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Identifying drivers of non-stationary climate-growth relationships of European beech

Christopher Leifsson [a],[*],[1], Allan Buras [a],[1], Stefan Klesse [b],[1], Claudia Baittinger [c],[2], Banzragch Bat-Enerel [d],[e],[2], Giovanna Battipaglia [f],[2], Franco Biondi [g],[2], Branko Stajić [ak],[2], Marius Budeanu [h],[2], Vojtěch Čada [i],[2], Liam Cavin [k],[2], Hugues Claessens [l],[2], Katarina Čufar [m],[2], Martin de Luis [n],[2], Isabel Dorado-Liñán [o],[2], Choimaa Dulamsuren [e],[2], Balázs Garamszegi [p],[2], Michael Grabner [q],[2], Andrew Hacket-Pain [r],[2], Jon Kehlet Hansen [s],[2], Claudia Hartl [t],[2], Weiwei Huang [s],[t],[2], Pavel Janda [i],[2], Alistair S. Jump [k],[2], Marko Kazimirović [ak],[2], Florian Knutzen [v],[2], Jürgen Kreyling [w],[2], Alexander Land [x],[2], Nicolas Latte [l],[2], François Lebourgeois [y],[2], Christoph Leuschner [d],[2], Luis A. Longares [n],[2], Edurne Martinez del Castillo [z],[2], Annette Menzel [aa],[2], Renzo Motta [ab],[2], Lena Muffler-Weigel [ac],[2], Paola Nola [ad],[2], Momchil Panayatov [ae],[2], Any Mary Petritan [h],[2], Ion Catalin Petritan [af],[2], Ionel Popa [h],[ag],[2], Cătălin-Constantin Roibu [ah],[2], Álvaro Rubio-Cuadrado [ai],[2], Miloš Rydval [i],[2], Tobias Scharnweber [aj],[3], J. Julio Camarero [j],[2], Miroslav Svoboda [i],[2], Elvin Toromani [al],[2], Volodymyr Trotsiuk [b],[2], Marieke van der Maaten-Theunissen [am],[2], Ernst van der Maaten [am],[2], Robert Weigel [ac],[2], Martin Wilmking [aj],[2], Tzvetan Zlatanov [an],[2], Anja Rammig [a],[1], Christian S. Zang [ao],[1]

[a] Technical University of Munich, TUM School of Life Sciences, Land Surface-Atmosphere Interactions, Hans-Carl-v.-Carlowitz-Platz 2, 85354 Freising, Germany
[b] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland
[c] The National Museum of Denmark, Environmental Archaeology and Materials Science, I.C. Modewegs Vej 11, DK - 2800 Kgs. Lyngby, Denmark
[d] Plant Ecology, University of Goettingen, 37073 Goettingen, Germany
[e] Applied Vegetation Ecology, Faculty of Environment and Natural Resources, University of Freiburg, 79106 Freiburg, Germany
[f] University of Campania Luigi Vanvitelli, via Vivaldi 43, 8100 Caserta, Italy
[g] DendroLab, Dept. of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557, USA
[h] National Institute for Research and Development in Forestry Marin Dracea, 13 Closca street, Brasov, Romania
[i] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamycka 129, Praha 6, Suchdol 16521, Czech Republic
[j] Instituto Pirenaico de Ecología (IPE), CSIC, Avda. Montañana 1005, 50080 Zaragoza, Spain
[k] Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK
[l] Forest is Life, ULiège, Passage des Déportés 2, B-5030 Gembloux, Belgium
[m] University of Ljubljana, Biotechnical Faculty, Department of Wood Science and Technology, Jamnikarjeva 101, 1000 Ljubljana, Slovenia
[n] Dpto. de Geografía y Ordenación del Territorio, IUCA, Universidad de Zaragoza, C/ Pedro Cerbuna s/n, 50009 Zaragoza. Spain
[o] Departamento de Sistemas y Recursos Naturales, Universidad Politécnica de Madrid, 28040 Madrid, Spain
[p] Institute of Forest Ecology, University of Natural Resources and Life Sciences, Vienna, Austria
[q] University of Natural Resources and Life Sciences, Vienna, Austria
[r] Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom
[s] Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark
[t] Nature Rings - Environmental Research & Education, 55118 Mainz, Germany
[u] Collaborative Innovation Center of Sustainable Forestry in Southern China of Jiangsu Province, Nanjing Forestry University, Nanjing 210037, China
[v] Climate Service Center Germany (GERICS), Helmholtz-Zentrum Hereon, Fischertwiete 1, 20095 Hamburg, Germany
[w] University of Greifswald, Experimental Plant Ecology, Soldmannstraße 15, 17498 Greifswald, Germany
[x] University of Hohenheim, Institute of Biology (190a), Garbenstraße 30, 70599 Stuttgart, Germany
[y] Université de Lorraine, AgroParisTech, INRAE, Silva, F-54000 Nancy, France
[z] Department of Geography, Johannes Gutenberg University Mainz, Mainz, Germany
[aa] Technical University of Munich, TUM School of Life Sciences, Ecoclimatology, Hans-Carl-v.-Carlowitz-Platz 2, 85354 Freising, Germany
[ab] Department of Agricoltural Forest and Food Sciences, University of Turin, Largo Paolo Braccini 2, 10095 Grugliasco, TO, Italy

* Corresponding author.
  E-mail address: christopher.leifsson@tum.de (C. Leifsson).

ac *Ecological-Botanical Garden, University of Bayreuth, 95447 Bayreuth, Germany*
ad *Department of Earth and Environmental Sciences, University of Pavia, Via S. Epifanio 14, I-27100 Pavia, Italy*
ae *University of Forestry, Dendrology Department, Forest Faculty, Sofia, Bulgaria*
af *Faculty of Silviculture and Forest Engineering, Department of Forest Engineering, Forest Management Planning and Terrestrial Measurements, Transilvania University of Brașov, Brașov, Romania*
ag *Center for Mountain Economy (CE–MONT), Vatra Dornei, Romania*
ah *Forest Biometrics Laboratory, Faculty of Forestry, "Stefan cel Mare" University of Suceava, Universitatii street, no. 13, Suceava RO720229, Romania*
ai *Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid. Ciudad Universitaria s/n, 28040 Madrid, Spain*
aj *Institute for Botany and Landscape Ecology, University Greifswald, 17487 Greifswald, Germany*
ak *University of Belgrade, Faculty of Forestry, Belgrade, Serbia*
al *Department of Forestry, Agricultural University Tirana, Tirana, Albania*
am *Chair of Forest Growth and Woody Biomass Production, TU Dresden, Dresden, Germany*
an *Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria*
ao *Weihenstephan-Triesdorf University of Applied Sciences, Department of Forestry, Hans-Carl-v.-Carlowitz-Platz 3, 85354 Freising, Germany*

HIGHLIGHTS

- Linear mixed-effects model used to derive individual and interactive effects.
- Growth variability and trends are more influential during wet conditions.
- Growth variables are decoupled and replaced by climate during dry conditions.
- Climate sensitivity decouples at driest conditions, indicating early-warning signal.

GRAPHICAL ABSTRACT

Drivers of non-stationary climate-growth relationships in F. sylvatica
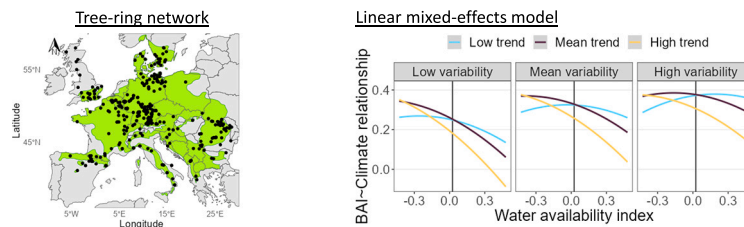
Growth variability, growth trends, and climatic water availability interact and significantly influence climate-growth relationships of growth in European beech

ABSTRACT

The future performance of the widely abundant European beech (*Fagus sylvatica* L.) across its ecological amplitude is uncertain. Although beech is considered drought-sensitive and thus negatively affected by drought events, scientific evidence indicating increasing drought vulnerability under climate change on a cross-regional scale remains elusive. While evaluating changes in climate sensitivity of secondary growth offers a promising avenue, studies from productive, closed-canopy forests suffer from knowledge gaps, especially regarding the natural variability of climate sensitivity and how it relates to radial growth as an indicator of tree vitality. Since beech is sensitive to drought, we in this study use a drought index as a climate variable to account for the combined effects of temperature and water availability and explore how the drought sensitivity of secondary growth varies temporally in dependence on growth variability, growth trends, and climatic water availability across the species' ecological amplitude.

Our results show that drought sensitivity is highly variable and non-stationary, though consistently higher at dry sites compared to moist sites. Increasing drought sensitivity can largely be explained by increasing climatic aridity, especially as it is exacerbated by climate change and trees' rank progression within forest communities, as (co-)dominant trees are more sensitive to extra-canopy climatic conditions than trees embedded in understories. However, during the driest periods of the 20th century, growth showed clear signs of being decoupled from climate. This may indicate fundamental changes in system behavior and be early-warning signals of decreasing drought tolerance. The multiple significant interaction terms in our model elucidate the complexity of European beech's drought sensitivity, which needs to be taken into consideration when assessing this species' response to climate change.

1. Introduction

Comprehensively understanding how forests' growth responds to the increasing frequency, severity, and duration of drought conditions is crucial for assessing their resilience to climate change (Anderegg et al., 2022; McDowell et al., 2020; Wang et al., 2023). The safeguarding of forests is necessary as they provide vital ecosystem services, including being a significant carbon sink of anthropogenic greenhouse gas emissions (Cabon et al., 2022; Friedlingstein et al., 2022; Pugh et al., 2019; Tagesson et al., 2020), contributing to biodiversity (FAO and UNEP, 2020; Leuschner and Ellenberg, 2017), providing biogeophysical feedback effects (Bonan, 2008; Liu et al., 2023; Makarieva and Gorshkov, 2007; Portmann et al., 2022; Smith et al., 2023) and contributing to human welfare and economy (FAO and UNEP, 2020; Hanewinkel et al.,

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1 Christopher Leifsson, Allan Buras, Stefan Klesse, Anja Rammig and Christian S. Zang are ordered manually.
2 Author's ordered alphabetically by their surnames
3 Deceased.

2014). The relatively stable climatic conditions that European forests have evolved under are on an unprecedented trajectory (IPCC, 2021), and the impacts of climate change on forests may be augmented by centuries of management, which has led to non-natural distributions of many species (Brunet et al., 2010; Forest Europe, 2020). Given the long lifespans and slow recruitment of trees, forest management is challenged by selecting tree species for rejuvenation that can cope with the projected climatic conditions in the 21st century and beyond (Anderegg et al., 2022; Berner and Goetz, 2022; Brodribb et al., 2020; Quetin et al., 2023).

To quantify trees' resilience to climate change, approximating annual increments in secondary growth using tree-ring width measurements (TRW) is frequently used. Secondary growth is directly linked to carbon storage and economic value (Fritts, 1976; Gea-Izquierdo and Sánchez-González, 2022; Hanewinkel et al., 2014) and has the advantage of providing spatially and temporally extensive information on acute and chronic growth changes in response to climate (Anderegg et al., 2015; Babst et al., 2013; Kannenberg et al., 2019; Leifsson et al., 2023). Converting TRW to basal area increments (BAI) can further improve the connection to secondary growth, as BAI is a more accurate predictor of actual annual biomass increments (Babst et al., 2014; LeBlanc, 1990; Visser et al., 2023). However, secondary growth has a limited capacity to reveal changes in the underlying mechanisms that govern growth in response to climate change. Recent studies have indicated these mechanisms are better elucidated by quantifying alterations in the sensitivity of growth to climate variables, as expressed by statistically quantifying climate-growth relationships (Heilmayr et al., 2023; Kannenberg and Maxwell, 2022; Peltier and Ogle, 2020) because climate sensitivity of growth varies in accordance with how limiting climate variables are for growth (Stine and Huybers, 2017). If those climatic limitations change, so does the climate sensitivity of growth, potentially revealing changes in the underlying mechanisms irrespective of responses of secondary growth, making it an essential aspect of tree-ring-based assessments of climate-change resilience (Kannenberg and Maxwell, 2022; Peltier and Ogle, 2020).

Climate sensitivity of growth is well understood to vary according to site-specific climatic conditions (Babst et al., 2013; Buras et al., 2018; D'Orangeville et al., 2018; Klesse et al., 2018b; Lange et al., 2018; Marchand et al., 2019; Muffler et al., 2020; Zeng et al., 2022) and to structural details of forests, such as strata, density, and composition (Keen et al., 2021; Marchand et al., 2019; Mausolf et al., 2018; Metz et al., 2020; Wang et al., 2023; Zang et al., 2012, 2014). Just as climate sensitivity of growth varies with spatial climate variability, climate also features a temporal variability called non-stationarity (Anderson-Teixeira et al., 2022; Babst et al., 2019; Harvey et al., 2020; Lange et al., 2018; Leifsson et al., 2023; Muffler et al., 2020; Peltier and Ogle, 2020; Szejner et al., 2020; Tumajer et al., 2022; Weigel et al., 2023). Remarkably, Wilmking et al. (2020) showed in their review of almost 2000 papers that 2/3 had not tested for non-stationary climate-growth relationships, while more than half of the remaining 1/3 did report non-stationary climate-growth relationships. Therefore, climate-change-induced deviations in climate-growth relationships must be quantified against the backdrop of the natural variability of climate-growth relationships.

