Interspecific differences in drought and pluvial responses for *Quercus alba* and *Quercus rubra* across the eastern United States

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A B S T R A C T

Quercus is one of the most important genera of plants in North America, but is currently undergoing a decrease in abundance and dominance of North American forest ecosystems. Of the two most common North American *Quercus* species, eastern white oak (*Quercus alba*) has experienced a slightly greater decline in dominance compared to northern red oak (*Quercus rubra*). Changes in *Quercus* demographics are likely due to multiple factors, but also highlight the importance of understanding the growth-climate relationships of these species under shifting climatic regimes. Therefore, we developed a network of tree-ring chronologies and stomatal conductance measurements where *Q. alba* and *Q. rubra* co-occur that spans the longitudinal extent of both species' geographic ranges. We compared growth reductions due to drought conditions, and growth increases due to pluvial conditions, of both species. The drought response (by reductions in radial growth and stomatal conductance) of *Q. alba* was consistently greater than *Q. rubra* irrespective of temporal or spatial drought dynamics. Similarly, the pluvial response (relative increase in growth) of *Q. alba* was greater than *Q. rubra*. We also found that both species exhibit nonlinear relationships to water availability, where increases in growth during pluvial conditions are less than the decreases in growth due to drought conditions. Thus, we concluded that *Q. alba* is moderately more sensitive to water availability than *Q. rubra*, which provides new insight for *Quercus* isohydricity classification, and may indicate different sensitivities to a changing precipitation regime in North America.

1. Introduction

The *Quercus* genus is arguably the most ecologically important genera of plants in North America (Monk et al., 1990; Abrams et al., 1995; Abrams, 1996; Dyer, 2001; Abrams, 2003; Cavender-Bares, 2016). Oaks are estimated to account for over 20% of total woody biomass, over 30% of total woody species, and sequester more carbon than any other woody group in the United States (Cavender-Bares, 2016). Although historically dominant in most regions where they occur, many studies have highlighted the diminishing importance and abundance of oaks as components of eastern North American forests (Abrams, 1992; Abrams, 2003; Fei et al., 2011; McEwan et al., 2011). Specifically, forest

inventory analysis of two of the most common and widespread North American oak species (Fig. 1), eastern white oak (*Q. alba*) and northern red oak (*Q. rubra*), shows slightly more widespread declines in *Q. alba* dominance compared to *Q. rubra* (Novick et al., 2022).

