



Drought and masting affect growth allocation along the stem axis in beech, oak, fir and spruce in temperate forests

Mareike Hirsch¹ · Evgenia Greiner-Müller¹ · Simon Boden² · Katharina Hillenmeyer¹ · Arno Mattes³ · Johanna Schuler⁴ · Peter Spathelf⁵ · Ernst van der Maaten⁶ · Marieke van der Maaten-Theunissen⁶ · Thomas Seifert^{7,8}

Received: 24 March 2025 / Accepted: 7 January 2026 / Published online: 10 February 2026
© The Author(s) 2026, modified publication 2026

Abstract

In temperate forests, tree growth and vitality are significantly influenced by drought, often reflected by low stem diameter growth. Additionally, masting, the cyclic production of seeds, can also affect growth, particularly through its interactions with environmental factors like drought. Despite extensive research on the individual impacts of drought and masting, their combined effects on growth allocation remain underexplored, especially for a broader variety of species. This study aims to bridge this gap by investigating how drought and/or masting influence growth patterns in the coniferous species *Abies alba* and *Picea abies*, as well as the deciduous broadleaved species *Fagus sylvatica* and *Quercus petraea*. Utilising tree-ring data collected over several decades, we analysed how basal area increment (BAI) at 1.3 m stem height as well as along the stem axis responds to various scenarios of drought and masting. Our results showed that drought consistently reduced BAI in all species. *F. sylvatica* and *P. abies* experienced significantly lower BAI during mast years that coincided with drought, suggesting a potential trade-off between vegetative and reproductive growth under resource limitation. In contrast, *Q. petraea* exhibited higher BAI during mast years, indicating a distinct carbon allocation strategy. Furthermore, our study revealed that differences in BAI between mast and non-mast years were most prominent in the upper stem in the deciduous species, particularly during drought periods. These findings highlight the complex interactions between environmental stress, stem diameter growth and seed production, emphasising the need for further research into whole-tree carbon allocation processes.

Key message

Drought and masting jointly affect basal area increment along the stem axis with species-specific patterns. Overall, beech and spruce are severely affected, while oak and particularly fir show less impact.

Keywords Carbon allocation · Fructification · Basal area increment · Dendroecology · Generative growth · Water availability

Communicated by F. Ripullone

✉ Mareike Hirsch
mareike.hirsch@wwd.uni-freiburg.de

¹ Chair of Forest Growth and Dendroecology, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany

² Fachbereich Wald, Landratsamt Ludwigsburg, Mühlstraße 34, 71665 Vaihingen/Enz, Germany

³ Landesforstverwaltung Baden-Württemberg/Forstdirektion Freiburg, Bertoldstraße 43, 79100 Freiburg, Germany

⁴ Fraunhofer Institute for Systems and Innovation Research ISI, Breslauer Straße 48, 76139 Karlsruhe, Germany

⁵ Eberswalde University for Sustainable Development, Alfred-Möller-Straße 1, 16225 Eberswalde, Germany

⁶ Chair of Forest Growth and Woody Biomass Production, TU Dresden, Pienner Str. 8, 01737 Tharandt, Germany

⁷ Chair of Forest Growth and Dendroecology, University of Freiburg, Tennenbacher Straße 4, Freiburg 79106, Germany

⁸ Department of Forest and Wood Science, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

Introduction

Drought has been recognised as a critical factor for tree growth and vitality in temperate forests (Bréda et al. 2006; Allen et al. 2010) and is associated with reduced stem diameter growth in a range of species (Vitasse et al. 2019; Song et al. 2021; Zimmermann et al. 2021). As sufficient turgor pressure is required for cell division and elongation, secondary wood formation is strongly controlled by water availability (Peters et al. 2021) and drought periods thus affect individual cell development (Stangler et al. 2021; Martínez-Sancho et al. 2022). At the tree-ring level, especially the rate of growth, but also its duration determine the overall stem radial increment (Larysch et al. 2021). Thus, drought periods that affect secondary xylem formation are likely to be reflected in low stem diameter growth. This has not only been observed as an immediate effect occurring in the year of the drought but also as a lagged effect in the subsequent year(s) (Vanoni et al. 2016; Fuchs et al. 2021; Rohner et al. 2021; Stangler et al. 2022). These lagged effects may be related to adverse effects on hydraulic functioning and/or carbon availability, or result from carbon allocation to other sinks than stem diameter growth (Kannenberg et al. 2020). While drought timing, intensity and duration are important factors (Werf et al. 2007; Gao et al. 2018; Huang et al. 2018), the responses to drought are also species-specific (Dănescu et al. 2018; Vitasse et al. 2019; Vanhellemont et al. 2019).

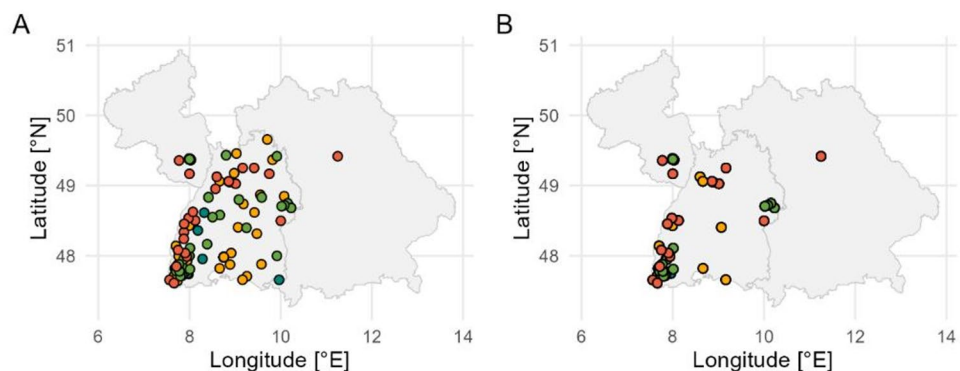
Further, the production of cones and seeds, especially in species with strong masting patterns (i.e. high inter-annual variability in reproductive growth) can also involve low stem diameter growth, as has been particularly shown for *Fagus sylvatica* (Hacket-Pain et al. 2018). Due to the complex inter-relationships between weather – and drought in particular –, masting and stem diameter growth, the (lagged) effects of drought and masting can be confounded. For instance, if low stem diameter growth is observed after a year with a severe drought period, this may not be a lagged drought effect but an indirect effect of a mast event, which was triggered by the warm and dry conditions in the previous year (Müller-Haubold et al. 2013; Hacket-Pain et al. 2015). Further, especially the co-occurrence of drought and masting can result in low stem diameter growth, as has been shown for *F. sylvatica* in Europe (Hacket-Pain et al. 2017) as well as for *Araucaria araucana* in South America (Mundo et al. 2021; Hacket-Pain et al. 2024). Although developing seeds are strong carbon sinks (Miyazaki 2013), it has been argued that reduced stem diameter growth in mast years is not simply caused by a trade-off in carbon allocation (Mund et al. 2020) but rather the result of complex interactions of direct and indirect endogenous and environmental effects, also related to the timing of the respective processes (Mund et al. 2010). It is important to consider that these interrelations

are also likely to differ between species, which do also differ in their masting strategies (Nussbaumer et al. 2021). While stem diameter growth is particularly low in mast years in *F. sylvatica*, no such effect has been found in *Quercus* sp. (Nussbaumer et al. 2021). In *Picea abies*, both no reduction in stem diameter growth in a mast year (Seifert and Müller-Starck 2009) and an effect depending on site elevation (Mencuccini and Piussi 1995) have been observed. As masting requires a large amount of resources, it could also be assumed to affect stem diameter growth in the year(s) following a mast event. While no such effect has been observed in *F. sylvatica* (Nussbaumer et al. 2021) and *Picea abies* (Seifert and Müller-Starck 2009), a minor reduction in basal area increment after a mast year was observed in *Quercus* sp. (Nussbaumer et al. 2021). These results point to species-specific patterns and lag effects, potentially also interlinked to climatic conditions in the respective years.

