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ORIGINAL PAPER

Climatic factors controlling stem growth of alien tree species at a mesic forest site: a multispecies approach

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Abstract

The introduction of non-native species with various ecological and functional traits to European forests may be a potential tool for mitigating climate risks. We analyzed the growth sensitivity to climate of seven alien (*Acer rubrum*, *Betula maximowicziana*, *Castanea sativa*, *Cryptomeria japonica*, *Metasequoia glyptostroboides*, *Thuja plicata* and *Tsuga heterophylla*) and two native (*Fagus sylvatica* and *Picea abies*) tree species on a productive forest site in western Germany in order to assess their potential suitability in light of climate change. Retrospective basal area increment at breast height (BAI) and total stem volume increment (VI) were statistically related to a total of 11 multiscale climatic variables showing minor discrepancies between BAI and VI in climatic sensitivity. Across the tree species, the strongest climate signals were found for the standardized precipitation evapotranspiration index (spei), vapor pressure deficit (vpd) and the number of frost days (nfr) representing water availability, heat and coldness, respectively. Growth of most species was positively affected by mild winters and growing season spei. Importance of the investigated variables differed among tree species with, e.g., *C. sativa* and *T. plicata* being mainly driven by winter vpd and *A. rubrum*, *C. japonica* and *P. abies* by water availability in the growing seasons. We conclude that particularly more anisohydric species (e.g., *C. sativa*) may profit from their low sensitivity to drier conditions. Highly sensitive and isohydric species (e.g., *A. rubrum)* will undergo significant growth reductions when climate becomes more variable.

Keywords Non-native tree species · Climate sensitivity · Stem analysis · Dendroecology · Global warming · Tree ring analysis

Introduction

Over the last two decades, adaptive forest management increasingly focuses on strategies to mitigate climate impacts on tree vitality and survival in European forests (Neumann et al. 2017; Thurm et al. 2018) and on a global scale (Allen et al. 2010). The ongoing climate change comprising climatic extremes (i.e., heat, drought and frost periods; IPCC 2013) is likely to increase environmental risks of European forest ecosystems (Bolte et al. 2010; Walentowski et al. 2017) such as declines in biodiversity (Archaux and Wolters 2006; Anderegg et al. 2013), shifting species composition and distribution (Dyderski et al. 2018; Buras and Menzel 2019) and increasing tree mortality (Anderegg et al. 2015; Neumann et al. 2017). One (active) measure to mitigate such climatic risks includes the introduction and cultivation of non-native tree species potentially better adapted to future climate conditions (Bolte et al. 2009). The recommended strategy basically focuses on the extension of the spectrum of tree species with various (different) ecological requirements and susceptibilities in order to prepare the forest ecosystems to various environmental future constellations. Thereby, the need for fulfilling multiple forest ecosystem services (e.g., economic yield, silvicultural integration, non-invasiveness) should be taken into account (Bolte et al. 2010; Eilmann and Rigling 2012).

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The complexity and variety of (endogenous and exogenous) factors driving species' climate sensitivity exacerbate the selection of appropriate tree species mitigating potential effects of climate change. In this context, the (evolutionary) long-term adaptation according to their ecological amplitudes in the natural range (Kölling et al. 2009; Kölling 2013) as well as morphological and functional traits (Bréda et al. 2006; Aubin et al. 2018) are of special importance (see Table 1 for details). For example, species distributed under broad ecological amplitudes such as the North American species *Acer rubrum* (Hart et al. 2012), *Thuja plicata* (Antos et al. 2016) or *Tsuga heterophylla* (Hennon 2011) are expected to possess large adaptive capacity to variable climate conditions. In particularly, the "super-generalist" (Abrams 1998) *Acer rubrum* is one of the most abundant and widespread tree species in eastern North America occurring under a huge ecological amplitude (Walters and Yawney 1990) indicating high adaptive potential. On the other hand, physiological and morphological traits and strategies have been considered as major factors controlling species-specific climate tolerance (Table 1; e.g., Brodribb et al. 2014, McCulloh et al. 2014). For example, the mesophilic and ring porous South European *Castanea sativa* (Bottacci 2011) follows a water spending strategy (anisohydric) and continues transpiration and wood formation when water resources become scarce (Gomes-Laranjo et al. 2012). This results in a general higher drought tolerance (e.g., Niinemets and Valladares 2006; Hoffmann et al. 2018a) or adaptive potential to new climatic conditions (Gomes-Laranjo et al. 2012; Thurm et al. 2018; Buras and Menzel 2019), even though during extreme drought events the species may tend to over-transpiration with increasing synergic risks (Conedera et al. 2010). A further anisohydric species, *Betula maximowicziana* (Ishii et al. 2013), originating from Northern Japan (Kurata 1971), is contrastingly characterized as a drought-intolerant species (e.g., Niinemets and Valladares 2006; Ranney et al. 1991). However, Hoffmann et al. (2018a) demonstrated a high growth stability during the European summer drought in 2003 on a West German forest site. Besides its heart-root system allowing extensive water uptake and its large climate amplitude including a higher summer drought and frost tolerance compared to European *Betula* species (Stephan and Liesebach 2011), this may indicate a general lower climate susceptibility. In contrast, isohydric and coniferous species such as Japanese *Cryptomeria japonica* (Kumagai et al. 2009) close stomata in early stages of water stress resulting in carbon starvation and lower wood productivity (McCulloh et al. 2014), in particular at dry sites (Matsumoto et al. 2006). A further isohydric tree species, the Chinese *Metasequoia glyptostroboides*, is characterized as a drought sensitive tree species (Vann 2005; Brodribb et al. 2014). Water stress produces high rates of membrane damage and low rates of root activity (Vann 2005). However, the widely cultivated *M. glyptostroboides* prospering in many geographic and climatic regions of the world is classified as climate-tolerant species, presumable due to its possibility to develop extensive, deeper root systems and to inhabit broad climatic amplitudes including regional extremes (Shen 2011; Williams 2005).

Climate impacts on tree growth can be determined by retrospective analyses of increment data. External stress situations (e.g., drought, heat, frost) may cause either cavitation-induced xylem disfunctions or a progressive depletion of stored carbohydrates, which both affect variation in stem growth (Choat et al. 2012; Eilmann and Rigling 2012). Besides classical climate variables (i.e., precipitation and temperature), a variety of climatic variables characterizing physiological stress conditions such as drought indicators or indices (WMO and GWP 2016) and evaporative demand may be more suitable to quantify growth reactions to climate events (Friedrichs et al. 2009). In addition, a complex interrelation of various environmental factors should be taken into account (Friedrichs et al. 2009; Scharnweber et al. 2011). Furthermore, the climate impact strongly depends on the temporal scale at which the climatic phenomena affect tree growth. So far, few climate–growth analyses have dealt with multiscale (monthly, cumulative *and* seasonal) climatic effects (e.g., Lévesque et al. 2013; Stojanović et al. 2018), or analyses were restricted to few timescales in the growing season such as 3- and 6-month periods. Information about both, dominant temporal scales and pervasive climatic parameters, may be crucial factors to derive complex relationships between climate variability and species-specific response patterns (Friedrichs et al. 2009; Lévesque et al. 2013).

Breast height series data can be related to diameter at breast height (DBH) and basal area (BA) measurements acting as useful predictors for approximating tree and stand characteristics (e.g., biomass production and stand density) in conventional forestry (Latte et al. 2016). In addition, several allometric models confirmed that tree taper stabilizes around breast height resulting in balanced and homogeneous growth (Chhin and Wang 2005; Kublin et al. 2013). As a consequence, climate-related interpretations in dendroecological research underly the assumption that breast height series approximately reflect the whole stem growth pattern or response to external factors (Chhin et al. 2010). However, a small number of comparative studies tested this hypothesis for European (e.g., Bouriaud et al. 2005; Sohn et al. 2012; Hoffmann et al. 2018a) or North American (Chhin et al. 2010) forest stands indicating both similarities and inconsistencies in climate–growth relationships between radial and volume increment (see Latte et al. 2016 for synthesis). Due to allometric discrepancies, additional measures connecting

Table 1 Species-specific properties and traits potentially related to climate sensitivity according to the literature (see Supplementary Information, SI Introduction, Appendix 1 for an overview of references used for species characterization)

Species	Native range	Ecological amplitudes			Physiological traits			Morphological traits		
		Precipitation (mm)	Temperature (°C)	Altitude (m a. s. l.)	Water-use strategy	Physiological tolerance*		Leaf	Root	Wood**
						Drought	Waterlogging			
Acer rubrum	Eastern & central North America	578–2289	"Wide range"	0–900	Isohydric	1.84 ± 0.16	3.08 ± 0.28	Deciduous broadleaf	Shallow	Diffuse porous
Betula maximowicziana	Japan	< 2500	6–13	200–1750	Anisohydric	1.57	1.25 ± 0.25	Deciduous broadleaf	Heart (surface near, extensive)	Diffuse porous
Castanea sativa	Southern Europe	600–1600	8–15	0–1800	Anisohydric	3.46 ± 0.18	1.32 ± 0.28	Deciduous broadleaf	Tap (stout)	Ring porous
Cryptomeria japonica	Japan	1000–3500	14–19	200–1200	Isohydric	2.75 ± 0.25	2 ± 1	Evergreen conifer	Shallow	Coniferous
Fagus sylvatica	Europe (large central area)	480–2000	4–14	0–1500	Anisohydric	2.4 ± 0.43	1.02 ± 0.01	Deciduous broadleaf	Heart	Diffuse porous
Metasequoia glyptostroboides	South-central China	557–1500	12–20	100–1500	Isohydric	2.38 ± 0.38	1.52 ± 0.48	Deciduous conifer	Extensive, deep	Coniferous
Picea abies	Northern, central & eastern Europe	550–1200	− 3 to 12	0–2400	Isohydric	1.75 ± 0.41	1.22 ± 0.12	Evergreen conifer	Shallow	Coniferous
Thuja plicata	Western North America	500–5750	5–11	0–1500	Isohydric	2.23 ± 0.25	1.01 ± 0.04	Evergreen conifer	Shallow***, extensive	Coniferous
Tsuga heterophylla	Western North America	380–6650	0.3–11.3	0–2130	Isohydric	1.17 ± 0.17	0.95 ± 0.05	Evergreen conifer	Shallow, extensive	Coniferous

*Standardized rankings according to Niinemets & Valladares (2006): very intolerant, 1; intolerant, 2; moderately tolerant, 3; tolerant, 4; very tolerant, 5

**According to Wagenführ (1999)

***Deeper than *T. heterophylla*'s root (Bennett et al. 2002) climatic impacts to volume-related tree growth are needed to better understand the species-specific climate sensitivity.

