



Case Report

The Future of European Beech in Northern Germany—Climate Change Vulnerability and Adaptation Potential

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Abstract: Earth's forests are increasingly exposed to climate risks through climate change-related drought and heat waves. Here, we review the climate vulnerability of European beech (*Fagus sylvatica*), the most abundant tree species of Central Europe's temperate forests, and its adaptation potential to a hotter and drier climate in northern Germany, close to the center of the species' distribution range. About two-thirds of the studied beech forests show persistent negative growth trends of their dominant trees since the onset of rapid warming in the early 1980s, driven primarily by long-term deterioration of the climatic water balance (CWB) in summer and, locally, long-term decrease in June precipitation. Lower water storage capacity of the soil increases the climate sensitivity of growth. Even though beech populations of drier sub-regions reveal some acclimation to drought (reduced stomatal conductance, turgor loss point reduction, higher C allocation to roots), they are more climate-vulnerable than populations at moister sites, visible in larger growth decreases and greater CWB sensitivity of growth. Even though beech mortality is still lower in the study region than in other parts of Central Europe, our results identify beech forest regions with <350 mm growing-season precipitation as vulnerable to recent climate conditions, which refers to half of the study region. With further climate warming and aridification, most of northern Germany likely will become unfavorable for beech growth within the next tree generation, which suggests choosing in many production forests alternative, more drought- and heat-resistant timber species.

Keywords: dendrochronology; drought adaptation; *Fagus sylvatica*; fine root system; growth trend; leaf water relations; mortality; northern Germany; sandy soils



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1. Introduction

Climate change and associated heat waves have a strong and sometimes irreversible impact on forest ecosystems. Droughts, combined with high temperatures and a rising atmospheric evaporative demand, are thought to be main causes of widespread increases in tree mortality globally [1,2] and in Europe [3,4]. Drought- and heat-induced mortality is often enhanced by pest and pathogen infestation, facilitated by trees' failure to defend against biotic attacks [5,6]. European beech (*Fagus sylvatica* L.), the most abundant tree species of Central Europe's temperate forests and an important timber species in several countries, has long been known to be fairly drought sensitive [7–9]. Yet, beech mortality rates have generally remained on a low level in Central Europe until recently [10]. In the European forest health monitoring network ICP Forests, beech reached a low average mortality of 0.3% yr^{−1}, which increased to 0.6% yr^{−1} only after the severe 2003 summer drought [11]; see also [12]. However, in the aftermath of the severe 2018–2020 heat wave and drought, beech showed foliage reduction and crown dieback in various forest regions of Central Europe, and mortality rose to >5% yr^{−1} in some regions [13–16], especially on shallow soils. Forest scientists and foresters alike are alarmed about the future of beech in the core of

the species' distribution range in the face of a rapidly warming and drying climate. For reducing the risk of failure of forestry in a changing climate, silvicultural decision making has to be based on the profound understanding of the species' drought and heat stress resistance and related hydrological and thermal limits. This must include information on the species' capacity to acclimate and adapt to climate change-induced stress.

Here, we develop a perspective of the future of beech in the face of climate change in the North German Lowlands, a large area (c. 140,000 km²) between the Dutch and Polish borders, by summarizing recent work on key water status-related traits (xylem embolism resistance, turgor loss point, foliar $\delta^{13}\text{C}$), long-term radial growth patterns, and fine root system structure and root dynamics of mature beech trees. The objective is to characterize (i) the vitality and growth performance of European beech in this region not far from the center of its range and (ii) to explore the species' adaptive potential to recent climate warming and aridification. By studying beech performance across a pronounced precipitation gradient (ca. 850 to <500 mm yr⁻¹ mean annual precipitation (MAP)), we sought to assess the adaptive potential of beech to water limitation by comparing populations with ample and limited water supply. The research addressed mature trees in a fairly large number of monospecific beech stands on sandy to sandy-loamy Pleistocene deposits, employing physiological, dendroecological, and fine root studies in order to achieve a comprehensive picture of recent tree vitality and growth responses to climate aridification. In order to support foresters in silvicultural decision-making, we searched for precipitation thresholds that may represent tipping points of beech vitality, with the aim to identify in the study region zones of beech vulnerability to current and future climatic conditions. Giving recommendations for silvicultural strategies is beyond the scope of this review.

2. Methods

This paper draws from published evidence and unpublished data in the fields of dendrochronology, plant hydraulics and tree water relations research, and root research on the drought and heat resistance of beech in northern Germany to develop a multi-disciplinary perspective of the species' anticipated vitality in the face of advancing climate warming and aridification. In the following, key methods used in the principal studies are briefly outlined. More methodological details and applied statistical methods are given in the cited publications and in Supplement S3.

2.1. Study Region

The study region comprises the entire North German Lowlands on Pleistocene deposits between the Dutch border in the west and the Polish border in the east, north of the lower mountain ranges of Central Germany. The climate of the study region is cool-temperate (mean annual temperature 8.5–9.7 °C; Table S1) with a shift in climate continentality from the oceanic, precipitation-rich north-west to the sub-continental, drier south-east. Thirty monospecific beech forests of mature age (typically 80–120 years, full range: 70–155 years) and about 28–32 m in height (range 24.9–36.8 m) with closed canopy and without ground-water influence were selected for study (for details see [17]). Another 10 beech stands were investigated in the study of Diers et al. 2022 [18]. Mean annual precipitation (MAP) decreases across the sampled beech forests from 848 mm yr⁻¹ to 498 mm yr⁻¹ (Table S1 and Figure 1). Soils are deep sandy to sandy-loamy (sand content 50%–90%) dystric (to eutric) Cambisols and Luvisols of low to medium base saturation and fertility.

2.2. Tree Sampling and Dendrochronological Analyses

Fifteen (co-)dominant trees of the upper canopy layer were selected in each stand in 2018 and 2019 for dendrochronological study, and stem wood cores were extracted. In a subsample of 10 trees, tree climbing was employed to collect leaf and branch samples from the uppermost sun canopy for ecophysiological and xylem anatomical investigations.

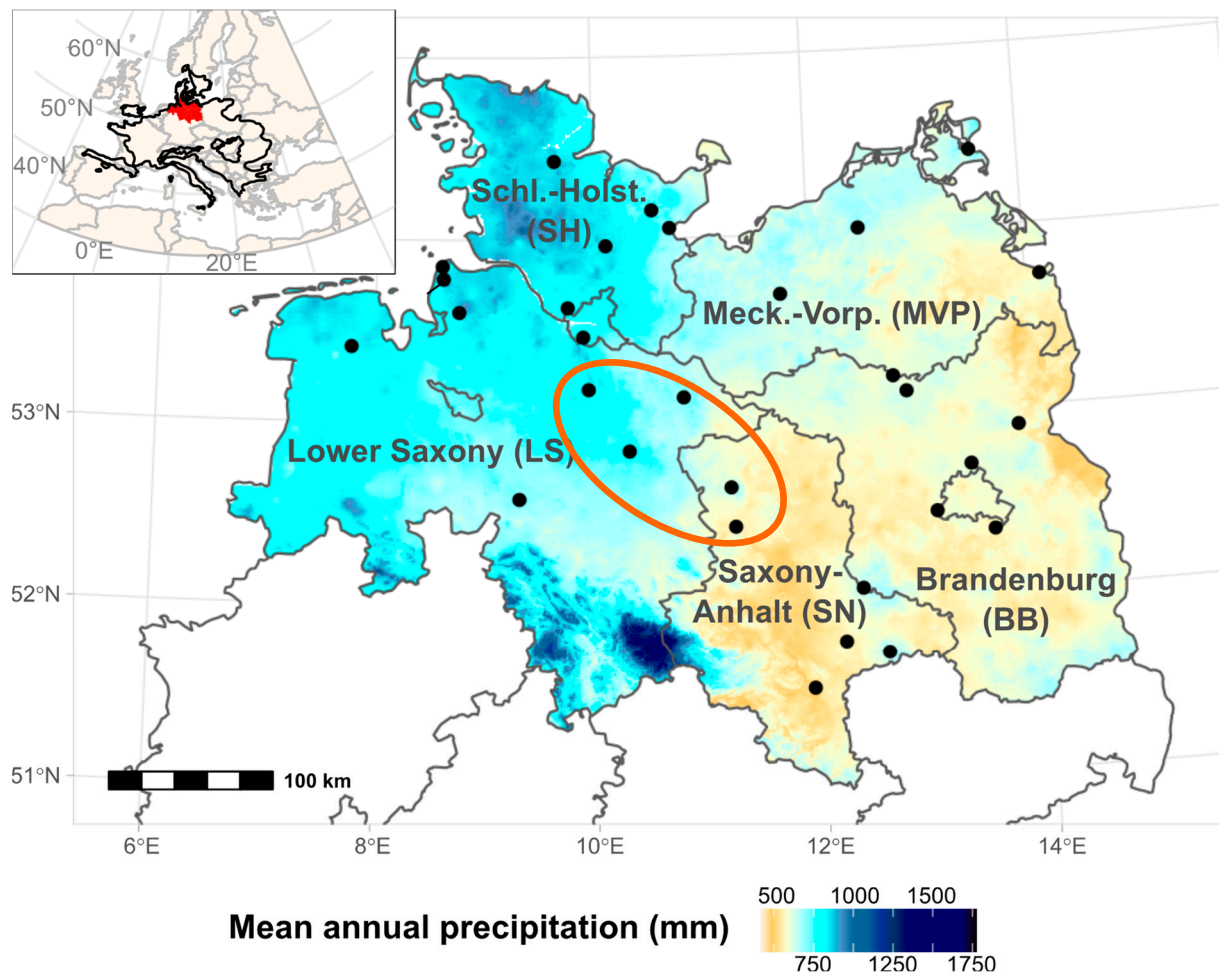


Figure 1. Location of the study region in northern Germany in the north of Central Europe along a marked precipitation gradient (distribution range of beech indicated in the small map). Black dots mark the location of the 30 beech stands of the core study (see Table S1). The red ellipse encloses intensive study sites along a steep section of the precipitation gradient, where root studies were additionally conducted. The German federal states are indicated with their abbreviations. Climate data (1991–2018 average) available from the climate data center of the German Weather Service.

