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# Drought timing influences the legacy of tree growth recovery

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## Abstract

Whether and how the timing of extreme events affects the direction and magnitude of legacy effects on tree growth is poorly understood. In this study, we use a global database of Ring-Width Index (RWI) from 2,500 sites to examine the impact and legacy effects (the departure of observed RWI from expected RWI) of extreme drought events during 1948–2008, with a particular focus on the influence of drought timing. We assessed the recovery of stem radial growth in the years following severe drought events with separate groupings designed to characterize the timing of the drought. We found that legacies from extreme droughts during the dry season (DS droughts) lasted longer and had larger impacts in each of the 3 years post drought than those from extreme droughts during the wet season (WS droughts). At the global scale, the average integrated legacy from DS droughts (0.18) was about nine times that from WS droughts (0.02). Site-level comparisons also suggest stronger negative impacts or weaker positive impacts of DS droughts on tree growth than WS droughts. Our results, therefore, highlight that the timing of drought is a crucial factor determining drought impacts on tree recovery. Further increases in baseline aridity could therefore exacerbate the impact of punctuated droughts on terrestrial ecosystems.

## KEYWORDS

drought timing, extreme drought, forest growth, legacy effect, tree-ring width

## 1 | INTRODUCTION

Global climate models project an increase in the frequency and intensity of climatic extreme events as a result of anthropogenic climate change during this century (IPCC, 2013). At the global scale, drought is expected to have widespread effects on terrestrial carbon cycling (Frank et al., 2015; Wang et al., 2014; Zscheischler et al., 2014). Extreme drought events have been reported in most regions over the globe, such as the Amazonia (Lewis, Brando, Phillips, Heijden, & Nepstad, 2011; Samanta et al., 2010), Europe (Ciais et al., 2005; Ivits, Horion, Fensholt, & Cherlet, 2014; Leuzinger, Zotz, Asshoff, & Körner, 2005), North America (Breshears et al., 2005; Hogg, Brandt, & Michaelian, 2008; Michaelian, Hogg, Hall, & Arsenaault, 2011; Schwalm et al., 2012; Wolf et al., 2016), East Asia (Zhang et al., 2014), and Australia (van Dijk et al., 2013; Horridge, Madden, & Wittwer, 2005). Droughts could fundamentally alter the

composition, structure, and function of terrestrial ecosystems (Assal, Anderson, & Sibold, 2016; Bréda, Huc, Granier, & Dreyer, 2006; Breshears et al., 2005; Frank et al., 2015; Hogg et al., 2008; Ivits et al., 2014; Leuzinger et al., 2005; Lewis et al., 2011; Ma, Huete, Moran, Ponce-Campos, & Eamus, 2015; Ponce Campos et al., 2013, and are generally associated with declines in vegetation productivity due to water stresses on ecosystem metabolism (Eamus, Boulain, Cleverly, & Breshears, 2013; Huang et al., 2017; Ivits et al., 2014; Leuzinger et al., 2005; Schwalm et al., 2012).

Particularly, drought can have a 'legacy effect' on terrestrial ecosystems (Anderegg et al., 2015; Camarero, Franquesa, & Sangüesa-Barreda, 2015; Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015; Frank et al., 2015; Gutschick & Bassirad, 2003; Walter, Jentsch, Beierkuhnlein, & Kreyling, 2013), which is defined as the lag in recovery or incompleteness in recovery that leads to persistent effects on performance (Gutschick & Bassirad,

2003). From an ecological response perspective, legacy effects can include both changes in ecosystem states or process rates after the termination of a climate extreme (Camarero, Gazol, et al., 2015; Corcuera, Camarero, & Gilpelegrin, 2004; Gutschick & Bassirirad, 2003; Ogle et al., 2015; Virlouvet & Fromm, 2015), as well as an altered postextreme ecosystem response to environmental conditions (Hacke, Stiller, Sperry, Pittermann, Mcculloh, 2001; Larcher, 2003; Anderegg et al., 2013; Walter et al., 2013), and are often related to changes in species composition and their functional attributes (Diez et al., 2012; Kreyling, Jentsch, & Beierkuhnlein, 2011; Smith, 2011; Suarez & Kitzberger, 2008; Zeiter, Schärer, Zweifel, Newbery, & Stampfli, 2016). For example, Corcuera et al. (2004) found that a severe summer drought could affect the leaf and internode growth in *Quercus ilex* for 2 years post drought as a result of enhanced leaf senescence and reduced leaf production during the drought year. Anderegg et al. (2013) reported lags in aspen mortality/dieback after an experimental drought due to drought-induced increased vulnerability to cavitation in subsequent stresses (also known as 'cavitation fatigue'; Hacke et al., 2001). Such lag/incompleteness in recovery of plants after severe droughts can have a major influence on an ecosystem's vulnerability to subsequent drought events, particularly if the drought return frequency is shorter than the drought recovery time (Anderegg et al., 2015).

Discrete climatic extreme events can have a disproportionate impact on ecosystems relative to the temporal scale over which they occur due to the pronounced seasonal cycle of many ecosystems and land uses (Allard, Ourcival, Rambal, Joffre, & Rocheteau, 2008; Camarero, Franquesa, et al., 2015; Chaves & Oliveira, 2004; De Boeck, Dreesen, Janssens, & Nijs, 2011; Dietrich & Smith, 2016; Lei et al., 2016; Misson, Limousin, Rodriguez, & Letts, 2010; Misson et al., 2011; Unger et al., 2009). For example, dry soil conditions in spring may suppress canopy development and peak leaf area (Misson et al., 2011; Noormets et al., 2008). Drought in summer may affect plant carbon status by reducing carbon use efficiency (Ciais et al., 2005). A drought during fall may accelerate leaf fall, shorten the growing season (Liu et al., 2016), and thus decrease the seasonal cumulative ecosystem productivity. In recent years, there is growing evidence indicating that the mode, direction, as well as magnitude of the direct, concurrent impacts of droughts on terrestrial ecosystems may vary depending on the timing of drought events (Allard et al., 2008; Camarero, Franquesa, et al., 2015; Misson et al., 2010, 2011). For Mediterranean *Quercus ilex* ecosystems, spring droughts had a larger impact on leaf-level photosynthesis (Misson et al., 2010) as well as leaf and flowering phenology (Misson et al., 2011) than autumn droughts because of the increasing atmospheric demand and typical leaf development during springtime (Misson et al., 2010). Besides, spring droughts were found to dramatically reduce the annual carbon balance of *Quercus ilex* forests, while increased severity and/or duration of summer droughts did not appear to have the potential to negatively impact the average carbon budget of this ecosystem (Allard et al., 2008). A more recent study by Camarero, Franquesa, et al. (2015) also reported that drought impacts on primary growth and phenological asynchrony depend on drought timing

and its interaction with other climatic stressors. They observed that defoliation and radial growth decline of Holm Oak were more pronounced in 2012, which was characterized by a dry previous winter and very warm conditions from that season until summer, than in the 2005 drought when spring and early summer were dry and hot (Camarero, Franquesa, et al., 2015). These findings suggest that the expected magnitude of drought legacies on terrestrial ecosystem likely depends on the timing of drought events. Nevertheless, main knowledge gaps remain regarding whether and how legacy effects depend on the drought timing.

