

Article

Climate Signals for Growth Variations of *F. sylvatica*, *P. abies*, and *P. sylvestris* in Southeast Germany over the Past 50 Years

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Abstract: Since recent drought events have already caused severe damage to trees and droughts in the near future are expected to occur even more frequently, this study investigated the response of forest ecosystems to changing climate conditions in the topographically complex region of Bavaria, southeast Germany. For this purpose, climate–growth relationships of important European deciduous and coniferous tree species were investigated over the past 50 years at three middle mountain ranges and corresponding basins. A response analysis between tree-ring width and climate variables was applied to detect modifications in tree responses comparing two 25-year periods at individual forest sites. Furthermore, tree responses to climatic extreme years and seasons were analyzed using a superposed epoch analysis. The results showed that Scots pine (*Pinus sylvestris*) proved to be the most vulnerable and least drought-resistant of all investigated tree species. Likewise, Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) revealed a higher drought sensitivity over the past 25 years, even though an extended growing season partially improved tree growth at high-elevation sites. In conclusion, all studied tree species were affected by drought events, even at humid high-elevation sites. Correlations with daily climate variables confirmed that even short-term weather conditions could strongly influence trees' radial growth. Tree responses to climate conditions have shifted significantly between past and present periods but vary considerably among sites and are generally stronger in humid regions than in already dry areas.

Keywords: tree-ring widths; climate–growth relationships; forest dynamics; climate variability; extreme climatic events; Bavaria; Germany

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1. Introduction

According to climate models, temperatures and summer drought stress will increase in southern Germany within the 21st century [1], but climate change is already perceptible: summer months have already become hotter and drier [2]. The previous summer heat record of 2003 [3,4] was recently exceeded by the heat record of 2018. In addition, 2019 was also listed as an exceptionally hot summer [5].

As water availability is the primary growth-limiting factor for most European tree species [6], current reports on the state of forests in Central Europe are alarming [5]. Scientists and foresters detected a decreasing vitality of European tree species and a rising incidence of tree mortality [4,5]. Since forest ecosystems are complex and influenced by numerous factors besides climate, the combination of environmental factors leading to tree mortality is not yet fully understood [7,8]. In addition, climate sensitivity differs between tree species, and the level of resilience is species-specific [6,7,9,10]. For example, *Picea abies*, which has been preferred in forestry and frequently planted outside of its natural distribution range, appears to be most vulnerable to future warming and drier climate conditions [11–16].

However, despite such negative effects, under certain conditions, climate warming can also enhance forest productivity in Europe, especially in mountainous regions and at sites not limited by water availability [17]. At higher elevations, warmer temperatures can lead to improved growth conditions [18] and a prolonged growing season [14,17,19]. Besides elevation effects, mountain regions also cause windward lee effects, which strongly modify precipitation patterns depending on the position of topographic barriers towards the dominant wind direction during precipitation events. Hence, climate change accompanied by increasing drought events may not affect all forest ecosystems equally, especially in complex topography. Consequently, the response of forest growth to altering climate conditions must be studied at a local scale, taking the modifying influence of topography into account.

Therefore, this study explores the climate–growth response of economically important broadleaved and conifer tree species in the Free State of Bavaria in southeast Germany with regard to increasingly drier and warmer weather conditions over the past 50 years. The investigated forests are located in Bavarian middle mountain ranges and nearby topographic basins, involving three different bioclimatic zones (intermediate, subcontinental, boreal), which comprise the ecological range for forest ecosystems [20]. Although several studies have already examined the climate–growth relationships of European tree species in southern Germany [6,21–23], this approach is new, because several tree species are compared at study sites exhibiting both an elevation and a precipitation gradient.

We hypothesize that climate–growth relationships have changed within the past 50 years and that significant differences in tree response between forest sites may occur even over very short distances due to the influence of topography on the local climatic conditions. Hence, climate–growth relationships of both coniferous and deciduous tree species were analyzed using the climate parameters air temperature, precipitation, and the associated standardized precipitation evapotranspiration index (SPEI) [24] in monthly resolution [25]. In addition, we correlated daily precipitation sums and daily maximum air temperatures with tree-ring widths to detect even short-term impacts of climate on growth responses [25,26].

2. Materials and Methods

2.1. Study Area and Sample Collection

The studied forest sites are located in southeast Germany, in the Free State of Bavaria. Three low- and three high-elevation sites from the middle mountain ranges were chosen for the analysis (Figure 1). As deciduous tree species, European beech (*Fagus sylvatica*) was selected because it is present at both altitudinal levels, whereas the coniferous tree species Norway spruce (*Picea abies*) is dominant at high-elevation and Scots pine (*Pinus sylvestris*) at low-elevation sites. The forests at Bad Brückenau (Rhoen), Wunsiedel (Fichtel Mountains), and Grafenau (Bavarian Forest) represent the high-elevation sites and are all located in Bavarian middle mountain ranges. In the following, we use a combination of symbolic letters for high-elevation (H) and low-elevation (L) sites with their location in the west (W), center (C), or east (E) of the study region, respectively. From west to east, the high-elevation sites are abbreviated with HW for Bad Brückenau, HC for Wunsiedel, and HE for Grafenau, while the low-elevation sites located in basins in the rain shadow of the mountain ranges are called LW for Würzburg, LC for Tennenlohe, and LE for Burglengenfeld (Table 1).

Due to these diverse topographic and elevation features, different climate conditions prevail at each site. The mean annual precipitation sum at high-elevation sites is higher than those of low-elevation sites and ranges between 580 mm a^{−1} at LW (Würzburg) and 1,140 mm a^{−1} in the Fichtel Mountains (HC) [27]. Mean annual temperature is higher at low-elevation sites and ranges between 9.7 °C at LW (Würzburg) and 6.4 °C at HC (Wunsiedel) [27].

At each sampling location, at least 15 dominant and healthy trees were sampled with a 5.0 mm diameter increment borer (Mora, Sweden) at breast height. To avoid anomalies caused by eccentric growth, at least two cores were taken from each tree [28]. Tree-ring-widths were measured with a LINTAB 6 measuring system (Rinntech, Heidelberg, Germany) with a precision of 0.01 mm.

