

# Earth's Future



## RESEARCH ARTICLE

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### Key Points:

- Negative asymmetry in tree growth was observed under regimes with seasonal extreme droughts
- Tree growth in arid and temperate dry regions is more vulnerable to extreme droughts in pre-growing-seasons than in growing-seasons
- Angiosperms are more sensitive to pre-growing-season water availability, and gymnosperms to legacy effects of the preceding tree growth

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Timing and Order of Extreme Drought and Wetness Determine Bioclimatic Sensitivity of Tree Growth

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**Abstract** Tree resistance to extreme droughts and post-drought recovery are sensitive to the drought timing. However, how the bioclimatic sensitivity of tree growth may vary with the timing and order of extreme droughts and wetness is still poorly understood. Here, we quantified the bioclimatic sensitivity of tree growth in the period of 1951–2013 under different seasonal extreme drought/wetness regimes over the extra-tropical Northern Hemisphere, using 1,032 tree ring chronologies from 121 gymnosperm and angiosperm species. We found a negative asymmetry in tree growth under regimes with seasonal extreme droughts. With extreme drought, tree growth in arid and temperate dry regions is more negatively impacted by pre-growing-season (PGS) extreme droughts. Clade-wise, angiosperms are more sensitive to PGS water availability, and gymnosperms to legacy effects of the preceding tree growth conditions in temperate dry and humid regions. Our finding of divergent bioclimatic legacy effects underscores contrasting trends in forest responses to drought across different ecoregions and functional groups in a more extreme climate.

**Plain Language Summary** The occurrence patterns of seasonal extreme drought and wetness events are dramatically shifting with climate warming. However, how will different seasonal extreme climate regimes affect the bioclimatic sensitivity of tree growth remains poorly understood. In this study, we investigated the sensitivity of tree growth to different seasonal climate factors and preceding tree growth conditions during 1951–2013 under different seasonal extreme drought/wetness regimes, using 1,032 tree ring chronologies covering 121 gymnosperm and angiosperm species. We found the magnitude in tree growth reduction caused by seasonal extreme drought events is much larger than that in tree growth stimulation by seasonal extreme wetness events in arid and temperate regions. Tree growth in arid and temperate dry regions is more negatively impacted by extreme drought events in pre-growing-seasons (PGSs) than in growing-seasons. We further found that angiosperms are more sensitive to PGS water availability, while gymnosperms are more sensitive to legacy effects of the preceding tree growth conditions in temperate dry and humid regions. These findings highlight divergent bioclimatic legacy effects on tree growth under different seasonal extreme climate regimes, and provide valuable insights into the future trajectories of forest growth across diverse ecoregions and functional groups in a more extreme climate.

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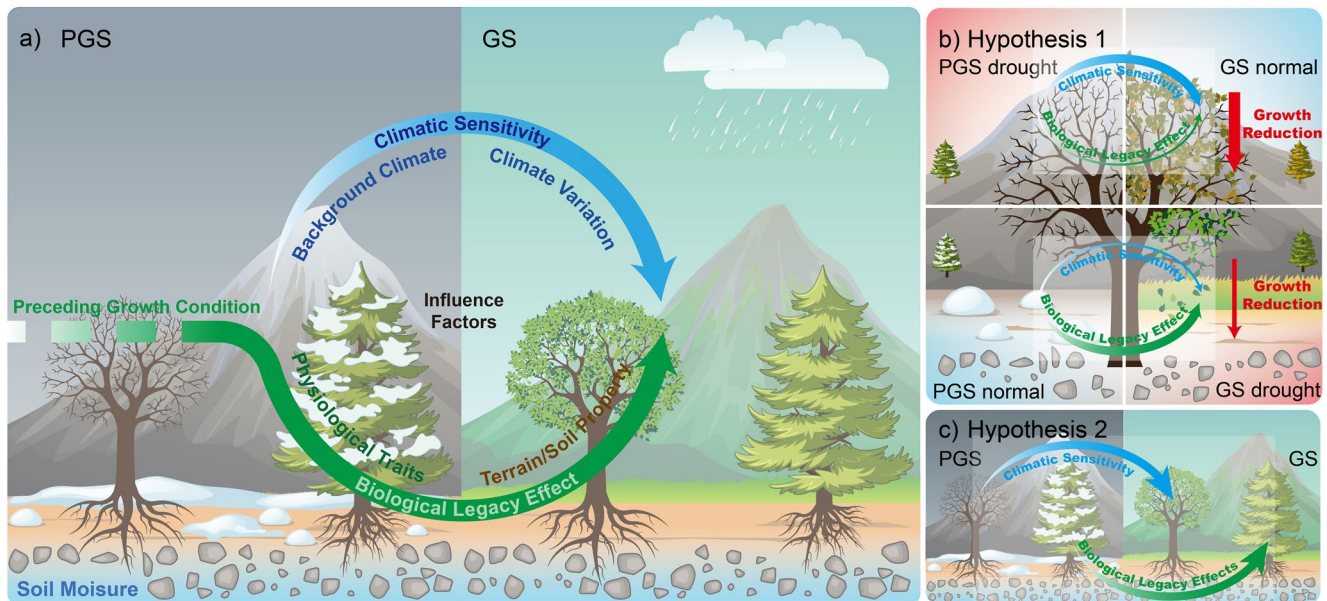
## 1. Introduction

Forests play a crucial and unique role in land carbon uptake and storage, and may have a large climate mitigation potential (Anderegg, Trugman, Badgley, Anderson, et al., 2020; Bastin et al., 2019; Doelman et al., 2020; N. L. Harris et al., 2021; Pan et al., 2011; Reichstein et al., 2013). Forests can, however, be threatened by severe droughts and other extreme climate events (Anderegg, Trugman, Badgley, Anderson, et al., 2020; Anderegg, Trugman, Badgley, Konings, et al., 2020; Breshears et al., 2005; Brodribb et al., 2020; Reichstein et al., 2013). Growing evidence shows that forests in many regions are increasingly susceptible to intensified climate extremes, and their complex interactions with disturbances such as insect outbreaks and fires (Allen et al., 2015; Anderegg, Hicke, et al., 2015; Anderegg, Trugman, Badgley, Konings, et al., 2020; Forzieri et al., 2021; Frank et al., 2015). This is exemplified by recent widespread forest dieback episodes, growth decline, and tree mortality triggered primarily by droughts accompanied with increasing temperature (Allen et al., 2010, 2015; Liu et al., 2013; van Mantgem et al., 2009; P. Zhang et al., 2020).

Several studies have assessed drought-induced tree growth decline and mortality (Allen et al., 2015; Anderegg, Hicke, et al., 2015; Bauman et al., 2022; Liang et al., 2016; Liu et al., 2013), forest resistance (ability to tolerate the drought impacts) and resilience (post-drought recovery rate) to drought (Bose et al., 2020; Gazol et al., 2018; Li et al., 2020), and their underlying physiological mechanisms (Brodribb et al., 2020; Choat et al., 2018). Extreme droughts often exert long-lasting legacy effects preventing or delaying growth recovery even when climatic droughts are over (Anderegg, Schwalm, et al., 2015; Wu, Liu, et al., 2018), suggesting the importance of both drought severity and post-drought bioclimatic features for understanding drought resistance and resilience. Most research, however, focused on documenting the effects of extreme drought during the growing-season (GS); and we know little about the impacts of extreme drought events that occur in different seasons, the impacts of a sequence of droughts, and recovery during follow-up wetness episodes (Hartmann et al., 2018; Lemoine et al., 2018; Peltier & Ogle, 2019). For example, when drought and wetness anomalies occur as a sequence, wetness pulses during the GS may re-stimulate tree growth and partially alleviate adverse impacts of previous extreme droughts (Jiang et al., 2019; Li et al., 2022). Such compensatory effects of seasonal wetness events on tree growth have been overlooked in quantifying the bioclimatic sensitivity of tree growth.