In our study, we analyzed the climate sensitivity of seven alien tree species and two native European tree species on a productive forest site in western Germany. Detailed stem analyses were applied to generate whole stem volume increment from stem disks at various tree heights. We hypothesized that climate sensitivity of tree growth is related to at least one of the following species-specific criteria: (1) ecological amplitude in the native range, (2) physiological traits and/or (3) morphological (external and internal) traits. Thus, a variety of species differing in these criteria was selected (see Table 1 for details). The objectives were to (1) identify most important climate factors controlling growth across tree species that can help evaluate the sensitivity of species to climate change, (2) detect dominant climatic temporal scales triggering species-specific growth and (3) evaluate whether climate–growth responses at breast height are good estimators for the whole stem responsiveness. Note: The same dataset was used in a previous study to analyze the sensitivity to specific, isolated drought events (e.g., 2003) at the study site providing additional information on drought tolerance of the mentioned species (see Hoffmann et al. 2018a for details).

Materials and methods

Study site and species selection

The study was carried out in the Arboretum Burgholz in North Rhine-Westphalia in western Germany (51° 13′ 7.226″ N, 7° 7′ 8.479″ E). In this forest district, different native and alien tree species have been cultivated under comparable site conditions since the late nineteenth century (Becker 2009). The Arboretum is characterized by advantageous climatic conditions (oceanic influence) for tree growth with high annual precipitation sums and a mild annual temperature average (1131 mm and 9.8 °C for the period 1960–2014, Fig. 1; DWD 2015). For the considered total growth period of the study trees (1960–2014), a clear warming trend during the last five decades was observed (Fig. S1). The forest soil in the Arboretum can be classified as a podzolic Cambisol, characterized by a poor to moderate nutrient supply, silty loam, good water supply and a mor humus layer.

For this study, the alien tree species *Acer rubrum* L., *Betula maximowicziana* Regel, *Castanea sativa* Mill., *Cryptomeria japonica* D. Don, *Metasequoia glyptostroboides* Hu et Cheng, *Thuja plicata* Donn and *Tsuga heterophylla* (Raf.) Sarg. were selected due to their favorable economic criteria and to their purported high climatic tolerances (e.g., Schenck 1939a; Burns and Honkala 1990a, b; Roloff et al. 2011; Praciak et al. 2013) as a function of their ecological properties and functional traits (see Table 1 for details). Additionally, two economically important native species, *Fagus sylvatica* L. and *Picea abies* H. Karst, were chosen as reference species. Within the Arboretum, the different tree species were mainly established as monospecific to mixed stands (dominated by the target tree) of 23 to 75 m^2 ha^{-1} in basal area (Table S1). Due to homogenous (soil and climatic) site conditions and the proximity of the selected stands (Fig. 1), the tree species grow under comparable environmental conditions. All stands were evenly aged (34–58 years) and had undergone the same silvicultural treatment (planting, thinning from above; Hoffmann et al. 2018b). The species names will be abbreviated by their genus name in the following (e.g., *Castanea sativa* = *Castanea*).

Growth data

We selected six to ten dominant or codominant (Kraft classes 1 and 2, Kraft 1884) trees per species. Cross-sectional stem disks were cut along the felled trees at 0.5 m, 1.3 m and subsequently every 2 m up to the tree top (max. height = 29.3 m). A total of 922 dried stem disks were progressively polished and scanned at 1200 dpi resolution (A3 scanner 2400S, Mustek). Annual radial increments were measured to the nearest 0.01 mm (Rinn 2006) along four radii at the main cardinal directions using LignoVision™ software (version 1.38e, Rinntech e. K., Heidelberg, Germany). Crossdating accuracy was checked visually and statistically by the parameters *Gleichläufigkeit* (Eckstein and Bauch 1969), *t*-value (Baillie and Pilcher 1973) and *Gleichläufigkeit*-significance (Rinn 2005) in a stepwise approach considering radial directions within a stem disk, different heights within a tree and different individuals per tree species (see Hoffmann et al. 2018a for details) using TSAP software (TSAP-Win professional version 4.68e Rinntech e. K., Heidelberg, Germany). A total of 19 stem disks of two trees that did not meet the statistical criteria were omitted from analyses.

Radial increment data were converted into (raw) basal area increment (BAI_r) to increase representation of whole stem growth using high-dimensional units (Hinckley and Lassoie 1981; Biondi and Qeadan 2008). Furthermore, (raw) total stem volume increment (VI_r) was calculated by the package *treeglia* using the function "StemAnalysis" (Bascietto and Scarascia-Mugnozza 2004) from the open-source software R (version 3.2.5, R Core Team 2016). Considering all height sections (stem heights) of individual trees, the application firstly interpolated annual stem heights (Carmean 1972). Annual volume increment was then computed according to both, Smalian's and cone's formulas (Bascietto and Scarascia-Mugnozza 2004). For comparative analyses, we restricted BAI_r series data to measurements at standard breast height

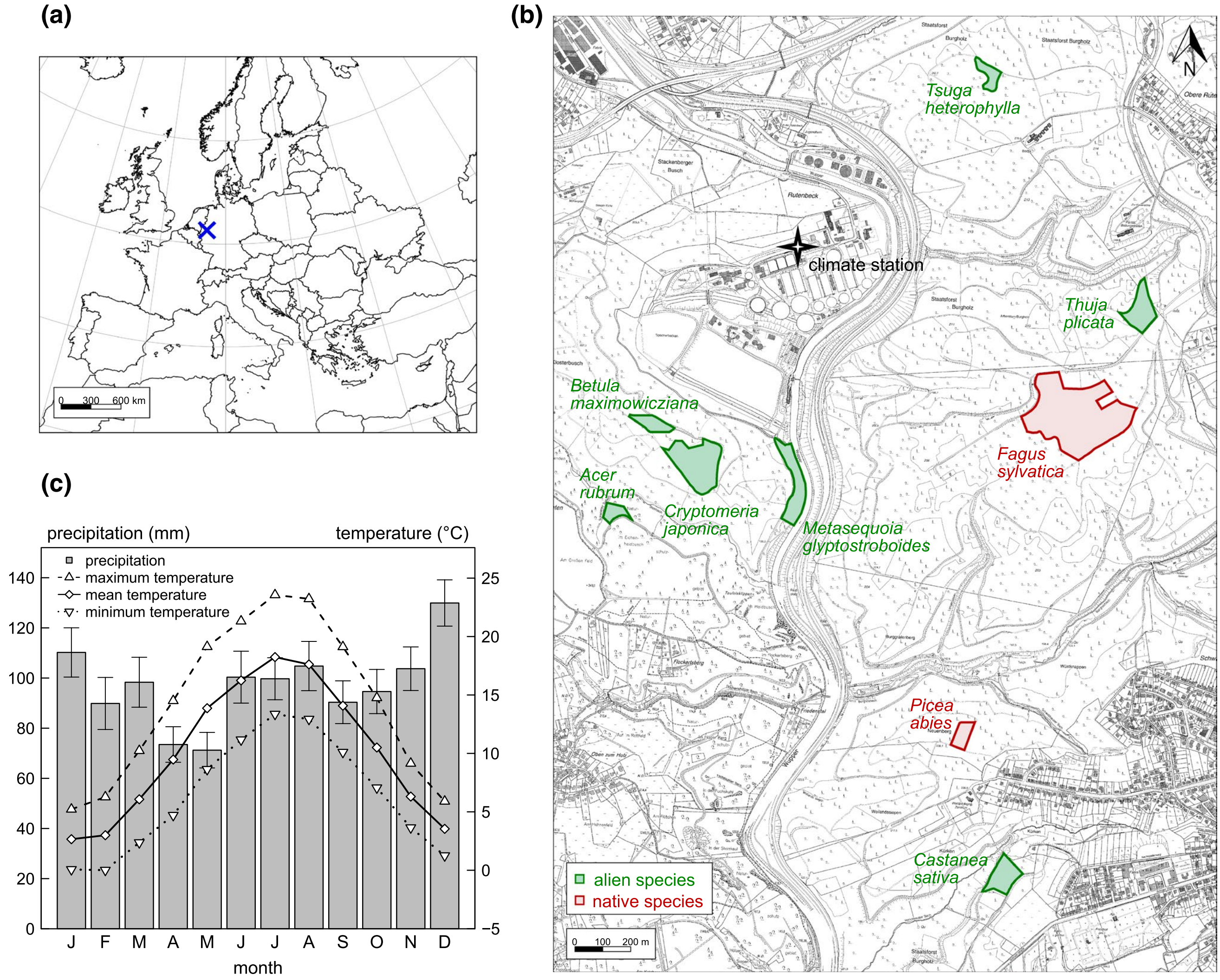


Fig. 1 **a** Location of the Arboretum Burgholz (blue cross), **b** distribution of the study stands in the Arboretum and **c** mean monthly precipitation sum (± standard error) and mean monthly temperature (maximum, mean, minimum) for the period 1985–2012 (DWD 2015). (Color figure online)

(1.3 m, in the following denoted by BAI). Additionally, VI_r data were used as a reference for the total stem growth (Table 3). Differences between tree species in mean BAI_r and VI_r were assessed by analysis of variance (ANOVA; BAI_r) and the nonparametric Kruskal–Wallis test by rank (VI_r), since homogeneity of variance of residuals or normal distribution of the values were not given for mean VI_r.

