Legacy effects of drought in the southwestern United States: A multi-species synthesis

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Abstract. Understanding impacts of drought on tree growth and forest health is of major concern given projected climate change. Droughts may become more common in the Southwest due to extreme temperatures that will drive increased evapotranspiration and lower soil moisture, in combination with uncertain precipitation changes. Utilizing ~1.3 million tree-ring widths from the International Tree Ring Data Bank representing 10 species (eight conifers, two oaks) in the Southwest, we evaluated the effects of drought on tree growth. We categorized ring widths by formation year in relation to drought (pre-drought, drought year, and post-drought), and we used a mixed-effects model to estimate the effects of current and antecedent precipitation and temperature on tree growth during the post-drought recovery period. This allowed us to assess changes in sensitivity of tree growth to precipitation and temperature at multiple timescales following multiple droughts, and to evaluate drought resistance and recovery in these species. The effects of precipitation and temperature on ring widths following drought varied among species and time since drought. Across species, 16% of the climate effects (i.e., "sensitivities") were significantly different from their pre-drought values. Species differed, with some showing increased sensitivities to precipitation and temperature following drought, and others showing decreased sensitivities. Furthermore, some species (e.g., *Abies concolor* and *Pinus ponderosa*) showed low resistance and slow recovery, with changes in growth sensitivities persisting up to 5 yr; others (e.g., *Juniper* spp.) showed high resistance, such that their climatic sensitivities did not change. Among species, the importance of different antecedent climate variables changed with time since drought. Though a majority of species responded positively to same-year precipitation pre-drought, all 10 species were positively affected by same-year precipitation the second year after drought. Our results demonstrate tree growth sensitivities vary among species and with time since drought, raising questions about physiological mechanisms and implications for forest health under future drought.

Key words: Bayesian; dendrochronology; drought resistance; lag responses; legacy effects; ecological memory; non-structural carbohydrates.

INTRODUCTION

In the southwestern United States (hereafter, "Southwest"), increasing temperatures and uncertain future precipitation conditions suggest that trees will face increased moisture stress in the coming decades (IPCC (2013). Droughts have serious consequences for tree and forest health, and have been implicated in forest diebacks across the western United States (Allen et al. 2010). Yet, the causes of and conditions leading to drought-related tree mortality are still not fully understood, and furthermore, the relative importance of hydraulic failure vs. carbon starvation for tree mortality during drought is debated (McDowell et al. 2008, Anderegg et al. 2012). Despite the surge of interest in

understanding mechanisms underlying drought-induced mortality, little is known about the recovery response of trees that survive drought events. Individual species respond differently to droughts, and often these differences are tied to physiological trade-offs (West et al. 2008, Mitchell et al. 2014). Recently, a global synthesis of stand-level tree-ring chronologies revealed widespread legacy effects of droughts, most prevalently in more arid sites and in conifer species (Anderegg et al. 2015). In this study, we focus on arid and semiarid sites in the Southwest to further explore such legacy effects and their differences within and among a number of taxonomic groups, including eight conifer species.

Tree-ring responses to drought, here defined by low precipitation, have been studied since the early days of dendrochronology. Droughts result in reduced growth, characterized by narrow or missing rings (Fritts 1976) and altered ring anatomy (Martin-Benito et al. 2013). Trees may also exhibit altered growth sensitivities if

stressed, where climatic and anthropogenic factors have been implicated in declining tree growth (Stahle et al. 1985, Becker 1989, Tainter et al. 1990, LeBlanc 1993). Severe droughts may result in sustained growth suppression for more than a single year, or impaired recovery (Jenkins and Pallardy 1995, Borghetti et al. 1998, Resco et al. 2009, Anderegg et al. 2015). Improved understanding of multi-year suppressions could prove useful in forest management and modelling applications in the coming decades.

Traditional dendrochronological analyses have been applied to reconstruct a variety of phenomena, including paleoclimates (Stockton and Meko 1975), fire histories (Swetnam 1993), insect outbreaks (Veblen et al. 1991), hydrologic records (Schulman 1946), forest demographics (Savage et al. 1996), and others (LaMarche and Harlan 1973, Babst et al. 2014). Methods for analysis of ring-width data are well established, including techniques for age standardization, detrending, and removal of auto-correlation within ring-width series (Fritts and Swetnam 1989). These methods allow determination of constant relationships between ring width and variables such as precipitation, temperature, or soil moisture. In these cases, medium-term (5–10 yr) autocorrelation in ring widths is often treated as noise since such variation is assumed to obscure, for example, potentially strong climate signals (Graumlich 1991). Such medium-term autocorrelation, arising from ecosystem (e.g., insect defoliation), edaphic (e.g., multi-year moisture storage), or physiological (e.g., masting) factors, is rarely explicitly considered in the statistical model, and methods for removing autocorrelation often rely on spline- or ARIMA-type approaches (Monserud 1986, Carrer et al. 2007, Di Filippo et al. 2007, Tegel et al. 2014). Increased understanding of the short-term (e.g., annual) and medium-term (e.g., 5–10 yr) variability in tree-ring widths could provide valuable insights into tree physiological responses.

Trends in tree-ring widths related to past years' conditions or growth have been observed for some time (Fritts 1976). More recently, modelling approaches have investigated the response of tree-ring widths to drought from a resistance–recovery–resilience perspective (Lloret et al. 2011). Growth following drought or low-growth episodes has been shown to be correlated with the levels of growth prior to the drought or low-growth period (Lloret et al. 2011, Martínez-Vilalta et al. 2012) as well as mean annual precipitation (Anderegg et al. 2015). Different species exhibit differing resistances to and abilities to recover from drought stresses (Pretzsch et al. 2013). However, existing approaches use average responses over multiple years that likely obscure important variability in tree growth rates following droughts, and rely on simplistic treatments of autocorrelation or ignore it entirely.

Determining the prevalence and severity of multi-year effects of drought on tree-ring widths may provide important information for further study of tree physiology, particularly if changes in climatic sensitivities following droughts vary among species. Insight into tree

growth responses to drought can potentially be gained from the International Tree Ring Data Bank (ITRDB), which houses millions of tree-ring records. We draw upon the ITRDB and focus on the Southwest to (1) quantify changes in both tree growth sensitivities following drought and the importance of antecedent climate conditions during the post-drought recovery period and (2) compare species' responses to drought from a resistance-recovery perspective that evaluates how these growth attributes vary over different timescales. To address these objectives, we employ time-indexed, hierarchical, nonlinear mixed effect regression models of tree-ring widths during "windows" of time centered on drought events during the 20th century in the Southwest.

<center>METHODS</center>

Data sources, selection, and quality control

Raw tree-ring records were downloaded from the ITRDB on 9 January 2007, and stored in Microsoft Access (Redmond, Washington, USA). We queried the MS Access database to obtain all ring widths from the Southwest (defined as south of 40° S latitude and west of 100° W longitude in the United States). Monthly temperature and precipitation data for approximately the last 100 yr in the Southwest were obtained from the UEA CRU TS3.1 data set, a gridded (0.5° resolution) monthly climate product (Harris et al. 2014). Ring width and climate data were matched by location in R (R Core Development Team 2014), and we subset both data sets to focus on drought periods. At each site, calendar years with total annual precipitation less than the 10th percentile of the 100-yr annual precipitation record for that site were defined as drought years. We chose this "low precipitation" index as a simple drought metric whose effect is easy to interpret within our analysis framework, but other drought indices could have been used (Williams et al. 2013). However, low annual precipitation likely captures the majority of drought events that have occurred in the last 100 yr in this region. Drought events were distributed throughout the 100 yr record, and the timing was not the same for each site. Histograms of precipitation received pre-drought, during drought, and post-drought associated with each drought year clearly show that the drought years we selected have much lower mean precipitation than the non-drought years (Fig. 1).