Forest ecosystems cover about one third of global land surface, and store nearly half of the carbon found in terrestrial ecosystem (Bonan, 2008). Drought can profoundly affect the functional, physiological, structural, and demographic properties of forest ecosystems (Assal et al., 2016). Forests are expected to exhibit the largest net effects of drought due to their large carbon pools and fluxes (Ahlström et al., 2015; Bonan, 2008), potentially large indirect and lagged impacts (Bréda et al., 2006; Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini, 2006; Frank et al., 2015; Kausrud et al., 2012; McDowell et al., 2011; Wendler, Conner, Moore, Shulski, & Stuefer, 2011), and long recovery time to regain previous stocks (Anderegg et al., 2015). At the same time, forests influence climate through complex biophysical and biochemical processes which affect planetary energy balance, the hydrological cycle, and atmospheric composition (Bonan, 2008). Therefore, the response of forest ecosystems to drought stresses has a significant impact on regional and global climate patterns and biogeochemical cycles.

In this study, we examined whether and how legacy effects on tree growth after drought differs according to drought timing using tree-ring width chronologies across the globe. Here tree-ring width was chosen as a proxy for tree growth because it is closely correlated with net primary productivity (Clark et al., 2001). We asked: (a) Do drought legacy effects on tree growth vary among drought events with different timing? (b) If so, how does drought timing affect the direction and the magnitude of drought legacies in tree growth? Addressing these questions will help improve current understanding of timing effects of severe drought on tree growth, and is of great importance to improving projecting impacts of extreme drought events on forest ecosystems under future climate change.

## 2 | MATERIALS AND METHODS

### 2.1 | Chronologies of Ring-Width Index

Tree-level tree-ring chronologies were downloaded from the International Tree Ring Data Bank (ITRDB, <https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>) at the National Oceanic and Atmospheric Administration (NOAA) Paleoclimatology Program and World Data Center for Paleoclimatology. Only chronologies meeting the following criteria were selected prior to further analyses: (a) chronologies measuring total ring-width, (b) chronologies containing at least 25 years during 1948–2008. To remove low-frequency ring-width fluctuations related to increasing

tree size and age, or to stand dynamics, the raw ring-width measurements were first converted to a standardized Ring-Width Index (RWI) (Anderegg et al., 2015; Cook & Kairiukstis, 2013). This was accomplished by dividing each measured ring-width by its expected value (Cook & Kairiukstis, 2013), which is estimated based on the 'cubic smoothing spline' approach with a frequency response cutoff at 0.50 and a wavelength of 30 years to enhance the climatic signal in tree growth (Bunn, 2008). Then tree-level RWI series from a site were averaged to form a single RWI series for each species and site (Cook & Kairiukstis, 2013). In addition, since annual tree-ring growth is generally affected by previous-year conditions (Cook & Kairiukstis, 2013), we also built prewhitened chronologies where autocorrelation was removed from each series before averaging. The prewhitening was performed by fitting an autoregressive model to the time series, where the adequate model complexity is selected using Akaike's information criterion (Venables & Ripley, 2013). All the processes of standardization, prewhitening and averaging were performed using the dendrochronology program library in R (dplR; Bunn, 2008). The final sample size of site-level chronologies of standardized RWI is 2,500 in this study, with 33 located in tropics (23°S–23°N), 1,815 in temperate regions (50°S–23°S, 23°N–50°N) and 652 in boreal regions (north of 50°N).

## 2.2 | Climate dataset and drought metrics

To detect drought events for each RWI site, we first calculated Climatic Water Deficit (CWD) (Stephenson, 1998) metrics from two gridded precipitation datasets and two gridded potential evapotranspiration (PET) datasets. The two precipitation datasets include: (a) Monthly precipitation datasets from Climatic Research Unit (CRU) TS 3.23 (PRE<sub>CRU</sub>) for the period 1901–2014 (Harris, Jones, Osborn, & Lister, 2014); (b) Monthly precipitation datasets from Global Precipitation Climatology Centre (GPCC) (PRE<sub>GPCC</sub>) for the period 1901–2013 (<https://www.dwd.de/EN/ourservices/gpcc/gpcc.html>). The two PET datasets include: (a) Monthly PET datasets from Climatic Research Unit (CRU) TS 3.23 (PET<sub>CRU</sub>) for the period of 1901–2014 (Harris et al., 2014); (b) Monthly PET datasets from Terrestrial Hydrology Research Group of Princeton University (PET<sub>Prin</sub>) for the period of 1948–2008 (Sheffield, Goteti, & Wood, 2006; Sheffield, Wood, & Roderick, 2012). PRE<sub>CRU</sub>, PRE<sub>GPCC</sub>, and PET<sub>CRU</sub> datasets have a spatial resolution of 0.5°×0.5°, while PET<sub>Prin</sub> has a spatial resolution of 1°×1°. Monthly CWD values were calculated as monthly precipitation minus monthly PET during over the entire period of overlap for all datasets (i.e., 1948–2008), and then aggregated over the course of each year to obtain annual CWD values. Given the different spatial resolution of PET<sub>Prin</sub> dataset compared to PET<sub>CRU</sub>, for each pixel of the latter, we simply extracted time series of PET data from the former accordingly.

We next extracted and averaged CWD values within a 3 × 3 pixel window around each RWI site from each gridded CWD map, obtained the detrended anomalies of CWD series, and calculated the partial correlation coefficient between the detrended anomalies of CWD series and RWI series with mean annual temperature and insolation (i.e., the sum of incoming short-wave solar radiation)

controlled for each site. The mean annual temperature was derived from monthly temperature data from Climatic Research Unit (CRU) TS 3.23 dataset during 1901–2014 with a spatial resolution of 0.5°×0.5°. The annual insolation sum was obtained from the CRU-NCEP version 5 datasets during 1901–2012 with a spatial resolution of 0.5°×0.5°. Considering the aim of this study is to quantify the memory effect of extreme drought events, we particularly displayed the results based on sites where RWI exhibited significantly ( $p < 0.05$ ) positive correlations with CWD anomalies ( $n = 392$ ; Supporting Information Figure S1) in addition to the results with all sites taken into consideration. Note that due to the intercorrelation between PET and temperature, we also conducted a supplementary partial correlation analysis in which CWD were replaced with annual total precipitation (Supporting Information Figure S2). Consistent result was observed with that derived from the analysis with CWD.

## 2.3 | Drought legacy on tree growth

We defined an 'extreme drought event' as the year with detrended anomaly of drought metric exceeding two standard deviations (2-SD dry anomaly). Based on partial autocorrelation function (PACF) coefficients, which is the simplest way to measure legacy effect (Scheffer et al., 2009), more than 60% of RWI sites show drought legacies for up to 3 years post drought (Supporting Information Figure S3a). For sites with significantly positive RWI-CWD relationships, drought legacies for at least 3 years were also observed for about 66% of these sites (Supporting Information Figure S3b). Therefore, legacy effects of droughts on tree growth were calculated as the difference between the observed postdrought growth and the predicted post-drought growth after an extreme drought event (Anderegg et al., 2015) over the following 3 years. Here the observed growth was determined by the detrended-only RWI chronologies, and the predicted growth was determined by the prewhitened chronologies derived using `DPLR` package (Anderegg et al., 2015). For each site and each extreme drought year, we calculated the integrated legacy effect of extreme droughts on tree growth as the sum of drought legacy of the 3 years post each extreme drought year. Note that only single drought events (no consecutive drought within 3 years post an extreme drought event) lasting no more than 1 year were considered in this study.