The stem wood cores were analyzed for ring width with a moveable measuring table (Linntab 5, Rinntech, Heidelberg, Germany) using the software TSAP-Win. From the data, chronologies were built for the 1948–2017 period for the 30 stands using the software dplR [19] in R v. 4.0.4 (R Core Team, Vienna, Austria). In the dendrochronological analyses, the 30 stands were grouped into four even-sized (7 or 8 sites) sub-regional precipitation classes according to mean growing-season precipitation (MGSP, April–September), distinguishing wettest sites (WW: 418–448 mm), wet sites (W: 364–417 mm), dry sites (D: 329–358 mm), and driest sites (DD: 306–328 mm) (Table S1). Long-term growth trends were analyzed by means of Sen’s slope coefficient s by regressing size-standardized basal area increment (BAI) against calendar year, using BAI data that were standardized to a fixed stem diameter (DBH, mean of all trees) by dividing the raw BAI values by their expected BAI at given DBH (for more details see [17]). We tested the influence of precipitation class (WW to DD) on the growth trend direction with an analysis of variance (F -test) with site ($N = 30$) as random grouping factor; differences in the proportion of trees with positive versus negative trend direction between the precipitation classes were tested for significance with Student’s t -test. For further methodological details incl. climate-growth analysis [20] see Supplement S3.

2.3. Hydraulic and Physiological Measurements

Branch hydraulic conductivity and embolism resistance were determined for about 30 cm long branch segments collected by tree climbing of each 10 trees per stand. The investigated branch samples were first-order side branches of a main branch collected in the uppermost sun-exposed tree top. Xylem cross-sectional area-specific hydraulic conductivity (K_s) was measured in a Xyl'ém embolism meter (Bronckhorst France, Montigny les Cormeilles, France) after flushing at high pressure (120 kPa) and establishing vulnerability curves in a flow centrifuge (Cavitron; [21]), starting at a pressure of -0.37 MPa (for details see [22]). Several leaf traits (leaf size, $\delta^{13}\text{C}$ of leaf mass, turgor loss point P_{tlp}) were determined between June and August 2018 and 2019 in fully expanded sun leaves of the uppermost crown (1–2 m below the tree tip) in each three branches per tree (10 trees per stand) using a vapor pressure osmometer (VAPRO 5600, Wescor, Logan, UT, USA) for P_{tlp} determination (see [23]).

The methodology of stand structural analysis (including leaf area index) and fine root studies is outlined in [24,25].

3. Natural and Recent Distribution of Beech Forests in Northern Germany

In the North German Lowlands, beech is the most abundant tree species of the potential natural forest vegetation. According to the potential natural vegetation map of Germany [26], beech forests would cover about 48.6% of the natural forest area in the study region, if human influence were absent [27]. The remaining forest area would mostly be occupied by broadleaf forests dominated by oaks, ash, birch, and other species. The forest area today consists to more than 95% of production forests, and only 6.6% are covered by beech, while Scots pine (*Pinus sylvestris* L.) plantations are the dominant forest type today (53.2% of the forest area). The large-scale conversion of beech (and other broadleaf forests) to pine stands has happened in the course of many centuries [28].

4. Climate Trends with Relevance for Beech Forest Health

The trend analysis of growth-relevant climate variables revealed for the study region a pronounced and significant temperature increase especially in April, June, and September in the 1983–2017 observation period, which is associated with marked decreases in the Standardized Precipitation-Evapotranspiration Index (SPEI) (significant in April and June; Figure 2a) [29]. In the 35 years from the 1948–1982 to the 1983–2017 period, June SPEI has decreased by up to 0.4 units in large parts of the study region (except for Schleswig-Holstein and the coastal regions of Lower Saxony and Mecklenburg-Vorpommern; Figure 2b). Later in the growing season (July–September), the trend toward higher aridity (lower SPEI) is not significant or absent (Figure 2a). Precipitation has significantly decreased during the 1983–2017 period in most of the study region in April, with a larger decrease in the drier regions, while a consistent precipitation increase has been recorded for August, especially at the coast [29]. June precipitation has declined by 10 mm or more in this 35-year period in the south of the study region, but it increased in the north (Figure 2c). Thus, pronounced climate aridification has happened in the 1983–2017 period especially in late spring and early summer (April to June), when flowering, leaf flushing, and peak stem cambial activity (June) take place in beech [17,30].

Growing-season climatic water balance (P-PET in April–September) has decreased by 20–30 mm from the 1948–1982 to the 1983–2017 period in the largest part of the study region (except for the North Sea coast, Figure 2d). Thus, the climate has become more arid especially in the already drier sub-continental parts of the study region in the south and south-east [29].

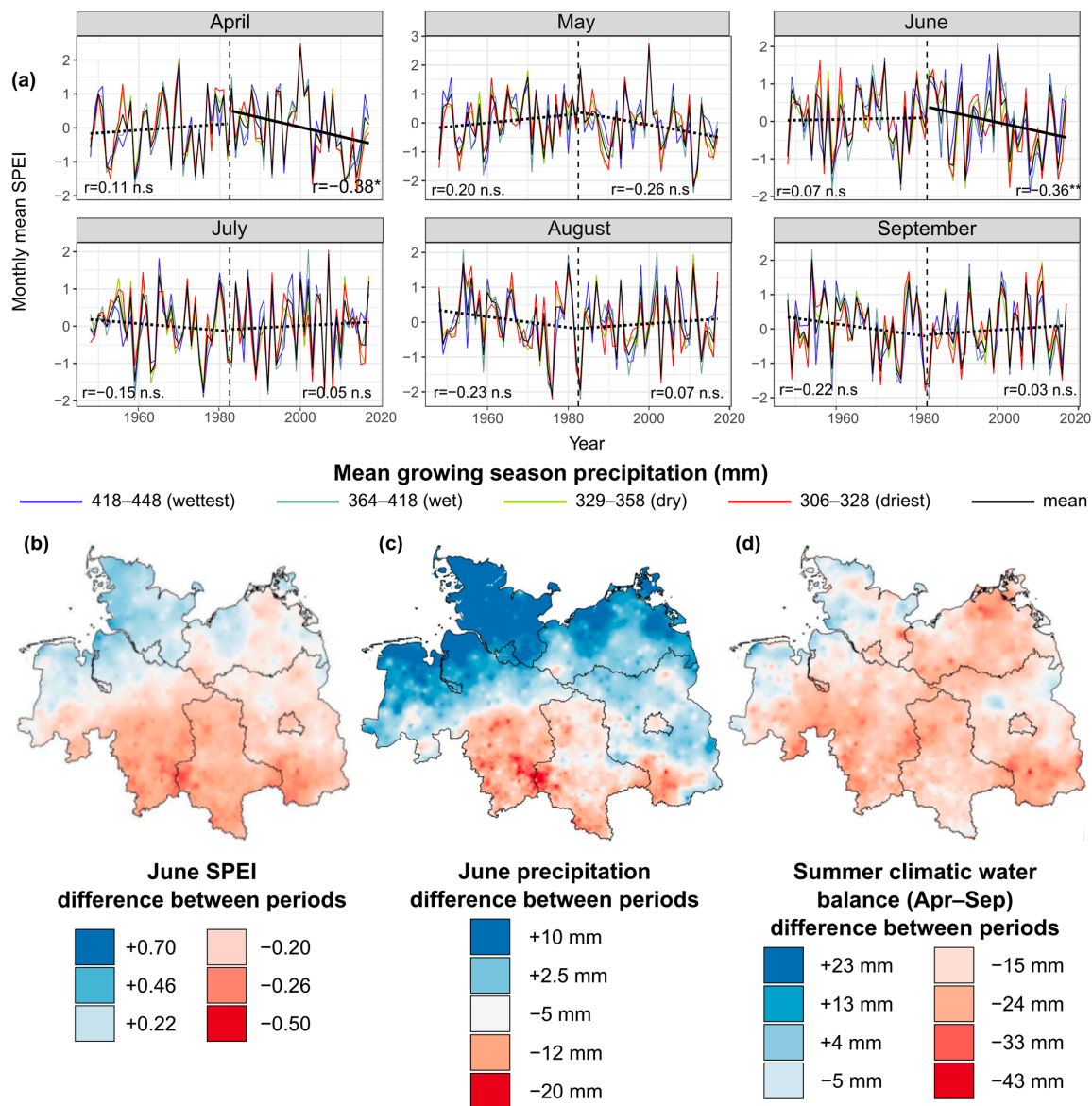


Figure 2. (a) Long-term trends of the mean SPEI of the growing season months (April–September) in the period 1948–2017 (split into the periods 1948–1982 and 1983–2017) extracted from gridded climate data of the German Weather Service for 30 beech forest locations across the whole study region. Given is the mean curve for all sites and the four curves for wettest, wet, dry, and driest MGSP classes. Significant trends are marked by solid trend lines ($p < 0.05$) and non-significant ones by dotted trend lines. * $p < 0.05$, ** $p < 0.01$ according to a Mann–Kendall trend test. (b) Long-term change in June SPEI, (c) June precipitation (in mm), and (d) summer climatic water balance (mm) in the study region. Given is the change between the means of the 1948–1982 and 1983–2017 periods. Modified from [29].