The individual BAI_r and VI_r series were detrended and standardized using a cubic smoothing spline (Cook and Peters 1981) with a 50% frequency cutoff at 67% of the series length (e.g., Zang et al. 2012; Restaino et al. 2016). Regarding the various tested detrending techniques, our results have been found to be robust if using fixed spline wavelengths (e.g., 10 years). We performed autoregressive modeling of the standardized series to remove first-order autocorrelation validated by Akaike information criterion (AIC). The resulting detrended residual series of each increment variable (BAI and VI) and tree species were averaged to site chronologies by a robust biweight mean (Cook 1985). Thus, a total of 18 chronologies for two increment variables and 9 tree species were constructed (Fig. 2). The common growth period from 1985–2012 was selected for statistical climate–growth analyses in order to reach comparability among species in series length. The chronologies were finally evaluated and compared using the descriptive statistics *mean sensitivity* (ms, a measure to quantify chronologies' interannual variation; Fritts 1976), *effective chronology signal* (es, an estimator to quantify signal strength between and within trees; Cook and Pederson 2011), *expressed population signal* (eps, which determines the representation of the theoretical population by the chronology; Buras 2017) as well as *Pearson*

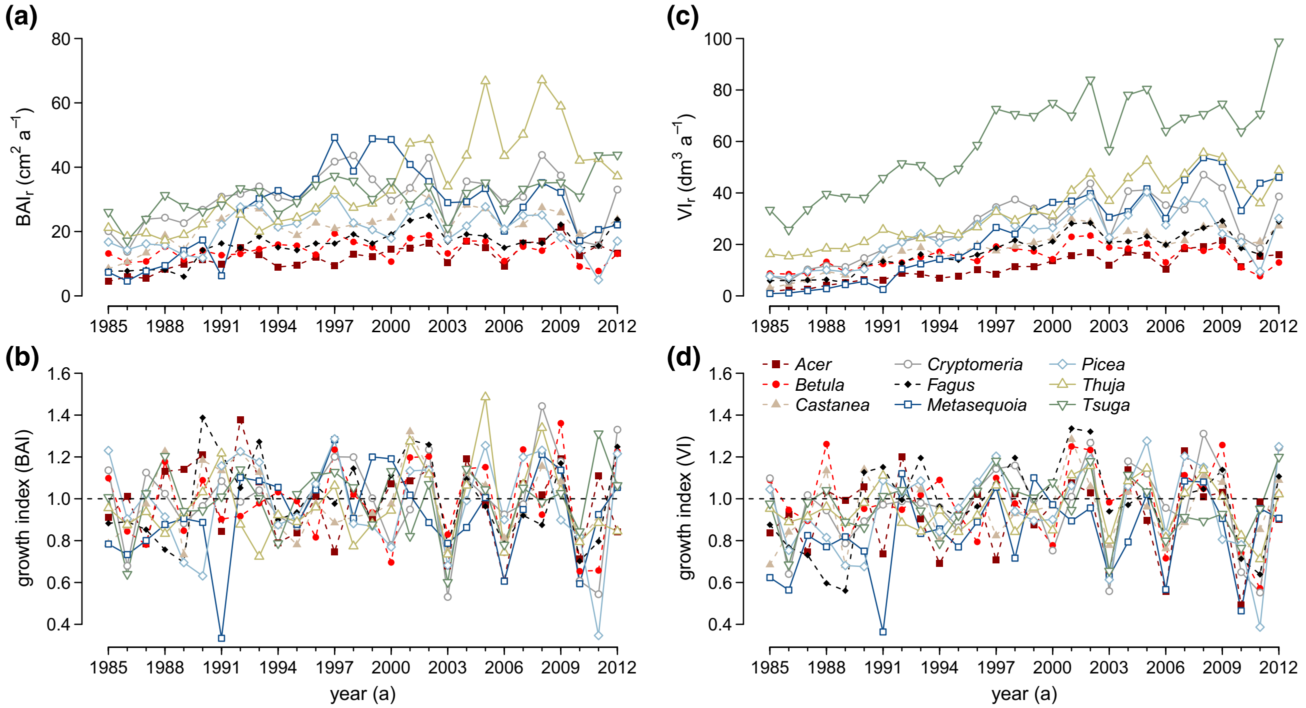


Fig. 2 Growth chronologies of **a** raw and **b** detrended basal area increment at breast height (BAI) as well as of **c** raw and **d** detrended volume increment (VI) of the coniferous (solid lines, blank symbols) and deciduous (dashed lines, filled symbols) tree species. (Color figure online)

correlation coefficient between VI and BAI chronologies (R_{VI}) and across the tree species. For consideration of temporal changes in the relationships of the chronologies, the common period was divided into two additional periods: 1985–1997 and 1998–2012.

Climate data

All climate data were accessed from the closest meteorological station "Wuppertal-Buchenhofen" (ID 5717, 51° 13.488′ N, 7° 6.318′ E, 130 m a.s.l.; National Meteorological Service of Germany, DWD 2015), located in the center of the Arboretum Burgholz (approximately 2.3 km distance to the furthermost study stand, Fig. 1). The climate records from 1960–2014 included daily average, maximum and minimum temperatures (tavg, tmax and tmin in °C), precipitation sums (prec in mm) and vapor pressure (vp in hpa). tavg, tmax and tmin were averaged to monthly values for climate–growth analyses. Additionally, the following physiological important monthly variables were computed: potential evapotranspiration (pet), vapor pressure deficit (vpd in hPa), degree day sum (> 5 °C and > 10 °C, sum$_{\Delta t05}$ and sum$_{\Delta t10}$), number of frost days (nfr), de Martonne aridity index (dmi; de Martonne 1926) and the standardized precipitation evapotranspiration index (spei; Vicente-Serrano et al. 2010; Table 2). For details on climate variables including calculations and individual cross-correlations, see Supplementary Information (SI Methods, Appendix 2: *Climate variables*; Eq. S1, S2; Fig. S2–S4; Table S2).

In addition to the monthly timescale, 2- to 6-month seasonal periods of climate variables were considered by averaging tavg, tmax, tmin, pet, vpd and dmi values, and summing prec, sum$_{\Delta t05}$, sum$_{\Delta t10}$, spei and nfr data ranging from April of the previous growth year to September of the current year. To account for potential vulnerability to coldness and (late) frost, tmin and nfr variables were restricted to the cold months from October of the previous year to April of the current year. Here, we excluded May data since solely two years (1996 and 2012) with one frost day each were detected. In total, 11 climate variables summing up to 1011 single- and multimonth possible predictor variables were obtained for climate–growth analyses.

The 11 climate variables were assigned to one of the three general categories according to its climatic origin and relevance for climate compatibility or vulnerability: (1) *water availability* (indicator for drought tolerance or demand), (2) *temperature* (indicator for heat tolerance or demand) and (3) *frost* (indicator for cold and [late] frost tolerance or demand; Table 2).

Climate–growth analyses

Climate–growth relationships between the species-specific BAI and VI chronologies and *single* monthly and seasonal

Table 2 Climatic categories and variables used for climate–growth analyses. For details on climate variables see Supplementary Information (SI Methods, Appendix 2: *Climate variables*)

Category	Indicator for	Variable code	Variable name and explanation
Water availability	Drought tolerance	prec	Precipitation sums (mm)
	Or water demand	dmi	de Martonne aridity index
		spei	Standardized precipitation evapotranspiration index
Temperature	Heat tolerance	tavg	Mean temperature (°C)
	Or demand	tmax	Maximum temperature (°C)
		pet	Potential evapotranspiration
		vpd	Vapor pressure deficit (hPa)
		$\mathrm{sum}_{\Delta t05}$	Degree day sum (> 5 °C)
		$\mathrm{sum}_{\Delta t10}$	Degree day sum (> 10 °C)
Frost	Cold and (late) frost	nfr	Number of frost days (days with < 0° C)
	Tolerance or demand	tmin	Minimum temperature (°C)

climate variables were assessed using classical correlation functions. Bootstrapped correlation coefficients (bcc) according to Biondi and Waikul (2004) with a 95% confidence interval were quantified by the R package *treeclim* (Zang and Biondi 2015) for the common period 1985–2012. To identify the most contributing climate factors across tree species, we firstly extracted lowest negative and highest positive bcc by species and growth variable. The highest total frequency of a climate variable (among species and increment variable) within each category (*water availability*, *temperature* or *frost*) was then assumed to be most appropriate to explain tree growth across species.