We defined the pre-drought period as the year prior to each drought event. Due to the large data set and large number of unique drought years (Fig. 2, Table 1), samples of the pre-drought year are unlikely to be biased by abnormal growth years. Even for the smallest data set (for *Q. kelloggii*), the pre-drought year sample represents 20 unique years at three different sites, while for the largest data sets, the number of unique pre-drought years is >50 (Fig. 2, Table 1). While drought years occur in some of the post-drought years (~12% on average),
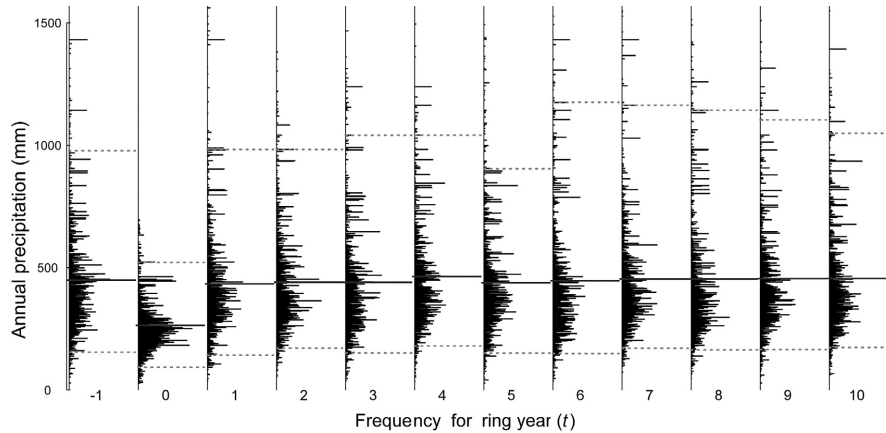
FIG. 1. Histograms of annual precipitation in each ring year, across all sites and species. Annual precipitation was used to select drought years. Years where annual precipitation was less than the 10th percentile of the record at that site were denoted as drought years (i.e., drought years differed across sites). Dark gray solid bars denote means and light gray dashed bars denote the 2.5th and 97.5th percentiles. Drought year occurs at $t = 0$.

the occurrence and timing of drought is relatively random across our data set (Fig. 1), and we draw on many different drought events at different sites, so this is unlikely to bias our results. The use of a single pre-drought year as the baseline for comparison of effects in post-drought years greatly reduces the likelihood of including a drought during the defined pre-drought period. For example, consecutive droughts are relatively unlikely (13.86% of annual precipitation data), but it is likely that two drought events could be separated by only 2–4 yr (32.90% of annual precipitation data). The mean, median, and mode of the interval between droughts were 6.45, 5, and 2 yr, respectively. Thus, we opted to only use one pre-drought year to minimize potential inclusion of a drought event during the pre-drought period.

Ring widths associated with the 5 yr prior to, the year of, and 10 yr after each drought were selected for analysis, resulting in 16-yr "windows" of tree-ring data associated with each drought event at each site. Ring-width years were indexed as being from 4 yr before to 10 yr after the drought. Tree age was estimated as the ring year minus the start year of each core; if there were multiple start years, the earliest was chosen and applied to all ring widths for a given core identification number. The final tree-ring data set included 10 species (eight conifers and two broadleaf) or species groups; due to the nature of the data in the ITRDB, some records were only identified as "*Pinyon*" or "*Pinyon* spp.," or "*Juniper*" or "*Juniper* spp." Therefore *Pinyon* spp. and *Juniper* spp. each represent two distinct species groups. There are five
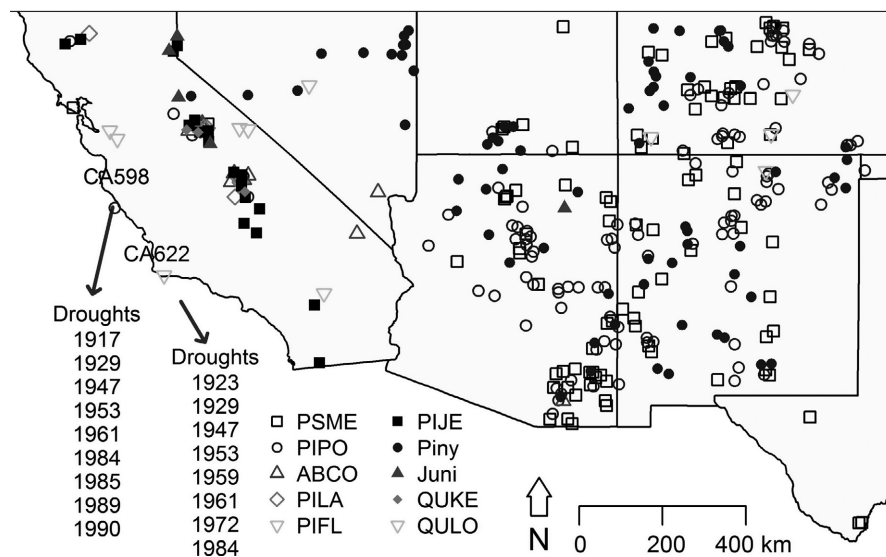

FIG. 2. Distribution of sites (jittered) across the southwestern United States. Associated sample sizes for each species appear in Table 1. Species codes are identified in Table 2. Actual drought series are provided for two example sites "CA598" and "CA622."

TABLE 1. Associated sample sizes for each species in Fig. 2.

Species	Droughts	Sites	Cores	Total n	Drought n
PSME	77	93	2,519	382,554	31,862
PIPO	73	108	2,773	368,738	30,701
Piny	66	69	1,932	251,837	20,982
PIJE	33	18	706	92,284	7,685
PILA	22	8	323	51,200	4,252
ABCO	90	10	277	42,898	3,569
PIFL	39	8	258	33,936	2,828
Juni	28	5	151	18,109	1,508
QULO	20	3	93	11,621	965
QUKE	20	3	89	14,963	1,244

Notes: Droughts, total number of unique drought years; sites, number of sites; cores, number of cores; total n, total sample size or number of rings used in the analysis; drought n, the number of rings that were formed during drought years. Species codes are identified in Table 2.

pines (including *Pinyon* spp.), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), junipers, and two oaks (*Quercus*) (data sets are summarized in Fig. 2 and Table 1).

Model description

We describe an approach that explicitly accounts for the different components of variance in tree-ring widths to explore variability in tree growth rates not typically accounted for by dendrochronological methods. We incorporated an individual-core-level, nonlinear age sub-model instead of detrending individual series prior to the analysis. We also explicitly accounted for non-constant variance in ring widths, and we incorporated first- through fourth-order autoregressive terms (Box and Jenkins 1976) to account for autocorrelation among consecutive rings. Finally, we estimated the effects of precipitation and temperature at multiple timescales using a mixed-effects modeling approach, thus allowing for effects of climate conditions occurring up to 4 yr prior to ring formation, as well as quantifying changes in these responses through time in the decade following drought. The choice of using a 4-yr lag for the climate variables was motivated by Anderegg et al. (2015) and Ogle et al. (2015). We categorize ring widths by the formation year in relation to a drought, and in this way can assess aggregate responses of trees to multiple droughts in the 20th century to quantify common patterns in tree-ring growth parameters through time. Finally, we implemented the analysis as a single, comprehensive model for each species, rather than the piece-wise approach taken by standard dendrochronological methods.