5. Drought-Related Foliage Reduction, Crown Damage, and Mortality Rate: Long-Term Trends and Influence of Site Conditions

With a measured increase in mean summer temperature (April–September) by about $1.3\text{ }^{\circ}\text{C}$ from 1983 to 2017, atmospheric vapor pressure deficit (VPD) in summer would have increased in the study region by $\sim 0.85\text{ hPa}$, if the water vapor pressure of the air had remained constant. This is a strong increase during this 35-year observation period, exposing the trees to a rising evaporative demand and progressively deteriorating their water balance. Moreover, the sequence of extreme droughts between 2015 and 2020 in Europe has been assessed as the most extreme episode in the past 2110 years [31]. As a

consequence of the extreme 2018/19 hot drought, beech forests showed premature foliage discoloration and leaf shedding, branch dieback, and elevated mortality in various lower mountain ranges in Switzerland, southern Germany, and elsewhere [16,32–34]. Forest health monitoring (which mainly addresses dominant trees) showed that damage was particularly severe in stands on shallow soils with low water storage capacity, on south-exposed slopes, in heavily thinned stands, and at forest edges ([35] and pers. obs.). In some cases, mortality could be attributed to catastrophic hydraulic failure [35,36].

On a forest patch scale, a few beech forests on steep slopes suffered mortality rates between 25 and >80% of the stems (e.g., in parts of Hainich National Park, central Germany, pers. obs., and in NW Switzerland [16,37]). However, when assessing more extended forest areas, annual mortality did rarely exceed 5% even in the most severely hit stands (e.g., 2.1% in NW Switzerland [16], up to 2.1% in Hesse, central Germany [10]). Certainly, mortality may increase in these stands in future decades, given the importance of legacy effects of past stress events on beech health [38,39].

In apparent contrast, most beech forests on deeper soil and at less exposed sites in the lowlands of northern Central Europe and at montane elevation were much less affected or even lacked weakness symptoms. For example, only slight increases in foliage reduction and crown damage were observed in the Luneburg Heath beech forests (Lower Saxony, N Germany) on deep sandy to loamy glacial deposits after the 2018/19 hot drought (pers. obs.). Annual forest health monitoring data from northern Germany reveal a long-term increase in foliage loss only for beech stands in Saxony-Anhalt (Figure 3a), where June precipitation and MAP are lowest in the region. In the other four federal states, estimated foliage reduction was stable in the 1991–2021 period. Nevertheless, after the severe 2018 drought, average foliage loss was in all states up to 20 percentage points higher (2019) than before, as had happened after previous droughts (as in 2004) as well.

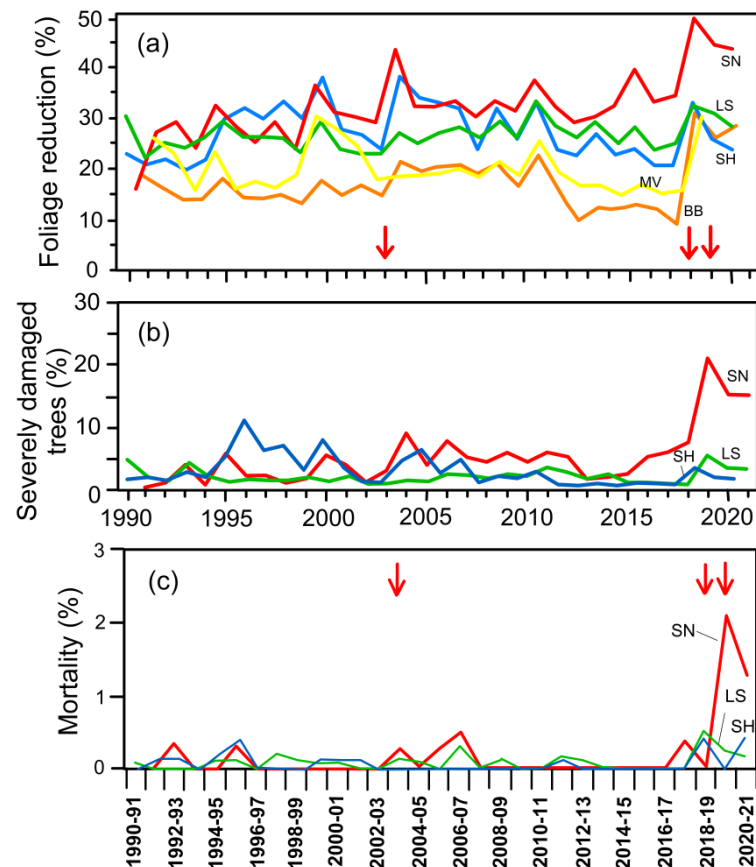


Figure 3. Variation in (a) visually assessed average canopy foliage reduction, (b) the percentage of severely damaged trees (>60% foliage reduction), and (c) annual mortality rate in northern German

beech stands that were monitored annually from 1991 to 2021 in the frame of the forest health monitoring program. Data averaged by federal state (BB: Brandenburg, LS: Lower Saxony, MV: Mecklenburg-Vorpommern, SH: Schleswig-Holstein, SN: Saxony-Anhalt). Red arrows indicate years with exceptionally dry summers. Drawn after data from Nordwestdeutsche Forstliche Versuchsanstalt, Göttingen.

Annual tree mortality in the period 1991–2018 remained at low levels (usually $\leq 0.3\%$ yr⁻¹, peak values up to 0.5% yr⁻¹), which probably mostly reflects within-stand competition processes. However, mortality rate increased after the severe 2018/19 drought to $>2\%$ yr⁻¹ in Saxony-Anhalt and reached 1.5% yr⁻¹ in 2020/21, and the proportion of severely damaged trees surpassed 20% (Figure 3b,c). In the moister regions (Lower Saxony and Schleswig-Holstein), no such increases were observed (Figure 3c). These ground-based damage assessments are in line with remote sensing (Sentinel-2 and Landsat-8) data that indicate in most northern German states annual canopy cover loss rates for larger tracts of broadleaf forest of $<0.2\%$ yr⁻¹ in 2018–2021, and only in Saxony-Anhalt and Brandenburg rates up to 0.4% yr⁻¹ [40]. More severe crown damage was observed after the 2018/19 drought only locally, e.g., near the drought limit of natural beech occurrence in southern Brandenburg at <550 mm yr⁻¹ MAP ([41] and pers. obs.).

6. Evidence of Climate Vulnerability of Beech: Radial Growth Dynamics and Growth Trends

Several recent dendrochronological studies in northern Germany have produced four pieces of evidence that demonstrate the vulnerability of beech to the current climate warming and aridification trend: (1) a multi-decadal decline in basal area increment; (2) a significant correlation between a negative long-term BAI trend and a multi-decadal decrease in June (or summer) climatic water balance; (3) an increasing strength of the June SPEI signal in tree-ring series with decreasing summer (or annual) precipitation; and (4) a persistent increase in within-population growth synchrony [17,18,42,43].

6.1. Long-Term Growth Trends and Their Dependence on Climatic and Edaphic Factors

The mean growth chronologies built for the four MGSP classes in the study region (wettest, wet, dry, driest) reveal for the 1983–2017 period stable size-standardized BAI rates or only weakly negative BAI trends (Sen's slope of the BAI trend < 0) in the wettest and wet classes (>360 mm MGSP) but more strongly decreasing BAI rates in the dry and driest classes (<360 mm; Figure 4c).

The proportion of trees in a stand with negative growth trend since ca. 1983 increases significantly from the wettest to the driest MGSP class (Figure 4a). Twenty-one of the thirty stands (70%) revealed on average negative (significant or non-significant) growth trends since ca. 1983, and only nine showed stable growth or positive trends. However, due to large variation in BAI trends among the 15 trees within a stand and also among the mean BAI trends of the 30 stands, the proportion of trees with negative BAI trend in a stand increased by 20 percentage points (from 35 to 55%) with a MGSP decrease from 450 to 300 m, but this trend was not significant (Figure 4b).