Large-scale tree-ring networks tend to be composed mainly of samples from dominant trees in proximity to the margins of the respective species' distributional range (Cook and Kairiukstis, 1990; Fritts, 1976; Grissino-Mayer and Fritts, 1997). Consequently, data from ecologically oriented productive and closed-canopy forests are comparatively underrepresented (Amoroso et al., 2017; Klesse et al., 2018a; Zhao et al., 2019). However, climate signals are weaker in these environments due to more moderate climatic conditions, more complex structural composition, and greater competition, with the latter two likely also influenced by forest management (Astigarraga et al., 2020; Dulamsuren et al., 2022; Keen et al., 2021; Marqués et al., 2022b; Mausolf et al., 2018; Rollinson et al., 2021; Wang et al., 2023). The implication for

estimating climate-growth relationships in closed-canopy forests is that they are likely influenced by changes in trees' social status within forest communities due to ontogeny, as there is a stark contrast between juvenile trees growing in the relatively moist and shaded understories compared to large (co-)dominant trees which are more exposed to macro-climatic conditions (Brienen et al., 2022; Leuschner et al., 2023a). The greater exposure to macro-climate of (co-)dominant trees may make them more susceptible to drought conditions and drought-induced stress, leading to lower or declining growth rates and higher growth variability and climate sensitivity (Anderson-Teixeira et al., 2022; Cailleret et al., 2019; Hansen et al., 2022; Jump et al., 2006; Wang et al., 2023), amplified by increasing climatic stress under climate change (Buras and Menzel, 2019; Wang et al., 2023). Low and negative growth trends have been connected to deteriorating tree vitality (Cailleret et al., 2017; Dobbertin, 2005; Dulamsuren et al., 2022; Klesse et al., 2022; Neycken et al., 2022, 2024; Pedersen, 1998; van der Maaten et al., 2024), while increasing growth variability and climate sensitivity have been connected to early warning signals of mortality following drought stress (Cailleret et al., 2019; Camarero et al., 2015; Keen et al., 2021).

The question that follows is if, and then how, growth trends and growth variability influence the sensitivity of BAI to climatic conditions. Detrending BAI, as done in some studies (Anderson-Teixeira et al., 2022; Bernal-Escobar et al., 2022; Jump et al., 2006; Pedersen, 1998; Weigel et al., 2023), leads to quasi-stationary BAI variability, but may mask crucial ecological information. Other studies limited their analyses to only mature trees after a juvenile period of rapid growth. However, defining juvenile periods is problematic in closed-canopy forests as growth patterns are more complex due to dependence on non-climatic environmental factors, such as variations in incoming radiation and resources due to competition. To the best of our knowledge, no study has comprehensively analyzed how climate sensitivity varies with growth rates expressed as BAI in closed-canopy forests.

Therefore, the specific aim of this study is to explore how growth trends, growth variability, and climatic conditions modulate climate sensitivity. For this purpose, we use a drought index as a climate variable, and will consequently, from here on, refer to drought sensitivity instead of climate sensitivity and drought conditions instead of climatic conditions. We furthermore use European beech (*Fagus sylvatica* L.) tree-ring data from a European-wide network of sites (Dorado-Liñán et al., 2022; Hacket-Pain et al., 2018; Martinez del Castillo et al., 2022). Contrary to the common issue of forest representativeness discussed above, the data in this network has been sampled for ecologically oriented purposes in closed-canopy forests. European beech is a native species across most of the European continent while also being one of the most dominant and economically important tree species (Hanewinkel et al., 2013; Leuschner and Ellenberg, 2017). Since beech is considered drought-sensitive and is widely known to feature a strong dependence on water availability (Dorado-Liñán et al., 2022; Leuschner, 2020; Mazza et al., 2024; Weigel et al., 2023), and has been shown to potentially decline in future abundance (Buras and Menzel, 2019), the species' future under climate change is of great importance for many European ecosystems and economies (Gessler et al., 2007; Leuschner, 2020). With an increasing focus on dendroecological studies in the complex environments of closed-canopy forests, significant knowledge gaps regarding the underlying drivers of altered drought sensitivity of secondary growth must be addressed, especially on a cross-regional scale, to accurately understand the species' future under global change.

To improve our understanding of the variability of climate-growth relationships in beech trees in closed-canopy forests, we tested the following hypotheses. (H1) Drought sensitivity is positively related to growth variability, and (H2) Drought sensitivity is negatively related to growth trends. Both of these hypotheses are based on the expectation that growth becomes increasingly governed by climatic stress due to climate change and due to an increasing influence of extra-canopy climate conditions when trees reach a (co-)dominant status. (H3a) Drought sensitivity is positively related to temporal variations in

drought conditions since climatic constraints on tree growth are amplified during drier conditions. Similarly, (H3b) drought sensitivity is higher at drier sites than wet sites since tree growth is more constrained by the drier conditions. Consequently, H3a and H3b are distinctly different in that they refer to temporal and spatial variations in drought conditions, respectively. Since it seems likely that these effects on drought sensitivity interact, we furthermore explore whether there are interactive and non-linear effects of the predictor variables growth trends, growth variability, and water availability that modulate their relationships with drought sensitivity.

2. Methods and materials

2.1. Tree-ring data

We obtained tree-ring width (TRW) measurements of European beech (*Fagus sylvatica* L.) from 344 sites from a European tree-ring network (Fig. 1) (Dorado-Liñán et al., 2022; Hacket-Pain et al., 2018; Martinez del Castillo et al., 2022). We calculated basal area increments (BAI) as $BAI_t = \pi R_t^2 - \pi R_{t-1}^2$ where R_t is the stem radius at the end of an annual increment and R_{t-1} is the stem radius at the beginning of the annual increment. For the trees where diameter at breast height (DBH) had been measured, BAIs were calculated by sequentially subtracting from the measured DBH towards the pith. When DBH had not been measured, BAIs were calculated by adding them up sequentially from the pith out. If the former option resulted in BAI being negative (due to a mismatch between measured DBH and sum of TRWs), BAI was calculated according to the second option (see the bai.out function of the dplR-package for details, Bunn et al., 2020). To retain absolute rates of basal area increments, we did not standardize the sites' BAI time series. However, they were log-transformed because BAI is multiplicative, and growth variability increases with increasing growth rates. Site-level chronologies were then calculated from the log-transformed BAI time series by robust averaging for all years with at least four trees (Fritts, 1976).
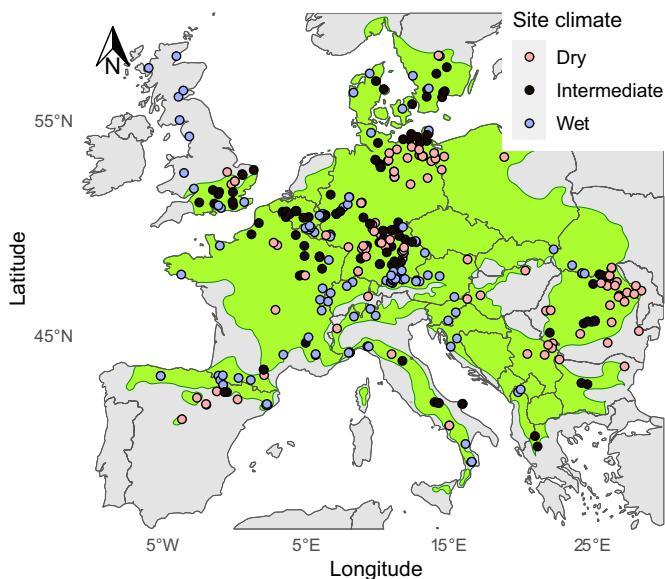
Fig. 1. Analyzed sites colored according to subsetted dry, intermediate, and wet tertile groups based on mean annual climatic water balance (see section 2.5 for details). Topography is a major factor in determining these categories and explains the close spatial proximity of dry and wet sites. The green background area indicates European beech's continuous geographical distribution (Caudullo et al., 2017).

2.2. Climate data

We obtained monthly minimum, mean, and maximum temperature data from 1901 until 2016, the year of the most recent tree-ring, at a spatial resolution of 0.5° from the Climate Research Unit (CRU) TS 4.04 dataset (Harris et al., 2020). Concurrent precipitation data was obtained at the same resolution from the Global Precipitation Climatology Center (GPCC) version 2018 (Schneider et al., 2014). To conform to local topographical effects, these gridded products were downscaled to 30-arc sec resolution using CHELSA version 1.2 (Karger et al., 2017). We used the drought index Standardized Precipitation-Evapotranspiration Index (SPEI) to represent the major climatic variability controlling tree growth as it accounts for the combined effects of both temperature and precipitation. To calculate SPEI, we first calculated modified Hargreaves potential evapotranspiration (PET) (Droogers and Allen, 2002; Hargreaves, 1994), then subtracted PET from precipitation to calculate climatic water balance ($CWB = P - PET$, Thornthwaite, 1948), which was then standardized into SPEI (Vicente-Serrano et al., 2010). Because light, temperature, and water resources are heterogeneously available between sites, the response of growth to the timing and time scale of these resources also differ between sites (Vicente-Serrano et al., 2013). To account for this variability, we identified the timing and time scale of SPEI that best explained tree-ring growth at each site (Leifsson et al., 2023) by calculating SPEI integrations of 2–12 months for April–September at every site and correlated all these time frames and integrational scales of SPEI with the respective sites' BAI chronologies. For each site, we then selected the one combination of SPEI timing and scale that showed the highest positive and significant correlation (Fig. S1), using Spearman's rank to account for potentially non-normally distributed data. This site-specific combination of timing and scale (from here on called SPEIx-month) selected for each site was the only one used for the respective sites for all further analyses.

2.3. Moving window analyses

We used a moving window approach to estimate the temporal variability of the BAI chronologies' drought sensitivity. We set the window length to 31 years to balance having enough data points for robust estimations and allowing for good temporal variability. Each window was always moved by one year at a time. Each site was analyzed individually to estimate the following variables for all available windows: 1) *Drought sensitivity* of BAI to the site-specific combination of SPEIx-month using Spearman's rank correlation. To avoid inflated correlations due to collinear overall trends of the relatively short 31-year windows and emphasize correlations of the high-frequency inter-annual variability, both BAI and SPEIx-month were detrended by linear regression against time in each window. 2) *Growth trend* of (log-transformed) BAI calculated as the regression coefficient between BAI and time. Contrary to BAI used for SPEI-sensitivity correlations; BAI is not detrended against time for the growth trends. 3) *Growth variability* determined as the standard deviation of the residuals of the growth trend just described. 4) *SPEI climatology* determined as the average undetrended SPEI, indicating drier and wetter climatic periods. Because all sites contained >40 years, a minimum of ten 31-year windows could be fit per site, resulting in at least ten of each of the above variables being calculated per site. Although strong collinearities between these moving window-derived variables within sites sometimes occurred, there were no overall collinearities across all sites (Fig. S2), supported by variance inflation (VIF) <1.5 for the explanatory variables (Zuur et al., 2010). We additionally performed further data exploration following the protocol of Zuur et al. (2010), ensuring that no assumptions were violated and lowering the risk of type I and type II errors. Finally, the inherent autocorrelation of these variables induced by the moving window method will be accounted for in the linear mixed-effects model explained in Section 2.4.

2.4. Linear mixed-effects model

The resulting time series of the moving window-derived variables were supplied to a linear mixed-effects model. To answer our hypotheses, growth trends, growth variability, and SPEI climatology were supplied as predictor variables, and drought sensitivity as the response variable. We tested for non-linear relationships between each site's response variable all predictor variables. Akaike Information Criterion (AIC) of linear and quadratic terms was compared, and it was shown that AIC was more frequently lower for quadratic terms than for linear terms (Fig. S3). Because of this we included non-linear terms of all predictor variables (Anderson-Teixeira et al., 2022). We additionally included all two-way interactions between the predictor variables, as drought conditions can influence both growth trends and variability (Astigarraga et al., 2020; Hansen et al., 2022), and growth trends may influence growth variability (Cailleret et al., 2019; Camarero et al., 2015; Klesse et al., 2018b; Neycken et al., 2022).