We begin with the data model, which gives the likelihood of the observed raw ring widths. For simplicity, we omit species indexing from model descriptions, but the model described below was applied to each species-level data set individually. The focal ring width ($r_{0,i}$) in a given year (lag = 0) was assumed to be normally distributed with mean μ_i and variance σ_i^2 for each observation i:

$$r_{0,i} \sim \text{Normal}(\mu_i, \sigma_i^2). \tag{1}$$

The estimated (or mean) ring width is modelled with a negative exponential age effect, plus a time-indexed multiple regression against 5 yr of annual precipitation ($P_{j,i}$) and mean monthly temperature ($T_{j,i}$), and four autoregressive effects for ring widths in the previous 4 yr, $r_{l,i}$ (for lag l).

A key component of our model is the incorporation of climate data at two distinct timescales. First, the *ring year* is the year of ring formation with respect to drought, and ranges from −1 (before a drought) to 10 (10 yr after). The first four of the 16 yr in our sample "windows" serve solely as covariates for the four autoregressive effects $r_{l,i}$, and thus are not indexed by ring year. Second, the *climate year* is the year of the climate data with respect to the ring year, and ranges from 0 (climate during the same year that a given ring is formed) to 4 (climate 4 yr prior to ring formation). Additionally, the notation $c(i)$ and $t(i)$ denote core c (that is, the index number of a given core; see Table 1 for species totals) and ring year t ($t = -1, 0, 1\ 2, \ldots, 10$) associated with observation i, j indexes the climate year j ($j = 0, 1, \ldots, 4$), and l indexes the lag associated with past ring widths ($l = 1, 2, 3,$ and 4 yr ago):

$$\mu_i = \alpha_{1,c(i)} e^{\alpha_{2,c(i)}(\text{Age}_i - 150)} + \sum_{j=0}^{4} \beta_{t(i),j} P_{j,i} + \sum_{j=0}^{4} \gamma_{t(i),j} T_{j,i} + \sum_{l=1}^{4} \delta_l r_{l,i} \tag{2}$$

Because both mean and variance of ring widths are typically larger in younger trees than in older trees, individual tree-ring series are usually detrended prior to analysis (Fritts and Swetnam 1989). In our model, we use an analogous negative exponential model for the age effect, with core-level parameters $\alpha_{1,c}$ and $\alpha_{2,c}$. The model is anchored near the mean tree age for the ring widths in the data set (~150 yr) to allow more meaningful interpretation of the intercept $\alpha_{1,c}$, the expected ring width of a

150-yr-old tree under average temperature and precipitation conditions (see next paragraph), as well as increasing the efficiency of the numerical approach for fitting the model.

To model the variation around the mean age effect due to climate, we used the time-indexed climate variables, $P_{j,i}$ and $T_{j,i}$, representing the annual precipitation and mean monthly temperature for each calendar year, respectively. Each was standardized (to facilitate comparison between different climate effects ($\beta_{t,j}$ and $\gamma_{t,j}$)) as the difference from the overall mean across the 100 yr of climate data, divided by the standard deviation. We also explored models involving monthly precipitation, August precipitation, maximum summer temperature, minimum winter temperature, summer precipitation, and precipitation by temperature interactions, but they performed similarly or resulted in implementation issues. As an example of a time-indexed climate effect, $\beta_{-1,3}$ represents the effect of precipitation that occurred 3 yr prior to ring formation ($j = 3$, $P_{3,i}$) on ring widths formed the year before the drought ($t = -1$). Similarly, $\gamma_{6,0}$ represents the effect of mean temperature during the year of ring formation ($j = 0$, $T_{0,i}$) on ring widths formed in the sixth year after drought ($t = 6$). These parameters ($\beta_{t,j}$ and $\gamma_{t,j}$) can be interpreted as the climatic sensitivities of tree growth. In this way, we can investigate the mean responses to climate (sensitivities) of all available series (trees) for a given species following all drought years in the Southwest in the 20th century.

To account for autoregressive effects not directly associated with tree age, we included the effects of past ring widths, δ_l, for each of the four past years ($l = 1, 2, 3, 4$ lags) prior to the focal year (Eq. 2). This is analogous to standard detrending methods in dendrochronology (Box and Jenkins 1976), but typically, only 1–2 lags are considered (Monserud 1986, Monserud and Marshall 2001, Tingley et al. 2012), whereas we include 4 lags simultaneously within a single analysis.

Rather than model the variance (σ_i^2, Eq. 1) indirectly as a function of age, as is often done via the aforementioned detrending techniques, we used a simple nonlinear regression of the variance as a function of the mean ring width of the four preceding years, $\bar{r}_i$, associated with observation i. This relationship explicitly incorporates the correlation between ring width variance and tree growth rates, where faster growing trees are expected to have higher variance than slower growing trees:

$$\sigma_i = e^{a+b\bar{r}_i}. \tag{3}$$

Notably, this differs from traditional methodology, in which both the ring widths and their variances across ages are standardized by dividing ring widths by their fitted detrended curves to create ring-width indices. For simplicity, individual tree differences in variance structure are ignored (i.e., we assume common parameters a and b across all individuals, or cores, within a species), and the decrease in variance with age (or growth rate) is modelled

at the species level (again, the model was applied to each species individually).

Hierarchical priors

The above model was implemented in a hierarchical Bayesian framework. We assume the core-level age effects ($\alpha_{p,c}$, for $p = 1, 2$; Eq. 2) are nested within species, such that they vary around species-level means, μ_{α_p}, with species-level variances, $\sigma_{\alpha_p}^2$, that describe variation among cores/trees within a species, leading to a hierarchical prior for each parameter p:

$$\alpha_{p,c} \sim \text{Normal}(\mu_{\alpha_p}, \sigma_{\alpha_p}^2). \tag{4}$$

The precipitation and temperature effects are split into two categories: pre-drought ($t = -1$) and drought/post-drought ($t = 0, 1, 2, \ldots, 10$). The drought/post-drought effects are modeled hierarchically, with each varying around overall mean effects, β_j^* or γ_j^*, respectively for each climate year (j), plus a random effect that varies by climate year ($j = 0, 1, \ldots, 4$) and ring year ($t = 0, 2, \ldots, 10$), $\varepsilon_{\beta,t,j}$ and $\varepsilon_{\gamma,t,j}$, resulting in 55 random effects each for each climate variable. The drought/post-drought random effects (ring years, t) for a given climate variable (precipitation or temperature) within a given climate year, j, are expected to be correlated to each other, as ring widths exhibit autocorrelation through time, independent of age, which may reflect autocorrelation in climate sensitivities. The correlation between the random effects is modelled using a multivariate normal distribution for the vectors ε_{β_j} and ε_{γ_j} with a zero mean vector of length 11, and 11×11 covariance matrices $\Sigma_{\beta,j}$ or $\Sigma_{\gamma,j}$:

$$\begin{aligned} \varepsilon_{\beta,j} &\sim \text{Normal}(\mathbf{0}, \Sigma_{\beta,j}) \\ \varepsilon_{\gamma,j} &\sim \text{Normal}(\mathbf{0}, \Sigma_{\gamma,j}) \end{aligned} \tag{5}$$

Where $\Sigma_{\beta,j}$ and $\Sigma_{\gamma,j}$ are parameterized according to the spatial exponential covariance function (Diggle et al. 2002), such that for row $t = r$ and column $t = k$:

$$\Sigma_{\beta,j}(r,k) = \sigma_{\beta,j}^2 e^{-\phi_j|r-k|} \tag{6}$$

and similarly for $\Sigma_{\gamma,j}$ with variance $\sigma_{\gamma,j}^2$ and correlation parameter ϕ_j, where the correlation among effects separated by one climate year ($|r-k| = 1$) is $e^{-\phi_j}$. Note that the covariance parameters ($\sigma_{\beta,j}^2, \sigma_{\gamma,j}^2, \phi_j$) are assumed to differ with respect to the climate year j, and that ϕ_j is assumed to be identical for the temperature and precipitation effects.