Another dendrochronological study by Knutzen et al. (2017) [42] of 11 beech stands along the steepest part of the precipitation gradient in the center of the study region (eastern Lower Saxony/western Saxony-Anhalt) corroborates the finding that two groups of stands can be distinguished, the first with >350 mm MGSP and positive BAI trends (or stable growth rates) and the second with <350 mm and negative growth trends since the 1980s or earlier (Figure 5a). The turning point of ~ 350 mm growing season precipitation matches the results of the larger 30-stand study (~ 360 mm MGSP, separating the wetter and drier MGSP classes). When mapping the regional variation in long-term growth trends in the 1983–2017 period, negative trends (or tendencies) prevail in a region covering the federal state of Saxony-Anhalt, Brandenburg, and the eastern part of Mecklenburg-Vorpommern (regions east of the red line in Figure 6). Based on the simple but straightforward threshold of ~ 350 mm MGSP, which separates positive and negative growth trends of dominant

trees, a vulnerability map of beech was drawn for northern Germany showing regions with <350 mm MGSP in red (Figure 6). Thus, more than two thirds of the beech forest area in the study region is characterized by negative growth trends since about the 1980s. Most of the affected stands do not yet show elevated levels of foliage reduction, crown damage, or mortality.

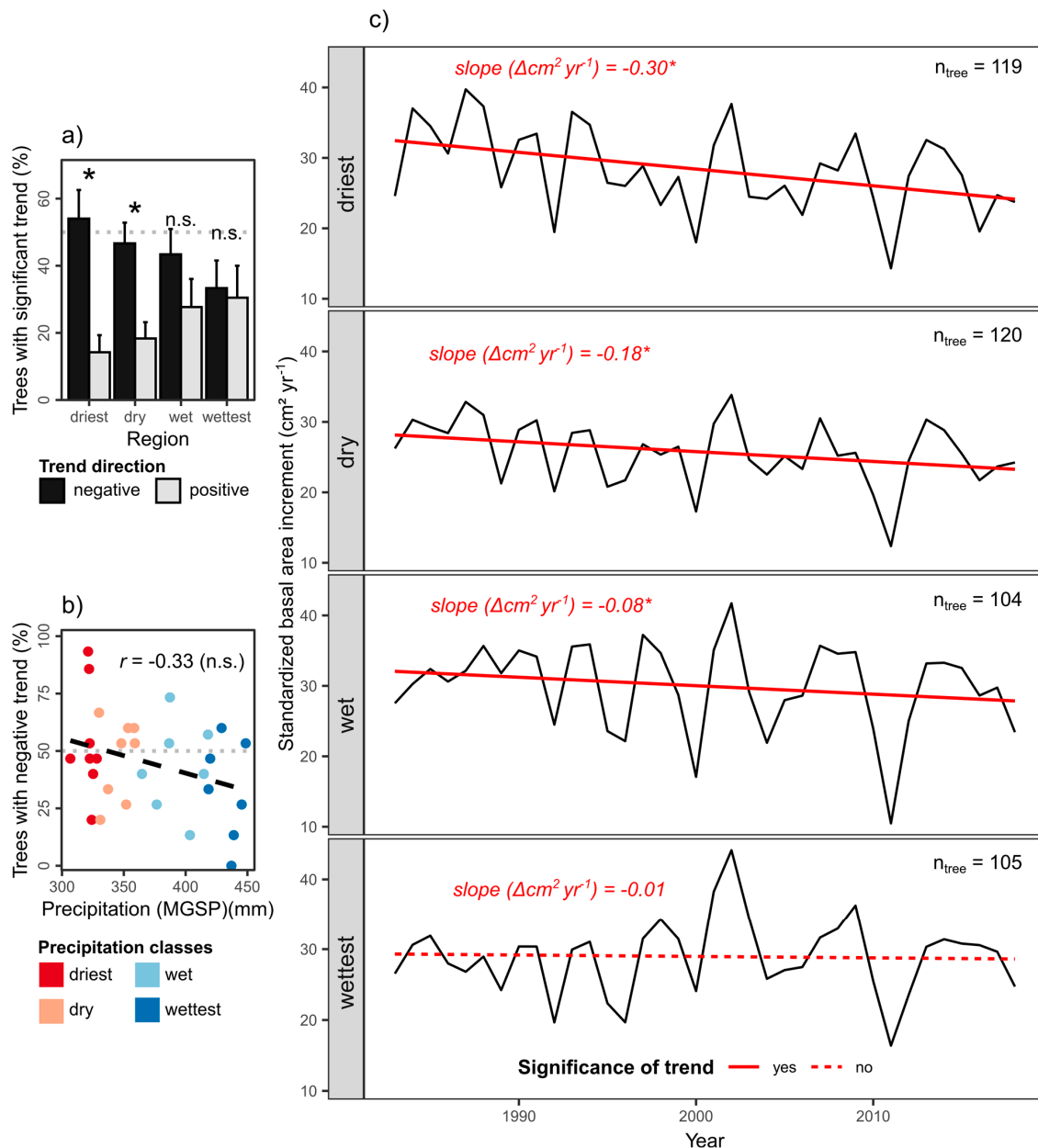


Figure 4. (a) Proportion of trees with negative or positive size-standardized BAI trends in the 1983–2017 period in the four growing-season precipitation classes ($N = 30$ stands; see Figure 2a). Asterisks indicate significant differences; n.s., non-significant differences (t -test) between the proportion of trees with negative or positive growth trends; (b) Pearson correlation (1000-fold bootstrap significance test) between the proportion of trees with negative growth trend at each site ($N = 30$) and mean growing season (April–September) precipitation (MGSP); (c) regional chronologies of basal area increment in the four precipitation classes and recent growth trends from 1983 to 2018 as quantified by Sen’s slope s and tested for significance with the Mann–Kendall trend test (* = trend significant at $p < 0.05$). The influence of tree size (positive correlation of BAI and diameter at breast height at time of ring formation) was removed from each tree-ring series prior to analysis. Modified from [17], with permission from the publisher.