The impacts of extreme droughts on tree growth are multidimensional, given the diverse characteristics of drought events (timing, severity, frequency, and duration) (Huang et al., 2018; Szejner et al., 2020). The effects of drought severity on tree growth and health were analyzed in diverse ecoregions (Anderegg, Schwalm, et al., 2015; Anderegg, Trugman, Badgley, Konings, et al., 2020; DeSoto et al., 2020; Kannenberg et al., 2019). By contrast, the effect of the timing of extreme drought has been less studied (Caldeira, 2019; D'Orangeville et al., 2018; Forner et al., 2018; Gao et al., 2018; Huang et al., 2018; Kannenberg et al., 2019). The seasonal nature of stem radial growth (which is species dependent) over middle and high latitudes of the Northern Hemisphere (NH) implies that hydroclimatic seasonality should determine the bioclimatic sensitivity of forest growth (D'Orangeville et al., 2018). In wet regions, longer drought recoveries were observed when extreme drought occurred in the late GS (Kannenberg et al., 2019). Oppositely, in drier regions, longer recoveries were observed when extreme drought occurred during the early GS (D'Orangeville et al., 2018; Gao et al., 2018; Huang et al., 2018). Those differences in response may further depend on edaphic and biophysiological factors (Kannenberg et al., 2019; Xu et al., 2021). Recent studies revealed that tree growth may be more sensitive to drought timing than to drought intensity in dry Mediterranean areas (Forner et al., 2018) and wet Eastern North America (D'Orangeville et al., 2018).

In addition to the impact of drought timing, post-drought effects also vary among ecoregions and tree species. For instance, gymnosperms and angiosperms exhibit different bioclimatic sensitivities explained by differences in ecophysiological traits (Li et al., 2020). Gymnosperms are commonly characterized by conservative water use adaptations, with more negative  $P_{50}$  (xylem water potential at 50% loss of hydraulic conductivity), higher wood density, and wider hydraulic safety margin (Choat et al., 2012, 2018; Li et al., 2020). This trait spectrum would make gymnosperms more resistant and less vulnerable to drought-induced xylem cavitation. By contrast, angiosperms have riskier embolism-tolerance strategies with higher  $P_{50}$  and narrower hydraulic safety margin, but may have a greater capacity to reverse hydraulic dysfunction and embolism (Choat et al., 2012). In addition, gymnosperms seemingly have stronger capacity to adaptively sustain soluble sugar concentrations in leaves and stems under extreme drought than angiosperms (He et al., 2020), which could lead to longer and more prominent legacy effects of preceding growth conditions on subsequent tree growth. However, the ecophysiological



**Figure 1.** Conceptual diagram for the bioclimatic sensitivity of tree growth under different seasonal extreme climate regimes. The climatic sensitivity (blue lines) and the biological legacy effects of preceding tree growth condition (green lines) on the subsequent tree growth are potentially differentiated among different climate zones and interactively controlled by climate variations, plant physiological traits, and local terrain and soil properties (a). We hypothesize that there is a greater growth reduction and lower drought resistance of tree growth in drier regions when extreme drought events occurred in pre-growing-season (PGS); while the legacy effects of preceding tree growth are likely more prominent when extreme drought events occurred in growing-season (GS) (i.e., hypothesis 1) (b); and that angiosperms are more sensitive to variations in water availability in PGS in regions suffering from strong water stress, while gymnosperms are more sensitive to legacy effects of preceding tree growth conditions prior to extreme drought (i.e., hypothesis 2) (c).

processes underlying bioclimatic legacy effects (i.e., legacy effects of preceding tree growth and climate conditions on subsequent tree growth) are poorly understood, and are under-represented in state-of-the-art dynamic global vegetation models (Anderegg, Schwalm, et al., 2015; Zhang et al., 2018). Such inadequacies limit their ability and performance in realistically predicting changes in both structure and functioning of forest biomes, as well as their response to interannual forcing.

Here, we address how timings and orders of seasonal extreme drought and/or wetness events within a biological year impact the sensitivity and resilience of tree growth to drought over northern forests (approximately 25°–75° N). We aim to test two hypotheses: (a) there is a greater growth reduction and a lower drought resistance of tree growth in drier regions when extreme droughts occur in the pre-growing-seasons (PGSs) than those occur in GSs. (b) Angiosperms are more sensitive to reductions in water availability in the PGS in regions suffering from strong water stress, while gymnosperms are more sensitive to legacy effects of preceding tree growth conditions before extreme drought (Figure 1).

## 2. Materials and Methods

### 2.1. Tree-Ring Chronologies

We compiled 1,032 tree-ring width series over the NH from the International Tree Ring Data Bank (ITRDB) (data obtained on December 1, 2019) (Zhao et al., 2019). The majority of tree-ring width series ended before 2013. The individual stand-level tree-ring width series, consisting of 121 tree species of evergreen needleleaf forest, deciduous needleleaf forest and deciduous broadleaf forest types (95 gymnosperms and 26 angiosperms), cover 47,204 site-years and span diverse bioclimatic regions. We removed longer-term (non-) climatic signals embedded in the raw ring-width series by fitting a consistent cubic smoothing spline detrending with a 50% frequency-response threshold of 20 years. The raw tree ring width measurements were divided by the corresponding fitted spline values, resulting in a unitless tree-ring index (TRI). The statistical quality of each tree-ring chronology was evaluated by the Expressed Population Signal, which considers sample size and the common signal among trees within a given geographic location (Fritts, 2001). We determined the reliable period for each tree ring chronology

with the Expressed Population Signal above 0.85. All TRI chronologies were further screened by meeting the following criteria: (a) there are full records of information on latitude, longitude, site elevation, species name, and sample numbers; (b) there is a minimum series length of 35 years in the study period of 1951–2013; and (c) the sample number (individual tree cores) for each site-year should be greater than 5.