## 2.4 | Effects of drought timing on drought legacy

To explore the relationship between drought timing and drought legacies on tree growth, we divided all extreme drought events into three groups according to whether each drought event was classified as occurring during the dry or wet season. Three separate categories were included: (a) extreme drought years where drought occurs in both the dry and wet seasons (DS+WS droughts), (b) extreme drought years with drought only in the dry season (DS droughts), and (c) extreme drought years with drought only in the wet season (WS droughts). To this end, for each drought metric, we first calculated the annual series of mean CWD during wet season and dry

season, respectively. For each year, dry/wet season is defined based on method adapted from Li and Fu (2004): the dry season arrival is determined by the first month when the monthly CWD values change from above to below the annual mean CWD, and vice versa for the wet season arrival. Then an extreme drought year is determined to occur if the detrended anomaly of mean CWD during dry season and/or during wet season exceeds one standard deviation (1-SD dry anomaly). To test the universality of this approach of dry/wet season detection, two pixels were selected from East Asia (31°N, 116°E) and Amazonia (7°S, 62°W), respectively. As shown in Supporting Information Figure S4, the arrival of dry/wet season were successfully and correctly captured using this approach, adding to support for the method from previous studies (East Asia: Xu, Du, Tang, & Wang, 2011; Zeng et al., 2014; Amazonia: Marengo, Liebmann, Kousky, Filizola, & Wainer, 2001; Li & Fu, 2004; Zeng et al., 2014).

For each of three types of extreme drought years, integrated drought legacies of 3 years post drought were averaged across all extreme drought events at the RWI sites. Particularly, we compared drought legacies under different drought timing for two main families represented in the dataset, i.e., Pinaceae (gymnosperms) and Fagaceae (angiosperm). These two families account for about 90% of chronologies analyzed in this study. Analysis of variance (ANOVA) was conducted to determine whether there is a statistically significant ( $p < 0.05$ ) difference regarding drought legacy between different drought types. To avoid the spatial variation of drought legacies biasing the linkage between legacy effects and drought timing, we further compared drought legacies between drought years with different drought timing for each of the RWI sites which have experienced at least two of the three drought types during the study period. In this case, the sample size of RWI sites with both DS+WS droughts and DS droughts, with both DS+WS droughts and WS droughts, and with both DS droughts and WS droughts is 31, 24, and 5, respectively. Considering the limited sample size, Wilcoxon signed-rank test was performed to determine whether drought legacies are significantly different between droughts with different timing.

To test if tree legacy effects were driven by drought severity (e.g., intensity, duration, etc.), we explored the relationship between tree legacy effects with drought intensity and duration, respectively. Here, drought intensity was indicated by the magnitude of SD of detrended CWD anomalies for each extreme drought event, and drought duration was determined by the number of months with negative CWD anomalies over the course of each extreme drought year.

### 3 | RESULTS

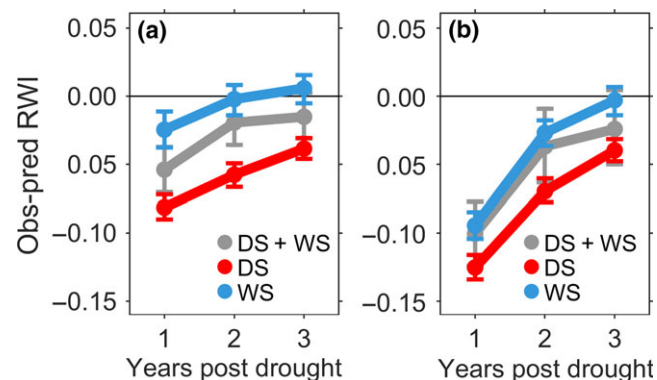
#### 3.1 | Legacy effects for 3 years post extreme drought events

Significant negative legacies in radial growth after extreme drought events, i.e., decrease in observed versus predicted growth after severe droughts, were found for DS+WS, DS, and WS droughts.

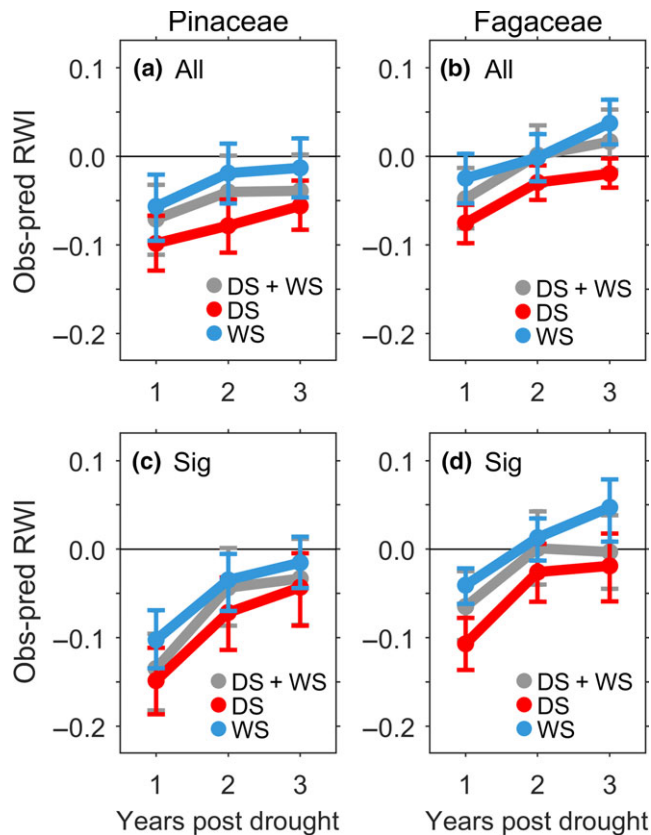
Pronounced differences were evident regarding both the duration and magnitude of drought legacies due to different drought timing (Figure 1). Legacy effects on tree growth lasted for more than 3 years for both DS+WS and DS droughts, while legacy effects disappeared in the second year when considering all RWI chronologies together (Figure 1a) or in the third year when considering only sites with significantly positive RWI–CWD relationship (Figure 1b). In terms of the magnitude of drought legacy, for each year post drought, DS droughts consistently show the largest legacy effects on forests, followed by DS+WS droughts, and then WS droughts (Figure 1). In the first year after drought, the legacy effects of DS droughts (a decrease in observed vs. predicted tree growth by 0.081) were ~1.5 times more pronounced to those of DS+WS droughts (0.054) and ~3.3 times to those of WS droughts (0.025) when all sites were taken into consideration (Figure 1a). For sites with significantly positive RWI–CWD relationships, extreme drought events with WS exhibited legacy effects with similar magnitude to those with WS + DS in the year 1 (0.10), but both showed smaller legacies than DS droughts (0.013) (Figure 1b). For the two main families (Pinaceae and Fagaceae) represented in the tree-ring dataset, a stronger and longer negative impacts of DS droughts on tree growth post drought compared to WS droughts were consistently observed for both families, even though the former displayed generally larger legacy effects (in terms of magnitude and duration) than the latter (Figure 2).

#### 3.2 | Integrated legacy for extreme drought events with different timing

DS droughts had a significantly ( $p < 0.05$ ) larger integrated legacies (the sum of drought legacies over 3 years post drought) on forest



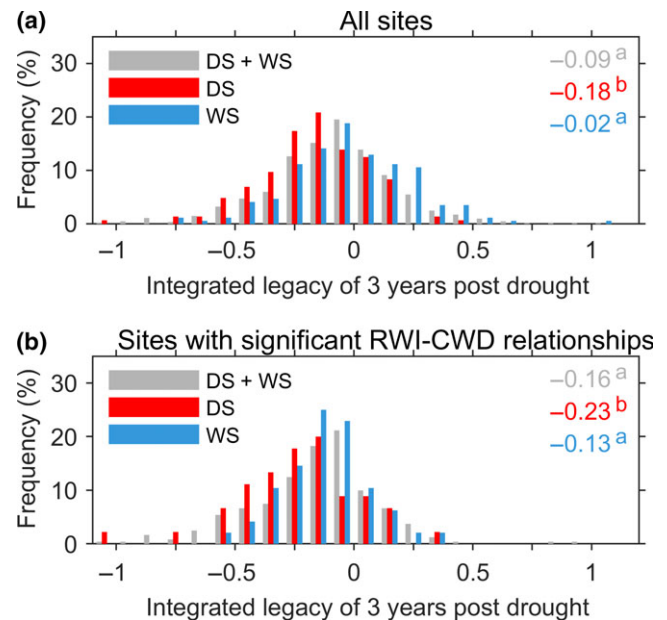
**FIGURE 1** Drought legacy during 1–3 years post an extreme drought year for droughts induced by both droughty dry and wet season (DS+WS drought), droughts induced by droughty dry season (DS drought), and droughts induced by droughty wet season (WS drought): (a) mean drought legacy across 2,500 tree-ring chronologies, (b) mean drought legacy across 392 tree-ring chronologies at sites that with significantly ( $p < 0.05$ ) correlations between Ring-Width Index (RWI) and climatic water deficit (CWD). The error bars represent the confidence interval from 1,000 bootstrap estimates