The impact of factors such as masting or drought on stem diameter growth are mostly studied at a stem height of 1.3 m (=breast height), and the observed effect is then used as a proxy for the response at the tree level (e.g. Zang et al. 2014; Camarero JJ et al. 2018). Yet, growth allocation along the stem can vary inter-annually, especially as affected by environmental factors. Drought has been observed to induce a stronger growth reduction at breast height than higher up the stem in *F. sylvatica* (Bouriaud et al. 2005; Peters et al. 2020), a pattern that is analogous to the growth decline recorded during hot summers in *P. abies* and *Abies alba* (van der Maaten-Theunissen and Bouriaud 2012). Under such unfavourable conditions, assimilates are likely to be primarily used within the crown and are less transported to the lower parts of the stem, thus increasing the impact on stem diameter growth as the distance between the site of carbon assimilation and the potential carbon sink increases (Fritts 1976; Lacointe 2000; van der Maaten-Theunissen and Bouriaud 2012). Thus, in this study we aimed to gain further knowledge on the effects of drought and/or masting on growth allocation patterns in the two coniferous species *A. alba* and *P. abies* as well as the two broadleaved species *F. sylvatica* and *Q. petraea*. In a first step, we investigated how basal area increment at 1.3 m stem height is affected by drought and/or masting conditional on the occurrence of drought and/or masting in the previous year. Then, focusing on stem diameter growth in the current year only, we analysed how the occurrence of masting and/or drought affects basal area increment along the stem axis.

Table 1 Number of trees per study and species (number of trees with samples at several stem heights per tree in brackets). A total of 986 (340) trees were considered

Source	<i>Abies alba</i>	<i>Picea abies</i>	<i>Fagus sylvatica</i>	<i>Quercus petraea</i>
A (Boden 2014)		31		
B (Diaconu 2016)			105	
C (Hauser 2003)			18	
D (Hillenmeyer 2021)		20 (20)	22 (22)	
E (Hirsch 2019)	45		204	
F (Lässig 1991)		18		
G (Mattes 2014)			40 (34)	39 (37)
H (Nutto 1998)				40 (9)
I (Schuler 2011)			58 (34)	67 (36)
J (Spathelf 1997)	25	43		
K (Tojic 2010)		26 (23)	16 (16)	
L (van der Maaten 2012)			54	
M (van der Maaten-Theunissen 2012)	70 (64)	45 (45)		
Sum	140 (64)	183 (88)	517 (106)	146 (82)

Fig. 1 Locations of sample trees in southern Germany for **A)** analysis at 1.3 m stem height and **B)** analysis at different stem heights per tree. Blue = *Abies alba*, Green = *Picea abies*, Yellow = *Fagus sylvatica*, Red = *Quercus petraea*

Material

Tree-ring data

Tree-ring data were extracted from the internal database of the Chair of Forest Growth and Dendroecology at the University of Freiburg and comprise of datasets of the four species *Abies alba*, *Picea abies*, *Fagus sylvatica* and *Quercus petraea* that were collected during the last decades within different research projects (s. Table 1 for the references). Samples were taken as either tree cores or stem discs. An overview of the number of trees per study is given in Table 1, the locations of the sampled trees are shown in Fig. 1 and the time period covered by the respective tree-ring series in Fig. 2.

Climate and masting data

Daily data on precipitation and minimum as well as maximum temperature were extracted for each location with the R-package *easyclimate* (Moreno and Hasenauer 2016; Pucher and Neumann 2022; Cruz-Alonso et al. 2023; Pucher

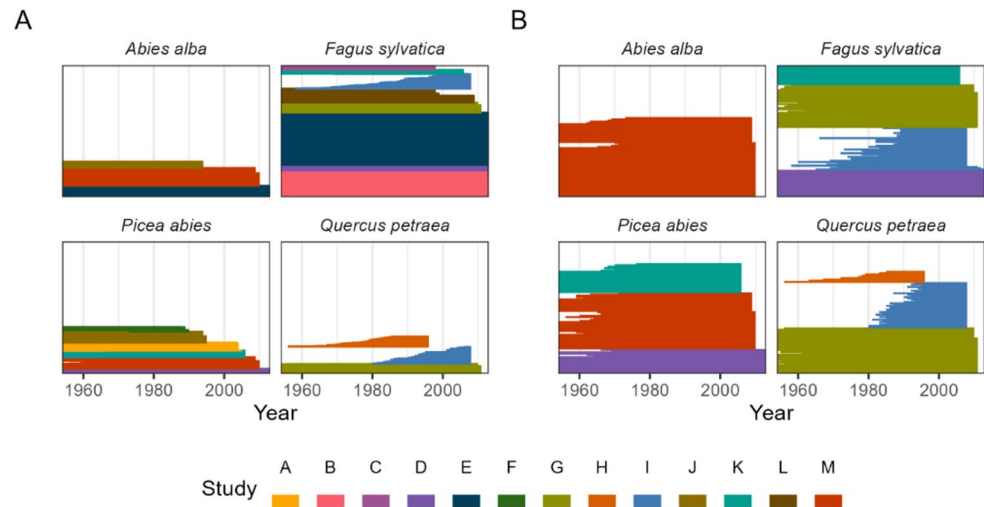
2023). As no records of masting activity were available for the sampled trees, data on mast intensity were extracted from the MASTREE+ database (Hacket-Pain et al. 2022). We obtained records of visual crop assessment available for our study region (Southwest Germany) and the time period of interest (1954–2013). Despite a certain degree of inter- and intra-regional variability, masting is generally strongly synchronised across large scales (Nussbaumer et al. 2016; Vacchiano et al. 2017; Bogdziewicz et al. 2021), allowing for the inference of masting activity of the sampled stands from these regional data.

Methods

Preparation of tree-ring data

For each tree, we averaged multiple tree-ring width series from the same stem height into a single series per tree and stem height, where applicable. Based on these series and the cumulative sums of tree-ring widths, basal area (at the respective stem height) and the annual basal area increment

Fig. 2 Overview of time series available between 1954–2013 for **A**) analysis at 1.3 m stem height and **B**) analysis at different stem heights per tree. Each horizontal line represents one tree-ring series (i.e. one tree, as annual values were averaged if series for different radii were available per tree), colours represent the different studies (cf. Table 1)



were calculated for each year. Tree age was estimated based on the number of rings at 1.3 m stem height. We added 15 years to the respective number to account for the time necessary to reach a tree height of 1.3 m, conceding that this is a rough estimate only with high inter- and intraspecific variability. Yet, as the aim was to account for ageing within a tree rather than comparing absolute values, we deemed this approach reasonable.

Estimation of absolute and relative height of trees and samples

In order to be able to compare basal area increment at different (relative) stem heights across trees, we converted the absolute stem heights at which samples were taken to relative stem heights. For that, we first had to estimate the absolute tree height at the point of sample collection, i.e. the missing length between the topmost sample taken and the apex. Based on the height of the topmost sample taken and the age of the tree at the stem height where the lowest sample was taken, we calculated the average annual height increment. Then, based on the cambial age of the topmost sample, we estimated the presumed length to the apex to calculate the overall tree height in the year of sampling. Considering that each tree continuously grows in both stem diameter and height, the next step was to calculate the relative stem height for each sample (i.e. absolute stem height at time of sampling) and year. To do so, we linearly interpolated the annual height increment between two samples (i.e. absolute stem heights) based on the respective cambial ages of these samples, resulting in an estimate for tree height in each year. Finally, the relative stem height at which the sample was taken was calculated as the percentage of the overall tree height in each respective year.

Preparation of climate and masting data

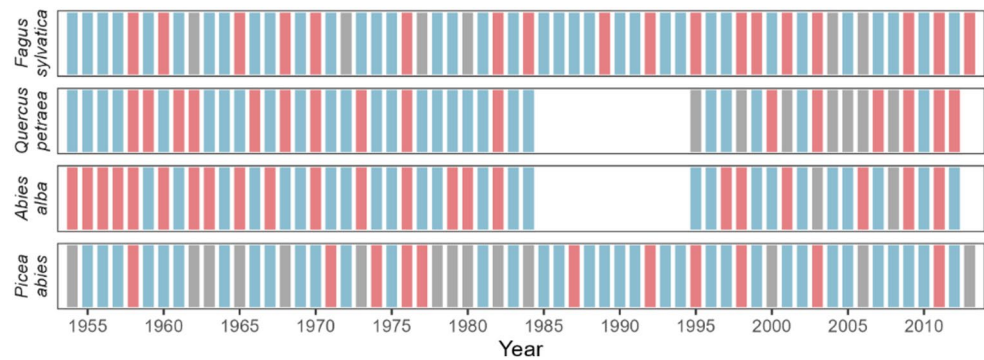
Daily mean temperature was calculated from the minimum and maximum values and then aggregated into monthly averages. Similarly, daily precipitation values were summed to derive monthly totals. Based on the monthly values and the latitude of each location, potential evapotranspiration (PET) was calculated using the Thornthwaite equation. From that, the climatic water balance was calculated as the difference between precipitation and PET and standardised as the SPEI using R-package *SPEI* (Beguería and Vicente-Serrano 2023). SPEI was calculated integrating a timescale of three months and the lowest value from May, June and July was selected to represent water availability in the period, in which stem diameter growth primarily takes place (Michelot et al. 2012; Larysch et al. 2021; Miller et al. 2022).