## 2.2. Gridded Climate Data Sets and Köppen-Geiger Climate Zones

Gridded monthly air temperature, precipitation, and potential evapotranspiration (PET) data with a spatial resolution of 0.5° and for the period 1951–2013 were obtained from the Climate Research Unit (CRU) TS 4.02 data set ([https://crudata.uea.ac.uk/cru/data/hrg/cru\\_ts\\_4.02/](https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/)), compiled by the Climate Research Unit of University of East Anglia (Harris et al., 2020). Gridded downward surface shortwave solar radiation data with a spatial resolution of 0.5° were obtained from the CRU-National Centers for Environmental Prediction (NCEP) product (CRU-NCEP version 7; <https://rda.ucar.edu/datasets/ds314.3/#!description>). The CRU-NCEP data is a harmonized product combining CRU TS 3.23 data and NCEP-NCAR reanalysis, providing 6-hourly meteorological forcing for global land surface model simulations (Viovy, 2018). Gridded monthly Standardized Precipitation-Evaporation Index (SPEI) data were obtained from the Global SPEI database (SPEIbase V2.5) (Begueria et al., 2010), with a spatial resolution of 0.5° and covering the period of 1901–2015. This data set has been widely used to evaluate drought severity and to quantify episodic extreme drought/wetness events for large-scale and long-term studies (D'Orangeville et al., 2018; Li et al., 2020), because it allows the comparison among sites with contrasting climate and accounts for both timing and duration of drought during the current and previous years (Vicente-Serrano et al., 2010, 2013).

Five major climate zones were regrouped based on the Köppen-Geiger climate classifications (<http://koepen-geiger.vu-wien.ac.at/present.htm>) over the middle and high-latitude NH (Kottek et al., 2006), including arid (AR), temperate dry (TA), temperate humid (TH), cold dry (CA), and cold humid (CH) regions (Table S1 in Supporting Information S1).

## 2.3. Determination of Seasonal Extreme Drought and Wetness Events

Extreme drought and wetness events were determined in PGSs and GSs, respectively, at each tree ring site. The remote sensing-derived Normalized Difference Vegetation Index (NDVI) data were used to identify the GS at each tree ring site (Appendix Text in Supporting Information S1). Analyses of NDVI-based vegetation phenology for the period of 1982–2015 reveal that the start of GS generally occurs in April or May in 58% of study sites over our study region, whereas the end of GS occurs in September or October in 65% of study sites (Appendix Text and Figure S1 in Supporting Information S1). Therefore, the PGS and GS for tree growth over the middle and high-latitude NH were consistently defined as previous October to current April and May to September, respectively, following previous studies of vegetation growth-climate responses over the northern NH (Peng et al., 2013; Piao et al., 2014; Wu, Liu, et al., 2018).

In this study, we identified the episodic, short-term extreme climate events in both PGSs and GSs at each forest stand using both SPEI at timescale of 6 months and the climatic water deficit (CWD). The 6-month timescale coincides approximately with the separation between PGS and GS in the northern hemisphere. The monthly CWD in the period of 1951–2013 was calculated using Equation 1 at each forest stand.

$$CWD_i = P_i - PET_i \quad (1)$$

where  $P_i$  and  $PET_i$  are total precipitation and PET in month  $i$ , respectively. Both the monthly precipitation and PET were obtained from the CRU TS 4.02 data set. The CWD considers the effects of both precipitation and PET on climatic water balance; and has been widely used to identify and characterize both the timing and severity of climatic droughts (Anderegg, Schwalm, et al., 2015; Wu, Liu, et al., 2018). Then, we calculated the mean CWD in the PGS and GS of each biological year at each forest stand for the 1951–2013 period. Years with CWD values exceeding mean  $\pm$  2SD (SD, temporal standard deviation) in either PGSs or GSs were defined as years with seasonal extreme wetness/drought events at each forest stand. Years with either extreme drought and/or extreme wetness in PGSs or GSs are marked as “extreme years” at each forest stand. The “normal years” were subsequently defined as those years without any extreme drought or wetness events in either PGSs or GSs. Consistently, a threshold of  $\pm$ 2.0 was applied for both mean PGS and GS SPEI series in the period of 1951–2013

to identify the extreme wetness ( $>2.0$ ) and drought ( $<-2.0$ ) events at each forest stand. Because SPEI values are normalized as  $z$  scores, an SPEI value of  $-2.0$  indicates a 2 SD drought. The bioclimatic sensitivity of tree growth in different seasonal extreme climate regimes derived from both SPEI and CWD was compared to validate the robustness of our findings.

Conceptually, there are eight possible regimes for sequential combinations of seasonal extreme climate events within a biological year. We denoted the sequential combinations of seasonal extreme climate events as  $^+I^-$  (e.g.), where  $I$  is seasonal mean CWD (or SPEI), the left and right superscripts represent PGS and GS, respectively; “-,” “+,” and “ $n$ ” in superscripts represent extreme drought events, extreme wetness events, and normal climate conditions, respectively. A preliminary exploration of different sequential extreme climate events showed that the following four extreme regimes ( $^-I^-$ ,  $^-I^+$ ,  $^+I^-$ , and  $^+I^+$ ) rarely occurred at any forest stand over the 1951–2013 period. The event samples of the four extreme regimes across all forest stands during the period of 1951–2013 are consistently less than 45. It indicates a low probability of the consecutive occurrence of “compound” extreme climate events in both PGS and the GS within a single biological year. Therefore, the four more common regimes, that is,  $^-I^n$ ,  $^nI^-$ ,  $^+I^n$ , and  $^nI^+$ , were retained as a focus of our analyses. In this study, only single extreme year effects were considered; that is, there is no seasonal extreme climate event within a given  $n = 2$  years period both preceding and after any “extreme year.” The number of events for the four seasonal extreme climate regimes in the five major climate zones during the 1951–2013 period is shown in Table S2 in Supporting Information S1.

#### 2.4. Quantification of Responses of Tree Growth to Bioclimatic and Other Factors

First, partial least squares regression (PLSR) was applied to determine the interannual sensitivity of TRI to variations of different seasonal climate factors, including PGS CWD ( $CWD_{pgs}$ ), GS CWD ( $CWD_{gs}$ ), mean GS temperature ( $T_{gs}$ ), total GS precipitation ( $P_{gs}$ ), and mean GS solar radiation ( $SR_{gs}$ ) in the period of 1951–2013, at each forest stand. The PLSR is an effective tool for handling the potential collinearity among multiple explanatory factors, and it is particularly useful for analyzing correlated predictor variables with a small sample compared with the number of predictors (Carrascal et al., 2009). All seasonal climate variables were linearly detrended and standardized before PLSR analyses. The standardized regression coefficients of PLSR are regarded as the interannual sensitivity of tree growth to variations in seasonal climate factors.

Then, a linear mixed effect model (LMM) was applied to identify the effects of multiple bioclimatic factors (seasonal climate factors and the preceding tree growth condition), topographical feature (i.e., site elevation), and tree species on tree growth for each of the four seasonal extreme climate regimes and across each of the five ecoregions. In this study, mean tree growth condition during the preceding 2 normal years ( $G_{pre}$ ) before an “extreme year” was introduced as a fixed effect variable into the LMM in addition to the above-mentioned seasonal climate factors. The 2-year timescale was selected to characterize the preceding mean tree growth before “extreme years,” given that previous studies revealed that the legacy effects of extreme climate events on subsequent tree growth normally last 1–4 years and in most cases 2 years (Kottek et al., 2006). Consistently, the  $G_{pre}$  variable was linearly detrended and normalized before the LMM analyses. For the LMM analyses, site elevation and tree species were introduced as random effect variables to account for the effects of topographical-dependent local site conditions (e.g., edaphic conditions and subsurface properties) (Bertrand et al., 2011) and tree species on tree growth under different seasonal extreme climate regimes and across the five ecoregions. We ranked all potential models (some considering the interactions among fixed effect variables) according to Bayesian information criterion (BIC) at each climate zone, and the best model was determined based on the lowest BIC value and largest Bayesian weight (see example in arid region in Table S3 in Supporting Information S1) (Astigarraga et al., 2020) to limit overfitting. Based on the model selection, the interaction effects among different seasonal climates and between seasonal climates and  $G_{pre}$  were not considered. The relative contribution (RC, %) of different fixed and random effect variables to variations in tree growth was estimated using the variance partitioning algorithm based on the package *partR2* (<https://cran.r-project.org/web/packages/partR2/index.html>) in *R*. We compared the results with seasonal extreme climate events identified by the SPEI at 6-month timescale to further confirm our findings. We displayed the findings with seasonal extreme climate events identified by CWD in the main text while putting the results derived from SPEI in the Supporting Information. The PLSR and LMM analyses were performed using the *pls* (<https://cran.r-project.org/web/packages/pls/index.html>) and *lme4* (<https://cran.r-project.org/web/packages/lme4/index.html>) packages, respectively, in the *R* environment.

