


Increasing Winter Temperatures Stimulate Scots Pine Growth in the North German Lowlands Despite Stationary Sensitivity to Summer Drought

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ABSTRACT

More than half of the forest area of the North German Lowlands is stocked with Scots pine-dominated forests, mostly plantations. Climate change suggests a declining suitability of Europe's temperate zone for conifer plantations, but only a few studies have examined the long-term growth trends of Scots pine in relation to environmental and site factors in this region. We studied the radial growth patterns of Scots pine over the last 60 years at ten sites along a precipitation gradient (830–530 mm mean annual precipitation) from an oceanic to a subcontinental climate, analyzing the spatial and temporal variability of the climate sen-

sitivity of growth to identify the main climatic factors influencing pine growth across this gradient, which covers a large part of the species' tolerated precipitation range. Annual radial increment was sensitive to late-winter temperatures (February, March) and summer drought and heat (June–August), with sensitivity increasing from the oceanic to the drier continental sites. Warmer late-winter periods apparently have stimulated growth during the last decades, while the sensitivity to summer-drought has remained fairly stable. Until recently, the negative impact of warming summers on growth has been compensated by the positive effect of late-winter warming, resulting in stable (or increasing) growth trends. However, our comparison of the climate sensitivity across sites suggests that the drought effect compensation through winter warming will in future be limited by increasing drought exposure. Thus, future productivity declines are likely in the northern German lowlands despite warming winters, discouraging large-scale pine plantations in the face of climate warming.

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Key words: climate sensitivity; dendrochronology; growth trends; precipitation gradient; sandy soil; summer drought; winter warming.

HIGHLIGHTS

- Radial growth of Scots pine is more drought-sensitive in subcontinental regions
- Late-winter warming compensates for drought and heat effects in summer
- Basal area increment increases despite growing sensitivity to climatic aridity in summer over time

INTRODUCTION

Forests play a key role for the global carbon and water cycles, and they harbor a large part of the earth's terrestrial biodiversity (Millennium Ecosystem Assessment 2005; Hill and others 2019). The last two decades have seen a rapid increase in the reporting of large-scale tree vitality loss and forest dieback in many regions of the world, which were attributed to the direct or indirect impact of drought and heat stress due to climate warming (van Mantgem and others 2009; Allen and others 2010; Carnicer and others 2011). In the temperate forests of Central Europe, widespread dieback occurred especially after the severe hot droughts of 2003 and 2018/2019, which primarily hit drought-sensitive Norway spruce (*Picea abies* Karst.), but also other main timbers such as European beech (*Fagus sylvatica* L.), and more locally Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Bigler and others 2006; Braun and others 2020; Schuldt and others 2020; Obladen and others 2021). This left foresters with the challenge of selecting drought-hardier timber species in order to achieve the declared goals of "climate-smart forestry", that is, maintaining (or increasing) timber yield in a warming climate, increasing forest resistance and resilience to drought and heat, and to increase the contribution of the forest sector to the climate change mitigation goals (Bowditch and others 2020; Verkerk and others 2020). In Central Europe's forests, the natural broadleaf forest cover has been largely replaced by conifer plantations. In Germany, for example, 54% of the current forest area is stocked by fast-growing conifers, such as Scots pine in the

northern lowlands (Thünen-Institut 2022a), where pine forests would naturally cover only about 2.3% (Förster and others 2021).

Due to its unproblematic establishment, tolerance of infertile soils and fast growth, pine has been planted on more than 9 million ha in Germany, Poland, and the Netherlands since about 250 years to meet the high demand for conifer wood (Hille and den Ouden 2004; Milnik 2007), often making it the economically most important timber species. Scots pine tolerates nutrient-poor and dry sites relatively well (Schütt and Stimm 2006; Roloff 2008), as is demonstrated by its natural occurrence on top of sand dunes at the Baltic coast (Dicrano-Pinion communities) and on shallow south-exposed slopes in limestone mountains (Erico-Pinion communities; Leuschner and Ellenberg 2017). Scots pine thrives under very different thermal and water balance conditions from the Mediterranean to the northern boreal zone and from the Atlantic coast to the Pacific coast (Caudullo and others 2017) partly as a consequence of drought-adjustment in the hydraulic system and enhanced stomatal control during periods of water shortage (Poyatos and others 2008; Martínez-Vilalta and others 2009).

Across its wide distribution range, the local climate-growth relationships of Scots pine differ largely. As expected, in cold regions, low temperatures limit both annual stem growth rates and seedling establishment (Rickebusch and others 2007; Mathisen and Hofgaard 2011; Matías and Jump 2014). In accordance, in a comparison of five pine populations across Europe, autumn, winter, and spring temperatures were more important for annual stem growth variability in the studied Central and Northern European populations, while interannual growth fluctuation was strongly sensitive to summer heat and drought at the drier southern sites (Matías and others 2017). That warmer winter and spring periods are currently promoting annual growth rates of Scots pine through an extension of growing season length, has also been reported by other studies, as evidenced by an increasingly strong winter/spring temperature-growth relationship (Lebourgeois and others 2010; Harvey and others 2020). At the species' southern distribution limit in the northern Mediterranean region, low spring and summer precipitation remain the main factors limiting annual growth rates of Scots pine (Andreu and others 2007; Matías and Jump 2012; Sánchez-Salguero and others 2012). In analogy with this large spatial variation in the climate sensitivity of annual growth rates, Scots pine long-term growth trends in

their dependence on climate change should also demonstrate regional variation across Europe. In fact, no distinct changes in long-term growth trends have usually been found in Central Europe (Kint and others 2012; Bauwe and others 2013, 2015), while positive growth trends were reported in the North, as in Lapland (Mielikäinen and Senov 1996). In contrast, decreasing growth trends have been observed in drought-affected regions of southern and central Europe, often in association with increasing mortality rates (Bigler and others 2006; Giuggiola and others 2010; Rigling and others 2013; Etzold and others 2019; Archambeau and others 2020).

