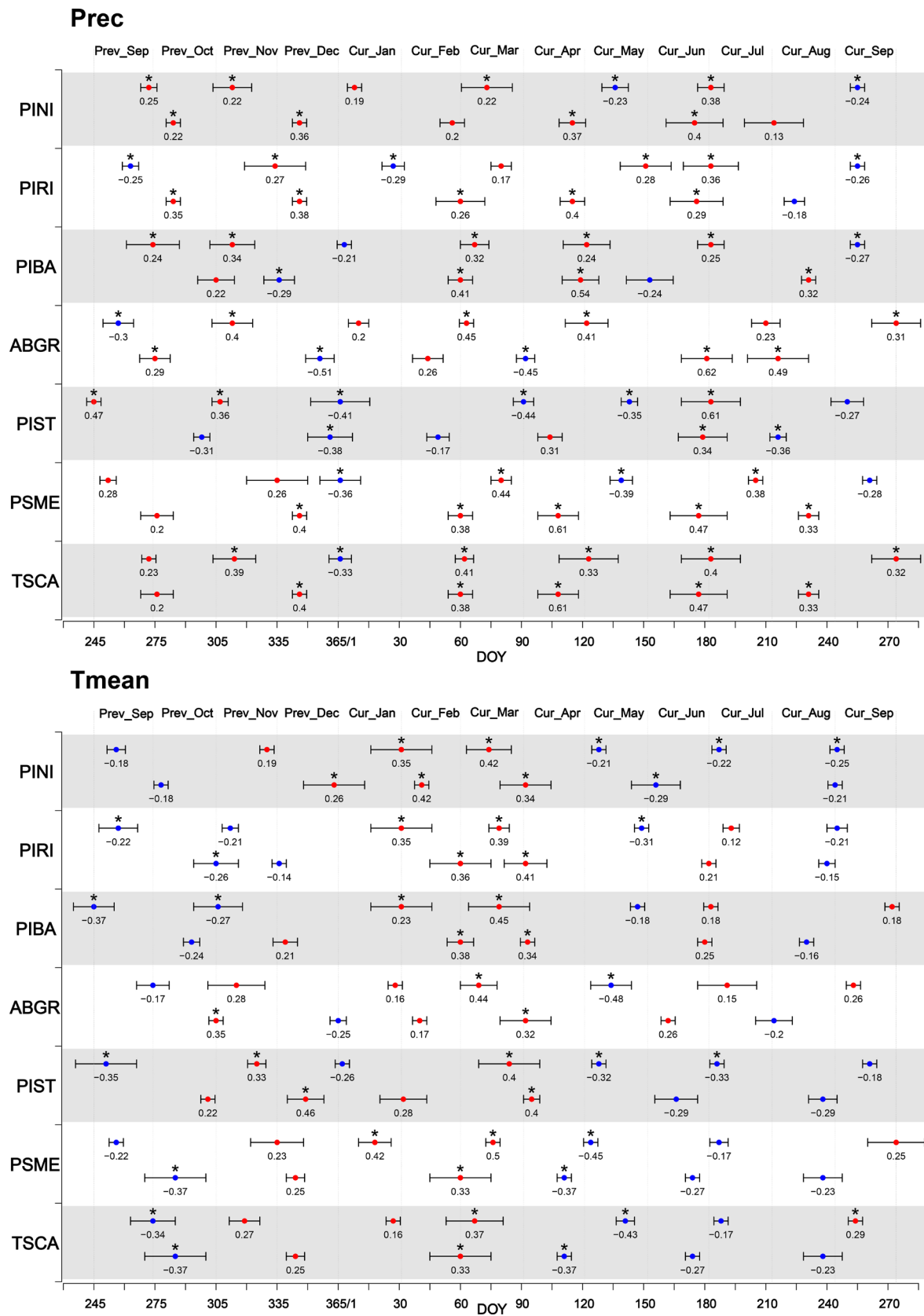


Fig. 4. Species-specific climate-growth relationships based on daily climate data. 14–60 day moving window correlations: between tree-ring width index (RWI) and precipitation (upper panel) and temperature (bottom panel). Red dots – positive correlations, blue dots – negative correlations, * demarcate a significance level of correlation ($p < 0.05$), horizontal whiskers demarcate window length, maximum correlation coefficient value shown below each whisker. For species IDs see data Table 1