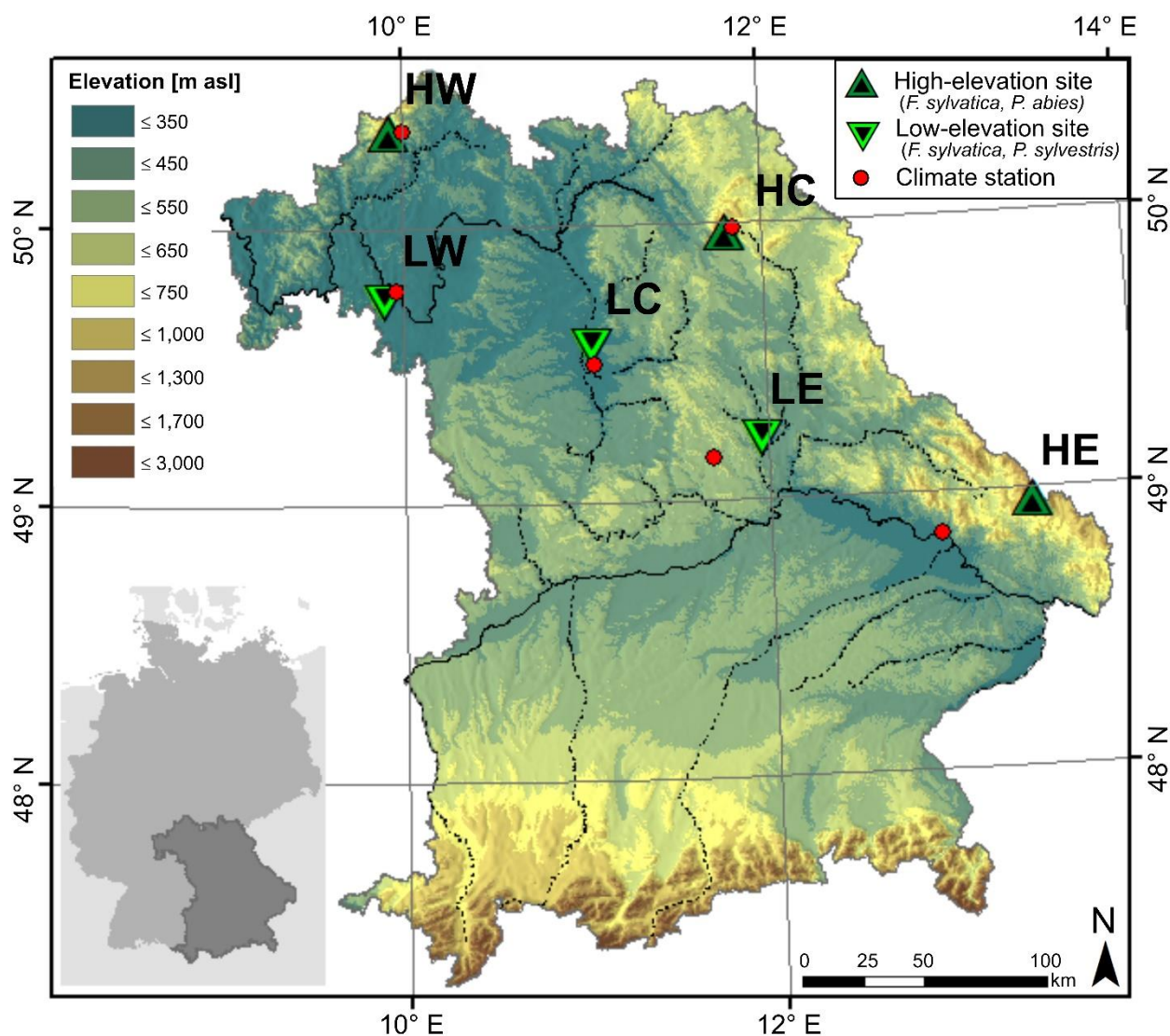


Figure 1. Location of the studied forests and climate stations at Bavaria, in southeast Germany. High-elevation sites from west to east: HW (Bad Brückenau), HC (Wunsiedel), and HE (Grafenau). Low-elevation sites from west to east: LW (Würzburg), LC (Tennenlohe), and LE (Burglengenfeld).

Table 1. Site characteristics: Geographic position (longitude degree °E, latitude degree °N, elevation m asl, location of climate station with mean annual precipitation sum (MAP) and mean annual temperature (MAT), geology, and predominant soils.

Site Name and Acronym	Species	lon[°E]	lat[°N]	Elev. [m asl]	Climate Station MAP/MAT	Geology	Soils
Bad Brückenau (HW)	<i>F. sylvatica</i> <i>P. abies</i>	9.93	50.35	810	10.0° E 50.35° N, 518 m 920 mm/8.1 °C	Basalt	Cambisols
Wunsiedel (HC)	<i>F. sylvatica</i> <i>P. abies</i>	11.80	49.97	795	11.84° E 49.98° N, 654 m 1140 mm/6.4 °C	Sandstone	Cambisols (podsolc)
Grafenau (HE)	<i>F. sylvatica</i> <i>P. abies</i>	13.43 13.53	48.96 48.91	975 990	12.92° E 48.85° N, 314 m 960 mm/8.4 °C	Granite	Cambisols Gleysols
Würzburg (LW)	<i>F. sylvatica</i> <i>P. sylvestris</i>	9.88	49.73	335	9.96° E 49.77° N, 268 m 580 mm/9.7 °C	Limestone	Cambi- sols/Luvisols
Tennenlohe (LC)	<i>F. sylvatica</i> <i>P. sylvestris</i>	11.03	49.55	300	11.05° E 49.5° N, 314 m 620 mm/9.3 °C	Sand	Cambi- sols/Podsols
Burglengenfeld (LE)	<i>F. sylvatica</i> <i>P. sylvestris</i>	11.95 12.07	49.21 49.20	415 395	11.69° E 49.15° N, 549 m 800 mm/8.0 °C	Limestone	Cambisols

2.2. Statistical Analysis

All tree-ring series were measured, visually cross-dated, and statistically evaluated by t-test and sign-test “Gleichläufigkeit” values using the software TSAP-Win (Rinntech, Heidelberg, Germany) [29,30]. The established ring-width site chronologies were cross-checked with tree-ring series obtained from the International Tree-Ring Data Bank (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>, accessed on 5 September 2019) [31].

After merging the individual cores of the same tree, the tree-ring series were detrended by applying a 25-year cubic smoothing spline within the package dplR [32] implemented in the open-source statistical language R [33]. In doing so, multidecadal and short-term variability related to climate variations were retained in the resulting tree-ring indices, whereas long-term biological growth trends were removed. Subsequently, a master chronology for each site was established by averaging the individual ring-width indices calculating a biweight robust mean [32]. Due to the availability of complete climate data and tree-ring chronologies, climate–growth analyses were performed with the final chronologies for the past 50 years (1970–2019). For that purpose, monthly as well as daily climate station data (precipitation sum, mean air temperature/maximum air temperature) for the common observation period were derived from the Climate Data Center (<https://cdc.dwd.de/portal/>, accessed on 3 November 2020) provided by the German Meteorological Service [27]. The Standardized Precipitation-Evapotranspiration Index (SPEI) was calculated for one, two, and three months based on monthly temperature and precipitation data of the individual climate stations within the R-package SPEI [24].

Using the R-package dendroTools [25], correlations between tree growth and climate variables were compared for one subperiod in the past (subperiod I: 1970–1994) and one recent subperiod (subperiod II: 1995–2019) based on daily and monthly climate data. The correlation between RWI and the drought index was calculated with a 2-month SPEI. All calculations were performed using Pearson’s correlation coefficients, significant at the confidence level of $p < 0.05$. In addition, the correlation coefficients were tested for robustness by applying a bootstrap procedure with 1000 replicates [34]. The resulting values illustrate the correlation coefficients of the first day of a time window (21 to 91 days). Therefore, each value represents an interval between three weeks and three months.

2.3. Pointer Year Analysis and Superposed Epoch Analysis

Abrupt growth variations were investigated by a pointer year analysis of each site’s tree-ring series using the R package pointRes [35]. In accordance with Schweingruber et al. [36], pointer years were defined as the five narrowest years relative to the average

growth of the four preceding years. To identify the climatic forcing underlying the growth declines, each pointer year was compared to local climate data. A Superposed Epoch Analysis (SEA) was carried out to assess tree response and resilience to pointer years [37]. The SEA was run with the package dplR [37] and shows the mean growth pattern prior to, during, and after a pointer year. To reveal the differences between local and larger-scale effects, SEA were calculated for exceptional known drought years in Europe (1976, 2003, and 2018), but also for local extreme years and seasons. Local extreme years were defined as the lowest decile in terms of precipitation sums at the respective climate stations.

3. Results

3.1. Climate–Growth Relationships

3.1.1. European Beech at High-Elevation Sites

Figures 2 and 3 illustrate the climate–growth relationships considering the months of the previous and current growth year based on daily maximum temperature and precipitation data. Comparing subperiods I and II, the response of beech growth to precipitation changed significantly at high elevations (Figure 2).