In the lowlands of north-east Germany, Bauwe and others (2013, 2015) found no climate change-induced turning point in the growth trends of Scots pine. This may be explained by the intermediate position of these stands in the transition zone between declining southern “rear edge” (Martínez-Vilalta and others 2008; Reich and Oleksyn 2008; Giuggiola and others 2010; Matías and Jump 2014) and northern “leading-edge” populations (Juntunen and others 2002; Reich and Oleksyn 2008; Kullman 2014; Matías and Jump 2014). Despite the wide distribution of Scots pine in the lowlands of northern Germany and Poland, only a few dendrochronological studies have been conducted in these pine populations so far (Bauwe and others 2013, 2015; Liang and others 2013; Stolz and others 2021). In this region, it thus remains unclear, under which environmental conditions Scots pine growth will shift from a growth-stimulating climate-warming effect to growth impairment due to drought and heat impacts. From the simplistic perspective of the species’ climate envelope, Germany’s forested area with its pronounced oceanic-to-continental climate gradient is expected to become in large parts more unfavorable for Scots pine growth with the expected twenty-first century warming (Kölling 2007), leaving the species’ future uncertain.

Against the background of a marked increase in mean annual temperature in Germany since 1881 by about 1.6 °C (DWD 2020) and the variety of pine growth–climate relationships observed across Europe, predicting future pine growth dynamics in Northern Germany and Central Europe requires a more comprehensive assessment of regional variation in growth dynamics, which takes soil hydrology and stand structure into account (Bose and others 2020). A better understanding of regional variation in climate-growth relationships and long-term growth trends is also needed to assist foresters in their efforts to establish more climate-

stable forests and chose appropriate tree species (Bowditch and others 2020; Verkerk and others 2020).

In this study, we investigated the radial growth dynamics of Scots pine along a climate gradient from the more oceanic western to the more continental eastern part of the North German Lowlands, thereby covering a longer climate gradient than done in previous studies. Study aim was to examine the sensitivity of Scots pine radial growth to climatic and edaphic factors in order to identify possible drought- and heat-induced limits of the species in northern Central Europe. The following questions guided our research: (1) Does the climate sensitivity of Scots pine growth increase toward drier regions? (2) Which climatic, edaphic, and stand structural factors are influencing growth most?

MATERIAL AND METHODS

Study Sites

The study took place in 10 Scots pine (*P. sylvestris* L.) stands in the North German Lowlands on Pleistocene sandy soils at elevations of 17 to 157 m a.s.l. All stands were managed 55- to 74-year-old even-aged cohorts that have been thinned regularly in the past. The stands are located along a climate gradient from a cool-temperate oceanic climate near the North Sea coast in the west to a cool-temperate sub-continental climate in the east close to the Polish border. Along this west–east gradient, mean annual temperature varies between 9.0 and 9.6 °C, while mean annual precipitation decreases from 823 mm year⁻¹ to 564 mm year⁻¹ (Table 1, Figure 2b). During the 1960–2017 observation period, winter and summer temperatures have increased by more than 2 °C, resulting in a higher evaporative demand, while summer precipitation changed only little (Figure A1) (Schönwiese and Janoschitz 2008; DWD 2020).

Tree-Ring Data

At each of the 10 sites, 10 sample plots were established in homogenous sections of the stand (see Diers and others 2021). Per plot, one wood core was extracted at breast height (1.3 m) from each two dominant, vital trees, resulting in 20 cores per site. Coring was conducted with a 5mm-increment corer (Haglöf, Längsele, Sweden) between December 2017 and April 2018 from either the western tree side or parallel to plot inclination to avoid the influence of tension and compression wood. The wood cores were glued onto wooden

Table 1. Summarized Statistics of Chronologies for Each Study Site (Name and ID Number in Figure 2)

Study site	Start year AC	AC1	Start year EPS + rbar	EPS	rbar	MAP (mm)	MAT (°C)
Weichel (04)	1952	0.61 ± 0.18	1968	0.86	0.24	823	9.5
Lüssberg (08)	1953	0.60 ± 0.15	1968	0.91	0.35	801	9.1
Süsing (09)	1952	0.52 ± 0.23	1968	0.86	0.23	794	9.2
Ewige Route (07)	1951	0.52 ± 0.11	1965	0.91	0.34	712	9.2
Kaarzer Holz (11)	1940	0.52 ± 0.17	1968	0.85	0.24	654	9.2
Authausener Wald (16)	1959	0.62 ± 0.13	1968	0.93	0.39	644	9.7
Weißhaus (18)	1947	0.58 ± 0.13	1968	0.94	0.43	623	9.5
Nievoidhagen (10)	1959	0.51 ± 0.19	1968	0.91	0.33	601	9.7
Eggesiner Forst (13)	1950	0.61 ± 0.16	1968	0.92	0.36	569	9.1
Ueckermünder Heide (14)	1960	0.71 ± 0.10	1968	0.96	0.53	564	9.2

Sorted in decreasing order according to MAP. AC1, First-order autocorrelation of the raw ring-width series; EPS, expressed population signal; rbar, mean interseries correlation between all pairs of trees per site calculated over the detrended tree-ring series (RWI); MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C).

mounts, and a plain surface was cut on the samples with a microtome. For better contrast, the samples were colored with safranin and then powdered with chalk.

Annual ring width was measured with a moveable measuring table (Lintab 5, Rinntech, Heidelberg) employing TSAP-Win software of Rinntech (Rinn 2012) for cross-dating. At all sites, each 20 tree-ring series had a similarity to each other of at least 65% (Gleichläufigkeit, Eckstein and Bauch 1969), a t-value of 3.5 (Baillie and Pilcher 1973), and an expressed population signal (EPS, Wigley and others 1984) > 0.85 (Table 1). The tree-ring series were detrended to obtain the dimensionless ring-width index (RWI) (function “detrend” in the dplR-package, Bunn and others (2021); R version 4.0.4) applying a smoothing spline function with a 50% frequency cut-off in a 20-year moving window (Cook and Peters 1981). The each 20 standardized RWI-series of a forest stand were then averaged (Tukey’s bi-weight robust mean, Bunn and Korpela (2021)) to obtain mean chronologies for the 10 study sites (Figure 2b). We further calculated annual basal area increment (BAI) from the raw tree-ring series and the diameter at breast height of each tree (function BAI.out in the dplR package, Bunn and others 2021).