We allow for the possibility that the correlation structure among the time-indexed climate sensitivities is different for the pre-drought effects. That is, the precipitation and temperature effects in pre-drought years ($t = -1$) are assigned normal priors with the same hierarchical means (β_j^* or γ_j^*) and variances (σ_β^2 or σ_γ^2) as the drought/post-drought years, but they are excluded from the auto-correlation structure, as we do not assume

that pre-drought climate sensitivities are correlated with those during or after the drought. This confers the analytical benefits of partial pooling with regards to multiple comparisons (Hill and Gelman 2007, Gelman et al. 2012),while allowing the pre-drought effects to be uncorrelated with the effects during ($t = 0$) or after drought ($t = 1,…, 10$):

$$\beta_{-1,j} \sim \text{Normal}(\beta_j^*, \sigma_{\beta,j}^2)$$
$$\gamma_{-1,j} \sim \text{Normal}(\gamma_j^*, \sigma_{\gamma,j}^2) \qquad (7)$$

Non-informative independent priors

The autoregressive effects, δ_l (Eq. 2), were given diffuse normal priors centered on zero. We assigned wide uniform (flat) priors to the species-level age effects, μ_{α_1} and μ_{α_2} (Eq. 4), with the restrictions $\mu_{\alpha_1} > 0$ and $\mu_{\alpha_2} < 0$. The species-level parameters in the variance model, a and b (Eq. 3), were given wide uniform priors and restricted to be >0. The overall climate effects (β^* or γ^*) were assigned diffuse normal priors, and the standard deviation (σ_β^2 and σ_γ^2) and correlation ($\rho_j = \exp(-\phi_j)$) terms in the spatial exponential covariance function (Eq. 6) were assigned uniform, U(0, A), priors, with A = 5 and A = 1, respectively (Gelman 2006).

Quantifying variation in growth sensitivity through time

To quantify variation in growth sensitivity to climate across ring years, we calculated effect differences (d values) for each of the random effects compared to its pre-drought ($t = -1$) value, resulting in 11 d values for each climate year for each climate variable, such that for $t = 0, 1, 2,…, 10$, $d_{\beta,t,j} = \beta_{t,j} - \beta_{-1,j}$ and $d_{\gamma,t,j} = \gamma_{t,j} - \gamma_{-1,j}$. The 95% credible intervals were computed for each d value, and those that do not overlap zero are considered significant at the $P < 0.05$ level.

To investigate resistance to and recovery from drought, we characterized species in terms of *response, lag, and recovery. Response* is defined as the sign (positive or negative) of the first significant d value (regardless of climate year), with respect to ring year during drought and post-drought ($t = 0, 1, …, 10$). *Lag* is the number of years after the drought year ($t = 0$) at which this first significant *response* occurs. *Recovery* represents the length of time that it takes for the post-drought climatic sensitivity to return to its baseline/pre-drought sensitivity; *recovery* is quantified as the first ring year, after the occurrence of the initial post-drought *response*, when d values for all five climate years are nonsignificant. For example, if the effect of precipitation was significantly higher than its pre-drought value in the second, third, and fourth years after drought, but not significantly different from the pre-drought value in all other years, the *response* would be positive, the *lag* would be 2 yr, and the *recovery* would be 5 yr. We note that multiple, simultaneous responses (i.e., in two different climate years) are possible. We also

indicate the significance level of the response, which is somewhat indicative of the magnitude or intensity of the response, as effects that are farther from the pre-drought effect will have smaller Bayesian P values (given similar credible intervals).

Implementation

The above model was fit to the ITRDB data via Markov chain Monte Carlo (MCMC) methods, implemented in JAGS (Plummer et al. 2003), and called by R (R Core Development Team 2014) via the package "rjags" (Plummer 2013). For each model, three parallel MCMC chains were run and assessed for convergence, in which case, all previous iterations were discarded and subsequently the MCMC chains were run sufficiently long to obtain 3000 relatively independent samples for each parameter.

RESULTS

Model fit

The model generally fit the ITRDB tree-ring data well, with R^2 values from regressions of observed vs. predicted ring widths ranging from 0.64 (*Pinyon* spp.) to 0.90 (*Abies concolor*), with a median R^2 of 0.80 across the 10 species (Table 2, Appendix S1). The observed vs. predicted ring widths generally fell around the 1:1 line, indicating little to no model bias (Table 2, Appendix S1).

Parameter estimates

Means, standard deviations, and 95% credible intervals (CIs) for all model parameters are reported in Appendix S4: Table S1, which includes the age effect parameters ($\mu_{\alpha_1}, \mu_{\alpha_2}, \sigma_{\alpha_1}^2$, and $\sigma_{\alpha_2}^2$), variance model parameters (a and b), and the climate effects standard deviations ($\sigma_{\beta,j}$ and $\sigma_{\gamma,j}$), which are not reported here. Here, we focus on the autoregressive effects (δ) and the actual climate effects (β and γ). Nearly all autoregressive effects were significant and positive, where ring width was more strongly coupled to more recent past widths (Fig. 3). The autoregressive effects varied among species; for example, the effect of previous year's ring width, δ_1, was the strongest and ranged from 0.367 [0.35, 0.384] for *Pinyon* spp. to 0.607 [0.562, 0.653] for *Q. kelloggii* (posterior means and 95% CIs). The effect of ring widths observed three and four years prior to the focal year, δ_3 and δ_4, were the weakest, depending upon species (Fig. 3).

The posterior estimates for the time-indexed effects of precipitation ($\beta_{t,j}$) and temperature ($\gamma_{t,j}$), were both positive and negative, depending on species, climate year, and ring year relative to the drought year. In general, there were similar numbers of significant positive effects of precipitation (188) and temperature (181), but more significant negative effects of precipitation compared to temperature (177 and 124, respectively; Table 3). In total,

Table 2. Model evaluation indices and species codes.

Species	Code	R^2	Coverage	Bias
Pseudotsuga menziesii (Mirb.) Franco	PSME	0.78	99.9%	0.97
Pinus ponderosa Dougl. ex Laws.	PIPO	0.84	99.8%	0.98
Pinyon spp.	Piny	0.64	99.9%	0.95
Pinus jeffreyi Grev. & Balf.	PIJE	0.87	99.9%	0.99
Pinus lambertiana Dougl.	PILA	0.86	99.9%	0.98
Abies concolor (Gord.) Lindl. ex Hildebr.	ABCO	0.90	99.9%	0.99
Pinus flexilis James	PIFL	0.79	99.9%	0.97
Juniper spp.	Juni	0.78	99.9%	0.98
Quercus lobata Nee	QULO	0.81	99.0%	1.01
Quercus kelloggii Newb.	QUKE	0.77	99.7%	0.98

Notes: The R^2 values were obtained from a regression of observed ring widths on the posterior means of predicted ring widths. Coverages are the percentage of observed values that fall within the 95% credible intervals for the predicted data. Bias is the slope of the linear regression of the observed vs. predicted plots (lack of bias is indicated by values equal to or close to 1). R^2 values, coverage, and bias were calculated from 3000 relatively independent samples of each predicted data point. Scatter plots of observed vs. predicted ring widths are provided in Appendix S1.

55.8% of the climate effects were significant (60.8% of precipitation effects and 50.8% of temperature effects). The number of significant climate effects varied widely between species, with some species showing less than 20% (e.g., *Juniper* spp.), and others showing ~75% (e.g., *P. menziesii*; Fig. 4).