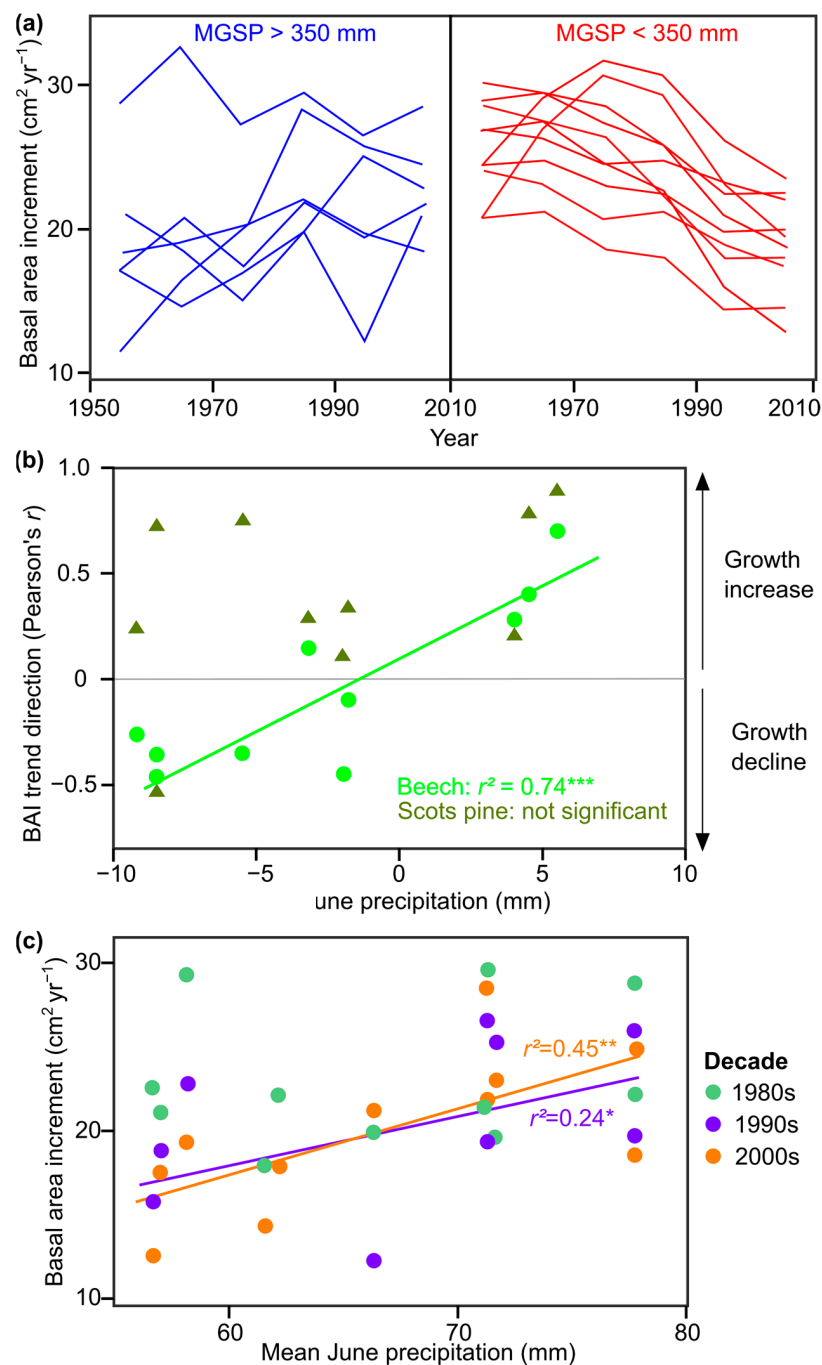


Figure 5. (a) Mean basal area increment (BAI) of each ten dominant trees per stand from 1951 to 2010 (given are decadal means) in six stands with $>350 \text{ mm}$ mean growing season precipitation (MGSP) (left) and five stands with $<350 \text{ mm}$ MGSP (right) along a steep precipitation gradient in Lower Saxony/Saxony-Anhalt (drawn after data in [42]); (b) Dependence of the mean basal area increment (BAI) trend (expressed as Pearson's r of the correlation between BAI and years) in ten pairs of beech (green) and Scots pine (black) stands of the study region in the 1989–2017 period on June precipitation change from the 1960–1988 to the 1989–2017 period, after data in [18]; (c) Relationship between mean basal area increment (BAI) of each ten dominant beech trees per stand with mean June precipitation in 11 stands along a precipitation gradient in Lower Saxony/Saxony-Anhalt in three decades (1980s to 2000s). The relationship between mean BAI and June precipitation was not significant in the 1981–1990 period but significant in the periods 1991–2000 ($y = 0.29 - 0.30x$, $R^2 = 0.24$, $p = 0.03$) and 2001–2010 ($y = -5.9 + 0.39x$, $R^2 = 0.45$, $p = 0.005$). Drawn after data in [42]. * = significant at $p < 0.05$, ** = significant at $p < 0.01$, *** = significant at $p < 0.001$.

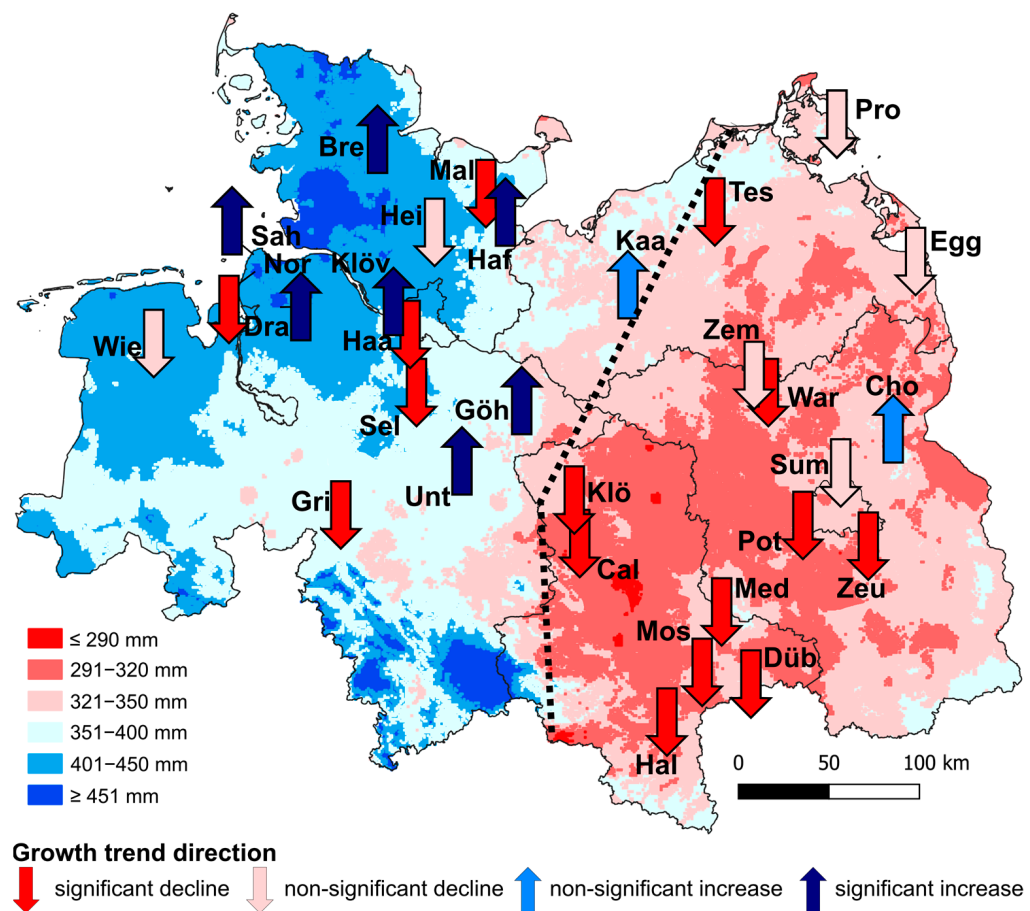


Figure 6. Prevailing growth trends of dominant beech trees in the 1983–2017 period in 30 stands in the study region (for explanation of site acronyms, see Table S1). The arrow directions indicate positive or negative long-term growth trends of size-standardized basal area increment (BAI) in the study region. The black dashed line delineates the westernmost extension of the area with widespread negative growth trends. Arrows are centered on the study site locations. The background color indicates classes of mean growing season precipitation (MGSP) in the study region (period 1983–2017). German federal state borders are also drawn (see Figure 1). For site IDs, see Table S1.

6.2. Drivers of Negative Growth Trends

A multiple regression model to explain the BAI trend direction identified long-term change in the summer climatic water balance (CWBs) from the 1948–1982 to the 1983–2017 period as the only climatic driver of the trend [17] (Figure 7). Other climatic variables such as SPEI, precipitation, and temperature of the summer months had no significant effect on the trend direction. A second influential factor, however, was the average distance between trees (as a proxy of competition intensity) at lower importance than the CWBs change (Figure 7). In another study that compared 10 paired beech and pine stands in the study region, a decrease in June precipitation from the 1960–1988 to the 1989–2017 period was associated with a negative BAI trend, while positive growth trends were found in regions with a long-term increase in June precipitation [18] (Figure 5b). In contrast, the growth trend direction of co-occurring Scots pines was not related to the recent change in June precipitation (Figure 5b). It appears that the strong effect of June precipitation on beech BAI developed only after 1990 (Figure 5c).

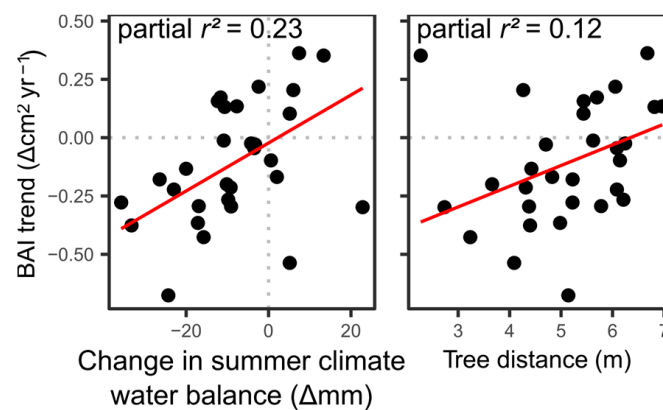


Figure 7. Basal area increment (BAI) trend (black dots) during the 1983–2017 period as explained by variation in climatic and stand structural factors for the 30-stand sample according to a multiple regression model (red lines; soil factors were without significant influence). The change in BAI was quantified for every stand with Sen’s slope (compare Figure 4). The change in summer climatic water balance (CWBs) is calculated as the difference between the CWBs of the periods 1983–2017 and 1948–1982. Mean stem distance serves as an indicator of competition intensity in the stand. The adjusted R^2 for the full model is 0.30, $p = 0.003$. Modified after [17], with permission from the publisher.

6.3. Spatial and Temporal Variation in the Climate Sensitivity of Growth

Climate aridification consists of two components, which may influence the physiology of beech trees in different ways: (1) the recorded increase in frequency and severity of irregular hot summer droughts in Central Europe [31,44,45]; and (2) the long-term increase in atmospheric evaporative demand and, thus, deterioration of the climatic water balance in the early growing season, which also proceeds in non-drought years and raises the ‘base stress level’ trees are exposed to [29]. It is thus plausible that current-year June SPEI emerged as the most important climate factor influencing the interannual variation in radial growth of beech in the study region [17] (see also Figure S1). According to a study in north-eastern Germany, the positive effect of a higher June SPEI (more favorable climatic water balance) seems to be stronger at sites with lower mean annual precipitation [43] (Figures 8a and S2). However, a multiple regression model for explaining drought signal strength (June SPEI) in the 30-stand sample did not include precipitation variables but indicated that the site’s mean summer temperature is the principal determinant of population differences in climate sensitivity (Figure 8b). Accordingly, growth sensitivity to June SPEI increases towards warmer sites in our study region, while site MAP itself is not influential. A higher soil sand content (and thus lower soil water storage capacity) and higher competition intensity (larger Hegyi index) also increased the growth sensitivity to June SPEI (Figure 8b).

The strength of the drought signal in the growth chronologies of the 30 stands has decreased since the 1980s for all five key climatic drivers of growth change (June and July SPEI, June precipitation, and temperature in June and previous July; Figure S1). The only exception is the June SPEI signal at the driest and dry sites (MGSP < 360 mm), which remained fairly constant at a high level during the whole observation period 1948–2017 (Figure S1: uppermost panel). The drier sites differ from the wetter ones by a tendency toward larger negative growth impact of lower SPEI values and high June temperatures, while the wetter sites tend to be more sensitive to higher drought exposure in July.

