



Growth characteristics and drought vulnerability of southwest German spruce and pine

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Abstract

Although it is evident that forest management needs to adapt to fast changing climate conditions, there are still many uncertainties about how European tree species will perform under predicted temperature increases and associated hydro-climatic extremes. Here, we present a dendrochronological network of 1934 trees from 46 sites across southwest Germany to assess the growth performance of Norway spruce and Scots pine between 100 and 820 m asl under recent climatic changes. Growth comparisons including basal area increment (BAI) show that spruce ($\text{BAI}_{\text{avg}} = 15.4 \text{ cm}^2 \text{ a}^{-1}$) grew twice than pine ($\text{BAI}_{\text{avg}} = 7.3 \text{ cm}^2 \text{ a}^{-1}$) between 1952 and 2009 CE. Drought is the dominant driver of spruce growth but shows a transition in seasonality along elevational gradients. Below 550 m asl, spruce is strongly limited by water availability during summer, while stands above 550 m asl become increasingly sensitive to previous-year moisture conditions. Positive correlations with February–March temperatures indicate an increasing importance of late-winter conditions for pine growth, likely related to rapidly rising air temperatures since the late 1980s and seasonal changes in photosynthetic activity. However, despite the benefits of warmer late-winter conditions for pine, significant moisture limitations and drought-induced growth decreases in both conifers underscore the need for more drought-resistant species in southwest Germany.

Keywords Climate signals · Dendroecology · *Picea abies* · *Pinus sylvestris* · Temperate forest · Tree-ring width

Introduction

Central European temperate forests are important terrestrial carbon sinks that mitigate global warming (Harris et al. 2021). However, the health and productivity of these forests

under future climate change is highly uncertain (Bonan 2008). While rising air temperatures extend the growing season and increase photosynthetic activity in spring and autumn, they also amplify the magnitude and duration of heatwaves and droughts (Masson-Delmotte et al. 2021).

Dendroecological studies offer the opportunity to quantify forest growth at annual resolution and assess its environmental forcing over past decades. Although assessing climate-growth responses in managed forests can be challenging (Esper et al. 2012), tree-ring width (TRW) is a reliable indicator of forest productivity (Xu et al. 2017) and vitality (Dobbertin 2005) that provides valuable insights into multi-decadal growth trends at regional to continental scales. In Europe, forest growth has recently shown divergent trends across tree species and space (Martínez del Castillo et al. 2022; Pretzsch et al. 2023; Kašpar et al. 2024). Most tree species benefit from the rising air temperatures at higher latitudes and altitudes but suffer substantial growth losses at low altitudes and in southern European regions. However, growth trends are less clear in the European lowlands, where precipitation patterns remain ambiguous

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(Aalbers et al. 2018) and silviculture recently faces unprecedented challenges (Senf et al. 2020).

Norway spruce (*Picea abies* [L.] Karst) and Scots pine (*Pinus sylvestris* L.) are the economically most important coniferous species in Europe, accounting for ~53% of the European-wide growing stock (Korhonen and Stahl 2020). Both conifers were widely cultivated since the 18th century, as they grow fast on various types of soil and ensured high timber yields (Spiecker 2003; Johann et al. 2004). Norway spruce is a shade-tolerant conifer with a shallow root system that prefers nutrient-rich soils and naturally grows in the cold and moist environments of the boreal zone and European mountains (Caudullo et al. 2016). In Europe, large portions of spruce were planted outside their natural distribution range, specifically in warmer and drier regions (Kölling et al. 2009). In these environments, Norway spruce is particularly susceptible to drought (Zang et al. 2014; Altman et al. 2017) and growth is frequently limited by summer precipitation (Lebourgeois 2007; Rybníček et al. 2010; Zang et al. 2011; Esper et al. 2012; van der Maaten-Theunissen et al. 2013; Debel et al. 2021), though effects on forest productivity vary with regional climate and site conditions (Krejza et al. 2021; Trembl et al. 2021).

Although Scots pine is more drought resilient than spruce due to a distinct plasticity in xylem anatomical structures and effective stomatal control mechanisms (Irvine et al. 1998; Eilmann et al. 2009), Central European pine growth is also frequently limited by summer water availability (Lévesque et al. 2014; Bose et al. 2020). In recent decades, late-winter temperatures became important for pine growth (Harvey et al. 2020; Janečka et al. 2020; Stolz et al. 2021; Diers et al. 2023, 2024), possibly reflecting a trade-off between enhanced winter and reduced summer photosynthesis. While the underlying physiological processes are not yet well understood, there is extensive evidence for analogous late-winter temperature signals in pine growth at several low-elevation temperate forest sites (Friedrichs et al. 2009; Lebourgeois et al. 2010; Koprowski et al. 2012; Seidling et al. 2012; Nagavciuc et al. 2019).

In the lowlands and low mountain ranges of southwest Germany, the region with the highest national forest density (BMEL 2023), there is a lack of TRW data integrating measurements from multiple sites. This gap limits our ability to assess the regional growth performance of spruce and pine and evaluate whether the climate sensitivities of these species have shifted in response to recent periods of rapid climate change in this region of significant forestry importance. To address this, we introduce a new TRW network for southwest Germany, comprising 46 sites, and aim to answer the following research questions:

- i) How did southwest German spruce and pine trees thrive during the late 20th and early 21st centuries, and how did growth patterns differ between the two species?

Hypothesis *We expect that both species have experienced growth increases over recent decades, with spruce exhibiting higher growth rates than pine.*

- ii) What are the key climatic drivers of regional spruce and pine growth?

Hypothesis *We expect summer drought to be the key climatic driver of growth for both species.*

- iii) How did climate sensitivities change over recent periods of climate change?

Hypothesis *We expect that both species have become increasingly sensitive to drought in response to recent warming.*

Materials and methods

Study area and climate

Between 2010 and 2021, a total of 1831 spruce (*Picea abies* [L.] Karst) and 1942 pine (*Pinus sylvestris* L.) core samples were collected to establish a network of 46 sites in southwest Germany (49°–51°N, 6°–9°E, Fig. 1a). The 22 spruce and 24 pine sites are located along altitudinal gradients ranging from 100 m asl in the Upper Rhine Plain to 820 m asl in the Rhenish Massif (Table 1). Scots pine is the dominant conifer in the lowlands (≤ 400 m asl), while Norway spruce prevails at higher elevations. The pine stands are slightly older (Fig. 1b) and predominant in the Palatinate Forest and Upper Rhine Plain on less fertile loamy sands and sandy clays, such as lean cambisols and fluvisols. In contrast, spruce grows mainly in the Rhenish massif on silty loams and clays, such as (podzolic) cambisols, luvisols, regosols, and stagnosols (Richter et al. 2007; Zech et al. 2014).

Within the southwest German TRW network, mean annual air temperatures vary from 10.5 °C at the lowest pine site (109 m asl) to 6.3 °C at the highest spruce site (819 m asl), while annual rainfall totals range from 643 mm to 944 mm. Consequently, the lowlands, especially the Upper Rhine Plain, are more affected by summer drought than the low mountain ranges (Fig. 2a–c). In recent decades (1952–2009 CE), annual maximum air temperatures ($T_{\max}$) and precipitation increased by 0.03 °C a⁻¹ and 1 mm a⁻¹, respectively (Fig. 2d–f). Temperature and precipitation changes, however, differ notably by month. $T_{\max}$ increased