Many hypotheses have been put forth to explain recent changes in oak regeneration and recruitment, including changing fire, precipitation, and soil moisture regimes (McEwan et al., 2011; Novick et al., 2022). While it is likely that multiple drivers are responsible for recent changes in North American oak demographics, the ongoing impacts of anthropogenic climate change underscore the importance of understanding the growth-climate relationships of these species. Although several studies have documented a shift towards increased precipitation
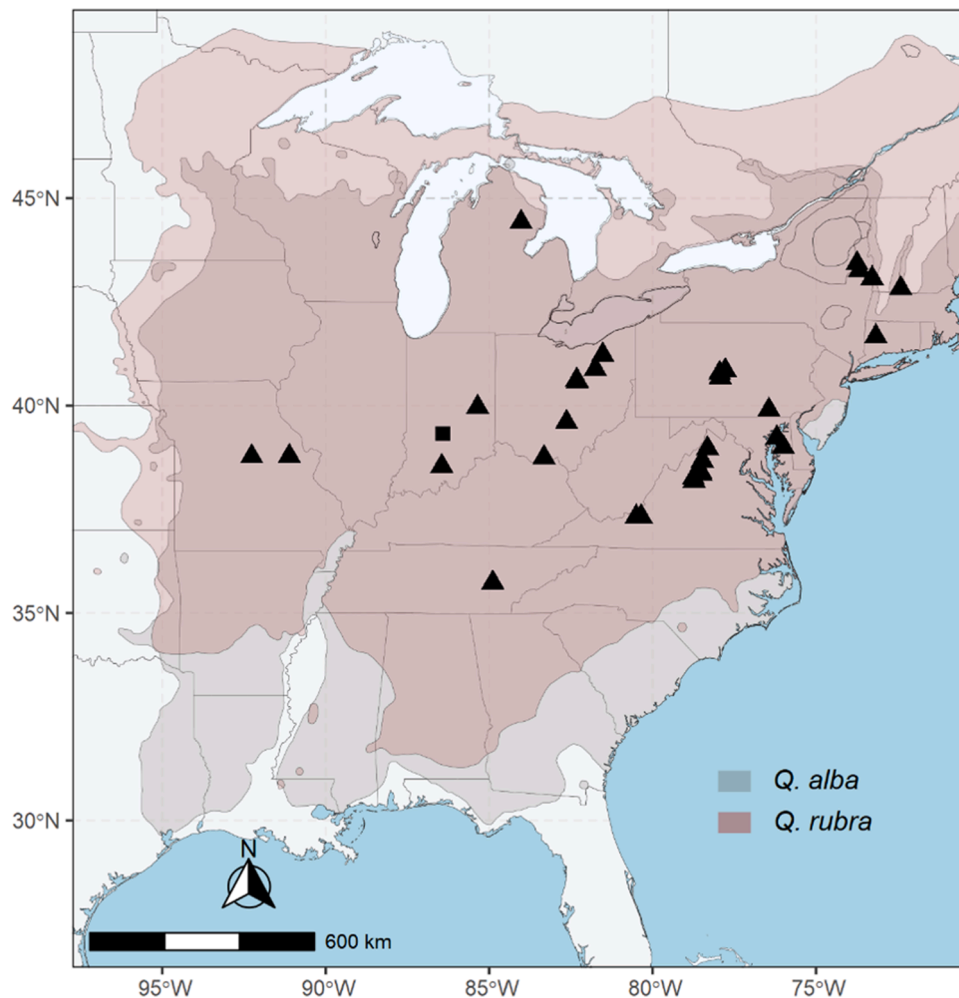
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Fig. 1. Locations of 35 tree-ring study sites (triangles) and one Ameriflux site (square), and the geographic range of *Q. alba* (gray) and *Q. rubra* (red) across the eastern United states. Each triangle represents a site from which both species co-occur and were sampled. Shading indicates geographic range of species (Prasad and Iverson, 2003).

and moisture availability across the midwestern and northeastern U.S. in recent decades (Mishra and Cherkauer, 2010; Horton et al., 2011; Seager et al., 2007; Maxwell and Harley 2017; Fei et al., 2017; Maxwell et al., 2016), climate extremes such as drought are projected to be more intense and frequent due to warming climate (IPCC et al., 2021). There is also strong evidence that the central and southwestern U.S. is seeing an enhanced risk of severe drought under an altered climate (Cook et al., 2015), and potentially a continental-scale drying across the U.S. (Ficklin and Novick, 2017). These periods of reduced moisture availability and prolonged drought reduce both tree growth and ecosystem-scale primary productivity (Novick et al., 2015; Piao et al., 2013; Ciais et al., 2005; Au et al., 2020). Within the context of changing precipitation patterns, areas with historically-high water limitations have experienced increases in *Q. alba* dominance, alongside simultaneous decreases in the dominance of *Q. rubra* (Novick et al., 2022).

The framework of iso/anisohydry is useful for characterizing responses to such water limitations in temperate forests (Roman et al., 2015), where more anisohydric species (like oaks) are found to maintain higher stomatal conductance rates in response to increasing water stress. This strategy, though, may expose anisohydric species to a greater risk of xylem cavitation (Benson et al., 2021; Novick et al., 2022). Several efforts to characterize the interspecific physiological responses of oaks to climatic variability have found broad similarities among species, notably so between *Q. alba* and *Q. rubra* (Cochard and Tyree, 1990; Abrams, 1990; Mediavilla and Escudero, 2004; LeBlanc and Terrell

2011; Schäfer, 2011; Roman et al., 2015; Kannenberg et al., 2019). However, limited evidence suggests that *Q. rubra* canopy conductance may be more sensitive to changes in vapor pressure deficit than *Q. alba*, particularly when soil moisture is low (Denham et al., 2021). Our understanding of these differences is further complicated by investigations of oak mortality following drought events, which have reported greater mortality rates in oaks of the red oak group (*Erythrobalanus*) compared to that of the white oak (*Leucobalanus*) group (Rosson, 2004; Shifley et al., 2006; Kabrick et al., 2008; Novick et al., 2022), suggesting a potentially more anisohydric strategy for dealing with moisture limitations in red oak group species that puts these oaks at greater mortality risk.