## 2.5. Resistance and Resilience of Tree Growth Under Seasonal Extreme Drought

Dimensionless and symmetric resistance ( $R_r$ , changes during drought) and resilience ( $R_s$ , recovery after drought) of tree growth were calculated for each drought year with extreme drought events occurring in either the PGS (i.e.,  $^{-}I^n$ ) or GS ( $^{n}I^{-}$ ) at each forest stand based on the definition proposed by Gazol et al. (2017). The  $R_r$  and  $R_s$  were calculated using Equations 2 and 3, respectively.

$$xR_r = TRI_d / TRI_{pre} \quad (2)$$

$$R_s = TRI_{post} / TRI_{pre} \quad (3)$$

where  $TRI_d$  is the  $TRI$  in a drought year under either  $^{-}I^n$  or  $^{n}I^{-}$  regime,  $TRI_{pre}$  and  $TRI_{post}$  are the  $TRI$  2 years before and after the corresponding extreme drought year. Higher values of  $R_r$  imply higher drought resistance (lower growth reduction). If seasonal extreme drought events lower tree growth, greater tree growth recovery leads to greater resilience (i.e., higher  $R_s$ ). We selected 2 years for forest recovery to quantify the resilience, based on prior studies of drought legacy effects (Anderegg, Schwalm, et al., 2015; Isbell et al., 2015). The difference in  $R_r$  and  $R_s$  between  $^{-}I^n$  and  $^{n}I^{-}$  within the same climate zone, and under the same seasonal extreme climate regime but among different climate zones was compared by Student's  $t$ -test and one-way ANOVA analysis (*stats* package, R).

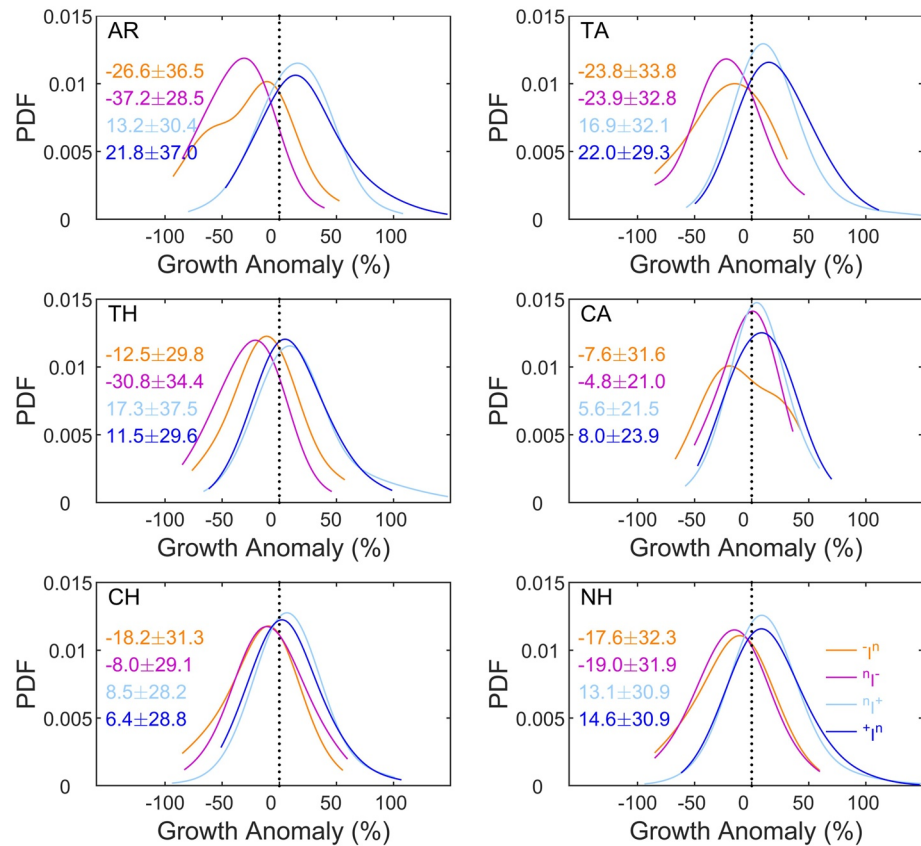
## 3. Results

### 3.1. Responses of Tree Growth to Bioclimatic Factors

Pervasive negative/positive anomalies in tree ring index ( $TRI$ ) are observed in cases where seasonal extreme drought/wetness events occurred within the biological year, respectively, in all of the five ecoregions. Stronger negative anomalies in  $TRI$  are observed in warmer and drier versus cooler and wetter ecoregions under both  $^{-}I^n$  (extreme drought event in PGS and normal climate condition in GS) and  $^{n}I^{-}$  regimes (normal climate condition in PGS and extreme drought events in GS) (Figure 2). Interestingly, the increased magnitude in  $TRI$  associated with seasonal extreme wetness events either occurred in GS or PGS (i.e.,  $^{n}I^{+}$  and  $^{+}I^n$ , respectively) is lower than the magnitude of reduction in  $TRI$  caused by seasonal extreme drought (Figure 2). This creates an asymmetry in tree growth anomalies in response to shifting seasonal water cycles. This indicates negative asymmetry in the response of  $TRI$  to seasonal extreme drought.

The PLSR analyses revealed significantly positive and negative response coefficients of  $TRI$  to  $CWD_{pgs}$  (PGS climatic water deficit) and  $T_{gs}$  (mean GS temperature), respectively, in the semi-arid southwestern North America. By contrast, the response coefficients of  $TRI$  to the other three climate factors were spatially heterogeneous (Figure 3). About 45% and 41% of  $TRI$  chronologies exhibit significantly ( $p < 0.05$ ) positive response to  $CWD_{pgs}$  in arid (AR) and temperate dry (TA) climate zones, respectively, while this proportion decreased to less than 14% in other climate zones. However, only 14% and 7% of  $TRI$  chronologies exhibit significantly positive response to  $CWD_{gs}$  (GS climatic water deficit) in AR and TA climate zones, respectively (Figure 3). The LMM analyses revealed significant positive effects of  $CWD_{pgs}$  on subsequent tree growth in both arid and temperate dry climate zones in cases when extreme drought events occurred during the PGS ( $^{-}I^n$ ); while  $T_{gs}$  exerts significantly negative effects on tree growth in arid regions under the  $^{-}I^n$  regime (Figure 4).