Due to the multiple linear, non-linear, and interaction terms, all variables were z-score standardized (Fig. S4). This improves the model performance by removing collinearities between the parameters of the main effects and their interactions, making them independent and interpretable (Gelman and Hill, 2007; Harrison et al., 2018; Schielzeth, 2010). The standardization was done at the level of each variable so that between-site variations within each variable were retained and could be accounted for in the model. A maximal model was created, including second-order polynomials of all variables and all two-way interactions. All estimated parameters were significant, except for the interaction between growth trends and growth variability, which was removed (Table S1). This resulted in the optimal model

$$DS_{ij} = \beta_0 + \beta_1 G_{ij} + \beta_2 G_{ij}^2 + \beta_3 V_{ij} + \beta_4 V_{ij}^2 + \beta_5 C_{ij} + \beta_6 C_{ij}^2 + \beta_7 GC_{ij} + \beta_8 VC_{ij}$$
$$+ \upsilon_j + \epsilon_{ij}$$

(1)

where DS_{ij} is the drought sensitivity of BAI, G_{ij} is the growth trend of BAI, V_{ij} is the growth variability, C_{ij} is the SPEI climatology, while GC_{ij} and VC_{ij} are the respective interactions. In all cases, i refers to an observation at site j, and hence υ_j refers to the random effect of the site-level intercept while ϵ_{ij} is the error associated with the ith observation at site j. β_{0j} and β_1, …,β_8 refer to the fixed effect intercept and the regression coefficients of all main effects, quadratic effects, and interactions common across all sites. An autocorrelation structure with calendar year as a continuous within-site time covariate was included in the model, successfully addressing the considerable autocorrelation in the data induced by the moving window method (Fig. S5). We set the method to maximum likelihood (ML) during the model selection process but changed to restricted maximum likelihood (REML) for parameter estimation following best statistical practice (Harrison et al., 2018; Pinheiro and Bates, 2000; Zuur et al., 2009).

2.5. Assessing the effect of site aridity on model predictions

While the model in Eq. 1 tests for the effect of temporal variations in SPEI climatology within sites, we also assessed how the model predictions differed depending on site climate. To do so, we created two subsets of sites, one with the driest and one with the wettest tertile of sites, based on the sites' mean annual CWB. The mean annual CWB was calculated over the whole period for which we had climate data (1901 to 2016), irrespective of the length of the TRW-chronologies of the respective sites, to avoid bias. Due to the lack of objective thresholds, we determined the dry and wet subsets based on tertiles. The mean annual CWB of the dry tertile group ranged between −439.5 and 125.8 mm y^{-1}, whereas the wet tertile group ranged between 349.5 and 1555 mm y^{-1} (Fig. 2). Comparing these sites by mean annual precipitation sum and mean annual temperature showed an overlapping border between the groups caused by the modified Hargreaves PET, taking into account differences in incoming radiation at different latitudes (Figs. 1 and 2).

The two subsets of relatively wet and relatively dry sites (high and low mean annual CWB, respectively) were applied to Eq. 1 individually, allowing group-specific estimations of all parameters (Table S2). The subset of sites with intermediate climatic conditions (middle tertile) was not analyzed.

2.6. Visualization of drought sensitivity responses

To show how drought sensitivity reacts to all three predictor variables, we created full factorial matrices of −2, 0, and + 2 standard deviations (σ) between all three pairwise combinations of growth variability, growth trends, and SPEI climatology, resulting in matrices with nine levels each. Each explanatory variable was combined in its continuous version with the categorical matrix of the other two variables, which were applied to Eq. 1. This allowed drought sensitivity to
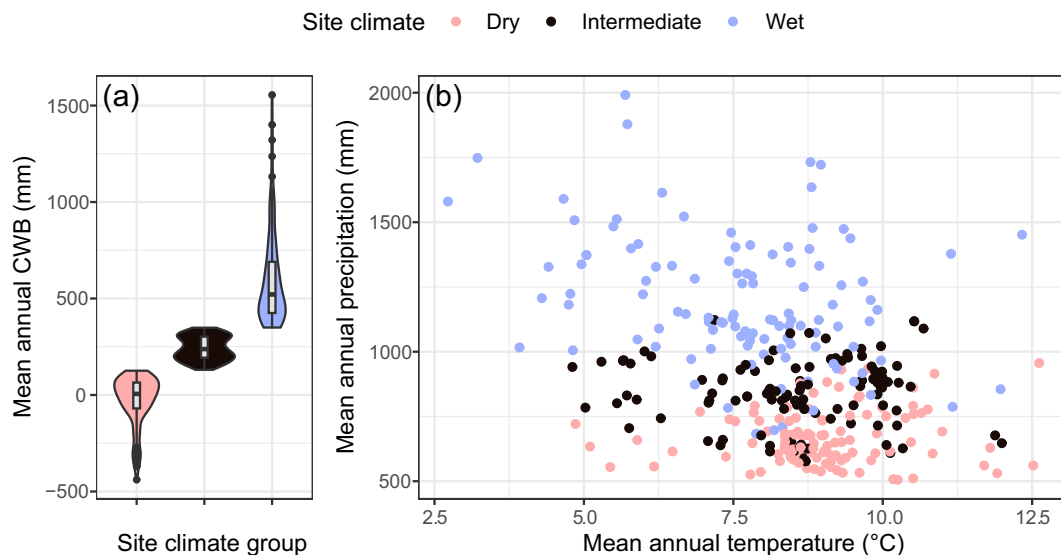
Fig. 2. Dry, intermediate, and wet tertile subsets of sites used to compare effects of site climate. Climatic conditions between 1901 and 2016 are shown as (a) mean annual climatic water balance (CWB) and (b) within their climate envelope. The overlap of groups in (b) is due to CWB accounting for differences in incoming radiation depending on latitude.

vary as a function of the continuous variable for each of the nine configurations of the other two predictor variables. Note that standard deviations are calculated from 31-year averages of all explanatory variables, as per the moving window approach (Section 2.3), and are therefore not equal to standard deviations of the initial input data (e.g. -2 σ in SPEI climatology $\neq$ -2 σ in SPEI). The predictions were calculated based on the group-specific model parameters to compare dry and wet sites.

3. Results

3.1. Model overview

Drought sensitivity was most sensitive and negatively related to SPEI climatology (Table 1), indicating drought sensitivity increased with increasingly dry conditions. Drought sensitivity was positively related and second most sensitive to growth variability, indicating drought sensitivity increased with higher growth variability. Drought sensitivity was least sensitive and negatively related to growth trends, indicating drought sensitivity decreased slightly with increasing growth trends (Table 1). All quadratic terms showed negative signs, indicating concave-down non-linear relationships between drought sensitivity and all explanatory variables. Drought sensitivity was again most sensitive to the quadratic term of SPEI climatology, but less sensitive to the quadratic term of growth variability compared to the respective term of growth trends, in contrast to their linear terms. The interaction between SPEI climatology and growth trends (GC) was negative, meaning that the relationships between these variables and drought sensitivity become more negative with higher (wetter) SPEI climatology and higher growth trends. In comparison, the interaction between SPEI climatology and growth variability (VC) was positive, meaning that the relationships between these variables and drought sensitivity became more positive with increasing (wetter) SPEI climatology and increasing growth variability (Table 1). Consequently, the negative relationship between SPEI climatology and drought sensitivity is influenced in opposite directions by growth trends and growth variability, the former enhancing the negative relationship and the latter mitigating and potentially reversing it. While all parameters in the model were significant, the explained variance was low, with marginal $R^2 \sim 0.08$ and conditional $R^2 \sim 0.08$ (Nakagawa et al., 2017), indicating high variance in the estimated parameters.

3.2. Response of drought sensitivity

To visualize how drought sensitivity reacts to all three predictor variables of the model (Table 1), the following three sections display drought sensitivity varying as a function of each continuous variable for each of the nine configurations of the other two predictor variables.

Table 1

Estimated parameters of the restricted maximum likelihood (REML) best model. G is growth trends, V is growth variability, and C is SPEI climatology. V^2, G^2, and C^2 are the quadratic terms of the respective linear terms. GC and VC are the interactions between the respective linear terms.

Parameter	Value	Std.Error	t-Value	p-Value
Intercept	0.083	0.038	2.184	0.029
G	−0.080	0.012	−6.686	0.000
G^2	−0.045	0.004	−10.608	0.000
V	0.148	0.010	14.847	0.000
V^2	−0.016	0.003	−5.225	0.000
C	−0.219	0.008	−27.742	0.000
C^2	−0.060	0.004	−14.384	0.000
GC	−0.093	0.007	−13.236	0.000
VC	0.059	0.006	9.505	0.000

3.2.1. Effects of growth variability on drought sensitivity

Drought sensitivity generally increased with increasing growth variability, with a comparably small quadratic effect due to an order of magnitude difference between the two terms (Table 1, Fig. 3). However, while the coupling of the positive relationship increased with wetter-than-average SPEI climatology, it decreased with drier-than-average SPEI climatology to the point that the relationship between growth variability and drought sensitivity was lost during the driest conditions, as indicated by the flat slope of the yellow lines in Fig. 3. The difference in drought sensitivity between the lower and upper ends of the growth variability range was 0.02, 0.12, and 0.22 for dry, average, and wet SPEI climatology, respectively. In comparison, the difference in mean drought sensitivity between dry and wet periods increased with increasing growth trends, as indicated by the increasing distance between lines between the facets in Fig. 3. During wet periods, mean drought sensitivity decreased significantly with increasing growth trends, 0.26, 0.19, and 0.04 for −2, 0, and + 2 σ, respectively. During dry periods, the difference was not as large and instead increased slightly with growth trends, 0.29, 0.37, and 0.38 for −2, 0, and + 2 σ, respectively. Consequently, while mean drought sensitivity increased with declining SPEI climatology (drier periods), this pattern was broken at low growth trends (Fig. 3a).

3.2.2. Effects of growth trends on drought sensitivity

The relationship between drought sensitivity and growth trends was relatively weak compared to the other variables. However, the quadratic term and interaction term with SPEI climatology were higher compared to the corresponding terms for growth variability (Table 1). Overall, drought sensitivity decreased with increasing growth trends and more so with higher (wetter) SPEI climatology (Fig. 4). The difference in drought sensitivity between −2 and + 2 σ of growth trends was −0.07 and − 0.22 for average and wet SPEI climatology, respectively (cyan and purple lines in Fig. 4a compared to Fig. 4c). However, the relationship between growth trends and drought sensitivity switched to become positive during dry climatic periods, with a corresponding difference in drought sensitivity of 0.09 (yellow lines in Fig. 4a compared to Fig. 4c). This was caused by the relatively high estimate of the interaction term between growth trends and SPEI climatology compared to the linear and quadratic terms of growth trends (Table 1). A consequence of this is that under average SPEI climatology, the highest drought sensitivity is found around a growth trend of approximately zero. In contrast, it is found at declining growth trends at wetter-than-average periods and at increasing growth trends at drier-than-average periods (Fig. 4).

The negative relationship between growth trends and drought sensitivity became more negative with increasing SPEI climatology. The difference in mean drought sensitivity between −2 and + 2 σ of SPEI climatology was 0.28 and 0.09 for −2 and + 2 σ of growth variability, respectively, although mean drought sensitivity was higher in the latter case. Furthermore, the interaction between growth trends and SPEI climatology led to a change from a negative to a positive relationship between growth trends and drought sensitivity in drier-than-average periods (yellow line compared to cyan and purple lines in Fig. 4).