Relationships between the growth chronologies (BAI and VI) and *multiple* climate variables were modeled using multiple stepwise regression analyses with forward selection for the same period 1985–2012. For these analyses, we used standardized climate variables (except for nfr) where the mean = 0 and standard deviation = 1 (Latte et al. 2016). The standardization enhanced the comparability of individual regression terms. The initial linear regression with growth data was performed using the "dredge"-function of the R package *MuMIn* (Barton 2016) for each climate variable and timescale (single- to 6-month) to preselect best-fit combinations of months (model selection of best-fit months of individual timescales). Here, the maximum number of regression terms in a single model was set to 4 and the regression model was selected by minimum AICc (Akaike information criterion, corrected for small sample sizes; Burnham and Anderson 2010). The best-fit predictor variables (months of individual timescales) were secondly merged for all timescales of individual climate variables (months of all timescales) used for subsequent linear regression with growth data. The regression models were determined by the same above-mentioned analyses with selection ("dredge," maximum number of terms = 4) of variable sets by minimizing the value of AICc (model selection of best-fit months of all timescales we will name *subset*). We thirdly applied the function "selMod" (R package *pgirmess*; Giraudoux 2017) to compare the selected subset models of different climate variables within the predefined categories (*water availability*, *temperature* and *frost*; *model selection of best-fit climate variable*). Similar to correlation functions, the climate variable with highest frequency within a category was assumed to be the best explaining climate variable across the tree species. *Final regression models* were determined by combining the pool of significant variables of the three categories using the "dredge"-function (maximum number of terms = 9). To identify and, consequently, reduce multicollinearity in models, we used stepwise variance inflation factor VIF selection (Zuur et al. 2007). Here, climate variables with highest VIF values were removed stepwise. The selection was repeated until all VIF values fell below the defined threshold of VIF = 1.5. The relative importance of an individual predictor variable (RIV) in each regression model was calculated by the function "calc.relimp" of the package *relaimpo* (Grömping 2006) using the "lmg"-method (i.e., R^2 contribution averaged over orderings among the regressors, e.g., Chevan and Sutherland 1991).

Results

Growth chronologies

For the period 1985–2012, mean (raw) BAI_r differed significantly from 12.2 (*Acer*) to 34.7 (*Thuja*) $\mathrm{cm}^2\ \mathrm{a}^{-1}$, and mean VI_r varied significantly from 10.9 (*Acer*) to 59.9 (*Tsuga*) $\mathrm{dm}^3\ \mathrm{a}^{-1}$ among tree species (Fig. 2; Table 3, all $p < 0.001$). The eps and es values of the detrended series ranged from 0.88 to 0.97 and 0.48 to 0.81, respectively, indicating a strong common signal and within- and between-tree correlation (Table 3). Comparing the increment variables, ms

Table 3 Tree characteristics at the point of disk sampling and chronology statistics of raw* (BAI_r, VI_r) and detrended (ms, es, eps, R_{VI}) series for the common period 1985–2012 (all data shown refer to data after crossdating and omitting trees and stem disks)

Species	*N*	Tree characteristics		Chronology statistics						
		dbh (cm)	Height (m)	incr	*n*	BAI_r ($cm^2\ a^{-1}$)* VI_r ($dm^3\ a^{-1}$)*	ms	es	eps	R_{VI}
Acer	8	22.6 ± 5.5	21.8 ± 1.1	BAI	8	12.2 ± 3.9	0.264	0.476	0.879	0.906
				VI	88	10.9 ± 5.4	0.289	0.564	0.912	1
Betula	6	25.3 ± 1.9	23.7 ± 1.6	BAI	6	14.1 ± 3.0	0.259	0.562	0.885	0.882
				VI	70	15.0 ± 4.4	0.211	0.582	0.893	1
Castanea	8	30.9 ± 4.3	20.3 ± 1.2	BAI	8	22.1 ± 5.7	0.184	0.578	0.916	0.938
				VI	86	18.5 ± 7.3	0.199	0.664	0.941	1
Cryptomeria	10	34.7 ± 6.3	21.7 ± 1.7	BAI	10	30.3 ± 8.4	0.255	0.614	0.941	0.960
				VI	113	27.0 ± 11.9	0.244	0.663	0.952	1
Fagus	8	29.0 ± 4.7	22.7 ± 1.2	BAI	8	15.9 ± 4.9	0.204	0.573	0.915	0.853
				VI	86	17.6 ± 7.4	0.173	0.658	0.939	1
Metasequoia	8	34.5 ± 5.4	23.0 ± 1.4	BAI	8	26.8 ± 13.0	0.245	0.620	0.929	0.878
				VI	97	24.8 ± 17.1	0.292	0.814	0.972	1
Picea	8	31.2 ± 4.1	23.2 ± 1.4	BAI	8	20.6 ± 6.2	0.269	0.713	0.952	0.936
				VI	94	23.3 ± 10.0	0.254	0.796	0.969	1
Thuja	10	40.5 ± 6.1	27.6 ± 1.4	BAI	10	34.7 ± 14.5	0.208	0.524	0.917	0.829
				VI	133	33.2 ± 12.6	0.155	0.745	0.967	1
Tsuga	9	43.4 ± 5.8	30.1 ± 1.7	BAI	9	31.2 ± 5.9	0.227	0.568	0.913	0.774
				VI	136	59.9 ± 18.0	0.173	0.720	0.959	1

N = number of trees, n = number of stem disks, incr = increment variable, BAI = basal area increment at breast height, VI = total stem volume increment

Tree characteristics: mean and standard deviation: dbh = diameter at breast height, height = tree height

*Raw chronologies: mean and standard deviation: BAI_r, VI_r

Detrended chronologies: ms = mean sensitivity, es = effective chronology signal, eps = expressed population signal, R_{VI} = correlation coefficient with VI chronologies (all $p < 0.001$)

varied between the investigated species, with highest ms for BAI measures for six of the nine tree species. VI chronologies highly corresponded to BAI series presenting high correlation coefficients within individual species (Table 3, $R_{VI} = 0.77$–0.96, $p < 0.001$). Comparing tree species, the correlation between BAI ($R = -0.02$–0.69) or VI (0.20–0.77) chronologies varied strongly across individual species with highest similarity for *Cryptomeria* and *Picea* trees (Fig. S4). The overall mean correlation across species' VI chronologies (1985–2012: $R = 0.52$) increased from $R = 0.28$ (1985–1997) to $R = 0.64$ (1998–2012), indicating a higher synchronicity and growth response to similar climatic factors with increasing tree age (see Hoffmann et al. 2018a for detailed analyses for the period 1998–2012).

Climate–growth relationships

Climate factors across tree species

Bootstrapped correlation functions in association with multiple linear regressions revealed species-specific differences for correlation and response patterns of the growth indices (BAI and VI) to climatic variables. Thus, growth was specifically driven by individual climate variables at individual month(s) and timescales (see Table S3 for details as an example for the correlation functions). Across the tree species and increment variables (BAI, VI), climate–growth analyses identified spei to be most important within the category *water availability* (including also prec and dmi) showing the largest number of highest bootstrapped correlation coefficients (bcc) and of best explaining variables, respectively (Table 4). For the six primarily *temperature*-controlled variables (tavg, tmax, pet, vpd, $sum_{\Delta t05}$, $sum_{\Delta t10}$), the most frequently and strongest relationships with tree growth were found for vpd. Within the climatic category *frost* (nfr, tmin), we found nfr as an overall reliable *frost*-indicator associating single and multiple climate–growth relationships (Table 4).

Species-specific response to single climate variables (correlation functions)

For BAI and VI detrended series, bootstrapped correlation functions indicated *Betula*, *Castanea, Fagus* and *Thuja* to be less sensitive to spei when compared with the remaining species (Fig. 3; see also Fig. S5; Table S4). Growth of

Table 4 Overall frequency of highest positive (pos) and lowest negative (neg) bootstrapped correlation coefficients (bcc) and, of the best explaining variables of the linear models within the climatic categories *water availability*, *temperature* and *frost* across the tree species and increment variables at the month and timescale of the year at which the highest correlation or lowest AICc was reached

Category	Variable	Correlation functions			Linear regression
		Number of highest and lowest bcc			Number of most explanatory variables
		bcc_{pos}	bcc_{neg}	bcc_{sum}	
Water availability	prec	5	4	9	1
	dmi	1	9	10	4
	spei	12	5	**17**	**13**
	null model	–	–	–	0
Temperature	tavg	2	1	3	1
	tmax	0	3	3	0
	pet	3	1	4	4
	vpd	11	5	**16**	**10**
	$\text{sum}_{\Delta t05}$	0	2	2	1
	$\text{sum}_{\Delta t10}$	2	6	8	2
	null model	–	–	–	0
Frost	nfr	0	18	**18**	**8**
	tmin	18	0	**18**	7
	null model	–	–	**–**	3

Null model indicates that none of the used climatic variables (nfr or tmin) improved the model (AICc)

Bold values indicate the highest frequency of strongest bcc and best explaining variables within the climatic categories

See Table 2 for abbreviations of climate variables

Tsuga, *Cryptomeria*, *Picea* and *Acer* (July) trees was negatively correlated with growing season vpd of the current year. For *Metasequoia*, *Acer* and *Betula*, nfr during October to April strongly inhibited the increment variables (BAI or VI; most frequently in January to April). In total, highest number of Pearson's correlation coefficients was found for *Fagus* (n = 105, primary positive relationships with previous vpd) as well as *Metasequoia* (n = 72) and Acer (n = 68), both revealing multiple correlations with spei, vpd and nfr. Lowest number of relationships was identified for *Castanea* (n = 12), *Betula* (n = 27) and *Thuja* (n = 51) trees indicating a general lower sensitivity to various climate constellations.

Multiple climate–growth relationships

Taking into account combinations and the partial contributions of the three selected climatic variables (spei, vpd, nfr), multiple regression models demonstrated significant coefficients of all predictor variables ($p < 0.05$) after variance inflation factor (VIF) selection (Table 5; see Table S5 for the relative importance values of predictor variables, RIV).