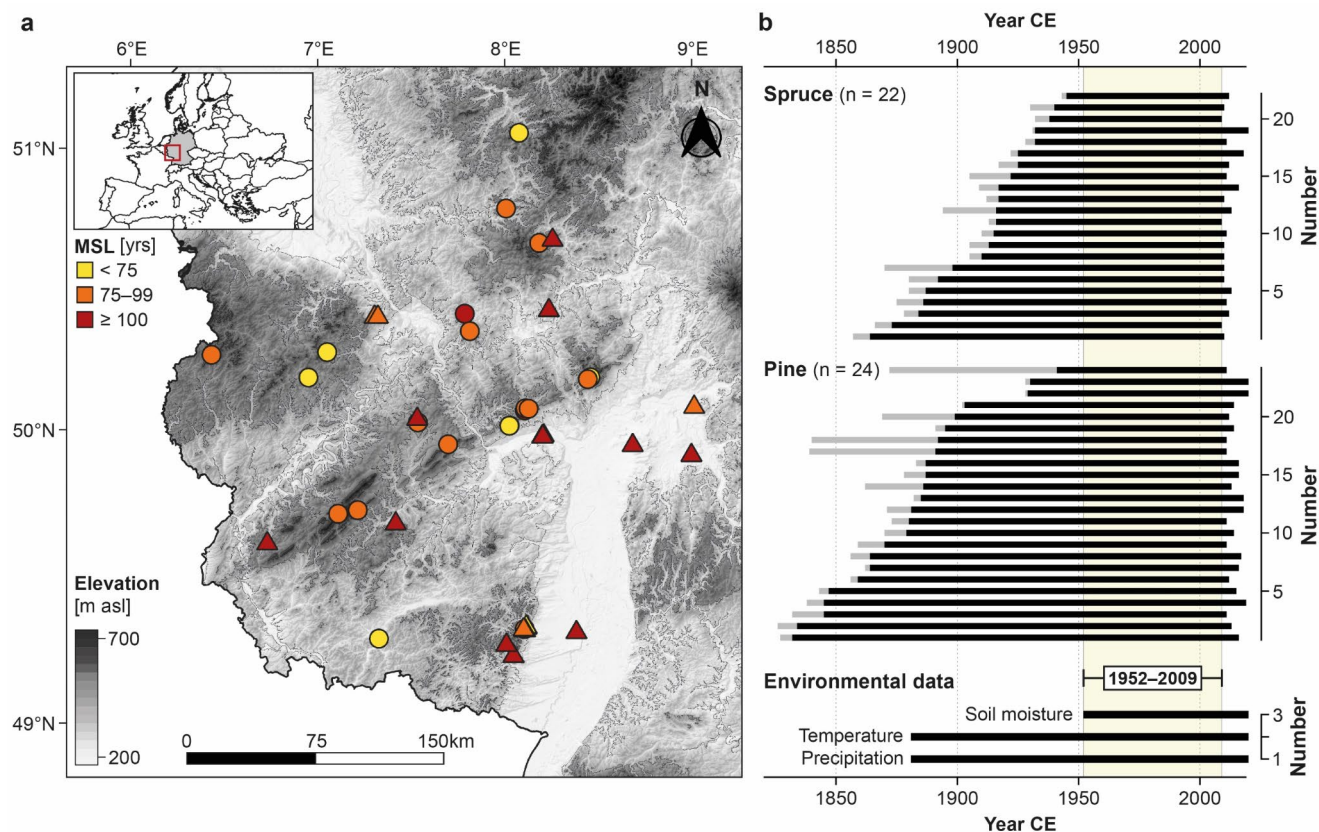


Fig. 1 Tree-ring and environmental data. **(a)** Topographic map showing spruce (circles) and pine (triangles) sites colored according to their mean segment lengths (MSL). **(b)** Periods covered by tree-ring chronologies and environmental records. Grey bars show the full tree-ring

records, black bars indicate lengths after truncation at $n \geq 10$ series. The common period of all series is highlighted in light yellow (1952–2009 CE)

Table 1 Characteristics of the southwest German tree-ring network

Species	Sites	n series trees	Elevation [m asl]	MSL ± 1 SE [years]	AGR ± 1 SE [mm]	$\bar{r}$
Norway spruce	22	1831 948	340–820	81 ± 3	2.35 ± 0.13	0.46
Scots pine	24	1942 986	100–570	115 ± 5	1.57 ± 0.10	0.50

MSL: mean segment length ± 1 standard error (SE), **AGR:** average growth rate [mm] calculated over the first 60 years of tree age (± 1 SE), $\bar{r}$: mean inter-series correlation of the 10SP chronologies (1952–2009 CE)

notably more in July and August, while June–August precipitation decreased contrary to the opposing trends in the other seasons (Fig. 2g–h). As a result, soil moisture availability increased from fall to spring but decreased in late-summer (Fig. 2i).

Tree-ring width and basal area increment data

At all sampling sites, one or two increment cores were collected at breast height (1.3 m) from dominant and suppressed conifers using a 5-mm increment borer. The network includes 948 spruce and 986 pine trees from managed, mostly even-aged monoculture stands. Sample size per site ranges from 39 to 148 series, with an average of 82 ± 3 (1 SE) series per site (Table S1). If more than one sample was collected, the cores were extracted from opposite stem

directions perpendicular to the slope to avoid compression wood. TRW was measured at an accuracy of 0.01 mm using the high-precision LINTAB 6 device (Rinntech, Germany) and TSAP-Win software (Rinn 2012). Visual and statistical crossdating was performed using skeleton plots (Stokes and Smiley 1996) and the COFECHA software (Holmes 1983).

TRW measurements were averaged (per tree) and converted to basal area increments (BAI; $\text{cm}^2 \text{a}^{-1}$) using the bai.out function of the R package *dplR* (Bunn 2008) considering:

$$BAI = \pi (r_n^2 - r_{n-1}^2) \quad (1)$$

where r_n is the distance from the pith to the outer tree-ring boundary of the actual year, and r_{n-1} is the distance from the pith to the outer ring boundary of the previous year (Fig. S1a). Unlike TRW, BAI accounts for geometrical

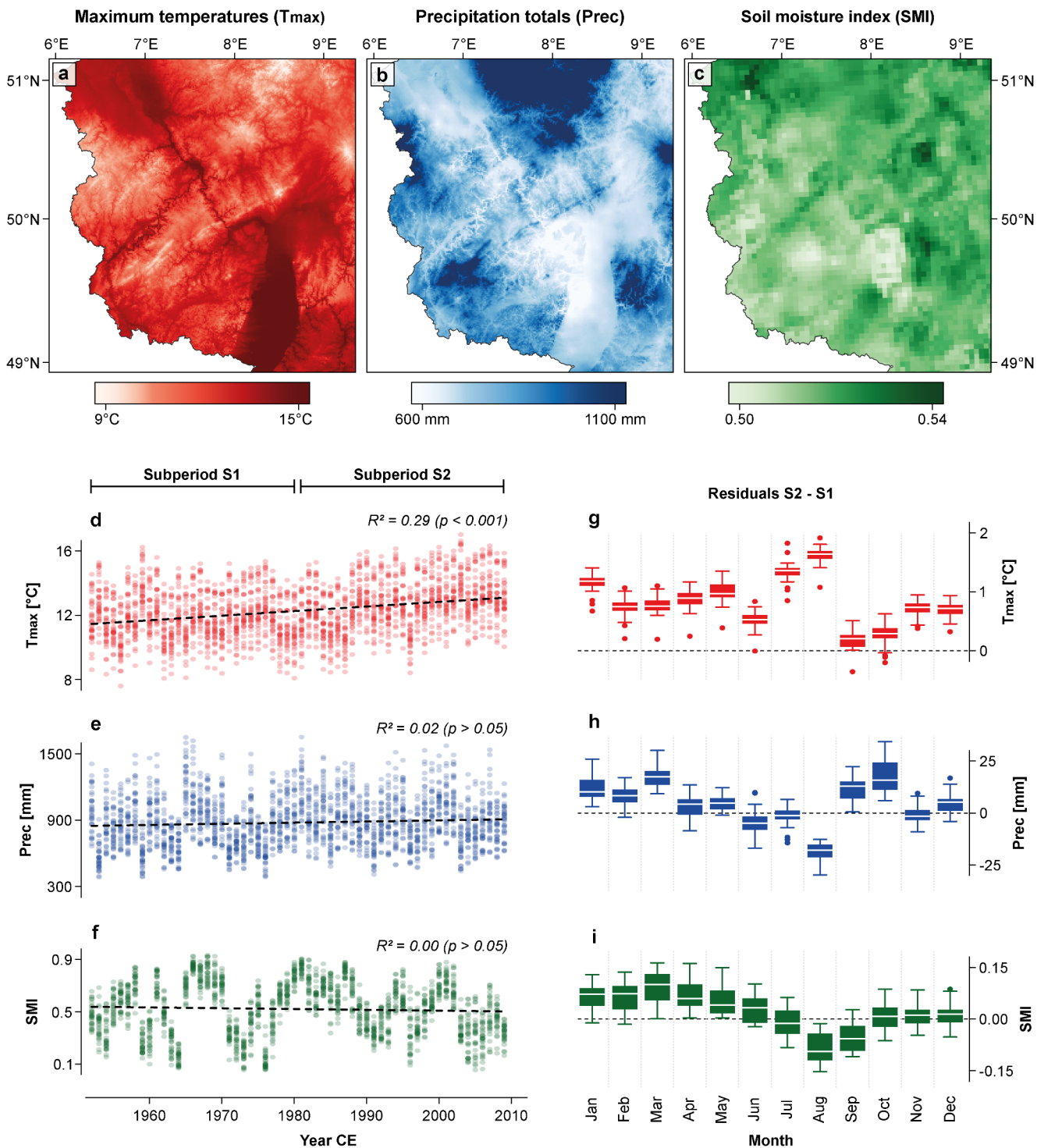


Fig. 2 Climate and soil moisture conditions in southwest Germany. Maps of annual (a) maximum air temperatures ($T_{\max}$), (b) precipitation totals (Prec), and (c) soil moisture indices (SMI). Time series of annual (d) $T_{\max}$, (e) Prec, and (f) SMI derived from nearby gridded data. Each dot represents one grid cell. Dashed lines show linear trends from 1952–2009 CE, R^2 values are the coefficients of determination (with respective p -values). Monthly (g) $T_{\max}$, (h) Prec, and (i) SMI

