Agricultural and Forest Meteorology 371 (2025) 110628

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Temperature-driven shifts in spatiotemporal stability of climate-growth responses of Douglas-fir (*Pseudotsuga menziesii*) from the southern Baltic Sea region

Marcin Klisz [a,*], Radosław Puchałka [b,c], Mariusz Gławenda [b,c], Marcin Koprowski [b,c], Roberts Matisons [d], Sandra Metslaid [e], Aleksei Potapov [e], Tobias Scharnweber [f], Eric Andreas Thurm [g], Rita Verbylaite [h,i], Adomas Vitas [j], Martin Wilmking [f], Jernej Jevšenak [k]

[a] *Dendrolab IBL, Department of Silviculture and Genetics, Forest Research Institute, Braci Lesnej 3, 05-090 Sekocin Stary, Poland*
[b] *Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100, Torun, Poland*
[c] *Centre for Climate Change Research, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Torun, Poland*
[d] *Latvian State Forest Research Institute 'Silava', 111 Rigas str., Salaspils, LV-2169, Latvia*
[e] *Chair of Forest and Land Management and Wood Processing Technologies, Institute of Forestry and Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51006, Tartu, Estonia*
[f] *DendroGreif, Working Group Landscape Ecology and Ecosystem Dynamics, University Greifswald, Greifswald, Germany*
[g] *Landesforstanstalt Mecklenburg-Vorpommern, Department of Forest Planning/Forest Research/Information Systems, Research Unit Silviculture and Forest Growth, Zeppelinstrasse 3, 19061, Schwerin, Germany*
[h] *Department of Forest Genetics and Tree Breeding, Institute of Forestry, Lithuanian Research Centre for Agriculture and Forestry, Liepu str. 1, Girionys, LT-53101, Kaunas distr., Lithuania*
[i] *Faculty of Environmental Engineering, Lietuvos inžinerijos kolegija Higher Education Institution, Tvirtovės al. 35, LT-50155, Kaunas, Lithuania*
[j] *Vytautas Magnus University, Kaunas, Lithuania*
[k] *Department for Forest and Landscape Planning and Monitoring, Slovenian Forestry Institute, Večna pot 2, 1000, Ljubljana, Slovenia*

ARTICLE INFO

Keywords:
Climate warming
Climate–growth relationships
Dendroecology
Europe
Tree growth

ABSTRACT

The southern Baltic region spans a significant part of the European continent with its forests under significant pressure due to climate changes. The implications of these changes are crucial for both native and non-native tree species. Under future climate scenarios, most native conifer populations might lose their climatic optima in the region. In contrast, for non-native Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), climatic conditions are expected to become optimal in the Baltic Sea region. Therefore, understanding the acclimatisation trajectory of Douglas-fir over the last century is essential to assess its potential to supplement retreating species and reduce pressure on local habitats. To study the region-wide acclimatisation in the secondary distribution, we established a network of 27 Douglas-fir tree-ring chronologies along the south Baltic Sea. We determined the spatio-temporal stability of the climate signal in tree rings and the potential coastal effect on the plasticity of the growth response. We found a region-wide trend of climate-growth relationships, with a dominant effect of the early-growth season temperatures being more pronounced for mature than young stands. Sites with higher mean annual temperatures exhibit a stronger positive temperature–growth correlation, demonstrating the sensitivity of Douglas-fir to climate warming. Douglas-fir could serve as a more heat-tolerant alternative to the declining European species of the Pinaceae family and contribute to the preservation of functionally comparable coniferous forest communities. However, forest practitioners should be aware that Douglas-fir may alter habitat conditions affecting microclimate and influencing species diversity.

---

* Corresponding author at: Dendrolab IBL, Department of Silviculture and Genetics, Forest Research Institute, Poland
E-mail address: m.klisz@ibles.waw.pl (M. Klisz).

https://doi.org/10.1016/j.agrformet.2025.110628
Received 16 September 2024; Received in revised form 7 May 2025; Accepted 11 May 2025

1. Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), is the most common non-native conifer in the entire Europe introduced from North America (Pötzelsberger et al., 2020). Still, it is unclear, how this species might be able to adapt to Europe's changing climate (Lévesque et al., 2014), how it potentially outcompetes native tree species (Miller et al., 2022), thereby changing local habitats (Podrázský et al., 2014; Schmid et al., 2014). The future of Douglas-fir in Europe is of great interest, since it is a very valuable, fast growing, and well-adapted tree to the climatic conditions in Europe. However, in the near future (2014-2060) this species may lose potential climate niches in western and central Europe regardless of whether the optimistic (SSP126) or pessimistic (SSP485) climate change scenario comes true while persisting in the southern and extending into the eastern and northern Baltic regions (Dyderski et al., 2018; Puchałka et al., 2023). In their natural range in North America, coastal and interior Douglas-fir populations show local adaptations that are expressed in different growth performance under changing climatic conditions (Klesse et al., 2020). Given the incomplete information on the genetic origin of trees (e.g. interior or coastal) growing today under non-analogue conditions in Europe (Fontes et al., 2003; Hintsteiner et al., 2018), other studies mainly focus on European provenance experiments (Chakraborty et al., 2018; Chakraborty et al., 2015; Krajnc et al., 2023) or recommend native provenances for planting in selected areas of Europe (Isaac-Renton et al., 2014). However, neither approach solves the acclimatisation of mature, old stands already growing in the species' secondary distribution. Therefore, numerous independent studies have attempted to assess the sensitivity of Douglas-fir to local climatic and habitat conditions (Enderle et al., 2024; Lassoie and Salo, 1981; Levanic and Straus, 2022) and its resilience to climate anomalies (Klisz et al., 2022; Sergent et al., 2014; Wrzesiński et al., 2024).

Studies on the climate sensitivity of Douglas-fir across various regions of Europe report the predominantly growth-accelerating effect of warm winters (Castaldi et al., 2020; Lévesque et al., 2014; Wrzesiński et al., 2024), suggesting an earlier onset of secondary meristem activity (Kriegel et al., 2021) or photosynthetic activity in winter, leading to a higher storage of non-structural carbohydrates (Wiley et al., 2018). With earlier growth activity, exposure of trees to climatic anomalies, particularly late frosts (Ma et al., 2019), can lead to injury and, consequently, to dysfunction of the xylem tissue (Klisz et al., 2022). Although the risk of damage to the vascular tissue is highest in juvenile trees (Arco Molina et al., 2016), as their bark layer does not insulate them sufficiently against low temperatures, frost-induced dysfunction of the tracheids in earlywood can effectively offset the positive effects of a longer growing season (Glerum and Farrar, 1966). A temporary dysfunction of the conductive tissue, after which the tracheids only regain their conductive capacity in the following season, may potentially lead to temporal changes in climate sensitivity (Zhirnova et al., 2022). Consequently, the stationarity of the climate signal can reflect both intrinsic and extrinsic factors, given a complex pattern of a species' acclimatisation at the local scale. To date, there are no region-wide studies in Europe that go beyond locally specific conditions on climate-growth relationships, especially in areas where Douglas-fir is expected to thrive under optimal climatic niches (Puchałka et al., 2023). Such a region-wide approach enables more reliable conclusions as it facilitates the study of spatial variability within geographically diverse area (Klesse et al., 2024; Leifsson et al., 2024; Martinez Del Castillo et al., 2024). One of the regions of Europe insufficiently explored in terms of climatic sensitivity is the southern Baltic coast with pronounced climatic gradient (Harvey et al., 2019; Weigel et al., 2018). The climatic conditions specific to the south Baltic Sea region were likely favorable for the growth of Douglas-fir in the last century (Feliksik and Wilczynski, 2004; Wilczynski and Feliksik, 2007). However, these findings have not been verified for the entire region under the changing climatic conditions of the first two decades of the 21st century. Over the past decades, Douglas-fir, like other trees, has experienced changes in climatic conditions, but its sensitivity to changing growth conditions has been attributed to its ontogenetic development (Trouillier et al., 2018). Unstable environmental conditions in conjunction with species-specific, variable climate sensitivity were thus expressed by the non-linear relationship (hereinafter non-stationarity) of the climate signal (Gribbe et al., 2024). For central Europe, there is clear evidence of a changing climate-growth relationship in the late 20th and early 21st centuries, although the character of this change as well as the interplay with the developmental stage of the trees has so far only been explored locally (Cavelier et al., 2025; Klisz et al., 2022; Wrzesiński et al., 2024).

Thus, assuming that the non-linear relationship between the growth of trees and their external factors is an ecological attribute of long-lived plants (Wilmking et al., 2020), it must be assumed that multiple co-occurring factors are responsible for the non-stationarity of the growth pattern. One of the main causes of non-stationarity in growth patterns is varying climatic conditions (Peltier and Ogle, 2020) and ontogenetic development, though in recent decades, trees have tended to change sensitivity from one environmental factor to another (Leifsson et al., 2024). This phenomenon is considered to be the result of an adaptation lag to rapid climate change (Frejaville et al., 2020). On the one hand, this phenomenon poses a challenge to climate reconstruction, carbon cycle, water cycle and future forest management (Buras et al., 2017; Jevšenak et al., 2024; Tumajer et al., 2023). However, it offers unique opportunities to study the plasticity and (mal)adaptation of trees in response to recent climate change (Matisons et al., 2021). With increasing interest in the non-stationarity of the relationships between tree growth and climatic conditions, methods for testing the temporal stability of climatic sensitivity have been developed (Beck et al., 2013; Jevšenak and Levanič, 2018; Zang and Biondi, 2015). The so-called running correlation approach for monthly and daily climate variables has become widely used (Leifsson et al., 2024; Tumajer et al., 2023). The successive advancement of analyses using high temporal resolution of climate variables now allows bootstrapped and partial correlation to be calculated (Jevšenak, 2020). In this study, we propose a further step in assessing the non-stationary correlations by calculating correlation patterns across various seasons and subsequently deriving parameters describing temporal trends, i.e., linear beta coefficients, for all seasonal combinations. The advantage of this approach lies in providing more detailed insights into changing climate sensitivity, which allows for the evaluation of the interdependency of different climatic parameters, as well as the identification of shifts in seasonal patterns. By analyzing these relationships over time, it becomes possible to identify how variations in one climatic factor influence others, revealing complex interactions that might otherwise go unnoticed. We established a tree-ring network of monospecific Douglas-fir stands, introduced in the late 19th and early 20th centuries across the southern Baltic coast to explore the effects of local climatic conditions on climate-growth correlations and their temporal stability at the regional scale over its century-long acclimatisation history.