The species *Castanea*, *Thuja*, *Fagus* and *Tsuga* were predominantly affected by the *temperature*-based vpd. In case of *Castanea*, vpd in December to January was the most influential factor according to the ranking of RIV (Table 5; Fig. 4). In addition, with positive effects of spei in current July on BAI and VI, climate variables explained the lowest variance in growth (29% and 36% for BAI and VI, respectively) when compared with the other tree species. VI of *Thuja* trees was predominantly facilitated by high winter vpd (January), followed by vpd in April–May of the previous and spei in spring (March–July) of the current year. As demonstrated by the single correlation functions (Fig. 3), vpd prior to the year of wood formation was the most promoting factor for *Fagus* trees (in combination with winter vpd: $R^2 = 0.64$ and $R^2 = 0.58$). Growth of *Tsuga* was primarily negatively affected by vpd in summer of the current year (July) revealing strong relationships between increment and together with secondary climate variables (summer or winter spei and vpd in January; $R^2 = 0.53$ and $R^2 = 0.55$).

In contrast, growth of *Acer*, *Cryptomeria*, *Picea* and *Betula* was triggered more dominantly by *water availability* (i.e., values of spei, Fig. 4; Table 5). spei in late summer of the current growth year promoted growth of *Acer* trees. In combination with a negative growth response to nfr in January (VI) and positive effects of winter or spring vpd, strong climate–growth relationships were found ($R^2 = 0.54$ and $R^2 = 0.49$). Climate response patterns of *Betula* were most different to the other tree species. High water availability (spei) in the current August (primarily VI and subordinately BAI) as well as in preceding December (BAI) negatively affected growth with secondary negative (early spring nfr) or positive (winter vpd positively) influencing variables of lower importance. Growth of *Cryptomeria* was predominantly related to 6-month water

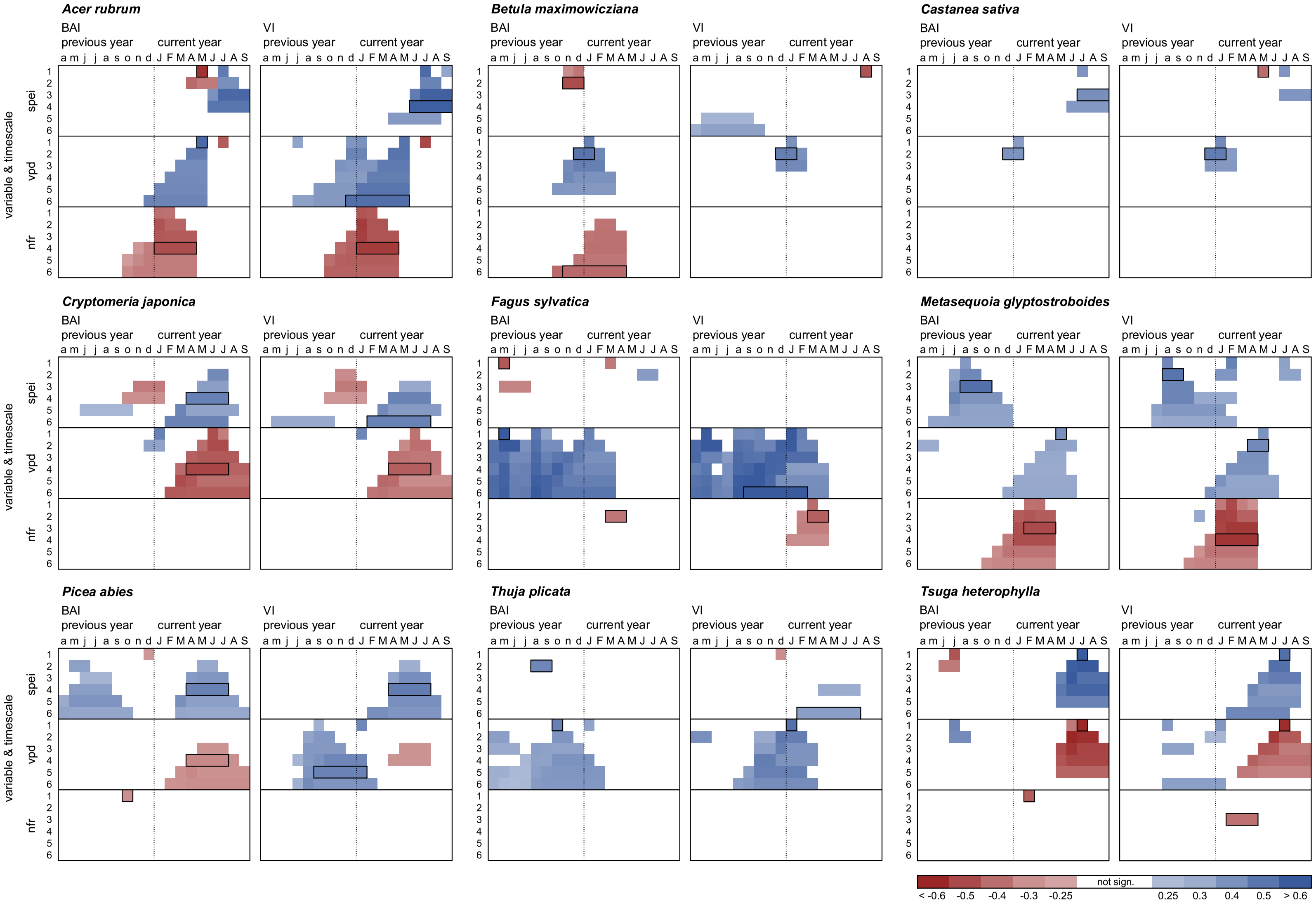


Fig. 3 Species-specific correlation coefficients between increment variables (basal area increment, BAI, and volume increment, VI) and monthly (timescale = 1) or seasonal (timescale = 2–6) standardized precipitation evapotranspiration index (spei), vapor pressure deficit (vpd) and the number of frost days (nfr) for the period 1985–2012 ($p < 0.05$). Lowercase abbreviations (a–d) denote months of the previous year (April–December), and uppercase abbreviations (J–S) indicate months of the current year (January–September). The month(s) and timescale at which the highest correlation was reached by species, increment variable and climate variable are framed in black. In the case of seasonal overlapping time windows, the respective subsequent correlation coefficients are indicated. (Color figure online)

Table 5 Summary of the linear regression models relating species-specific increment variables (incr) to the best explaining climate variables (v1, v2, v3) at the month(s) and timescale of the year at which the lowest AICc was reached