changes between the subperiods S2 (1981–2009 CE) and S1 (1952–1980 CE). Boxplots show the distribution among grid cells. White bars are the medians, boxes the 25%- and 75%-quartiles, whiskers the min and max values within 1.5x the interquartile range, and dots are outliers. Positive residuals indicate higher values in the recent subperiod S2 compared to subperiod S1

constraints of adding a cross-sectional area to an expanding stem radius. However, as age-related BAI trends may distort comparisons among different tree and stand ages (Weiner and Thomas 2001), we additionally calculated average growth rates (AGR) over the first 60 years of tree age by aligning each TRW series according to its cambial age (Fig. S1b). The arithmetic means of the age-aligned series are referred to as regional curves (Esper et al. 2003). Potential dependencies of BAI and AGR on tree age, elevation, and microclimatic conditions (air temperature, precipitation and soil moisture) were evaluated using linear regression models. As interactions between these microclimatic conditions may themselves play a crucial role in driving tree growth variability, we opted for simple regression models rather than multiple regression models.

Detrending and chronology development

Non-climatic trends were removed from the TRW series by calculating residuals from cubic smoothing splines with a 50% frequency-response cutoff at 10 years (10SP) and from negative exponential curves (EXP; Fig. S1c). Alternative spline detrendings were applied to evaluate standardization effects on high-to-low frequency chronology variance and network covariance (Fig. S2). Prior to each detrending, a data-adaptive power transformation was used to minimize the heteroscedastic structure of the raw TRW data (Cook and Peters 1997). Site chronologies were produced using the ARSTAN software (ARS41d; Cook et al. 2017) by calculating bi-weight robust means of the detrended series. Site chronologies were variance-stabilized (Frank et al. 2007) and truncated at $n < 10$ series. Inter-series correlations ($\bar{r}$) were computed over 30-year segments with a 29-year overlap to estimate changes in covariance inherent in the site chronologies (Cook and Kairiukstis 1990). Network covariance was assessed by calculating Pearson correlations between the detrended site chronologies over the 1952–2009 CE common period.

Climate data and calibration

High-resolution temperature and precipitation data (1×1 km) from the German Weather Service (<http://www.dwd.de/cdc>; Kaspar et al. 2013) and soil moisture data (4×4 km) from the German Drought Monitor (<https://www.ufz.de/index.php?en=37937>; Zink et al. 2016) were used to characterize the conditions at each sampling site. We extracted monthly time series of $T_{\max}$, precipitation and soil moisture index (SMI) from grids closest to each site and calculated seasonal means. The SMI indicates water availability in the top 180 cm of the soil (Zink et al. 2016). April–October was defined as the growing season based on

monthly temperature and daily dendrometer data (Klippel et al. 2017).

Climate-growth relationships were assessed by computing Pearson correlations between the 10SP site chronologies and the environmental variables using the R package *treeclim* (Zang and Biondi 2015). As with TRW, the environmental data were high-pass filtered prior to correlation analyses by calculating residuals from cubic smoothing splines with a 50% frequency cutoff at 10 years. Bootstrap correlations ($n = 1000$) were computed over the 1952–2009 CE period using an 18-month time window ranging from previous-year May to current-year October, and 21-year running correlations were applied to assess the stationarity of climate signals.

Results

Southwest German growth characteristics

The regional curves of the age-aligned TRW series show distinct negative exponential trends that are fairly homogeneous across the 22 spruce and 24 pine sites (Fig. 3a–d). TRW decreases as a function of tree age, though AGRs of spruce are significantly higher than those of pine ($1.2\text{--}3.5 \text{ mm a}^{-1}$ versus $1.0\text{--}2.7 \text{ mm a}^{-1}$, $p < 0.01$). The lower AGRs of pine are due to a steeper TRW decline in the first ~25 years of cambial age and persistently lower values thereafter. The total number of rings per series varies from five to 154 years among the 1831 individual spruce series ($\bar{x} = 82$ years) and from 16 to 190 years among the 1942 individual pine series ($\bar{x} = 118$ years), indicating a higher average tree age for the pine samples.

The BAI chronologies reveal significant ($p < 0.001$) growth differences between spruce ($15.4 \pm 1.0 \text{ cm}^2 \text{ a}^{-1}$; mean ± 1 SE) and pine ($7.3 \pm 0.6 \text{ cm}^2 \text{ a}^{-1}$) over the 1952–2009 CE period (Fig. 3e–f). While spruce BAI increased strongly by $\sim 0.17 \text{ cm}^2 \text{ a}^{-1}$ throughout the 20th century, the pine BAI rose moderately by $\sim 0.08 \text{ cm}^2 \text{ a}^{-1}$ during the first half of the 20th century and remained fairly stable thereafter. Alignment of the BAI series by cambial age outlines notable age trends consisting of growth increases up to ~110 years, followed by a stationary growth plateau and declining phase (only for pine) as the trees become older (Fig. S3). The initial growth acceleration is much stronger in spruce than in pine, explaining the substantial BAI differences between the overall younger spruce and older pine stands.

Despite the observed growth rate differences, the mean BAI chronologies of spruce and pine correlate at $r = 0.59$ from 1952 to 2009 CE, pointing to a common climatic forcing across the network. Covariance is particularly high among the spruce sites ($r_{1952-2009} = 0.66$) compared to pine