We hypothesise that (i) the south Baltic Sea region generally provides favorable conditions for Douglas-fir growth, (ii) these conditions vary spatially and temporally leading to distinct variations in the stability of the climate signal, and (iii) spatial variation of climate sensitivity is driven by regional climate patterns in the Southern Baltic Sea.

2. Materials and methods

2.1. Study region

The study focused on the southern Baltic Sea region, spanning from ~ 52 to 59°N and 10 to 27°E, an area where Douglas-fir has been introduced over the last two centuries (Table A1, Fig. A1) (Brus et al., 2019). The western and central part of this region (northern Germany and Poland), are located in Pleistocene lowlands shaped by the last glaciation. These areas feature relatively uniform forest complexes, primarily located on ground and terminal moraines. In the northeastern part of the region (Latvia, Lithuania, Estonia), on the other hand, the relief is flatter, with a high proportion of wetlands within the glacial depressions. According to the Köppen-Geiger classification, the growing conditions in the western part of the region are shaped by a temperate humid climate (Cfb), while the eastern part experiences a more continental humid climate with cold, moist winters and warm, wet summers (Dfb) (Kottek et al., 2006; Peel et al., 2007). Mean annual temperatures range from 5.4 – 9.1°C, and annual precipitation ranges from 556 – 839 mm (Table A1, period 1979–2013 CHELSA Bioclim database) (Karger et al., 2017). Over the past century, the southern Baltic Sea region has experienced a warming of the summer season, although the increased temperatures in winter have led to reduced snow cover and partially decreasing soil temperatures (Weigel et al., 2021). The increase in annual temperature has been more pronounced in the eastern and northern latitudes, while precipitation has shown a decreasing trend in the south-western part of the region. Despite this overall pattern, there have been some hotspots with increased precipitation of up to 60 mm per year (Fig. 1). In the Baltic Sea region, the heterogeneity of summer precipitation has the tendency to increase, hence the incidence of prolonged hot droughts increases (Meier et al., 2022).

2.2. Study sites

In selecting the study sites, our primary aim was to select the oldest existing Douglas-fir pure stands in the region. Younger developmental stages were only considered as acceptable alternatives when this criterion could not be met (i.e. in north-eastern Poland and eastern Lithuania). The second criterion in selecting the study sites was to ensure the study sites represented the diverse climatic conditions of the South Baltic Sea region, aiming to capture the most comprehensive climatic range (Fig. 1). In order to achieve the most complete climate coverage possible for the region, 27 study sites were selected, with a mean age ranging from 49 to 130 years (mean age of 90 years), located at elevations up to 231 m above sea level (Fig. A1; Table A1).

2.3. Tree-ring data

At each of the 27 selected study sites, 20 to 25 sample trees were chosen from among the dominant and visually healthy individuals. Two increment cores were collected from each tree using an increment borer from random directions perpendicular to each other at a height of approximately 1.3 meters above the ground (Gut et al., 2019), the fieldwork was conducted between 2019 and 2021. The wood samples were processed by a standard sample preparation procedure, sanded with progressively finer sandpaper to ensure ring border identification, and digitized at 2400 dpi (Epson Expression XL12000). Subsequently, ring width measurements with an accuracy of 0.01 mm and cross-dating were performed using digital measuring software (CooRecorder and CDendro v.9.0, respectively). Two growth series per tree were only averaged to create individual tree-ring series if the minimum Pearson correlation criterion of 0.20 was met. Growth series that did not meet this criterion were excluded from further analyses. Consequently, each

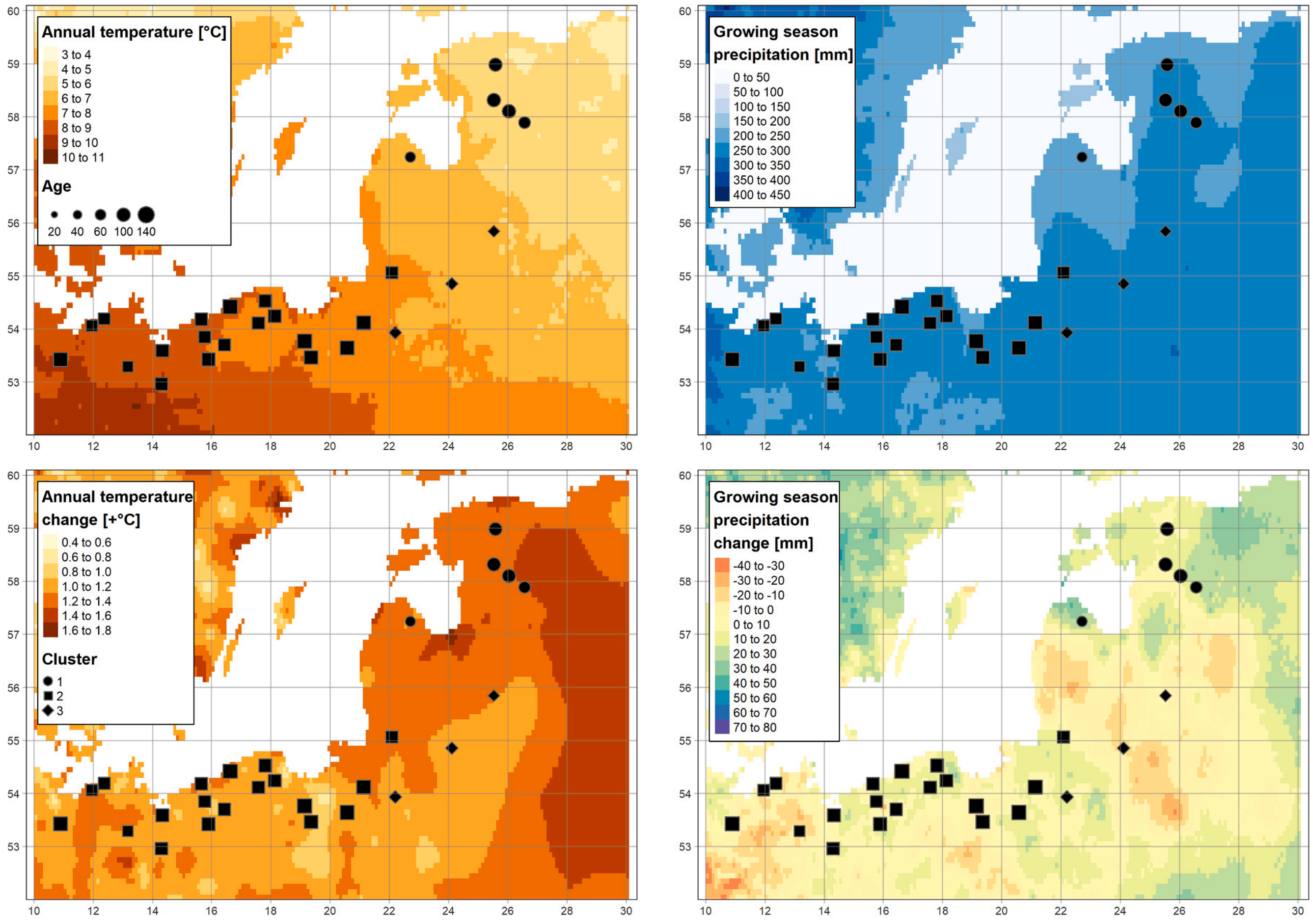

Fig. 1. Climatic conditions of the South Baltic region for mean annual temperature (upper left panel) and growing season precipitation sums (upper right panel) for the period 1950–2020. Changes in climatic conditions of the study region calculated as a difference between the early (1950–1985) and late (1986–2021) periods for mean annual temperature (bottom left panel) and growing season precipitation sums (bottom right panel). Size of black circles indicates the mean age of Douglas-fir stands, while the symbol indicates the cluster group.

study site was represented by 14 to 23 trees (Table A2). To exclude age-related trends and other non-climatic influences on growth, the raw growth series were detrended using a cubic smoothing spline with a cut-off of 50 % of the frequency at a wavelength of 32 years (Cook and Peters, 1981; Speer, 2010). In the next step, pre-weighting was applied with the first-order autoregressive model to remove autocorrelation and emphasize the high-frequency signal in growth (Cook and Kairiukstis, 2013). Finally, to create residual chronologies, bi-weighted robust means were used (Table A2). The quality of the established chronologies was verified with Gleichläufigkeit (Glk, i.e. the coherence coefficient) (Buras and Wilmking, 2015; Eckstein and Bauch, 1969) and the mean correlation between individual tree ring series (mean rbt, an indicator of the strength of the common signal) (Cook and Kairiukstis, 2013; Wigley et al., 1984). To test the suitability of the created chronologies for climate-growth analyses, we applied the sub-sample signal strength (SSS), first-order autocorrelation (AR1, an indicator of the effect of the previous year's conditions on the current year's growth) and signal-to-noise ratio (SNR, the proportion of the explainable variation of the chronology due to climate divided by the unexplainable variation) (Wilczyński and Kulej, 2013). A threshold value greater than 0.95 was used as an entry criterion for the SSS (Table A2).