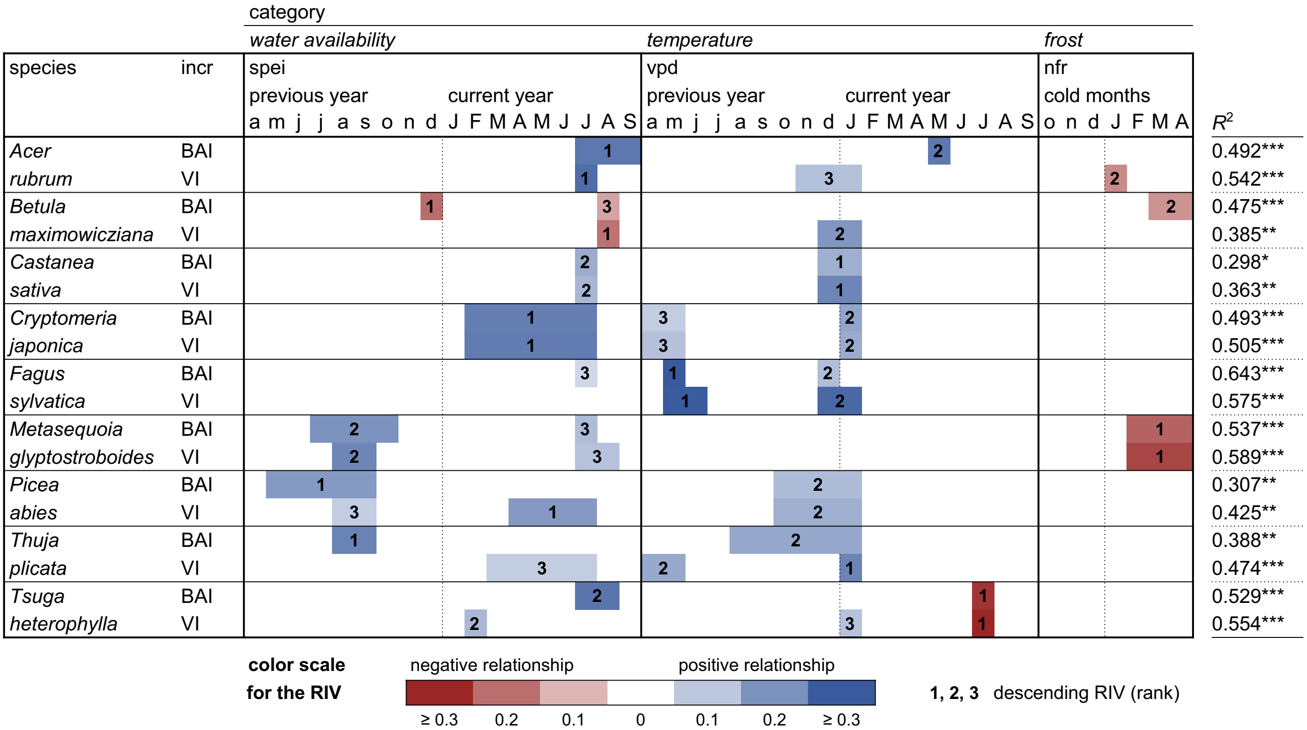
Species	incr	Intercept	Climate variable (descending RIV→)			Model	
			v1	v2	v3	R^2	p
Acer rubrum	BAI		spei.JUL-SEP	vpd.MAY			
		0.983 (<0.001)	0.086 (0.004)	0.085 (0.004)		0.492	<0.001
	VI		spei.JUL	nfr.JAN	vpd.nov-JAN		
		0.913 (<0.001)	0.092 (0.001)	−0.065 (0.020)	0.055 (0.045)	0.542	<0.001
Betula maximowicziana	BAI		spei.dec	nfr.MAR-APR	spei.AUG		
		0.989 (<0.001)	−0.104 (0.002)	−0.082 (0.011)	−0.074 (0.020)	0.475	0.001
	VI		spei.AUG	vpd.dec-JAN			
		0.984 (<0.001)	−0.072 (0.015)	0.072 (0.015)		0.385	0.002
Castanea sativa	BAI		vpd.dec-JAN	spei.JUL			
		0.991 (<0.001)	0.063 (0.029)	0.063 (0.031)		0.298	0.012
	VI		vpd.dec-JAN	spei.JUL			
		0.947 (<0.001)	0.073 (0.007)	0.058 (0.026)		0.363	0.004
Cryptomeria japonica	BAI		spei.FEB-JUL	vpd.JAN	vpd.apr-may		
		0.992 (<0.001)	0.116 (0.002)	0.079 (0.024)	0.073 (0.041)	0.493	<0.001
	VI		spei.FEB-JUL	vpd.JAN	vpd.apr-may		
		0.969 (<0.001)	0.109 (0.001)	0.069 (0.032)	0.076 (0.023)	0.505	<0.001
Fagus sylvatica	BAI		vpd.may	vpd.dec	spei.JUL		
		0.996 (<0.001)	0.128 (<0.001)	0.064 (0.014)	0.055 (0.031)	0.643	<0.001
	VI		vpd.may-jun	vpd.dec-JAN			
		0.973 (<0.001)	0.102 (<0.001)	0.097 (0.001)		0.575	<0.001
Metasequoia glyptostroboides	BAI		nfr.FEB-APR	spei.jul-oct	spei.JUL		
		0.932 (<0.001)	−0.094 (0.004)	0.098 (0.003)	0.083 (0.010)	0.537	<0.001
	VI		nfr.FEB-APR	spei.aug-sep	spei.JUL-AUG		
		0.831 (<0.001)	−0.092 (0.002)	0.088 (0.003)	0.068 (0.015)	0.589	<0.001
Picea abies	BAI		spei.may-sep	vpd.oct-JAN			
		0.980 (<0.001)	0.113 (0.009)	0.096 (0.023)		0.307	0.010
	VI		spei.APR-JUL	vpd.oct-JAN	spei.aug-sep		
		0.947 (<0.001)	0.086 (0.019)	0.074 (0.042)	0.071 (0.044)	0.425	0.004
Thuja plicata	BAI		spei.aug-sep	vpd.aug-JAN			
		0.972 (<0.001)	0.095 (0.003)	0.082 (0.010)		0.388	0.002
	VI		vpd.JAN	vpd.apr-may	spei.MAR-JUL		
		0.953 (<0.001)	0.052 (0.008)	0.049 (0.016)	0.044 (0.027)	0.474	0.001
Tsuga heterophylla	BAI		vpd.JUL	spei.JUL-AUG			
		0.992 (<0.001)	−0.072 (0.008)	0.065 (0.015)		0.529	<0.001
	VI		vpd.JUL	spei.FEB	vpd.JAN		
		0.959 (<0.001)	−0.076 (<0.001)	0.047 (0.021)	0.040 (0.045)	0.554	<0.001

For each model, coefficients (estimates and p values in parentheses) of the intercept, climatic predictor variable (spei, vpd, nfr) and abbreviation of the month and timescale of the regression term as well as multiple R^2 and p values of the whole model are shown. Lowercase abbreviations (apr–dec) denote months of the previous year (April–December), and uppercase abbreviations (JAN–SEP) indicate months of the current year (January–September). The regression terms are listed in descending order according to its relative importance of the predictor variables (RIV)

BAI, basal area increment at breast height; VI, total stem volume increment; spei, standardized precipitation evapotranspiration index; vpd, vapor pressure deficit; nfr, number of frost days (<0 °C)

availability (spei) in February–July in the year of tree ring formation with second-order variables being winter and previous spring vpd. Similarly to *Cryptomeria*, annual increment of *Picea* was limited by spei during growing seasons in the prior (BAI and VI) and current year (VI) as well as vpd in the preceding November to January.

Multiple regression analyses of *Metasequoia* confirmed the observed vulnerability of growth to *frost* occurrence (nfr)



species	incr	R^2
Acer rubrum	BAI	0.492***
	VI	0.542***
Betula maximowicziana	BAI	0.475***
	VI	0.385**
Castanea sativa	BAI	0.298*
	VI	0.363**
Cryptomeria japonica	BAI	0.493***
	VI	0.505***
Fagus sylvatica	BAI	0.643***
	VI	0.575***
Metasequoia glyptostroboides	BAI	0.537***
	VI	0.589***
Picea abies	BAI	0.307**
	VI	0.425**
Thuja plicata	BAI	0.388**
	VI	0.474***
Tsuga heterophylla	BAI	0.529***
	VI	0.554***

Fig. 4 Graphical illustration of the linear regression models relating species-specific increment variables (incr) to the best explaining climate variables (spei, vpd, nfr) at the month(s) and timescale of the year at which the lowest AICc was reached. For each model, climate variables promoting growth (positive relationships) are presented in blue, and variables inhibiting growth (negative relationships) are highlighted in red. The numerals (1, 2, 3) indicate the hierarchical importance of the climate variable as a function of its listed relative importance of the predictor variable (RIV) in each regression model in descending order (1 = highest RIV, 3 = lowest RIV, all $p < 0.05$). Lowercase abbreviations (a–d) denote months of the previous year (April–December), and uppercase abbreviations (J–S) indicate months of the current year (January–September). R^2 = multiple R^2. Significance levels of the models: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. (Color figure online)

in February–April (Fig. 4). Furthermore, summer spei in both, previous and current years, positively influenced the annual increment.

Differences between breast height and stem increment in response to climate

Climate sensitivity slightly varied between BAI and VI depending on the tree species (Figs. 3, 4). However, across tree species no clear trend in growth response to climate regarding the considered increment variables was found. VI slightly differed in terms of the greater impact of temperature (vpd) in the spring and winter season prior to the year of wood formation (*Acer*, *Betula*, *Castanea*, *Fagus*, *Picea*, *Thuja*, *Tsuga*). Furthermore, VI appeared to be marginally more sensitive to water availability (spei) in the current growing season (*Acer*, *Betula*, *Picea*, *Thuja*) with no sensitivity of VI to current year summer spei for *Fagus* and *Tsuga* trees. BAI tended to be more affected by water availability (spei) in the preceding growing season (*Picea, Thuja*) or by nfr (*Betula*) when compared with VI. The overall strongest discrepancies in climate sensitivity between BAI and VI were found for *Betula*, *Picea* and *Thuja* trees ($\Delta R^2 = 0.09$, 0.12 and 0.09, respectively, Fig. 4). The lowest discrepancies in response to climate between BAI and VI were observed for *Cryptomeria* ($\Delta R^2 = 0.01$) and *Tsuga* ($\Delta R^2 = 0.02$) trees (Fig. 4).

Discussion

Our analysis confirmed that growth was significantly driven by climatic factors that function at different time periods at the mesic forest site. Temperature-controlled vapor pressure deficit (vpd) in preceding cold periods tended to be the most important driver across the tree species for current growth. Additionally, water availability represented by the standardized precipitation evapotranspiration index (spei) in the growing seasons (prior and current to the year of wood formation) strongly affected tree growth.

Effects of climate factors on tree growth

Our findings underline the effects of vapor pressure deficits (vpd) on tree growth observed by different authors. Williams et al. (2012) and Restaino et al. (2016) reported a consistent and strong impact of growing season deficits on the growth of coniferous tree species throughout western US forests. In contrast to temperature that limits growth as a function of decreasing photosynthesis at given thresholds of leaf temperature, vpd is linked to stomatal closure which ultimately reduces growth due to prevented CO_2 uptake (Restaino et al. 2016). Thus, growing season vpd seems to be a reliable indicator for physiological plant stress that is more directly associated with tree productivity. However, the inverse and positive effects of vpd in non-growing season do not reflect the stress-related evaporative demand, particularly astonishing for deciduous species ceasing photosynthesis in winter. For the coniferous evergreen species, the lower saturation pressure in winter months (in comparison with growing season) and consequently weaker deficit might be sufficient to induce transpiration processes without drought damage due to available water supply at the study site. In this regard, vpd might be as low to prevent stomatal closure. Because of the nonlinear (exponential) response of saturation vapor pressure to temperature, increasing temperature increasingly affects vpd given constant relative humidity and even more strongly given constant absolute humidity. This is why we consider vpd as a matrix for temperature. The strong sensitivity of vpd to air temperature (tavg; Fig. 3) might be a further generalized explanation for the across species' dependency on high vpd in cold months. The importance of winter temperatures and temperature-related variables to tree growth had been reported for various tree species in Central (e.g., Feliksik and Wilczyński 2009; Lebourgeois et al. 2010; van der Maaten 2012; Land et al. 2017) and Southern Europe (e.g., Granda et al. 2013; Martin-Benito et al. 2013; Żywiec et al. 2017). The general positive growth response to winter vpd might be related to decreasing winter embolism with increasing temperature in cold months (Lebourgeois et al. 2010; van der Maaten 2012). The risk of cavitation restraining water transport processes is of larger importance for ring porous tree species with large vessels (Améglio et al. 2002) such as *Castanea sativa*. In diffuse-porous species, the number of embolized xylem conduits can either increase (e.g., in *Acer* or *Fagus* trees) or decrease during winter, while coniferous species are less vulnerable to winter embolism (Améglio et al. 2002). A warm winter may further encourage soil warming and mycorrhizal root growth as well as promote bud burst phenology and needle and shoot maturation, thus prolonging the growing season of the following year (Lebourgeois et al. 2010). As supported by the findings of Restaino et al. (2016), the lagged impact of temperature-driven variables such as vpd in non-growing seasons is higher for regions where water is less limiting. Thus, the relatively high dependence of tree growth on previous vpd may be related to the general high water supply of our study site.