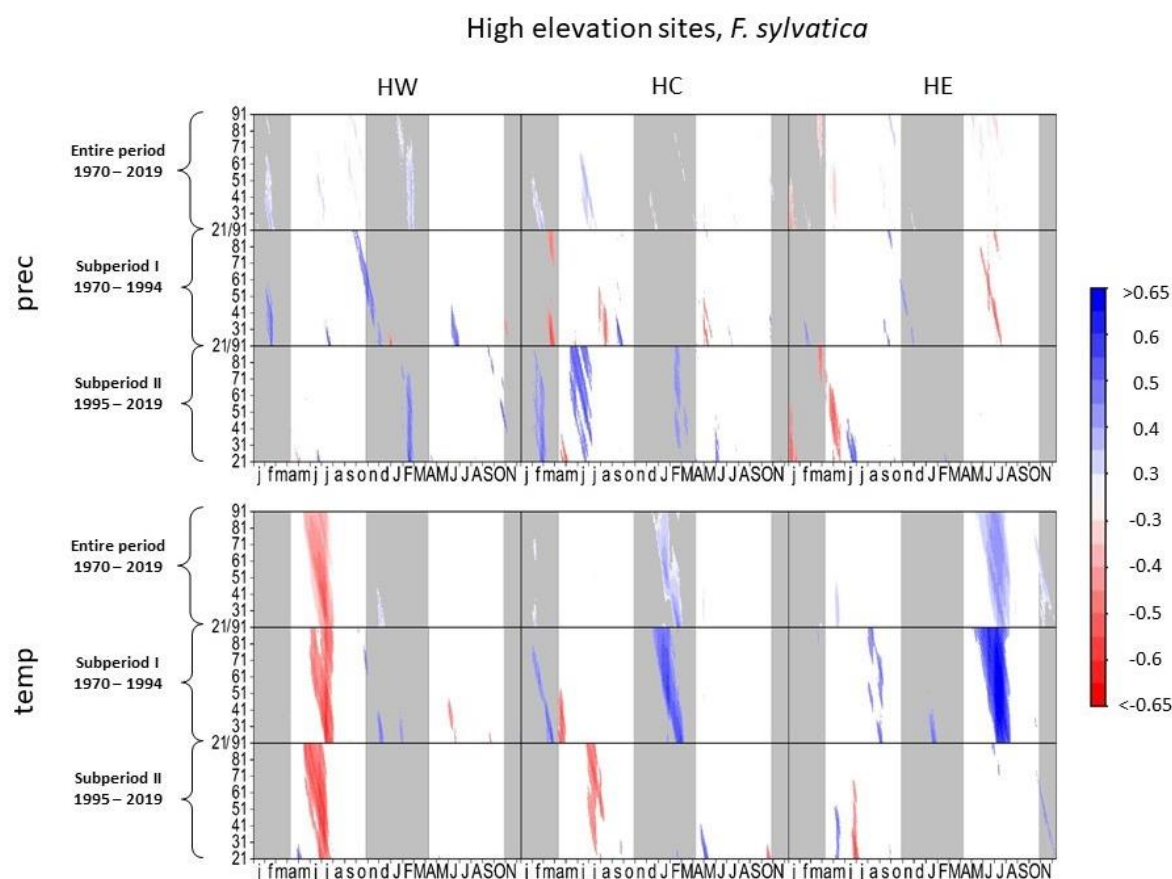


Figure 2. Correlations between daily precipitation/maximum daily temperature and tree-ring width of *Fagus sylvatica* at high-elevation sites. Each value illustrates the beginning of the considered window. Only significant correlation coefficients are shown ($p < 0.05$). Lower case letters in the abscissa axis represent month of previous growing season, and capital letters indicate the month of the current growing season until November. Grey shading indicates the biologically inactive phase. The ordinate axis displays the window lengths.

High precipitation in current and previous spring and summer was detrimental to tree growth at HE and HC in subperiod I, whereas the correlation patterns in spring and summer reversed in subperiod II. Higher precipitation in the current (HC) and previous year (HC and HE) enhanced tree growth. Growth variation of beech at HW responded

positively to summer precipitation in subperiod I, while this correlation pattern is rarely observed during subperiod II. Late summer temperatures of the previous year correlated negatively with beech growth at all high-elevation sites in subperiod II. Higher temperatures in the current summer at HE and in the current and previous spring at HC positively affected beech growth in subperiod I. In subperiod II, HC was the only site where a significant positive response to higher temperatures in the current year still occurred.

3.1.2. Norway Spruce at High-Elevation Sites

Summer precipitation had a negative effect on radial growth of spruce at HE in subperiod I, though the negative effect decreased in subperiod II (Figure 3). In contrast, tree growth was positively influenced by precipitation in previous September to October in subperiod II. At HW and HC, spruce showed low correlations between tree growth and precipitation in the current year in subperiod I. In subperiod II, however, tree growth at HW and HC correlated positively to summer and autumn precipitation.

High summer temperatures at HW and autumn temperatures at HC negatively influenced radial growth of spruce at these sites in subperiod II, whereas in subperiod I, spruce growth at HE correlated positively to higher temperatures between March and June, a complete signal loss towards temperature occurred in subperiod II.

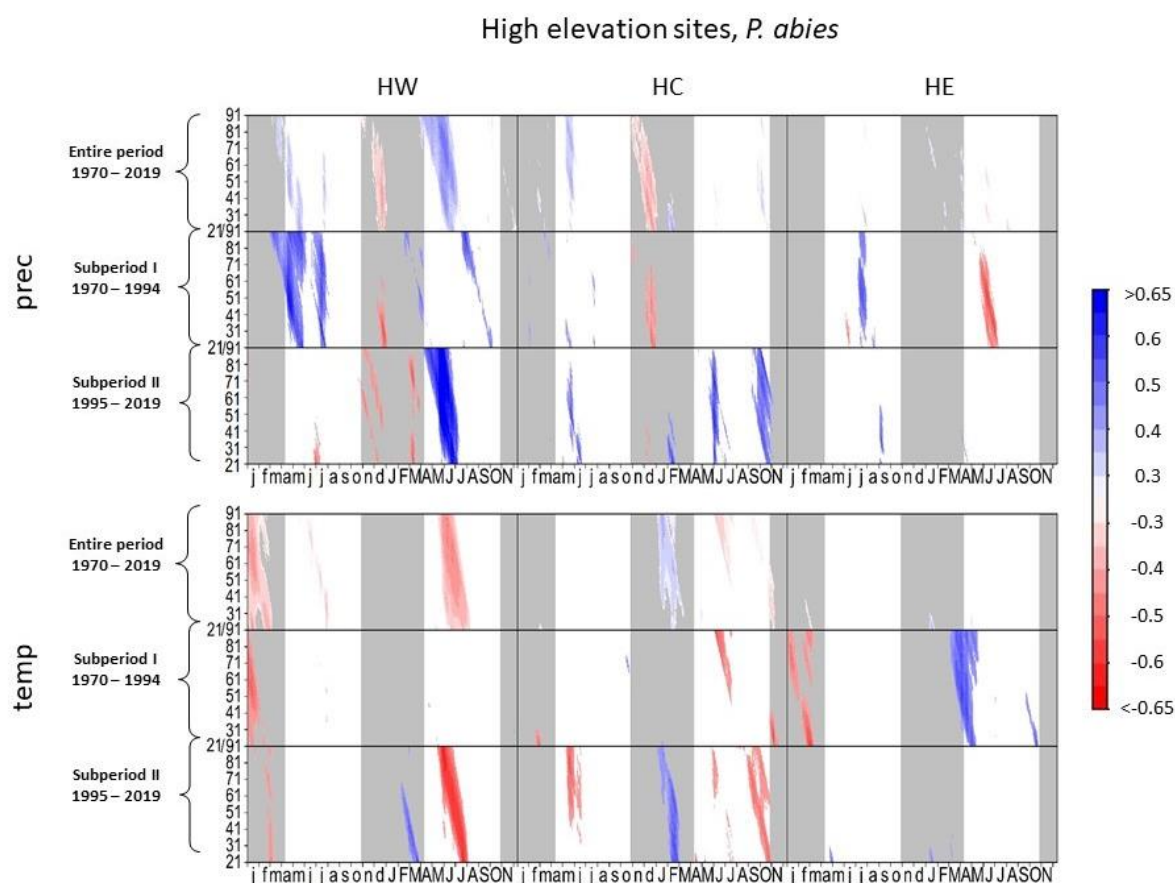


Figure 3. Correlations between daily precipitation/maximum daily temperature and tree-ring width of *Picea abies* at high-elevation sites. Each value illustrates the beginning of the considered window. Only significant correlation coefficients are shown ($p < 0.05$). Lower case letters in the abscissa axis represent month of previous growing season, and capital letters indicate the month of the current growing season until November. Grey shading indicates the biologically inactive phase. The ordinate axis displays the window lengths.