2.4. Spatial variation of radial growth pattern

We applied hierarchical clustering to detrended site chronologies to assess similarities in radial growth patterns. The analysis covered the period 1975–2019, the common timeframe with available data for all 27 sites. A Euclidean distance matrix was computed to quantify pairwise dissimilarities between observations. We considered five different clustering methods, single and complete linkage, average, weighted and Ward's method were tested according to their clustering structure of the dataset (Kaufman and Rousseeuw, 2009). Finally, we chose Ward's method, since it expressed the highest value of the agglomerative coefficient. The Ward method minimizes the total variance within clusters.

2.5. Climate data

Given the broad geographic coverage of the study sites and the variation in quality among instrumental climate data from five countries in the southern Baltic Sea region, we utilized uniform daily climate data from the E-OBS version 24.0e with a $0.1^{\circ} \times 0.1^{\circ}$ spatial resolution (Haylock et al., 2008). More specifically, we used the mean daily air temperatures and daily precipitation sums for the period 1920-2022. To verify the climatic niches of Douglas-fir across its native North American range and its secondary distribution in Europe, we used two bioclimatic variables, BIO7 – Annual range of air temperature and BIO18 – Precipitation of warmest quarter (Fig. A2B). These variables were obtained from CHELSA Bioclim database, which provides high resolution climate data for Earth's land surface areas at a spatial resolution of 30 arcsec from 1979-2013 (Karger et al., 2017), allowing unbiased comparison of areas with different annual temperature and precipitation distributions (Klisz et al., 2022; Puchałka et al., 2023).

2.6. Tree growth responses to climate

To assess the site-specific climate sensitivity of the Douglas-fir population, we calculated climate-growth correlation coefficients using day-wise aggregated climate variables (mean temperature and precipitation), considering all season lengths (aggregation windows) between 21 and 180 days, from April of the previous year to October of the current year. Specifically, we used the *daily_response()* function implemented in the latest version of the R package dendroTools for this purpose (Jevšenak, 2020; Jevšenak and Levanič, 2018). We ran a large number of correlation tests, which could result in increased type I error (Torbenson et al., 2024). To avoid drawing conclusions solely based on p-values, we have removed all weaker correlations and retained only those exceeding the 75th percentile of the absolute correlation values for each site. In addition, the timings and seasons of the most significant correlations are all well-within the expected seasons, and we thus argue that they can be trusted. To avoid any spurious correlations related to temporal trends in the climatic series, each climate series was detrended before the calculation of the correlation series (Ols et al., 2023). To do so, we used linear detrending, which involves fitting a linear regression model to represent the long-term trend across the climate series and subsequently subtracting this trend component from the original observations. In addition to the site-specific climate sensitivity analyses, we also aimed at identifying a general trend of climate-growth correlations through all combinations of season lengths for all study sites and calculated average correlation coefficients.

2.7. Temporal stability of climate–growth relationships

To derive site-specific temporal trends of the relationships between tree rings and climate, we first subdivided each chronology and corresponding climate data into 30-year time windows and calculated correlation coefficients for each season, defined as a combination of season length (from 21 to 180 days) and season start (from 150 DOY of the previous year to 360 DOY of the current year). We then repeated these calculations using a moving window that was successively shifted by one year at a time for the entire period 1950 – 2021.

This process resulted in period-specific correlation coefficient matrices (heatmaps) for each site, with each pixel representing a specific season. These matrices were ordered by time, and the beta coefficients from pixel-wise linear models were extracted (Eq. 1), representing increasing or decreasing climate sensitivity across the seasons (Popa et al., 2024).

$$\rho_{\mathrm{i}}(\mathrm{t}) = \beta_{\mathrm{i}}\mathrm{t} + \alpha_{\mathrm{i}} \tag{1}$$

where: $\rho_i(t)$ represents the correlation coefficient for the *i-th* seasonal combination at time *t*, β_i is the slope, indicating the rate of change of correlation over time for the *i-th* seasonal combination, α_i is the intercept for the *i-th* seasonal combination (the expected ρ_i when $t = 0$), *t* is the time variable (*year* in our study).

These calculations were performed independently for each climate variable (mean temperature and precipitation) and study site. As a result, we obtained a heatmap of beta coefficients for each combination of site chronology and climate variable, indicating climate-growth correlation stability over time. Finally, to obtain a general trend for Douglas-fir in the temporal stability of climate sensitivity, we averaged site-specific heatmaps of beta coefficients for each climate variable, while results for individual sites are reported in Appendix A (Figs. A5 and A6). Finally, we produced seasonal heatmaps of mean beta coefficients (β_i). A positive β_{i} denotes growing climate sensitivity for variables with positive effects and diminishing sensitivity for those with negative effects, whereas a negative β_{i} denotes the opposite – decreasing sensitivity for positive-effect variables and increasing climate sensitivity for negative-effect variables, relative to the climate factor under study. To further elaborate on spatial variations in the obtained beta coefficients, we modeled them as a function of long-term annual temperature data from 1950 to 2022, which exhibited a distinct gradient across the study sites (Fig. 1). Although we also evaluated other variables, such as annual and growing season precipitation, longitude, latitude, and distance to the Baltic Sea, they were less significant in explaining the variability in beta coefficients and, therefore, not used in the final models. Thus, in the results section, we present the models for the seasons with the highest explained variance, highlighting the main trends in climate sensitivity across the study region, while additional results showing consistency across similar seasons can be found in the Appendix A.

3. Results

3.1. Chronology statistics and growth pattern

The NRA and ELK chronologies demonstrated the strongest common signal in radial growth patterns (rbar > 0.65), while the RAM and SLA chronologies exhibited the weakest signal (rbar < 0.40; Table A2). However, this pattern is not evident in either the coherence coefficient (Glk) or the first-order autocorrelation (AR1, inverse trend). The RAM, SLA and ROK had a significantly weaker environmental signature in radial increment (SNR < 10) among site chronologies than the ELK and NRA populations (SNR > 30; Table A2). All the chronologies showed relatively high site-specific growth patterns (SSS > 0.95), yet the DRA chronology had a slightly lower subsample signal strength (0.93; Table A2).

Three distinct clusters were identified: 1) The first cluster comprised two younger sites from Lithuania and one younger northeastern site from Poland. 2) The second cluster included all Baltic sites from Estonia and Latvia. 3) The third and largest cluster contained the remaining 19 chronologies, which could be further divided into two subclusters. One subcluster primarily consisted of northeastern Polish sites and one Lithuanian site (RAM), while the other included sites from northwestern Poland and northern Germany. These results reveal distinct spatial radial growth patterns, with notable differences between mature and younger forest stands (Fig. 2).

3.2. Climate–growth relationships

Climate sensitivity analyses across the study sites, situated along a temperature gradient (Fig. A3), revealed a predominant positive influence of early season temperatures on the radial growth of Douglas-fir (Fig. 3). This pattern intensifies with higher annual temperatures, where the selected youngest sites (ELK, ROK) represent the only and the most significant outlier to this pattern (Fig. A3). The growth reaction to precipitation, while less marked, was also noteworthy, but was relatively uniform across the sites without significant precipitation pattern. High precipitation from early spring to late summer, generally had a positive effect on the Douglas-fir trees across all sites, with the exception of the youngest site (ROK) in Lithuania, where a negative relationship with previous years' precipitation was observed. Warmer sites showed slightly stronger correlation with both the previous and current season rainfall, while cooler sites responded positively solely to precipitation in the current year. Notably, some sites exhibited a substantially weaker precipitation signal (ROK, KAM, OI, BYT and IDPM, Fig. A4).

3.3. Temporal stability of climate-growth relationships

The temporal stability analysis of climate signals revealed distinct, climate variable-specific patterns. From 1950 to 2021, the positive effect of the current summer temperature decreased, while the influence of the previous autumn temperature increased. This trend, observed within the 30-year moving window, coincided with a weakening effect of the late summer temperatures (Fig. 4). During the current summer, we generally observe a reduced climate sensitivity to precipitation, while beta coefficients for temperature remain close to zero, indicating no significant change. However, we also detected decreasing negative correlation trends for temperature in late summer to early autumn. Regarding the previous growing season, we observed more site-specific responses related to changes in climate sensitivity. At a few sites, growth showed negative correlations with previous summer temperatures (Fig. A3) and correspondingly significant negative beta coefficients (Fig. A5), indicating intensified adverse temperature effects. However, most sites exhibited non-significant correlations with previous-summer temperatures, suggesting that this season is not critical for tree growth. During the same period, precipitation also showed a general increase in its correlation strength (Fig. 3), but variability among sites was relatively pronounced (Fig. A6). Finally, temperature effects from the previous late autumn indicate heightened temperature sensitivity, whereas precipitation exhibited the opposite trend, suggesting reduced influence. Concurrently, changes in the effects of previous season temperature were associated with an inverse relationship with precipitation, confirming an interdependency between temperature and precipitation trends. However, other environmental factors could also explain this apparent interdependency, such as soil moisture availability, drought