Summarizing the significant precipitation effects across species within each climate year (j) by ring year (t) combination (e.g., the effect of prior year precipitation on ring widths formed 7 yr after drought) revealed 39 effects that were common to more than half of the species, indicating clear patterns in sensitivities of ring width to antecedent climate variables. For nearly all ring years, a majority of species showed positive effects of focal ($j = 0$) and prior ($j = 1$) year precipitation, and negative effects of precipitation received two years prior to ring formation ($j = 2$; Table 3). A smaller number of species (two to seven) were characterized by significant negative effects of precipitation received three ($j = 3$) and four ($j = 4$)

years prior to ring formation, and none ($j = 3$) or a very small number (~1, primarily *Q. kelloggii*, $j = 4$) of species were positively affected by precipitation received during these past time periods. Prior to and during drought ($t = -1$ and 0), 70–80% of the showed positive effects of both focal ($j = 0$) and prior ($j = 1$) year precipitation. However, due to increased sensitivity in *P. lambertiana*, *P. flexilis* and *A. concolor*, all 10 species showed positive effects of focal year precipitation in the second year after drought ($t = 2$), which was the only unanimous climate effect (Table 4). While uncommon, we note that four and three species showed positive effects of 4 yr prior ($j = 4$) precipitation in the first ($t = 1$) and third ($t = 3$) years after drought respectively, compared to only one species for all other ring years (Table 3).

Patterns in significant temperature effects of ring width were less uniform, and effects varied more with time since drought. More than half of species showed negative effects of focal year ($j = 0$) temperature in most ring years,
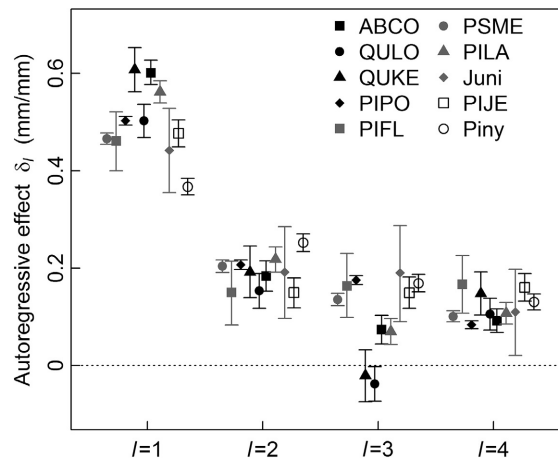

FIG. 3. Means and 95% credible intervals (CIs) of first- through fourth-order autoregressive parameters (δ_l) for each species; l indicates the lag corresponding to past ring widths. Parameters whose 95% CIs do not include zero (dashed line) are considered significant. Different symbols and colors represent different species. See Table 2 for species codes.

TABLE 3. Summary of significant positive (top) and negative (bottom) precipitation (β effects, left) and temperature (γ effects, right) effects.

Ring year t	Species with significant β effect					Species with significant γ effect				
	$j = 0$	$j = 1$	$j = 2$	$j = 3$	$j = 4$	$j = 0$	$j = 1$	$j = 2$	$j = 3$	$j = 4$
Positive										
−1	8	8	0	0	1	4	2	4	5	3
0	7	8	1	0	1	4	2	6	4	4
1	9	7	0	0	4	4	3	2	3	3
2	10	5	0	0	1	3	5	1	3	2
3	8	5	0	0	3	4	3	1	4	3
4	9	6	0	0	1	3	1	2	5	3
5	7	6	0	0	1	4	1	5	5	3
6	8	6	0	0	1	3	1	1	4	5
7	8	4	0	0	1	2	4	2	4	3
8	9	5	1	0	1	3	3	1	3	2
9	9	4	0	0	1	3	1	3	4	3
10	8	5	0	0	1	2	2	2	3	3
Negative										
−1	0	0	8	7	4	6	4	1	0	0
0	0	0	6	5	4	6	3	0	1	0
1	0	0	7	5	4	6	3	0	1	1
2	0	0	6	3	4	6	3	1	2	1
3	0	0	8	4	3	5	3	1	0	0
4	0	0	7	3	3	4	5	2	0	0
5	0	0	8	3	4	6	4	0	1	0
6	0	1	7	2	4	4	5	0	1	0
7	0	1	7	2	5	6	3	0	1	0
8	0	0	6	6	4	6	2	1	1	0
9	0	0	7	3	4	6	4	0	1	0
10	0	0	7	2	3	4	3	0	0	0

Notes: Values indicate the number of species (out of 10) with a significant effect for a given climate variable, e.g., for precipitation received or temperature experienced j "years ago" (climate year) with respect to the year of ring formation, and for ring year, t, relative to the drought year (e.g., $t = -1$ is the year before, and $t = 0$ is the drought year). Effects are considered significant at $P < 0.05$ when their 95% credible intervals (CIs) do not include zero.

but effects of prior year temperature were mixed (negative and positive), and negative effects of 2–4 yr prior temperature were uncommon (Table 3). With respect to the effects of past temperature on growth, one-half or more of the species showed positive effects of temperature of the prior year ($j = 1$) during the second year after drought ($t = 2$), of 2 yr prior ($j = 2$) during the drought year ($t = 0$) and the fifth year after drought ($t = 5$), 3 yr prior ($j = 3$) in the pre-drought year ($t = -1$) and the fourth and fifth years after drought ($t = 4$ and 5), and 4 yr prior ($j = 4$) in the sixth year after drought ($t = 6$; Table 3).

Effects relative to pre-drought responses

Evaluation of the d values ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$, see *Methods*) lends insight into species-specific differences between the effects of climate during the drought ($t = 0$) and post-drought ($t = 1, 2, \ldots, 10$) relative to the effects in the pre-drought year ($t = -1$). In total, 16% of the d values were significant ($P < 0.05$) across all species, though the number of significant d values per species ranged from zero (*Juniper* spp., *Q. kelloggii*, and *P. flexilis*) to 43 (*P. menziesii*) out of a total of 110 per species (5 climate

years × 11 ring years × 2 climate variables), indicating large differences in resistance to and recovery from drought among species (Table 4, Appendix S4: Table S1). All species, except *Juniper* spp., *P. flexilis*, and *Q. kelloggii*, showed one or more significant d values during the 10-yr period after drought. Some species, such as *P. menziesii*, exhibited altered growth sensitivities to climate for many years following drought (Fig. 4, Appendix S2), while the d values of others, such as *Q. lobata*, exhibited variability immediately following drought, though significant d values could occur many years after drought (Fig. 5, Table 4, Appendix S3).