Environmental Variables

We obtained climate data (monthly temperature and precipitation) from the Climate Data Center (DWD Climate Data Center (CDC) 2019a, b) of the German Weather Service (Deutscher Wetterdienst, Offenbach) for the period from 1959 to 2017 (R package “rdwd” v.1.4.0, Boessenkool (2021)). The Standardized Precipitation–Evapotranspiration Index (SPEI) as an indicator for climatic aridity and the occurrence of drought periods was calculated

with the R package “SPEI” v.1.7 (Beguería and Vicente-Serrano 2017).

Forest structure data were available for every plot and used in the analysis as site means. Variables employed in the analysis were the stand density index after Reineke (1933), the mean number of living and standing trees per hectare [$n \text{ ha}^{-1}$], the diameter of mean basal area at breast height [cm], the timber volume of living and standing trees per hectare [$\text{m}^3 \text{ ha}^{-1}$], the cumulative basal area of living trees per hectare [$\text{m}^2 \text{ ha}^{-1}$], stand age [years], and the time since last thinning operation [years].

Soil chemical data were collected in a soil profile dug in each sample plot (Diers and others 2021), which were averaged to obtain site means ($n = 10$ per site). Soil chemical variables include profile totals (0–60 cm of mineral soil, “ms”) of the salt-exchangeable base cations (BC_{ms} [$\text{mol}_c \text{ m}^{-2}$]) potassium (K), calcium (Ca) and magnesium (Mg), soil organic carbon content (C_{ms} [Mg ha^{-1}]), total nitrogen content (N_{ms} [kg ha^{-1}]), plant-available phosphorus content (resin-exchangeable P, P_{resin} [g m^{-2}]), and profile averages of base saturation (BS_{ms} [%]), C:N ratio (CN_{ms} [g g^{-1}]), pH(KCl) (pH_{ms}), and clay content (cl_{ms} [%]). In addition, the total amounts of base cations (BC_{ol} [kg ha^{-1}]), organic carbon (C_{ol} [Mg ha^{-1}]), total nitrogen (N_{ol} [kg ha^{-1}]), and total phosphorus (P_{total} [kg ha^{-1}]) were determined for the organic layer (“ol”, O horizon), as well as the base saturation (BS_{ol} [%]), C:N ratio (CN_{ol} [g g^{-1}]), and pH(KCl) (pH_{ol}) of this layer.

Statistical Analysis

In order to analyze tree growth–climate relationships separately for each site, we correlated the RWI data with the annual time series of monthly climate variables (monthly averages from previous year’s

June to current-year September) (“dcc” function in the “treeclim” package of R v.2.0.5.1, Zang and Biondi 2015) and used Pearson’s r to express the strength of relationships. To account for non-stationarity of climate–growth relationships (Wilmking and others 2020) during the observation period, we split this analysis into an earlier (1960–1988) and a later period (1989–2017) of 29 years each. According to this initial correlation analysis, we selected the major growth-limiting climate factors and investigated their temporally variable importance in a moving-window analysis over the entire 58-year observation period for each site (“dcc” function with a window size of 30 years and 1-year offset).

We also applied linear multiple regression analyses to examine, how climate, forest structure, and local edaphic factors influence tree growth rates (BAI) across sites. We first set up a climate-only model in order to explain site-average (1960–2017) BAI by site averages (1960–2017) of the major growth-limiting climate factors as detected in the climate-sensitivity analysis. Then, we attempted to increase the performance of this initial model by iteratively adding and dropping factors related to forest structure and soil chemistry. We used Akaike’s Information Criterion (AIC) to select the best model (Akaike 1974) and took care to exclude autocorrelation between the explanatory variables in the model (Figures A3 and A4, appendix). We calculated the explained variance of each environmental factor in the final models using the R-package “variancePartition” (v.1.20.0, Hoffman and Schadt (2016); Hoffmann (2020)).

RESULTS

Climate Sensitivity of Scots Pine Growth

The climate sensitivity analysis shows that late-winter and early-spring temperatures were the most important climatic drivers of pine radial growth in the study region, when considering the whole 58-year observation period. Most sites revealed a significant positive relation of growth with March or February temperature (Figure 1a). The other most influential climatic factor was a water deficit in summer (Figure 1a). High temperatures in current-year June (and to a lesser degree in May) tended to affect growth negatively (not significant). We detected no consistent effects of previous-year weather conditions on growth. When comparing the earlier (1960–1988) and the later period (1989–2017), the largest differences in sensitivity were found for the temperature of the winter months, as the share of significant winter

temperature correlations increased from the earlier (no significant correlation with February temperature at any site) to the later period (nine sites with a significant February temperature signal) (Figure 1b). In contrast, the growth sensitivity to mid-summer drought (negative correlation with July/August precipitation and SPEI) persisted across both observation periods; yet, the sensitivity to low early-summer (June) precipitation weakened from the earlier to the later period (Figure 1b and Figure A2 in the Appendix). Analyzing growth responses to aggregate measures of summer drought intensity (MSP, mean June–August precipitation total) reveals that summer drought has a strong negative effect on pine growth at nearly all studied sites, especially at the drier sites (Figure 2). An aggregate measure of late-winter/early-spring temperature (February–March temperature average) correlated positively with growth at all sites except for one (Figure 2b right panel), without a dependence on the precipitation gradient in the study area (correlation of winter temperature sensitivity with MAP: $r^2 = 0.08$; data not shown).

The moving window analysis shows that the growth-promoting influence of warm periods late in winter (especially February and the average of February–March) has increased continuously during the last six decades at most of the ten sites (Figure 3). At one of the wetter sites, tree growth seemed to profit more from a warmer February than at the other sites, while one of the driest stands seemed not to profit at all over the 58-year period. Further, the correlation strength of June precipitation to growth decreased in the last two decades at most sites, while that of July precipitation increased (Figure 3). This shift is more pronounced at the wetter sites. On the other hand, the sites with lowest mean annual precipitation maintained their high precipitation sensitivity in June during the observation period (Figure 3). The growth sensitivity to SPEI of July, August, or the summer months (June–August) was particularly high in the driest stands throughout the observation period; it decreased slightly in the last 20 years. At the moistest sites, the growth correlations with the SPEI of July and of the summer period tended to increase over the observation period, but not so for the August SPEI (Figure 3).