Tree growth condition in the preceding 2 years (i.e.,  $G_{pre}$ ) was found to have significantly positive effects (with a relative contribution  $-RC-$  of 31%) on subsequent tree growth in the arid climate zone under extreme PGS drought ( $^{-}I^n$ ). When extreme drought events occur in the GS ( $^{n}I^{-}$ ), tree growth was significantly ( $p < 0.05$ ) and negatively related to  $T_{gs}$  in the arid climate zone.  $G_{pre}$  exerts significantly positive effects on subsequent tree growth in arid and temperate climate zones (i.e., AR, TA, and TH), where the relative contribution ranges from 16% to 38% under  $^{n}I^{-}$ . Interestingly, the effects of  $G_{pre}$  on subsequent tree growth are prominent and become the most important factor (with highest explanation power) for tree growth in nearly all climate zones when extreme wetness events occur in either the PGS or GS (i.e.,  $^{+}I^n$  or  $^{n}I^{+}$ ) (Figure 4). Lower contribution of  $G_{pre}$  to subsequent tree growth is observed in cases with seasonal extreme wetness events than that with seasonal extreme drought events that occurred in either the PGS or the GS in both arid and temperate dry climate zones (Figure 4). Our



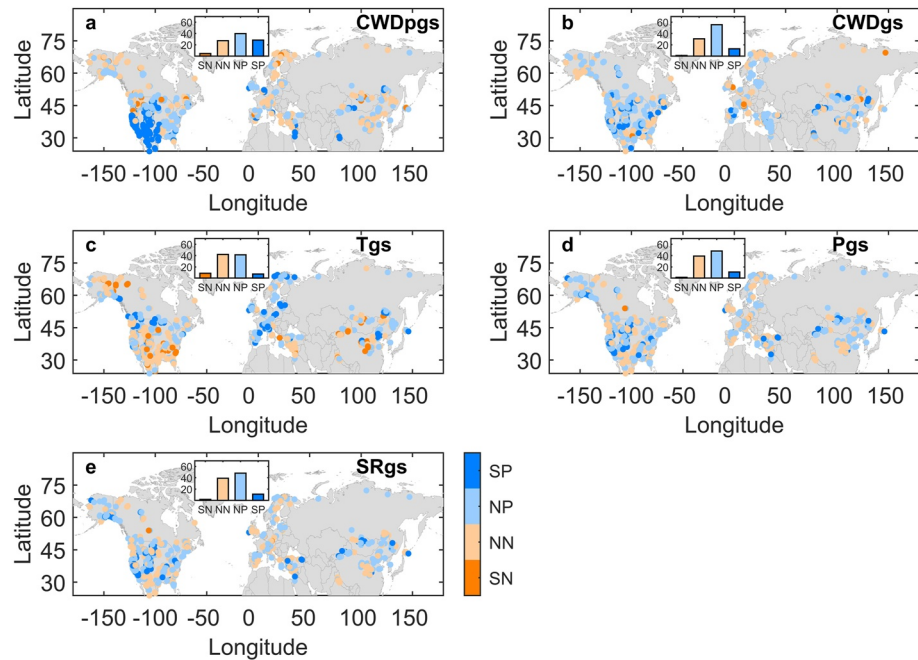
**Figure 2.** The probability density function (PDF) of anomalies in tree ring index (TRI) under four seasonal extreme climate regimes in five major climate zones over the northern hemisphere (NH) for the 1951–2013 period. Major climate zones considered include: arid (AR), temperate dry (TA), temperate humid (TH), cold dry (CA), and cold humid (CH) regions. Anomalies in TRI under  $-I^n$  (orange line, with extreme drought event in pre-growing-season (PGS) and normal climate condition in growing-season [GS]),  ${}^nI^-$  (purple line, with normal climate condition in PGS and extreme drought event in GS),  $+I^n$  (blue line, with extreme wetness event in PGS and normal climate condition in GS), and  ${}^nI^+$  (light blue line, with normal climate condition in PGS and extreme wetness event in GS) and over the five major climate zones and entire northern hemisphere (NH) are displayed. Values shown in different panels are mean  $\pm$  SD (SD, standard deviation) for the TRI anomalies. Anomalies in TRI are displayed as percentages (%).

results are consistent across a choice of water stress index, as a consistent pattern is also observed when using the SPEI drought index instead of the CWD (Figure S2 in Supporting Information S1).

The two random effect variables (i.e., site elevation and tree species) contributed different effects to tree growth variations across different combinations of climate zones and seasonal extreme climate regimes. Higher relative contributions were observed under both PGS ( $-I^n$ ) and GS ( ${}^nI^-$ ) extreme drought regimes in arid and temperate climate zones (Table S4 in Supporting Information S1). Overall, the introduced fixed and random effect variables explain a lower proportion of TRI variance in cases when seasonal extreme wetness events occurred, relative to cases when seasonal extreme drought events occurred (Figure 4, Table S5 in Supporting Information S1).

### 3.2. Divergent Responses of Gymnosperms and Angiosperms to Bioclimatic Factors

Significantly positive responses of tree growth to  $CWD_{pgs}$  are observed for both gymnosperms and angiosperms in the temperate dry climate zone (Figure 5). Negative responses to  $CWD_{pgs}$  are observed for both groups in temperate humid regions (TH) under PGS drought ( $-I^n$ ) (Figure 5). The relative contributions of  $CWD_{pgs}$  to tree growth of angiosperms and gymnosperms are 33% and 19% in temperate dry climate zone, and 62% and 22% in temperate humid climate zone, respectively, under PGS extreme drought regime ( $-I^n$ ) (Figure 5). This finding implies greater sensitivity of angiosperms to variations in  $CWD_{pgs}$  than gymnosperms. Higher contributions of



**Figure 3.** Spatial patterns in the interannual responses of tree growth to seasonal climate variables for the 1951–2013 period. Different colors in the color bar indicate the four types of tree growth responses to variations in seasonal climate, while SP, NP, NN, and SN represent significantly positive, non-significantly positive, non-significantly negative, and significantly negative responses, respectively. The insets show the proportions of the four response types. Five kinds of seasonal climate variables are included: pre-growing-season climatic water deficit ( $CWD_{pgs}$ ), growing-season (GS) climatic water deficit ( $CWD_{gs}$ ), mean GS temperature ( $T_{gs}$ ), total GS precipitation ( $P_{gs}$ ), and mean GS solar radiation ( $SR_{gs}$ ).