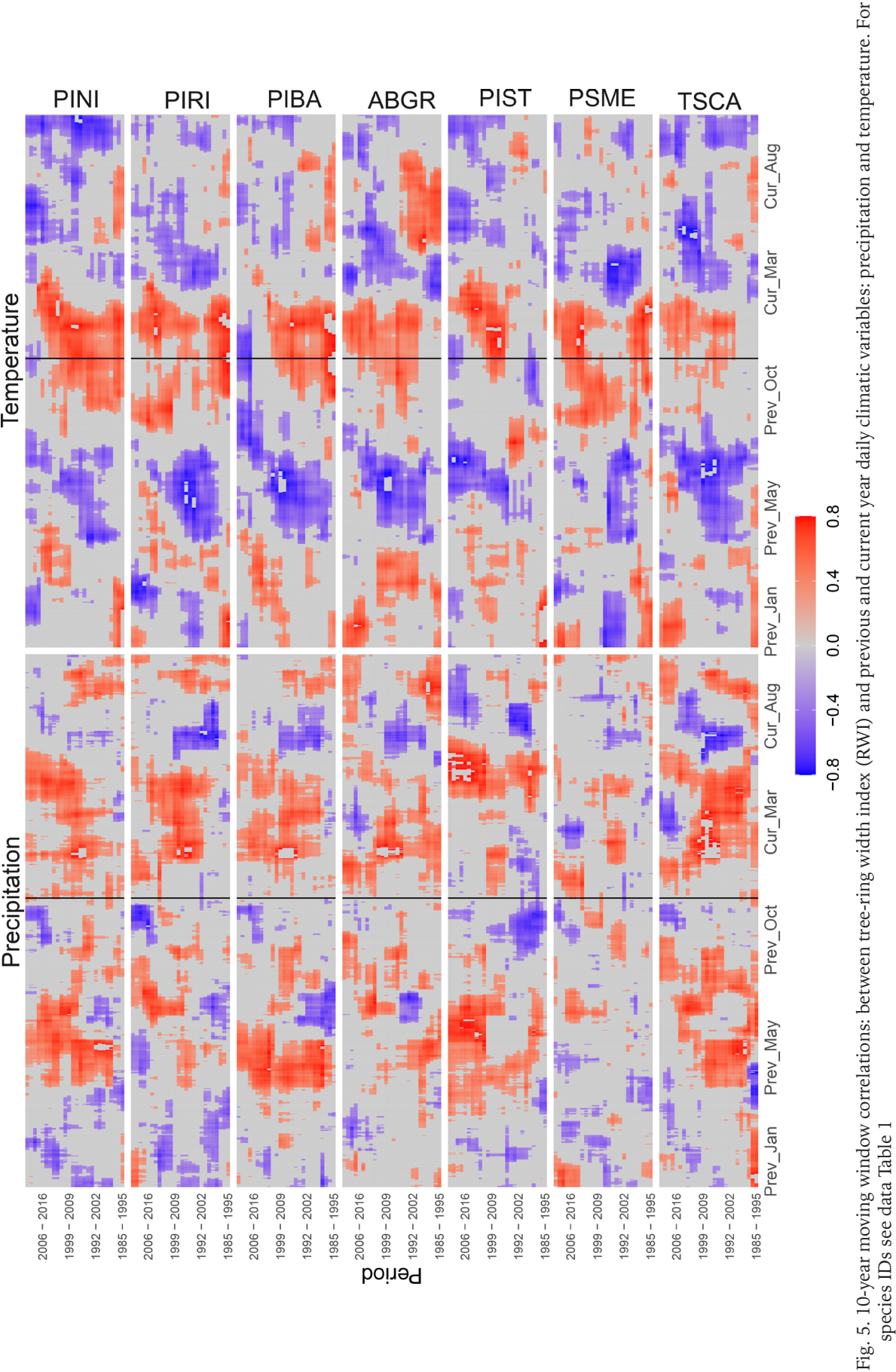


Fig. 5. 10-year moving window correlations: between tree-ring width index (RWI) and previous and current year daily climatic variables: precipitation and temperature. For species IDs see data Table 1