Long-Term Growth Trends

The annual BAI of all ten forest sites reveals a strong increase over the 58 observation years (Figure 4b). The increase at sites with low mean annual precipitation (MAP) tended to be somewhat smaller than at sites with high MAP, but one dry site also showed a

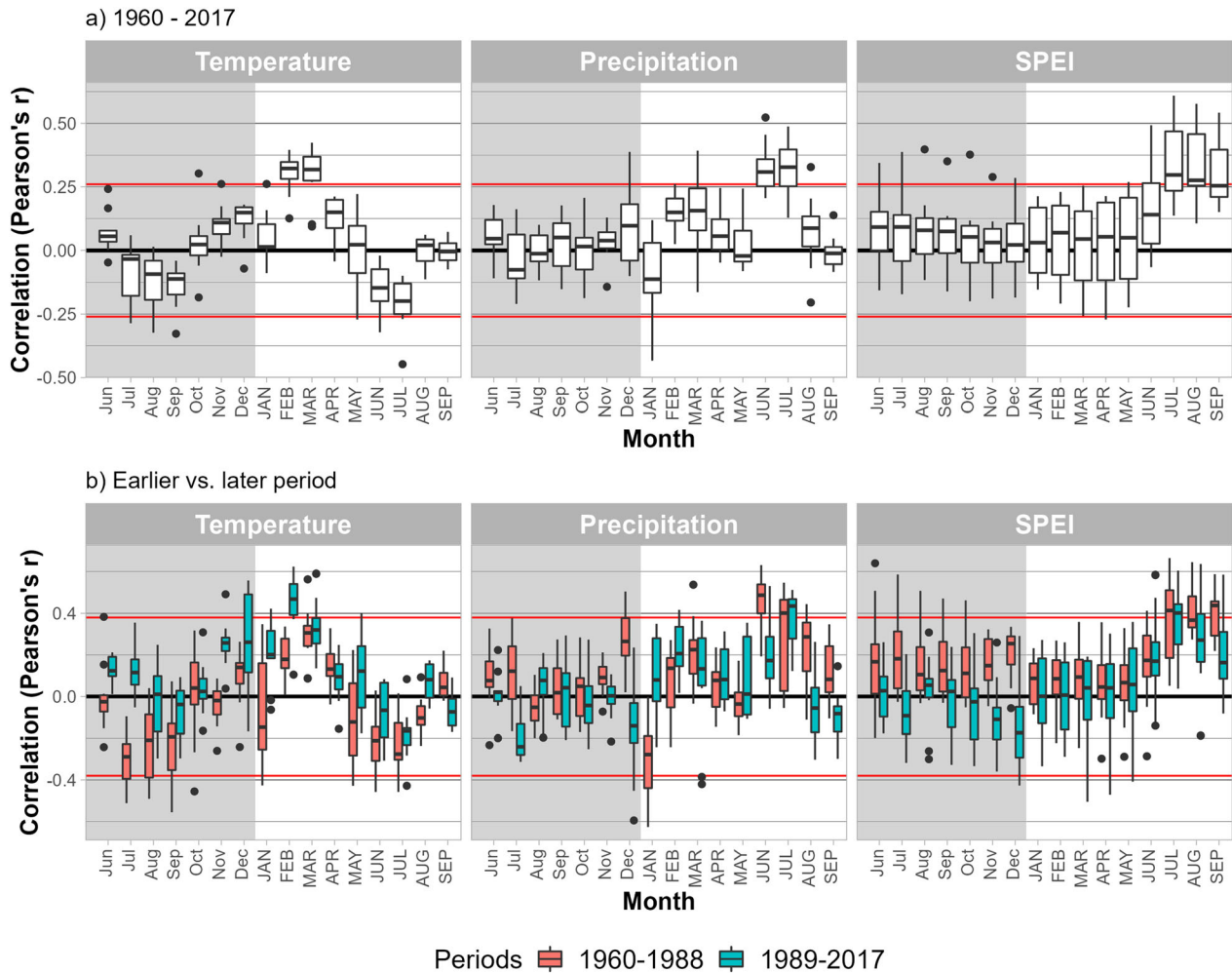


Figure 1. Correlation coefficients for the relationship of ring width index (RWI) with monthly temperature, precipitation and Standardized Precipitation–Evapotranspiration Index (SPEI), calculated separately for each of the 10 pine stands (each whisker-box represents 10 sites = 10 individual correlations) for January to September of the current year (in capitals) and June to December of the previous year (grey background) based on the data of the whole observation period (1960–2017) (a) and split into the periods 1960–1988 (red boxes) and 1989–2017 (blue boxes) for demonstrating temporal shifts in climate sensitivity of growth (b). The threshold for significant correlations is indicated by the red lines. For the full period ($n = 58$ years), $p < 0.05$ corresponds to $|r| > 0.26$ and for the split periods ($n = 29$ years), $p < 0.05$ corresponds to $|r| > 0.38$. The black dots mark outlying correlation coefficients of individual stands.

marked basal area growth increase over time (Figure 4b). When the trees are divided into age cohorts, both young and old trees show a strong increase in growth rates since about the 1980s. Strikingly, the youngest trees grew faster already during their juvenile stage (~ 1980) than their older conspecifics during their juvenile stage (1960 and before).