In general, the responses to drought (i.e., significant d values; see *Quantifying variation in growth sensitivity through time*) could be positive or negative and could occur in any climate year ($j = 0, 1, \ldots, 4$). Simultaneous responses in multiple climate years were common, and many responses were highly significant (i.e., "intense"), however, species showed important differences in resistance and recovery metrics (Table 4). For example, of the five species for which a response to drought occurred during the focal year (i.e., for which $j = 0$ in Table 4), all four conifers responded negatively to precipitation (β statistics) or temperature
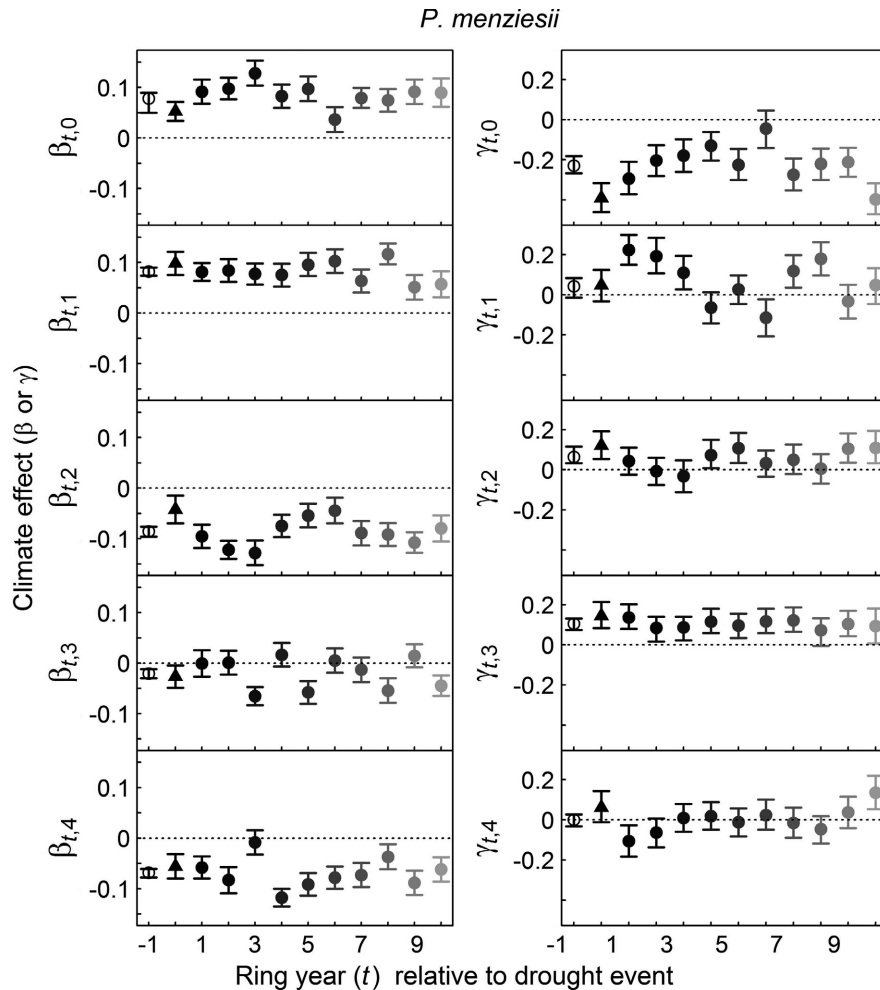
P. menziesii

FIG. 4. Means and 95% credible intervals (CIs) for the effects of standardized precipitation (β, left) and standardized temperature (γ, right) on ring widths for a conifer species (*Pseudotsuga menziesii*), showing some of the most complex patterns we observed. Plots are ordered vertically by climate year ($j = 0$ [focal year, top] to $j = 4$ [4 yr prior to ring formation, bottom]). Ring year (t) is denoted on the x-axis such that within each plot, there are 12 values, corresponding to (from left to right) the parameter values for the pre-drought year ($t = -1$), the year of the drought ($t = 0$), and for each of 10 years after the drought ($t = 1, 2, …, 10$). Pre-drought effects are denoted by empty circles, drought year effects by triangles, and post-drought effects by circles with darker shading for years closer to the drought.

(γ statistics), while one angiosperm (*Q. lobata*) responded positively to precipitation (Table 4). Altered climatic sensitivities occurred 1 yr following drought (Lag = 1) in *Q. lobata* and *P. jeffreyi*, while responses were immediate (during the drought year, Lag = 0) in all other species that responded to drought (Table 4). While some species recovered from drought within 1–2 yr, others required three (*P. lambertiana*, *Q. lobata*) or even 5 yr (*A. concolor*, *P. menziesii*, *P. ponderosa*, *Pinyon* spp.) to return to pre-drought climatic sensitivities (Table 4).

We note that while the above summaries of the climate sensitivities ($\beta_{t,j}$ and $\gamma_{t,j}$) and d values ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$) reveal general patterns across species, they conceal important year to year and between-species variability in any given climate effect, such as long lags, positive, negative, or mixed effects of climate, and sign switching of effects through time (for examples, see Fig. 6, Appendices S2, S3). Longer lags were common when considering climate years individually (vs. across all climate years, as shown in Table 4), and patterns across ring years (t) were highly species specific. For example, for the effect of prior year temperature ($j = 1$) on ring widths in *P. lambertiana*, the first significant d value occurred in the fifth year after drought, vs. the Lag = 0 yr across all j as in Table 4 (Fig. 6).

DISCUSSION

To quantify variability in the climatic growth sensitivity of tree rings associated with droughts in the 20th century, we evaluated the effects of precipitation and temperature on growth using a time-indexed, nonlinear, mixed-effects model. We utilized two distinct time indices, ring year ($t = -1, 0, 1, …, 10$) in relation to the timing of a drought,

TABLE 4. Summary of significant positive (+) and negative (−) d values ($d_{\beta,t,j} = \beta_{t,j} − \beta_{−1,j}$ and $d_{\gamma,t,j} = \gamma_{t,j} − \gamma_{−1,j}$) across climate years, for the effects of precipitation (β) and temperature (γ) in ring year t relative to pre-drought ($t = 0$), for climate year j.

Species	Difference values for β effects						Difference values for γ effects					
	+	−	Response		j	Lag	Recovery	+	−	Response		j	Lag	Recovery
PSME	12	15	−/+	*/***	0/2	0	1	7	9	−	***	0	0	5
PIPO	12	11	+/+	**/***	1/2	0	2	11	8	−/+	**/*	0/2	0	5
Piny	6	7	+	*	4	0	5	5	3	−/+	*/*	0/3	0	1
PIJE	2	2	+	**	4	1	2	1	1	+/−	*/*	3/4	10	
PILA	6	9	+/−	**/***	2/4	0	3	5	4	+	**	2	0	3
ABCO	9	7	−/+	**/**	0/2	0	5	3	4	−	**	3	0	1
PIFL	0	0						0	0					
Juni	0	0						0	0					
QULO	6	6	+/−	*/*	0/2	1	2	3	2	+	*	4	1	3
QUKE	0	0						0	0					

Notes: For each species, we report the response, lag, and recovery indices, where (1) response is the sign of the first significant d value, along with the climate year (j) that this response first occurred; (2) lag is the number of ring years (t) after the drought year that the response occurred, which could be zero if the response occurred during the DROUGHT; and (3) recovery is the first ring year (t) after the first significant response that the climate effects become indistinguishable (nonsignificant) from the baseline (pre-drought) values across all climate years (j). Blank cells indicate species that had no significant d values. Levels of significance indicate the intensity or magnitude of the d values associated with each response, and are denoted by ***$P < 0.001$, **$P < 0.01$, and *$P < 0.05$. For instances when there are multiple climate years for which the first significant d value occurs, a "/" is used to separate the sign, significance, and climate year (j) associated with each of these simultaneous responses. Lower (more significant) Bayesian P values are indicative of lower resistance to drought. See Table 2 for species codes.

and climate year (j = 0, 1, 2, 3, 4) with respect to past years in relation to the year of ring formation. Across species, common patterns in significant climate effects for different ring year by climate year combinations demonstrate the importance of focal year and antecedent climate for tree growth, and the variability in growth responses to climate drivers following drought. After accounting for age trends and autocorrelation, 16% of the growth sensitivities differed significantly from pre-drought values, indicating widespread variability in growth sensitivities following drought. Significantly different climate effects following drought relative to pre-drought effects (i.e., d values) were found in a majority of conifers, and in one oak species. Species-specific patterns of variability in these response and associated recovery times, as revealed by d values ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$), suggest that these responses may be related to species-specific physiologies, and we discuss potential mechanisms below.

Antecedent climate and potential physiological mechanisms

Growth during the drought year was only related to the intensity of the drought (i.e., the amount of precipitation received during a drought year) for 70% of the species. The effect of focal year precipitation was important for more species prior to or subsequent to drought. This is surprising, however, recent work has shown that drought intensity is not strongly related to the intensity of legacy effects (Anderegg et al. 2015). Furthermore, we show that the relative importance of different climate variables changes through time following droughts, resulting in lagged responses. For example, all species respond positively to focal year precipitation in the second year

after drought ($\beta_{2,0}$, Table 3), and five species responded positively to prior year temperature in the second year after drought ($\gamma_{2,1}$), but only two species responded to prior year temperature in the pre-drought year ($\gamma_{−1,1}$) and drought year ($\gamma_{0,1}$). This demonstrates the prevalence of drought legacy effects in some species, as well as the transience and complexity of responses to climate through time. Lagged responses could reflect cumulative impacts of drought-induced tissue damage. For example, leaves or needles may be damaged or dropped during drought stress (Berg and Chapin 1994), and their replacement may delay subsequent growth responses to favorable precipitation conditions (Fritts 1976).