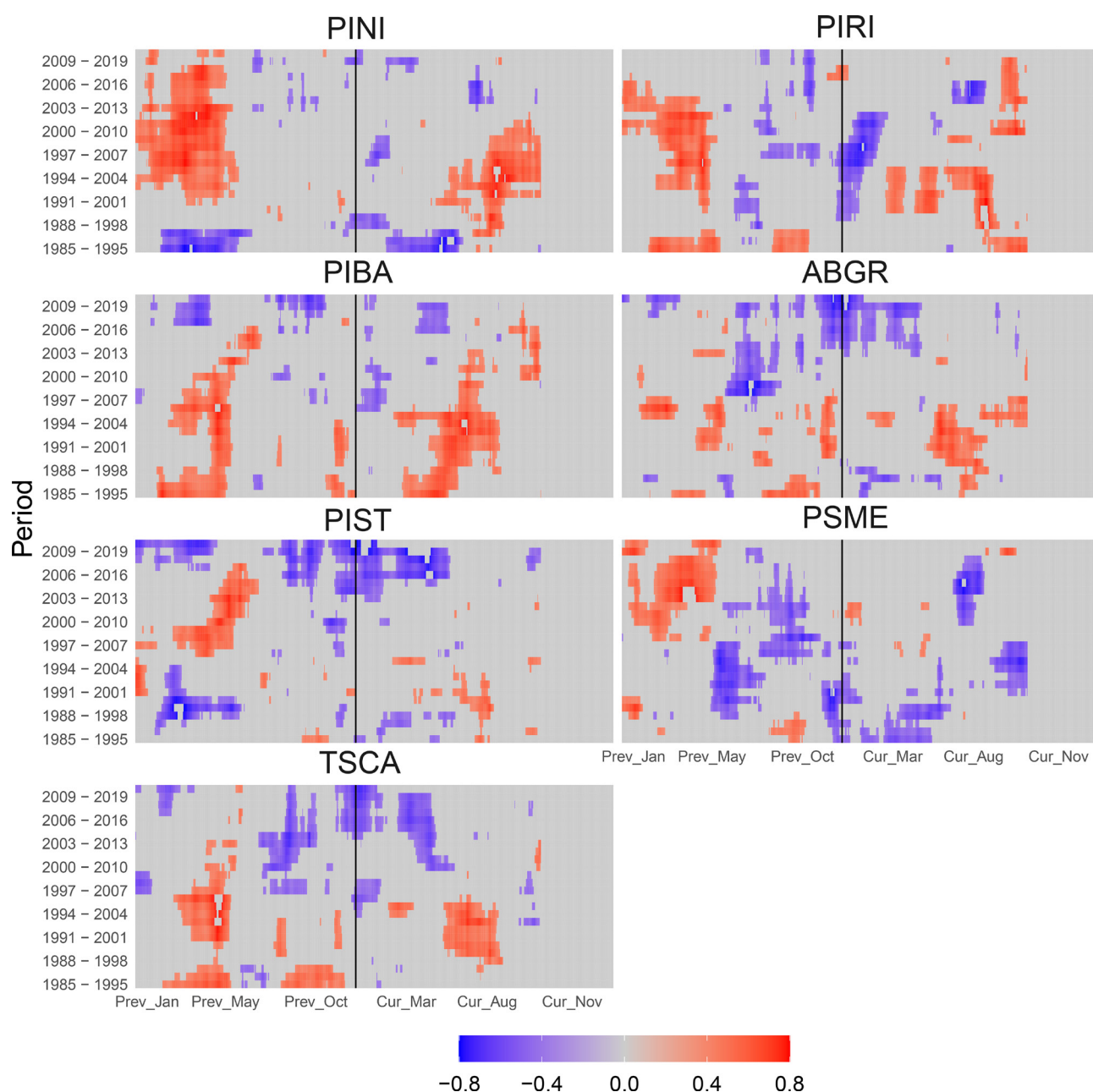


Fig. 6. 10-year moving window correlations between tree-ring width index (RWI) and previous and current year daily SPEI. For species IDs see data Table 1