**FIGURE 2** Drought legacy during 1–3 years post an extreme drought year for droughts induced by both droughty dry and wet season (DS+WS drought), droughts induced by droughty dry season (DS drought), and droughts induced by droughty wet season (WS drought). Drought legacy was calculated across both the whole 2,500 tree-ring chronologies that support either of the two main families represented, Pinaceae and Fagaceae (a, b), and the 392 tree-ring chronologies at sites that with significantly ( $p < 0.05$ ) correlations between Ring-Width Index (RWI) and climatic water deficit (CWD) for these two families (c, d). The error bars represent the confidence interval from 1,000 bootstrap estimates

ecosystems than either DS+WS droughts or WS droughts (Figure 3a). On average, the integrated legacy from DS droughts (0.18) was about twice the magnitude of integrated legacy from DS+WS droughts (0.09), and was about nine times the magnitude of that from WS droughts (0.02). There seems no statistically significant difference when comparing integrated legacy between DS + WS droughts and WS droughts. Similar results were observed when only sites with significantly positive RWI–CWD relationships were taken into consideration (Figure 3b), but with an overall stronger legacy effect, as well as when RWI chronologies for either Pinaceae or Fagaceae were selected for the comparison of drought legacy with different timing (Table 1).

We next mapped the spatial pattern of integrated legacies over 3 years post drought for DS+WS droughts, DS droughts, and WS droughts, respectively (Figure 4a–c; Supporting Information Figure S5). Among the three groups, DS droughts exhibited the largest percentage of RWI chronologies with negative integrated legacies



**FIGURE 3** Frequency distribution of integrated legacies of 3 years post an extreme drought year for droughts induced by both droughty dry and wet season (DS + WS drought), droughts induced by droughty dry season (DS drought), and droughts induced by droughty wet season (WS drought): (a) mean drought legacy across 2,500 tree-ring chronologies, (b) mean drought legacy across 392 tree-ring chronologies at sites that with significantly ( $p < 0.05$ ) correlations between Ring-Width Index (RWI) and climatic water deficit (CWD). The numbers on the right side in each panel refer to the mean value of integrated legacy for DS+WS, DS, and WS droughts, respectively. Different letters indicate statistically significant differences among drought timing at  $p < 0.05$

**TABLE 1** Comparison of the integrated legacies of 3 years post an extreme drought year for droughts induced by both droughty dry and wet season (DS + WS drought), droughts induced by droughty dry season (DS drought), and droughts induced by droughty wet season (WS drought) for the two main families represented, Pinaceae and Fagaceae. The uncertainties were estimated from 1,000 bootstrap estimates. Different letters indicate statistically significant differences among drought timing at  $p < 0.05$

		DS + WS	DS	WS
All <sup>1</sup>	Pinaceae	$-0.17 \pm 0.06^a$	$-0.25 \pm 0.05^b$	$-0.09 \pm 0.05^c$
	Fagaceae	$-0.03 \pm 0.05^a$	$-0.15 \pm 0.03^b$	$-0.02 \pm 0.01^a$
Sig <sup>2</sup>	Pinaceae	$-0.21 \pm 0.12^{ab}$	$-0.28 \pm 0.10^a$	$-0.15 \pm 0.01^b$
	Fagaceae	$-0.07 \pm 0.08^a$	$-0.18 \pm 0.06^b$	$0.03 \pm 0.01^c$

<sup>1</sup>All the 2,500 tree-ring chronologies. <sup>2</sup>The 392 tree-ring chronologies at sites that with significantly ( $p < 0.05$ ) correlations between Ring-Width Index (RWI) and climatic water deficit (CWD).

(0.77; Figure 4b). The most pronounced legacy effects (a reduction in observed tree growth compared to predicted growth larger than 0.4) appeared mainly in central Canada, northern and middle United States, and sparsely in northern Europe as well as central and east Asia (Figure 4b). In comparison, for droughts with only dry WS, only half RWI chronologies showed negative legacy effects, among which

10% had a magnitude less than 0.3 (Figure 4c). Relatively stronger legacy effects ( $>0.4$ ) were only sparsely located in parts of western United States, southern Europe, and south Asia (Figure 4c).

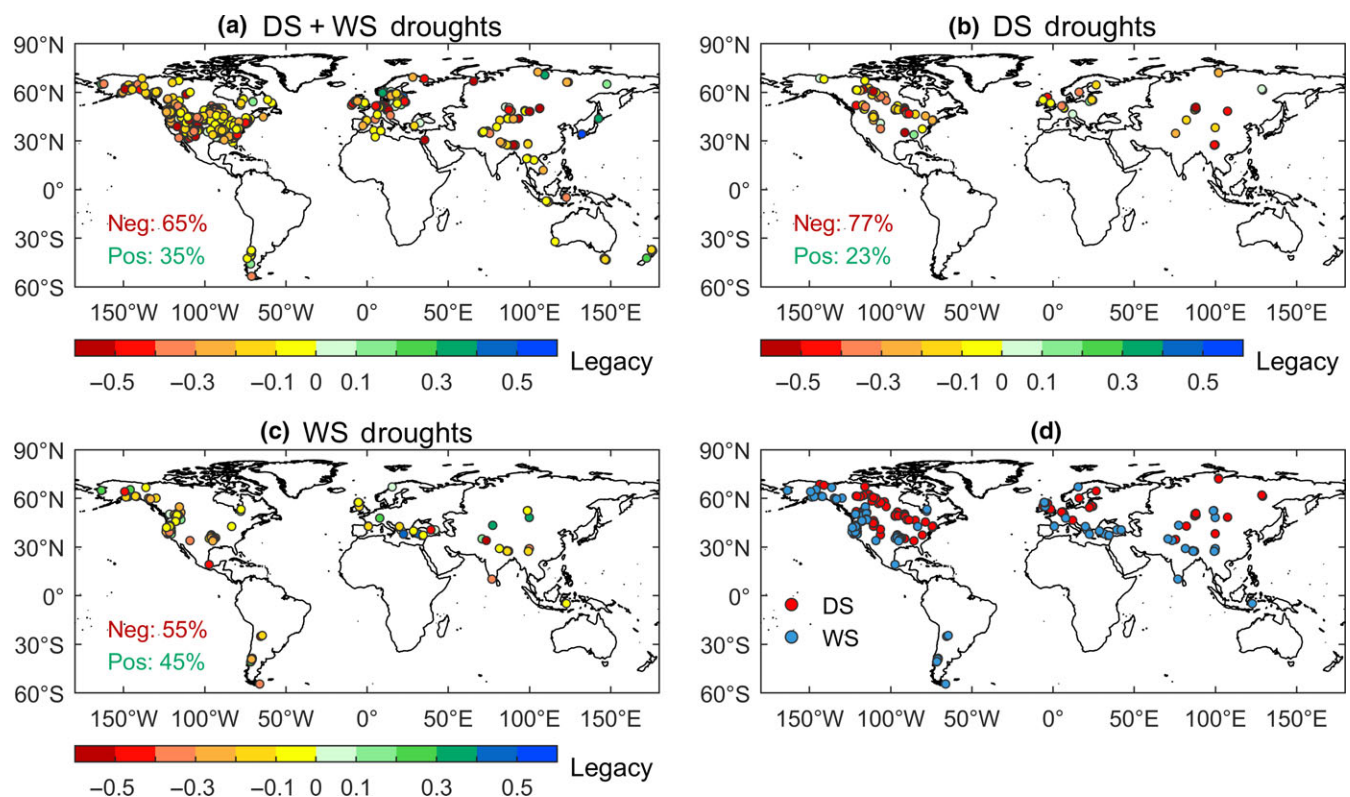
Particularly, we found that extreme drought events with only dry DS mainly appeared in central and eastern Canada, middle and eastern United States and northern Europe, while extreme drought events with only dry WS were concentrated in western Canada, western United States, and southern Europe (Figures 4d and Supporting Information Figure S5). We further mapped the distribution of RWI sites for two drought classifications (DS droughts and WS droughts) for different periods of the study period, i.e., 1948–1959, 1960–1969, 1970–1979, 1980–1989, 1990–1999, and 2000–2008, respectively. The results showed that such spatial patterns of drought timing were generally preserved in each of the period (Supporting Information Figures S6 and S7).