An increasing number of comparative dendroecological studies of various tree species recently confirmed that water availability and drought stress during the growing season rank among the dominant climatic factors driving growth of European forests (e.g., Zang et al. 2014; Bhuyan et al. 2017; Vitali et al. 2017; Stojanović et al. 2018). The use of extended drought indices considering such physiological stress conditions has greatly increased. The applied standardized precipitation evapotranspiration index (spei) benefits from the involvement of a water balance giving thresholds for regional water availability above or below average conditions for a given climate record (Vicente-Serrano et al. 2010). However, recent studies emphasize that negative spei do not represent sites' water shortage per se, suggesting not to apply spei as a standalone index for detection of drought severity, especially in a global context (Zang et al. 2020). In this study, the response to spei particularly differed between tree species with respect to the temporal scale of water availability or shortage, respectively (Figs. 3, 4). When water becomes low, xylem water potentials decrease, and leaf stomata closure causes a rapid cessation of photosynthetic CO_2 assimilation (Choat et al. 2018). As a consequence, carbon storage and wood formation are inhibited. Over longer drought periods, low photosynthesis rates in association with cavitation-induced gas emboli throughout the xylem reduce hydraulic conductance and water transport, and carbohydrate pools can be depleted (Choat et al. 2018). Since strategies to avoid water stress (e.g., anisohydric or isohydric) strongly differ among tree species (e.g., Thomsen et al. 2013; Fardusi et al. 2016) as a function of drought duration, this emphasizes the need for considering cumulative effects of water availability. As reported by Bhuyan et al. (2017), spei of short- and intermediate-term scales seems to be appropriate to capture drought signals of tree growth in temperate forests.

In dendroecology research, the rare application of the number of frost days (e.g., Gazol et al. 2019) or derived spring frost measures based on accumulated degree day sums (e.g., Vanoni et al. 2016; Vitasse et al. 2019) may be linked to the fact that this meteorological parameter simplifies the absolute values of (minimum) temperature records. Furthermore, calibration (of frost day signals in growth series) over summer months is impaired due to lack of days below freezing point. However, our analyses demonstrated that the cumulative occurrence of frost can have significant impacts on tree growth when restricted to cold month including spring data (Figs. 3, 4). As frost events are expected to become more frequent in earlier starting and longer lasting growing seasons, especially in Europe (Liu et al. 2018), this variable will gain increasing importance in the future when evaluating tree response to climate.

In total, interactions of climate parameters considering water- and temperature-related (including frost occurrence) conditions seem to play a major role in species-specific growth dynamics (Table 5; Fig. 4). The combination of high vpd in preceding winter periods with high water availability during growth periods was the most significant complex of factors in the growth variation across the tree species. On the other hand, the multiple approaches demonstrated individualistic climate response of species to a unique set of climate parameters.

Species-specific response to climate factors

The climate–growth analyses revealed species-specific patterns with respect to growth dominating climatic parameters and timescales. Tree growth of *Castanea*, *Thuja* and *Fagus* was mainly affected by vpd in winter or spring (*Fagus*) with slightly lower dependency on spei. For *Acer*, *Cryptomeria* and *Picea*, water availability during growing seasons was the dominant factor facilitating tree growth. High vpd in current July reduced growth of *Tsuga*, and *Betula* was negatively affected by high water availability in current August. Growth of *Metasequoia* was strongly limited by frost occurrence in the beginning of a year. These climate–growth patterns may result from specific ecological properties or morphological and functional traits. The species' water-use strategies seem to be a crucial factor regarding the sensitivity to water availability and drought. Thus, anisohydric and water spending species such as *Betula*, *Castanea* and *Fagus* were generally less affected by spei in comparison with the isohydric species. This effect can be supported by morphological traits such as the development of deep root systems facilitating the exploitation of water resources. The long-term adaption due to the ecological amplitudes might additionally control the species-specific climate sensitivity, e.g., when the mesic conditions of the study site coincide with optimum climate conditions of a species' range (e.g., *Fagus*). On the other hand, if the study site represents the ecological distributional edge of a species (e.g., in terms of temperature), a higher sensitivity was found (e.g., sensitivity to frost of *Metasequoia*). As the individual characteristics may specifically trigger climate sensitivity, all criteria should be considered. For a comprehensive assessment of species' climate vulnerability, we further suggest the incorporation of all three analyzed climatic aspects weighted in the following order: water availability (spei), temperature (vpd) and frost (nfr).

Our analyses shows a positive effect of water availability on anisohydric *Castanea sativa* growth only in late summer, while the positive effect of winter vpd was stronger (Fig. 4). Due to its affinity on high summer temperatures (22–30 °C, Gomes-Laranjo et al. 2012) or degree days (Bottacci 2011), *Castanea* is expected to shift northwards to Central Europe where future conditions will become more favorable, e.g., in terms of milder winters (Broadmeadow et al. 2005; Thurm et al. 2018; Buras and Menzel 2019). In total, *Castanea* trees provided the lowest sensitivity to multiple climate factors with relatively low dependency on water availability.

For a further anisohydric species, *Betula maximowicziana*, water availability even affected tree growth negatively (Fig. 4). At mesic sites where water is less limiting such as the study site Burgholz, oversupply of precipitation and waterlogging can cause oxygen deprivation inhibiting root functioning and growth with negative feedbacks on transpiration and photosynthesis, leading to potential growth losses (Repo et al. 2016). The high sensitivity to waterlogging of *Betula* species such as *Betula pendula* (Wang et al. 2016) and, in particular, *Betula maximowicziana* (Niinemets and Valladares 2006) may be linked to our observed negative impact of spei in August. This, in turn, indicates a lower demand for water and coincides with the reported high resistance to extreme summer drought in 2003 with particularly low precipitation amounts in August (Hoffmann et al. 2018a).

Additionally, the European native *Fagus sylvatica* seems to benefit from its water spending (anisohydric) behavior (e.g., Pretzsch et al. 2013) resulting in a low growth response to water availability (Figs. 3, 4). As shown in a previous study (Hoffmann et al. 2018a), beech trees were of rather medium to high drought tolerance supporting the secondary dependence on water availability at the study site. In contrast, temperature and vpd in the preceding year strongly triggered tree growth. These (first-order) lags between temperature and growth response of *Fagus* had been observed in several studies. Thus, temperature in months of the preceding summer to autumn (e.g., Čufar et al. 2008; Castagneri et al. 2014; Dulamsuren et al. 2017) or winter (e.g., Lebourgeois et al. 2005; van der Maaten 2012; van der Maaten-Theunissen and Bouriaud 2012) positively influenced *Fagus* growth at different European forest sites. However, no further analyses supporting such (positive) ongoing heating effects were found. We hypothesize that the mesic study site with deep soils and high precipitation amounts reflects nearly optimal climate conditions for *Fagus* trees where additional heat and transpiration do not limit (stress), but facilitate photosynthesis and wood formation. However, the currently increasing number of observations of beech crown dieback after the extraordinary summer drought in 2018 (e.g., Asche and Meier zu Beerentrup 2019; Buras et al. 2020) may indicate a rapid increase in drought vulnerability when such climate extremes accumulate. This "new phenomena" may particularly hold for shallow and sandy soils with low water holding capacity (personal observation) and is in line with projected decrease in beech abundance over large parts of Central Europe (Buras and Menzel 2019).

In our analysis, water availability of the isohydric (McCulloh et al. 2014) and drought-resistant (Grossnickle and Russell 2010; Hoffmann et al. 2018a) *Thuja plicata* was of lower importance for tree growth with little response of volume increment (Fig. 4). Comparable to the growth reaction of *Fagus*, the greater importance of vpd in the previous year may be related to the favorable mesic conditions of the study site facilitating ongoing transpiration and photosynthesis. As reported by Schaberg et al. (2010), root sensitivity to frost damages due to a limited cold tolerance and shallow rooting may further explain the positive effect of vpd in winter months. The wide ecological amplitude of the shadow-tolerant (Minore 1990) *Thuja* trees might furthermore explain the general lower climate sensitivity (Fig. 4).

For *Tsuga heterophylla*, our findings confirm the frequently observed strong sensitivity (negative influence) to growing season temperature (Ettinger et al. 2011) and vpd (Hoffmann et al. 2018a) with highest impact in July (Figs. 3, 4). Heat-induced evaporative demand and subsequently early stomatal closure (isohydric) seem to be of special importance for the growth of *Tsuga* trees. Furthermore, water availability (spei) in the current growth year with focus on the vegetation period is a further climatic factor limiting annual tree growth. For the mesic study site, the observed strong climate sensitivity does not coincide with findings primary classifying *Tsuga* as a rather climate-tolerant tree species (Ettinger et al. 2011) due to its distribution under broad ecological amplitudes (Burns and Honkala 1990a).