3.1.3. European Beech at Low-Elevation Sites

In the entire period, radial growth of European beech responded positively to precipitation in late spring and summer at LW and LC (Figure 4). At LC, the positive correlation between precipitation and tree growth increased during the complete growing season between subperiod I and subperiod II, with the highest correlation coefficients between mid-June and mid-July ($r = 0.75$, DOY 530, 32-day interval). At LW, the level of significance of climate-proxy relationships with precipitation in the current growing season increased during subperiod II. However, in subperiod II, the highest correlations occurred for previous autumn precipitation. Beech at LE showed positive correlations to spring and summer precipitation in subperiod I, while in subperiod II, no correlations to precipitation occurred in the current year.

Beech negatively correlated to spring and summer temperature at all low elevation sites in subperiod I (Figure 4). However, the negative impact of temperature on tree growth decreased in subperiod II, especially at LW and LE. At these two sites, beech correlated positively to higher temperatures in previous September and October.

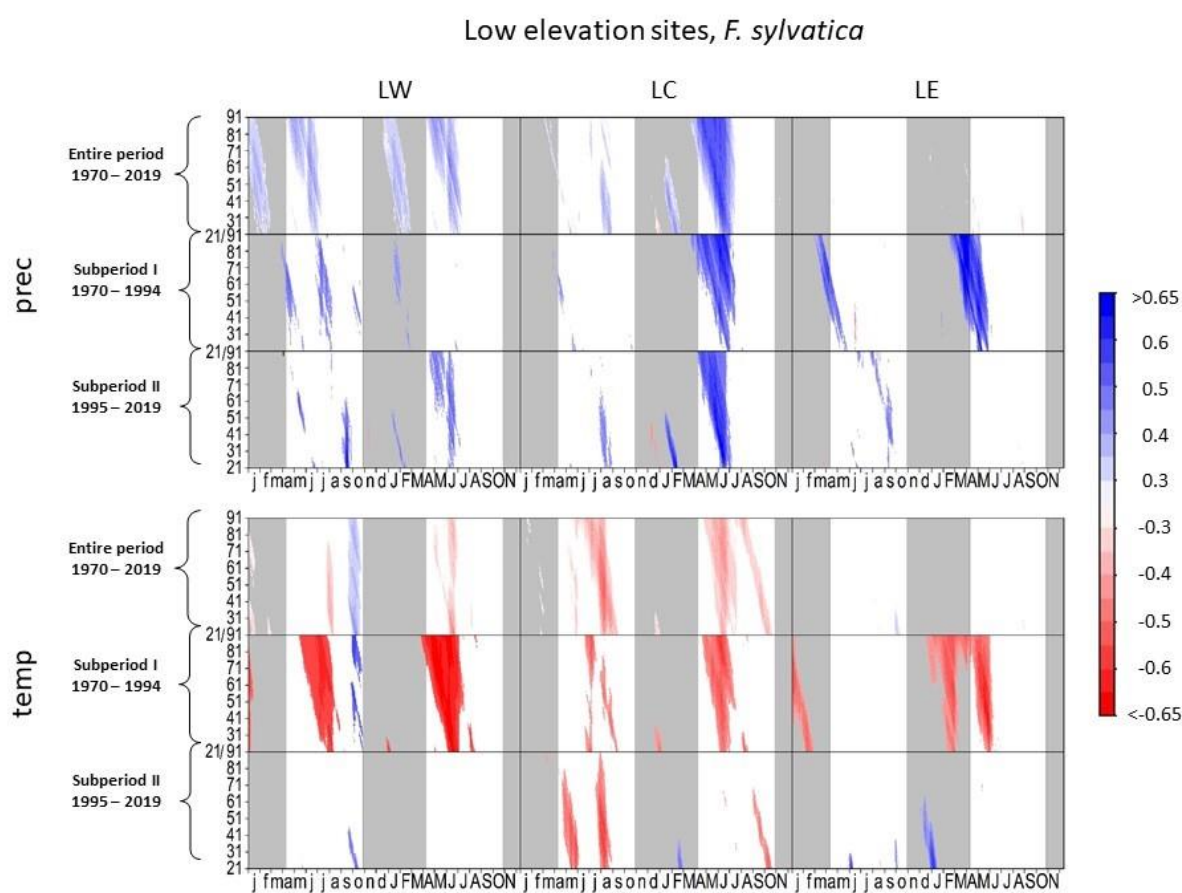


Figure 4. Correlations between daily precipitation/maximum daily temperature and tree-ring width of *Fagus sylvatica* at low-elevation sites. Each value illustrates the beginning of the considered window. Only significant correlation coefficients are shown ($p < 0.05$). Lower case letters in the abscissa axis represent month of previous growing season, and capital letters indicate the month of the current growing season until November. Grey shading indicates the biologically inactive phase. The ordinate axis displays the window lengths.

3.1.4. Scots Pine at Low-Elevation Sites

Increased precipitation in the current growing season is favorable for tree growth of Scots pine at all low-elevation sites over the entire investigated period, whereby the summer precipitation positively affected tree growth more strongly in subperiod II (Figure 5). In subperiod I, early spring precipitation and longer periods of precipitation correlated

best. In subperiod II, high correlation coefficients around 0.7 between tree growth of pine and daily precipitation occurred in June/July at all low-elevation sites (LW: $r = 0.69$, $p < 0.001$, DOY 553, 23-day interval; LC: $r = 0.79$, $p < 0.001$, DOY 521, 60-day interval; LE: $r = 0.69$, $p < 0.001$, DOY 557, 21-day interval). Correlation coefficients for monthly precipitation in subperiod II were around 0.5 or higher (LW: $r = 0.6$, $p < 0.01$, July; LC: $r = 0.66$, $p < 0.001$, July; LE: $r = 0.47$, $p < 0.05$, July).

At all low-elevation sites, radial growth of Scots pine was negatively affected by increased temperatures in the entire period. Particularly higher summer and autumn temperatures during the current growth period revealed the most negative impact on tree growth. Despite the predominant negative effects of high temperatures on tree growth at all sites, higher temperatures in February/March positively influenced tree growth in subperiod II at LW and LC.