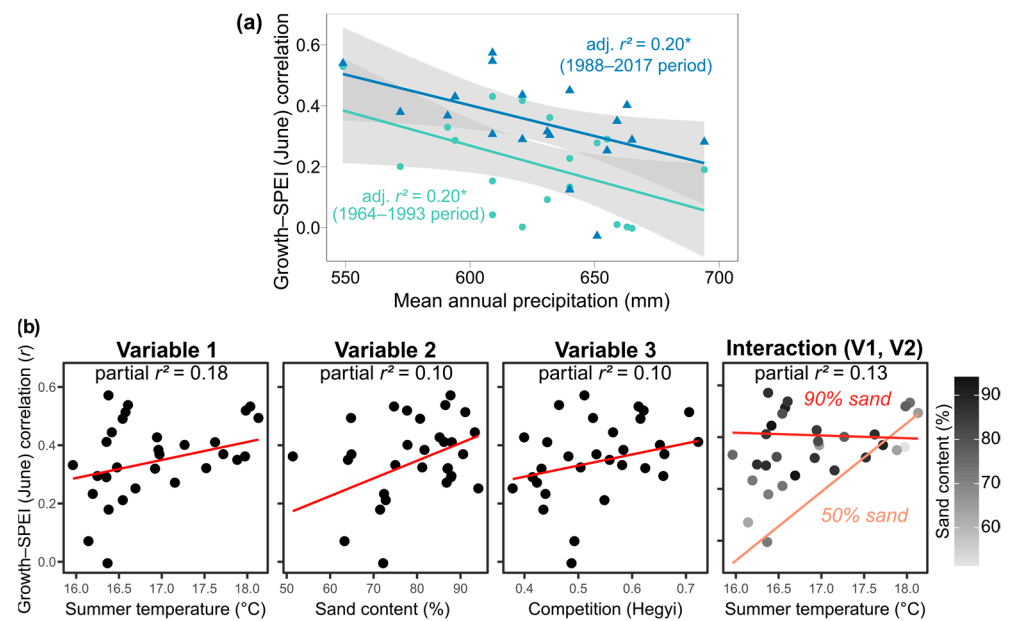


Figure 8. (a) Dependence of the radial growth—June SPEI correlation on mean annual precipitation in 19 stands in Mecklenburg-Vorpommern. Modified from [43], with permission (* = relationship significant at $p < 0.05$). (b) Dependence of the radial growth—June SPEI correlation (calculated for the full period 1948–2017; black dots) on mean summer temperature, soil sand content, competition intensity (Hegyi Index) (red lines: relationships of the three significant factors), and the interaction of summer temperature and sand content in the 30-stand sample according to a multiple regression model (right panel: relationship given for 50% and 90% sand content); The adjusted R^2 of the full model is 0.42, $p = 0.001$. Modified after [17], with permission from the publisher.

6.4. Growth Synchrony

Within-population growth synchrony (expressed by the \bar{r} value, i.e., the average correlation between the ring width series of a population) has significantly increased from the 1948–1982 to the 1983–2017 period in the 30-stand sample (ANOVA with period and site as explanatory factors, $F_{\text{period}} = 8.4$, $p_{\text{period}} = 0.007$) (Figure S2). This was associated with a higher interannual growth fluctuation in the more recent than in the earlier period ($F_{\text{period}} = 9.2$, $p_{\text{period}} < 0.05$). Growth synchrony was not dependent on MGSP or MAP of the site ($F_{\text{MGSP}} = 1.4$, n.s.). A model run with a variety of climatic, edaphic, and stand structural variables revealed that growth synchrony increases toward sites with more frequent June drought (measured as the frequency of years with June SPEI < -1) and toward sites with lower plant-available soil water storage capacity (Figure S3). \bar{r} also increased with tree age, but this effect was less influential than that of the two drought-related factors.

7. Leaf-, Branch-, Stem-, and Root-Level Responses as Possible Causes of the Growth Decline

Persistent growth reduction can have various causes, among them high tree age, competitive inferiority, abiotic and biotic stressors that harm tree functions such as carbon assimilation and hydraulic conductance, or allocation shifts to organs other than the stem cambium, induced by environmental signals. We can exclude high age, competitive inferiority, and biotic stressors, since the studied 80–130 year-old trees that were well ahead of the age of biological senescence [39] were not visibly affected by leaf herbivory or insect and fungal attack and were not suppressed by neighbors, as all studied trees were dominant individuals in the upper canopy. The marked difference in growth trends between stands at wetter and drier sites in northern Germany is strong evidence for the assumption that the affected beech populations have crossed thresholds of necessary minimum water availability and/or maximum tolerable heat exposure. These drivers likely have reduced radial growth well before the trees succumb to crown dieback and death. Catastrophic

hydraulic failure, a plausible cause of crown dieback and tree mortality in beech in other regions [36], is an unlikely driver of the decade-long growth decline at our sites because growth trends shifted gradually from positive to negative, and visual canopy damage is still low at most sites.

Reduced carbohydrate availability for stem growth in the course of a deteriorating summer water balance is a more likely driver, either due to reduced stomatal conductance [23] and lowered photosynthetic carbon gain or due to increased resource allocation toward root growth at the cost of radial stem increment [24,25]. Both factors may have contributed to growth decreases at the drier sites. First, sun-leaf mass $\delta^{13}\text{C}$ increased across the 30 beech stands from ca. $-29.5^0/_{00}$ to $-27.5^0/_{00}$ with a decrease in spring climatic water balance (March to May) from +5 to -190 mm [23] (Figure 9a), indicating that mature beech trees reduce leaf conductance progressively with decreasing MAP.

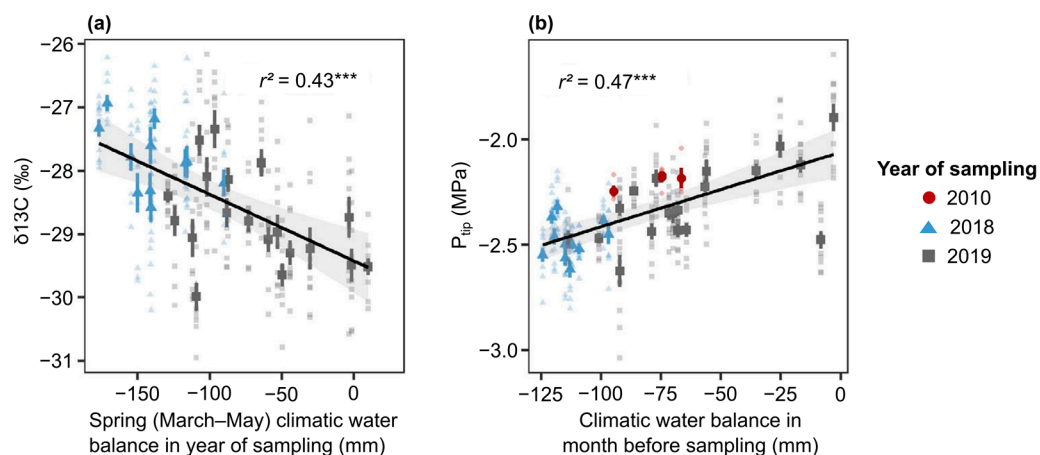


Figure 9. (a) Dependence of the $\delta^{13}\text{C}$ signature and (b) of turgor loss point (P_{tlp}) of upper-canopy sun leaves on the cumulative climatic water balance in spring (a) or the climatic water balance of the month before sampling (b) in 34 beech stands in the study region (means \pm SE). Modified after [23], with permission from the publisher. *** = significant at $p < 0.001$.

Second, beech adapts to a MAP reduction in the study region by increasing its fine root biomass profile total (from ~ 350 g m^{-2} to >600 g m^{-2} in the mineral topsoil (0–30 cm) plus organic layer with a precipitation reduction from c. 850 mm yr^{-1} to c. 650 mm yr^{-1} ; Figure 10a) as well as by increasing fine root productivity (from ca. 150 g m^{-2} yr^{-1} to 400 g m^{-2} yr^{-1} , Figure 10b) [25]. This suggests more rapid fine root turnover under lower than higher MAP (only non-significant tendency; Figure 10c). On the other hand, beech does not root deeper at drier sites [46]. Root sampling to 2.4 m depth produced no evidence of a deeper extension of the fine root system at sites with lower MAP (Figure S4a). Mast fruiting events, partly triggered by drought, can also cause C allocation shifts away from stem growth in beech [47–49].

Long-term reduction in carbon gain, partial hydraulic failure, and continued below-ground C allocation shifts all have the potential to weaken a tree's stem growth potential and its capacity to return to pre-drought growth levels [50]. This could be one explanation of the negative growth trends at the drier sites. A role for water limitation is suggested by xylem anatomical data that showed a significant long-term decrease in mean vessel diameter in the stem xylem over the last decades in Central German beech trees, opposite to the general ontogenetic trend of conduit widening with increasing age [51]. Beech trees of a given diameter decreased their vessel diameters from 1951 to 2010 by 2.35% per decade, while vessel density increased by 6.80% per decade. Since this anatomical modification was linked to a continuous reduction in stem growth rate (and thus ring width), a reduction in stem hydraulic conductance might well have negatively affected canopy water status, which could reduce carbon gain.