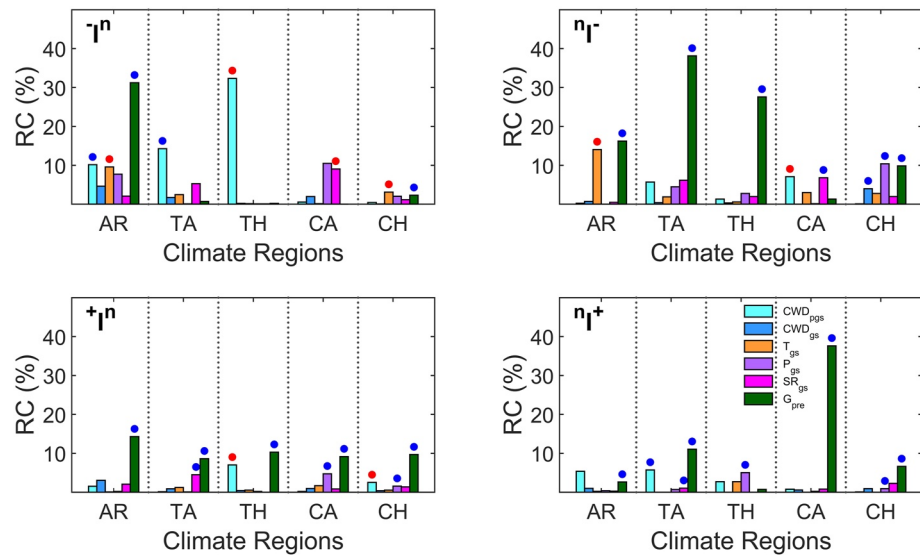
$CWD_{pgs}$  to tree growth of angiosperms than gymnosperms are consistently observed in other seasonal extreme climate regimes in both temperate dry and temperate humid climate zones (Figure 5). No clear divergence in the responses of tree growth to other climate factors is observed between gymnosperms and angiosperms in either temperate dry or temperate humid climate zones under any seasonal extreme climate regime (Figure 5).

Tree growth of gymnosperms is more sensitive to preceding tree growth condition ( $G_{pre}$ ) than angiosperms in temperate dry regions under all climate regimes, except for  $-I^+$  (Figure 5). There is a much higher contribution of  $G_{pre}$  to subsequent tree growth in gymnosperms than angiosperms under  $-I^-$  (45% for gymnosperms and insufficient samples for angiosperm),  $+I^+$  (12% vs. 2%), and  $+I^-$  (13% vs. 6%) in the temperate dry climate zone (Figure 5). Such analyses are not conducted for other three climate zones due to limited samples for both functional groups under different seasonal extreme climate regimes.

### 3.3. Effects of Seasonal Extreme Droughts on Tree Growth Resistance and Resilience

We further compared the drought resistance ( $R_r$ ) and drought resilience ( $R_s$ ) of tree growth between two seasonal drought regimes (i.e.,  $-I^+$  and  $+I^-$ ) and among different climate zones (i.e., under the same seasonal extreme drought regime but for different climate zones). No significant difference is observed in either drought resistance or drought resilience between  $-I^+$  and  $+I^-$  in any climate zone (Figure 6). However, we observe significantly lower drought resistance and resilience in arid regions than in other climate zones under  $-I^+$  (Figure 6). Significant lower drought resistance was observed in angiosperm than in gymnosperm under both  $-I^+$  and  $+I^-$  in temperate arid region and under  $-I^+$  in temperate humid region (Figure S3 in Supporting Information S1). Significant lower drought resilience was observed in angiosperm than in gymnosperm under  $-I^+$  in temperate arid region (Figure S3 in Supporting Information S1).





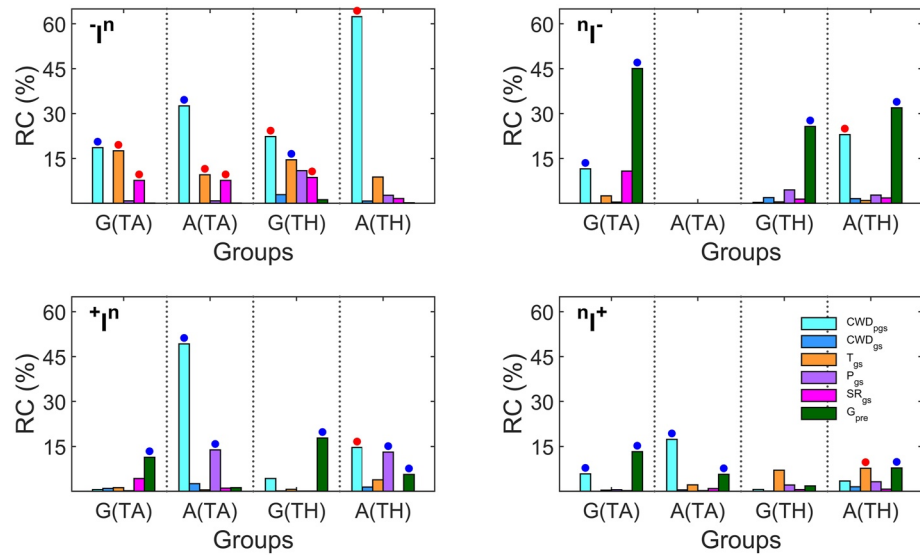
**Figure 4.** The relative contribution (RC, %) of different bioclimatic factors to variations in tree growth among the five climate zones and different seasonal climate extreme regimes. Six kinds of bioclimatic variables are considered in this analysis, including pre-growing-season (PGS) climatic water deficit (CWD<sub>pgs</sub>), growing-season (GS) climatic water deficit (CWD<sub>gs</sub>), mean GS temperature ( $T_{gs}$ ), total GS precipitation ( $P_{gs}$ ), mean GS solar radiation ( $SR_{gs}$ ), and preceding 2-year mean tree-ring width index ( $G_{pre}$ ). The five major climate zones are arid (AR), temperate arid (TA), temperate humid (TH), cold arid (CA), and cold humid (CH) regions. Four seasonal extreme climate regimes are considered, including  $-I^n$  (with extreme drought event in PGS and normal climate condition in GS),  $-I^-$  (with normal climate condition in PGS and extreme drought event in GS),  $+I^n$  (with extreme wetness event in PGS and normal climate condition in GS), and  $+I^+$  (with normal climate condition in PGS and extreme wetness event in GS); where  $I$  denotes the seasonal mean CWD. Blue and the red dots above the bars represent significantly ( $p < 0.05$ ) positive and negative responses of tree growth to the corresponding bioclimatic variables.

## 4. Discussion

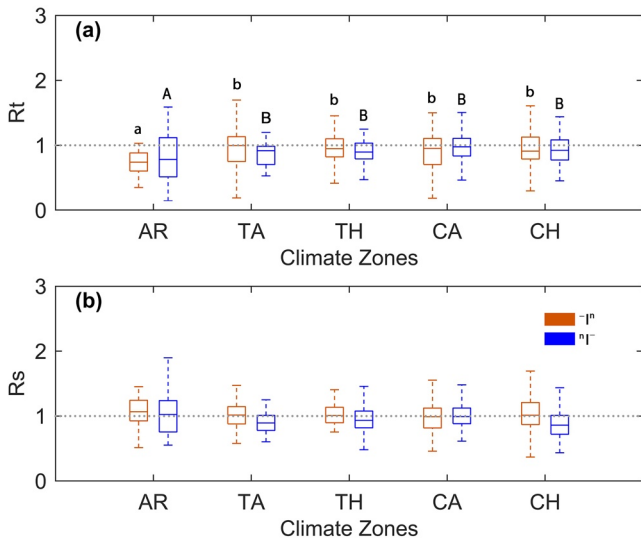
### 4.1. Bioclimatic Legacy Effects Associated With Timing of Seasonal Climate Extremes

Our findings confirm our first hypothesis that tree growth is more vulnerable to water deficit when extreme drought occurred in the PGSs than in the GSs in arid and temperate dry regions (Figure 1). Extreme drought events in the PGSs lead to much lower drought resistance of tree growth in arid region than other wetter regions. By contrast, tree growth turns out to be more sensitive to legacy effects of preceding tree growth conditions when seasonal extreme wetness occurred. These findings highlight that the timing of seasonal extreme climate events is a critical driver for understanding the bioclimatic sensitivity of tree growth and accurately predicting future trajectories of forest ecosystems facing climate change induced shifts in seasonal hydrothermal regimes (Dannenberg et al., 2019; Huang et al., 2018; Pendergrass et al., 2017).