Changes in growth sensitivities following drought could also reflect allocation to xylem refilling and embolism repair (Sperry et al. 1987, Hacke and Sauter 1996). Older xylem conduits are less likely to be refilled, and so total hydraulic conductance, carbon assimilation, and growth may decrease during growth years following drought (Sperry et al. 1994, West et al. 2008, Resco et al. 2009). The common positive effect of precipitation received 1 yr prior to ring formation on growth during the drought year ($\beta_{0,1}$; Table 3) suggests trees receiving more precipitation in the year before a drought are less impacted by the subsequent drought event. In contrast, negative sensitivities to precipitation received 2 yr ago were extremely common (Table 3). This may represent an associated cost of past tree vigor or high growth rate during subsequent periods of stress. Trees receiving more precipitation accumulate more biomass, both above- and belowground (Pregitzer et al. 1993), particularly at moisture-limited sites favored by dendrochronologists (Fritts and Swetnam 1989). Maintenance respiration poses a greater cost to large, fast growing trees (Ogle and Pacala 2009), and
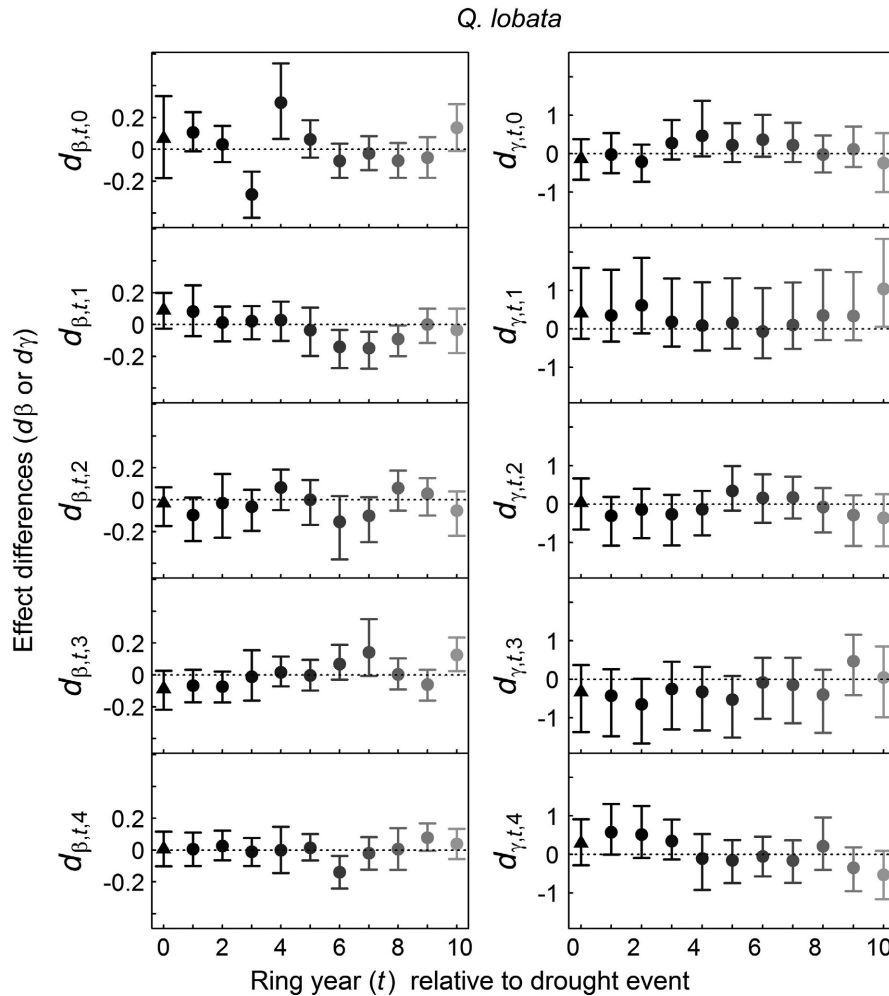
Fig. 5. Means and 95% credible intervals (CIs) for the d values ($d_{\beta,t,j}$ and $d_{t,j}$) associated with standardized precipitation (β, left) and standardized temperature (γ, right) effects for one of the two angiosperm species (*Quercus lobata*). Plots are ordered vertically by climate year ($j = 0$ [focal year, top] to $j = 4$ [4 yr prior to ring formation, bottom]). Ring year (t) is denoted on the x-axis such that within each plot, there are 11 values, corresponding to (from left to right) the difference between the effect estimated for the year of the drought ($t = 0$) and for each of 10 years after the drought ($t = 1, 2, ..., 10$), relative to the pre-drought effect. Differences for the drought year are denoted by triangles, and post-drought differences by circles with darker shading for years closer to the drought. Difference values with 95% CIs that do not overlap zero (dashed line) are significant ($P < 0.05$); values greater than zero indicate increased sensitivity of ring widths to climate, while values less than zero indicate decreased sensitivity to climate.

under certain conditions, fast-growing or more sensitive trees can have higher mortality risk (Jenkins and Pallardy 1995, Ogle et al. 2000, Suarez et al. 2004), though the opposite has also been shown (e.g., Bigler et al. 2007, Macalady and Bugmann 2014).

Both coniferous and deciduous temperate trees rely on existing stores of non-structural carbohydrates (NSC), particularly early in the growing season when leaves, or annual needle crops, have yet to form, and growth conditions are poor (low temperatures, shorter days) (Dickson 1989, Kagawa et al. 2006, Kuptz et al. 2011, Michelot et al. 2012). The common pre-drought importance of previous year's precipitation ($\beta_{-1,1}$; Table 3) may correspond to early-season growth dependence on NSC (Barbaroux and Bréda 2002). The rapid increase in sensitivity