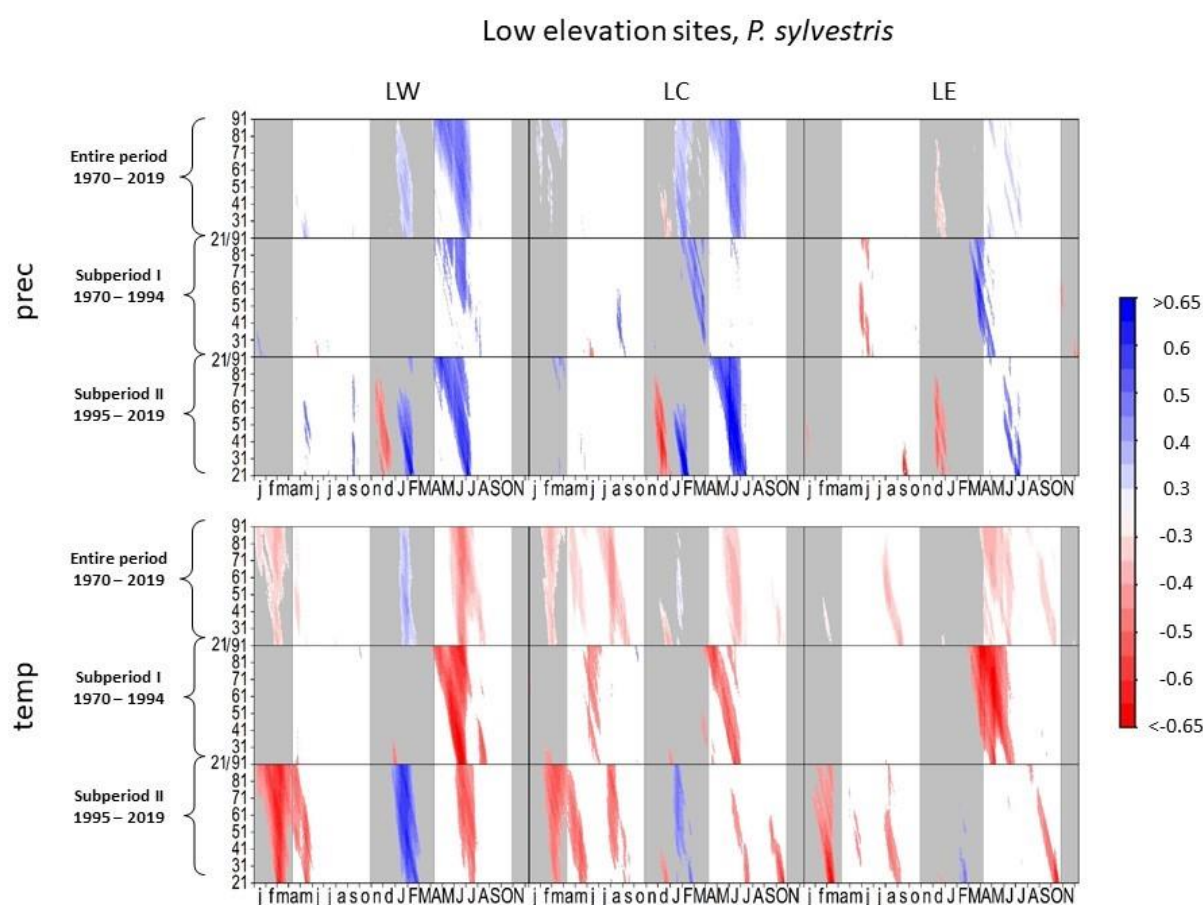


Figure 5. Correlations between daily precipitation/maximum daily temperature and tree-ring width of *Pinus sylvestris* at low-elevation sites. Each value illustrates the beginning of the considered window. Only significant correlation coefficients are shown ($p < 0.05$). Lower case letters in the abscissa axis represent month of previous growing season, capital letters indicate the month of the current growing season until November. Grey shading indicates the biologically inactive phase. The ordinate axis displays the window lengths.

3.2. Tree Responses to 2-Month SPEI

Correlations between a 2-month SPEI and tree growth changed at some study sites between the two investigated subperiods (Figure 6). Except for beech at HE, which correlated negatively to July/August SPEI in subperiod I, no significant correlations occurred in the growing season for beech at high-elevation sites in both subperiods.

In contrast, spruce at HW showed positive correlations to previous May/June-, and previous July/August, and August/September-SPEI in subperiod I. This correlation shifted to a highly significant correlation to current June/July-SPEI in subperiod II. Tree

growth of spruce at HC was not correlated to SPEI in subperiod I but showed significant correlations with June/July-SPEI in subperiod II. Spruce at HE correlated negatively to June/July-SPEI in subperiod I, but showed no significant correlations in subperiod II.

Beech at LW showed significant correlations to previous July/August-, August/September-, and current February/March-SPEI but no significant correlation in subperiod II. Conversely, beech at LC correlated to May/June-, June/July-, and July/August-SPEI in subperiod I. In the most recent 25 years, however, only previous August/September- and current June/July-SPEI induced tree responses. (Figure 6). Beech at LE responded especially to April/May- and May/June-SPEI in subperiod I, but no significant correlations occurred in subperiod II.

Pine at LW correlated significantly to May/June-, June/July-, and July/August-SPEI in subperiod I, whereas only June/July- and July/August-SPEI showed significant correlations in subperiod II. At LC, pine responded to previous February/March- and current-March/April -SPEI in subperiod I. In subperiod II, the correlation shifted to previous February/March, March/April, and April/May and current June/July- and July/August-SPEI. Tree growth of pine at LE was positively correlated to April/May- and May/June-SPEI in subperiod I, whereas no significant correlation remained for pine at LE in subperiod II.

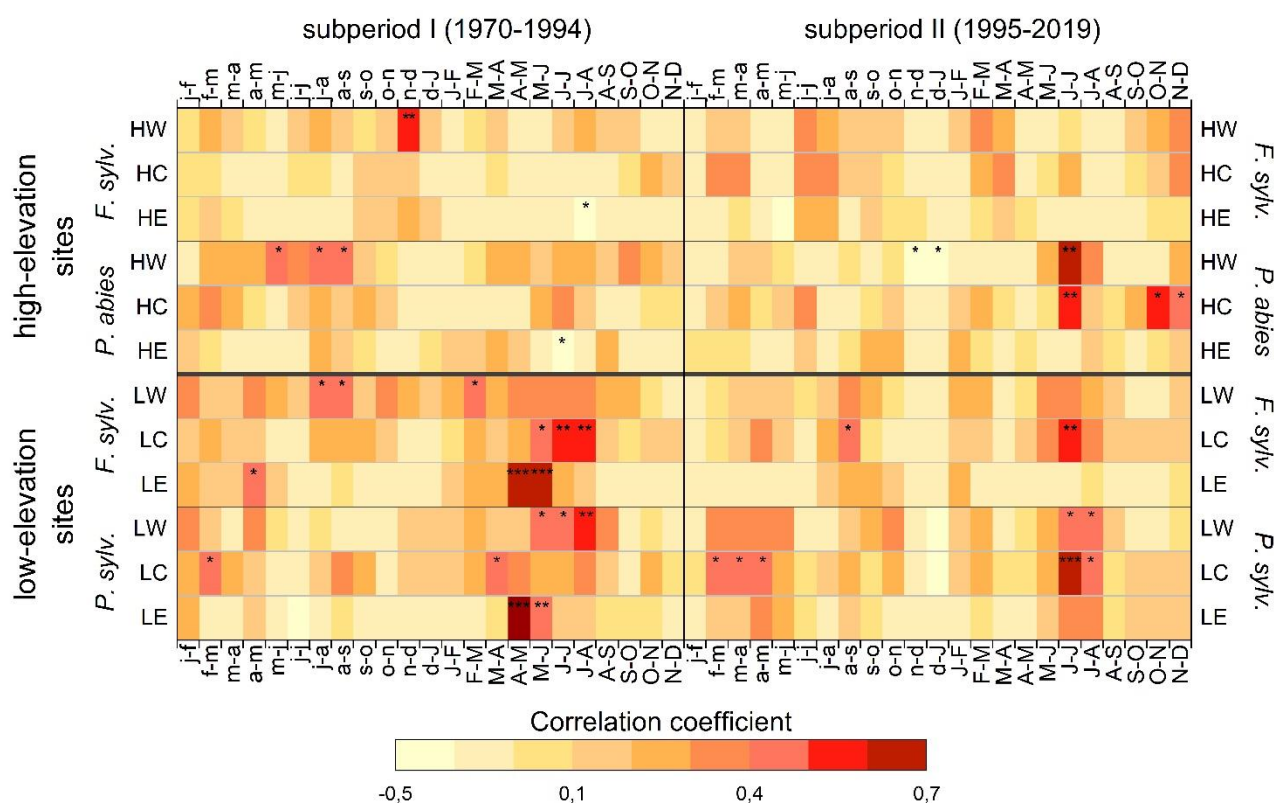


Figure 6. Pearson's correlation coefficients between a 2-month SPEI (Standardized Potential Evapotranspiration Index) and RWI calculated for both 25-year subperiods. High-elevation sites are HW, HC, and HE. Low-elevation sites are LW, LC, and LE. Months of the year preceding tree growth are shown in lower case letters. Level of significance for the correlations are indicated at $p < 0.05$, < 0.01 and < 0.001 as *, **, and ***, respectively.

3.3. Pointer Year Analysis and Superposed Epoch Analysis (SEA)

Table 2. Pointer years and the affected study sites, as well as probable climate-induced reasons. Ordered by frequency of occurrence in the chronologies.