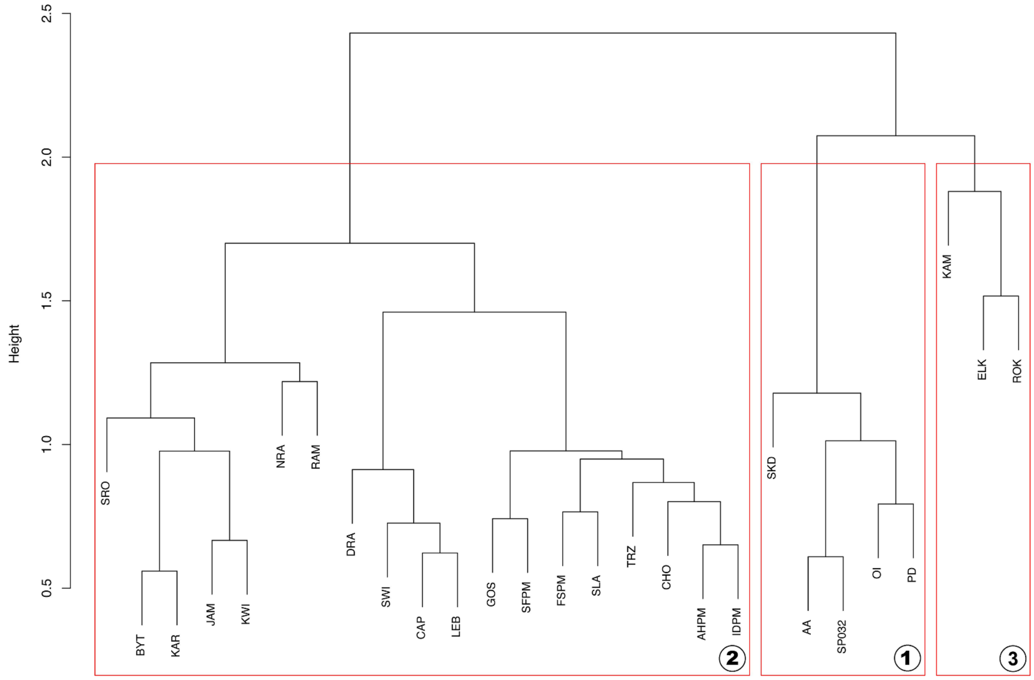

Fig. 2. Hierarchical clustering of the RWI mean site chronologies, using the Euclidean distance and Ward's minimum variance clustering method. Numbers in circles denote cluster groups. For chronology IDs, see Table A1.

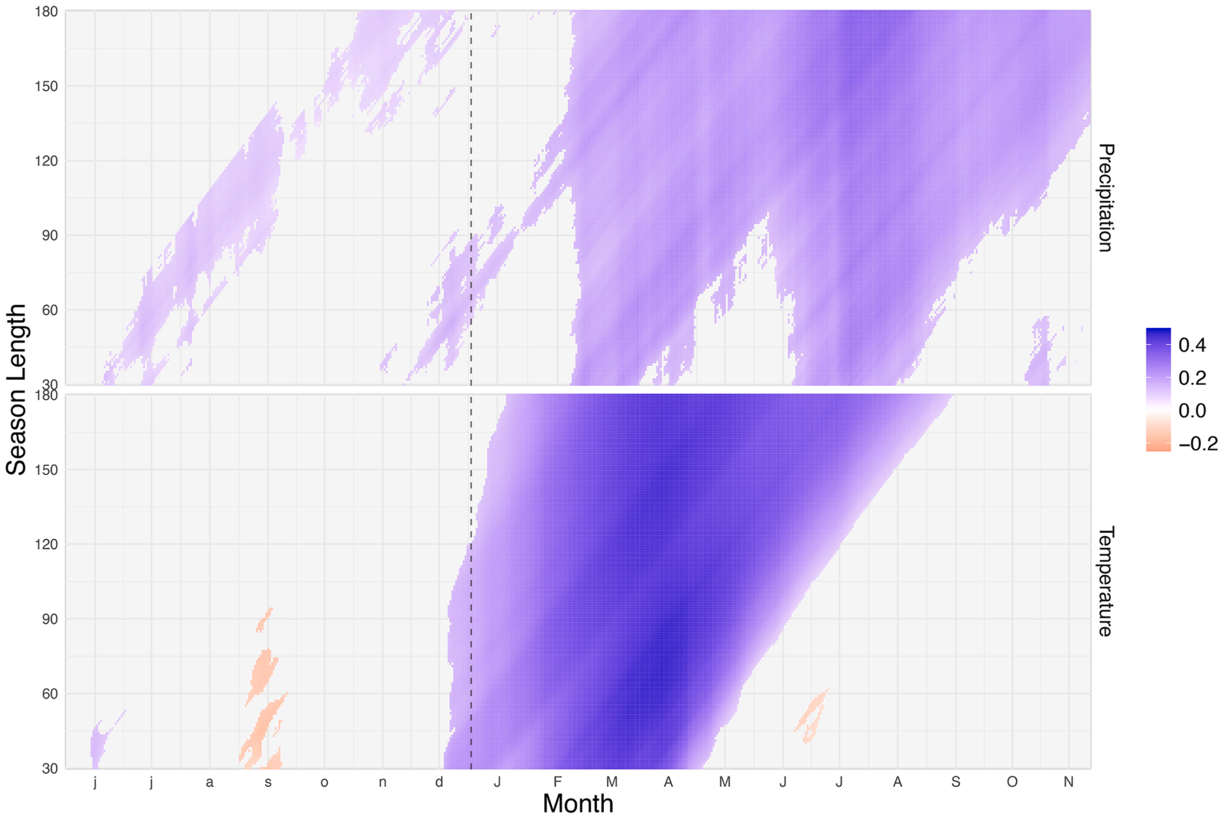

Fig. 3. Pearson correlation coefficients exceeding the 75th percentile for each site, averaged across study sites, between Douglas-fir ring-width index chronologies and aggregated (over specified season) daily variables: precipitation (upper panel) and temperature (bottom panel). Dashed vertical line marks the border between previous and current year. The position of each correlation coefficient corresponds to the end of season window, used for the calculation. Results for individual sites are shown in Fig. A3 and A4.

legacy effects, or large-scale atmospheric event.

Regarding site-specific temporal stability, the temperature signal was linked to the mean annual temperature across the study sites. Cooler sites exhibited a weakening of the temperature effect, whereas warmer sites demonstrated an amplification of this effect (Fig. A5). However, a similar relationship between the stability of the climate signal and the temperature gradient was not observed for precipitation (Fig. A6). Nonetheless, signal weakening was observed for the two youngest stands, ROK and KAM.

3.4. Spatial patterns in non-stationarity of climate-growth correlations

Trends in temporal stability of climate signal were strongly related to annual climate patterns (Fig. A7), however distance from Baltic Sea coast also appears to play a role (Fig. A8). More specifically, temporal trends in temperature correlations were mainly explained by the annual temperature pattern for both the current and the previous season (R^2 0.67 and 0.57, respectively, Fig. 5), and less by the distance to the coast (R^2 0.37 and 0.17, respectively, Fig. A8). Models explaining precipitation correlation's temporal stability for the current and previous growing season showed slightly less pronounced temperature gradient, but still highly significant (R^2 0.56 and 0.53, respectively, Fig. 5). In contrast, for distance to the coast, the model for precipitation correlation's temporal stability showed a similar gradient for both current and previous seasons (R2 0.30 and 0.36, respectively, Fig. A8). Here we show the models that exhibited the strongest temperature gradient (see Table A3 for detailed season description). However, in Figure A7 we show that the obtained patterns are strongly consistent across related seasons.

4. Discussion

The growth of Douglas-fir in the southern Baltic Sea region is mainly controlled by the temperature at the beginning of the growing season and, to a much lesser extent, by the precipitation of the previous and current seasons (Fig. 3). This trend can also be observed in other parts of Europe, regardless of the climate zone (Castaldi et al., 2020; Cavelier et al., 2025; Feliksik and Wilczynski, 2004; Levanic and Straus, 2022), and the elevation (Lévesque et al., 2014; Song et al., 2021). This finding aligns with observations for native Douglas-fir populations in North America (Chen et al., 2010). Although more favourable pluvial conditions prevail in the coastal region of Central Europe (Meier et al., 2022), a weakening of the precipitation signal may be observed regardless of the distance to the sea (e.g., IDPM, BYT, KAM; see Figs. A4 and A8). The growth of Douglas-fir in areas with a negative water balance are strongly controlled by summer season precipitation (Gazol et al., 2022; Sergent et al., 2014). The potentially suitable growing conditions in the South Baltic Sea can therefore be limiting for Douglas-fir to a certain extent due to deficient precipitation. Due to the temporal and spatial variability of the climate sensitivity of Douglas-fir across the study area, it is crucial to consider the entire region rather than focusing solely on selected study sites when assessing the performance of this non-native tree species in Europe. Over recent decades, the effect of temperatures on tree growth in the preceding end-of-summer and autumn has increased, while the significance of the winter and end-of-summer precipitation has decreased (Fig. 4). The amplifying effect of temperature on growth increases with higher site-specific mean annual temperatures (Fig. 5). Douglas-fir has so far benefited from warming in a region where end-of-winter temperatures have so far been limiting for the species' growth (Wilczynski and Feliksik, 2007). While in regions that are already warm and dry, warming during the growing season impairs the