### 3.3 | Site-specific comparison between legacy effects from droughts with different timing

Based on Wilcoxon signed-rank test, integrated legacies from DS+WS droughts were significantly ( $p < 0.05$ ) larger than those from WS droughts (Table 2), with 60% sites showing legacy effects when experiencing the former than the latter (Figure 5b). Although there did not appear a statistically significant ( $p < 0.1$ ) difference between integrated legacies between DS and WS droughts (Table 2), larger

impacts of DS droughts than WS droughts were observed in four out of the five sites experiencing both DS and WS droughts during the study period except for one site in western Canada (Figure 5c). Thus, we next extracted the five RWI chronologies with both DS droughts and WS droughts during the study period, and compared the legacy effects between different drought events for each site as case study (Figure 6).

Among these five RWI sites, three of these RWI sites are located in western Europe ( $56^{\circ}\text{N}$ ,  $3^{\circ}\text{W}$ ), and the rest sites are located in western Canada ( $49^{\circ}\text{N}$ ,  $118^{\circ}\text{W}$ ). For the three European sites, in each year post drought, DS droughts generally had stronger negative impacts (Figure 6b,c) or weaker positive impacts (Figure 6c) on tree growth post drought compared to WS droughts. The negative legacy effects also lasted for a longer period after DS drought than after WS drought (Figure 6b,c). Therefore, the average difference between integrated legacy from DS and WS droughts were 0.20 across the three sites (0.10, 0.23, and 0.26, respectively) (Figure 6a–c). For one of the two RWI chronologies in western Canada, DS drought displayed negative legacy effects except in the third year post drought, while WS drought consistently showed positive legacy effect in each of the 3 years post drought (Figure 6d). Integrated over 3 years post drought, a slightly negative legacy effect (a reduction of 0.01 in observed vs. predicted growth post drought) was found for the extreme drought year with dry DS, while a positive integrated legacy effect (0.27) were observed for the one with dry WS (Figure 6d). By



**FIGURE 4** Spatial patterns of integrated legacies of 3 years post an extreme drought year for (a) droughts induced by both droughty dry and wet season (DS + WS drought), (b) droughts induced by droughty dry season (DS drought), and (c) droughts induced by droughty wet season (WS drought) for 2,500 tree-ring chronologies. The percentage of positive and negative integrated legacies is shown in the left bottom for panel (a)–(c). Panel (d) refer to the spatial pattern of sites experiencing DS droughts and WS droughts during the study period

**TABLE 2** Site-level comparison of integrated legacies post droughts among different drought timing based on Wilcoxon signed-rank test

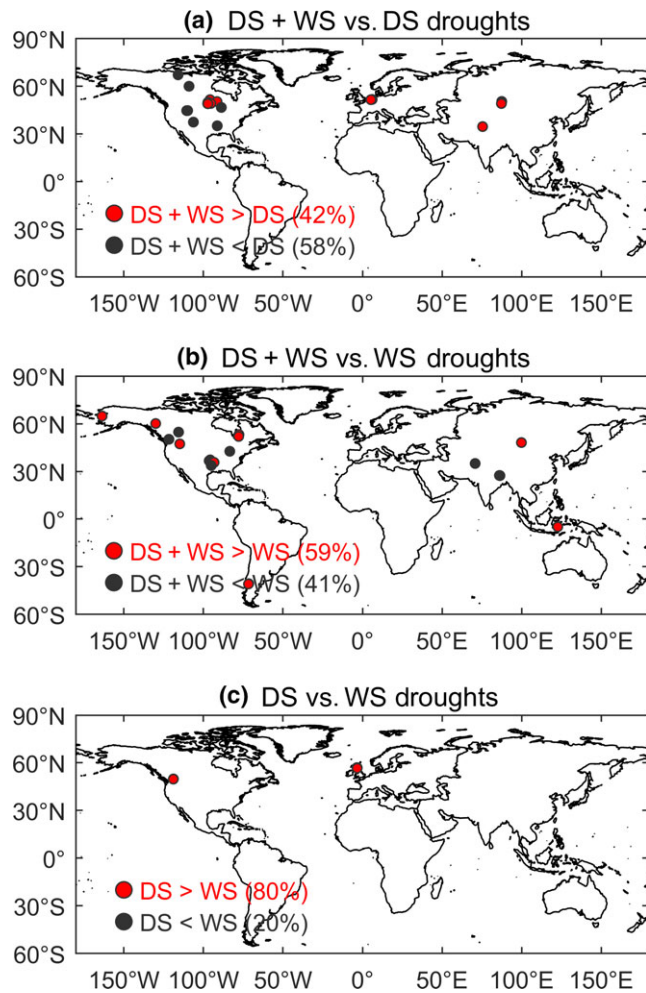
	DS + WS <sup>a</sup>	DS <sup>b</sup>	WS <sup>c</sup>
DS + WS		NS <sup>d</sup>	Legacy <sub>DS + WS</sub> < Legacy <sub>WS</sub> <sup>d</sup>
DS	31		NS
WS	24	5	

<sup>a</sup>Droughts induced by both droughty dry season and droughty wet season.

<sup>b</sup>Droughts induced by droughty dry season.

<sup>c</sup>Droughts induced by droughty wet season.

<sup>d</sup>Indicates statistically significant at the 95% ( $p < 0.05$ ) level, and NS indicates statistical insignificance.



**FIGURE 5** Site-level comparison of drought legacies between droughts with different timing: (a) droughts induced by both droughty dry and wet season (DS + WS drought) vs. droughts induced by droughty dry season (DS drought), (b) DS + WS droughts vs. droughts induced by droughty wet season (WS drought), (c) DS droughts vs. WS droughts

contrast, the other site in western Canada exhibited exactly the opposite results. WS drought at this site led to a decrease of 0.45 in real tree growth compared with predicted growth, while DS drought resulted in a positive legacy effect with the magnitude of 0.12 (Figure 6e).