The time series of masting activity were first converted to binary values, i.e. observations of no or scarce masting were categorised as “non-mast” years and observations of intermediate and heavy masting as “mast” years. As, depending on the species and year, observations of up to 15 series were available, we tested for intra-annual agreement per species by calculating the mean and did then exclude any years, where the mean value was <0.66 for mast years or >0.33 for non-mast years. Thus, we did only retain years with high synchrony across our study region in order to increase applicability of the data to our sample trees and the robustness of our analysis (Fig. 3).

Statistical analysis

All analyses were carried out for the time period 1954–2013 ($\triangleq 60$ years) using R (R Core Team 2023).

Fig. 3 Overview of available masting data and masting activity between 1954–2013. Mast years are indicated by red bars, non-mast years by blue bars. Grey bars indicate years, in which there was insufficient agreement between series and which were thus excluded from the analysis



Effect of masting and drought on basal area increment at 1.3 m stem height

For each of the four species, a generalised additive model was formulated with the basal area increment (BAI_t) as the response variable. The minimum SPEI-3 of the period May–July of the current ($SPEI-3\ MJJ_t$) and preceding year ($SPEI-3\ MJJ_{t-1}$) were included as a tensor smooth interaction, and the different combinations of mast occurrence in the current and preceding year were included as factor-by-smooths in order to analyse the effects of masting in interaction with potential drought conditions. In addition, stem basal area at 1.3 stem height and tree age were included as smooth predictors. To account for underlying growth trends, calendar year was included as a smooth effect to address global temporal trends, such as rising temperatures or increasing atmospheric CO_2 levels. Additionally, an interaction between calendar year and tree ID was modeled using Duchon splines to capture individual growth effects over time, such as competition and release (Nothdurft and Vospernik 2018). To address spatial autocorrelation, the coordinates of each location were included as an anisotropic tensor product smooth. The Gamma family was used with a log-link. For all but the individual tree effect we employed P-splines with a second-order difference penalty in order to balance flexibility and potential overfitting (Eilers and Marx 1996). We further applied the double penalty approach to allow a term to be entirely removed from the model (Marra and Wood 2011). In order to fit biologically plausible fits that have limited wigglyness we fitted the temporal and spatial components with a maximum of ten basis functions and all other terms with a maximum of five basis functions. Model diagnostics were carried out using a simulation-based approach to compare observed to expected residuals using R-package *DHARMA* (Hartig 2022). The estimates of the smooth effects were extracted using R-package *gratia* (Simpson 2023). In order to compare the effect of masting and SPEI-3 MJJ on annual basal area increment, we calculated the estimated marginal means based on the different combinations of masting in the current and preceding year

using R-package *emmeans* (Lenth 2023). To this end, three values were calculated for SPEI-3 MJJ that represent the mean conditions as well as one standard deviation difference to represent below-average and above-average conditions.

Effect of masting on basal area increment at different stem heights and under different drought scenarios

In this step, we focussed on the effect of masting in the current year only. In order to analyse the joint effect of drought and masting along the stem, we modelled relative stem height and SPEI-3 MJJ_t as a tensor-product smooth, which accounts for the different units of both variables and added mast as a factor-by-smooth. This allows to create a separate smooth of the interaction of relative stem height and SPEI-3 MJJ_t for mast and non-mast years, respectively. To account for the general effect of masting on BAI_t , it was also included as a fixed effect. The maximum number of basis functions for relative stem height was set to eight. All remaining predictors and settings as well as diagnostics were the same as for the models described above.

Results

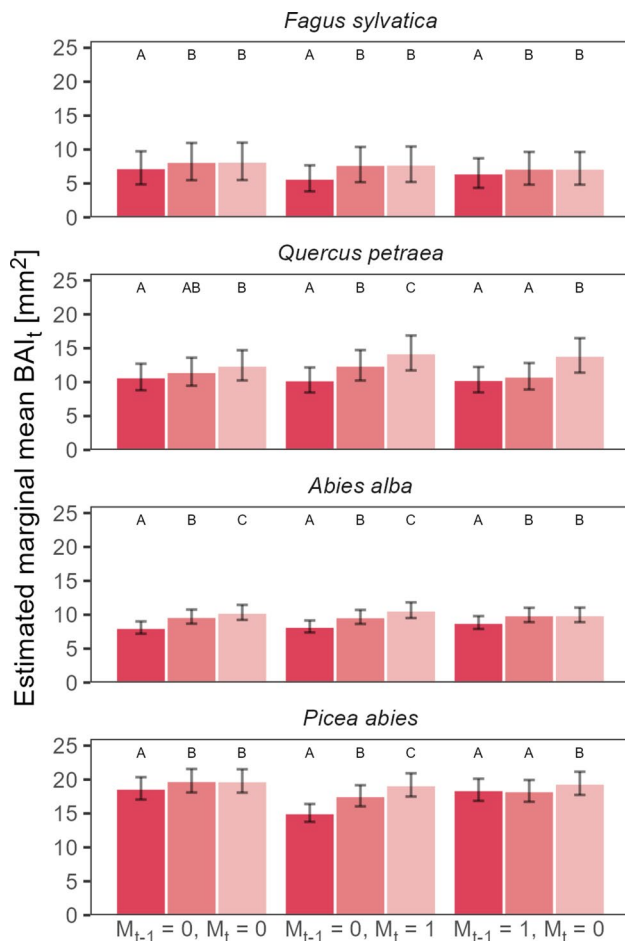
The effects of masting and drought on basal area increment at 1.3 stem height

In a first step, we assessed the effect of masting in the current or previous year on basal area increment at a stem height of 1.3 m based on the estimated marginal means of the first model. It is important to note that the reference grids differed between species, i.e. with respect to (mean) tree age and basal area, so that increment levels should not be compared between species. In Table 2, the estimated marginal means are shown for the respective SPEI-3 values representing average and dry conditions. In years with average conditions, both *F. sylvatica* and *P. abies* showed significantly lower BAI_t in mast years and years following a mast year

Table 2 Estimated marginal means of annual basal area increment in different scenarios of mast year sequences for both years with average min. SPEI-3 MJJ and lower than average min. SPEI-3 conditions

Average conditions (Mean minimum SPEI-3 MJJ _t)								
	<i>Fagus sylvatica</i>		<i>Quercus petraea</i>		<i>Abies alba</i>		<i>Picea abies</i>	
$M_{t-1} = 0, M_t = 0$	8.2 ± 2.7	C	11.6 ± 2.1	AB	9.8 ± 1	B	19.8 ± 1.7	C
$M_{t-1} = 0, M_t = 1$	7.7 ± 2.6	B	12.6 ± 2.3	A	9.8 ± 1	B	17.5 ± 1.5	A
$M_{t-1} = 1, M_t = 0$	7.2 ± 2.4	A	11 ± 2	B	10 ± 1.1	B	18.3 ± 1.6	B
Dry conditions (Mean minimum SPEI-3 MJJ _t - SD)								
	<i>Fagus sylvatica</i>		<i>Quercus petraea</i>		<i>Abies alba</i>		<i>Picea abies</i>	
$M_{t-1} = 0, M_t = 0$	7.3 ± 2.4	C	10.8 ± 2	A	8.1 ± 0.9	AB	18.7 ± 1.6	B
$M_{t-1} = 0, M_t = 1$	5.8 ± 1.9	A	10.3 ± 1.8	A	8.3 ± 0.9	A	15.1 ± 1.3	A
$M_{t-1} = 1, M_t = 0$	6.5 ± 2.2	B	10.4 ± 1.9	A	8.9 ± 0.9	B	18.7 ± 1.6	B

Letters indicate significant differences in BAI_t within species. Average conditions correspond to SPEI-3 MJJ_t values of -1.2 in *F. sylvatica* and *P. abies*, -1.3 in *Q. petraea* and -1.1 in *A. alba*. Dry conditions correspond to SPEI-3 MJJ_t values of -1.7 in *F. sylvatica* and *P. abies*, -1.8 in *Q. petraea* and -1.6 in *A. alba*.