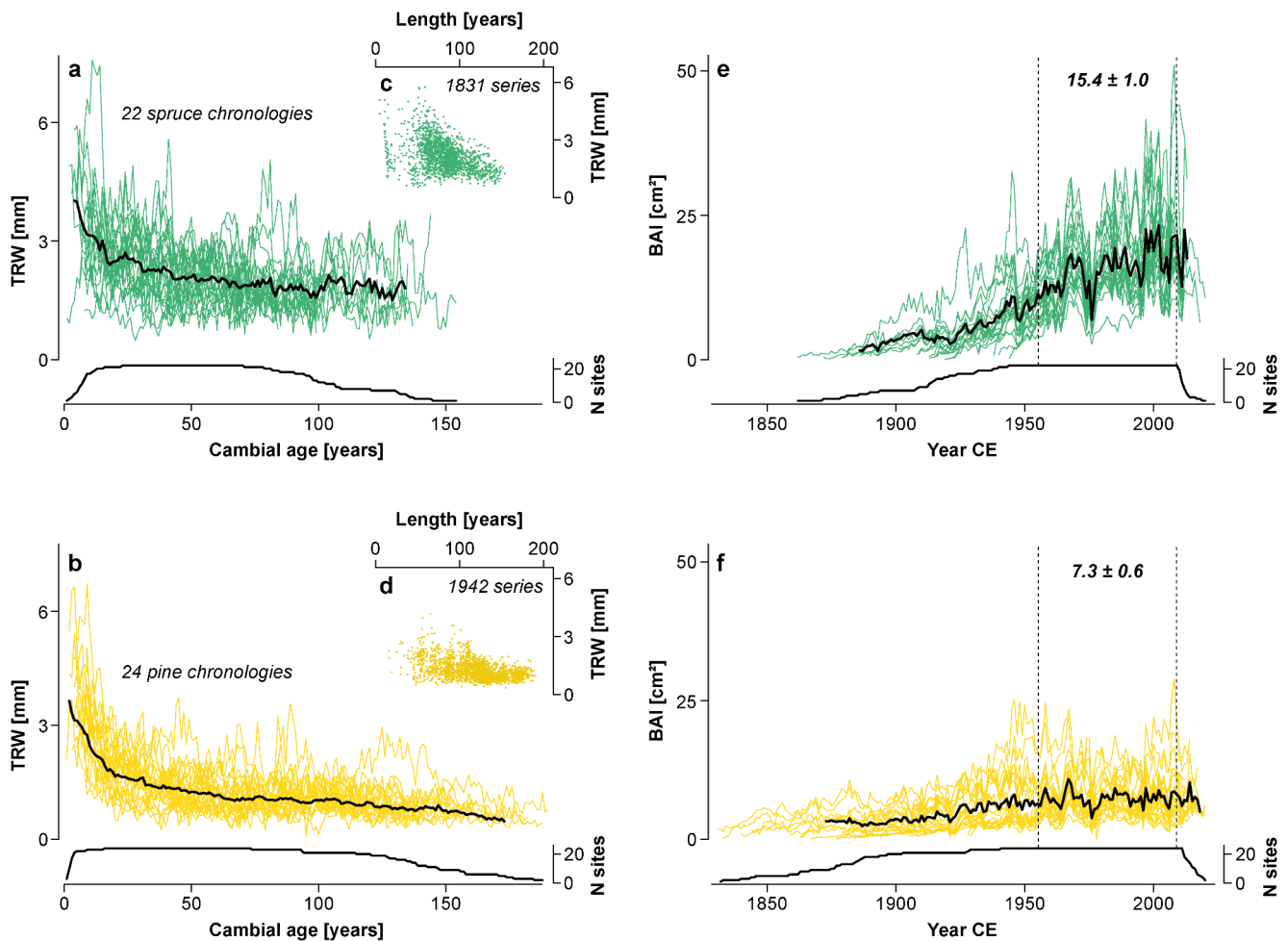


Fig. 3 Spruce and pine growth characteristics. Regional curves of the (a) spruce (green) and (b) pine (yellow) sites truncated at < 10 series. Black lines are the arithmetic means at $n \geq 5$ sites. Bottom panels show the number of integrated site chronologies. Relationship between segment length and mean tree-ring width (TRW) of all (c) spruce and (d) pine series. Each dot represents one individual series. Basal area

($r_{1952-2009} = 0.46$), and the BAI chronologies synchronize particularly well in years of severe growth decline that coincide with low growing-season SMI values (SMI_{A-O} ; Fig. 4a). In the six driest growing seasons ($SMI_{A-O} < 0.30$), BAI values drop between -19% and -68% for spruce, and -14% and -61% for pine compared to previous years. The greatest growth losses were recorded in 1976 CE for both species. BAI and SMI series correlate at $r = 0.85-0.86$ after 10–20-year band-pass filtering, indicating the importance of decadal-scale soil moisture fluctuations for conifer growth in southwest Germany (Fig. 4b).

Inter-site BAI differences are weakly explained by tree age, elevation, growing-season T_{max} , precipitation, or soil moisture availability (Fig. 4c-l). While none of the factors is significant for pine, spruce BAI indicates a weak but significant positive dependence ($R^2 = 0.19$, $p < 0.05$) on growing-season precipitation and the SMI. Highest BAIs (> 20

increment (BAI) chronologies of (e) spruce and (f) pine truncated at < 10 series. Black lines are the arithmetic means at $n \geq 5$ sites. Numbers between the vertical dashed lines indicate the mean BAI ± 1 standard error calculated for 1952–2009 CE. Bottom panels show the number of integrated site chronologies

$cm^2 a^{-1}$) are found in young ($MSL < 90$ years) and moist ($SMI_{A-O} > 0.52$) spruce stands. AGRs show no significant association with growing-season precipitation or the SMI but a significant ($p < 0.01$) dependence on MSL, explaining 40% of the variance among the spruce sites (Fig. S4). No significant relationship was found between the stand-specific AGR and MSL of pine.

Network covariance

The detrended TRW chronologies share high fractions of common variance and synchronize well in negative pointer years such as 1976 CE (Fig. 5a). Covariance among spruce sites is slightly higher (mean $r_{1952-2009} = 0.66$) than among pine sites (mean $r_{1952-2009} = 0.62$), considering the 10SP series, and declines with increasing inter-site distance (Fig. 5b-c). The regional spruce and pine chronologies

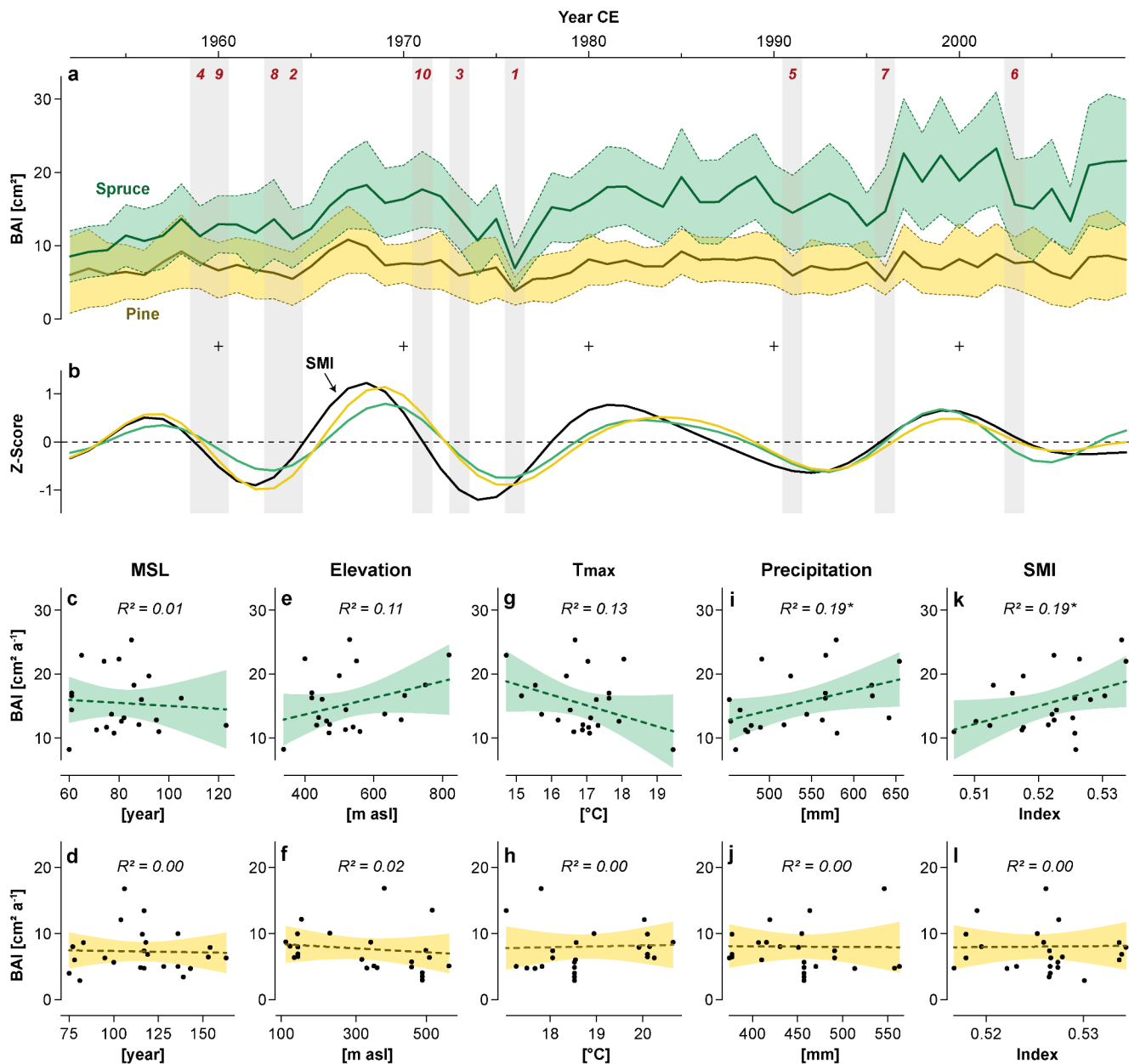


Fig. 4 Growth response to soil moisture variability. (a) Basal area increment (BAI) of spruce (green) and pine (yellow) from 1952–2009 CE. Thick curves are the average BAI of all spruce and pine sites, respectively. Colored shadings indicate ± 1 standard deviation. Red numbers and grey shadings label the ten driest growing seasons (1 = lowest SMI). (b) Band-pass filtered (10–20 years) z-scores of the growing-season SMI (black) shown together with spruce (green) and pine (yellow) BAI. (c–d) Average BAI (1952–2009 CE) of spruce (top

panels) and pine (bottom panels) as a function of mean segment length (MSL), (e–f) elevation, (g–h) maximum air temperature ($T_{\max}$), (i–j) precipitation, and (k–l) SMI. The latter three variables are calculated for the growing season (April–October). Each dot represents one site. Dashed lines show linear trends. Colored areas are the 95% confidence intervals of the regression slopes. Asterisks behind R^2 indicate significance at $p < 0.05$

correlate at $r_{10SP} = 0.63$ and $r_{EXP} = 0.71$ from 1952 to 2009 CE, suggesting that the TRW variability across the network is synchronized by environmental (climatic) forcing and that this forcing is also relevant at decadal scale, as reflected in the EXP data. Striking inconsistencies among the site chronologies are rare and confined to single years, such as 1978 CE, when two pine 10SP chronologies deviate negatively. $\bar{R}$

values of the 10SP chronologies fluctuate around a mean of 0.46 (pine) and 0.42 (spruce), and are relatively stable from 1952 to 2009 CE. $\bar{R}$ values of the EXP chronologies are generally lower and show a downward trend toward the present.