Environmental Factors Explaining Basal Area Increment

The average summer temperature (MST, 1960–2017) of a site and thus thermal site differences were the most important factor explaining BAI differences

among sites, with MST and BAI being negatively related to each other (Table 2). Interestingly, a site's average summer precipitation as the second-most important variable was associated with mean BAI also negatively, that is, a higher precipitation level was related to lower average BAI. The third-most important variable, average February/March temperature, on the contrary, had a strong positive effect on growth. The comparison of slope coefficients shows that the positive effect of a 1 K warmer winter is larger than the negative effect of 1 K warmer summer across the sites (Table 2). Of the soil factors, only the mineral soil C/N ratio remained as a significant factor in the model (negative effect of C/N ratio

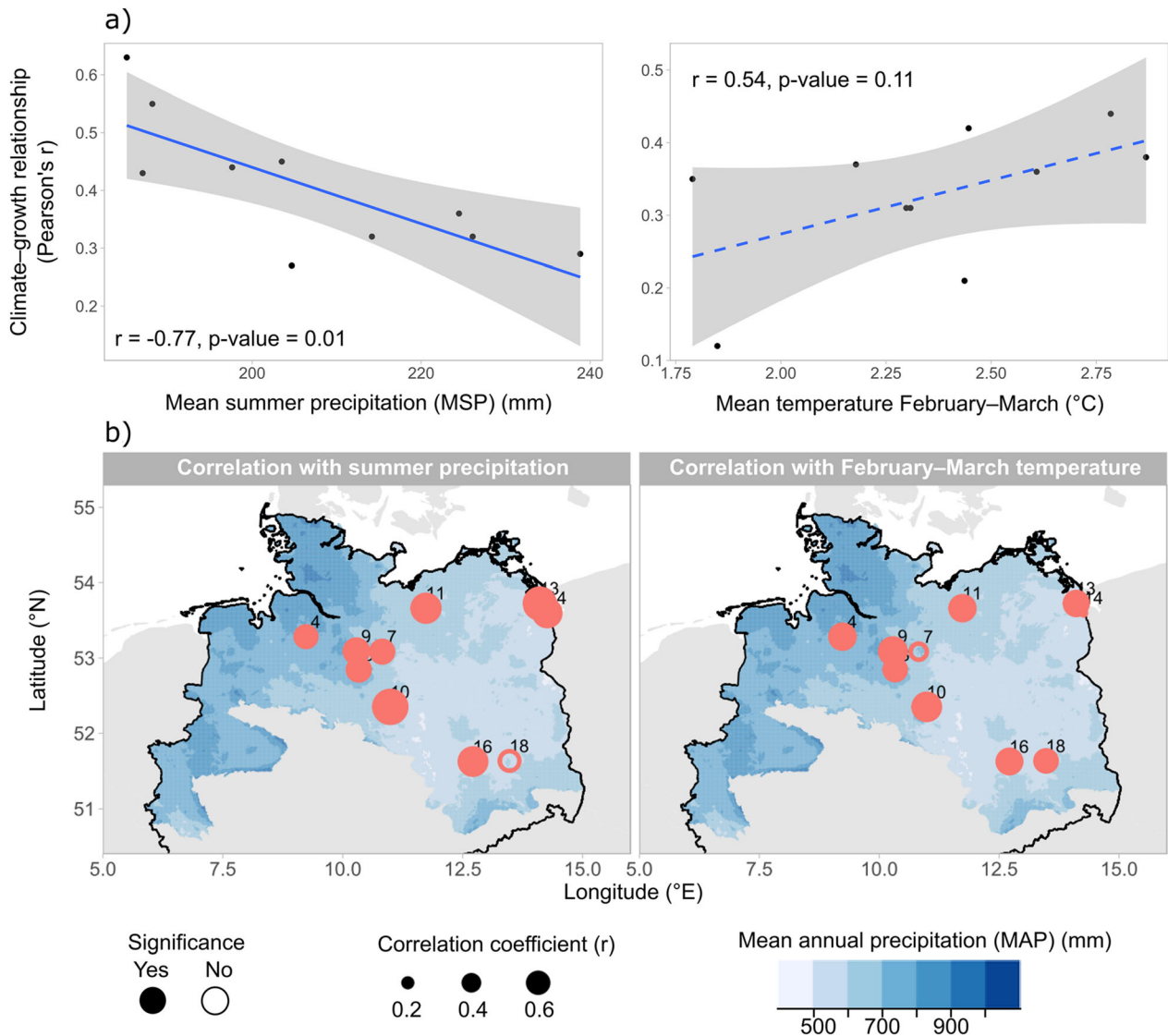


Figure 2. **a** Correlation strength of summer precipitation (June–August total) and growth, and winter temperature (February–March) and growth, respectively, in the 10 pine stands in northern Germany regressed against the average climate of the sites. Numbers indicate the different forest sites. **b** Summer precipitation and winter temperature signals (tree growth–climate correlations) at the 10 pine forest sites across the climatic landscape of the North German Lowlands.

and positive effect of soil N content). Mean BAI was not influenced by forest structure at any of the sites. In sum, most of the explained growth variance is related to differences in average climate conditions between sites, while the influence of soil conditions (C/N ratio) is small (but significant) (Table 2).

DISCUSSION

Higher, Yet Recently Decreasing, Drought Sensitivity at the Drier Sites

Our results show that the radial growth of Scots pine in northern Germany is more drought-sensi-

tive at drier sites with a less humid subcontinental climate (Figure 2, Figure A2), which is in line with the findings of Stolz and others (2021) from a shorter rainfall gradient in the northeast German lowlands and with pan-European patterns that revealed greater drought sensitivity in southern dry regions than in wetter and cooler northern parts of Europe (Matías and Jump 2012; Henttonen and others 2014; Camarero and others 2021). Our results indicate that Scots pine growth in this northern Central European region is impacted by both winter warming and summer drying, and the trees thus seem to operate in the transition zone from temperature limitation in the north (Harvey