3.2.3. Effects of SPEI climatology on drought sensitivity

Drought sensitivity was most sensitive to the respective linear and quadratic terms of SPEI climatology, in addition to SPEI climatology being the only explanatory variable that significantly interacted with the other explanatory variables (Table 1). SPEI climatology had an overall negative relationship with drought sensitivity, though it reversed to a positive relationship due to interactions (Fig. 5). As indicated in Figs. 3 and 4, drought sensitivity became insensitive to variations in growth variability and growth trends at very low (dry) SPEI climatology (left edges of facets in Fig. 5). At low (dry) SPEI climatology, the difference in drought sensitivity between −2 and + 2 σ of growth variability was 0.02 for all values of growth trends. This was in contrast to high (wet) SPEI climatology (right edges of facets in Fig. 5), where drought sensitivity
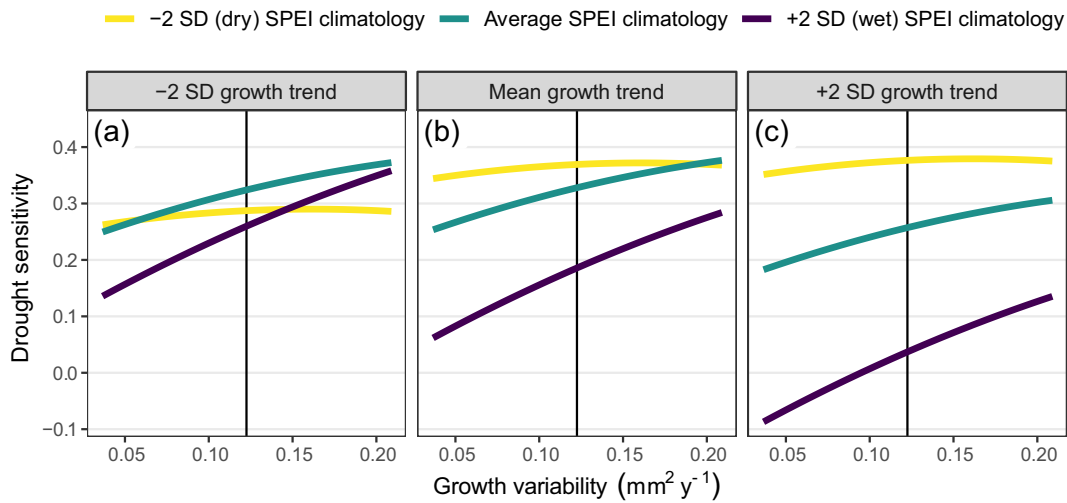
Fig. 3. Drought sensitivity (DS) as a function of growth variability (V) for −2, mean, and + 2 standard deviations of SPEI climatology (C, colors; yellow, teal, and purple, respectively) and growth trend (G, facets; (a), (b) and (c), respectively). The left and right edges of the facets represent −2 and + 2 standard deviations of the distribution of growth variability values, respectively. X- and y-axes are presented as non-standardized variables to improve interpretation. Predictions based on the x-axis variable outside ±2 standard deviations have been cut to adhere to the same distribution range as the categorized variables (colors and facets). The black vertical line indicates the mean of the distribution of growth variability. The data shown are fixed effects level predictions. The corresponding figure distinguishing between dry and wet sites can be found in Fig. S7.
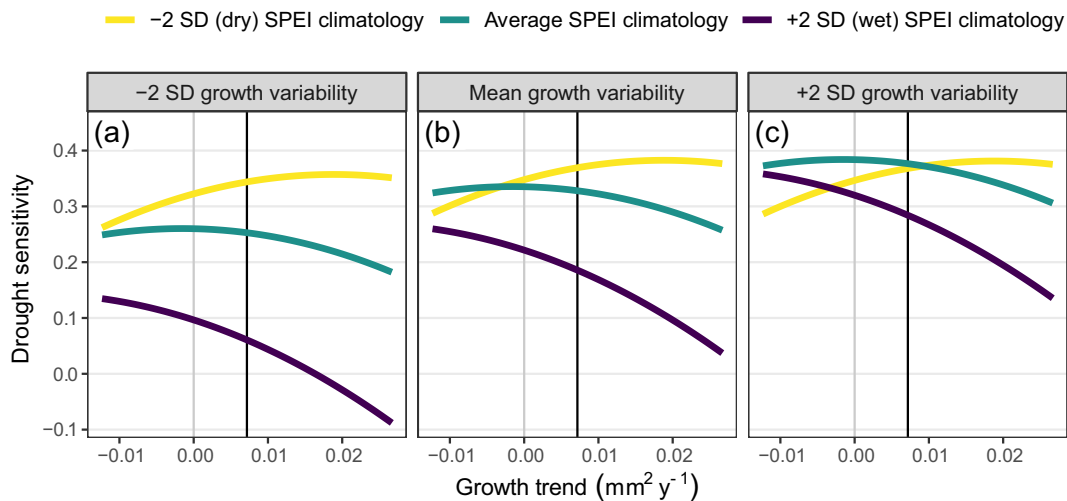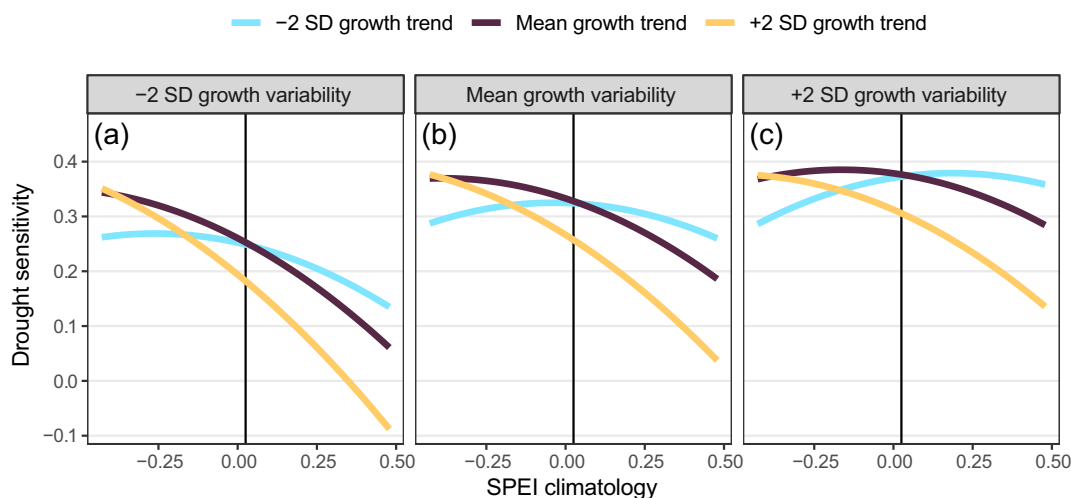

Fig. 4. Drought sensitivity (DS) as a function of growth trend (G) for −2, mean, and + 2 standard deviations of SPEI climatology (C, colors; yellow, teal, and purple, respectively) and growth variability (V, facets; (a), (b) and (c), respectively). The left and right edges of the facets represent −2 and + 2 standard deviations, respectively, of the distribution of growth trend values. X- and y-axes are presented as non-standardized variables to improve interpretation. Predictions based on the x-axis variable outside ±2 standard deviations have been cut to adhere to the same distribution range as the categorized variables (colors and facets). The black vertical line indicates the mean of the distribution of growth trends, while the gray vertical line indicates the point of no growth trend, separating increasing and decreasing trends (corresponding to −0.73 standard deviations from the mean). The data shown are fixed effects level predictions. The corresponding figure distinguishing between dry and wet sites can be found in Fig. S8.

declined rapidly with decreasing growth variability and increasing growth trends, resulting in a corresponding difference in drought sensitivity of 0.22. Consequently, there was a shift in maximum drought sensitivity towards higher (wetter) SPEI climatology with increasing growth variability and decreasing growth trends. At below-average growth variability and above-average growth trends (purple and orange lines in Fig. 5a), maximum drought sensitivity was found at $< -2\,\sigma$ of the SPEI climatology distribution (i.e., more negative than the minimum SPEI climatology shown in Fig. 5a). At above-average growth variability and below-average growth trends, this point shifted to inside the $\pm 2\,\sigma$ distribution of SPEI climatology (i.e., inside Fig. 5c). At $-2\,\sigma$ of growth trends and $+ 2\,\sigma$ of growth variability (cyan line in Fig. 5c), maximum drought sensitivity occurred at wetter-than-average SPEI

climatology, with the consequence of a strong decline in drought sensitivity towards drier-than-average periods.

3.2.4. Effect of site aridity on drought sensitivity

The model parameters created for dry and wet tertiles of sites were largely similar but with some differences (Fig. 6, Table S2). The more notable difference was a large difference in intercept, which was positive for dry sites but negative for wet sites. The consequence was a considerably higher mean drought sensitivity for dry sites than wet sites (Fig. S6a and S7-S9). Other differences in model parameters between dry and wet tertiles of sites were higher effects for the linear term for growth variability (V), the quadratic term for growth trends (G^2), and the interaction between growth variability and SPEI climatology (VC), as

Fig. 5. Drought sensitivity (DS) as a function of SPEI climatology (C) for −2, mean, and + 2 standard deviations of growth trend (G, colors; turquoise, black, and orange, respectively) and growth variability (V, facets; (a), (b) and (c), respectively). The left and right edges of the facets represent −2 and + 2 standard deviations, respectively, of the distribution of SPEI climatology values. X- and y-axes are presented as non-standardized variables to improve interpretation. Predictions based on the x-axis variable outside ±2 standard deviations have been cut to adhere to the same distribution range as the categorized variables (colors and facets). The black vertical line indicates the mean of the distribution of SPEI climatology. The data shown are fixed effects level predictions. The corresponding figure distinguishing between dry and wet sites can be found in Fig. S9.
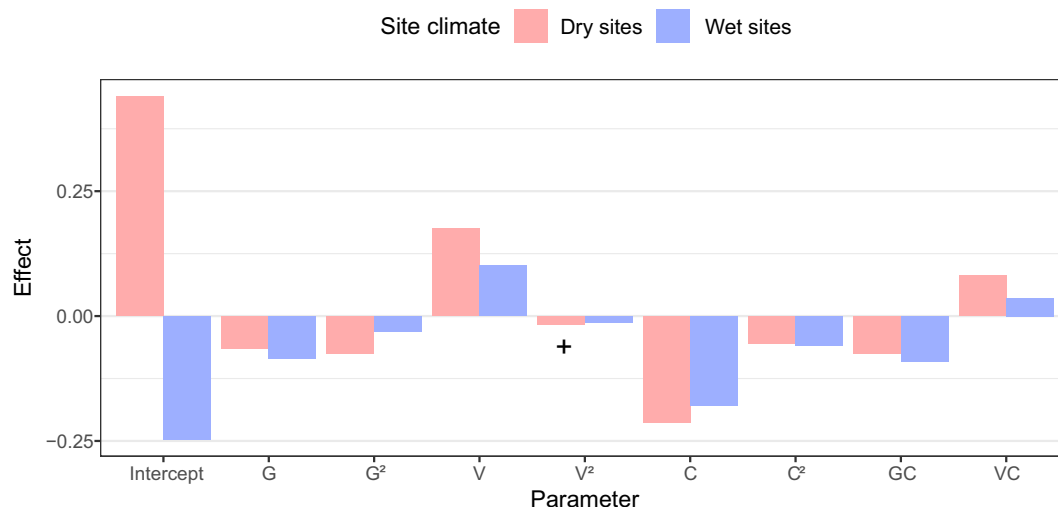
Fig. 6. Comparison of parameter effects for dry and wet subsets of sites after being supplied to Eq. 1 (Table S2). Non-significant parameters are indicated by a '+' and were kept as the model was created based on all data (see section 2.4).

well as a somewhat higher effect of the linear term for SPEI climatology (C), in dry sites compared to wet sites (Fig. 6). The model for dry sites did not show that the quadratic term for growth variability was significant, though the effect was still marginally higher than that for wet sites (Fig. 6). These effects were underlined by slight positive shifts in the distributions of growth trends and growth variability for dry sites compared to wet (Fig. S6b and c).

The greater effect of the linear term for growth variability for dry sites resulted in an overall much more sensitive relationship with drought sensitivity (Fig. S7). However, the interaction between growth trends and SPEI climatology was also greater, resulting in a similar relationship between growth variability and drought sensitivity for dry and wet sites at the driest distribution range of SPEI climatology (compare the increasing difference in sensitivity between yellow and purple lines in Fig. S7).

Comparing the relationship between growth trends and drought sensitivity between dry and wet sites showed that, on the one hand, the

linear term was higher for wet sites, but on the other hand, the quadratic term was higher for dry sites (Fig. S8). The relationship consequently showed a more pronounced peak drought sensitivity for the dry sites, especially for average and wetter-than-average SPEI climatology, which more frequently occurred within $\pm 2\,\sigma$ of the growth trends distribution, in contrast to the wet sites where it occurred at lower growth trends than $-2\,\sigma$ (Fig. S8).

The relationship between SPEI climatology and drought sensitivity showed the least difference between the dry and wet sites' respective model terms (Fig. S9). The greatest difference was the greater interaction term between SPEI climatology and growth variability for dry sites, which was most pronounced at the lower range of the distribution of growth variability, where the relationship between growth variability and drought sensitivity was more negative than for wet sites (compare the steepness of the slopes of dry and wet sites in Fig. S9a). As a result, the difference in drought sensitivity between dry and wet sites increased with drying SPEI climatology, which is also evident in the corresponding

figure for growth variability (compare the distance between dashed and solid lines in Fig. S7a to Fig. S7c).

3.3. Temporal trends of variables

The distributions of the four variables, drought sensitivity of growth (DS), growth trends (G), growth variability (V), and SPEI climatology (C), all showed different temporal trends (Fig. S10). The response variable, drought sensitivity, showed a significant positive trend ($P < 0.01$), as did growth variability ($P = 0.019$). Growth trends showed a positive trend until approximately 1960 ($P < 0.001$), after which it shifted to a negative trend that continued until the present ($P < 0.001$). SPEI climatology exhibited a more complex long-term fluctuation. In the 1930s–50s, the distributions of values had medians slightly lower than 0, indicating that most sites were slightly drier than on average. This shifted towards the 1970s–80s when the medians of the distributions were slightly >0, indicating that most sites were slightly wetter than on average. Since the 1980s, the distributions trended towards average climatic conditions, with the most recent median being approximately 0 (Fig. S10). Note that the SPEI climatology shown here is that of the analyzed sites (Fig. 1) and is not representative of the region that makes up the ecological amplitude of beech, let alone Europe as a whole. Furthermore, the annual distributions of variable values do not reveal potential trends within individual sites.

4. Discussion

4.1. Effects of growth variability on drought sensitivity (H1)

The model identified growth variability as having an overall positive influence on drought sensitivity (i.e., a tightened coupling) in accordance with our first hypothesis (H1). This is in line with the central claim in dendroclimatology that increased inter-annual growth variability is driven by a stronger translation of climatic variability into growth variability, i.e., drought sensitivity, rather than originating from internal processes decoupled from climate (Bunn et al., 2013; Fritts, 1976; LaMarche, 1978). The relationship can partly be explained by changes in trees' social status within forest communities due to ontogeny and partly by increasingly dry climatic conditions. Juvenile trees are embedded in the relatively moist micro-climate of the understory, preventing a strong influence of ambient climate outside the canopy layer. This understory embedding is removed as the trees reach a (co-)dominant status once their crowns become increasingly exposed to incoming radiation and extra-canopy climatic conditions (Brienen et al., 2022; Leuschner et al., 2023a). Furthermore, growth variability is negatively correlated with SPEI climatology (Fig. S2), indicating that increasingly dry climatic conditions (i.e., decreasing SPEI climatology) lead to increasing growth variability and thereby indirectly influencing drought sensitivity. The increasing influence of climate on growth equals greater drought sensitivity and consequently inter-annual growth variability (Bunn et al., 2013; Carrer and Urbinati, 2004; Leuschner et al., 2023a; Thom et al., 2023; Weigel et al., 2023; Zang et al., 2014). This may further explain the more sensitive relationship between growth variability and drought sensitivity at drier sites compared to wetter sites during wet climatic periods (Fig. S7), as the dry sites are in greater need of water due to typically dry conditions.