Higher inter-series and inter-site correlations in the 10SP data indicate strong covariance and external forcing of high-frequency network growth variability. The

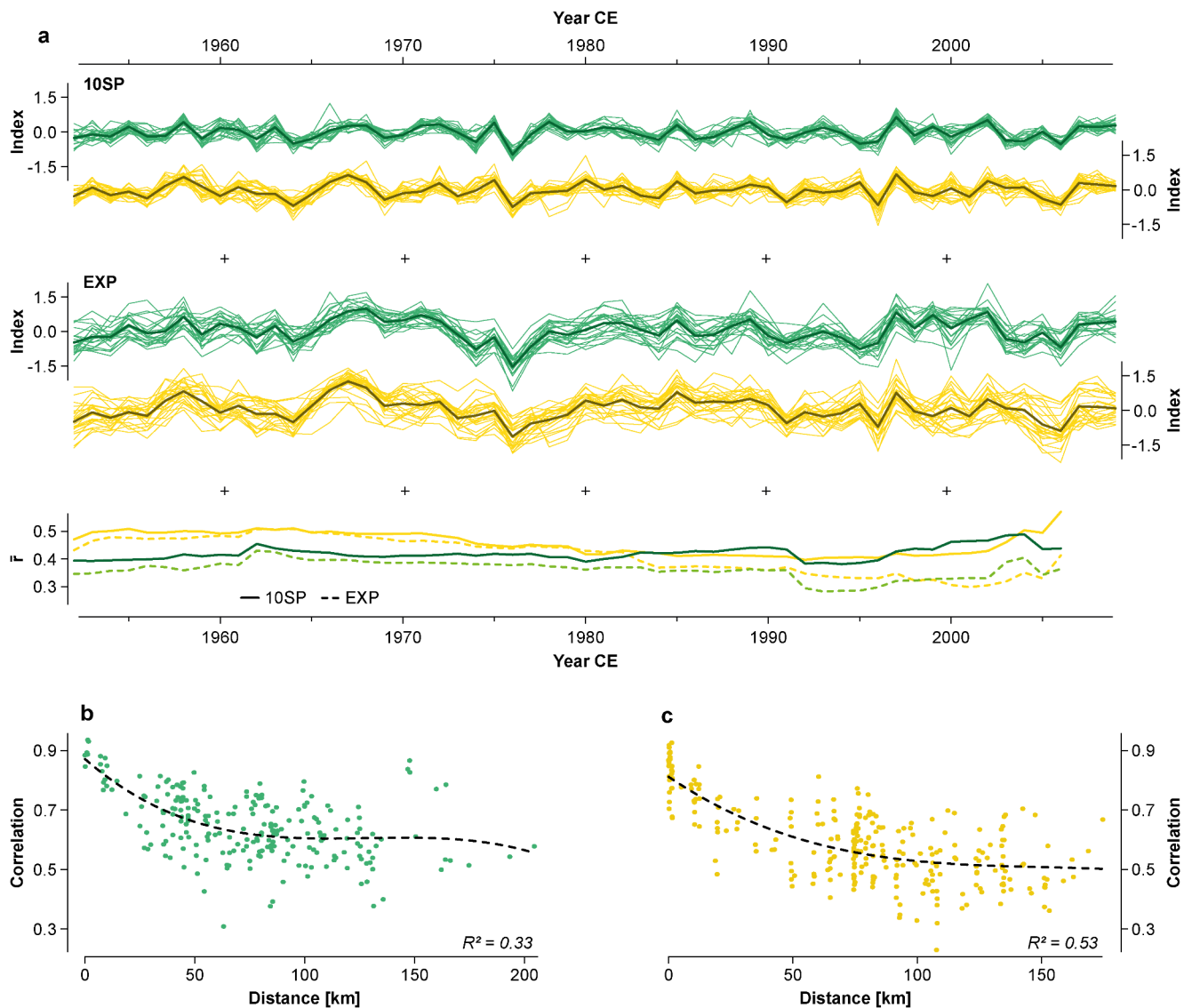


Fig. 5 Detrended tree-ring width (TRW) chronologies. **(a)** Spruce (green) and pine (yellow) site chronologies after detrending using 10-year smoothing splines (10SP, top panel) and negative exponential curves (EXP, middle panel), shown together with their 30-year running inter-series correlations ($\bar{r}$, bottom panel). Thick curves (top and

middle panel) are the regional mean chronologies. **(b–c)** Correlations between the 10SP spruce and pine chronologies as a function of distance. Dashed lines indicate third-order polynomial trends of all possible spruce ($n=231$) and pine ($n=276$) pairings

varying retained frequencies are visible in the TRW site chronologies (Fig. 5a) and expressed in first-order autocorrelations decreasing from $AC1_{avg}=0.61$ in the EXP data to $AC1_{avg}=0.07$ in the 10SP data, demonstrating the removal of decadal to multi-decadal variability from the latter. $AC1$ values do not differ significantly between the two species according to the Mann-Whitney U test ($p>0.05$), neither in the raw nor in the detrended data.

Network climate sensitivity

Climate conditions in early spring and mid-summer are most important for southwest German conifer growth

(Fig. 6a). For spruce, highest correlations are found with July–September T_{max} of the previous year (pJAS) ranging from $r = -0.15$ to $r = -0.55$ between the sites (1952–2009 CE). Twenty of the 22 spruce stands show significant ($p<0.05$) negative correlations with pJAS T_{max} , and the regional spruce chronology correlates at $r_{1952-2009} = -0.47$ ($p<0.001$). In contrast, only seven of the 24 pine stands are significantly correlated with pJAS T_{max} ($p<0.05$), of which five stands are located at the southern border of the tree-ring network in the Palatinate Forest (49–49.5°N/ 8–8.25°E). The species-specific differences in pJAS- T_{max} correlations are significant at $p<0.001$ and are related to a fading