for ring width and daily SPEI (from previous January to current September) clearly demonstrated interspecies variation in climate sensitivity (Fig. 6). The negative water balance ($\text{SPEI} < 0$) of the winter months had a limiting effect on the growth of ABGR, PIST and TSCA, while this relationship was not observed for PSME and PIRI and only weakly for PIBA and PINI. Extremely dry seasons ($\text{SPEI} < -2$) resulted in growth reduction only in PIST and PINI (Fig. S2), while in PIST the growth response occurred in the same year, a two-year delay was observed in PINI.

Discussion

The frequency of frost-related xylem deformation was strongly dependent on cambial age (Fig. 2, 3A and 3B), while late wood-like tracheids in early wood occurred in different years independent of cambial age (Fig. 2, 3C and 3D). Both types of growth anomalies, FR and IADF, distinguish non-native species in their susceptibility to adverse growing conditions associated with low temperatures and water deficit effects. Although the main climatic drivers determining secondary growth were common to all species

(summer precipitation and end-of-winter and spring temperatures), species-specific climate sensitivity related to pluvial and thermal conditions of the previous autumn and winter were confirmed. Similar to the stationary correlations with climatic conditions, temporal variation in climate sensitivity revealed common pattern for all species. Nonetheless, certain patterns in temporal variation in climate-growth relationships varied among species groups e.g.: PIST and PINI differ from TSCA, ABGR and PIRI in terms of spring and summer precipitation effects. The most pronounced interspecific variation was found for the growth response to drought events (as determined by the SPEI). While interspecific variation in tolerance to drought episodes is well documented for native tree species in Europe (Zang et al., 2014; Kunz et al., 2018; Harvey et al., 2020), similar evidence for drought-tolerant non-native species is scarce and relates mainly to comparisons between key non-native and native species for European forestry (Lévesque et al., 2014; Miller et al., 2022). Thus, our studies, although local in nature, provide valuable insights into the potential for acclimatization of non-native species in light of observed climate change in Europe.

The uniformly high frequency of FRs in the first cambial years in all non-native tree species reflects previous findings from studies across different bioclimatic zones (e.g. Gurskaya & Shiyatov, 2006; Kidd et al., 2014; di Filippo et al., 2021). The reasons for this trend may lie in specific aspects of conifer ecology, in particular: a thinner bark layer isolating the cambium cell layer in young trees (Gurskaya & Shiyatov, 2002, 2006; Gurskaya et al., 2016; Arco Molina et al., 2016; Bräuning et al., 2016; Muñoz-Salazar et al., 2022), a different cambial phenology reflected in an earlier timing of cambial reactivation in younger trees (Rossi et al., 2008; Li et al., 2013; Zeng et al., 2018), and higher growth rate during the juvenile phase of trees, exposing tracheids to frost damage during the differentiation phase (Schweingruber, 2007; Jiang et al., 2021). Although these factors co-occur, this does not mean that they are equally important for frost damage vulnerability (Li et al., 2019).

The highest frequency of FR in the first cambial years was observed in PSME and TSCA ($\geq 50\%$ of trees, Figs 2 and 3). This pattern has previously been confirmed only for PIBA in the natural range of this species (Kidd et al., 2014) and thus under climatic conditions different from those in Central Europe (Fig. S1). The higher vulnerability of PSME and PSCA to cambium tissue damage caused by early spring frosts, which is particularly pronounced in the first growth rings, could be related not only to species-specific characteristics (thinner bark or earlier cambium reactivation) but also to tree age (Carrer & Urbinati, 2004). For species represented by older trees (PINI, PIRI, and PIBA), cambium cell damage

was caused by late frosts between 1930 and 1950, whereas for species represented by younger trees (PSME and TSCA) it was caused by weather events between 1970 and 2000. Given the changes in intensity and frequency of climatic anomalies observed in recent years, generalizations of our results should be made with caution (Ma et al., 2019).