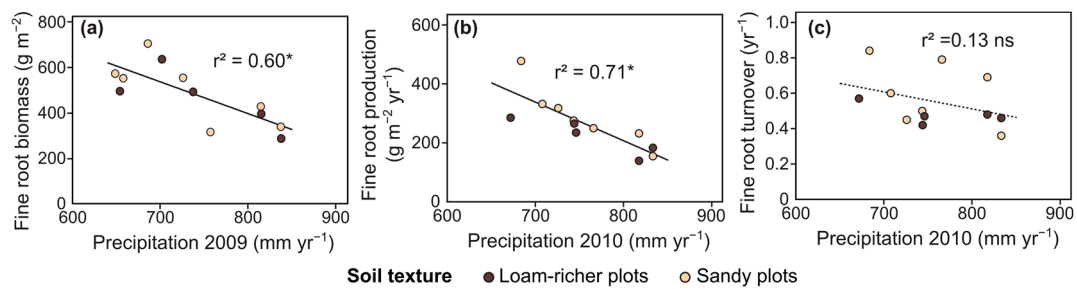


Figure 10. (a) Fine root biomass, (b) annual fine root production, and (c) fine root turnover in the organic layer and the mineral topsoil (0–30 cm) in dependence on annual precipitation in the sampling year in 12 stands along a precipitation gradient in the center of the study region. Modified after [25], with permission. * = significant at $p < 0.05$, ns = non-significant.

8. The Climate Change Acclimation and Adaptation Potential of Beech

The recent hot droughts demonstrate that climate change is exposing beech even in the center of its distribution range to physiological conditions that are close to, or even beyond, the tolerated limits. The trees respond to this stress with acclimation, i.e., non-heritable, reversible shifts in phenotype (often termed phenotypic plasticity), or genetic adaptation through natural selection at the population level, exploiting the large intraspecific genetic variation of the species [52]. A genetic study using highly polymorphic microsatellite markers in five beech populations along our precipitation gradient in northern Germany found more than 97% of genetic variation within populations and <3% between populations [53]. Intraspecific genetic variation among individuals must thus be a major source of trait variation in the study region [54]. Correspondingly, a large fraction of the observed variation in xylem anatomical traits (52%–71%), hydraulic traits (57%–78%), and leaf morphological and physiological traits (24%–52%) among the 30 stands was attributed to differences between individuals [22,23,55], reflecting pronounced genetic, phenotypic, and micro-site differences among the trees. The wide intra-population genetic variation might represent a strong basis for future climate change adaptation of beech [56]. Epigenetic factors are also likely playing an important role [57,58].

Comparing population-level trait means across our precipitation gradient suggests that significant adaptive modifications in response to drought and heat have occurred at leaf, branch, and root levels. With a decrease in MAP (or MGSP), we found decreases in stomatal conductance levels and turgor loss point [55], a reduction in branch xylem vessel diameter [55], and an increase in fine root biomass and productivity [24,25], all of which may help avoid tissue desiccation. One of the most effective modifications to sustain tree growth in a drier climate is thought to be osmotic adjustment in leaf, root, and other tissues [59,60]. In our 30-stand sample, sun-leaf turgor loss point was reduced during mid-summer by about 0.3 MPa per 100 mm decrease in CWB (measured in the month before sampling), indicating that climate aridification has triggered active osmotic adjustment in the beech sun foliage [23] (Figure 9b). Water potential reduction through active osmolyte accumulation may thus be an element of the foliar drought response of anisohydric beech [61].

The above-mentioned adaptive, putatively drought-alleviating modifications of beech are counteracted by obvious maladaptations, notably the surprising increase in mean leaf size towards drier sites in northern German beech populations. This response was observed in the 30-stand sample in our study region [23] and in another precipitation gradient study in central Germany, where leaf size increased by about 1.55 cm² per MAP decrease by 100 mm yr^{−1} [24], accompanied by an increase in mean specific leaf area by about 1.62 m² kg^{−1} per 100 mm yr^{−1} MAP decrease (Figure 11a,b). Even more surprising, stand leaf area (LAI) increased toward drier sites by roughly 0.45 m² m^{−2} per 100 mm yr^{−1} MAP decrease [24] (Figure 11c).

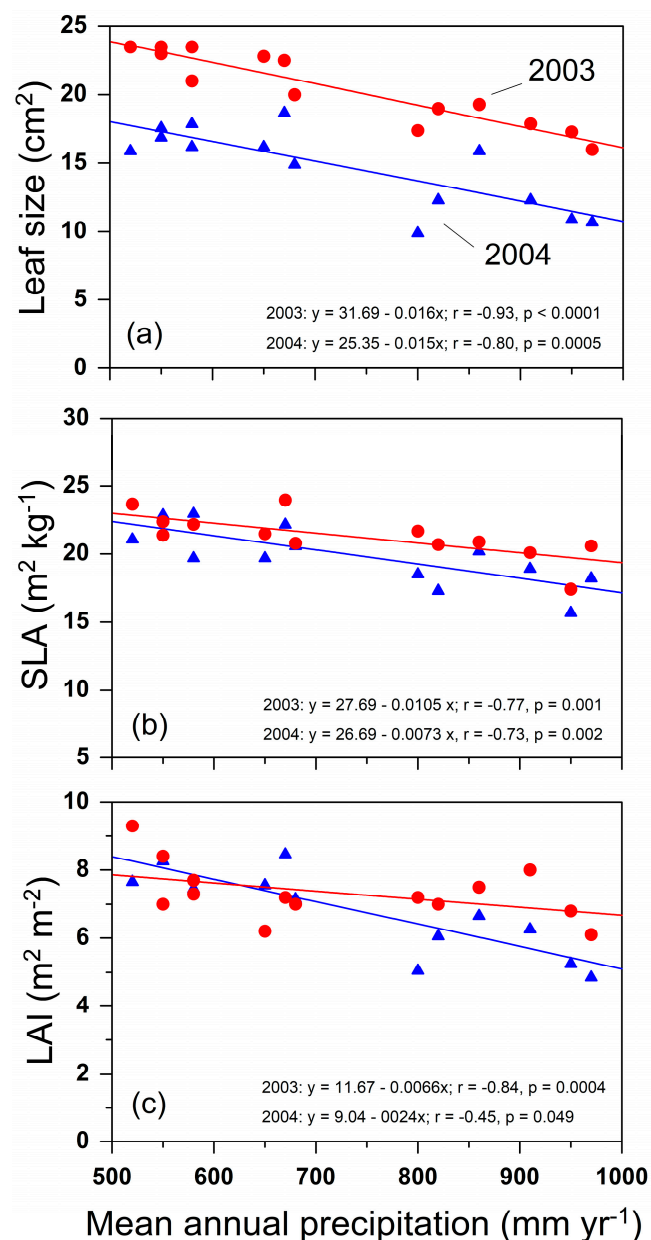


Figure 11. Change in mean leaf size (a), specific leaf area (SLA) (b), and leaf area index (c) in 14 beech stands along a steep precipitation gradient (970 to 520 mm yr⁻¹ MAP) in central Germany on acid sandstone bedrock in the summers 2003 and 2004. Modified after [24], with permission from the publisher.

The apparent lack of an embolism resistance increase toward drier sites in our study region [22] also seems to be maladaptive: Sun-branch P50 value (the xylem pressure where 50% of hydraulic conductance is lost) did neither depend on MAP nor CWB in the 30-stands sample (Figure S5a,b). This contrasts with an earlier study along a steep, but shorter, precipitation gradient (850–540 mm yr⁻¹) in the center of the study region, which revealed a P50 decrease by 0.33 MPa, i.e., by about 0.13 MPa per 100 mm yr⁻¹ MAP decrease [62]. Yet, we found a P50 reduction by ~0.3 MPa with a decrease in plant-available soil water capacity from 300 to 50 mm, indicating increasing embolism resistance with a decrease in soil water availability (Figure S5c). Thus, the influence of water deficits on P50 seems to be inconsistent in the study region.

The small genetic distances between populations suggest that the above-mentioned adaptive physiological and morphological modifications are largely a result of phenotypic

plasticity, rather than caused by genetic differences. The more negative growth trends at the drier sites indicate that acclimation was obviously not sufficient to counteract the stress experienced by the trees from a decade-long decrease in the climatic water balance. This is corroborated by the greater growth sensitivity to a hot and dry June at drier sites. One possible explanation of this pattern is that these populations have during the last decades not sufficiently acclimated to fully buffer beech growth against increasing drought and heat stress exposure, either due to a restricted capacity for sufficient acclimation to cope with the recent climate aridification, or because time was too short for full acclimation. Assisted migration of presumably more drought- and heat-tolerant beech genotypes from greater distance (e.g., southern and south-eastern Europe) might be a promising option with respect to drought adaptation, which has been investigated in various common garden growth trials [63–65].