These studies highlight the complex nature of identifying differences in responses to water availability at the species scale. Though tree growth exhibits a high sensitivity to variation in climate, it can also be influenced by site factors, including aspect and stand density (Hurteau et al., 2007; Au et al., 2020). To account for this, we examine growth responses at a network of sites where both species co-occur, which minimizes the impact of site influence on growth differences. Tree growth is also the result of physiological processes within the tree itself, where hydraulic stress, due to soil or atmospheric water limitations, can reduce carbon uptake (Grossiord et al., 2020). Therefore, the objective of this paper is to examine how northern red (*Quercus rubra*) and eastern white oak (*Quercus alba*) responses to drought and pluvial conditions differ, using a combination of both growth (tree-ring) and
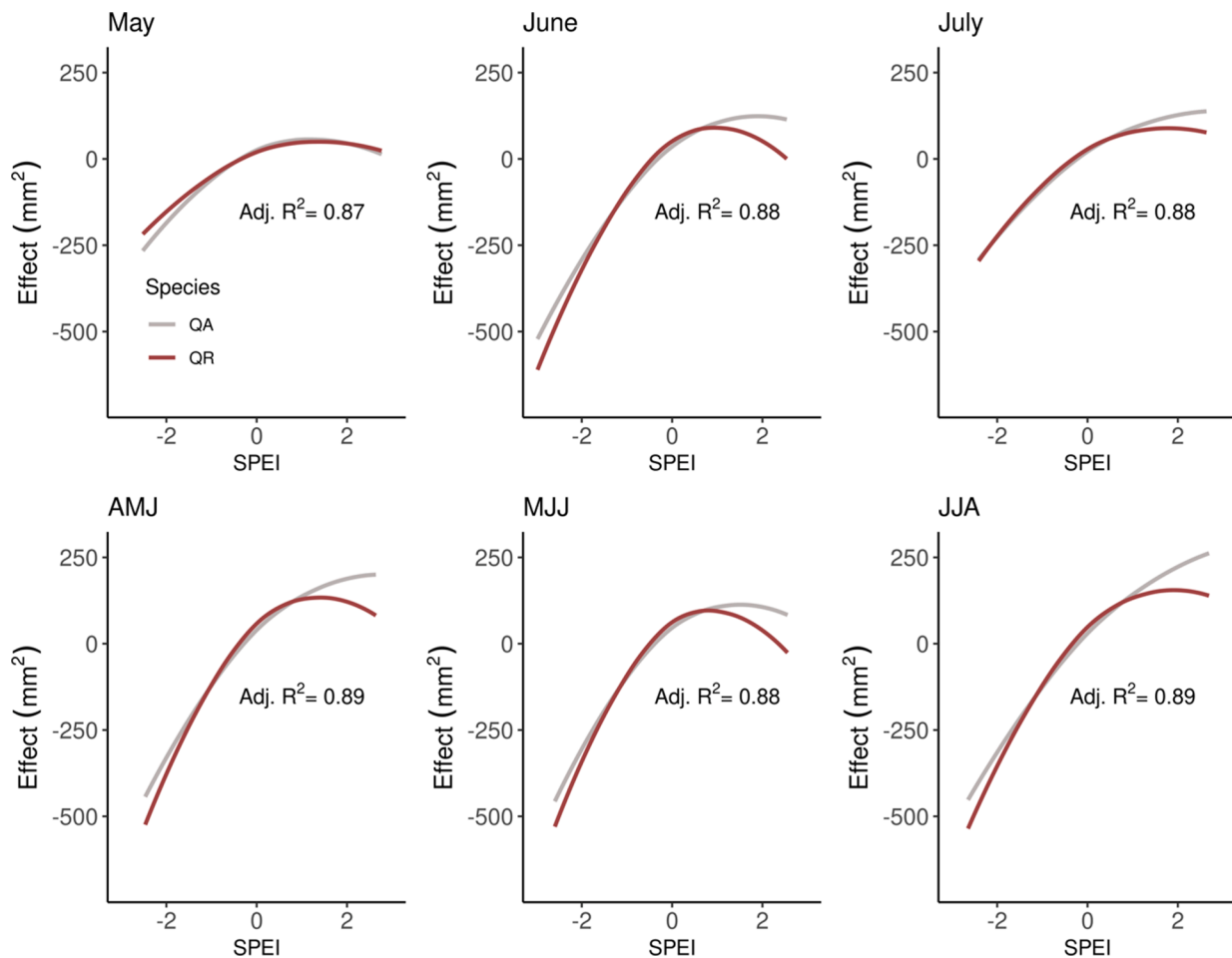
Fig. 2. Sensitivity plots of BAI to SPEI for each species. Sensitivity plots were constructed by applying the mean year for each chronology to the model to evaluate the independent effect of SPEI on BAI.