Studies addressing the frequency of occurrence of IADF in the xylem structure of non-native conifer species growing in Europe are scarce and involve species considered particularly important for European forestry (Wimmer et al., 2000; Wimmer, 2002; George et al., 2019). However, work on these species conducted in their native habitat suggests that they tend to form anomalies in xylem structure due to fluctuating climatic conditions (Hoffer & Tardif, 2009; Marchand & Fillion, 2012). Here we present evidence that all seven non-native conifer species alter xylem structure under Central European climatic conditions to produce IADF (Fig. 2). Although the non-native species show a diverse predisposition to form IADF structures, PIST stands out with the highest frequency of anomalies in the xylem structure (Fig. 3D). This could indicate a high sensitivity of PIST to short term water stress both in its natural range and in its secondary distribution (Marchand & Fillion, 2012). The response to water stress manifested in the formation of IADF observed in PIST is also confirmed by the reduction of radial growth in response to spring droughts (2005–2020, Fig. 6). Similar sensitivity to water deficit to PIST is manifested by PSME and TSCA which is in accordance with the results of provenance studies in Central Europe (George et al., 2019). In the case of PSME, there is no doubt about intraspecific variability in response to water stress under continental climate conditions induced by climate transfer (Klisz et al., 2022). There is no evidence to date that similar variability exists in other alien species (Alizoti et al., 2022), despite provenance experiments confirm intraspecific variation in wood density (Nabais et al., 2018). Our studies indicate that climate transfer may have been one of the factors contributing to the species-specific growth response (see bio2 and bio4; Fig. S1). According to Prasad & Leites (2022), eastern white pine reached the highest growth potential in the “warm” zone located in the southern part of its natural range in North America. Growing conditions at the study site appear to be most closely linked in terms of the temperature-related bioclimatic parameters to ‘cold’ or possibly ‘middle’ intraspecific regions within the natural range of eastern white pine (Prasad & Leites, 2022; Fig. S1). Thus, we can speculate that this species has not found optimal conditions in Central Europe, although previous studies indicate its high invasive potential (Hadincová et al., 2008; Münzbergová et

al., 2013). Our assumptions are supported by specific xylem modifications, namely frost rings and IADF, which are substantially more frequent in PIST than in other species (Fig. 2 and 3).

In general, the main climatic drivers, common to all seven species (mean temperature of February–April and precipitation of June–July; Fig. 4) correspond with previous studies on these species from Central Europe (Feliksik & Wilczyński, 1999a; 1999b, 2004; Cedro et al., 2013; Bijak et al., 2016; Wojtan & Tomusiak, 2018; Wilczyński, 2020). However, the varying period of responsiveness observed among non-native species may indicate species-specific climate sensitivity, which has not been reported so far. These trends are even more pronounced for the minimum and maximum temperature effects (Fig. S3). PINI the only European species among the seven non-native species, had the longest period of responsiveness with respect to the mean temperature effect, spanning from the previous December to the current mid-April (Fig. 4). This may indicate that PINI can take advantage of an earlier onset of the growing season (Poljanšek et al., 2019). However, recent findings on cambium phenology suggest that the onset of cambium activity of PINI, as with PIRI, may be delayed compared to other pine species, PISY and PIST (Puchałka, personal communication). The other species besides PINI with a relatively long responsiveness period was found to be PSME, which according to Miller et al. (2022) should give it an advantage in superior growth performance. In contrast, ABGR and PIST had the shortest periods of responsiveness, from March to mid-April. This in turn may indicate that both species fail to take advantage of favorable early spring conditions for earlier reactivation of the secondary meristem. Our finding only partially corresponds with previous studies from Denmark, where a positive effect of winter warming was observed in PINI and ABGR but did not persist for spring temperatures (Song et al., 2021). This discrepancy in climate sensitivity could be due to divergent effect of climatic conditions of study sites, specifically jet stream latitude and the associated strong anticyclonic anomalies that disrupt the westerly airflow (atmospheric blocking) in Europe (Dorado-Liñán et al., 2022). Considering the positive effect of spring temperature and summer precipitation, a longer period of responsiveness may indicate that species originating from the same continent (Europe) but from a different climatic zone have adapted better to local conditions than species from North America. A longer period of responsiveness can be beneficial for tree growth, although when it occurs at the beginning of radial growth it can also contribute to higher sensitivity to late frost events (Gurskaya, 2021). In our study, the predominance of frost rings was observed in early wood tracheids, although cell