While decreasing growth rates often reflect a vitality reduction, they could also be a consequence of acclimation to drought, when they result from xylem anatomical modifications that increase hydraulic safety [66]. However, an observed reduction in mean vessel diameter of sun-branch xylem in response to a MAP reduction from 900 to 540 mm across our 30-stand sample [55] had no effect on branch xylem embolism resistance, since P50 was unrelated to vessel diameter [22]. Further, the climate sensitivity of growth increased toward drier sites, pointing at long-term impairment of plant functioning rather than increased plant fitness [17,43]. Moreover, if smaller rings with narrower vessels in branches and stem were an acclimation to drought, such a modification should lead to growth recovery after several years, which was not observed. Thus, it is unlikely that smaller annual rings are primarily indicators of successful drought acclimation of our beech stands.

Our findings of only limited acclimation contrast with dendrochronological results from larger (continent-wide) studies which found a lower drought sensitivity of mature beech trees in dry-marginal beech populations as compared to more mesic central populations, pointing at successful drought adaptation of these genetically more distant populations [67–69]. Similarly, many common garden experiments with beech seedlings and saplings of different European origins revealed a higher drought resistance and/or faster drought recovery of populations from drier and warmer sites [9,70,71], which seems to contrast with our results. That the beech populations of the drier sites of our study were not successful in maintaining growth under increasingly stressful climatic conditions might be a consequence of the relatively small genetic distances found between our populations [53] and perhaps insufficient genetic adaptation to the rapid climate aridification in recent time. Clearly, some genotypes in the studied populations may well exhibit better drought and heat adaptation than the bulk of trees, as seems to be indicated by the positive growth trend of a minority of trees at the drier sites. Judged from the velocity of recent climate change, it seems unlikely that the force of natural selection will act rapidly enough to optimize the drought and heat adaptation of beech populations that recently face negative growth trends in the study region [72].

9. The Future of Beech in Northern Germany

With typical rotation periods of 100 to >120 years in Central Europe, beech forest management operates with planning horizons that reach from present toward the mid of the 22nd century, when mean temperatures might well be 2.5 to 3.5 °C higher than today [73]. Projecting our results on hydrological thresholds of beech vitality from the 2020s to the next century is a hazardous and probably flawed undertaking, because the trajectories of drought and heat intensity and frequency can only roughly be approximated with regional climate scenarios, and long-term adaption of the trees is not well understood. Moreover, beech growth is frequently subject to long-lasting memory effects of past stress impact that can result in decade-long periods of reduced growth and eventual death [38,39,74], complicating predictions about future vitality and growth. A dendroecological modelling study based on growth chronologies from 324 beech forests in Europe extrapolated growth

from the 1986–2016 to the 2060–2090 period under projections of the mild SSP1-2.6 CMIP6 climate scenario and the more extreme SSP5-8.5 CMIP6 scenario. The study predicts for large parts of northern Germany growth reductions of up to 20% and 50%, respectively, in the coming 40 to 70 years for the two scenarios [75] (Figure S6), which is in line with our findings.

When extrapolating these dendrochronological findings to stand-level wood production, it has to be kept in mind that most dendrochronological studies (including ours) focus on the tallest, dominant trees, which might be more climate-sensitive than trees of lower canopy strata. Forest health monitoring programs also assess predominantly trees of the upper canopy layer. Therefore, the drought and heat sensitivity of the whole stand could be overestimated by these approaches, if sub-dominant individuals were less affected by climate hazards. This could be one possible explanation of the apparent contradiction between frequently observed negative growth trends of dominant trees and often stable or increasing stand-level wood increment rates in beech (e.g., [76]). Dendrochronological results from subordinate trees are needed to clarify this issue.

Strong and long-lasting growth decline is often a precursor of tree mortality [77,78], and the negative BAI trends that prevail since the 1980s in the drier part of our study region may well be indicators of an elevated mortality risk of mature trees in future decades. In Swiss beech forests, long-term reduction in growth rate and higher inter-annual growth variation were related to greater crown damage in subsequent years [35]. Severe droughts could push beech trees that already suffer from reduced growth to a trajectory of decline, which starts with partial crown defoliation and proceeds to crown dieback and, finally, tree death, with the consequence that closed stands are opened up, and the characteristic forest interior climate decays [79]. As was observed in beech forests on shallow soil that were hit by severe droughts early in the 21st century, changing light and air humidity conditions will then accelerate stand break-down and eventually may lead to replacement of beech by more drought-tolerant tree species, if man does not interfere [12]. Attack by pest organisms and pathogens such as *Phytophthora* sp., which are promoted by weather extremes, can speed up the decline [6]. This does not necessarily exclude that beech still persists in the lower forest strata.

10. Conclusions

This review of the current knowledge about the health status of European beech in northern Germany produces multiple evidence of widespread vitality loss of dominant trees in a large region not far from the species' distribution center. About two-thirds of the studied trees showed negative growth trends since about the 1980s, when the recent warming period started. Using a persistent negative growth trend as a criterion, nearly half of the beech forest area in the North German Lowlands must today be assessed as vulnerable. Yet, assessing beech vulnerability by means of the 350 mm-MGSP isohyete, as done in Figure 6, must be viewed as an over-simplification, as other influential factors such as soil water storage capacity and stand structure are ignored in this approach. As sand content (and, thus, soil water availability) influence both the climate sensitivity of growth and growth synchrony in the study region, beech vitality is impaired in regions with <350 mm MGSP especially at sandy sites. Moreover, silvicultural planning cannot be based on assessments of recent climate vulnerability alone but should ideally also consider the expected climate change during the entire rotation period, i.e., for the next 100 years or so. The high uncertainty, which comes with all regionalized projections of hydrometeorological parameters well into the next century, suggests introducing 'safety margins' into beech vulnerability maps that may allow coping with further declines in the summer climatic water balance in the decades to come. Choosing a 50 mm safety margin and thus adopting a MGSP of 400 mm as a putative tipping point of beech vitality would extend the vulnerable zone to the entire north-east of Germany, leaving only parts of the federal states of Schleswig-Holstein and Lower Saxony with oceanic climate beyond the 400 mm-isohyete as presumably safe regions for beech growth in our region. With the

adoption of even more pessimistic climate scenarios, which become more likely with failure to implement effective climate change mitigation measures, and, consequently, the need for larger safety margins, the area with climate conditions suitable for vital beech growth would reduce even more to small regions close to the coast.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14071448/s1>, Figure S1: Moving-window (25-year) climate–growth correlation analysis for the 1948–2017 period (mid years of moving windows 1960–2005) of the five most influential growth-limiting climate factors calculated for the four MGSP classes. Modified from [17], with permission from the publisher; Figure S2: Change in within-population tree growth synchrony from the 1948–1982 to the 1983–2017 period (r_{bar} value) in 30 beech stands assigned to four MGSP classes (driest to wettest). The difference between periods is significant, and the differences between classes (regions) are not; Figure S3: Partial plots of a multiple regression model explaining within-stand growth synchrony ($adj. R^2 = 0.32$; $p = 0.004$) (calculated for the full observation period 1948–2017) with climatic, edaphic, and stand structural properties of the study sites. June/July drought frequency is the percentage of years with SPEI < −1. August water balance is August precipitation minus potential evapotranspiration. Modified after [17], with permission from the publisher; Figure S4: (a) Density of fine root biomass (diameter < 2 mm, g dm L^{−1}) and (b) of small coarse roots (diameter 2–5 mm, roots per m²) in dependence on soil depth in six beech forests along a steep precipitation gradient in the center of the study region (means ± SE of each three soil pits per stand). After [46], with permission from the publisher; Figure S5: Dependence of embolism resistance (P50) of sun-canopy branches on (a) mean annual precipitation, (b) climatic water balance (full year), and (c) the soil storage capacity for plant-available water (c) in the 30 stands across the study region. Modified after [22], with permission from the publisher; Figure S6: Expected relative change in basal area increment of beech trees in northern Central Europe from the 1986–2016 to the 2060–2090 period under projections of the mild SSP1-2.6 CMIP6 (a) and the more extreme SSP5-8.5 CMIP6 climate scenarios (b) based on dendrochronological data from 324 beech sites in Europe and a generalized linear mixed effects model of beech growth in Europe in dependence on climate. Modified after [75], with permission from the publisher; Table S1: Stand structural and climatic characteristics of the 30 studied beech forests in northern Germany. Given are means (±SE) of the stands. MAP—mean annual precipitation, MGSP—mean growing season precipitation, MAT—mean annual temperature (period 1983–2017). Precip. class: WW (wettest; 419–448 mm MGSP), W (wet; 364–418 mm), D (dry; 329–358 mm), DD (driest; 306–328 mm). Sites are ranked according to MGSP; Table S2: Pearson correlation analysis of the relationship between mean tree height, mean tree age and mean DBH on mean annual precipitation (MAP), mean growing season precipitation (MGSP), climatic water balance (CWB) and plant-available soil water storage capacity (AWC) in the 30-sites sample. Pearson correlation coefficients in italics, p values in bold (no significant correlations present); Supplement S3: Methods of dendrochronological analysis.

Author Contributions: C.L. conceived the research idea, developed the principal study design, and organized the funding in the framework of different projects. G.W. conducted most of the ecophysiological field work and analyzed the related data. B.B.-E. collected the dendrochronological and climatic data and conducted basic data analyses. R.W. conducted the bulk of dendrochronological analyses. C.L. surveyed the data analysis and wrote the first version of the manuscript with support by R.W. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Data available from the authors upon request.

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