**Fig. 4** Estimated marginal means of BAI_t for different mast scenarios and SPEI-3 MJJ conditions (dark red=mean - SD, medium red=mean, light red=mean+SD). Mean (standard deviation) of SPEI-3 MJJ corresponds to -1.2 (0.5) in *F. sylvatica* and *P. abies*, -1.3 (0.5) in *Q. petraea* and -1.1 (0.5) in *A. alba*

than in non-mast years, which were also preceded by a non-mast year. On the contrary, BAI_t in *Q. petraea* was higher in mast years than non-mast years, although the difference was only significant when comparing with a non-mast year

following a mast year. For *A. alba*, however, there were no significant differences in BAI_t at all.

In dry years, *A. alba* did show slight differences, where BAI_t was significantly higher in a non-mast year following mast than in a mast year. In turn, there were no significant differences in *Q. petraea*. In *F. sylvatica* and *P. abies*, BAI_t was again significantly lower in mast than in non-mast years.

Within each category (no masting, masting in preceding year, masting in current year) we assessed the effect of SPEI-3 MJJ_t, while assuming average conditions of SPEI-3 MJJ_{t-1}. In all species, BAI_t was significantly lower in dry years compared to average and/or wet years regardless of the occurrence of masting (Fig. 4).

The plots for the joint effects of SPEI-3 MJJ in the current and preceding year show that there was a general tendency of a positive effect of less negative SPEI-3 MJJ in the current and/or preceding year (Fig. 5). Yet, within species this effect was slightly modified when comparing the different scenarios of mast occurrence.

The effect of masting and drought on basal area increment along the stem axis

The second set of models was employed in order to quantify the effect of SPEI-3 MJJ_t on basal area increment along the stem axis, again considering potential differences in mast and non-mast years. In Fig. 6, the fitted values of BAI_t as affected by relative stem height, SPEI-3 MJJ_t and mast are shown. In order to gain further insight into the effect of masting, the ratios of the estimated marginal means between mast and non-mast years were calculated in 10%-steps from 5% to 95% relative stem height (where 0% corresponds to the base of the stem and 100% to the apex). The four species showed different, distinct patterns with respect to basal area increment along the stem axis as affected by masting and drought (Fig. 7). For *P. abies*, basal area increment at the respective stem height was almost always higher in

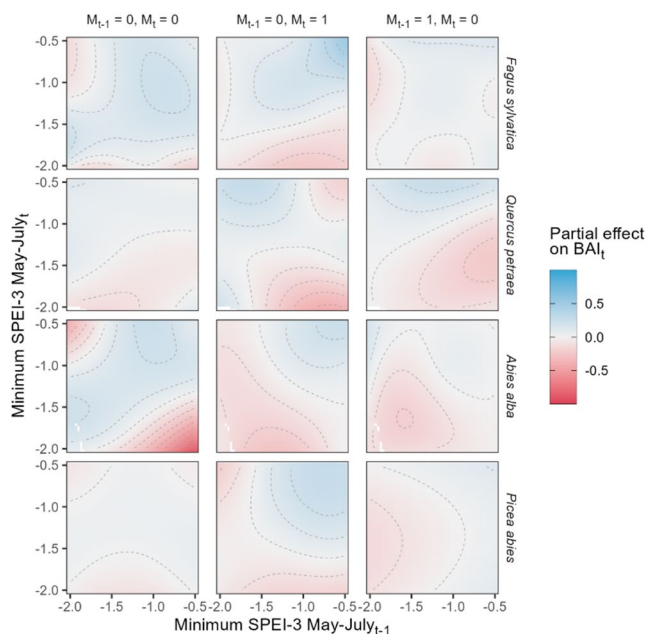


Fig. 5 Partial effect of minimum SPEI-3 MJJ of current and previous year on basal area increment at $d_{1.3}$ for different scenarios of mast year sequences (no mast in current or previous year, mast in the current year, mast in the previous year). To aid interpretation, dashed lines trace contours of selected equal values of estimated basal area increment

non-mast than mast years along the complete stem axis. In *F. sylvatica* and *A. alba*, however, this was only true for dry years, whereas in average and wetter-than-average years, the difference was only significant in the upper parts of the tree. In *Q. petraea*, under average and wetter-than-average conditions, BAI_t was higher in mast than non-mast year, if significantly different at all. This relation shifted in the upper 15% of the tree. Interestingly, under dry conditions, there was no significant difference in BAI_t except for in the top part, where BAI_t was then however mostly higher in non-mast years than mast years.

Discussion

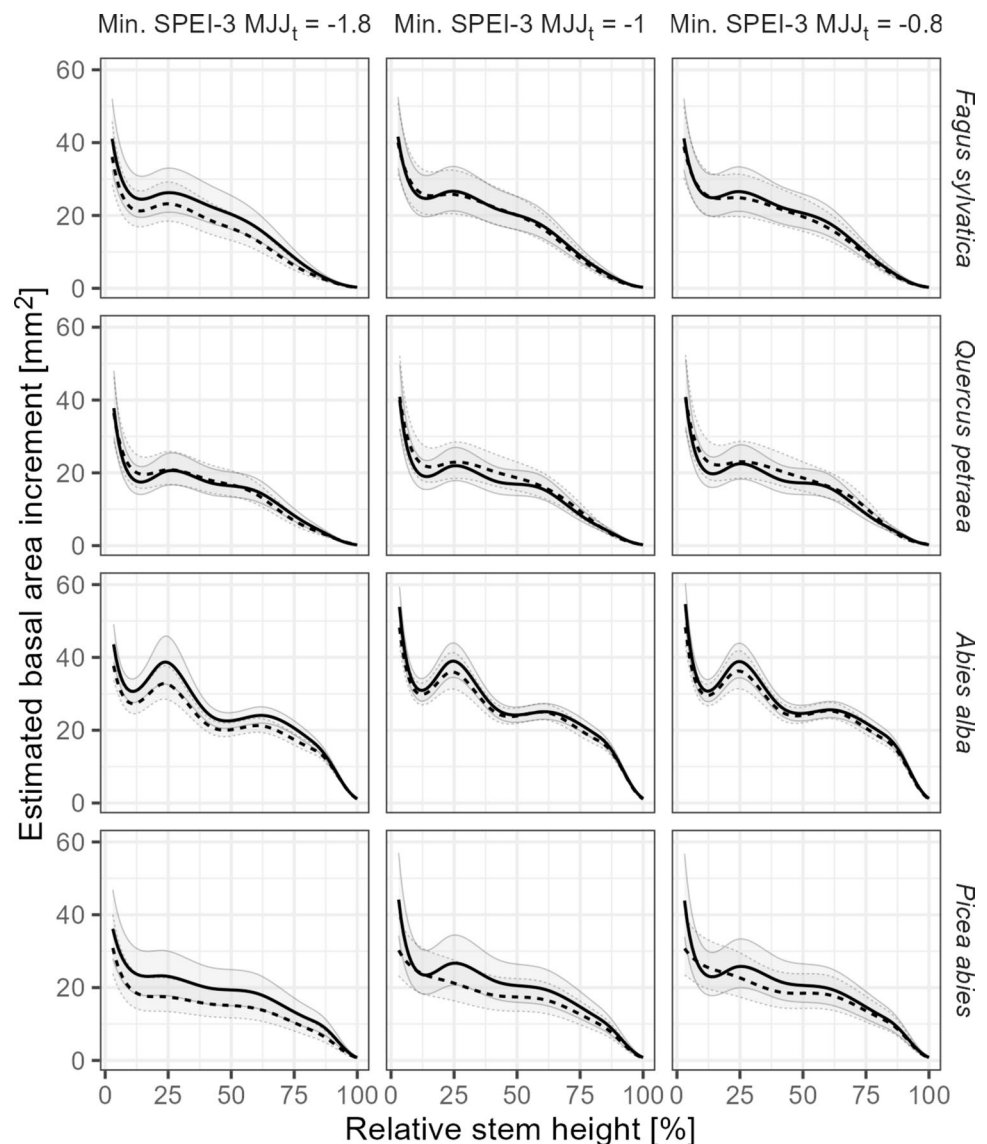
Analysing the effects of growing conditions (i.e. water availability) and masting on basal area increment gave insight into complex interactions, which were also subject to inter-specific differences. While we cannot compare (relative) carbon allocation to different sinks based on our analysis, investigating the effects of masting on growth (at different stem heights) under different drought scenarios may help to understand these species-specific patterns.

How do masting and drought affect basal area increment at 1.3 m stem height?

For this analysis, we investigated the joint effects of drought and mast in the same year as well as a potential lagged effect of masting, and finally a combined effect of drought in the current and preceding year given the different mast scenarios.