However, the non-linear relationship tapers off with increasing growth variability, eventually reaching a saturation point and suspending the translation between climate variability and growth variability (Bunn et al., 2013). This occurs at lower values of growth variability with increasingly dry conditions, when mean drought sensitivity is also higher, possibly due to greater exposure to extra-canopy climatic conditions. The likely conclusion is that a climatic threshold has been passed beyond which the physiological mechanisms can tolerate (i.e., beyond an optimum response curve discussed in Wilmking et al., 2020). This is in contrast to the increasing climate sensitivity

expected if the climate is more growth-limiting, as is the case for most of the SPEI climatology range (Fig. 5). This explains the higher mean drought sensitivity during wetter-than-average periods and low and declining growth trends (purple and teal lines in Fig. 3a and 4) as such growth rates may be related to stressed trees, which are more sensitive to drought conditions (Neycken et al., 2022), raising drought sensitivity under wetter-than-average conditions but lowering drought sensitivity under dry conditions. Likewise, the lower mean drought sensitivity during wetter-than-average periods and high growth trends (purple and teal lines in Fig. 3c and 4) also concur with trees' social status within forest communities. High growth rates are more likely to be related to juvenile trees, which are more likely to be embedded in the moist and shaded understory where they are less responsive to inter-annual variability of climate during wet periods but better able to utilize temporarily warm periods compared to declining trees (Thom et al., 2023; Wang et al., 2023).

The lack of a clear relationship between drought sensitivity and growth variability (i.e., decoupling) during dry periods (yellow lines in Fig. 3) may also be an effect of increasing climatic stress due to climate change. This might explain why mean drought sensitivity is lower at low growth trends, as trees with these growth rates may be more vulnerable to increased climate stress. In comparison, while the relationship between drought sensitivity and growth variability is also decoupled at high growth trends, the higher mean drought sensitivity may be explained by the considerable buffering capacity against extra-canopy climate in understories of beech forests (Leuschner et al., 2023a). Lastly, when comparing dry and wet sites during dry periods, there is no apparent difference in the sensitivity of the relationship between growth variability and drought sensitivity. In contrast, it is considerably more sensitive in dry sites than in wet sites during wet periods (Fig. S7). This may suggest that beech in dry sites, while generally more sensitive to inter-annual drought conditions, have also adapted to the locally dry conditions.

4.2. Effects of SPEI climatology on drought sensitivity (H3)

In agreement with H3a, the relationship between SPEI climatology and drought sensitivity was generally negative and in line with Liebig's law of the minimum (Stine and Huybers, 2017). However, the higher non-linear effect of SPEI climatology had the effect that peak drought sensitivity more frequently occurred within $\pm 2\,\sigma$ of the SPEI climatology distribution with higher growth variability and lower growth trends (Fig. 5). These results show that during the dry end of the climatic conditions over the course of the 20th century, maximum drought sensitivity was surpassed, resulting in a reversal and decline in drought sensitivity, in contrast to H3a. This is in general accordance with the optimum response curves presented by Wilmking et al. (2020) as well as other studies showing that drought sensitivity of secondary tree growth is non-stationary (Anderson-Teixeira et al., 2022; Babst et al., 2019; Mazza et al., 2024; Tumajer et al., 2022; van der Maaten et al., 2024; Weigel et al., 2023). The decline in the climate signal towards drier conditions may indicate an early-warning signal for an approaching tipping point (Duffy et al., 2021), e.g., due to cavitation fatigue (Hacke et al., 2001). This is corroborated by the decoupling in climate signal of growth with decreasing growth trends (cyan line in Fig. 5c). Consequently, a continued drying of the European climate may lead to further fatigue and detrimental effects due to insufficient time to recover, especially if trees are also faced with potential legacy effects following drought events (Leifsson et al., 2023).

A limitation of our study is that it cannot distinguish the effects of either juvenile trees that are exposed to extra-canopy climate, such as in the case of gaps in the canopy, or the influence of larger and deeper root systems of larger trees (Annighöfer, 2018; Brinkmann et al., 2019; but see also Gessler et al., 2022). Regarding the juvenile trees, a problem arises from the bias of the data against such occurrences in favor of closed-canopy conditions because of the ecologically oriented sampling.

Regarding both the juvenile and large trees, the respective effects are masked in the current results. In the case of juvenile trees, it would require knowing how the gaps affect growth trends and variability, which, however, is unknown. In the case of large trees, better access to (deeper) groundwater would lower the drought sensitivity during dry SPEI climatology, a partial influence that is likewise unknown. It should, however, also prevent the declining drought sensitivity towards the drier SPEI climatology, which is not the case (Fig. 5).

The predicted drought sensitivity was considerably higher for dry sites than wet sites, agreeing with H3b (Fig. S6 and S9). Consequently, the impact of site aridity on mean drought sensitivity overruled the corresponding effect of temporal SPEI climatology. The exceptions, when drought sensitivity was relatively similar between dry and wet sites, were at very low growth variability and high growth trends (orange lines in Fig. S9a). Assuming that these conditions relate to moist and shaded understories as discussed above, it indicates that juvenile trees are relatively equally sensitive to extra-canopy climatic conditions across beech's ecological amplitude, despite a divergence towards lower growth trends. In the case of the remainder of the data, the higher drought sensitivity at dry sites agrees with many reports (Knutzen et al., 2017; Weber et al., 2013; Weigel et al., 2023; Zimmermann et al., 2015), though notably there are many reports of the opposite (Cavin and Jump, 2017; Friedrichs et al., 2009; Muffler et al., 2020). In contrast, Hacket-Pain et al. (2016), the only other study covering a comparable climatological range as our study, reported a lack of difference between dry and wet sites, as did van der Maaten-Theunissen et al. (2016) in their comparison of two sites of contrasting available soil water holding capacity. However, except for Hacket-Pain et al. (2016), all of the referenced studies performed their analyses on a more limited climatological and geographical scale, and it may be that some of these studies reveal a more pronounced influence of specific local details, e.g., topography (Didion-Gency et al., 2021; Miranda et al., 2022), forest composition (Didion-Gency et al., 2021), and edaphic factors (Leuschner, 2020; Weigel et al., 2023).

4.3. Effects of growth trends on drought sensitivity (H2)

Our results showed a generally negative relationship between growth trends and drought sensitivity. Interestingly, however, this was not always the case because of the non-linear and interaction effects, in addition to differences between dry and wet sites, providing a more nuanced perspective on the relationship (Fig. 4 and S8). Consequently, there was divergent support for H2. As with site climate, the literature is equivocal about whether negative growth trends are related to increasing climate stress. In agreement with the overall effect of our results, negative growth trends have been reported to occur in conjunction with increasingly dry conditions (Jump et al., 2006; Neycken et al., 2024; Piovesan et al., 2008; Weigel et al., 2023). However, Diers et al. (2022) found a decline in drought sensitivity with declining growth trends, which in our results was the case during drier-than-average periods, especially at drier sites (yellow lines in Fig. 4 and S9). Marqués et al. (2022a) and Mazza et al. (2024) found that beech with declining growth rates showed lower sensitivity to precipitation and an intensified negative sensitivity to temperature, contrary to Knutzen et al. (2017), who found an increased sensitivity to precipitation with declining growth rates. All of these results can also be discerned under specific conditions in our results. Neycken et al. (2022) and van der Maaten et al. (2024) did not find clear differences in climate sensitivity between vital and declining beech. Hacket-Pain and Friend (2017) found climate sensitivity to decrease for both decreasing and increasing growth rates, while Camarero et al. (2021) reported declining growth rates to occur in conjunction with both declining and unchanging sensitivity to precipitation. The relationship between growth trends and climate sensitivity in beech is evidently complicated and highly variable. However, because of the non-linear terms and interactions in our model, many of these responses can be found in our

results depending on the details of all variables and site climate. This study is, to the authors' knowledge, the most comprehensive analysis of the relationship between growth trends and climate sensitivity, and the results shown here were only revealed through our multivariate and multidimensional approach where we analyzed the effects of growth variability, growth trends and SPEI climatology on drought sensitivity simultaneously.

4.4. Decoupled relationships with drought sensitivity

The dry climatic conditions our sites experienced in the 20th century led to drought sensitivity decoupling from growth variability, and the relationship with growth trends reversed from increasing to decreasing under low and negative growth trends. Such indications may be signs of early-warning signals prior to drought-induced mortality (Cailleret et al., 2019, 2017). While the evidence of such a decoupling is not consistent across angiosperms (Cailleret et al., 2019), beech may be assumed to be more sensitive compared to other angiosperms because of its comparably more anisohydric hydraulic strategy (Gessler et al., 2007; Leuschner et al., 2021; Walthert et al., 2021) which allows for maintained carbon assimilation despite drought stress (Gebhardt et al., 2023; Motte et al., 2023; Zang et al., 2014). However, the observed decoupling of growth variability and growth trends from drought sensitivity may likewise be due to adaptation mechanisms, as beech has been reported to have a good ability to acclimate (Arend et al., 2022; Leuschner et al., 2023b). Still, growth rates in beech trees have been reported to decline following drought events (Camarero et al., 2021; Meyer et al., 2020; Schmied et al., 2023), as has mortality (Buras et al., 2020; Frei et al., 2022; Schuldt et al., 2020) which drier climatic conditions may worsen (Frei et al., 2022).

5. Conclusion

This study has elucidated the complex nature of climate sensitivity of secondary growth in European beech across its geographical and climatological distribution. Our novel approach allowed us to determine the influence of growth trends, growth variability, and spatial and temporal SPEI climatology on drought sensitivity at unprecedented detail, dealing with all individual and interactive components simultaneously. The main conclusion to be drawn is the highly non-stationary nature of drought sensitivity of growth, which depends on not only SPEI climatology but also growth characteristics, including their interactions. While drought sensitivity increases with growth variability and decreases with growth trends, increasingly dry climatic conditions also increase drought sensitivity, potentially intensified by climate change. However, drought sensitivity is decoupled from growth variability and growth trends during dry periods.

While other studies have reported non-stationary climate sensitivity of secondary growth, to the authors' knowledge, none have clearly shown the continuous, non-linearity presented in this study. Our results can largely be explained by both increasingly dry climatic conditions due to climate change and by trees' rank progression within forest communities. However, drought sensitivity declined during the driest periods the trees experienced in the 20th century. This may indicate a tipping point and that further drying of European climate could lead to a continued decline of climate sensitivity and a critical slowing down due to an accumulation of legacy effects caused by continually dry conditions and insufficient recovery time.

The results of this study improve our understanding of how climate-growth relationships vary in closed-canopy European beech forests and reveal underlying causes. This possibly explains the widely diverging observations on climate sensitivity and growth characteristics found in the literature and may consequently guide future research towards a unified theory of European beech's drought sensitivity in a changing climate.