Year	Study Site	Species	Reason
1976	HW	<i>F. sylvatica</i> / <i>P. abies</i>	Drought year+ Year after a dry year
	HC	<i>P. abies</i>	
	LW	<i>F. sylvatica</i> / <i>P. sylvestris</i>	
	LC	<i>F. sylvatica</i> / <i>P. sylvestris</i>	
	LE	<i>F. sylvatica</i> / <i>P. sylvestris</i>	
2011	HW	<i>F. sylvatica</i>	Late frost event in spring
	HC	<i>F. sylvatica</i> / <i>P. abies</i>	
	HE	<i>F. sylvatica</i> / <i>P. abies</i>	
	LW	<i>F. sylvatica</i>	
2018	HW	<i>P. abies</i>	Drought year
	HC	<i>P. abies</i>	
	LC	<i>F. sylvatica</i> / <i>P. sylvestris</i>	
	LE	<i>P. sylvestris</i>	
2019	HW	<i>P. abies</i>	Year after a drought year+ drought year/dry summer
	HC	<i>P. abies</i>	
	HE	<i>P. abies</i>	
	LW	<i>P. sylvestris</i>	
	LC	<i>P. sylvestris</i>	
2003	LW	<i>F. sylvatica</i> / <i>P. sylvestris</i>	Drought year
	LC	<i>F. sylvatica</i>	
1998	LC	<i>F. sylvatica</i> / <i>P. sylvestris</i>	Year after a dry year + dry spring/summer
	LW	<i>F. sylvatica</i>	
1991	HW	<i>P. abies</i>	Drought year
	HE	<i>P. abies</i>	
2012	LW	<i>P. sylvestris</i>	Dry spring/summer
	LE	<i>P. sylvestris</i>	
2009	LW	<i>F. sylvatica</i>	Dry summer/autumn
	LE	<i>F. sylvatica</i>	
2000	HC	<i>F. sylvatica</i>	Dry and warm spring
	LE	<i>F. sylvatica</i>	
2013	LC	<i>P. sylvestris</i>	Dry spring+ Year after a dry year
	LE	<i>P. sylvestris</i>	
2004	HW	<i>F. sylvatica</i>	Year after a drought year
	HC	<i>F. sylvatica</i>	
2010	HW	<i>F. sylvatica</i>	Year after a warm summer/autumn
	LE	<i>F. sylvatica</i>	
1987	HC	<i>F. sylvatica</i>	Wet and cold summer
	HE	<i>F. sylvatica</i>	
1996	HE	<i>F. sylvatica</i> / <i>P. abies</i>	Cold summer

The SEA linking to pointer years (presented in Supplementary Figure S1) indicated significant growth declines for these years at all sites, whereas beech at LC also showed a significant growth decline after the year with the marked growth decline. The SEA for assessing tree response to the climatic extreme years 1976, 2003, and 2018 (Figure 7) at low-elevation sites showed similar results. However, no significant response occurred at LE for beech, whereas growth of beech and pine declined in the following year at LC as well. At high-elevation sites, the drought years did not significantly affect spruce growth at HE or beech growth at HC and HE. Spruce at HW and HC responded to the drought

years with a growth decline in the same year, whereas beech at HW responded in the following year (Figure 7).

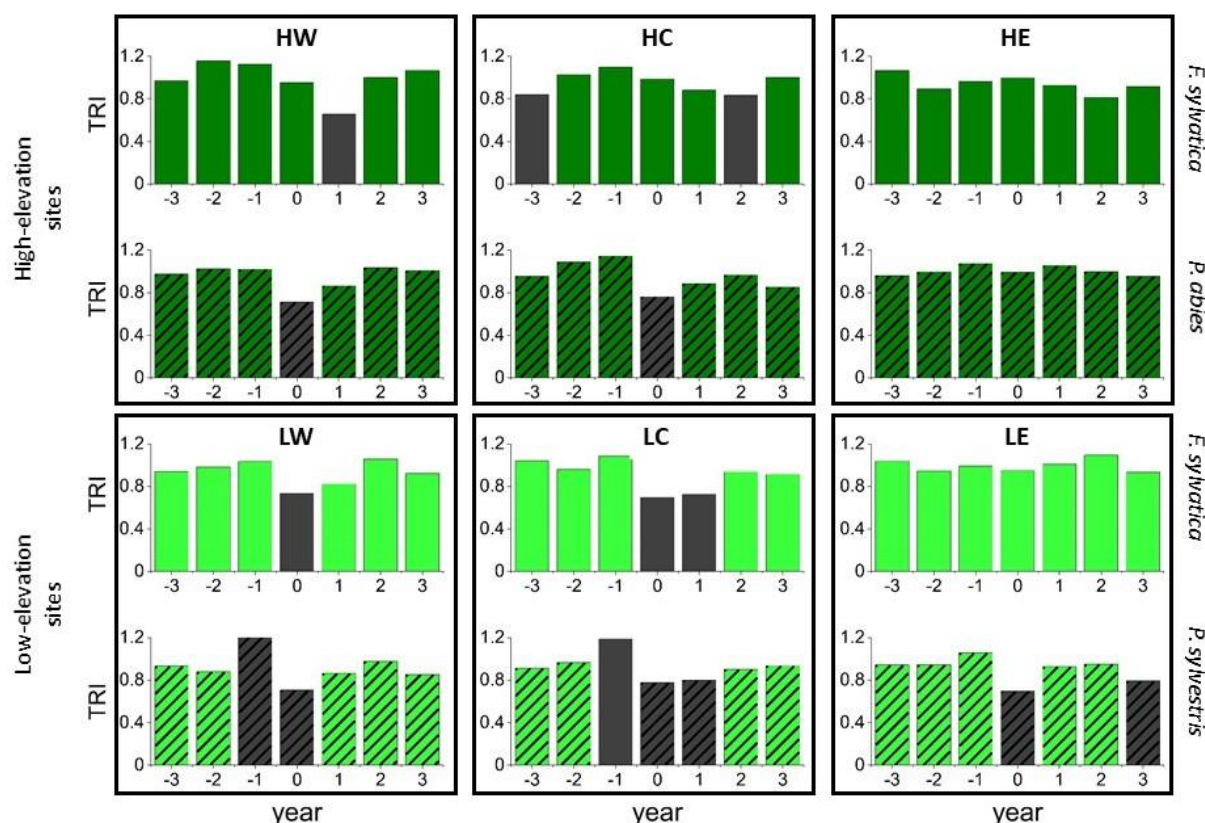


Figure 7. Superposed epoch analysis showing the impact of the extreme drought years 1976, 2003, and 2018 on the tree-ring index (TRI). Dark green bars illustrate high-elevation sites (HW, HC, HE); light green bars show low-elevation sites (LW, LC, LE). Hatching indicates conifers, grey bars indicate significant values with $p < 0.05$.

Superposed Epoch Analyses using local weather extremes revealed that a dry growing season and even a dry spring or summer negatively affected most species at low-elevation sites, except for beech at LE (results not shown). Dry growing seasons also negatively affected beech growth in the following year at LW and LC and pine growth at LC. Dry summer seasons did not significantly affect beech at LW. However, dry autumn months resulted in a growth decline the following year for beech at LW and pine at LW and LC. At high-elevation sites, spruce at HW responded negatively to a dry growing season, as did beech at HW in the following year. Spruce at HC showed decreased growth in a year with a dry season and also in the following year. Beech at HE benefited from a dry growing season and showed positive tree growth for these years. Otherwise, only dry summer months negatively influenced the tree growth of spruce at HW and HC.