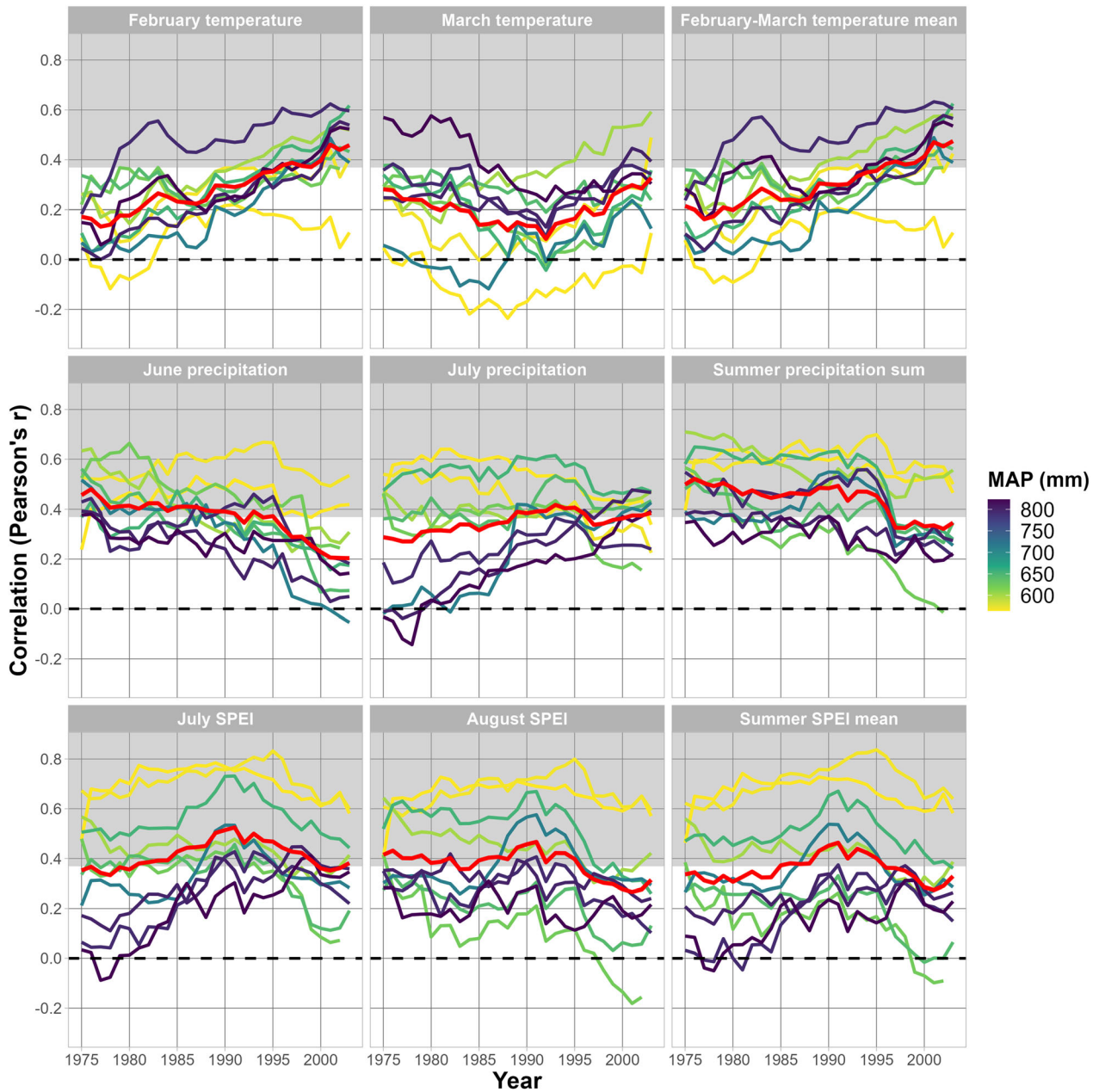


Figure 3. Moving-window correlation analysis of climate variables with ring width index (RWI) for the months with greatest influence and aggregated precipitation, Standardized Precipitation–Evapotranspiration Index (SPEI) and temperature means/totals of the summer period (June–August). The x-axis shows the central year of the 30-year moving window. Each line represents one forest site (colored according to the mean annual precipitation (MAP)) and the mean correlation of all 10 sites (red). The grey background corresponds to $|r| > 0.37$ at $p < 0.05$ for $n = 30$ years.

and others 2020; Janecka and others 2020) to drought limitation more in the south (Bogino and others 2009; Matías and Jump 2012; Camarero and others 2021).

The observed shifts in climate sensitivity over time might be caused by both climatic changes and age-related effects. The pronounced warming since the 1980s was accompanied by a decrease in summer SPEI by about 0.4 units (DWD 2020). Thus, the

evaporative demand of the atmosphere and the climatic water deficit has increased especially in early summer at most sites, irrespective of changes in summer rainfall that has decreased in parts of the region but increased in others (Bat-Enerel and others 2022). These climate trends are not mirrored in an increasing growth sensitivity to drought-related climate variables in *P. sylvestris* during the last two decades. A similar decoupling of the climate