to focal year precipitation for *P. lambertiana*, *P. flexilis*, and *A. concolor* from the drought year to the first and second years after drought is suggestive of a decoupling of growth and photosynthesis during drought. Growth can be inhibited prior to, or more severely than photosynthesis, during droughts (Goulden et al. 1996, McDowell 2011) or seasonal drydown (Barbaroux and Bréda 2002), potentially building up, rather than depleting NSCs. Therefore, trees may maintain high NSC concentrations after mild droughts, showing increased post-drought growth, though NSC may be used to mitigate stresses, or offset respiratory costs (Chapin et al. 1990). In contrast, the lagged effect of prior-year temperature on ring widths after drought ($\gamma_{2,1}$, Table 3) may indicate drought stress depleted reserves, which then limited growth in the year
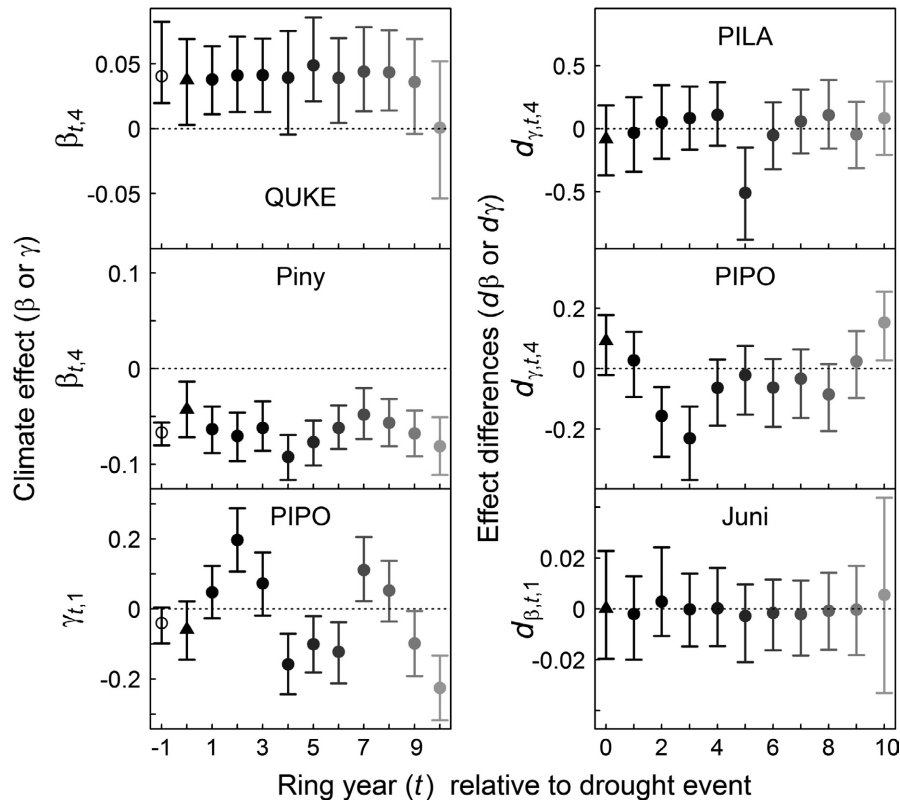
Fig. 6. A selection of the diverse patterns in climate sensitivities ($\beta_{t,j}$ and $\gamma_{t,j}$, left) and d values ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$, right) that we observed. Interpretation is equivalent to either Figs. 3 or 4. Means and 95% credible intervals (CIs) are presented for all applicable ring years (t) for a given parameter, and inset text denotes species. Parameter and climate year ($j = 0, 1, \dots, 4$) are denoted on the y-axis. Ring year (t) is denoted on the x-axis and indicates the pre-drought year ($t = -1$, only for climate effects, left), the year of the drought ($t = 0$), and each of 10 years after the drought ($t = 1, 2, \dots, 10$). Pre-drought effects are denoted by empty circles, drought year effects or effect differences by triangles, and post-drought effects or effect differences by circles with darker shading for years closer to the drought.

after drought for some species (Galiano et al. 2011), but warmer temperatures may have allowed for accumulation of new NSC. Subsequently, trees responded positively to same year precipitation ($\beta_{2,0}$), potentially due to availability of recently stored NSC and new photosynthates following depletion of NSC during drought (Keel et al. 2007, Dietze et al. 2014).

Fewer species were significantly affected by climate conditions that occurred 3–4 yr prior to ring formation (Table 3). These relatively long climate lags may reflect the contribution older pools of NSC to growth. Recent work suggests there are multiple NSC pools in trees that turn over at different rates (Carbone et al. 2013, Richardson et al. 2015), which agrees well with evidence that older NSC may be less available, or even unavailable, to trees compared to more recently fixed carbohydrates (Millard et al. 2007, Sala et al. 2010). We would expect the importance and availability of "old" (e.g., 3–4 yr old) NSC pools to be indicated by a positive effect of precipitation received 3–4 yr ago. Yet, only one species—an angiosperm, Q. kelloggii—showed a consistently positive effect of 4 yr prior ($j = 4$) precipitation. This could be attributed to its wood anatomy, which is expected to

promote greater NSC storage (Ogle and Pacala 2009). The other oak species (Q. lobata) in our data set, which has similar wood anatomy does not show this pattern, but this may be due to differences in their habitat (Q. lobata is more abundant at lower, potentially more stressful elevations) and/or life history characteristics (Q. kelloggii acorns require 2 yr to mature, and stress-induced abortion reduces seed crops; Nixon et al. 1997). Ring widths of the eight conifer species were either uncorrelated or negatively correlated with precipitation received 3–4 yr ago. Given that conifers have potentially limited capacity to store NSC in their stems (Ogle and Pacala 2009), we may have expected greater importance of recent precipitation and temperature and high reliance on recently stored or produced NSC; again, the negative effect of past precipitation likely reflects delayed biomass or respiration costs.

Variability through time and across species

The prevalence of significant d values ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$) shows significant, complex, and persistent changes in growth sensitivity to climate following droughts for many tree species in the Southwest. Strikingly, while

consideration of a "normal" or "baseline" (e.g., pre-drought) growth sensitivity (Lloret et al. 2011, Anderegg et al. 2015) is a useful conceptual model for studying tree recovery from drought, many of the species we studied (including conifers and one angiosperm) exhibited variable climate sensitivities throughout the entire 12-yr window defined by a drought event. Clark et al. (2007) found a temporal trend in tree growth between 1993 and 2006, which they attributed to climate effects, and our model shows that similar temporal trends may still emerge even after accounting for climate effects. Lagged mortality due to drought has been documented (Pedersen 1998, Bigler et al. 2007), and we also show that lagged changes in growth are common in the Southwest (Table 4, Fig. 6). Taken together, our results suggest potential for more research into the interacting physiological processes controlling lagged responses to precipitation and temperature following drought.

Species-specific differences in drought responses suggest a role for differing tree physiologies. For example, of the five species with a response to focal year climate (where $j = 0$, Table 4), the uniform initial response (positive) of all four conifers to focal year climate contrasts with that of *Q. lobata* (negative). Oaks rely heavily on stored NSCs for construction of earlywood, while conifers draw on a mix of stored NSC and recent photosynthates (Barbaroux and Bréda 2002, Michelot et al. 2012). The lack of significant *d* values in *Juniper* spp. (Fig. 6), though potentially due to insufficient data, is consistent with work showing zero drought legacy effects in *Cupressaceae* (Anderegg et al. 2015). This could be explained by the observation that these anisohydric species are resistant to moderate drought stress (West et al. 2008). In contrast, long recovery times for widely distributed conifer species (*P. ponderosa*, *P. menziesii*, *A. concolor*, etc.; Table 4) demonstrate that legacy effects are common in important tree species in the Southwest, and that these species may be vulnerable to climate change. These legacy effects should be taken into account when quantifying the growth or ecosystem effects of these foundation species (Ellison et al. 2005).

Conclusion

The changes in growth sensitivities predicted by our statistical model could represent normal variability in tree growth. However, as the significance of any given climate effect ($\beta_{t,j}$ and $\gamma_{t,j}$) or *d* value ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$) requires hundreds to thousands of trees over large spatial scales to respond in the same way following multiple, site-level droughts, we argue that this variation represents individual, or at least, stand-level responses to environmental conditions related to or contemporaneous with drought. A number of species (*P. ponderosa*, *P. menziesii*, *A. concolor*, *P. lambertiana*) were characterized by a high number of significant *d* values ($d_{\beta,t,j}$ and $d_{\gamma,t,j}$) defining differences in growth responses to climate through time, and variation in these *d* values among species points to

important variation in drought resistance and recovery. It is likely that the magnitudes of these changes in growth sensitivities are larger on smaller spatial scales. Within each species, trees occurring across large areas (including different sub-species) were pooled for our analyses, and different mechanisms are likely more important in different locations or populations, potentially lessening the magnitude of shared responses to drought. Future research is necessary to explore this variability in tree growth sensitivities associated with drought applied at finer spatial scales, across broader spatial domains, and for more species. Tests of the hypothesized mechanisms we have presented could further our understanding of tree carbon allocation, water use, and the impacts of drought and legacy effects, which will be valuable given projected climate change in the Southwest.

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