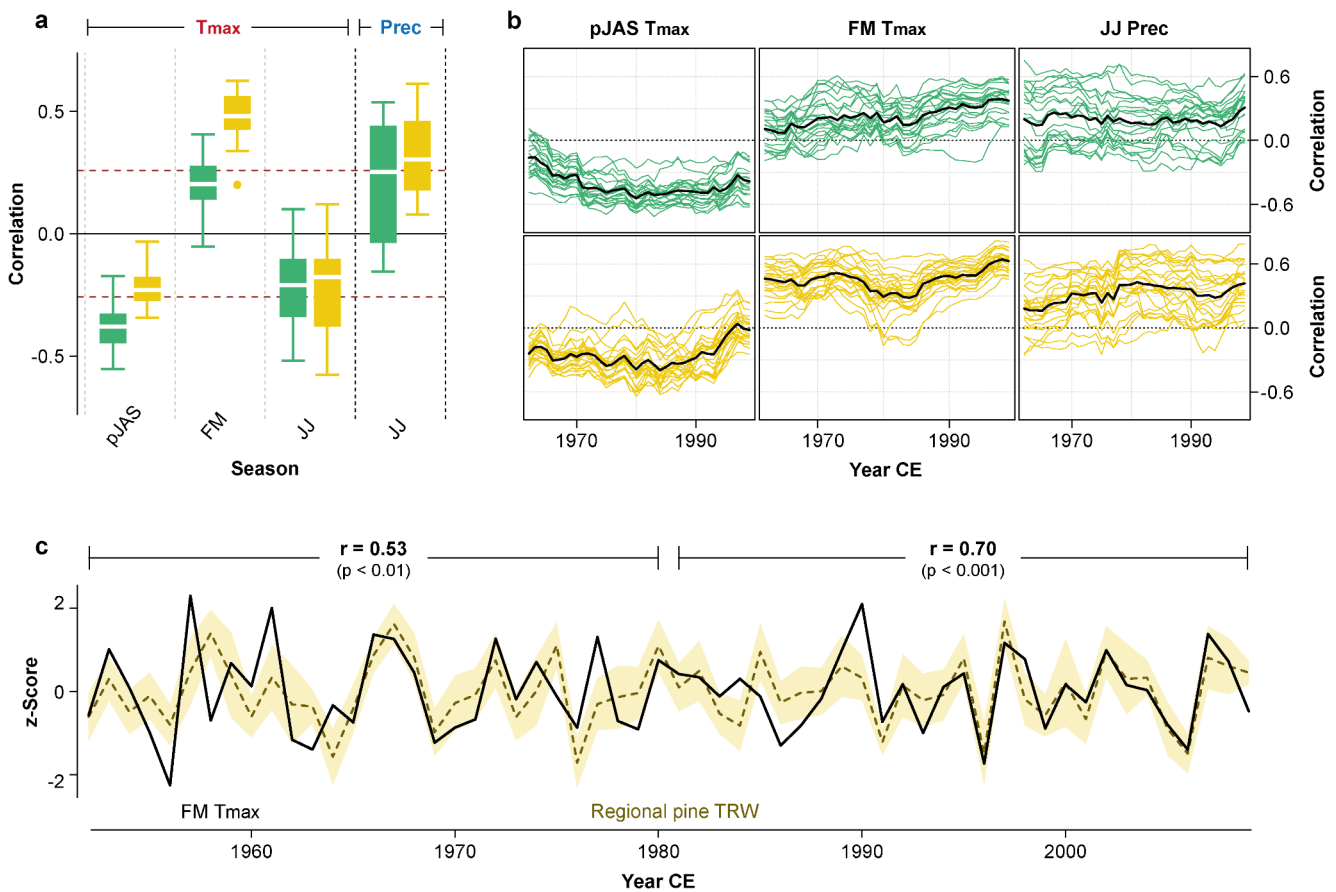


Fig. 6 Climate-growth relationships. (a) Distribution of bootstrap correlations of the 10SP chronologies (spruce=green, pine=yellow) with seasonal maximum air temperatures (T_{max}) and precipitation (Prec) from 1951–2009 CE. Boxplots show the median (white bar), 25%- and 75%-quartiles (box), min and max values within 1.5x the interquartile range (whiskers), and outliers (points). Horizontal dashed

lines mark $p < 0.05$. (b) 21-year running correlations between the TRW site chronologies and seasonal T_{max} and precipitation. Black curves are the mean. (c) Z-Scores of the 10SP regional pine chronology (brown dashed line) and high-pass filtered February-March T_{max} (black solid line). Yellow shadings represent $\pm 1\sigma$ of all pine chronologies. R values refer to 1952–1980 and 1981–2009 CE

temperature sensitivity of pine growth toward the end of the 20th century (Fig. 6b).

For pine, the highest correlations are found with February-March (FM) T_{max} , ranging from $r = 0.20$ to $r = 0.63$ for 1952–2009 CE. Twenty-three of the 24 pine chronologies display significant ($p < 0.05$) positive correlations with FM T_{max} . Southeastern pine sites in the Upper Rhine Plain and the Palatinate Forest show the highest correlations with $r \geq 0.50$. Correlations between spruce TRW and FM T_{max} ($r_{avg} = 0.20$) are substantially lower compared to pine ($r_{avg} = 0.47$) and are only significant ($p < 0.05$) at sites below 550 m asl (eight of the nine sites). However, correlations between TRW and FM T_{max} have increased noticeably for both species in recent decades, particularly for pine (Fig. 6c).

June-July (JJ) T_{max} responses are less coherent across the network. Site correlations range from $r = 0.10$ ($p > 0.05$) to $r = -0.52$ ($p < 0.001$) for spruce and from $r = 0.12$ ($p > 0.05$) to $r = -0.58$ ($p < 0.001$) for pine. Strongest negative correlations ($r \leq -0.40$) with JJ T_{max} are found in pines below

140 m asl in the Upper Rhine Plain (49.5–50°N/ 8–9.5°E) and in spruce from the Palatinate Forest. Running correlations reveal that both species' summer T_{max} response has declined since the late 1980s. Positive correlations between TRW and JJ precipitation mirror the strong negative correlation between summer T_{max} and precipitation ($r_{JJ} = -0.62$, $p < 0.001$) but also point to the importance of water supply during summer resulting from mutual interactions between precipitation and evapotranspiration. The regional TRW chronologies correlate at $r_{spruce} = 0.27$ ($p < 0.05$) and $r_{pine} = 0.41$ ($p < 0.01$) with JJ precipitation from 1952 to 2009 CE, suggesting that current-year summer precipitation is more important for pine than for spruce.

Correlations of the 46 TRW chronologies with monthly soil moisture indices show that spruce and pine growth are strongly affected by summer drought (Fig. 7a). Correlations with monthly SMI values are generally higher than with monthly T_{max} and precipitation totals (Fig. S5), indicating greater importance of soil water availability compared to

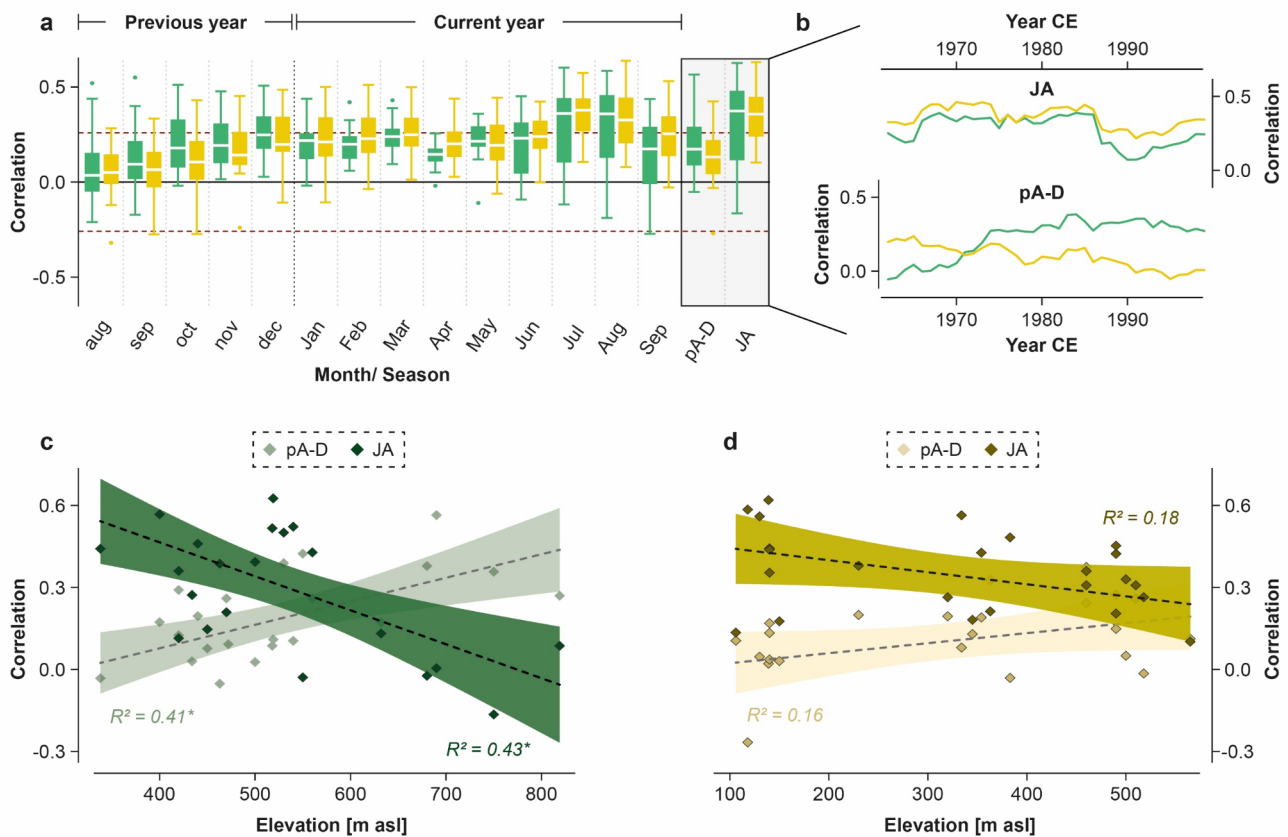


Fig. 7 Soil moisture sensitivity. **(a)** Distribution of bootstrap correlations of 10SP chronologies (spruce=green, pine=yellow) with monthly and seasonal soil moisture indices from 1951–2009 CE. Boxplots show the median (white bar), 25%- and 75%-quartiles (box), min and max values within 1.5x the interquartile range (whiskers), and outliers (points). Horizontal dashed lines mark $p < 0.05$. **(b)** Mean 21-year running correlations of the species with current-year July-August (JA)

and previous-year August-December (pA-D) soil moisture indices. Soil moisture sensitivity of **(c)** spruce and **(d)** pine as a function of elevation. Each dot represents one site. Light colors indicate correlations (1952–2009 CE) with the pA-D SMI, dark colors indicate correlations with the JA SMI. Dashed lines show linear trends. Colored areas are the 95% confidence intervals of the regression slopes. Asterisks behind R^2 indicate significance at $p < 0.01$

individual climate factors. The highest correlations between TRW and SMI values are obtained for July-August (JA). Thirteen spruce (59%) and 18 pine stands (75%) are significantly ($p < 0.05$) positively correlated with the JA SMI, and the regional TRW chronologies correlate at $r_{\text{spruce}} = 0.38$ ($p < 0.01$) and $r_{\text{pine}} = 0.49$ ($p < 0.001$) from 1952 to 2009 CE. Running correlations between TRW and the JA SMI remain fairly stable until 1985 CE, but weaken considerably thereafter (Fig. 7b).