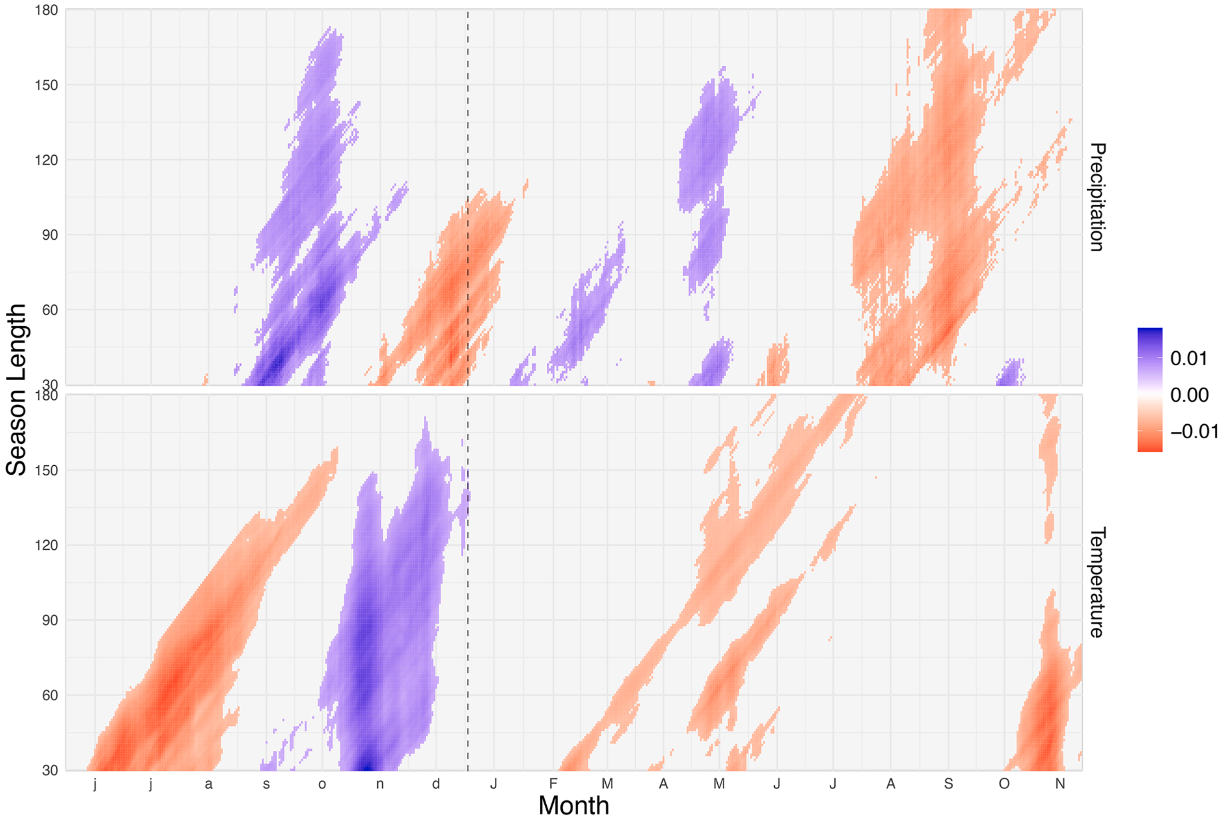

Fig. 4. Mean beta coefficients, indicating trends in climate sensitivity of study sites for temperature (bottom panel) and precipitation (upper panel). A positive beta coefficient indicates an increase in climate sensitivity towards present for positive correlations, while a negative coefficient indicates a decrease. The position of each beta coefficient corresponds to the end of season window, used for the model calculation. Trends for individual sites are shown in Figs. A5 and A6.

growth of Douglas-fir stands (Eckhart et al., 2019). Furthermore, under temperate climate warming during the dormant season can disrupt the reproductive processes of this species (Jastrzębowski et al., 2021) and thereby contribute to secondary growth as a result of resource relocation (Hacket-Pain et al., 2018).

4.1. Climate sensitivity evidence supports current and future potential distribution

The consequences of projected climate change will be particularly profound for long-lived organisms such as trees due to their relatively slow migration rates and high maturation age for generative reproduction (Aitken et al., 2008). Species distribution models (SDM) support delineating potential areas of range expansion and contraction (Booth, 2018; Dolos et al., 2015). However, the climate or site suitability for tree species, as defined by SDMs, may not align with their optimal growth conditions. This is because the fundamental niche reflects trade-offs between environmental factors necessary for completing the full life cycle of trees and establishing stable populations. Our study provides an opportunity to access growth responses of the mature Douglas-firs in northeastern Europe, an area where this species can still maintain or even expand its potential ranges in the south and southeast Baltic Sea region (Dyderski et al., 2025; Puchałka et al., 2023). Given the observed climate warming, particularly evident with increased annual temperatures in the western sites (Table A1, Fig. 1), the temperatures in the early growing season might favour Douglas-fir growth (Fig. 3). On the other hand, a warming climate in Europe is expected to lead to a higher frequency of late spring frost (Zohner et al., 2020). This can potentially damage young Douglas-fir trees, which are sensitive to low temperatures at the beginning of the growing season (Chakraborty et al., 2019; Malmqvist et al., 2018). However, this pattern is not as pronounced for the precipitation effect of the summer season (Fig. 4), as some of the warm sites (SWI, IDPM) were characterised by only a weak climate signal (Fig. A4). We can, therefore, speculate that the predicted persistence of the potential range in the southern Baltic Sea region will likely result from the favourable thermal conditions at the onset of the growing season, with summer precipitation playing a secondary role. Differences in the strength of the climate-growth relationships for precipitation (current season) and temperature (previous season) between warm and cold sites (Fig. 5) indicates that SDM predictions need to take into account the peculiarities of the south Baltic coast (Harvey et al., 2019), adjacent to the shallow, often frozen inner sea (Meier et al., 2022), and local climatic conditions (Klisz et al., 2023). Interestingly, studies on the European Douglas-fir tree stands growing under mountain climate conditions have shown a remarkably consistent growth pattern, regardless of the mountain range, with a strong influence of maximum winter temperature and much weaker summer precipitation signal (Castaldi et al., 2020; Levanic and Straus, 2022; Lévesque et al., 2014; Wrzesiński et al., 2024). In contrast, lowland stands of this species manifest a site-specific response to climatic conditions, particularly to climate extremes such as droughts (Cavelier et al., 2025; Klisz et al., 2022; Sergent et al., 2014; Vejpustková and Čihák, 2019). Soil sorption properties, fertility and mycorrhiza likely play an important role here (Lassoie and Salo, 1981; Pickles et al., 2015; Sergent et al., 2014). Unfortunately, due to data availability limitations of overly complex models, current predictions of potential ecological niches of woody species usually do not consider soil properties as variables (Brun et al., 2019). Although an earlier and warmer spring with a warming climate should be favourable for Douglas-fir in southern Baltic Sea region (Fig. A3), younger stands in our network do not appear to be benefiting from climate warming. Therefore, regions with a projected persistence of the species (e.g. the southern Baltic Sea region) (Puchałka et al., 2023) may, in the future, offer conditions that are favourable for growth of old stands but not necessarily for newly planted stands (Fig. 2).

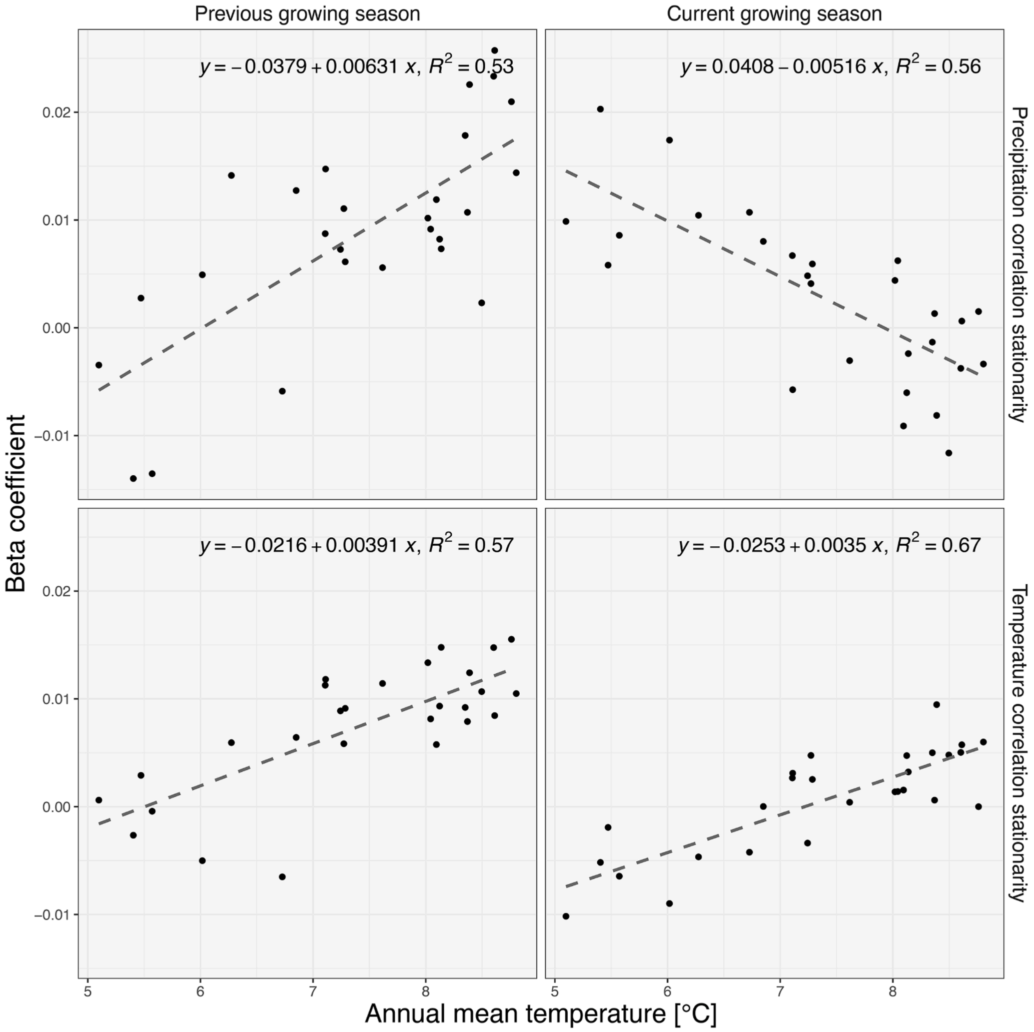

Fig. 5. Effect of long-term annual temperature patterns on the temporal stability of growth response to precipitation (upper panels) and temperature (bottom panels) correlations (beta coefficient) of the current (right panels) and previous (left panels) growing seasons. Stationarity of climate-growth relationship is expressed by beta coefficients. Here we highlight trends for seasons with the highest explained variance (see Table A3 for more detailed season definitions), but we show that the trends are strongly consistent across related seasons (see Fig. A9).