Basal area increment (BAI) was significantly lower in dry years compared to BAI in years with average conditions in most species and mast scenarios, but at least compared to years with wetter-than-average conditions (Fig. 4). Such low growth resistance to drought and particularly a negative effect of low water availability and/or high temperature in spring/summer has been shown in previous studies across all of our studied species (Vanhellemont et al. 2019; Vitasse et al. 2019; Petritan et al. 2021). At least to some degree, it can be explained by the direct effect of reduced water availability on cell production and enlargement rates for wood formation, to the extent that drought may even induce the premature cessation of cell enlargement (Larysch et al. 2021, 2022). While the adverse effects of drought on stem diameter growth have been vastly studied, their interaction with effects of masting are less known, especially for species other than *F. sylvatica* (Hacket-Pain et al. 2017). Yet, from our study based on interactive effects of SPEI in the current and previous year with mast in current and previous year, it is apparent that both effects have to be considered in combination across species. Especially for *F. sylvatica* and *P. abies*, in a dry mast year, BAI was substantially reduced, both in comparison to BAI in non-mast dry years and to mast years with average conditions in May-July (Table 2; Fig. 4). For *P. abies*, this is in contrast to the results of a previous study, where no trade-off between biomass investment into stem diameter growth and cones was observed (Seifert and Müller-Starck 2009). However, a reduction of stem diameter growth in mast years has also been found to be dependent on elevation and competition in this species, highlighting the influence of site and growing conditions (Mencuccini and Piussi 1995). In *F. sylvatica*, BAI was particularly reduced in years, in which mast and drought co-occurred, suggesting that a potential trade-off between vegetative and generative growth depends on the concomitant weather conditions in this species (Hacket-Pain et al. 2017). Yet, such observed trade-off does not necessarily imply a general carbon limitation (Mund et al. 2010, 2020). Rather, other sinks such as storage may be prioritised over stem diameter growth to ensure sufficient carbon supply in the long run (Sala et al. 2012). Moreover, as cambial activity and cell elongation can be directly affected by water shortage due to reduced turgor (Hsiao 1973), studies on intra-annual xylem formation and phenology are necessary

Fig. 6 Fitted values of annual basal area increment along the stem axis (as relative stem height) in non-mast (solid line) and mast (dashed line) years for different values of SPEI-3 MJJ_t, representing drier than mean (−1.8), mean (−1) and wetter than mean (−0.8) conditions. Shaded ribbons show the respective confidence intervals



to investigate if and how tree hydraulics are modified by the production of flowers, cones or seeds. In contrast to *F. sylvatica* and *P. abies*, BAI was (partly significantly) higher in mast years than non-mast years in *Q. petraea* in years with average climatic conditions. This confirms results from previous studies where no immediate negative effect of masting on stem diameter growth has been observed (Lebourgeois et al. 2018; Nussbaumer et al. 2021), which suggests that oaks do not follow a “resource-switching”-strategy such as beech (Kelly and Sork 2002). It is currently under debate whether *Quercus* sp. exhibits a resource-matching strategy instead (Lebourgeois et al. 2018; Nussbaumer et al. 2021). That *Q. petraea* showed a higher BAI in mast compared to non-mast years in our study could indeed indicate such pattern, i.e. high resource availability does not only enable strong fructification but also high stem diameter growth at the same time. *Q. petraea* has been found to generally prioritise

carbon allocation to storage more than *F. sylvatica*, which is potentially related to the differences in wood anatomy – in ring-porous oaks the large earlywood vessels get embolised in winter, requiring the formation of new earlywood vessels in spring before leaf unfolding occurs and new carbon is assimilated (Genet et al. 2010). Thus, tracing back to the different wood anatomies, *Q. petraea* and *F. sylvatica* potentially follow distinct strategies of carbon storage and utilisation, which are then also reflected in their growth potential in mast years. However, this pattern did not show in dry years, in which there was no significant difference in BAI across the different masting scenarios. This would suggest that in mast years with adverse conditions, *Q. petraea* is also limited in resources – or allocates them to other sinks but stem diameter growth. Interestingly, in the coniferous *A. alba*, such lack of significant differences in BAI became apparent in years with average climatic conditions instead.

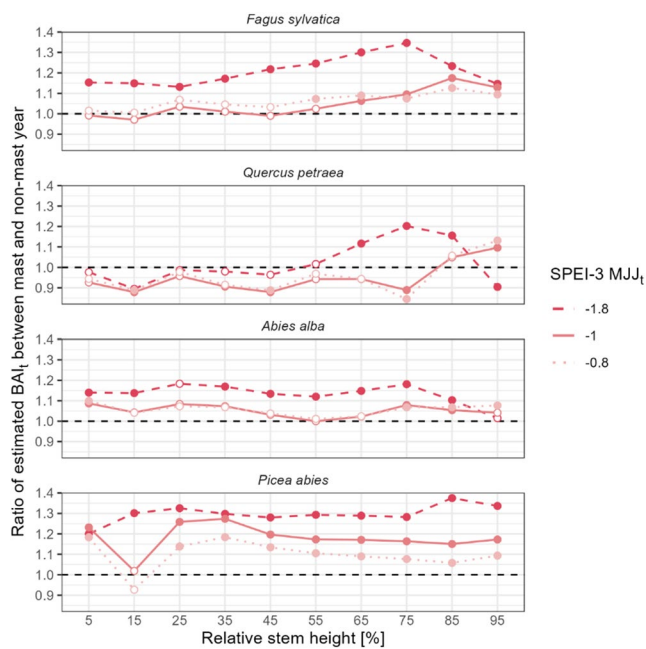


Fig. 7 Ratios of estimated marginal means of basal area increment along the stem axis (10% steps from 5 to 95% relative stem height) in years with average SPEI-3 MJJ_t (medium red solid line), lower than average SPEI-3 MJJ_t (dark red dashed line) and higher than average SPEI-3 MJJ_t (light red dotted line). Values > 1 indicate that BAI is higher in non-mast than mast years, values < 1 indicate that BAI is higher in mast than non-mast year. Filled circles indicate significant differences in estimated BAI between mast and non-mast years within species and relative stem height

In dry years, while partly significant, differences were small as well, indicating that masting neither in the current nor preceding year substantially affected stem diameter growth in this species.

When regarding basal area increment as the result of carbon allocation patterns, one could also assume a lasting or lagged effect of mast on BAI in the subsequent year. Indeed, in a year with average SPEI-3 MJJ_t, a mast event in the previous year had a similar effect on BAI as masting in the current year in *F. sylvatica*, *A. alba* and *P. abies*. Nussbaumer et al. (2021) have observed a similar effect and attributed this to resource depletion as a result of high allocation to generative growth in the preceding year. This seems reasonable, given that e.g. in *F. sylvatica*, up to 20% of the carbon used for xylem formation at the beginning of the growing season originated from reserves (Skomarkova et al. 2006). Yet, no depletion of NSCs in the branch or stem xylem has been observed as a consequence of masting (Körner 2003; Hoch et al. 2003). This illustrates that further knowledge is required concerning the conditions under which carbon from which source (current assimilation vs. reserves) is available or utilised for which process (Dietze et al. 2014). In contrast to the other three species, BAI was significantly lower in a year following a mast event than in a mast year

itself in *Q. petraea* under average weather conditions. This is in line with a recent study, in which BAI was slightly reduced in the two years after a mast event, attributed to a potentially moderate resource depletion (Nussbaumer et al. 2021). However, as BAI in such year was comparable to that in a non-mast year following a year without mast event, this may not be a lagged effect but an indication of a resource-matching strategy. Yet, in *P. abies* and *F. sylvatica*, where BAI was significantly reduced in non-mast years following a mast event compared to years without masting in neither the current nor preceding year, such a lagged effect seems more plausible.