Preceding bioclimatic conditions have crucial legacy effects on subsequent tree growth and drought sensitivity/resilience across a broad spectrum in climate, demography, and site conditions (D'Orangeville et al., 2018; Hackett-Pain et al., 2018; Kannenberg et al., 2020; Karban & Pezzola, 2017; Ogle et al., 2015; Peltier et al., 2016; Peltier & Ogle, 2019; Scharnweber et al., 2020; Szejner et al., 2020). Legacy effects of preceding water availability on tree growth appear to be pervasive in both temperate and boreal forests globally (Anderegg, Schwalm, et al., 2015; Au et al., 2020; Kannenberg et al., 2020; Scharnweber et al., 2020; Wu et al., 2019), especially in water-limited regions and those regions prone to drought stress (Peltier et al., 2016; Szejner et al., 2020) (Figures 3 and 4). Drought in the PGS can reduce tree growth in the following GS due to potential legacy effects on soil water supply, nutrition availability, allocation of carbohydrates and hydraulic functioning (Babst et al., 2012, 2013; Girardin et al., 2016; Scharnweber et al., 2020; Wu et al., 2019), while the prevalence of these legacy effects on subsequent tree growth is ecoregion- and species-dependent. Tree growth in drought-stressed regions tends to be increasingly susceptible to further amplification in seasonal hydroclimatic variability under a warmer and drier climate (Dannenberg et al., 2019; Wu et al., 2019). In drier regions, the respective positive and negative responses of tree growth to CWD<sub>pgs</sub> and  $T_{gs}$  illustrate the important positive legacy effects of



**Figure 5.** The relative contribution (RC, %) of different bioclimatic factors to variations in tree growth between gymnosperms (G) and angiosperms (A) in temperate dry (TA) and temperate humid (TH) regions under different seasonal climate extreme regimes. Six kinds of bioclimatic variables are considered in this analysis, including PGS climatic water deficit ( $CWD_{pgs}$ ), growing-season (GS) climatic water deficit ( $CWD_{gs}$ ), mean GS temperature ( $T_{gs}$ ), total GS precipitation ( $P_{gs}$ ), mean GS solar radiation ( $SR_{gs}$ ), and preceding 3-year mean tree-ring width index ( $G_{pre}$ ). Four seasonal extreme climate regimes are considered, including  $-I^n$  (with extreme drought event in PGS and normal climate condition in GS),  $-I^-$  (with normal climate condition in PGS and extreme drought event in GS),  $+I^n$  (with extreme wetness event in PGS and normal climate condition in GS), and  $+I^+$  (with normal climate condition in PGS and extreme wetness event in GS); where  $I$  denotes the seasonal mean CWD. Blue and red dots above the bars represent significantly ( $p < 0.05$ ) positive and negative responses of tree growth to the corresponding bioclimatic variables.



**Figure 6.** Drought resistance (a,  $R_t$ ) and resilience (b,  $R_s$ ) of tree growth under two seasonal extreme drought regimes ( $-I^n$  and  $+I^-$ ) across five major NH climate zones. Different lower and upper cases above the boxes in plot (a) indicate significant ( $p < 0.05$ ) differences in  $R_t$  under the regimes of  $-I^n$  (extreme drought in pre-growing-season [PGS] and normal condition in growing-season [GS]) and  $+I^-$  (normal climate condition in PGS and extreme drought in GS), respectively, among the five major climate zones. The five major climate zones are arid (AR), temperate dry (TA), temperate humid (TH), cold dry (CA), and cold humid (CH).

PGS water availability on subsequent tree growth, particularly when extreme drought events occurred in PGSs. This positive legacy effect weakens with high temperatures (Figures 3 and 4) and consecutive GS drought (Girardin et al., 2016; Peltier et al., 2016). Tree growth is increasingly vulnerable to PGS drought and warming in the subsequent spring in many regions (Peltier & Ogle, 2019), particularly in drought-prone ecosystems (Peltier et al., 2016; Wu et al., 2019) (Figures 3 and 4). It showed that tree growth can be influenced by the legacy effect of preceding precipitation over up to 4 years back in time (Ogle et al., 2015). Increasing evidence demonstrated that changes in winter processes (e.g., snow cover and melting, frozen soil dynamics, etc.), attributing to both climate warming and shift in seasonal precipitation regimes, played an increasing role in regulating tree growth (Reinmann et al., 2019; Wu et al., 2019). Declined snow cover and earlier snow melting are expected along with a warmer climate (Déry & Brown, 2007; Musselman et al., 2021), which deteriorates the snowmelt water supply for sustaining the subsequent tree growth in regions suffering from strong water stress (Wu et al., 2019). Earlier snow melting could advance spring phenology and extend the GS length. This results in increased exposure to spring freezing and stronger water stress in mid- and late-GS owing to seasonal biophysical feedbacks, which in turn limits tree growth (Hu et al., 2010; Kreyling, 2010). The legacy effects of preceding soil water availability are strongly dependent on the complex interplayed associations between rooting system and local topographical features (Míguez-Macho & Fan, 2021; Wu, Liu, et al., 2018). Difference in rooting systems, soil texture, and topography among different forest stands might partially explain the diverse sensitivity of tree growth to seasonal climate variability even in regions with similar background climate

conditions (Figure 3). More interestingly, forests in regions not even suffering strong water limitation (such as eastern North America) are still sensitive to PGS droughts (Figure 3).

The drought sensitivity of tree growth could also change after extreme climate events, and such change depends on phylogenetic controls (Anderegg, Trugman, Badgley, Konings, et al., 2020; Babst et al., 2013; Peltier et al., 2016), owing to potentially cumulative impacts on ecophysiological functioning. This change additionally depends on the ambient environmental conditions (Babst et al., 2013), which shape diverse adaptive strategies to climate variability. However, the degree to which the magnitude and duration of such legacy effects vary across different tree species and climate zones across the NH is still poorly understood.

Beyond climatic factors, our analyses reveal a significant legacy effect of preceding tree growth conditions (Figure 1). We further discovered that this legacy effect is strongly affected by seasonal extreme climate regimes, long-term climate conditions, and species-dependent functional traits. This effect is more prominent in cases when extreme drought events occurred in the GSs and when extreme wetness events occurred in either the PGS or GS (Figure 4). The observed legacy effects of preceding growth conditions may be partially attributed to the lifetime of functional organs and the storage of carbon reserves (Ogle et al., 2015; Peltier et al., 2016; Zweifel & Sterck, 2018). A process-based tree model confirmed that tree species with longer lifetimes of organs and reserves were normally characterized with longer and stronger legacy effects of preceding growth conditions and responded more strongly to historic climate conditions and buffered their growth responses to current conditions (Zweifel & Sterck, 2018). However, such legacy effects of preceding tree growth conditions seem to be overridden by seasonal water balance impacts, particularly the PGS water deficit, under the regime  $\tau^m$  for all climate zones except for arid regions (Figure 4).