4.2. *West Coast conifer can benefit from South Baltic climate*

Among the most commonly introduced conifers from North America to Europe, species from the West Coast dominate, with *P. menziesii* undisputedly leading the way (Brus et al., 2019; Dimitrova et al., 2022). Conifers originating from the east coast of North America are less common on the European continent. The selection of sites and climatic conditions for introduction was based on their similarity to the native conditions of the non-native species. West coast species were introduced to the European Atlantic coast, while species from the east coast, as well as from the interior, were introduced to eastern and central Europe (Nyssen et al., 2016). When introduced to Europe, interspecies competition with co-occurring species in their native habitats was removed for these North American conifer species (Bianchi et al., 2018; He and Duncan, 2003). This may have accounted for their divergent growth strategy and different climate sensitivity compared to their native range (Thurm et al., 2016). Our studies have clearly demonstrated that Douglas-fir growth under the temperate climate of Central Europe with the moderating influence of the Baltic Sea is mainly determined by the temperatures at the beginning of the growing season and not by a moisture deficit as in British Columbia (Fig. 3) (Griesbauer and Green, 2010; Griesbauer et al., 2019). Variations in growth reaction may be due to the different distribution of annual precipitation over the two continents (Fig. A2B) as well as specific competitive constraints, interspecific in native populations and intraspecific in introduced populations (Finkelstein and Truppi, 1991; Zveryaev, 2004). In general, Douglas-fir stands were plastic enough under secondary range conditions to adapt their growth to the climate of Central Europe (Figs. 3 and 4). Looking in more detail, the western populations from Germany and Poland, growing under a moist temperate climate, seem to have an advantage over the northeastern populations from the Baltic countries, growing under a moist continental climate (Fig. 2, A3 and A4). On the other hand, the growth response to temperatures of the current season seems to be less stable with increasing distance from the Baltic Sea (Fig. A8). Thus, in the first hundred years of growth since its introduction, the climate of the western part of the South Baltic region appeared to be more favourable for Douglas-fir. However, this trend could change with the projected warming in Europe. In the next 20–60 years, this species may find suitable fundamental niches in the eastern and even northern parts of the Baltic Sea region (Puchałka et al., 2023). In contrast, eastern North American *P. strobus* appeared drought-sensitive under moist continental climate conditions of eastern part of the southern Baltic region (Jansone et al., 2023; Läänelaid and Helama, 2020). With the scarcity of dendroclimatic studies from this region of Europe, definite conclusions cannot be drawn on the advantage of western over eastern conifers in acclimatisation to a humid temperate climate. However, it is evident that Douglas-fir finds the conditions in the western part of the study region suitable for growth. With projected climate change, the eastern part of the region may also become favourable for this species.

4.3. Potential benefits and risks of Douglas-fir introductions

Recent studies suggest that European conifers, which are currently important in the southern Baltic region may lose their climatic optima in the near future (Bombi et al., 2017; Dyderski et al., 2018). The negative effects of a warming climate on the growth and vitality of spruce and pine stands (Diers et al., 2024; Kharuk et al., 2016), are already evident. This means a loss of the most economically valuable native species suitable for cultivation on poor sandy soils. It is also a loss of dominant species that shape the habitat conditions for *Vaccinium* spp. and fungi and many others. One way to preserve the proximal ecosystem services provided by pine and spruce stands may be to introduce species that are phylogenetically and functionally close to native conifers, and that have similar interspecific interactions. Unfortunately, two potential alternatives from drier and hotter regions, *P. nigra* and *P. rigida* appear to respond similarly to *P. sylvestris* to extreme droughts and heat waves (Klisz et al., 2023). Moreover, they provide less valuable woody material (Bellon, 1977), making them of less economic value. The cultivation of *P. strobus*, which is the only coniferous species benefiting from climate change, is nevertheless risky because of its susceptibility to fungal infections (Puchałka et al., 2023; Radu, 2008). Therefore, an alternative species for the southern Baltic Sea region could be *P. menziesii and Abies alba*, which are expected to maintain its climatic niches in the coming decades (Dyderski et al., 2025; Puchałka et al., 2023). Douglas-fir has similar interspecific interactions and similarly affects soil conditions in similar way to native conifers (Wohlgemuth et al., 2022), suggesting that it could replace them in the event of a large-scale decline. On the other hand, it is also a host to many common pests and pathogens for the members of the Pinaceae family (Potzelsberger et al., 2021), which could pose further risks for native conifers. In general, most ecological studies have shown more negative impacts on soil properties and biodiversity (Wohlgemuth et al., 2022). The observed differences in effects of Douglas-fir may be due to the habitat properties into which the species was introduced. For example, in deciduous forests, Douglas-fir has strong negative effects on forest specialists (Bärmann et al., 2023; Viewegh et al., 2014). It is associated with soil acidification and altered light regimes, which are detrimental to the understory plants. Therefore, Douglas-fir should only be considered for habitat introduction in nutrient-poor habitats where its presence does not alter the species composition of natural coniferous forests. Furthermore, it should be planted in a mixture with other species and at a density that prevents excessive shading of the forest understorey. Its cultivation should also take into account the risk of uncontrolled spread, which undoubtedly poses a threat to biodiversity (Wohlgemuth et al., 2022).

5. Conclusions

Our study reveals a region-wide trend in climate-growth relationships, particularly the influence of early-growing-season temperature and previous-year precipitation. However, across 30-year intervals from 1950 to 2022, this relationship is temporally and spatially unstable, suggesting an increasing dependence on temperature as warming continues. Older stands of Douglas-fir in the western part of the southern Baltic region appear to be well-acclimated and plastically adapted to recent climate changes. However, this area may not be equally suitable for young trees, which showed weaker or even negative correlations with temperature in our study. Although the potential range of Douglas-fir in Europe is expected to decline significantly, stable climatic niches are likely to persist in the Baltic region. As a close relative of the declining European species within the Pinaceae family and functionally similar to them, the Douglas-fir could serve as a more heat-tolerant alternative. With the expected turnover of native conifers by both native and introduced broadleaved species, Douglas-fir may help to maintain functionally comparable conifer forest communities. It promotes species interactions and creates light and soil conditions similar to those of native conifers. To maintain forest ecosystem services, forestry practices should take into account the ecological influence of Douglas-fir, particularly its ability to modify habitat conditions, alter microclimatic regimes, and affect biodiversity.

Data availability statements

The research was based mainly on the following datasets from the GBIF database: GBIF.org (26 April 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.8pa6n5 The gaps in species distribution data were supplemented from literature data listed in Appendix A. Climatic data were obtained from the WorldClim2.1 database https://www.worldclim.org/data/worldclim21.html The data that support the findings of this study are available from the corresponding author upon reasonable request.

Funding

The study was elaborated within the framework of the research project entitled “Adaptive potential of silver fir and Douglas-fir in the gradient of the climatic conditions of northern Poland” (no 90.02.47) financed from the subsidy funds received by the Forest Research Institute from Polish Ministry of Education and Science. This article is based upon work from COST Action CA21138 (CLEANFOREST) “Joint effects of CLimate Extremes and Atmospheric depositioN on European FORESTs”, supported by COST (European Cooperation in Science and Technology). J.J. acknowledges the support of the Slovenian Research and Innovation Agency (ARIS) through the Program and Research Group “Forest Biology, Ecology, and Technology” (P4-0107). M.Kl. acknowledges the support of the INTERREG Central Europe Programme, Project RE-ENFORCE: “Transnational Cooperation on nature-based solutions for restoring degraded forests of Central Europe” (grant no. CE0200902). This work is linked to activities conducted within the COST FP1403 ‘NNEXT’, COST CA21138 ‘CLEANFOREST’ and the COST CA19128 ‘PEN-CAFoRR’ networks.