Climate–growth relationships of *Metasequoia glyptostroboides* indicate a strong sensitivity to various climate constellations (particularly given by the high number correlations; Fig. 3) which does scarcely match with its common characterization as a climate-tolerant tree species (Williams 2005; Shen 2011). Our findings suggest a strong limitation of annual increment in response to frost occurrence in January to April of the current growth year (Figs. 3, 4). Thus, the reported risk to late frost damage due to early bud break (Burrichter and Schoenwald 1968) could be partially confirmed, while its cold tolerance could not (Williams 2005). The reduced drought tolerance (Vann 2005) is furthermore reflected by the growth response to spei in the previous growing season. However, negative effects of (too) strong transpiration (indicated by high vpd) on tree growth (Burrichter and Schoenwald 1968) were not found and may be explained by the general good water supply (Fig. 1).

The response patterns of European native *Picea abies* to climate parameters largely corresponded with those of *Cryptomeria* trees (Fig. 3). This isohydric species has widely been classified as susceptible to water stress during drought in European forests (e.g., Pretzsch et al. 2013; Zang et al. 2014; Vitali et al. 2017) and is expected to largely disappear from Central European lowlands under future scenarios (Buras and Menzel 2019). Our analysis suggests that accumulated water availability (long-term spei) during the growing season is the dominant factor driving tree growth, even for sites with a favorable water supply (Fig. 4).

The strong sensitivity to water availability during growing seasons (Fig. 4) of the isohydric *Cryptomeria japonica* corresponds with findings (or classifications) of various studies and expert assessments (e.g., Schenck 1939b; Schober 1978; Matsumoto et al. 2006; Tange et al. 2009). Therefore, its high water demand, but low ability to transport water from the soil according to its large hydraulic resistance (Matsumoto et al. 2006), may explain the observed drought vulnerability (Hoffmann et al. 2018a). Besides strong regulation of leaf water potential (Kumagai et al. 2009), a shallow root system (Konôpka et al. 2006) additionally inhibits water uptake from deeper soil layers during drought. For *Cryptomeria* trees, high values of vpd in the current growing season may induce physiological stress caused by high evaporative demand (Fig. 3). However, mild conditions in the preceding winter positively influenced growth, which may be related to reduced winter embolisms or prolonged vegetation periods.

Against common characterizations as an adaptable, undemanding and climate-tolerant tree species (Walters and Yawney 1990; Abrams 1998), *Acer rubrum* surprisingly tended to be very sensitive to all investigated climatic parameters (spei, vpd and nfr, Figs. 3, 4). Growth was strongly driven by water availability in summer that may be related to the early cease of transpiration by stomatal closure when water becomes short (isohydric, Thomsen et al. 2013). vpd in winter largely promoted growth, whereas the occurrence of frost had a negative effect. This resulted in a complex interaction of climatic conditions indicating uncertainty in estimates of growth response. Our findings strongly differ from results of Teets et al. (2018) concluding *Acer* to exhibit a greater plasticity to fluctuating climate conditions due to the lack of significant climate–growth relationships in the most northeastern USA (Maine). However, findings of Hart et al. (2012) in the more central eastern USA (Tennessee) indicate some accordance with our results as the authors found a positive growth response to temperature in winter and to precipitation in spring, but negative correlations with summer temperature.

Comparison of breast height and stem volume response to climate factors

Overall, BAI and VI responded similarly to climate events. Climate sensitivity only marginally and species-specifically differed within trees. We found no universal response pattern that would give indications for growth allocation in relation to climate factors. VI appeared to be marginally more sensitive to temperature-driven vpd in spring or winter of the previous year and to water availability (spei) in the current year growing season. BAI tended to be slightly more sensitive to spei in the previous year growing season. Considering that VI represents growth response in upper stem segments stronger when compared with BAI (as VI incorporates a relatively higher amount of increment measurements above breast height), two general mechanisms may explain growth allocation (e.g., Gower et al. 1995; Sevanto et al. 2003; Ryan et al. 2006): 1) carbon allocation and 2) hydraulic limitations:

During unfavorable growth conditions (e.g., drought), reduced carbon assimilates are used for respiration first, and remaining assimilates are exploited for wood formation. Upper stem parts, close to the organs of photosynthesis (foliage), profit most (allocation at tree tops) and the basipetal (top-down) transport of carbohydrates is reduced (Gower et al. 1995; van der Maaten-Theunissen and Bouriaud 2012). Consequently, relatively low growth rates at lower stem sections lead to higher growth variations under more variable and unfavorable conditions. The lagged growth response at breast height to spei may be related to a reduced availability of carbohydrate reserves and limited allocation to the lower stem. On the other hand, during favorable conditions represented by mild winter and spring (high vpd), the maximum growth shifts downwards resulting in a relative increase in increment on the lower bole (Larson 1963) or, in turn, in a higher sensitivity of upper stem represented by VI.

In contrast, hydraulic and gravitational limitations are proposed as a potential mechanism reducing water availability at the top of tall trees (Ryan et al. 2006; Kerhoulas and Kane 2012; Latte et al. 2016). Thus, climate sensitivity is expected to increase with stem height (Kerhoulas and Kane 2012) and may explain the observed stronger sensitivity of species' VI to current year spei.

Our findings suggest that mechanisms (carbon allocation and hydraulic limitation) driving growth allocation are not uniform across tree species and may interact (Ryan and Yoder 1997). Allocations may be further influenced by other factors such as microclimate, fruit production and cambial reactivation and cessation (Chhin et al. 2010; van der Maaten-Theunissen and Bouriaud 2012; Latte et al. 2016). The general strong allometric relationships between increment at breast height and of the whole stem support the overall similarity of growth response to climate parameters for BAI and VI (corresponding with Corona et al. 1995; Latte et al. 2016). In spite of marginal species-specific differences in climate sensitivity between BAI and VI, radial growth at breast height seems to be a reliable estimate for tree sensitivity.

Methodical limitations

We consider our results to be representative for mesic forest sites with a strong oceanic influence and deep, well water-supplied, but nutrient-poor soils as represented by our Arboretum site (Fig. 1). Thus, implications regarding a general growth behavior of the tree species should be limited to comparable site conditions. The inclusion of site-specific gradients by extension of study sites with, e.g., decreasing water supply or altitudes (e.g., Vanoni et al. 2016; Dulamsuren et al. 2017) would be helpful to derive species-specific climatic site suitability. Further physiological mechanisms difficult to reconstruct such as fruit production and defense mechanisms can influence and superimpose growth responses to climate (Hacket-Pain et al. 2015, 2018).

On chronology-level, the climatic signal component is strongly affected by the number of observations and period length (Schweingruber 1983). In this study, new information about whole stem response to climate had been derived at the expense of the sample size. Despite its general reliable signal strength (estimated by, e.g., eps), a short series length may additionally mask a certain sub-period referring to juvenile growth. Thus, superimpositions of age-related effects on species' climate response in the first years cannot be completely excluded hindering the transferability to old-growth forest stands (in particular for the younger stands of *M. glyptostroboides* or *B. maximowicziana*). We applied a similar detrending method (67% spline) to maintain a maximum comparability across tree species.

Our study only weakly considered the influence of tree size and stand density (including competition) on annual stem growth, even though these factors may bias climate signals in growth series (e.g., Zang et al. 2012; Sohn et al. 2016; Pretzsch et al. 2018). As our aim was to minimize local endogenous and stand level exogenous effects on increment by selecting dominant individuals, we emphasize to take these factors into account when analyzing climate susceptibility of different tree species in future studies.

Conclusion and implications for alien tree species

Focusing on site-specific climate factors, the parameters spei, vpd and nfr were the most important climatic variables explaining growth patterns across seven alien and two native tree species at a productive study site in western Germany. By finding universal variables for describing climate sensitivity, tree responses to climate can be compared between species. We could show that mild winter conditions strongly promote tree growth of several species at mesic forest sites where water availability is less limiting. However, cumulative water shortage in the growing seasons may negatively affect tree growth.

Castanea sativa and *Betula maximowicziana* showed the lowest sensitivity to climatic factors, may therefore exceed climate tolerance levels of native species and may show great potentials to future wood production facing climate change. For *B. maximowicziana*, it was further shown that extreme drought events such as the European summer drought in 2003 are likely to be compensated for (Hoffmann et al. 2018a). For both species, growth seems to be promoted by a water spending, anisohydric physiology during drought when considering the investigated time period. Furthermore, the anisohydric *Fagus sylvatica* seems to benefit from a relatively low vulnerability to variations in water availability in our dataset. For these three anisohydric species, however, increasing (in frequency and strength) severe drought may lead to irreversible damages of essential organs with follow-up dieback phenomena as already observed for European beech stands (particularly at shallow soils). Due to high drought tolerance (Hoffmann et al. 2018a) with major limitations of growth by vpd, *Thuja plicata* and *Tsuga heterophylla* can be classified as tree species with moderate climate sensitivity. *Metasequoia glyptostroboides*, *Picea abies*, *Cryptomeria japonica* and *Acer rubrum*, on the other hand, revealed a strong sensitivity to complex climate conditions and are least suitable among those species that we investigated to mitigate climatic risks.

Based on this study and responses to drought investigated by Hoffmann et al. (2018a), the investigated species can be ranked by an increasing climatic susceptibility as follows: *C. sativa* < *B. maximowicziana* < *T. plicata* < *F. sylvatica* < T. heterophylla < *M. glyptostroboides* < *P. abies* < *C. japonica* < *A. rubrum* . Our species assessment may facilitate decision making when it comes to increasing the share of non-native species in European temperate forests.

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