4. Discussion

4.1. Climate–Growth Relationships

4.1.1. European Beech and Norway Spruce at High-Elevation Sites

Since high summer precipitation sums imply high cloudiness and reduced insolation and accordingly low photosynthesis rates [38–42], precipitation during the growing season was negatively correlated with tree growth at the two high elevation sites within the boreal bioclimatic zone (HC and HE) (Figures 2 and 3) [20]. Yet, increased mean temperatures in subperiod II (Figure 8) [27] caused a shift in environmental conditions at humid

mountainous sites as well (Figure 9a). Trees first benefited from higher temperatures and additional insolation due to a prolonged growing season [14,17,18]. In subperiod II, however, this pattern reversed: beech and spruce showed positive correlations to summer precipitation and negative correlations to summer temperature (Figures 2 and 3), which indicates an increased sensitivity towards drier conditions [43]. Correlations between SPEI and tree growth (Figure 6) revealed a higher susceptibility to summer drought in subperiod II for spruce at HW and HC, confirming its drought intolerance [15,44]. Scharnweber et al. [45] observed similar effects and identified stronger growth responses to drought at sites with higher water availability compared to drier sites.

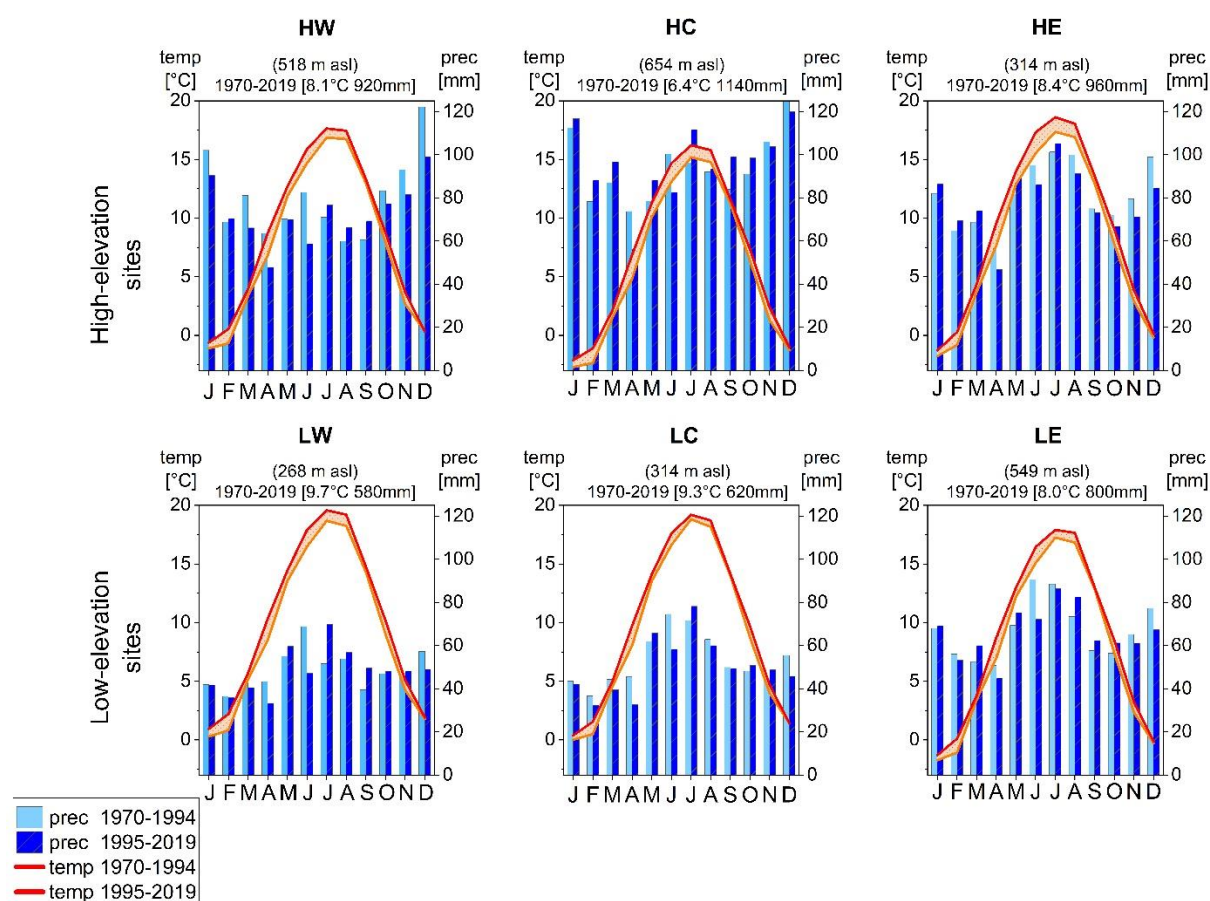


Figure 8. Climate diagrams of the climate stations close to each research site showing mean monthly temperature and mean total monthly precipitation for subperiod I and subperiod II.

Since the soil type for spruce at HE is classified as Gleysols (Table 1), the risk of reduced soil water availability is minimal, as reflected by a lack of significant correlations with precipitation and temperature (Figure 3). However, since the climate station for the HE site is located at a lower altitude (elevation difference of 600 m), small deviations in climate–growth relationships may also be due to differences in precipitation totals and temperatures at HE. Nevertheless, shifts in tree responses between subperiod I and subperiod II can be a first indication that even at forest sites with moist conditions, increasing temperatures and reduced summer precipitation may lead to a growth decline in the near future. In summary, this study reveals that even at moist high-elevation sites seen as limited by temperature and radiation [46], water availability in the summer months gains an increasing influence on tree growth, especially for spruce (Figure 9a).

4.1.2. European Beech and Scots Pine at Low-Elevation Sites

Water availability is considered the primary growth-limiting factor for trees [6]; consequently, for beech, the highest correlation coefficients with precipitation for the entire investigated period were observed during late spring and summer (Figure 4). These distinct relationships confirm previous findings that beech radial growth depends on soil water content in early summer [38,41,47,48] and that June is the most important month for tree-ring formation [21]. However, in recent years, the mean total precipitation in June has decreased at all sites from subperiod I to subperiod II (Figure 8). In consequence, growth is more sensitive to summer precipitation, especially at low-elevation sites (Figures 4 and 9b).

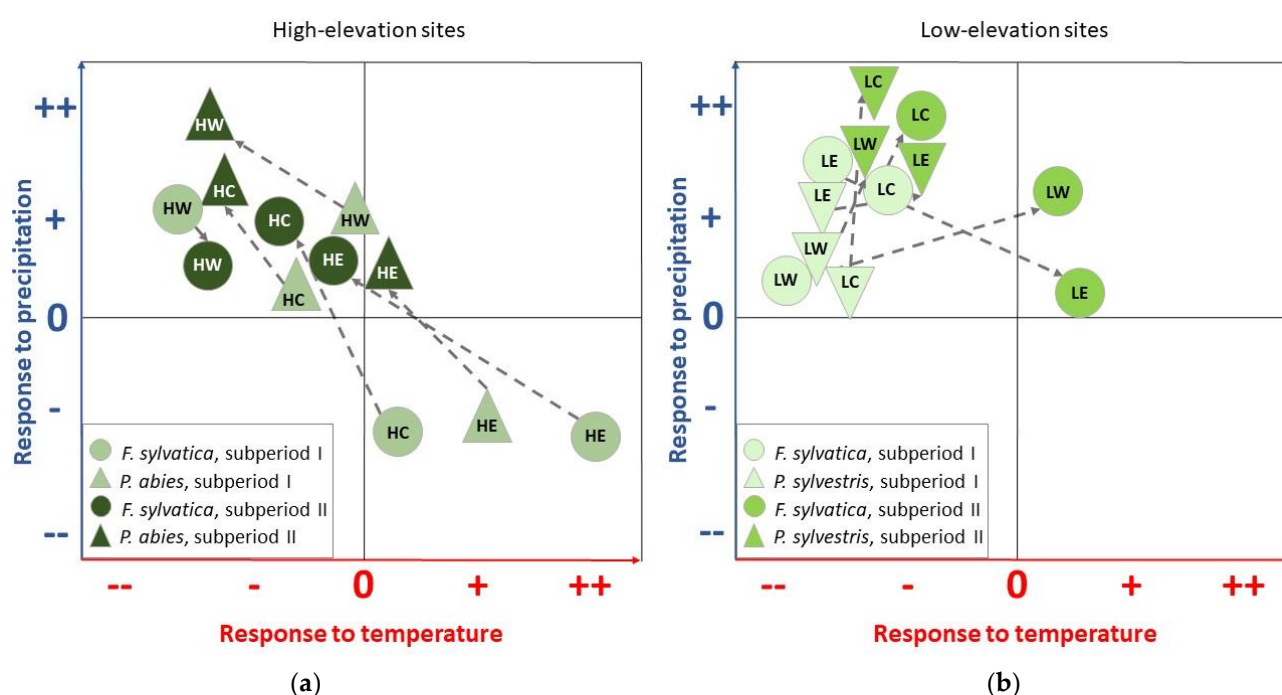


Figure 9. Schematic illustration of the shift in climate–growth relationships between subperiod I (1970–1994) and subperiod II (1995–2019), with respect to precipitation and temperature. (a) Changes for *F. sylvatica* and *P. abies* at the high-elevation sites HW, HC, and HE. (b) Changes for *F. sylvatica* and *P. sylvestris* at the low-elevation sites LW, LC, and LE.