ecophysiological (stomatal conductance) data. We hypothesize that *Q. alba* exhibits a greater sensitivity to water availability than does *Q. rubra*. Additionally, we hypothesize that the differential responses between the two species varies spatially with respect to historical hydroclimatic patterns and the extent of their respective geographic ranges.

2. Materials and methods

2.1. Tree-ring data

Using data from multiple sources, we developed a network of co-occurring *Q. alba* and *Q. rubra* tree-ring chronologies at 35 sites, where both species were sampled, that span the eastern United States (Fig. 1, Table A.1). The co-occurrence of both species allowed for a novel, paired comparison of drought and pluvial response across the study region. The network contains previously published chronologies from the FORAST dataset (McLaughlin et al., 1986), which had the goal of obtaining a representative sample of overstory trees from a large number of sites distributed across the eastern half of the United States. We also gathered chronologies from published studies (Pederson et al., 2004; Pederson et al., 2013; Maxwell et al., 2015; Maxwell and Harley 2017; Strange et al., 2019; Dye et al., 2019), some of which were archived at the International Tree-Ring Data Bank (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data).

Lastly, we collected data from two additional sites. At each site, two cores were obtained, at breast height, from a minimum of 10 canopy dominant trees for each species. Sub-canopy trees are typically more sensitive to climate, though canopy-dominant trees have been found to sequester more carbon, thus, some species-specific responses may not be captured within the network due to the lack of sub-canopy trees (Dye et al., 2019; Rollinson et al., 2021).

To quantify the magnitude of annual growth of each species at the site level, we used the "dplR" R package (Bunn et al., 2019) to calculate basal area increments (BAI; Biondi and Qeadan 2008) of each series for each species before averaging across samples to build site chronologies. This produced a dataset of 5160 site-species-year observations. Diameter-at-breast-height (DBH) is needed to estimate BAI, but DBH data were not available at all sites. Given that using the sum of the ring widths to estimate DBH can produce substantial underestimates of BAI, we used the modeling approach developed by Lockwood et al. (2021) – which uses a model calibrated using sites where DBH data are available, and produces estimates of DBH with lower errors than using either the ring widths alone or pith locators – to reduce these biases by reconstructing the diameter of those sampled trees that lacked DBH measurements (five sites for each species).