Correlations between TRW and previous-year SMI values are generally weak. However, nine spruce (41%) and five pine (21%) stands show significant ($p < 0.05$) positive correlations with the August-December SMI of the previous year (pA-D). While running correlations between pine TRW and the pA-D SMI decrease slightly from 1952 to 2009 CE, increasing correlations between spruce TRW and the pA-D SMI indicate an enhanced growth response to previous-year soil moisture conditions, especially above 550 m asl (Fig. S6). Linear regression models reveal a significant ($p < 0.01$)

dependence of SMI correlations on elevation (Fig. 7c). With increasing altitude, spruce TRW shows a decreasing response to the JA SMI and an increasing response to the pA-D SMI. No significant relationship was found for pine (Fig. 7d).

Discussion

Conifer growth characteristics

Including more than 1900 spruce and pine trees, our network is the largest TRW dataset in southwestern Germany. The well-replicated data fill a spatial gap between networks in northeastern France (Lebourgeois et al. 2010), southern Germany (Boden et al. 2014; Zang et al. 2014; Debel et al. 2021), and the low mountain ranges in west-central Germany (Friedrichs et al. 2009; Esper et al. 2012), and provide

new insights into the regional growth performance of spruce and pine over several decades.

The AGRs of Norway spruce ($2.3 \pm 0.6 \text{ mm a}^{-1}$) and Scots pine ($1.6 \pm 0.5 \text{ mm a}^{-1}$) are similar to nearby sites in western Germany and northeastern France (Friedrichs et al. 2009; Lebourgeois et al. 2010). Average BAIs are similar between the conifers during the first 20 years of cambial age ($\sim 2.9 \text{ cm}^2 \text{ a}^{-1}$), but increasingly diverge thereafter due to the strong growth acceleration in spruce. The observed growth trends and inter-species differences align well with data across Central European temperate forests (Bouriaud and Popa 2009; Seidling et al. 2012; Treml et al. 2021; Pretzsch et al. 2023).

In addition to species effects, the observed growth differences between spruce and pine may also be influenced by factors such as elevation, climate, and site conditions. Since the pine stands are, on average, ~ 30 years older than the spruces, age-related growth disparities are likely, particularly when considering the different environmental conditions each species experienced during their early growth stages. These growth differences are likely further amplified by elevational site variations and associated soil properties. While spruce predominates above 400 m asl on soils with higher water retention capacities, pines are primarily planted below 550 m asl on sandy soils (Richter et al. 2007), exposing them to greater drought stress. This is compounded by lower rainfall sums and higher air temperatures in the lowlands (Fig. S7). Different soil properties may also explain intra-species growth differences, as suggested by the reduced or absent precipitation response in spruce growing on well-developed stagnosols (Klippel et al. 2017). However, the effects of soil properties on conifer growth within our network remain unclear due to the lack of high-resolution soil measurements at the individual sites.

The assessment of mean BAI data from 1952 to 2009 CE shows that soil water supply during summer is of decisive importance for spruce. Spruce BAI increases with increasing growing-season moisture supply, with the highest growth rates ($\text{BAI}_{\text{avg}} > 20 \text{ cm}^2 \text{ a}^{-1}$) being recorded in young ($\text{MLS} < 90$ years) and moist ($\text{SMI}_{\text{A-O}} > 0.52$) stands. The lower BAI of spruce at drier sites and lack of comparable dependencies in pine likely reflect the higher drought vulnerability of spruce in the Central European lowlands and low mountain ranges (Zang et al. 2014; Treml et al. 2021).

Despite the observed age-trends in BAI, differences in stand age do not explain intra-species BAI differences. However, the significant negative relationship ($r = -0.63$, $p < 0.01$) between spruce AGR and MSL shows that older stands are characterized by lower initial growth rates than the younger stands. Although only living trees were included in this study and thus maximum tree ages cannot be determined, our results suggest that slow juvenile growth

prolongs the life expectancy of spruce (Bigler and Veblen 2009; Rötheli et al. 2012; Castagneri et al. 2013). There are many explanations for such a putative trade-off between longevity and growth rate including the greater resilience of slow-growing trees to external disturbances (Schulman 1954), slower regulation of growth-related processes in taller trees (McDowell et al. 2008), as well as differences in root architecture (Hamberg et al. 2018) and hydraulic resilience (Ryan and Yoder 1997). No significant relationship was found between stand-level AGR and MSL in pine. However, a weak but significant correlation ($r = -0.24$, $p < 0.001$) was observed when accounting for the individual growth rates of the 986 pines (Fig. S8), supporting similar findings from other European sites (Bigler 2016; Büntgen et al. 2019).

Network covariance

Cross-correlation, Principal Component Gradient and Hierarchical Cluster analyses (Fig. S2) reveal that network covariance is most distinct in the high-frequency domain and likely driven by several environmental (climatic) factors (Debel et al. 2021; Friedrichs et al. 2009; Lebourgeois 2007; Mäkinen et al. 2002; Vitali et al. 2017). Compared to treeline sites, where inter-annual TRW variability is synchronized and increased by a single growth-limiting climatic factor, the more favorable conditions in temperate forests promote the formation of more invariable (complacent) tree rings. High-pass filters, such as the 10-year splines, emphasize inter-annual variance by eliminating low-frequency information (Esper and Gärtner 2001) and thereby synchronize TRW variance within and between sites. Higher inter-site correlations in the 10SP data compared to the EXP data support this conclusion and indicate stronger climatic forcing in the high-frequency domain.

The lower covariance in the EXP data may also be related to the impact of silvicultural treatments such as wood harvesting and thinning, which can induce long-term growth releases by reducing competition for light and nutrients (Kramer 2019). Negative exponential detrending does not mitigate such rapid non-climatic trends and thereby distorts the synchronizing influence of climate variability across the network. Although this contradicts findings of Esper et al. (2012), who report only minor effects of logging on spruce precipitation sensitivity in western Germany, several studies support that silvicultural practices and local disturbances may alter long-term growth trends (Mörling 2002; Mehtätalo et al. 2014; Lehtonen et al. 2023). Insect outbreaks can affect high-frequency covariance strongly, as shown by the strong TRW deviations of two pine stands in the late 1980s caused by pine sawfly (*Diprion pini* L.) outbreaks in 1977 CE near Speyer and Aschaffenburg (Bogenschütz 1981).

The singularity of such striking events, however, does not substantially affect the covariance of the 10SP data across southwest Germany.

Growth responses to summer drought

The assessment of species-specific climate-growth relationships shows that summer drought is the dominant climatic driver of southwest German spruce and pine growth. Although correlations between TRW and climate variables are generally weak, the uniform network growth responses to current-year summer $T_{\max}$ and precipitation underline the importance of adequate water supply during the time of xylem formation. The positive association of TRW with summer precipitation and the negative association with $T_{\max}$ appear physiologically meaningful, as low summer rainfall and high temperatures intensify evapotranspiration and soil moisture deficit, and thereby reduce turgor pressure in the xylem and associated cell enlargement processes (Peters et al. 2021). Stronger correlations with summer precipitation than with $T_{\max}$ point to a higher relevance of summer rain for both conifers, but the significant inverse relationship between summer temperature and precipitation ($r_{JJA} = -0.65$) makes a clear distinction between the two factors difficult. The precipitation sensitivity is in line with findings by Friedrichs et al. (2009) and Esper et al. (2012), who report similar growth responses to May–July precipitation at several spruce and pine stands in the Rhenish Massif. Comparable relationships between TRW and May–July precipitation were found in lowland Poland (Koprowski and Zielski 2006) and the lower French Alps (Desplanque et al. 1998). TRW correlations with the SMI peak slightly later in summer (July–August), likely due to delayed responses of the hydro-pedological system (Entekhabi et al. 1996).