Legacy effects of preceding climate and tree growth conditions may also be confounded by other factors such as stand disturbances, edaphic conditions (D'Orangeville et al., 2018), subsurface properties and stand heterogeneity (Preisler et al., 2019; Sugden, 2019), and species-specific traits (De Grandpre et al., 2019; Scharnweber et al., 2020) (Tables S4 and S5 in Supporting Information S1) (Figure 1). Detailed information for stand disturbance history, tree and stand traits (e.g., diameter, age, height, and density), and subsurface properties (e.g., water table depth, root zone water availability) for forest stands at hemispheric scale is lacking. The linear mixed effects model analyses elucidate that local site properties (represented by site elevation) and tree species exert significant effects on the bioclimatic sensitivity of tree growth (Table S4). Our analyses do not consider the long-term (e.g., longer than 1 year) legacy effects of hydroclimatic conditions on subsequent tree growth, although a few studies report that such legacy effects can usually last up to 2 years (Anderegg, Schwalm, et al., 2015; Isbell et al., 2015; Wu, Liu, et al., 2018). Other biochemical factors, such as CO<sub>2</sub> fertilization, mycorrhizal associations and/or anthropogenic nitrogen deposition (Ibanez et al., 2018), could also play important roles in regulating climate-growth sensitivity. Two species-specific physiological traits—rooting depth and  $P_{50}$ —are widely used to understand the drought vulnerability of tree growth. However, some studies revealed that mean species traits have marginal explanatory power for predicting broad-scale drought impacts on tree growth (D'Orangeville et al., 2018), given that plant traits vary greatly within the same species (Bose et al., 2020). Instead, large-scale studies generally report the dominant role of environmental factors which override species-specific traits in governing long-term variations in forest growth and climate-growth sensitivity (Anderegg, 2015; Bose et al., 2020; Gazol et al., 2017).

#### 4.2. Divergent Bioclimatic Sensitivity of Gymnosperms Versus Angiosperms

Our analyses further confirm our second hypothesis that angiosperms are more susceptible to PGS water deficit (Figure S3), while gymnosperms are more sensitive to legacy effects of the preceding 2 years of growth conditions, particularly in temperate dry region (Figures 1 and 5). These findings show that the sensitivity of tree growth to variations in seasonal climate and preceding tree growth conditions is functional-specific (DeSoto et al., 2020; Fei et al., 2017; Klockow et al., 2018; Zweifel & Sterck, 2018). Gymnosperms and angiosperms displayed divergent bioclimatic sensitivity, consistent with their contrasting trait syndromes and drought response strategies (Anderegg, Schwalm, et al., 2015; Anderegg, Trugman, Badgley, Konings, et al., 2020; Blackman et al., 2019; Carnicer et al., 2013; Choat et al., 2012; Hammond & Adams, 2019; Li et al., 2020). First, angiosperms normally have ring-porous or diffuse wood structure, allowing them to maintain relatively higher hydraulic conductivity than gymnosperms during droughts (Liesche et al., 2015; Vicente-Serrano et al., 2013; Vose et al., 2016), and are in turn characterized with high sensitivity to and low resistance to extreme drought (Figure S3 in Supporting Information S1) (DeSoto et al., 2020; Klockow et al., 2018). Second, the ring-porous species form new, large

earlywood vessels during the early part of the current GS. Third, angiosperms have narrower hydraulic safety margins, lower leaf capacitance, and higher minimum leaf conductance than gymnosperms, making them more vulnerable to xylem embolism under extreme droughts (Blackman et al., 2019; Choat et al., 2012; Hammond & Adams, 2019). These may partially explain why angiosperms are found in this study to be more vulnerable to PGS water deficit than gymnosperms in temperate dry regions (Figure 5, Figure S3 in Supporting Information S1). A recent study indicates that angiosperms are more vulnerable to variations in both atmospheric and soil water deficits than gymnosperms (Brodribb et al., 2020). However, the drought resistance and resilience for angiosperms show no marked temporal changes over the last century (Li et al., 2020), suggesting that a critical threshold of drought resistance for angiosperms has not been achieved despite the intensified drought in recent decades. Notably, the underrepresented angiosperm tree species than gymnosperms in the studied data set could add uncertainties to the conclusions regarding the bioclimatic sensitivity of angiosperms.

For gymnosperms, legacy effects of seasonal extreme drought might persist for a longer time than for angiosperms owing to a more conservative drought response strategy and longer organ lifetimes (Anderegg, Schwalm, et al., 2015; Blackman et al., 2019; DeSoto et al., 2020; Gazol et al., 2017; Zweifel & Sterck, 2018). The more conservative stomatal regulation and slower rate of desiccation in gymnosperms may partially explain why gymnosperms are more sensitive to legacy effects of previous growth conditions (Figure 5) (Au et al., 2020; Cailleret et al., 2017; Gazol et al., 2020; Zweifel & Sterck, 2018). The long-term memory effects of preceding tree growth in gymnosperms could also be associated with the longer lifetimes of functional organs and reserves (e.g., leaf, stem, and root), their internal carbon use economy and hydraulic functioning (DeSoto et al., 2020; Zweifel & Sterck, 2018). Previous studies showed that gymnosperms had low capacity to repair xylem embolism once it occurs under drought and they were more vulnerable to repeated drought events (Anderegg, Trugman, Badgley, Konings, et al., 2020; DeSoto et al., 2020).

Undoubtedly, large within-group and within-species variations in climate-growth sensitivity exist for both angiosperms and gymnosperms (D'Orangeville et al., 2018; Fei et al., 2017; Peltier et al., 2016), which may be attributed to different traits driven by differentiated climatic regimes, phenotypic plasticity, evolutionary history, and historical selection pressure. With projected dramatic changes in climate regime and potential forest demographics, more comprehensive understandings of the species-specific growth-bioclimatic relationship under shifting seasonal extreme climate regimes are urgently needed. Further understanding of the eco-physiological responses of tree growth to interactions between intensified drought and extremely high-temperature exposures is also needed (Wu, Guo, et al., 2018), which could provide valuable insights into potential tree species distribution shifts, forest health monitoring, and sustainable management.

## Data Availability Statement

The gridded monthly air temperature, precipitation, and potential evapotranspiration were obtained from the CRU TS 4.02 data set ([https://crudata.uea.ac.uk/cru/data/hrg/cru\\_ts\\_4.02/](https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/)). The gridded downward surface shortwave solar radiation data were obtained from CRU-NCEP data set (version 7) (<https://rda.ucar.edu/datasets/ds314.3/#!description>). The gridded monthly SPEI data were obtained from the SPEIbase V2.5 (<https://climate-dataguide.ucar.edu/climate-data/standardized-precipitation-evapotranspiration-index-spei>). The Köppen-Geiger climate map with a spatial resolution of 0.5° was obtained from <http://koeppen-geiger.vu-wien.ac.at/present.htm>.

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