While potential lag effects of masting require further research, legacy effects of drought on tree growth and vitality have been vastly observed (McDowell et al. 2008; Schuldt et al. 2020). These can result from direct effects – e.g. resource limitation, reduced leaf area or hydraulic failure (Bréda et al. 2006; McDowell 2011) – or indirect effects, as drought has been found to trigger masting in a number of species (Nussbaumer et al. 2018), which itself can be concomitant with low vegetative growth in some species, as shown above. We thus investigated the combined effect of the current as well as previous year's SPEI-3 MJJ for the different mast scenarios (Fig. 5). For *F. sylvatica*, the negative effect of masting on BAI in the subsequent year, described above, was particularly enhanced if this mast year was also characterised by dry conditions in May–July. This indicates that under such conditions, the combination of high carbon demand and potentially limited supply lasts throughout the following year. In mast years, less dry conditions in the previous year did also have a positive effect on BAI, especially in combination with less negative SPEI3-MJJ in the current year, underlining the direct effect of favourable weather conditions on BAI in mast years (Mund et al. 2020). In contrast, low SPEI-MJJ in the previous year rather had a more positive effect on BAI in *Q. petraea*, especially when masting occurred in either of those years. Across Europe, growth in *Q. petraea* has been shown to hardly respond to precipitation in previous year's spring and summer and was also characterised by high recovery after spring and especially summer droughts (Bose et al. 2021). The observed pattern could thus be related to the resource dynamics in this species – a single summer drought may not have substantial effects on overall resource storage in this species, and low stem diameter growth in a dry year (Fig. 4) may even entail higher resource availability for wood formation in the following year. The opposite is visible in *A. alba*, where particularly the combination of dry conditions in the current and previous year had a negative effect on BAI, at least when masting occurred in either of these years. This is in line with a recent study showing increased drought sensitivity of stem diameter growth in this species, especially regarding drought

legacy effects (Stangler et al. 2022). *P. abies* showed similar patterns – and weather conditions in the previous year were especially relevant when they co-occurred with masting, which may also hint at a certain degree of resource depletion under such unfavourable conditions, in which resource demand for cone production is high.

It has to be noted that, while our analysis offers insights into the complex interactions between drought, masting and the respective lag effects, we did not consider other environmental variables or time periods. Further, as we were not able to account for intra-annual variability in masting within our study, the results need to be verified based on dendro-ecological studies combined with masting observations in the respective trees.

How does masting affect growth partitioning along the stem under differing drought conditions?

So far, only few studies exist that investigate the effect of drought on growth allocation along the stem but these do consistently show that basal area increment in *F. sylvatica*, *P. abies* and *A. alba* is particularly impaired at the lower stem parts (Bouriaud et al. 2005; van der Maaten-Theunissen and Bouriaud 2012; Peters et al. 2020). To our knowledge, our study is the first to assess the effect of masting on BAI at different stem heights. While we did not compare relative growth allocation between different stem positions, the ratio of BAI in mast compared to non-mast years showed relatively stable patterns within a given SPEI-3 MJJ_t scenario in most species in the lower half of the tree, indicating that the effect of masting becomes particularly apparent in the crown (Fig. 7).

The production of flowers, cones and seeds is a strong carbon sink (Seifert and Müller-Starck 2009; Müller-Haubold et al. 2013; Mund et al. 2020) and of high priority in mast years, even under drought conditions (Hesse et al. 2021). In deciduous species, once the leaves have flushed, carbon reserves are refilled simultaneously with stem diameter growth (Klein et al. 2016; Zahnd et al. 2024). If masting occurs, the required carbon is in general fully provided from current assimilation taking place in the respective branchlets (Hoch 2005; Hoch et al. 2013). While carbon reserves in the branches at the end of the growing season generally show low between-year variability, indicating that (environmental) conditions do not substantially affect refilling, particularly low starch levels have been observed in *F. sylvatica* in a year, in which drought and mast co-occurred (Zahnd et al. 2024). This potential inability to fully refill reserves in years, in which unfavourable conditions and a high demand for masting coincide could likely be reflected in a particularly strong difference in BAI between mast and non-mast years under drought conditions, if related to an overall

carbon limitation. Indeed, in *F. sylvatica*, the difference in BAI was particularly strong in dry years, and in average and wet years only significant in the upper half of the tree (Fig. 7). Thus, while carbon allocation to secondary growth was reduced throughout the stem in dry years, only the crown was affected in non-drought years. Here, the flower and seed production was likely favoured over the secondary growth of branches, potentially along with the refilling of reserves (Sala et al. 2012). Thus, even in non-drought years, BAI in this part of the tree seemed to be limited or of lower priority. In contrast, in *Q. petraea*, BAI in average and wet years was similar, or higher in mast than non-mast years along the complete stem axis except for the very top, underlining the indication of a resource-matching strategy in this species as described above (Fig. 7). Interestingly, in the upper third of the tree, BAI was significantly higher in non-mast than in mast years. The carbon for seed production in *Q. petraea* is entirely provided by current assimilation (Hoch et al. 2013) and reduced diameter growth of branches may indicate some resource limitation or at least low prioritisation of secondary growth to occur in this species as well, at least when conditions are unfavourable. In *A. alba* and *P. abies*, the responses to drought and masting observed at 1.3 m stem height mostly correspond to those along the complete stem axis, where the difference between BAI in mast and non-mast years is particularly strong in dry years and lower or even not significantly different under more favourable conditions. In these two coniferous species, the effect of mast on growth allocation is however mostly consistent throughout the length of the tree, and thus less affected by the distance to the sites of carbon assimilation as well as cone and seed production.

Conclusion

Species-specific effects of drought and mast need to be considered in combination

Our study confirms the ubiquitous negative impact of drought on BAI across species. However, our analysis clearly showed that it is difficult to identify species-specific responses of stem diameter growth to masting. Rather, the impacts of drought and masting should be considered jointly so as to avoid confounding effects. In *F. sylvatica* and *P. abies*, BAI showed a strong reduction in mast compared to non-mast years, particularly when drought co-occurred. This potentially indicates a resource switching strategy, especially under unfavourable conditions. In *Q. petraea*, however, BAI was higher in mast than non-mast years, at least under average climatic conditions, potentially related to the generally stronger prioritisation of carbon storage in

this species as well as a resource-matching strategy. *A. alba* showed small effects of masting on BAI overall. Our results show that the interrelations between the effects of drought and masting are further complicated by potential lag effects of both factors, necessitating a deeper understanding of carbon allocation dynamics and the prioritisation of different sinks.

Effect of masting on BAI is particularly pronounced in the upper tree but allocation patterns are also affected by drought

Our analysis of BAI along the stem axis offered some first clues with regard to intra-tree variability in biomass allocation. While the impact of masting was rather uniform along the lower part of the stem across species, more substantial differences in BAI between mast and non-mast years showed in the upper part of the tree/crown area, especially in the two broadleaved species. In this part, the co-occurrence of drought did further modify these patterns. While we could not determine the underlying processes, our study highlights that whole-tree processes related to carbon allocation need to be investigated further in order to improve the understanding the effect of masting on tree growth.

Acknowledgements We would like to thank Daniela Diaconu, Sandra Hauser, Reinhard Lässig, Leif Nutto and Karl Tojic for providing tree-ring width data.

Author contributions MH and TS conceived the study. MH and EGM developed the methods. MH carried out the analysis and wrote the first draft of the manuscript, TS and EGM edited the manuscript. SB, KH, AM, JS, PS, EM and MMT provided tree ring data and edited the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. MH was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 454840041.

Data availability Data is available upon reasonable request.