deformations induced by late frosts were equally frequent in species with long and relatively short response periods (Fig. 2, 3A, 3B).

The positive effect of spring temperature associated with spring warming (Ma et al., 2016) was observed in all species, but the temporal stability of this relationship was species-specific. While a stable climate signal was observed in PIBA, PINI, and PIRI; ABGR, PIST, and TSCA did not respond to spring warming until the last decade of the twentieth century (Fig. 5). The species-specific temporal stability of the climate signal may indicate that some species still find favourable conditions for radial growth despite the warming of the winter-spring period, while others are only now benefiting from climate warming. However, this pattern of climate-growth relationships may only be valid to the Central European lowlands and may change depending on environmental conditions (Lévesque et al., 2014). Nevertheless, the positive effect of winter-spring warming on the growth of non-native species (Fig. 5) suggests that these species, at least in Central Europe, may benefit from climate change. While the effect of winter-spring temperature changes appears to be common, the effect of summer precipitation deficit is markedly different (Fig. 5). Summer water deficit reduces radial growth most significantly in PIST and PINI (Fig. S2), with the latter species simultaneously adapting xylem structure to adverse conditions by developing an IADF structure much more frequently than the other species (Fig. 3D). Assuming that negative pointer years can be associated with drought events, the CPY analysis provides no basis for distinguishing groups of NNTs sharing a common response to these weather anomalies (Fig. 2). However, extreme water deficits could be responsible for the reduction in radial growth common to majority of the species (e.g., 1996, Fig. 2). Again, our findings on the drought tolerance of alien species should be interpreted with caution. Site conditions, species composition, local climate, and intra-species variability undoubtedly shape the vulnerability of these species to drought events as demonstrated for PSME (Sergent et al., 2014; Montwé et al., 2015; Thurm et al., 2016; Vitali et al., 2018). As recent research has demonstrated, the effect of severe drought events on wood-related traits is largely stable across broad climate gradients (Serra-Maluquer et al., 2022). Nevertheless, wood density, a proxy for the relationship between growth and drought, is modified by climate transfer effects, which is particularly important when non-native tree species are considered (Nabais et al., 2018). In our study, it is not possible to determine the effects of climate transfer because the origin of seeds of non-native species is unknown and these species cover a wide range of ecological conditions in their natural range (except for PINI, Fig. S1).

Conclusions

Under lowland climate conditions of Central Europe, warming of the winter-spring period appears to favour growth of both southern European and North American conifer species, as reflected in the extended responsiveness period. However, the same warming with concurrent late frosts effectively limits acclimatization of non-native species, especially during the juvenile phase. Deficits in summer precipitation exacerbated by high temperatures result in reduced growth and anomalies in xylem structure-IADF in earlywood. PIST is one of the fastest growing non-native conifers despite its high susceptibility to frost-induced cambium damage and sensitivity to summer drought. However, the data set used in this study has obvious limitations due to local environmental conditions, but at the same time represents a unique set of seven alien conifer species that have not yet been studied in Europe. Therefore, here we call for new local studies on the acclimatization of non-native coniferous species to complete the picture for Europe.

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