2.2. Climate data

The 1-month and 3-month Standardized Precipitation-Evapotranspiration Index (SPEI) were chosen as the site-level climate variables. The SPEI provides a measure of moisture availability (i.e., water supply in the form of precipitation minus water demand in the form of evapotranspiration) that is standardized relative to local climate conditions, with zero indicating typical (median) conditions (Beguería et al., 2014). SPEI data for the period 1901 to 2017 were acquired from
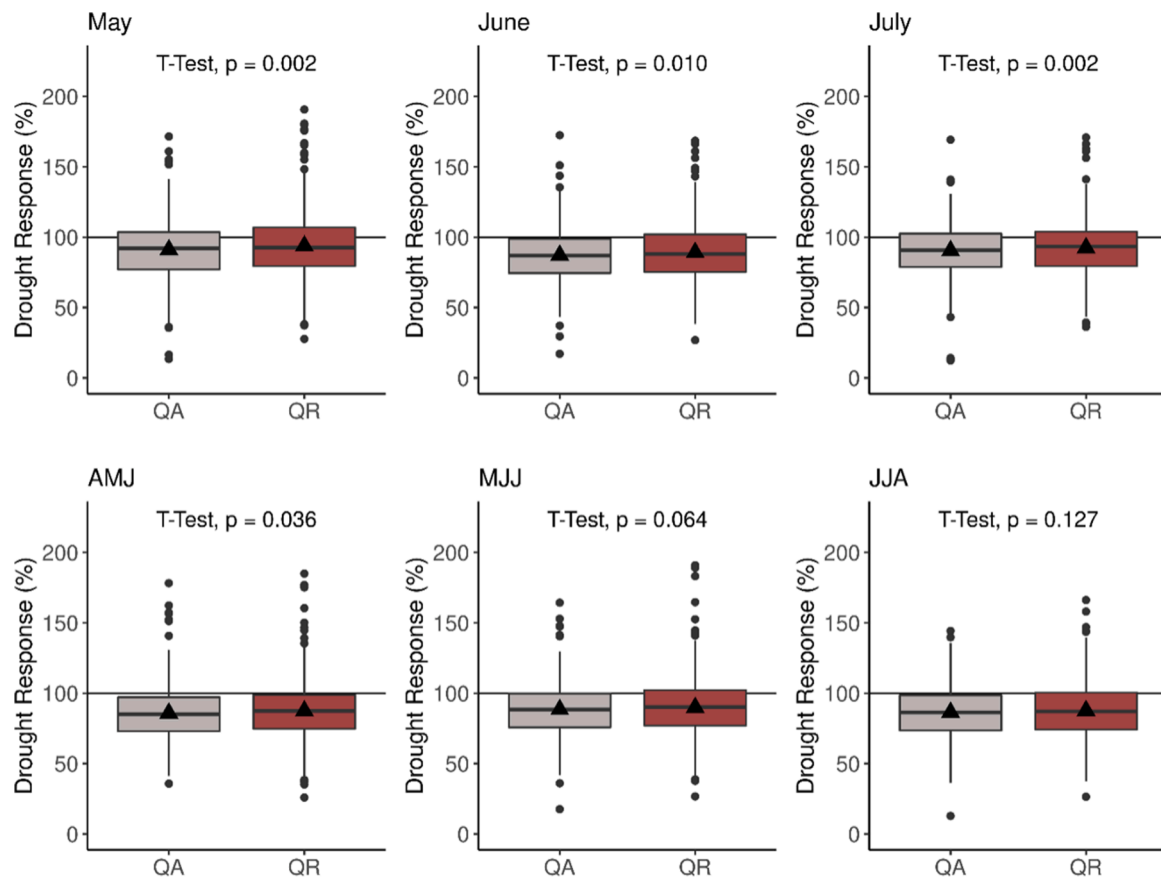
Fig. 3. Drought response, as the percent of BAI during drought years compared to non-drought years, for monthly combinations of May, June, July, April-June, May-July, and June-August with paired *t*-test p-values. Boxplot shows interquartile range (IQR) of drought response, with whiskers indicating the fences no further than 1.5 times the IQR with points indicating outliers beyond the whiskers (https://cran.r-project.org/web/packages/ggplot2/ggplot2.pdf).

Table 1
ANOVA table of Multivariate model results for interspecies drought response paired difference.

Term	F-value	p-value
Adjusted $R^2 = 0.08$, $p < 0.001$		
Year	2.44	0.118
Site	7.91	< 0.001
Year:Site	2.41	< 0.001
SPEI	2.22	0.137

the Global Drought Monitor (http://spei.csic.es/index.html) at 0.5-degrees spatial resolution. To evaluate the sensitivity of growth during different portions of the growing season, we used May, June, and July 1-month SPEI, and April-June, May-July, and July-August 3-month SPEI combinations. We also calculated historical June potential evapotranspiration (PET) at each site for the period 1971 to 2000 to represent longer term, historical site conditions. Average June minimum and maximum temperatures and precipitation data were obtained at each site from the high resolution (30 arc-second) database WORLDCLIM version 2.1 (Fick and Hijmans, 2017) and used with site latitude to calculate June PET over the 1971–2000 period with a simplified Hargreaves algorithm.