CRediT authorship contribution statement

Marcin Klisz: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Radosław Puchałka:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Mariusz Gławenda:** Writing – review & editing, Resources. **Marcin Koprowski:** Writing – review & editing, Resources. **Roberts Matisons:** Writing – review & editing, Resources. **Sandra Metslaid:** Writing – review & editing, Resources. **Aleksei Potapov:** Writing – review & editing, Resources. **Tobias Scharnweber:** Writing – review & editing, Resources. **Eric Andreas Thurm:** Writing – review & editing, Resources. **Rita Verbylaite:** Writing – review & editing, Resources. **Adomas Vitas:** Writing – review & editing, Resources. **Martin Wilmking:** Writing – review & editing, Resources, Conceptualization. **Jernej Jevšenak:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

In memory of Dr. Tobias Scharnweber, whose invaluable contributions to sampling and study design we sincerely acknowledge. We kindly thank the Bytów, Czaplinek, Chojna, Drawsko, Ełk, Gościerzyna, Jamy, Kartuzy, Kwidzyn, Lębork, Nowe Ramuki, Sławno, Srokowo, Świdno, Trzebnica Forest Districts for granting access and assistance with site selection and sample collection. We thank Urszula Wojciechowska for assistance with field and laboratory and help with graphical abstract preparation.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110628.

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolution. Appl. 1 (1), 95–111.

Arco Molina, J.G., Hadad, M.A., Patón Domínguez, D., Roig, F.A., 2016. Tree age and bark thickness as traits linked to frost ring probability on Araucaria araucana trees in northern Patagonia. Dendrochronologia 37, 116–125.

Bärmann, L., Kaufmann, S., Weimann, S., Hauck, M., 2023. Future forests and biodiversity: Effects of Douglas-fir introduction into temperate beech forests on plant diversity. Forest Ecol. Manag. 545.

Beck, W., Sanders, T.G.M., Pofahl, U., 2013. CLIMTREG: Detecting temporal changes in climate–growth reactions – A computer program using intra-annual daily and yearly moving time intervals of variable width. Dendrochronologia 31 (3), 232–241.

Bellon, S., Tumiłowicz, J., Król, S., 1977. Obce Gatunki Drzew w Gospodarstwie Leśnym. PWRiL, Warszawa.

Bianchi, S., Hale, S., Cahalan, C., Arcangeli, C., Gibbons, J., 2018. Light-growth responses of Sitka spruce, Douglas-fir and western hemlock regeneration under continuous cover forestry. Forest Ecol. Manag. 422, 241–252.

Bombi, P., D'Andrea, E., Rezaie, N., Cammarano, M., Matteucci, G., 2017. Which climate change path are we following? Bad news from Scots pine. PLoS One 12 (12), e0189468.

Booth, T.H., 2018. Species distribution modelling tools and databases to assist managing forests under climate change. Forest Ecol. Manag. 430, 196–203.

Brun, P., et al., 2019. Model complexity affects species distribution projections under climate change. J. Biogeogr. 47 (1), 130–142.

Brus, R., et al., 2019. Extent, distribution and origin of non-native forest tree species in Europe. Scand. J. For. Res. 34, 533–544.

Buras, A., Wilmking, M., 2015. Correcting the Calculation of Gleichläufigkeit, Dendrochronologia. Elsevier GmbH., pp. 29–30

Buras, A., Zang, C., Menzel, A., 2017. Testing the stability of transfer functions. Dendrochronologia 42, 56–62.

Castaldi, C., Marchi, M., Vacchiano, G., Corona, P., 2020. Douglas-fir climate sensitivity at two contrasting sites along the southern limit of the European planting range. Journal of Forestry Research 31 (6), 2193–2204.

Cavelier, G., Weigel, R., Enderle, L., Leuschner, C., 2025. Douglas fir - A victim of its high productivity in a warming climate? Predominantly negative growth trends in the North German Lowlands. Sci. Total Environ. 973, 179100.

Chakraborty, D., Matulla, C., Andre, K., Weissenbacher, L., Schueler, S., 2019. Survival of Douglas-fir provenances in Austria: site-specific late and early frost events are more important than provenance origin. Annals Forest Sci. 76 (4).

Chakraborty, D., Schueler, S., Lexer, M.J., Wang, T., 2018. Genetic trials improve the transfer of Douglas-fir distribution models across continents. Ecography 42 (1), 88–101.

Chakraborty, D., et al., 2015. Selecting populations for non-analogous climate conditions using universal response functions: the case of Douglas-fir in central Europe. PLoS One 10 (8), e0136357.

Chen, P.Y., Welsh, C., Hamann, A., 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biol. 16 (12), 3374–3385.

Cook, E.R., Kairiukstis, L.A., 2013. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology Applications in the Environmental Sciences. Springer Science+ Business Media B.V., pp. 1–394

Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bulletin.

Diers, M., Leuschner, C., Dulamsuren, C., Schulz, T.C., Weigel, R., 2024. Increasing winter temperatures stimulate scots pine growth in the north german lowlands despite stationary sensitivity to summer drought. Ecosystems.

Dimitrova, A., et al., 2022. Risks, benefits, and knowledge gaps of non-native tree species in Europe. Frontiers Ecol. Evolut., 908464

Dolos, K., Bauer, A., Albrecht, S., 2015. Site suitability for tree species: Is there a positive relation between a tree species' occurrence and its growth? Eur. J. Forest Res. 134 (4), 609–621.

Dyderski, M.K., Paz, S., Frelich, L.E., Jagodzinski, A.M., 2018. How much does climate change threaten European forest tree species distributions? Global Change Biol. 24 (3), 1150–1163.

Dyderski, M.K., Paz-Dyderska, S., Jagodzinski, A.M., Puchalka, R., 2025. Shifts in native tree species distributions in Europe under climate change. J. Environ. Manage. 373, 123504.

Eckhart, T., et al., 2019. Forest stand productivity derived from site conditions: an assessment of old Douglas-fir stands (Pseudotsuga menziesii (Mirb.) Franco var. menziesii) in Central Europe. Annals Forest Sci. 76 (1), 19.

Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwissenschaftliches Centralblatt 230–250.

Enderle, L., et al., 2024. A warmer climate impairs the growth performance of Central Europe's major timber species in lowland regions. Sci. Total Environ., 173665

Feliksik, E., Wilczynski, S., 2004. Dendroclimatic regions of Douglas fir Pseudotsuga menziesii (Mirb.) Franco in western and northern Poland. Dendrobiology 52, 9–15.

Finkelstein, P.L., Truppi, L.E., 1991. Spatial distribution of precipitation seasonality in the United States. J. Clim. 4, 373–385.

Fontes, L., Savill, P., Luis, J.S., Harris, S., 2003. Identification of the origin of Portuguese Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] provenances. Silvae Genetica 266–273.

Frejaville, T., Vizcaino-Palomar, N., Fady, B., Kremer, A., Benito Garzon, M., 2020. Range margin populations show high climate adaptation lags in European trees. Global Change Biol. 26 (2), 484–495.

Gazol, A., Valeriano, C., Cantero, A., Vergarechea, M., Camarero, J.J., 2022. Douglas fir growth is constrained by drought: delineating the climatic limits of timber species under seasonally dry conditions. Forests 13 (11).

Glerum, C., Farrar, J., 1966. Frost ring formation in the stems of some coniferous species. Can. J. Bot. 44, 879–886.

Gribbe, S., et al., 2024. Recent growth decline and shifts in climatic growth constraints suggest climate vulnerability of beech, Douglas fir, pine and oak in Northern Germany. Forest Ecol. Manag. 566.

Griesbauer, H.P., Green, D.S., 2010. Regional and ecological patterns in interior Douglas-fir climate–growth relationships in British Columbia, Canada. Can. J. For. Res. 40 (2), 308–321.

Griesbauer, H.P., Klassen, H., Saunders, S.C., Spittlehouse, D.L., 2019. Variation in climate-growth relationships for Douglas-fir growth across spatial and temporal scales on southern Vancouver Island, British Columbia. Forest Ecol. Manag. 444, 30–41.

Gut, U., et al., 2019. No systematic effects of sampling direction on climate-growth relationships in a large-scale, multi-species tree-ring data set. Dendrochronologia, 125624.

Hacket-Pain, A.J., et al., 2018. Climatically controlled reproduction drives interannual growth variability in a temperate tree species. Ecol. Lett. 21 (12), 1833–1844.

Harvey, J.E., et al., 2019. Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests. Global Change Biol., 14966

Haylock, M.R., et al., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. J. Geophys. Res., D20119

He, F., Duncan, R.P., 2003. Density-dependent effects on tree survival in an old-growth Douglas fir forest. J. Ecol. 88 (4), 676–688.

Hintsteiner, W.J., van Loo, M., Neophytou, C., Schueler, S., Hasenauer, H., 2018. The geographic origin of old Douglas-fir stands growing in Central Europe. European Journal of Forest Research 137 (4), 447–461.

Isaac-Renton, M.G., Roberts, D.R., Hamann, A., Spiecker, H., 2014. Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. Glob Chang Biol 20 (8), 2607–2617.

Jansone, D., Matisons, R., Straupe, I., Jansons, Ā., 2023. Weather sensitivity of radial increment of Pinus strobus in an experimental plantation in the western part of Latvia. Forestry Wood Process. 38, 48–54.

Jastrzębowski, S., Ukalska, J., Guziejko, A., Puchałka, R., 2021. Current and predicted future winter warm spells would affect douglas fir (Pseudotsuga menziesii (mirb.), franco) seeds in the early stage of germination more than in the late stage of germination. Forests 796.

Jevšenak, J., 2020. New features in the dendroTools R package: Bootstrapped and partial correlation coefficients for monthly and daily climate data. Dendrochronologia.

Jevšenak, J., Buras, A., Babst, F., 2024. Shifting potential for high-resolution climate reconstructions under global warming. Quat. Sci. Rev. 325.