CRediT authorship contribution statement

Christopher Leifsson: Writing – review & editing, Resources. **Allan Buras:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Stefan Klesse:** Writing – review & editing, Resources, Methodology. **Claudia Baittinger:** Writing – review & editing, Resources. **Banzragch Bat-Enerel:** Writing – review & editing, Resources. **Giovanna Battipaglia:** Writing – review & editing, Resources. **Franco Biondi:** Writing – review & editing, Resources. **Branko Stajić:** Writing – review & editing, Resources. **Marius Budeanu:** Writing – review & editing, Resources. **Vojtěch Čada:** Writing – review & editing, Resources. **J. Julio Camarero:** Writing – review & editing, Resources. **Liam Cavin:** Resources. **Hugues Claessens:** Writing – review & editing, Resources. **Katarina Čufar:** Writing – review & editing, Resources. **Martin de Luis:** Writing – review & editing, Resources. **Isabel Dorado-Liñán:** Writing – review & editing, Resources. **Choimaa Dulamsuren:** Writing – review & editing, Resources. **Balázs Garamszegi:** Writing – review & editing, Resources. **Michael Grabner:** Writing – review & editing, Resources. **Andrew Hacket-Pain:** Writing – review & editing, Resources. **Jon Kehlet Hansen:** Writing – review & editing, Resources. **Claudia Hartl:** Writing – review & editing, Resources. **Weiwei Huang:** Writing – review & editing, Resources. **Pavel Janda:** Writing – review & editing, Resources. **Alistair S. Jump:** Writing – review & editing, Resources. **Marko Kazimirović:** Writing – review & editing, Resources. **Florian Knutzen:** Writing – review & editing, Resources. **Jürgen Kreyling:** Writing – review & editing, Resources. **Alexander Land:** Writing – review & editing, Resources. **Nicolas Latte:** Writing – review & editing, Resources. **François Lebourgeois:** Writing – review & editing, Resources. **Christoph Leuschner:** Writing – review & editing, Resources. **Luis A. Longares:** Writing – review & editing, Resources. **Edurne Martinez del Castillo:** Writing – review & editing, Resources. **Annette Menzel:** Writing – review & editing, Resources. **Renzo Motta:** Writing – review & editing, Resources. **Lena Muffler-Weigel:** Writing – review & editing, Resources. **Paola Nola:** Writing – review & editing, Resources. **Momchil Panayatov:** Writing – review & editing, Resources. **Any Mary Petritan:** Writing – review & editing, Resources. **Ion Catalin Petritan:** Writing – review & editing, Resources. **Ionel Popa:** Writing – review & editing, Resources. **Cătălin-Constantin Roibu:** Writing – review & editing, Resources. **Álvaro Rubio-Cuadrado:** Writing – review & editing, Resources. **Miloš Rydval:** Writing – review & editing, Resources. **Tobias Scharnweber:** Resources. **Miroslav Svoboda:** Writing – review & editing, Resources. **Elvin Toromani:** Writing – review & editing, Resources. **Volodymyr Trotsiuk:** Writing – review & editing, Resources. **Marieke van der Maaten-Theunissen:** Writing – review & editing, Resources. **Ernst van der Maaten:** Writing – review & editing, Resources. **Robert Weigel:** Writing – review & editing, Resources. **Martin Wilmking:** Writing – review & editing, Resources. **Tzvetan Zlatanov:** Writing – review & editing, Resources. **Anja Rammig:** Writing – review & editing, Supervision. **Christian S. Zang:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Gridded historical temperature data is available at the Climatic Research Unit *https://crudata.uea.ac.uk/cru/data/hrg/* and gridded historical precipitation data is available at the Global Precipitation Climatology Centre *https://opendata.dwd.de/climate_environment/GPCC /html/*. European beech tree-ring data is not publicly available,

contact Christian Zang (christian.zang[*at*]hswt.de) for inquiries.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.173321.

References

Amoroso, M.M., Daniels, L.D., Baker, P.J., Camarero, J.J. (Eds.), 2017. Dendroecology: Tree-Ring Analyses Applied to Ecological Studies. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-61669-8.

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528–532. https://doi.org/10.1126/science.aab1833.

Anderegg, W.R.L., Wu, C., Acil, N., Carvalhais, N., Pugh, T.A.M., Sadler, J.P., Seidl, R., 2022. A climate risk analysis of Earth's forests in the 21st century. Science 377, 1099–1103. https://doi.org/10.1126/science.abp9723.

Anderson-Teixeira, K.J., Herrmann, V., Rollinson, C.R., Gonzalez, B., Gonzalez-Akre, E. B., Pederson, N., Alexander, M.R., Allen, C.D., Alfaro-Sánchez, R., Awada, T., Baltzer, J.L., Baker, P.J., Birch, J.D., Bunyavejchewin, S., Cherubini, P., Davies, S.J., Dow, C., Helcoski, R., Kašpar, J., Lutz, J.A., Margolis, E.Q., Maxwell, J.T., McMahon, S.M., Piponiot, C., Russo, S.E., Šamonil, P., Sniderhan, A.E., Tepley, A.J., Vašíčková, I., Vlam, M., Zuidema, P.A., 2022. Joint effects of climate, tree size, and year on annual tree growth derived from tree-ring records of ten globally distributed forests. Glob. Chang. Biol. 28, 245–266. https://doi.org/10.1111/gcb.15934.

Annighöfer, P., 2018. Stress relief through gap creation? Growth response of a shade tolerant species (Fagus sylvatica L.) to a changed light environment. For. Ecol. Manag. 415-416, 139–147. https://doi.org/10.1016/j.foreco.2018.02.027.

Arend, M., Link, R.M., Zahnd, C., Kahmen, A., 2022. Lack of hydraulic recovery as a cause of post-drought foliage reduction and canopy decline in European beech. New Phytol. 11 https://doi.org/10.1111/nph.18065.

Astigarraga, J., Andivia, E., Zavala, M.A., Gazol, A., Cruz-Alonso, V., Vicente-Serrano, S. M., Ruiz-Benito, P., 2020. Evidence of non-stationary relationships between climate

and forest responses: increased sensitivity to climate change in iberian forests. Glob. Chang. Biol. 26, 5063–5076. https://doi.org/10.1111/gcb.15198.

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., Panayotov, M., Urbinati, C., Bouriaud, O., Ciais, P., Frank, D., 2013. Site- and species-specific responses of forest growth to climate across the European continent: climate sensitivity of forest growth across Europe. Glob. Ecol. Biogeogr. 22, 706–717. https://doi.org/10.1111/geb.12023.

Babst, F., Bouriaud, O., Alexander, R., Trouet, V., Frank, D., 2014. Toward consistent measurements of carbon accumulation: A multi-site assessment of biomass and basal area increment across Europe. Dendrochronologia 32, 153–161. https://doi.org/10.1016/j.dendro.2014.01.002.

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century redistribution in climatic drivers of global tree growth. Sci. Adv. 5, eaat4313 https://doi.org/10.1126/sciadv.aat4313.

Bernal-Escobar, M., Zuleta, D., Feeley, K.J., 2022. Changes in the climate suitability and growth rates of trees in eastern North America. Ecography 2022, e06298. https://doi.org/10.1111/ecog.06298.

Berner, L.T., Goetz, S.J., 2022. Satellite observations document trends consistent with a boreal forest biome shift. Glob. Chang. Biol. 28, 3275–3292. https://doi.org/10.1111/gcb.16121.

Bonan, G.B., 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449. https://doi.org/10.1126/science.1155121.

Brienen, R., Helle, G., Pons, T., Boom, A., Gloor, M., Groenendijk, P., Clerici, S., Leng, M., Jones, C., 2022. Paired analysis of tree ring width and carbon isotopes indicates when controls on tropical tree growth change from light to water limitations. Tree Physiol. 42, 1131–1148. https://doi.org/10.1093/treephys/tpab142.

Brinkmann, N., Eugster, W., Buchmann, N., Kahmen, A., 2019. Species-specific differences in water uptake depth of mature temperate trees vary with water availability in the soil. Plant Biol. 21, 71–81. https://doi.org/10.1111/plb.12907.

Brodribb, T.J., Powers, J., Cochard, H., Choat, B., 2020. Hanging by a thread? Forests and drought. Science 368, 261–266. https://doi.org/10.1126/science.aat7631.

Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in european beech forests - a review with recommendations for sustainable forest management. Ecol. Bull. 77–94.

Bunn, A., Jansma, E., Korpela, M., Westfall, R.D., Baldwin, J., 2013. Using simulations and data to evaluate mean sensitivity as a useful statistic in dendrochronology. Dendrochronologia 31, 250–254. https://doi.org/10.1016/j.dendro.2013.01.004.

Bunn, A.G., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2020. dplR: dendrochronology program library in r.

Buras, A., Menzel, A., 2019. Projecting tree species composition changes of european forests for 2061-2090 under RCP 4.5 and RCP 8.5 scenarios. Front. Plant Sci. 9, 1986. https://doi.org/10.3389/fpls.2018.01986.

Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.-J., Menzel, A., 2018. Are scots pine forest edges particularly prone to drought-induced mortality? Environ. Res. Lett. 13, 025001 https://doi.org/10.1088/1748-9326/aaa0b4.

Buras, A., Rammig, A., Zang, C.S., 2020. Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. Biogeosciences 17, 1655–1672. https://doi.org/10.5194/bg-17-1655-2020.

Cabon, A., Kannenberg, S.A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., Delpierre, N., Guerrieri, R., Maxwell, J.T., McKenzie, S., Meinzer, F.C., Moore, D.J. P., Pappas, C., Rocha, A.V., Szejner, P., Ueyama, M., Ulrich, D., Vincke, C., Voelker, S.L., Wei, J., Woodruff, D., Anderegg, W.R.L., 2022. Cross-biome synthesis of source versus sink limits to tree growth. Science 376, 758–761. https://doi.org/10.1126/science.abm4875.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Calderon, J.C.L., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., Rodríguez, R.L., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Chang. Biol. 23, 1675–1690. https://doi.org/10.1111/gcb.13535.

Cailleret, M., Dakos, V., Jansen, S., Robert, E.M.R., Aakala, T., Amoroso, M.M., Antos, J. A., Bigler, C., Bugmann, H., Caccianiga, M., Camarero, J.-J., Cherubini, P., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanic, T., Linares, J.-C., Lombardi, F., Mäkinen, H., Mészáros, I., Metsaranta, J.M., Oberhuber, W., Papadopoulos, A., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Smith, J.M., Stan, A.B., Stojanovic, D.B., Suarez, M.-L., Svoboda, M., Trotsiuk, V., Villalba, R., Westwood, A.R., Wyckoff, P.H., Martínez-Vilalta, J., 2019. Early-warning signals of individual tree mortality based on annual radial growth. Front. Plant Sci. 9, 1964. https://doi.org/10.3389/fpls.2018.01964.

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., Vicente-Serrano, S.M., 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. J. Ecol. 103, 44–57. https://doi.org/10.1111/1365-2745.12295.

Camarero, J.J., Colangelo, M., Gazol, A., Azorín-Molina, C., 2021. Drought and cold spells trigger dieback of temperate oak and beech forests in northern Spain. Dendrochronologia 66, 125812. https://doi.org/10.1016/j.dendro.2021.125812.

Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in Larix Decidua and Pinus Cembra. Ecology 85, 730–740. https://doi.org/10.1890/02-0478.

Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data Brief 12, 662–666. https://doi.org/10.1016/j.dib.2017.05.007.

Cavin, L., Jump, A.S., 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. Glob. Chang. Biol. 23, 362–379. https://doi.org/10.1111/gcb.13366.

Cook, E.R., Kairiukstis, L.A., 1990. Methods of Dendrochronology. Springer, Dordrecht. https://doi.org/10.1007/978-94-015-7879-0.

Didion-Gency, M., Bachofen, C., Buchmann, N., Gessler, A., Morin, X., Vicente, E., Vollenweider, P., Grossiord, C., 2021. Interactive effects of tree species mixture and climate on foliar and woody trait variation in a widely distributed deciduous tree. Funct. Ecol. 35, 2397–2408. https://doi.org/10.1111/1365-2435.13898.

Diers, M., Weigel, R., Leuschner, C., 2022. Both climate sensitivity and growth trend of European beech decrease in the north German lowlands, while scots pine still thrives, despite growing sensitivity. Trees. https://doi.org/10.1007/s00468-022-02369-y.

Dobbertin, M., 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. Eur. J. For. Res. 124, 319–333. https://doi.org/10.1007/s10342-005-0085-3.

Dorado-Liñán, I., Ayarzagüena, B., Babst, F., Xu, G., Gil, L., Battipaglia, G., Buras, A., Čada, V., Camarero, J.J., Cavin, L., Claessens, H., Drobyshev, I., Garamszegi, B., Grabner, M., Hacket-Pain, A., Hartl, C., Hevia, A., Janda, P., Jump, A.S., Kazimirovic, M., Keren, S., Kreyling, J., Land, A., Latte, N., Levanič, T., van der Maaten, E., van der Maaten-Theunissen, M., Martínez-Sancho, E., Menzel, A., Mikoláš, M., Motta, R., Muffler, L., Nola, P., Panayotov, M., Petritan, A.M., Petritan, I.C., Popa, I., Prislan, P., Roibu, C.-C., Rydval, M., Sánchez-Salguero, R., Scharnweber, T., Stajić, B., Svoboda, M., Tegel, W., Teodosiu, M., Toromani, E., Trotsiuk, V., Turcu, D.-O., Weigel, R., Wilmking, M., Zang, C., Zlatanov, T., Trouet, V., 2022. Jet stream position explains regional anomalies in European beech forest productivity and tree growth. Nat. Commun. 13, 2015. https://doi.org/10.1038/s41467-022-29615-8.

D'Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., Houle, D., Arseneault, D., Beier, C.M., Bishop, D.A., Druckenbrod, D., Fraver, S., Girard, F., Halman, J., Hansen, C., Hart, J.L., Hartmann, H., Kaye, M., Leblanc, D., Manzoni, S., Ouimet, R., Rayback, S., Rollinson, C.R., Phillips, R.P., 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Glob. Chang. Biol. 24, 2339–2351. https://doi.org/10.1111/gcb.14096.

Droogers, P., Allen, R.G., 2002. Estimating reference evapotranspiration under inaccurate data conditions. Irrig. Drain. Syst. 16, 33–45. https://doi.org/10.1023/a:1015508322413.

Duffy, K.A., Schwalm, C.R., Arcus, V.L., Koch, G.W., Liang, L.L., Schipper, L.A., 2021. How close are we to the temperature tipping point of the terrestrial biosphere? Sci. Adv. 7, eaay1052 https://doi.org/10.1126/sciadv.aay1052.

Dulamsuren, C., Bat-Enerel, B., Meyer, P., Leuschner, C., 2022. Did stand opening 60 years ago predispose a European beech population to death? Trees, Forests and People 8, 100265. https://doi.org/10.1016/j.tfp.2022.100265.