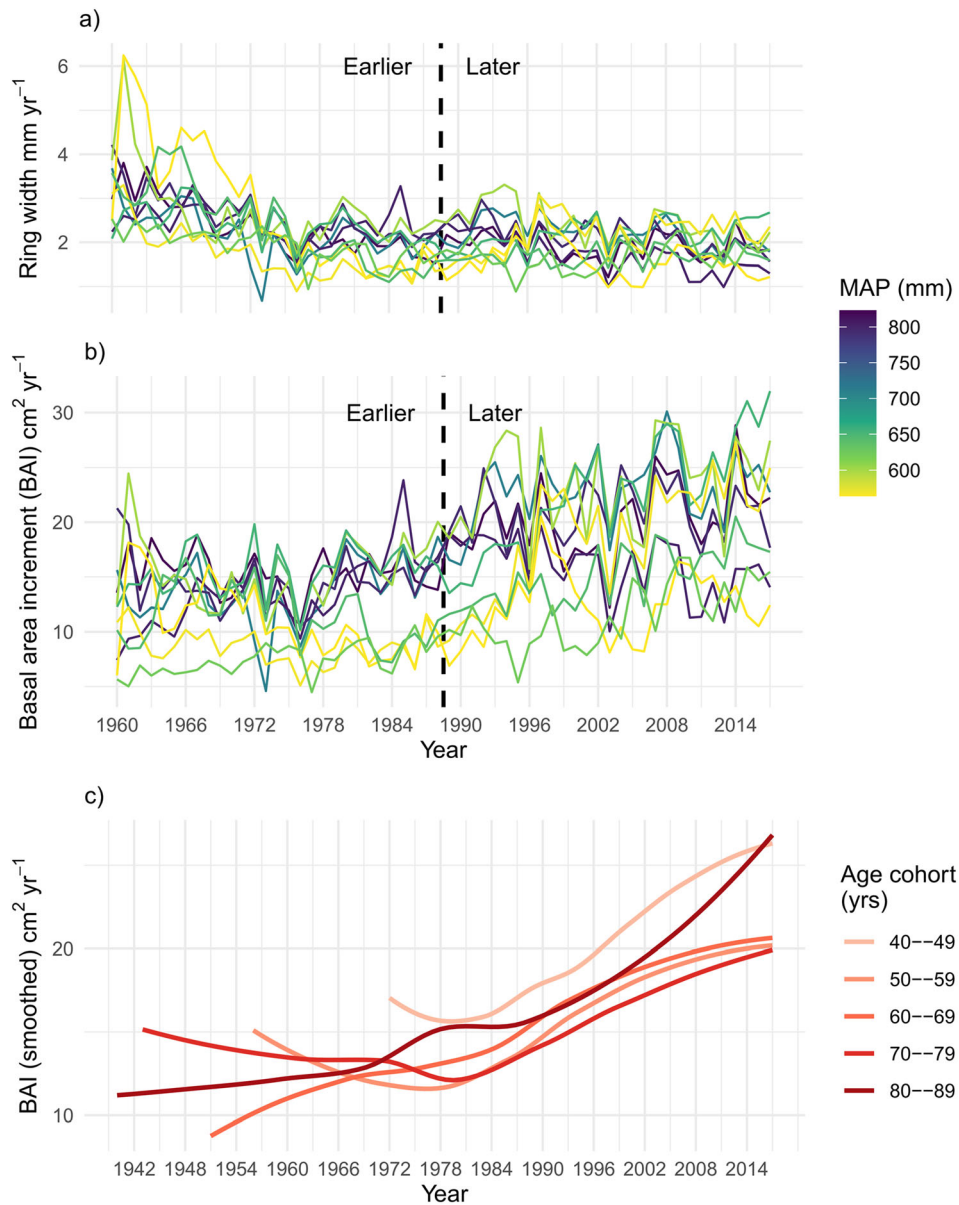


Figure 4. **a** Ring-width chronologies (average of 20 trees per site) and **b** the derived mean basal area increment (BAI) per year over the 58-year period used for climate–growth analysis. Lines are colored according to the mean annual precipitation (MAP, 30-year mean) of each site; **c** mean basal area increment (BAI) of different tree age cohorts across all forest sites. The tree age of each individual tree at the time of sampling was estimated from the length of the tree-ring series.

Table 2. Model Results on the Influence of Environmental Variables on BAI in a Comparison of Sites

Variable	Effect (Coef)	F-value	p-value	Expl.Var.p.Var (%)
Mean temperature Feb./Mar.	1005.87	32.3393	0.0047	24.18
Mean summer temperature (MST)	-674.07	40.8889	0.0030	30.58
Mean summer precipitation (MSP)	-12.70	40.1959	0.0031	30.06
Mean CN-ratio mineral soil	-21.35	9.8171	0.0350	7.37
Sum				92.19

sensitivity of growth from climate trends has been observed in other temperate tree species as well (*Acer platanoides*, *Fraxinus excelsior*, *Tilia cordata*: Fuchs and others (2021), *Quercus petraea*: Dobrovolný and others (2016)) and could result from successful drought acclimation, but other explanations such as deeper root penetration with increasing age or growth release after larger thinning operations are also possible.

Increasing Growth Stimulation by Late-Winter/Early-Spring Warming

Low winter temperatures have been identified as a growth-limiting factor in various studies on Scots pine in central and northern Europe, and the positive influence of climate warming on growth seems to increase toward colder environments (Reich and Oleksyn 2008; Lebourgeois and others 2010; Matías and others 2017; Harvey and others 2020). In general, winter-cold sensitivity is found in both evergreen conifers and broadleaf deciduous trees, which may relate to fine root damage by strong soil frost events in mid-winter (Pederson and others 2004; Weigel and others 2018, 2021), among other negative effects of cold. However, we found a greater influence of temperatures on the brink of winter to spring than during the mid-winter months with lowest temperatures. This should rule out mid-winter frost damage as an explanation for smaller annual growth rings with lower winter temperatures. In our study region, temperature-induced ring width variation is more likely caused by the positive effect of a warmer spring. The onset of xylogenesis is thought to be a threshold response to critical spring temperatures (Liang and Camarero 2018), which now likely have been crossed at most studied pine forest sites in the course of climate warming since the 1980s. Hence, a positive relationship between late-winter temperature and growth has emerged, and an extending growing season length seems to act as a major driver of stable or increasing annual growth rates in Scots pine in our region, despite increasing drought exposure (Henttonen and others 2017; Babst and others 2019). Our dendrochronological finding of increasing growth trends in tree individuals is also in line with recent findings of stand-level productivity increases of Scots pine in the study area (Pretzsch and others 2023).

Growth Trends and the Role of Regional Climate

Long-term trends in basal area increment may provide valuable information on climate-driven

vitality declines (Jump and others 2006). One explanation of the continued rise in BAI of the studied pine trees is certainly the regular thinning of the stands, which has promoted the growth of the remaining trees in the stand. This also indicates that the climatic changes experienced especially since the 1980s have in total not reduced tree productivity so far. In fact, the growth conditions of pine must have markedly improved during the last century in northern Central Europe, as indicated by a height growth increase of 29% in Poland in the period 1900–2000 (Socha and others 2021). Our separate analysis for different age-cohorts also shows that growth has increased in recent decades across all ages, and younger trees have grown faster than previous cohorts right from the start. Similarly, even in several southern-marginal pine populations in Spain, growth rates have increased at least at the wetter sites in recent time (Martínez-Vilalta and others 2008). As suggested by Bose and others (2020), we also accounted for local habitat factors to explain differences in average tree growth rate across sites. However, stand structural variables do not explain the differences in average growth rates between sites across the precipitation gradient in our BAI model. This points at a common abiotic driver such as growth period extension, increased atmospheric [CO₂], or continued N deposition, which has stimulated growth despite the recent increase in climatic aridity (Begović and others 2023). Martínez-Vilalta and others (2008) suggested the increased atmospheric CO₂ concentration as a key driver, which might be canceled out by increasing drought exposure in the long run (Peñuelas and others 2011). In northern Germany, atmospheric nitrogen deposition is also most likely contributing to the growth increase in the past decades, as foliar N concentrations have markedly increased (Sardans and others 2016; Wellbrock and Bolte 2019; Prietzel and others 2020), suggesting decades of growth stimulation. In correspondence, our model shows that smaller topsoil C:N ratios (indicating faster soil N mineralization) enhance average radial growth at the different sites, even though the effect is weak compared to the strong influence of climatic factors in our BAI model.