Jevšenak, J., Levanič, T., 2018. dendroTools: R package for studying linear and nonlinear responses between tree-rings and daily environmental data. Dendrochronologia 32–39.

Karger, D.N. et al., 2017. Climatologies at high resolution for the earth's land surface areas, Scientific Data. The Author(s), pp. 1–20.

Kaufman, L., Rousseeuw, P.J., 2009. Finding Groups in Data: An Introduction to Cluster Analysis. John Wiley & Sons.

Kharuk, V.I., Im, S.T., Dvinskaya, M.L., 2016. Decline of spruce (Picea abies) in forests of Belarus. Russian J. Ecol. 47 (3), 241–248.

Klesse, S., et al., 2020. Continental-scale tree-ring-based projection of Douglas-fir growth: Testing the limits of space-for-time substitution. Global Change Biol. 26 (9), 5146–5163.

Klesse, S., et al., 2024. No future growth enhancement expected at the northern edge for european beech due to continued water limitation. Global Change Biol. 30 (10), e17546.

Klisz, M., et al., 2022. Coping with Central European climate – xylem adjustment in seven non-native conifer tree species. Dendrobiology 105–123.

Klisz, M., et al., 2023. Local site conditions reduce interspecific differences in climate sensitivity between native and non-native pines. Agric. For. Meteorol., 109694

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World Map of the Köppen-Geiger climate classification updated. Meteorol. Z. 15 (3), 259–263.

Krajnc, L., Gričar, J., Jevšenak, J., Hafner, P., Brus, R., 2023. Tree rings, wood density and climate–growth relationships of four Douglas-fir provenances in sub-Mediterranean Slovenia. Trees 37 (2), 449–465.

Kriegel, P., Matevski, D., Schuldt, A., 2021. Monoculture and mixture-planting of non-native Douglas fir alters species composition, but promotes the diversity of ground beetles in a temperate forest system. Biodivers. Conserv. 30 (5), 1479–1499.

Läänelaid, A., Helama, S., 2020. White pine and Scots pine tree-ring chronologies as indicators of climate-related non-native and native tree growth patterns in Estonia. Baltic Forestry 26 (2).

Lassoie, J.P., Salo, D.J., 1981. Physiological response of large Douglas-fir to natural and induced soil water deficits. Can. J. For. Res. 11 (1), 139–144.

Leifsson, C., et al., 2024. Identifying drivers of non-stationary climate-growth relationships of European beech. Sci. Total Environ. 937, 173321.

Levanic, T., Straus, H., 2022. Effects of Climate on Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) Growth Southeast of the European Alps. Plants (Basel) 11 (12).

Lévesque, M., Rigling, A., Bugmann, H., Weber, P., Brang, P., 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agric. For. Meteorol. 197, 1–12.

Ma, Q., Huang, J.G., Hanninen, H., Berninger, F., 2019. Divergent trends in the risk of spring frost damage to trees in Europe with recent warming. Global Change Biol. 25 (1), 351–360.

Malmqvist, C., Wallertz, K., Johansson, U., 2018. Survival, early growth and impact of damage by late-spring frost and winter desiccation on Douglas-fir seedlings in southern Sweden. New Forests 49 (6), 723–736.

Martinez Del Castillo, E., et al., 2024. Contrasting future growth of norway spruce and scots pine forests under warming climate. Global Change Biol. 30 (11), e17580.

Matisons, R., et al., 2021. Non-linear regional weather-growth relationships indicate limited adaptability of the eastern Baltic Scots pine. Forest Ecol. Manag. 479.

Meier, H.E.M., et al., 2022. Climate change in the Baltic Sea region: a summary. Earth System Dynamics 13 (1), 457–593.

Miller, T.W., et al., 2022. Longer and faster: Intra-annual growth dynamics of Douglas fir outperform Norway spruce and silver fir over wide climatic gradients. Agric. For. Meteorol., 108970

Nyssen, B., Schmidt, U.E., Muys, B., Lei, P.B.v.d., Pyttel, P., 2016. History of introduced and invasive tree species. In: Krumm, F., Vítková, L. (Eds.), Introduced Tree Species in European Forests. European Forest Institute, EFI, Freiburg, pp. 44–56.

Ols, C., et al., 2023. Detrending climate data prior to climate–growth analyses in dendroecology: a common best practice? Dendrochronologia.

Peel, M.C., Finlayson, B.L., Mcmahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. Discuss. 4 (2), 439–473.

Peltier, D.M.P., Ogle, K., 2020. Tree growth sensitivity to climate is temporally variable. Ecol. Lett. 23 (11), 1561–1572.

Pickles, B.J., Twieg, B.D., O'Neill, G.A., Mohn, W.W., Simard, S.W., 2015. Local adaptation in migrated interior Douglas-fir seedlings is mediated by ectomycorrhizas and other soil factors. New Phytol. 207 (3), 858–871.

Podrázský, V., Martiník, A., Matějka, K., Viewegh, J., 2014. Effects of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) on understorey layer species diversity in managed forests. J. Forest Sci. 60 (7), 263–271.

Popa, A., Jevšenak, J., Popa, I., Badea, O., Buras, A., 2024. In pursuit of change: Divergent temporal shifts in climate sensitivity of Norway spruce along an elevational and continentality gradient in the Carpathians. Agric. For. Meteorol. 358.

Potzelsberger, E., et al., 2021. Biotic threats for 23 major non-native tree species in. Europe. Scientific Data 8 (1), 210.

Pötzelsberger, E., et al., 2020. Growing non-native trees in european forests brings benefits and opportunities but also has its risks and limits. Current Forestry Reports 6 (4), 339–353.

Puchałka, R., et al., 2023. Predicted range shifts of alien tree species in Europe. Agric. For. Meteorol. 341.

Radu, S., 2008. Pinus strobus: past and future in Europe. A page of silvicultural history and international scientific cooperation. Annals Forest Res. 51 (1), 133–140.

Schmid, M., Pautasso, M., Holdenrieder, O., 2014. Ecological consequences of Douglas fir (Pseudotsuga menziesii) cultivation in Europe. Eur. J. Forest Res. 133, 13–29.

Sergent, A.-S., Rozenberg, P., Bréda, N., 2014. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Annals Forest Sci. 71 (6), 697–708.

Song, Y., et al., 2021. Growth of 19 conifer species is highly sensitive to winter warming, spring frost and summer drought. Ann. Bot. 128, 545–557.

Speer, J.H., 2010. Fundamentals of Tree-Ring Research. University of Arizona Press.

Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. Forest Ecol. Manag. 376, 205–220.

Torbenson, M.C.A., Stagge, J.H., Chen, F., Ziaco, E., Esper, J., 2024. Adjusting the significance of daily climate responses in tree-ring proxies. J. Forestry Res. 36 (1).

Trouillier, M., et al., 2018. Size matters—a comparison of three methods to assess age- and size-dependent climate sensitivity of trees. Trees 33 (1), 183–192.

Tumajer, J., et al., 2023. Ecological and methodological drivers of non-stationarity in tree growth response to climate. Global Change Biol. 29 (2), 462–476.

Vejpustková, M., Čihák, T., 2019. Climate response of douglas fir reveals recently increased sensitivity to drought stress in central europe. Forests 10 (2).

Viewegh, J., Podrázský, V., Matějka, K., 2014. Characteristic of forest floor developed under Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) stands in commercial forest in Czech Republic. Sylwan 158 (4), 277–284.

Weigel, R., et al., 2021. Ecosystem Processes Show Uniform Sensitivity to Winter Soil Temperature Change Across a Gradient from Central to Cold Marginal Stands of a Major Temperate Forest Tree, Ecosystems. Springer US.

Weigel, R., et al., 2018. Winter matters: Sensitivity to winter climate and cold events increases towards the cold distribution margin of European beech (Fagus sylvaticaL.). J. Biogeogr. 45 (12), 2779–2790.

Wigley, T.M., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Appl. Meteorol. Climatol. 201–213.

Wilczynski, S., Feliksik, E., 2007. Local chronologies and regional diversity of dendrochronological signal of Douglas-fir in Poland. Geochronometria: J. Methods Appl. Absolute Chronol. 26, 69–80.

Wilczyński, S.B., Kulej, M., 2013. The influence of climate on the radial increment of larches of different provenances on the basis of the experiment in the Carpathian Mountains in Southern Poland. Eur. J. Forest Res. 132 (5-6), 919–929.

Wiley, E., Rogers, B.J., Griesbauer, H.P., Landhausser, S.M., 2018. Spruce shows greater sensitivity to recent warming than Douglas-fir in central British Columbia. Ecosphere 9 (5), 02221.

Wilmking, M., et al., 2020. Global assessment of relationships between climate and tree growth. Global Change Biol. 26 (6), 3212–3220.

Wohlgemuth, T., et al., 2022. Impact of non-native tree species in Europe on soil properties and biodiversity : a review. NeoBiota 45–69.

Wrzesiński, P., Klisz, M., Niemczyk, M., 2024. Looking for a drought-tolerant tree species among native and introduced mountain conifers. Trees.

Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38 (4), 431–436.

Zhirnova, D.F., et al., 2022. Spatial-coherent dynamics and climatic signals in the radial growth of siberian stone pine (Pinus sibirica Du Tour) in subalpine stands along the western Sayan Mountains. Forests 13 (12).

Zohner, C.M., et al., 2020. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. Proc. Natl. Acad. Sci. USA. 117 (22), 12192–12200.

Zveryaev, I.I., 2004. Seasonality in precipitation variability over Europe. J. Geophys. Res.: Atmos. 109 (D5).