Declarations

Competing Interests No conflicts of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage* 259:660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Begueria S, Vicente-Serrano SM (2023) SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index. <https://spei.csic.es>, <https://github.com/sbegueria/SPEI>
- Boden S (2014) Resilienz ausgewählter Jahrringparameter von Fichten (*Picea abies* (L.) Karst.) in Zeiten mit geringer Wasserverfügbarkeit in Baden-Württemberg. Dissertation, Albert-Ludwigs-Universität Freiburg
- Bogdziewicz M, Hacket-Pain A, Ascoli D, Szymkowiak J (2021) Environmental variation drives continental-scale synchrony of European beech reproduction. *Ecology*. <https://doi.org/10.1002/ecy.3384>
- Bose AK, Scherrer D, Camarero JJ et al (2021) Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe. *Sci Total Environ* 784:147222. <https://doi.org/10.1016/j.scitotenv.2021.147222>
- Bouriaud O, Bréda N, Dupouey J-L, Granier A (2005) Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Can J Res* 35:2920–2933. <https://doi.org/10.1139/x05-202>
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63:625–644. <https://doi.org/10.1051/forest:2006042>
- Cruz-Alonso V, Pucher C, Ratcliffe S et al (2023) The easyclimate R package: easy access to high-resolution daily climate data for Europe. *Environ Model Softw*. 161:105627. <https://doi.org/10.1016/j.envsoft.2023.105627>
- Diaconu D (2016) Impact of thinning and aspect on growth and drought tolerance of European beech: analyses on a cellular-, tree- and stand-level. Dissertation, Albert-Ludwigs-Universität Freiburg
- Dietze MC, Sala A, Carbone MS et al (2014) Nonstructural carbon in woody plants. *Annu Rev Plant Biol* 65:667–687. <https://doi.org/10.1146/annurev-arplant-050213-040054>
- Dănescu A, Kohnle U, Bauhus J et al (2018) Stability of tree increment in relation to episodic drought in uneven-structured, mixed stands in southwestern Germany. *For Ecol Manage* 415:148–159. <https://doi.org/10.1016/j.foreco.2018.02.030>
- Eilers PHC, Marx BD (1996) Flexible smoothing with B-splines and penalties. *Stat Sci* 11:89–102. <https://doi.org/10.1214/ss/1038425655>
- Fritts HC (1976) Tree rings and climate. Academic, London
- Fuchs S, Schuldt B, Leuschner C (2021) Identification of drought-tolerant tree species through climate sensitivity analysis of radial growth in Central European mixed broadleaf forests. *For Ecol Manage* 494:119287. <https://doi.org/10.1016/j.foreco.2021.119287>
- Gao S, Liu R, Zhou T et al (2018) Dynamic responses of tree-ring growth to multiple dimensions of drought. *Glob Chang Biol* 24:5380–5390. <https://doi.org/10.1111/gcb.14367>
- Genet H, Bréda N, Dufrene E (2010) Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiol* 30:177–192. <https://doi.org/10.1093/treephys/tpp105>
- Hacket-Pain A, Foest JJ, Pearse IS et al (2022) MASTREE+: time-series of plant reproductive effort from six continents. *Glob Chang Biol* 28:3066–3082. <https://doi.org/10.1111/gcb.16130>
- Hacket-Pain AJ, Ascoli D, Vacchiano G et al (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>
- Hacket-Pain AJ, Friend AD, Lageard JGA, Thomas PA (2015) The influence of masting phenomenon on growth-climate relationships in trees: explaining the influence of previous summers' climate on ring width. *Tree Physiol* 35:319–330. <https://doi.org/10.1093/treephys/tpv007>
- Hacket-Pain AJ, Lageard JGA, Thomas PA (2017) Drought and reproductive effort interact to control growth of a temperate broad-leaved tree species (*Fagus sylvatica*). *Tree Physiol* 37:744–754. <https://doi.org/10.1093/treephys/tpx025>
- Hacket-Pain A, Roig FA, Ascoli D et al (2024) Reconstruction of araucaria Araucana cone production reveals warming intensifies regionally synchronized masting. *Ecosphere* 15:1–14. <https://doi.org/10.1002/ecs2.70087>
- Hartig F (2022) Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6
- Hauser S (2003) Dynamik hochaufgelöster radialer Schaftveränderungen und des Dickenwachstums bei Buchen (*Fagus sylvatica* L.) der Schwäbischen Alb unter dem Einfluss von Witterung und Bewirtschaftung. Dissertation, Albert-Ludwigs-Universität Freiburg
- Hesse BD, Hartmann H, Rötzer T et al (2021) Mature beech and spruce trees under drought – Higher C investment in reproduction at the expense of whole-tree NSC stores. *Environ Exp Bot* 191:104615. <https://doi.org/10.1016/j.envexpbot.2021.104615>
- Hillmeyer K (2021) Abschätzung der Produktivität verschiedener Baumarten für ausgewählte Standorte auf der Grundlage von Höhenanalysen. Dissertation, Albert-Ludwigs-Universität Freiburg
- Hirsch M (2019) Das Stammdickenwachstum von Buchen und Tannen in Baden-Württemberg unter dem Einfluss von Witterung und Klimaveränderungen - Langfristige Trends und kurzfristige Reaktionen auf Trockenheit. Dissertation, Albert-Ludwigs-Universität Freiburg
- Hoch G (2005) Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees. *Plant, Cell Environ* 28:651–659. <https://doi.org/10.1111/j.1365-3040.2004.01311.x>
- Hoch G (2005) Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees. *Plant Cell Environ* 28:651–659. <https://doi.org/10.1111/j.1365-3040.2004.01311.x>
- Hoch G, Richter A, Körner C (2003) Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ* 26:1067–1081. <https://doi.org/10.1046/j.0016-8025.2003.01032.x>
- Hoch G, Siegwolf RTW, Keel SG et al (2013) Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia* 171:653–662. <https://doi.org/10.1007/s00442-012-2579-2>
- Hsiao TC (1973) Plant responses to water stress. *Annu Rev Plant Biol* 24:519–570. <https://doi.org/10.1146/annurev.pp.24.060173.002511>
- Huang M, Wang X, Keenan TF, Piao S (2018) Drought timing influences the legacy of tree growth recovery. *Glob Chang Biol* 24:3546–3559. <https://doi.org/10.1111/gcb.14294>
- Julio Camarero J, Gazol A, Sangüesa-Barreda G et al (2018) Forest growth responses to drought at Short- and Long-Term scales in Spain: squeezing the stress memory from tree rings. *Front Ecol Evol* 6:1–11. <https://doi.org/10.3389/fevo.2018.00009>
- Kannenberg SA, Schwalm CR, Anderegg WRL (2020) Ghosts of the past: how drought legacy effects shape forest functioning and carbon cycling. *Ecol Lett* 23:891–901. <https://doi.org/10.1111/ele.13485>
- Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol Syst* 33:427–447. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095433>
- Klein T, Vitasse Y, Hoch G (2016) Coordination between growth, phenology and carbon storage in three coexisting deciduous tree species in a temperate forest. *Tree Physiol* 36:847–855. <https://doi.org/10.1093/treephys/tpw030>
- Körner C (2003) Carbon limitation in trees. *J Ecol* 91:4–17. <https://doi.org/10.1046/j.1365-2745.2003.00742.x>
- Lacointe A (2000) Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. *Ann Sci* 57:521–533. <https://doi.org/10.1051/forest:2000139>
- Larysch E, Stangler DF, Nazari M et al (2021) Xylem phenology and growth response of European beech, silver fir and Scots pine along an elevational gradient during the extreme drought year 2018. *Forests* 12:75. <https://doi.org/10.3390/f12010075>
- Larysch E, Stangler DF, Puhlmann H et al (2022) The 2018 hot drought pushed conifer wood formation to the limit of its plasticity: consequences for woody biomass production and tree ring structure. *Plant Biol* 24:1171–1185. <https://doi.org/10.1111/plb.13399>
- Lebourgeois F, Delpierre N, Dufrêne E et al (2018) Assessing the roles of temperature, carbon inputs and airborne pollen as drivers of fructification in European temperate deciduous forests. *Eur J Forest Res* 137:349–365. <https://doi.org/10.1007/s10342-018-1108-1>
- Lenth R (2023) Emmeans: estimated marginal means. aka Least-Squares Means
- Lässig R (1991) Zum Wachstum von Fichtensolitären [*Picea abies* (L.) Karst.] in Südwestdeutschland. Dissertation, Albert-Ludwigs-Universität Freiburg
- Marra G, Wood SN (2011) Practical variable selection for generalized additive models. *Comput Stat Data Anal* 55:2372–2387. <https://doi.org/10.1016/j.csda.2011.02.004>
- Martínez-Sancho E, Treydte K, Lehmann MM et al (2022) Drought impacts on tree carbon sequestration and water use – evidence from intra-annual tree-ring characteristics. *New Phytol* 236:58–70. <https://doi.org/10.1111/nph.18224>
- Mattes A (2014) Zuwachs und Konkurrenz in Buchen- / Eichenmischbeständen unter sich ändernden Klimabedingungen. Dissertation, Albert-Ludwigs-Universität Freiburg
- McDowell NG (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol* 155:1051–1059. <https://doi.org/10.1104/pp.110.170704>
- McDowell N, Pockman WT, Allen CD et al (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Mencuccini M, Piussi P (1995) Production of seeds and cones and consequences for wood radial increment in Norway spruce (*Picea abies* (L.) karst). *G Bot Ital* 129:797–812. <https://doi.org/10.1080/11263509509436170>
- Michelot A, Bréda N, Damesin C, Dufrêne E (2012) Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *Ecol Manage* 265:161–171. <https://doi.org/10.1016/j.foreco.2011.10.024>
- Miller TW, Stangler DF, Larysch E et al (2022) Longer and faster: Intra-annual growth dynamics of Douglas fir outperform Norway spruce and silver fir over wide climatic gradients. *Agric Meteorol* 321:108970. <https://doi.org/10.1016/j.agrformet.2022.108970>
- Miyazaki Y (2013) Dynamics of internal carbon resources during masting behavior in trees. *Ecol Res* 28:143–150. <https://doi.org/10.1007/s11284-011-0892-6>
- Müller-Haubold H, Hertel D, Seidel D et al (2013) Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. *Ecosystems* 16:1498–1516. <https://doi.org/10.1007/s10021-013-9698-4>