Besides the drought response during xylem formation, spruce reveals a definite sensitivity to previous-year late-summer (July–September) conditions. This lag-response is consistent with other tree-ring studies (Rybníček et al. 2010; Zang et al. 2011; Seidling et al. 2012; van der Maaten-Theunissen et al. 2013) and supports the significance of carry-over effects on earlywood formation (Lebourgeois et al. 2010). The negative relationship between spruce TRW and prior-summer $T_{\max}$ can likely be attributed to drought-induced reductions in carbohydrate accumulation, impairment of fine root formation, and increased crown dieback, limiting radial growth in the following year (St. George 2014). The latter explanation is supported by results of Solberg (2004) and Seidling et al. (2012), who found positive correlations between summer temperature and the crown transparency of spruce. Summer droughts favor needle defoliation and discoloration in fall, thereby reducing photosynthesis and growth in subsequent growing seasons (Solberg

2004). High summer temperatures may also promote flowering and seed production in consecutive years and thereby inhibit growth by limiting the amount of available resources (Selås et al. 2002).

Even though TRW variations among the spruce stands are highly synchronous ($r_{\text{avg}} = 0.66$ for 10SP data), the SMI signals are significantly altered by elevation. Current-summer SMI correlations decrease by ~ 0.1 per 100 m, while previous-year SMI correlations increase towards higher elevations. Twelve of the thirteen spruce stands that are significantly correlated with the JA SMI are located below 550 m asl, and six of the eight stands that are significantly correlated with the pA–D SMI are at or above 550 m asl. Linear regression models show that elevation explains 43% of the drought signal differences. Van der Maaten-Theunissen et al. (2013) found a similar gradient ($R^2 = 0.33$) along elevational transects in the Black Forest. The variations in drought sensitivity are consistent with the fact that spruce at drier sites is most susceptible to current growing-season conditions, while wetter stands at intermediate elevations frequently lack such signals (Wilson and Hopfmueller 2001; Leal et al. 2007; Hartl-Meier et al. 2014; Sidor et al. 2015; Jevšenak et al. 2021). Park and Spiecker (2005) show that spruce at drier sites tend to form more latewood cells with thicker walls, while spruce at wetter sites generally form larger earlywood cells, which might explain the stronger response to previous-year conditions at mid-elevations, as earlywood formation is closely related to the mobilization of stored photoassimilates (Kagawa et al. 2006).

Running correlations between TRW and SMI values indicate that previous August–December moisture conditions became increasingly important for spruce. Although these correlations are calculated over a short time window, the fairly coherent patterns across the network point to an increasing growth response of spruce to previous-year climatic conditions, particularly above 550 m asl. These results support the findings of previous studies from eastern Europe (Rybníček et al. 2010; Čermák et al. 2019). The increasing responses to water supply in previous late-summer and autumn may be related to the strong warming and decreasing rainfall in July and August, limiting accessible soil moisture in recent decades. Droughts can reduce fine root formation and recovery (Nikolova et al. 2009), which may adversely affect growth in the following growing season, especially as late-summer is a distinct growth period for roots in southwestern Germany (Xu et al. 1997).

Growth responses to late-winter temperatures

FM temperature signals in pine TRW have previously been reported from several temperate forest sites (Friedrichs et al. 2009; Lebourgeois et al. 2010; Koprowski et al. 2012;

Seidling et al. 2012; Bauwe et al. 2013; Debel et al. 2021; Stolz et al. 2021; Diers et al. 2023, 2024), indicating a large-scale growth-promoting influence of air temperatures during the dormancy period across Central Europe. However, despite the extensive empirical evidence, physiological mechanisms explaining the growth-stimulating influence of winter temperatures are still poorly understood. While an onset of growth in February–March is unlikely, elevated air temperatures during late winter may favor physiological processes supporting cambial reactivation during quiescent dormancy (Begum et al. 2013). At the lowest elevations (~100 m asl), 38% of the February–March days exceeded a mean temperature of 6 °C and 25% exceeded 8 °C (Fig. S9), indicating that thermal thresholds for xylogenetic activity are only sporadically reached, but temperatures could be sufficient to promote photosynthesis (Tanja et al. 2003; Rossi et al. 2008). Such effects appear plausible as evergreen conifers can remain photosynthetically active in winter and modulate their capacities within a few days (Nippert et al. 2004; Mäkelä et al. 2004). A temperature-driven stimulation of photosynthesis in late winter could also explain the lack of significant correlations between spruce TRW and FM $T_{\max}$ above 550 m asl.

In the temperate regions of France, early- and latewood width of fir, pine and spruce are positively related to February temperatures, suggesting that warm late winters not only promote growth in spring but also favor growth processes throughout the growing season, probably related to an enhanced photoassimilate accumulation prior to the onset of cambial activity (Lebourgeois et al. 2010). This inference is supported by findings of Giberti et al. (2022), who report positive relationships between January–March temperatures and carbon sequestration in Polish pines. Since warmer winters are accompanied by higher rainfall, as shown by the positive correlation between FM $T_{\max}$ and precipitation ($r=0.43$), the FM response may also reflect an increased water availability in late winter into spring. The lack of significant precipitation correlations, however, indicates that FM temperature is the key climatic driver. Besides the effects on photosynthetic biochemistry, high late-winter temperatures might also promote soil warming and mycorrhizal growth (Domisch et al. 2002) and reduce the risk of winter desiccation (Sevanto et al. 2006; Ensminger et al. 2008).

Increasing running correlations between TRW and FM $T_{\max}$ indicate that late-winter temperatures have become noticeably more important for southwest German spruce and pine growth in recent decades. Our results support previous studies from the south Baltic region (Harvey et al. 2020; Janecka et al. 2020; Diers et al. 2023, 2024) and add evidence that late-winter temperatures are gaining importance for Central European forest growth. Decreasing

correlations with JJ $T_{\max}$ and increasing correlations with FM $T_{\max}$ since the 1980s point to putative trade-offs between enhanced winter and reduced summer photosynthesis (Stolz et al. 2021), which may result from a strong inter-seasonal warming (Fig. S10a). Even if FM $T_{\max}$ correlations may be strengthened by the higher variance of cold-season temperatures (Fig. S10b), the increasing relevance of late-winter temperatures for conifer growth is in line with long-term phenological observations indicating earlier plant development and fruiting (Chmielewski et al. 2004; Büntgen et al. 2022).

Conclusion

We introduce a TRW network to assess the growth performance of Norway spruce and Scots pine along elevational gradients from 100 to 820 m asl in southwest Germany and identify climatic drivers of regional forest growth. The data reveals that spruce has grown twice that of pine in recent decades, partly due to differences in tree age and site conditions. Decadal BAI fluctuations of both conifers are closely related to long-term soil moisture variability, but only spruce indicates a significant dependence on growing-season water supply, which likely reflects the higher drought vulnerability of this species at locations beyond its natural distribution range. Correlations using high-pass filtered TRW and climate data support that summer drought is the dominant climatic driver of southwest German spruce growth, but the seasonality of the signal changes with elevation. Sites below 550 m asl show a stronger growth response to current-summer soil moisture conditions, whereas spruce sites above 550 m asl are particularly sensitive to previous-year moisture conditions. Possible reasons for the changing seasonality along the elevational gradient are discussed, but remain conjectural due to the sole focus on radial stem growth, underlining the need to address the complex interactions between above- and below-ground biomass productivity in future research. In addition, increasing growth responses to late-winter temperatures hint at potential changes in the photosynthetic seasonality of Scots pine, likely related to an abrupt temperature increase in the late 1980s and possibly reflecting a trade-off between enhanced winter and reduced summer photosynthesis. Our results provide new insights into the growth performance of southwest German spruce and pines under recent climate change, which call for a change in planting strategies towards more drought-resistant tree species and may help refine future projections for temperate forests.

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Author contributions P.R. and J.E. conceived and planned the study. P.R., F.R., O.K., L.K., and J.E. conducted fieldwork. P.R. performed the final analyses and drafted the manuscript with input from E.M., F.R., M.C.A.T., U.B. and J.E. All authors provided discussion and agreed to the final version of the manuscript.

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Data availability The data is made publicly accessible through the International Tree-Ring Data Bank (ITRDB; <https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>).

Code availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

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