In the subcontinental zone, beech growth at LC revealed the strongest sensitivity to June/July precipitation. Since the region around LC in particular has become drier since 1995 [27], mean growing season and summer precipitation dropped below the threshold for vital beech growth in subperiod II (mean growing season precipitation (MGSP): <350 mm, summer precipitation (JJA): <250 mm). [21]. Strong and significantly negative correlations to the SPEI reveal a severe drought stress for beech (Figure 6). Nevertheless, vital growth below the precipitation threshold is possible, as revealed by beech at LW, where growth conditions with summer precipitation and MGSP below the threshold prevailed since at least 1970 [27]. Other studies also suggest that forest ecosystems thriving in dry conditions are less drought-sensitive than those in more humid conditions [45,49,50]. Although beech is more vulnerable and drought-sensitive compared to other broadleaf species [51,52], beech vitality is not solely controlled by summer precipitation, as visible in subperiod II at LE. Here, a significant correlation between beech growth and spring and summer precipitation completely disappeared in subperiod II (Figure 4). Increasing summer precipitation in subperiod II at LE decreased water stress during the summer months at this site. The negative effect of high summer temperatures decreased in subperiod II, and beech radial growth even increased due to increasing temperatures in previous September and October and/or February (Figures 4 and 9b). Sykes and Prentice [53] assumed

a threshold of $>5^{\circ}\text{C}$ for tree growth. Accordingly, temperatures above 5°C in autumn and early spring result in an extended growing season and hence may increase radial growth. Higher temperatures in February trigger cambial reactivation and consequently result in an earlier start of wood production in spring [6,23].

For Scots pine, higher correlation coefficients with summer precipitation in subperiod II and strong negative correlations to summer temperature signify an increasing influence of drought periods on growth (Figures 5 and 9b). Although radial growth is assumed to occur mainly in spring [54], the strong correlations between the 2-month SPEI (Figure 6) and pine growth in the summer months in subperiod II (LC: $r = 0.67$, $p < 0.001$, June/July) confirm that the negative effects of high temperatures and low precipitation sums in summer amplified at LC [55–58].

In general, these results support observations of low drought resistance of Scots pine [59]. Furthermore, as soil textures at LC are sandy and feature a low water-storing capacity. These edaphic conditions result in pine being most susceptible to dry periods at this study site (Figures 6 and 9b) [60].

4.2. Pointer Year Analysis and Superposed Epoch Analysis

Most negative pointer years defined by tree-ring width were equivalent to years with long-time drought periods in spring, summer, and/or previous autumn in combination with high temperatures, such as in 1976, 2003, 2018, and 2019. The late frost event in spring 2011 [61,62] also resulted in a depletion in tree growth at several sites (Table 2). Other years with significant reduced growth can be explained by local weather phenomena, such as dry periods in the current and in the previous year. Drought years were defined as years with an annual precipitation sum within the first quartile of the mean annual precipitation sum between 1970 and 2019. Dry years and dry seasons (spring (MAM)/summer (JJA)/autumn (SON)) signify a respective precipitation sum within the 33rd percentile, whereas warm seasons indicate temperatures above the third quartile (Table 2). In some cases, pointer years at high elevation sites occurred in association with long periods of precipitation (annual precipitation sum above the third quartile) and/or low temperatures (mean annual temperature in the first quartile) (e.g., for beech in 1987 at HC/HE, for beech and spruce in 1996 at HE) [58]. For some pointer years, no obvious climate-related reasons were found (e.g., for beech in 1995 at HE and in 1970 at HW). Here, the growth decline might be caused by non-weather-related factors (beetle attacks, storms, masting, or human activity) [21,63,64].

The SEA showed that for both tree-ring-based pointer years and climatic event years, tree growth of beech and pine at LC was most vulnerable, followed by beech and pine at LW and beech and spruce at HW. The State of the Forests report of the Bavarian State Ministry of Food, Agriculture and Forestry [5] also observed high vital disturbances for Scots pine, such as mistletoe-induced crown-degradation, as well as needle loss of up to almost 32% in 2019 close to LC [5]. Beech at LW and LC showed a significant growth decline after hot and dry growing seasons in the current as well as in the subsequent year, confirming previous findings of drought reaction of beech in this part of Bavaria [65]. The declining influence of spring and summer precipitation on beech growth at LE may be explained by a generally more humid climate, in comparison to LW and LC. On the contrary, higher temperatures could have caused more favorable growing conditions during the beginning and the end of the vegetation season.

Considering the dryer and hotter summers occurring in recent years [27], most trees showed narrower rings. Such long-time growth depressions may bias the pointer year analysis, so that specific pointer years do not stand out any longer as individual extreme events [66].

5. Conclusions

Comparing the results of the climate–growth relationships and the SEA, all studied species responded specifically to changing climate conditions at all observed study sites. However, all results revealed increasing susceptibility and sensitivity of trees to droughts, even in the more humid regions.

Outcomes suggest that *P. sylvestris* is the most vulnerable, least drought-resistant, and least resilient of the three studied species. Even though *P. abies* first benefited from higher temperatures at low mountain ranges, it also became more dependent on summer precipitation in subperiod II (1994–2019). Therefore, the initially positive effect of higher temperatures at high elevation sites possibly shifted to a negative impact due to an increasing risk of drought stress. Although *F. sylvatica* responded differently at each study site, two general tendencies can be identified. First, beech became in general more drought-sensitive over time, but the exact timing of drought periods within the course of the year is site-specific. For instance, beech at LC was most vulnerable to summer droughts, even to short dry phases. Conversely, beech at LW rather responded to long-lasting dry periods, as well as to dry spells in spring and the previous autumn. Second, an extended growing season due to warmer temperatures in spring and autumn resulted in increasing wood production at both low- and high-elevation sites.

Overall, increasing frequencies of dry periods will pose a serious threat to all analyzed tree species. A loss of vitality due to higher temperatures and an increased frequency of dry periods already proceeds. However, the differences in growth–climate responses between the past and the recent subperiod indicate that changing climate dynamics also crucially alter the response of tree radial growth. Therefore, climate variables at a daily resolution are very useful to identify amplification or damping of growth correlations, since even short intervals of specific weather conditions can heavily affect radial tree growth. In addition, climate scenarios at local scales are essential to provide better estimates of how drought frequency and intensity and daily maximum temperatures will evolve in the future. Topographically diverse regions such as Bavaria show that weather phenomena over Europe can result in locally differing weather conditions, which accordingly imply different tree responses.

Our regional example from Bavaria in southeast Germany demonstrates that it is thus imperative to improve our knowledge of local climate patterns and to compare climate–growth relationships with future expected climatic conditions at each site to reliably simulate the future development of forest ecosystems in European forest areas in complex topographic regions.

Supplementary Materials: The following are available online at www.mdpi.com/article/10.3390/f12111433/s1, Figure S1: Superposed Epoch Analyses showing the impact of pointer years.

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