## 4 | DISCUSSION

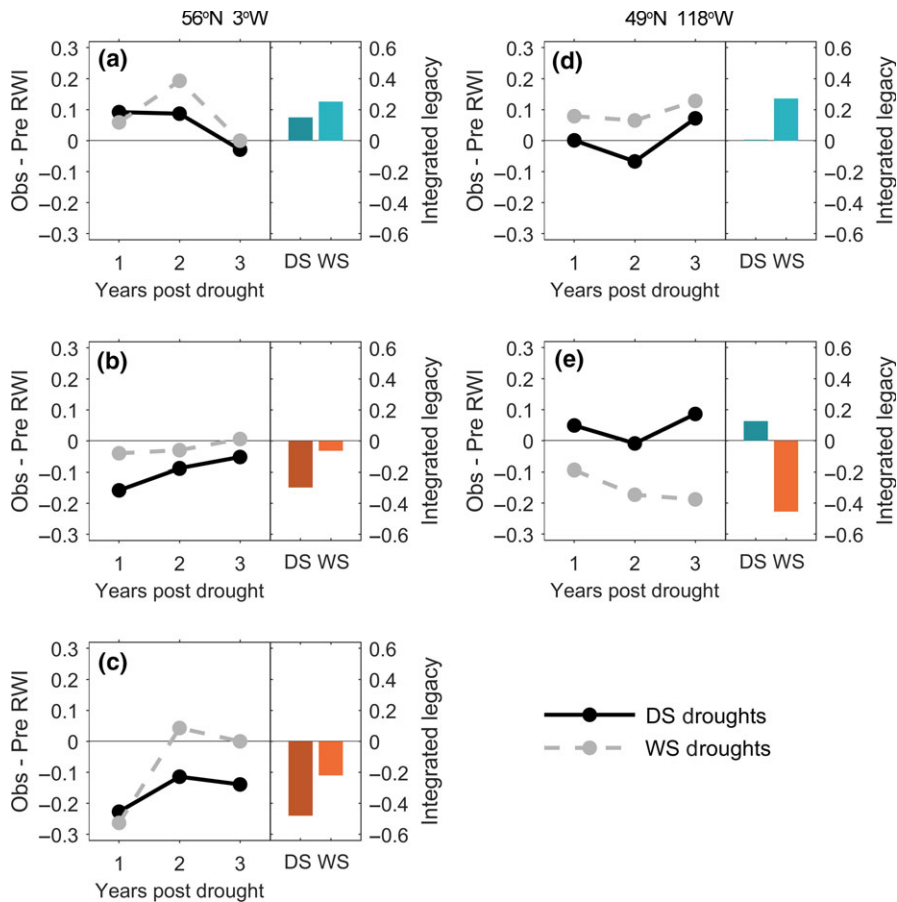
To distinguish drought legacy effects on tree growth by extreme drought events with different timing, we observed significantly larger legacies from extreme droughts with dry DS than those with only dry WS based on comparisons at both global (Figure 3) and local scales (Figure 6). Four of the five sites experiencing both DS and WS droughts during the study period display stronger negative impacts or weaker positive impacts of DS droughts on tree growth post drought compared to WS droughts (Figure 6). Although extreme droughts with different timing may differ in drought intensity and duration, we did not find a strong linkage either between the magnitude of drought legacy effect and drought intensity ( $p > 0.1$ ) or between the magnitude of drought legacy effect and drought duration ( $p > 0.1$ ). Our result suggests that the timing of drought is a crucial factor determining tree recovery after drought that extreme DS droughts show more pronounced negative impacts on tree recovery than WS droughts. As shown in Supporting Information Figure S8, for the five sites we selected for the case study, the period of dry season (from April to September) was generally overlapped with the growing season of the forests in corresponding regions (from May to October). In addition, the dry season overlapped with the growing season of the local vegetation for at least 60% of the length of dry season in over 80% of the RWI sites in our analyses. Therefore, we presume that such distinctions in legacy effects may result from the fact that an extreme drought event can affect plant physiological recovery from drought via different environmental-biological processes according to its timing.

### 4.1 | Legacy effects of extreme drought events through plant processes

Plants respond to drought stress by a series of structural or physiological adjustments (Bréda et al., 2006; Frank et al., 2015; Lambers, Chapin, & Pons, 2008; Larcher, 2003), which potentially have lagged impacts on tree growth in the years following the year of an extreme drought (Frank et al., 2015). Drought-induced reductions in photosynthesis (Bréda et al., 2006; Ciais et al., 2005; Leuzinger et al., 2005; Schwalm et al., 2012) and changes in photosynthate allocation (Aaltonen, Lindén, Heinonsalo, Biasi, & Pumpanen, 2017) after the drought period are both possible reasons explaining the decreased tree-ring width during years following severe droughts (see also Figure 7).

First, drought directly decreases CO<sub>2</sub> assimilation rates (process I in Figure 7) by reducing the CO<sub>2</sub> supply to Rubisco due to stomata closure (Bréda et al., 2006; Chaves, Flexas, & Pinheiro, 2009; Chaves & Oliveira, 2004; Konings & Gentine, 2017; Misson et al., 2010; Reddy, Chaitanya, & Vivekanandan, 2004), by suppressing mesophyll conductance to CO<sub>2</sub> diffusion (Chaves et al., 2009; Flexas, Bota, Loreto, Cornic, & Sharkey, 2004; Flexas et al., 2007; Grassi & Magnani, 2005; Keenan, Sabate, & Gracia, 2010; Misson et al., 2010; Reddy et al., 2004), and/or by decreasing the activity and concentrations of photosynthetic enzymes (Chaves & Oliveira, 2004; Chaves et al.,

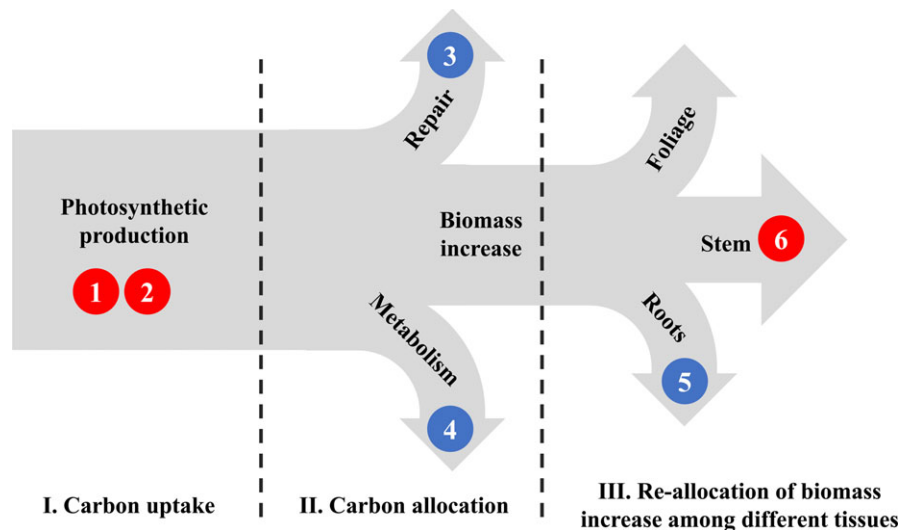




**FIGURE 6** Site-level comparison of drought legacy effects over 3 years post drought for RWI chronologies at sites experiencing both droughts induced by droughty dry season (DS drought) and those induced by droughty wet season (WS drought) during the study period. Three RWI chronologies are from the site in western Europe (56°N, 3°W), and two RWI chronologies are from the site in western Canada (49°N, 118°W). In each panel, blue bars indicate positive legacies post drought, while orange bars indicate negative legacies post drought