FAO, UNEP, 2020. The State of the World's Forests 2020. Forests, Biodiversity and People. Rome.

Forest Europe, 2020. State of europe's Forests. Bratislava.

Frei, E.R., Gossner, M.M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., Wohlgemuth, T., 2022. European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. Plant Biol. 24, 1132–1145. https://doi.org/10.1111/plb.13467.

Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I.T., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S.R., Alkama, R., Arneth, A., Arora, V.K., Bates, N.R., Becker, M., Bellouin, N., Bittig, H.C., Bopp, L., Chevallier, F., Chini, L.P., Cronin, M., Evans, W., Falk, S., Feely, R.A., Gasser, T., Gehlen, M., Gkritzalis, T., Gloege, L., Grassi, G., Gruber, N., Gürses, Ö., Harris, I., Hefner, M., Houghton, R.A., Hurtt, G.C., Iida, Y., Ilyina, T., Jain, A.K., Jersild, A., Kadono, K., Kato, E., Kennedy, D., Klein Goldewijk, K., Knauer, J., Korsbakken, J.I., Landschützer, P., Lefèvre, N., Lindsay, K., Liu, J., Liu, Z., Marland, G., Mayot, N., McGrath, M.J., Metzl, N., Monacci, N.M., Munro, D.R., Nakaoka, S.-I., Niwa, Y., O'Brien, K., Ono, T., Palmer, P.I., Pan, N., Pierrot, D., Pocock, K., Poulter, B., Resplandy, L., Robertson, E., Rödenbeck, C., Rodriguez, C., Rosan, T.M., Schwinger, J., Séférian, R., Shutler, J.D., Skjelvan, I., Steinhoff, T., Sun, Q., Sutton, A.J., Sweeney, C., Takao, S., Tanhua, T., Tans, P.P., Tian, X., Tian, H., Tilbrook, B., Tsujino, H., Tubiello, F., van der Werf, G.R., Walker, A.P., Wanninkhof, R., Whitehead, C., Willstrand Wranne, A., Wright, R., Yuan, W., Yue, C., Yue, X., Zaehle, S., Zeng, J., Zheng, B., 2022. Global carbon budget 2022. Earth System Science Data 14, 4811–4900. https://doi.org/10.5194/essd-14-4811-2022.

Friedrichs, D.A., Trouet, V., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009. Species-specific climate sensitivity of tree growth in central-West Germany. Trees 23, 729–739. https://doi.org/10.1007/s00468-009-0315-2.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London, Great Britain.

Gea-Izquierdo, G., Sánchez-González, M., 2022. Forest disturbances and climate constrain carbon allocation dynamics in trees. Glob. Chang. Biol. 28, 4342–4358. https://doi.org/10.1111/gcb.16172.

Gebhardt, T., Hesse, B.D., Hikino, K., Kolovrat, K., Hafner, B.D., Grams, T.E.E., Häberle, K.-H., 2023. Repeated summer drought changes the radial xylem sap flow

profile in mature Norway spruce but not in European beech. Agric. For. Meteorol. 329, 109285 https://doi.org/10.1016/j.agrformet.2022.109285.

Gelman, A., Hill, J., 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models, Analytical Methods for Social Research. Cambridge University Press, Cambridge ; New York.

Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007. Potential risks for European beech (Fagus sylvatica L.) in a changing climate. Trees - Structure and Function 21, 1–11. https://doi.org/10.1007/s00468-006-0107-x.

Gessler, A., Bächli, L., Rouholahnejad Freund, E., Treydte, K., Schaub, M., Haeni, M., Weiler, M., Seeger, S., Marshall, J., Hug, C., Zweifel, R., Hagedorn, F., Rigling, A., Saurer, M., Meusburger, K., 2022. Drought reduces water uptake in beech from the drying topsoil, but no compensatory uptake occurs from deeper soil layers. New Phytol. 233, 194–206. https://doi.org/10.1111/nph.17767.

Grissino-Mayer, H.D., Fritts, H.C., 1997. The international tree-ring data Bank: an enhanced global database serving the global scientific community. The Holocene 7, 235–238. https://doi.org/10.1177/095968369700700212.

Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J., McCulloh, K.A., 2001. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of Xylem1. Plant Physiol. 125, 779–786. https://doi.org/10.1104/pp.125.2.779.

Hacket-Pain, A.J., Friend, A.D., 2017. Increased growth and reduced summer drought limitation at the southern limit of Fagus sylvatica L., despite regionally warmer and drier conditions. Dendrochronologia 44, 22–30. https://doi.org/10.1016/j.dendro.2017.02.005.

Hacket-Pain, A.J., Cavin, L., Friend, A.D., Jump, A.S., 2016. Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. Eur. J. For. Res. 135, 897–909. https://doi.org/10.1007/s10342-016-0982-7.

Hacket-Pain, A., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M., Drobyshev, I., Dorado-Liñán, I., Friend, A.D., Grabner, M., Hartl, C., Kreyling, J., Lebourgeois, F., Levanič, T., Menzel, A., van der Maaten, M., van der Maaten-Theunissen, Ernst, Muffler, L., Motta, R., Roibu, C.-C., Popa, I., Scharnweber, T., Weigel, R., Wilmking, M., Zang, C.S., 2018. Climatically controlled reproduction drives interannual growth variability in a temperate tree species. Ecol. Lett. 21, 1833–1844. https://doi.org/10.1111/ele.13158.

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., Zimmermann, N.E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Chang. 3, 203–207. https://doi.org/10.1038/nclimate1687.

Hanewinkel, M., Cullmann, D.A., Michiels, H.-G., Kändler, G., 2014. Converting probabilistic tree species range shift projections into meaningful classes for management. J. Environ. Manag. 134, 153–165. https://doi.org/10.1016/j.jenvman.2014.01.010.

Hansen, W.D., Schwartz, N.B., Williams, A.P., Albrich, K., Kueppers, L.M., Rammig, A., Reyer, C.P.O., Staver, A.C., Seidl, R., 2022. Global forests are influenced by the legacies of past inter-annual temperature variability. Environmental Research: Ecology 1, 011001. https://doi.org/10.1088/2752-664X/ac6e4a.

Hargreaves, G.H., 1994. Defining and using reference evapotranspiration. J. Irrig. Drain. Eng. 120, 1132–1139. https://doi.org/10.1061/(ASCE)0733-9437(1994)120:6 (1132).

Harris, I., Osborn, T.J., Jones, P., Lister, D., 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Scientific Data 7, 109. https://doi.org/10.1038/s41597-020-0453-3.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E. D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6, e4794. https://doi.org/10.7717/peerj.4794.

Harvey, J.E., Smiljanić, M., Scharnweber, T., Buras, A., Cedro, A., Cruz-García, R., Drobyshev, I., Janecka, K., Jansons, Ā., Kaczka, R., Klisz, M., Läänelaid, A., Matisons, R., Muffler, L., Sohar, K., Spyt, B., Stolz, J., van der Maaten, E., van der Maaten-Theunissen, M., Vitas, A., Weigel, R., Kreyling, J., Wilmking, M., 2020. Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests. Glob. Chang. Biol. 26, 2505–2518. https://doi.org/10.1111/gcb.14966.

Heilmayr, R., Dudney, J., Moore, F.C., 2023. Drought sensitivity in Mesic forests heightens their vulnerability to climate change. Science 382, 1171–1177. https://doi.org/10.1126/science.adi1071.

IPCC, 2021. Climate Change 2021 the Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, 1st ed. Cambridge University Press. https://doi.org/10.1017/9781009157896.

Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Glob. Chang. Biol. 12, 2163–2174. https://doi.org/10.1111/j.1365-2486.2006.01250.x.

Kannenberg, S.A., Maxwell, J.T., 2022. Disentangling the drivers of non-stationarity in tree growth. Tree Physiol. 42, 1128–1130. https://doi.org/10.1093/treephys/tpac031.

Kannenberg, S.A., Novick, K.A., Alexander, M.R., Maxwell, J.T., Moore, D.J.P., Phillips, R.P., Anderegg, W.R.L., 2019. Linking drought legacy effects across scales: from leaves to tree rings to ecosystems. Glob. Chang. Biol. 25, 2978–2992. https://doi.org/10.1111/gcb.14710.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data 4, 170122. https://doi.org/10.1038/sdata.2017.122.

Keen, R.M., Voelker, S.L., Wang, S.-Y.S., Bentz, B.J., Goulden, M.L., Dangerfield, C.R., Reed, C.C., Hood, S.M., Csank, A.Z., Dawson, T.E., Merschel, A.G., Still, C.J., 2021. Changes in tree drought sensitivity provided early warning signals to the California drought and forest mortality event. Glob. Chang. Biol., gcb.15973 https://doi.org/10.1111/gcb.15973.

Klesse, S., Babst, F., Lienert, S., Spahni, R., Joos, F., Bouriaud, O., Carrer, M., Filippo, A. D., Poulter, B., Trotsiuk, V., Wilson, R., Frank, D.C., 2018a. A combined tree ring and vegetation model assessment of European Forest growth sensitivity to interannual climate variability. Glob. Biogeochem. Cycles 32, 1226–1240. https://doi.org/10.1029/2017GB005856.

Klesse, S., Wohlgemuth, T., Meusburger, K., Vitasse, Y., von Arx, G., Lévesque, M., Neycken, A., Braun, S., Dubach, V., Gessler, A., Ginzler, C., Gossner, M.M., Hagedorn, F., Queloz, V., Samblás Vives, E., Rigling, A., Frei, E., 2022. Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in Fagus sylvatica. Sci. Total Environ. 851, 157926 https://doi.org/10.1016/j.scitotenv.2022.157926.

Klesse, Stefan, DeRose, R.J., Guiterman, C.H., Lynch, A.M., O'Connor, C.D., Shaw, J.D., Evans, M.E.K., 2018b. Sampling bias overestimates climate change impacts on forest growth in the southwestern United States. Nat. Commun. 9, 5336. https://doi.org/10.1038/s41467-018-07800-y.

Knutzen, F., Dulamsuren, C., Meier, I.C., Leuschner, C., 2017. Recent climate warming-related growth decline impairs European beech in the Center of its Distribution Range. Ecosystems 20, 1494–1511. https://doi.org/10.1007/s10021-017-0128-x.

LaMarche, V.C., 1978. Tree-ring evidence of past climatic variability. Nature 276, 334–338. https://doi.org/10.1038/276334a0.

Lange, J., Buras, A., Cruz-García, R., Gurskaya, M., Jalkanen, R., Kukarskih, V., Seo, J.-W., Wilmking, M., 2018. Climate regimes override Micro-site effects on the summer temperature signal of scots pine at its northern distribution limits. Front. Plant Sci. 9, 1597. https://doi.org/10.3389/fpls.2018.01597.

LeBlanc, D.C., 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Can. J. For. Res. 20, 1399–1407. https://doi.org/10.1139/x90-185.

Leifsson, C., Buras, A., Rammig, A., Zang, C., 2023. Changing climate sensitivity of secondary growth following extreme drought events in forest ecosystems: a global analysis. Environ. Res. Lett. 18, 014021 https://doi.org/10.1088/1748-9326/aca9e5.

Leuschner, C., 2020. Drought response of European beech (Fagus sylvatica L.)A review. Perspectives in Plant Ecology, Evolution and Systematics 47, 125576. https://doi.org/10.1016/j.ppees.2020.125576.

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe, I. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-43042-3.

Leuschner, C., Schipka, F., Backes, K., 2021. Stomatal regulation and water potential variation in European beech: challenging the iso/anisohydry concept. Tree Physiol., tpab104 https://doi.org/10.1093/treephys/tpab104.

Leuschner, C., Hohnwald, S., Petriţan, A.M., Walentowski, H., 2023a. Vertical temperature and air humidity gradients in beech and oak forests, and the forest interior climate created by beech. Flora 305, 152317. https://doi.org/10.1016/j.flora.2023.152317.

Leuschner, C., Weithmann, G., Bat-Enerel, B., Weigel, R., 2023b. The future of European beech in northern GermanyClimate change vulnerability and adaptation potential. Forests 14, 1448. https://doi.org/10.3390/f14071448.

Liu, Q., Peng, C., Schneider, R., Cyr, D., Liu, Z., Zhou, X., Du, M., Li, P., Jiang, Z., McDowell, N.G., Kneeshaw, D., 2023. Vegetation browning: global drivers, impacts, and feedbacks. Trends Plant Sci. 28, 1014–1032. https://doi.org/10.1016/j.tplants.2023.03.024.

van der Maaten, E., Stolz, J., Thurm, E.A., Schröder, J., Henkel, A., Leinemann, L., Profft, I., Voth, W., van der Maaten-Theunissen, M., 2024. Long-term growth decline is not reflected in crown condition of European beech after a recent extreme drought. For. Ecol. Manag. 551, 121516 https://doi.org/10.1016/j.foreco.2023.121516.

van der Maaten-Theunissen, M., Bümmerstede, H., Iwanowski, J., Scharnweber, T., Wilmking, M., van der Maaten, E., 2016. Drought sensitivity of beech on a shallow chalk soil in northeastern Germany a comparative study. Forest Ecosystems 3. https://doi.org/10.1186/s40663-016-0083-6.