2.3. Drought and pluvial response

Annual tree growth exhibits nonlinear patterns both over time (Fritts, 2012) and in response to climatic variables (Maxwell et al., 2016; Anderson-Teixeira et al., 2021). To examine these nonlinearities, we used the "mgcv" package in R to fit a generalized additive model to

quantify the relationship between tree growth and water availability (Wood and Wood, 2015; Pedersen et al., 2019):

$$BAI = s\ (SPEI) + s(Year) \tag{1}$$

where *Year* is included to account for a positive growth trend (Figs. A.1 and A.2), and *s* is a smooth function equation, or spline, fit for each species:

$$s(SPEI) = \sum_{k=1}^{3} \beta_k b_k(SPEI) \tag{2}$$

where *k* represents the number of weights, β represents the weighted values and *b* is the basis functions.

Reductions in annual tree growth have been used to identify species-level differences in response to drought conditions in the eastern US (Kannenberg et al., 2019; Au et al., 2020). Responses to pluvial conditions are comparatively understudied, though recent findings suggest variation in responses is present across site types and taxonomic classes (Jiang et al., 2019) Here, we identified drought conditions by selecting the years with SPEI < −1for each 1- and 3-month period. We defined pluvial conditions by selecting the years with SPEI > 1. In terms of their cumulative probabilities, these SPEI values are equivalent to one standard deviation departure from mean site conditions. We defined drought response as:

$$Drought\ response = \ (BAI(d)\ /\ \overline{BAI(nd)}) * 100 \tag{3}$$

where *BAI(d)* represents the BAI during a given drought year, and $\overline{BAI(nd)}$ represents the mean of BAI during non-drought years. Pluvial response was calculated using the same procedure for pluvial and non-
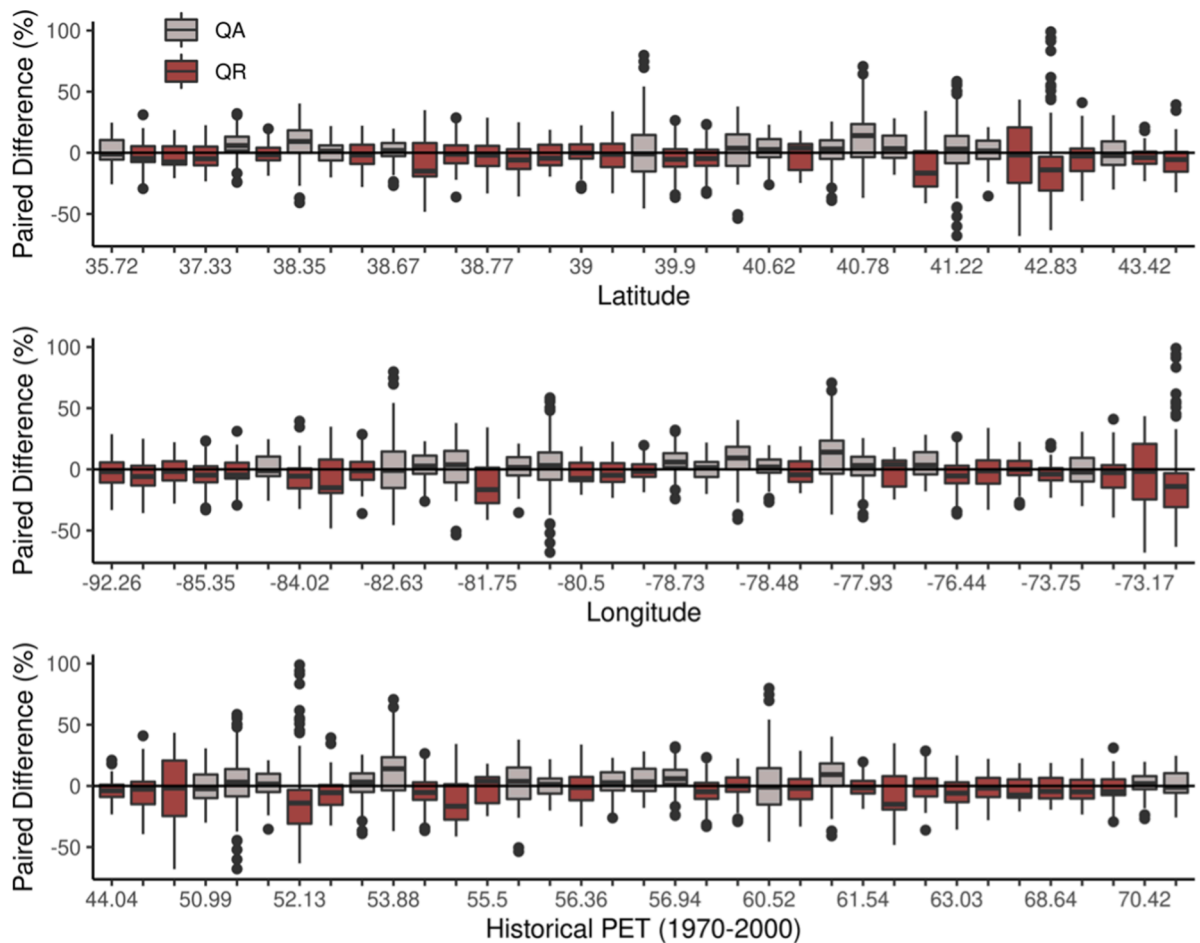
Fig. 4. Paired difference in drought response during all drought years by site according to increasing site latitude, longitude, and historical PET. Positive numbers indicate a greater drought response in *Q. rubra* for a given year while negative numbers represent a greater response in *Q. alba*. Boxplots are colored according to greater mean drought response in *Q. alba* (gray) or *Q. rubra* (red). Boxplot shows interquartile range (IQR) of drought response, with whiskers indicating the fences no further than 1.5 times t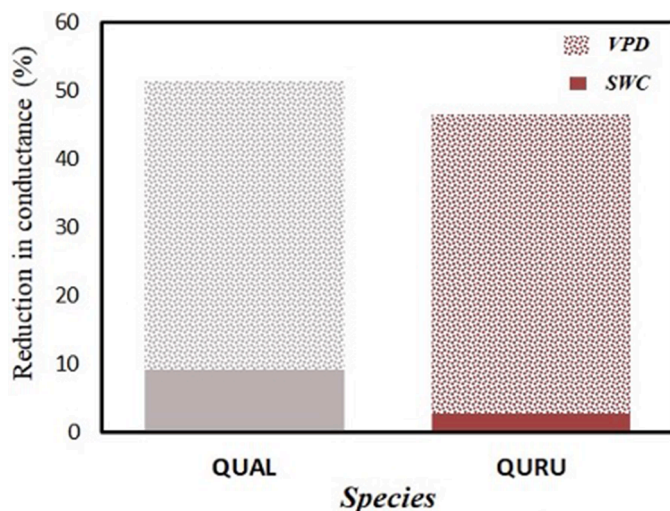he IQR with points indicating outliers beyond the whiskers (https://cran.r-project.org/web/packages/ggplot2/ggplot2.pdf).