2009; Flexas et al., 2006; Lawlor & Cornic, 2002; Misson et al., 2010; Reddy et al., 2004). For example, based on gas exchange measurements on ash and oak trees in sub-Mediterranean ecosystems, Grassi and Magnani (2005) found a much more pronounced summer decline of light-saturated net photosynthesis (60%–75%) during a severe water stress of year 2003 compared to that of normal year (15%–20%) for these forests as a result of the combination of stomatal, mesophyll conductance, and biochemical limitations during severe drought. In addition to limitations in regard to photosynthetic rates, drought-induced leaf shedding (Achten et al., 2010) could damage photosynthetically active leaf area in the canopy (Bréda et al., 2006; Galvez, Landhäuser, & Tyree, 2011; Keith, Van, Jacobsen, & Cleugh, 2012; Magnani, Mencuccini, & Grace, 2000). In a greenhouse study, Galvez et al. (2011) found that the total leaf area in *Populus tremuloides* Michx. seedlings growing under a severe 3-month drought treatment decreased by 52.7% over the whole experiment (12 weeks), while that in the control group increased threefold during the length of experiment. Such a decline in leaf area could eventually affect the amount of assimilate produced during the drought year. Therefore, the amount of photosynthetic production is largely reduced for the drought year (Bréda et al., 2006; Ciais et al., 2005; Galvez et al., 2011; Hommel et al., 2016; Keith et al., 2012; Schwalm et al., 2012). As a consequence, tree-ring width is expected to be reduced during several years following a severe drought (Bréda et al., 2006; Keith et al., 2012; Palacio, Hoch, Sala, Körner, & Millard, 2014).

In the meantime, tree growing under drought conditions must allocate existing stored reserves among the demands for repair, tissue maintenance, growth, and defense (Bréda et al., 2006; Galvez et al., 2011; McDowell et al., 2011; Sala, Woodruff, & Meinzer, 2012; Palacio et al., 2014; process II in Figure 7). In this case, any additional demand on already limited reserves may delay the recovery of growth (Bréda et al., 2006; Galvez et al., 2011). On one hand, for example, drought-induced damage on physiological disorders have to be required before normal processes can resume (Bréda et al., 2006). On the other hand, during drought, plants have to maintain an efficient water transfer from soil to leaves (Sperry, Hacke, Oren, & Comstock, 2002; Mencuccini, 2003; Bréda et al., 2006; Sala et al., 2012) with the purpose to keep leaf water potential above cavitation thresholds (Bréda et al., 2006; Sperry et al., 2002). This process requires a large amount metabolic energy, since tree transpiration is largely reduced during drought (Lambers et al., 2008). Tree-level studies have found that the sum of soluble sugars and starch in root tissues was 73.7% higher in aspen seedlings growing under drought conditions than that in the control group (Galvez et al., 2011). This suggests that plants experiencing droughts tend to increase the allocation of assimilated carbon to nonstructural carbohydrate reserves in the root system, which can be potentially used for osmoregulation and osmoprotection during severe water stress and are likely used for additional growth in the nonstressed seedlings (Galvez et al., 2011; Hommel et al., 2016).



**FIGURE 7** Conceptual diagram of the legacy effects of extreme drought events on radial growth recovery through plant processes. Numbers shading in blue (red) refer to the positive (negative) effects of an extreme drought event on a certain aspect of plant processes. Effect #1: reducing CO<sub>2</sub> assimilation rates (e.g., Grassi & Magnani, 2005); Effect #2: damaging photosynthesis active leaf area through drought-induced leaf shedding (e.g., Galvez et al., 2011); Effect #3: increasing carbon demand for repairing drought-induced damage on physiological disorders (e.g., Bréda et al., 2006); Effect #4: increasing carbon demand to maintain an efficient water transfer from soil to leaves (e.g., Sala et al., 2012); Effect #5: increasing below-ground biomass allocation to improve water foraging capacity in deep soil layers (e.g., Aaltonen et al., 2017); Effect #6: reducing sapwood section due to enhanced duraminization in the sapwood to heartwood transition zone (e.g., Bréda et al., 2006)

Furthermore, in order to reduce the vulnerability to severe water deficit, plants have to re-allocate the limited carbohydrate used for biomass increase among different tissues of tree individuals (e.g., the photosynthetic tissue, foliage; the water-conducting tissue, stems; as well as the water-absorbing tissue, roots) (DeLucia, Maherali, & Carey, 2010; Mencuccini, 2003; Bréda et al., 2006; process III in Figure 7). Although drought can decrease fine root biomass due to decreased root elongation, and increased root cavitation and mortality in the short term (Jackson, Sperry, & Dawson, 2000; Joslin, Wolfe, & Hanson, 2000), several researches have consistently suggest that in the long-term, tree species growing under drier conditions tend to increase below-ground biomass allocation to improve water foraging capacity in deep soil layers (Aaltonen et al., 2017; Achten et al., 2010; Markesteijn & Poorter, 2009; Schlesinger et al., 2016). For example, Aaltonen et al. (2017) compared the carbon allocation in Scots pine seedlings with and without drought treatments, and found that the fine root-to-shoot ratio in the drought treatment was 36% higher than that in the control, which suggests more carbon allocation to root biomass than to the aboveground biomass by drought-treated seedlings. Simultaneously, severe droughts are suggested to result in a reduction of sapwood section due to enhanced duraminization in the sapwood to heartwood transition zone (Bréda et al., 2006). Overall, the combination of drought-induced reduction of assimilated carbon allotted to growth and changes in the allocation strategy of plants jointly causes the decreased tree-ring width following extreme drought events.

In summary, an extreme drought could negatively affect radial growth after droughts through its impacts on different stages of vegetation growth. Drought could (a) directly reduce the amount of assimilate produced during the drought year (Effect #1 and #2

during process I); (b) indirectly lead to a decline of carbon allocation to growth recovery after drought through increasing the allocation to tissue repair and metabolism (Effect #3 and #4 during process II); and (iii) have a negative influence on the re-allocation of biomass increase to postdrought radial growth both directly (reducing sapwood section, Effect #6 during process III) and indirectly (increasing root biomass, Effect #5 during process III).

#### 4.2 | Legacy effects of extreme drought events through soil processes

Water retention has been suggested to decrease after drought as a result of drought-induced changes to soil structure and soil hydrophobicity which promote preferential flow during the drought recovery period (Bloor & Bardgett, 2012). Based on a drying-rewetting experiment using soil columns from Norway spruce forest, Muhr, Franke, and Borken (2010) found that rewetting could not restore soil moisture of the dry soil to the level of the control group (under continuously moist conditions), presumably because of preferential flow and water repellency of soil organic matter post drought. In addition to the direct impacts via reduced soil water content (Bloor & Bardgett, 2012; Manzoni, Vico, Porporato, & Katul, 2013; Moyano, Manzoni, & Chenu, 2013; Muhr et al., 2010), droughts can affect tree growth following drought via changes in the nutrient availability of the rhizosphere after severe droughts (Fuchslueger, Bahn, Fritz, Hasibeder, & Richter, 2014; Muhr et al., 2010; Schlesinger et al., 2016; Sheik et al., 2011). Nevertheless, the effects of drought on postdrought nutrient availability are also quite complex and remains equivocal so far (Fuchslueger et al., 2014; Moyano et al., 2013).