Although the temperature differences are small across our study region (MAT varies from 9.0 to 9.6 °C), they appear to be large enough to have an impact on BAI. In fact, pine trees tended to be more productive at sites with a lower mean summer temperature. In the light of increasing summer temperatures, this finding may suggest that the potential of Scots pine to maintain its elevated growth rates and to adapt to further summer

warming and heat exposure may be limited. It is possible that summer heat is harming the Scots pine foliage directly (Way and Sage 2008; Gette and others 2020), as the maximum quantum yield of photosystem II (F_v/F_m) of Scots pine needles was found to decrease by 5% at 41.9 °C, and by 50% at 47.8 °C according to measurements in Bavaria, southern Germany (Kunert and others 2022). This points to greater heat sensitivity than in European beech and some other temperate broad-leaved tree species (Kunert and Hajek 2022). On the other hand, pine trees tended to grow on average somewhat better at the drier sites in our region (negative MSP-growth relation; Table 2), despite the more prominent drought signal in the tree-ring series at the drier sites, which caused greater growth reduction in the ring width index data in exceptionally dry years at these sites. This unexpected spatial pattern is also mirrored in the National Forest Inventory data from 2011, where the stand-level growth rates (in $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) tended to increase from the North Sea coast toward the drier eastern part of the study area (Figure A5). We can only speculate that the generally lower cloudiness and higher sunshine duration at the drier, more continental sites are causing this growth increase with decreasing precipitation. Unfortunately, the quality of sunshine duration data is too poor for accurate spatial comparisons, and the strong spatial autocorrelation with precipitation in our study area makes it impossible to separate radiation and precipitation effects in a modeling approach. Although our northeastern sites are relatively dry with $< 600 \text{ mm}$ MAP, they seem to remain in all years, except for extraordinary dry summers, still above the threshold pine can tolerate (Kölling 2007). In the 2018/2019 drought, however, which probably was the severest drought in Central Europe since 2000 years (Büntgen and others 2021), various pine stands in the eastern German state of Brandenburg and elsewhere suffered crown damage and dieback (Obladen and others 2021; MLUK-BB 2022; NW-FVA and MWTLF-SA 2022), and widespread infection of weakened pines by the fungal endophyte *Sphaeropsis sapinea* occurred (Rohde and others 2021). It is too early to draw conclusions on the resulting growth trends of the surviving pine trees in response to this millennial drought. Scots pine populations in Southern Europe and also in the Central Alps have been found to suffer from decreasing growth trends (Giuggiola and others 2010; Matías and Jump 2014). In these regions, widespread dieback in response to severe droughts has been recorded which was worst at micro-

habitats with highest mesoclimatic and edaphic drought exposure (Giuggiola and others 2010; Rigling and others 2013; Buras and others 2018; Etzold and others 2019; Archambeau and others 2020), confirming the species' sensitivity to severe water deficits.

Compared to the negative influence of hot summer droughts, late winter/early spring temperature was similarly important for explaining spatial differences in average growth rates according to the explained variance in our model. This factor exerts an even stronger impact on radial growth than summer temperature, as evidenced by the large slope coefficients in the model, suggesting that pine growth today still profits at many sites in principal from the recent climate warming (Harvey and others 2020; Stolz and others 2021). In accordance, the climate-driven growth models of Bauwe and others (2013, 2015) predict for north-east German Scots pine stands neither a strong increase nor a strong decrease in productivity with advancing climate warming, as the positive effects of an extended growing season might well be canceled out by the negative effects of increased drought exposure. However, we doubt that the stimulating effect of late-winter warming will in future be large and persistent enough to balance the negative impact of increasingly hot and dry summers on pine growth in northern Central Europe, given the higher growth sensitivity of the drier stands to summer precipitation and SPEI. Moreover, repeated exposure to extreme droughts could lead to additive negative drought effects on Scots pine growth (Bose and others 2020), which might drive the trees closer to their limits.

CONCLUSIONS

While foresters in Central Europe have valued Scots pine as an undemanding timber species, our growth records based on basal area increment evidence the species' sensitivity to hot and dry summers, especially in the more continental regions. Even though climate warming still has a positive effect on pine productivity in the region, the greater drought sensitivity of the drier stands of our sample, together with increased crown damage and pine mortality especially in the German states of Saxony-Anhalt and Brandenburg after the extreme 2018/19 drought, indicate that pine vitality likely will decrease in future at sites with a negative climatic water balance in summer and low soil water storage capacity. Although Scots pine is an economically important timber species in northern Germany and in Poland, the Netherlands and other

Central European countries, silvicultural decision making, which is driven by the high demand for conifer wood of local and international markets, should avoid large-scale pine plantations, as these bear a high risk of failure due to fire, pest attack and a predicted decline in tree vitality (Reich and Oleksyn 2008). Moreover, the evapotranspiration of pine stands is relatively high in comparison to the locally native beech forests (Müller and Bolte 2009), and pine stands are thus usually exacerbating site water deficits and soil drying (Leuschner and others 2022). Possible alternatives are more drought-resistant native broadleaf trees such as *Acer platanoides*, *Quercus petraea*, *Carpinus betulus* and *Tilia cordata* (Fuchs and others 2021), which however requires adapting wood markets to more hardwood supply. Our results demonstrate large temporal and also spatial variation in climate-growth relationships of the same species, which has to be considered in tree vitality and growth projections in a warming and drying climate.

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DATA AVAILABILITY

Data can be found at: <https://doi.org/10.25625/S7LTJP>.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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