Makarieva, A.M., Gorshkov, V.G., 2007. Biotic pump of atmospheric moisture as driver of the hydrological cycle on land. Hydrol. Earth Syst. Sci. 11, 1013–1033. https://doi.org/10.5194/hess-11-1013-2007.

Marchand, W., Girardin, M.P., Hartmann, H., Gauthier, S., Bergeron, Y., 2019. Taxonomy, together with ontogeny and growing conditions, drives needleleaf species' sensitivity to climate in boreal North America. Glob. Chang. Biol. 25, 2793–2809. https://doi.org/10.1111/gcb.14665.

Marqués, L., Ogle, K., Peltier, D.M.P., Camarero, J.J., 2022a. Altered climate memory characterizes tree growth during forest dieback. Agric. For. Meteorol. 314, 108787 https://doi.org/10.1016/j.agrformet.2021.108787.

Marqués, L., Peltier, D.M.P., Camarero, J.J., Zavala, M.A., Madrigal-González, J., Sangüesa-Barreda, G., Ogle, K., 2022b. Disentangling the legacies of climate and management on tree growth. Ecosystems 25, 215–235. https://doi.org/10.1007/s10021-021-00650-8.

Martinez del Castillo, E., Zang, C.S., Buras, A., Hacket-Pain, A., Esper, J., Serrano-Notivoli, R., Hartl, C., Weigel, R., Klesse, S., Resco de Dios, V., Scharnweber, T., Dorado-Liñán, I., van der Maaten-Theunissen, M., van der Maaten, E., Jump, A., Mikac, S., Banzragch, B.-E., Beck, W., Cavin, L., Claessens, H., Čada, V., Čufar, K., Dulamsuren, C., Gričar, J., Gil-Pelegrín, E., Janda, P., Kazimirovic, M., Kreyling, J., Latte, N., Leuschner, C., Longares, L.A., Menzel, A., Merela, M., Motta, R., Muffler, L., Nola, P., Petritan, A.M., Petritan, I.C., Prislan, P., Rubio-Cuadrado, Á., Rydval, M., Stajić, B., Svoboda, M., Toromani, E., Trotsiuk, V., Wilmking, M., Zlatanov, T., de Luis, M., 2022. Climate-change-driven growth decline of European beech forests. Communications Biology 5, 1–9. https://doi.org/10.1038/s42003-022-03107-3.

Mausolf, K., Wilm, P., Härdtle, W., Jansen, K., Schuldt, B., Sturm, K., Von Oheimb, G., Hertel, D., Leuschner, C., Fichtner, A., 2018. Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests. Sci. Total Environ. 642, 1201–1208. https://doi.org/10.1016/j.scitotenv.2018.06.065.

Mazza, G., Monteverdi, M.C., Altieri, S., Battipaglia, G., 2024. Climate-driven growth dynamics and trend reversal of Fagus sylvatica L. and Quercus cerris L. in a low-elevation beech forest in Central Italy. Sci. Total Environ. 908, 168250 https://doi.org/10.1016/j.scitotenv.2023.168250.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368, eaaz9463. https://doi.org/10.1126/science.aaz9463.

Metz, J., Annighöfer, P., Westekemper, K., Schall, P., Schulze, E.-D., Ammer, C., 2020. Less is more: effects of competition reduction and facilitation on intra-annual (basal area) growth of mature European beech. Trees 34, 17–36. https://doi.org/10.1007/s00468-019-01894-7.

Meyer, B.F., Buras, A., Rammig, A., Zang, C.S., 2020. Higher susceptibility of beech to drought in comparison to oak. Dendrochronologia 64, 125780. https://doi.org/10.1016/j.dendro.2020.125780.

Miranda, J.C., Calderaro, C., Cocozza, C., Lasserre, B., Tognetti, R., von Arx, G., 2022. Wood anatomical responses of European beech to elevation, Land use change, and climate variability in the central Apennines, Italy. Front. Plant Sci. 13, 855741 https://doi.org/10.3389/fpls.2022.855741.

Motte, F., Rötzer, T., Biber, P., Uhl, E., Pritsch, K., Pretzsch, H., 2023. Growth of European beech recovered faster than that of Norway spruce after a five-year experimental drought in a mixed forest stand. Trees. https://doi.org/10.1007/s00468-023-02453-x.

Muffler, L., Weigel, R., Hacket-Pain, A.J., Klisz, M., van der Maaten, E., Wilmking, M., Kreyling, J., van der Maaten-Theunissen, M., 2020. Lowest drought sensitivity and decreasing growth synchrony towards the dry distribution margin of European beech. J. Biogeogr. 47, 1910–1921. https://doi.org/10.1111/jbi.13884.

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14, 20170213. https://doi.org/10.1098/rsif.2017.0213.

Neycken, A., Scheggia, M., Bigler, C., Lévesque, M., 2022. Long-term growth decline precedes sudden crown dieback of European beech. Agric. For. Meteorol. 324, 109103 https://doi.org/10.1016/j.agrformet.2022.109103.

Neycken, A., Wohlgemuth, T., Frei, E.R., Klesse, S., Baltensweiler, A., Lévesque, M., 2024. Slower growth prior to the 2018 drought and a high growth sensitivity to previous year summer conditions predisposed European beech to crown dieback. Sci. Total Environ. 912, 169068 https://doi.org/10.1016/j.scitotenv.2023.169068.

Pedersen, B.S., 1998. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology 79, 79–93. https://doi.org/10.1890/0012-9658(1998)079[0079:TROSIT]2.0.CO;2.

Peltier, D.M.P., Ogle, K., 2020. Tree growth sensitivity to climate is temporally variable. Ecol. Lett. 23, 1561–1572. https://doi.org/10.1111/ele.13575.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS, Statistics and Computing. Springer, New York, NY, US.

Piovesan, G., Biondi, F., Filippo, A.D., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (Fagus sylvatica L.) forests of the central Apennines, Italy. Glob. Chang. Biol. 14, 1265–1281. https://doi.org/10.1111/j.1365-2486.2008.01570.x.

Portmann, R., Beyerle, U., Davin, E., Fischer, E.M., De Hertog, S., Schemm, S., 2022. Global forestation and deforestation affect remote climate via adjusted atmosphere and ocean circulation. Nat. Commun. 13, 5569. https://doi.org/10.1038/s41467-022-33279-9.

Pugh, T.A.M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., Calle, L., 2019. Role of forest regrowth in global carbon sink dynamics. Proc. Natl. Acad. Sci. 116, 4382–4387. https://doi.org/10.1073/pnas.1810512116.

Quetin, G.R., Anderegg, L.D.L., Boving, I., Anderegg, W.R.L., Trugman, A.T., 2023. Observed forest trait velocities have not kept pace with hydraulic stress from climate change. Glob. Chang. Biol. 29, 5415–5428. https://doi.org/10.1111/gcb.16847.

Rollinson, C.R., Alexander, M.R., Dye, A.W., Moore, D.J.P., Pederson, N., Trouet, V., 2021. Climate sensitivity of understory trees differs from overstory trees in temperate Mesic forests. Ecology 102, e03264. https://doi.org/10.1002/ecy.3264.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1, 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x.

Schmied, G., Pretzsch, H., Ambs, D., Uhl, E., Schmucker, J., Fäth, J., Biber, P., Hoffmann, Y.-D., Šeho, M., Mellert, K.H., Hilmers, T., 2023. Rapid beech decline under recurrent drought stress: individual neighborhood structure and soil properties matter. For. Ecol. Manag. 545, 121305 https://doi.org/10.1016/j.foreco.2023.121305.

Schneider, U., Becker, A., Finger, P., Meyer-Christoffer, A., Ziese, M., Rudolf, B., 2014. GPCC's new land surface precipitation climatology based on quality-controlled in situ data and its role in quantifying the global water cycle. Theor. Appl. Climatol. 115, 15–40. https://doi.org/10.1007/s00704-013-0860-x.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C.,

Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on central European forests. Basic and Applied Ecology 45, 86–103. https://doi.org/10.1016/j.baae.2020.04.003.

Smith, C., Baker, J.C.A., Spracklen, D.V., 2023. Tropical deforestation causes large reductions in observed precipitation. Nature 615, 270–275. https://doi.org/10.1038/s41586-022-05690-1.

Stine, A.R., Huybers, P., 2017. Implications of Liebig's law of the minimum for tree-ring reconstructions of climate. Environ. Res. Lett. 12, 114018 https://doi.org/10.1088/1748-9326/aa8cd6.

Szejner, P., Belmecheri, S., Ehleringer, J.R., Monson, R.K., 2020. Recent increases in drought frequency cause observed multi-year drought legacies in the tree rings of semi-arid forests. Oecologia 192, 241–259. https://doi.org/10.1007/s00442-019-04550-6.

Tagesson, T., Schurgers, G., Horion, S., Ciais, P., Tian, F., Brandt, M., Ahlström, A., Wigneron, J.-P., Ardö, J., Olin, S., Fan, L., Wu, Z., Fensholt, R., 2020. Recent divergence in the contributions of tropical and boreal forests to the terrestrial carbon sink. Nature Ecology & Evolution 4, 202–209. https://doi.org/10.1038/s41559-019-1090-0.

Thom, D., Ammer, C., Annighöfer, P., Aszalós, R., Dittrich, S., Hagge, J., Keeton, W.S., Kovacs, B., Krautkrämer, O., Müller, J., von Oheimb, G., Seidl, R., 2023. Regeneration in European beech forests after drought: the effects of microclimate, deadwood and browsing. Eur. J. For. Res. 142, 259–273. https://doi.org/10.1007/s10342-022-01520-1.

Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. Geogr. Rev. 38, 55–94.

Tumajer, J., Begović, K., Čada, V., Jenicek, M., Lange, J., Mašek, J., Kaczka, R.J., Rydval, M., Svoboda, M., Vlček, L., Treml, V., 2022. Ecological and methodological drivers of non-stationarity in tree growth response to climate. Glob. Chang. Biol. https://doi.org/10.1111/gcb.16470.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1.

Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., Lopez-Moreno, J.I., Azorin-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Moran-Tejeda, E., Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes. Proc. Natl. Acad. Sci. 110, 52–57. https://doi.org/10.1073/pnas.1207068110.

Visser, H., van der Maaten-Theunissen, M., van der Maaten, E., 2023. BAI BAI bias an evaluation of uncertainties in calculating basal area increments from cores. Dendrochronologia 78, 126066. https://doi.org/10.1016/j.dendro.2023.126066.

Walthert, L., Ganthaler, A., Mayr, S., Saurer, M., Waldner, P., Walser, M., Zweifel, R., von Arx, G., 2021. From the comfort zone to crown dieback: sequence of physiological stress thresholds in mature European beech trees across progressive drought. Sci. Total Environ. 753, 141792 https://doi.org/10.1016/j.scitotenv.2020.141792.

Wang, J., D'Orangeville, L., Taylor, A.R., 2023. Tree species growth response to climate warming varies by forest canopy position in boreal and temperate forests. Glob. Chang. Biol. 29, 5397–5414. https://doi.org/10.1111/gcb.16853.

Weber, P., Bugmann, H., Pluess, A.R., Walthert, L., Rigling, A., 2013. Drought response and changing mean sensitivity of European beech close to the dry distribution limit. Trees 27, 171–181. https://doi.org/10.1007/s00468-012-0786-4.

Weigel, R., Bat-Enerel, B., Dulamsuren, C., Muffler, L., Weithmann, G., Leuschner, C., 2023. Summer drought exposure, stand structure, and soil properties jointly control the growth of European beech along a steep precipitation gradient in northern Germany. Glob. Chang. Biol. 29, 763–779. https://doi.org/10.1111/gcb.16506.

Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., Smiljanic, M., Trouillier, M., 2020. Global assessment of relationships between climate and tree growth. Glob. Chang. Biol. 00, 1–9. https://doi.org/10.1111/gcb.15057.

Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in scots pine, Norway spruce and common oak. Trees 26, 557–569. https://doi.org/10.1007/s00468-011-0617-z.

Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., Menzel, A., 2014. Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Glob. Chang. Biol. 20, 3767–3779. https://doi.org/10.1111/gcb.12637.

Zeng, X., Hu, Z., Chen, A., Yuan, W., Hou, G., Han, D., Liang, M., Di, K., Cao, R., Luo, D., 2022. The global decline in the sensitivity of vegetation productivity to precipitation from 2001 to 2018. Glob. Chang. Biol. 28, 6823–6833. https://doi.org/10.1111/gcb.16403.

Zhao, S., Pederson, N., D'Orangeville, L., HilleRisLambers, J., Boose, E., Penone, C., Bauer, B., Jiang, Y., Manzanedo, Rubén D., 2019. The international tree-ring data Bank (ITRDB) revisited: data availability and global ecological representativity. J. Biogeogr. 46, 355–368. https://doi.org/10.1111/jbi.13488.

Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate warming-related growth decline affects Fagus sylvatica, but not other broad-leaved tree species in central European mixed forests. Ecosystems 18, 560–572. https://doi.org/10.1007/s10021-015-9849-x.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-87458-6.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.