First, drought may influence nutrient mobility and retention in the soil during the drought recovery period (Bloor & Bardgett, 2012; Fuchslueger et al., 2014; Muhr et al., 2010). On one hand, droughts reduce the mobility of nutrients in the soil (Bloor & Bardgett, 2012), thereby disconnecting organisms from substrates (Fuchslueger et al., 2014), because less nutrients are dissolved in soil solution owing to reduced soil water content (Bloor & Bardgett, 2012; Manzoni et al., 2013; Moyano et al., 2013; Muhr et al., 2010). On the other hand, droughts affect nutrient losses in the soil, but the direction and magnitude of this effect are still not clear (Bloor & Bardgett, 2012; Fuchslueger et al., 2014). For example, droughts may adversely affect soil nutrient retention through changes in soil hydrophobicity (Bloor & Bardgett, 2012; Muhr et al., 2010) and/or increased leachate concentration (Bloor & Bardgett, 2012). In addition, droughts may also lead to decreased nutrient losses as a result of decreased volumes of drainage water (Bloor & Bardgett, 2012). Using an outdoor mesocosm experiment to examine grassland responses to a simulated one per century extreme summer drought event, Bloor and Bardgett (2012) reported that postdrought losses of both dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were generally lower in droughted mesocosms throughout the drought recovery time compared to the nondroughted mesocosms owing to the lower volumes of drainage water after drought treatment.

Moreover, droughts may result in changes in the structure and activity of soil microbial communities (Bardgett, Freeman, & Ostle, 2008; Birch, 1958; Bloor & Bardgett, 2012; Fuchslueger et al., 2014; Moyano et al., 2013; Muhr et al., 2010; Schimel, Balsler, & Wallenstein, 2007; Sheik et al., 2011). For example, droughts may select for more resistant microbial groups, which can result in the shift of an existing microbial community (Allison & Martiny, 2008; Castro, Classen, Austin, Norby, & Schadt, 2010; Sheik et al., 2011). Besides, droughts can affect microbial-driven ecosystem functions through the impacts on microbial activities (Bardgett et al., 2008; Lennon & Jones, 2011; Meisner, Rousk, & Bååth, 2015; Wallenstein & Hall, 2012), which may be initiated by various mechanisms such as a decreased input of labile carbon into the soil due to reduced plant productivity (Araus, Slafer, Reynolds, & Royo, 2002; Göransson, Godbold, Jones, & Rousk, 2013; Reddy et al., 2004), and altered soil nutrient retention and availability (Bloor & Bardgett, 2012; Muhr et al., 2010). For instance, the respiratory responses in drought-exposed soils were slower and reached lower rates than control soils, translating to less C mineralized after rewetting (Göransson et al., 2013). Another example is that the net nitrogen mineralization over the course of the whole experiment in soil with a drying-rewetting treatment was reduced to 52%–77% of that kept under continuously moist conditions (Muhr et al., 2010). All these changes in soil microorganism in conjunction with nutrient mobility may jointly have an influence on the soil nutrient availability during years following drought events, eventually affecting the tree growth post drought. Such changes in plant productivity then in turns affect the quantity and quality of the input of plant carbon into the rhizosphere (Baldocchi, Tang, & Xu, 2006; Bardgett et al., 2008) as a feedback, aggravating the negative legacy effects of extreme drought events on tree growth.

### 4.3 | Legacy effects of droughts with different timing

For sites with a dry season overlapping with the period of active vegetation growth (which are selected as case study in this study), an extreme drought year induced by dry DS implies that drought can have a legacy effect on postdrought tree growth directly by influencing plant photosynthetic processes and carbon allocation, and indirectly by altering the environment for soil microorganisms. In comparison, dry WS refers to water stress beyond the photosynthetic active period of vegetation for these sites. For deciduous forests particularly, there is seldom photosynthetic activity for during the period of vegetation dormancy (Larcher, 2003). In this case, drought legacies due to dry WS can be only initiated via drought-induced changes in soil processes discussed above, of which the direction and magnitude remains unclear (Fuchslueger et al., 2014; Moyano et al., 2013). Such different environmental-biological processes through which droughts with different timing influence tree recovery probably explain our results that DS droughts had larger negative effects on postdrought vegetation growth indicated by tree-ring width compared to WS droughts.

To test the hypothesis that (for the five selected RWI chronologies) severe water deficits during the period of active photosynthesis may leave a more pronounced negative impacts on biomass accumulation than water stress in a period of senescence or low growth because of direct damages on the key phases of plant photosynthesis (Bréda et al., 2006; Ciais et al., 2005; Galvez et al., 2011; Hommel et al., 2016; Keith et al., 2012), we compared the RWI of the drought year with dry DS and that of the drought year with dry WS for the selected sites with both dry DS and dry WS droughts during the study period. As shown in Supporting Information Figure S9, four of the five sites show smaller RWI in DS drought than in WS Drought, suggesting that DS droughts affect stem growth more severely than WS droughts. Such different impacts of drought on photosynthesis depending on the timing of drought event were also observed in a *Quercus ilex* ecosystem (Misson et al., 2010). Through experimentally inducing exceptional spring and autumn drought conditions using a rainfall shelter, Misson et al. (2010) found that spring rainfall exclusion carried out during leaf development had a larger impact on photosynthesis than autumn exclusion conducted at a time of mature foliage. Only one RWI site in western North America show similar RWI in DS and WS droughts; and for this site, DS drought had less negative impacts on postdrought tree growth than WS drought (Figure 6e). We next examined the correlations between RWI and climatic variables (temperature, water availability and solar radiation) for each of the five sites. The result shows that for this site, RWI are more strongly associated with temperature and insolation rather than CWD (Supporting Information Figure S10). In this case, drought timing may not prominently affect the magnitude of drought legacies since tree growth here is primarily driven by variations in temperature. Furthermore, less precipitation may suggest less cloudy days and more insolation, which can positively affect the tree growth over this region.

However, there may still exist a risk that the drought timing effects on the legacy of tree growth recovery may be confounded

by plant phenology, considering that for more than 80% of the RWI sites in our analyses (including the selected sites as case study), at least 60% of the length of DS overlapped with the growing season of the local vegetation. Therefore, we further compared drought legacies between drought years with different drought timing only for RWI chronologies in extratropical sites where the dry season overlaps with the period of active photosynthesis for local vegetation for less than 70% of the length of dry season (24% of the whole RWI chronologies in this study). Similar results are observed as shown in Supporting Information Figures S11 and S12, suggesting our conclusion is robust to interactions between growing season and dry/wet seasons. Such phenomenon could also be conceptualized as the “dose dependency” of extreme drought events for tree growth recovery. That is, in theory, DS drought would be much harsher if the trees are already close to their tolerance limit to low moisture during the dry season. Conversely, the threshold value of CWD will be less easily passed if the water availability decreases from optimum when drought occurs during wet season. Under real conditions, such dependence of drought recovery on the background moisture condition has also been reported in terms of the microbial responses to drying-rewetting. A recent study of Meisner, Leizeaga, Rousk, and Bååth (2017) found that moisture content before rewetting affected the bacterial growth pattern after rewetting. However, the threshold value of CWD determining whether severe drought would result in a significantly stronger legacy effect on tree growth remain poorly understood, particularly for tropical ecosystems without a clear boundary between growing season and nongrowing season.

In conclusion, using tree-ring width data for the last six decades, we found stronger and longer negative impacts of DS droughts on tree growth post drought compared to WS droughts. Our result suggests that the timing of drought is a crucial factor determining its impacts on tree recovery after severe drought. Nevertheless, the state-of-art ecosystem models generally lack the representation of drought legacies (Anderegg et al., 2015), let alone the effects of drought timing on the magnitude of legacies. Our study, therefore, suggests the importance in including the missing mechanisms leading to timing dependent response to extreme climatic events into global ecosystem models. Further experiments and observational designs on other ecosystems such as grasslands are also needed to test such timing effects on drought legacies for other species. Moreover, shifts in the timing of drought are expected under some climate change scenarios (Christensen & Christensen, 2007; Kunkel & Liang, 2004). The information provided by our analyses constitutes a crucial step for a better understanding and more accurate prediction of ecosystem responses to drought events under future climate change scenarios.

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## SUPPORTING INFORMATION

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