- Moreno A, Hasenauer H (2016) Spatial downscaling of European climate data. *Int J Climatol* 36:1444–1458. <https://doi.org/10.1002/joc.4436>
- Mund M, Herbst M, Knohl A et al (2020) It is not just a ‘trade-off’: indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest. *New Phytol* 226:111–125. <https://doi.org/10.1111/nph.16408>
- Mund M, Kutsch WL, Wirth C et al (2010) The influence of climate and fructification on the inter-annual variability of stem growth and net primary productivity in an old-growth, mixed Beech forest. *Tree Physiol* 30:689–704. <https://doi.org/10.1093/treephys/tpp027>
- Mundo IA, Sanguinetti J, Kitzberger T (2021) Multi-centennial phase-locking between reproduction of a South American conifer and large-scale drivers of climate. *Nat Plants* 7:1560–1570. <https://doi.org/10.1038/s41477-021-01038-1>
- Nothdurft A, Vospernik S (2018) Climate-sensitive radial increment model of Norway spruce in Tyrol based on a distributed lag model with penalized splines for year-ring time series. *Can J Res* 48:930–941. <https://doi.org/10.1139/cjfr-2018-0027>
- Nussbaumer A, Gessler A, Benham S et al (2021) Contrasting resource dynamics in mast years for European beech and oak—a continental scale analysis. *Front Forests Glob Change* 4:1–17. <https://doi.org/10.3389/ffgc.2021.689836>
- Nussbaumer A, Waldner P, Apuhtin V et al (2018) Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe. *For Ecol Manage* 429:336–350. <https://doi.org/10.1016/j.foreco.2018.07.011>
- Nussbaumer A, Waldner P, Etzold S et al (2016) Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. *For Ecol Manage* 363:237–251. <https://doi.org/10.1016/j.foreco.2015.12.033>
- Nutto L (1998) Neue Perspektiven für die Begründung und Pflege von jungen Eichenbeständen. Ergebnisse einer Untersuchung zur Kronenentwicklung, Astreinigung und Dickenwachstum junger Stiel- und Traubeneichen in Europa (*Quercus robur* L. und *Quercus petraea* (Matt.) Liebl. Dissertation, Albert-Ludwigs-Universität Freiburg
- Peters RL, Steppe K, Cuny HE et al (2021) Turgor – a limiting factor for radial growth in mature conifers along an elevational gradient. *New Phytol* 229:213–229. <https://doi.org/10.1111/nph.16872>
- Peters RL, von Arx G, Nievergelt D et al (2020) Axial changes in wood functional traits have limited net effects on stem biomass increment in European beech (*Fagus sylvatica*). *Tree Physiol* 40:498–510. <https://doi.org/10.1093/treephys/tpaa002>
- Petrutan AM, Petrutan IC, Hevia A et al (2021) Climate warming predispose sessile oak forests to drought-induced tree mortality regardless of management legacies. *For Ecol Manage*. <https://doi.org/10.1016/j.foreco.2021.119097>
- Pucher C (2023) Description and Evaluation of Downscaled Daily Climate Data Version 4
- Pucher C, Neumann M (2022) Description and Evaluation of Downscaled Daily Climate Data Version 3
- R Core Team (2023) R: A Language and Environment for Statistical Computing
- Rohner B, Kumar S, Liechti K et al (2021) Tree vitality indicators revealed a rapid response of beech forests to the 2018 drought. *Ecol Indic* 120:106903. <https://doi.org/10.1016/j.ecolind.2020.106903>
- Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: feast or famine? *Tree Physiol* 32:764–775. <https://doi.org/10.1093/treephys/tpr143>
- Schuldt B, Buras A, Arend M et al (2020) A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl Ecol* 45:86–103. <https://doi.org/10.1016/j.baae.2020.04.003>
- Schuler JK (2011) Astentwicklung und Astreinigung in Abhängigkeit vom Dickenwachstum bei Buche (*Fagus sylvatica* L.) und Eiche (*Quercus petraea* (Matt.) Liebl.; *Quercus robur* L.). Dissertation, Albert-Ludwigs-Universität Freiburg
- Seifert T, Müller-Starck G (2009) Impacts of fructification on biomass production and correlated genetic effects in Norway spruce (*Picea abies* [L.] Karst.). *Eur J For Res* 128:155–169. <https://doi.org/10.1007/s10342-008-0219-5>
- Simpson G (2023) Gratia: graceful ggplot-Based graphics and other functions for GAMs. Fitted using mgcv
- Skomarkova MV, Vaganov Ea, Mund M et al (2006) Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. *Trees* 20:571–586. <https://doi.org/10.1007/s00468-006-0072-4>
- Song Y, Sass-Klaassen U, Sterck F et al (2021) Growth of 19 conifer species is highly sensitive to winter warming, spring frost and summer drought. *Ann Bot* 128:545–557. <https://doi.org/10.1093/aob/mcab090>
- Spathelf P (1997) Orientierungshilfe zur Prognose und Steuerung des Wachstums von Fichten (*Picea abies* (L.) Karst.) und Tannen (*Abies alba* Mill.) in Überführungswäldern mit Hilfe der relativen Kronenlänge. Dissertation, Albert-Ludwigs-Universität Freiburg
- Stangler DF, Kahle H-P, Raden M et al (2021) Effects of intra-seasonal drought on kinetics of tracheid differentiation and seasonal growth dynamics of Norway spruce along an elevational gradient. *Forests* 12:274. <https://doi.org/10.3390/f12030274>
- Stangler DF, Miller TW, Honer H et al (2022) Multivariate drought stress response of Norway spruce, silver fir and Douglas fir along elevational gradients in Southwestern Germany. *Front Ecol Evol* 10:1–15. <https://doi.org/10.3389/fevo.2022.907492>
- Tojic K (2010) Einordnung des Wachstums von Buche (*Fagus sylvatica* L.) und Fichte (*Picea abies* [L.] Karst) im Zeitraum zwischen den zwei Bundeswaldinventuren (1987 und 2002) in den längerfristigen Kontext. Dissertation, Albert-Ludwigs-Universität Freiburg
- Vacchiano G, Hackett-Pain A, Turco M et al (2017) Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytol* 215:595–608. <https://doi.org/10.1111/nph.14600>
- van der Maaten ECD (2012) Intra- and interannual growth responses of European beech (*Fagus sylvatica* L.) to climate, aspect and thinning in the Swabian Alb - southwestern Germany. Dissertation, Albert-Ludwigs-Universität Freiburg
- van der Maaten-Theunissen M, Bouriaud O (2012) Climate–growth relationships at different stem heights in silver fir and Norway spruce. *Can J For Res* 42:958–969. <https://doi.org/10.1139/x2012-046>
- van der Maaten-Theunissen MJC (2012) Growth responses of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) to climate along an altitudinal gradient in southwestern Germany. Dissertation, Albert-Ludwigs-Universität Freiburg
- Vanhellemont M, Sousa-Silva R, Maes SL et al (2019) Distinct growth responses to drought for oak and beech in temperate mixed forests. *Sci Total Environ* 650:3017–3026. <https://doi.org/10.1016/j.scitotenv.2018.10.054>
- Vanoni M, Bugmann H, Nötzli M, Bigler C (2016) Quantifying the effects of drought on abrupt growth decreases of major tree species in Switzerland. *Ecol Evol* 6:3555–3570. <https://doi.org/10.1002/ece3.2146>
- Vitasse Y, Bottero A, Cailleret M et al (2019) Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. *Glob Chang Biol* 25:3781–3792. <https://doi.org/10.1111/gcb.14803>
- Werf GW, Sass-Klaassen UGWW, Mohren GMJJ et al (2007) The impact of the 2003 summer drought on the intra-annual growth pattern of Beech (*Fagus sylvatica* L.) and oak (*Quercus Robur* L.)

- on a dry site in the Netherlands. *Dendrochronologia* 25:103–112. <https://doi.org/10.1016/j.dendro.2007.03.004>
- Zahnd C, Zehnder M, Arend M et al (2024) Uniform carbon reserve dynamics along the vertical light gradient in mature tree crowns. *Tree Physiol.* <https://doi.org/10.1093/treephys/tpae005>
- Zang C, Hartl-Meier C, Dittmar C et al (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>
- Zimmermann J, Link RM, Hauck M et al (2021) 60-year record of stem xylem anatomy and related hydraulic modification under increased summer drought in ring- and diffuse-porous temperate broad-leaved tree species. *Trees* 35:919–937. <https://doi.org/10.1007/s00468-021-02090-2>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.