Fig. 5. Percent reduction in stomatal conductance attributed to soil water content (SWC) and vapor pressure deficit (VPD).

pluvial years. Given that BAI increased over time in some chronologies, we calculated means of non-drought or non-pluvial conditions within blocks that split each chronology length into thirds. This approach reduces the effect of the growth trend on drought and pluvial response

calculations while retaining the units of BAI that would otherwise be lost in a detrended chronology. We then used paired t-tests to test for interspecies differences in mean drought and pluvial response. In addition to the mean response, interannual variation in drought and pluvial responses between the two species may be a useful indicator of intra-species ecophysiological differences. Thus, we used the interquartile range of growth reductions and increases, followed by an F-test to evaluate differences in variances of the responses of the two species. To determine if site characteristics or climatic conditions influence the interspecies difference in drought and pluvial response, we calculated paired difference in responses by subtracting *Q. rubra* drought and pluvial response from the *Q. alba* for each occurrence. We then used this difference as the response variable in a multivariate model with drought/pluvial timing (month), drought/pluvial severity (SPEI), historical PET, latitude, and longitude as predictors.

2.4. Stomatal conductance

To examine the differences in physiological responses between *Q. alba* and *Q. rubra*, which may in turn produce differences in growth response, we collected sap flux measurements from 2011 to 2013, to estimate stomatal conductance (G_c) for both species at a single site located centrally within both species' ranges (Denham et al., 2021). Stomatal conductance is commonly used to characterize species along the isohydric/anisohydric gradient (Hochberg et al., 2018).

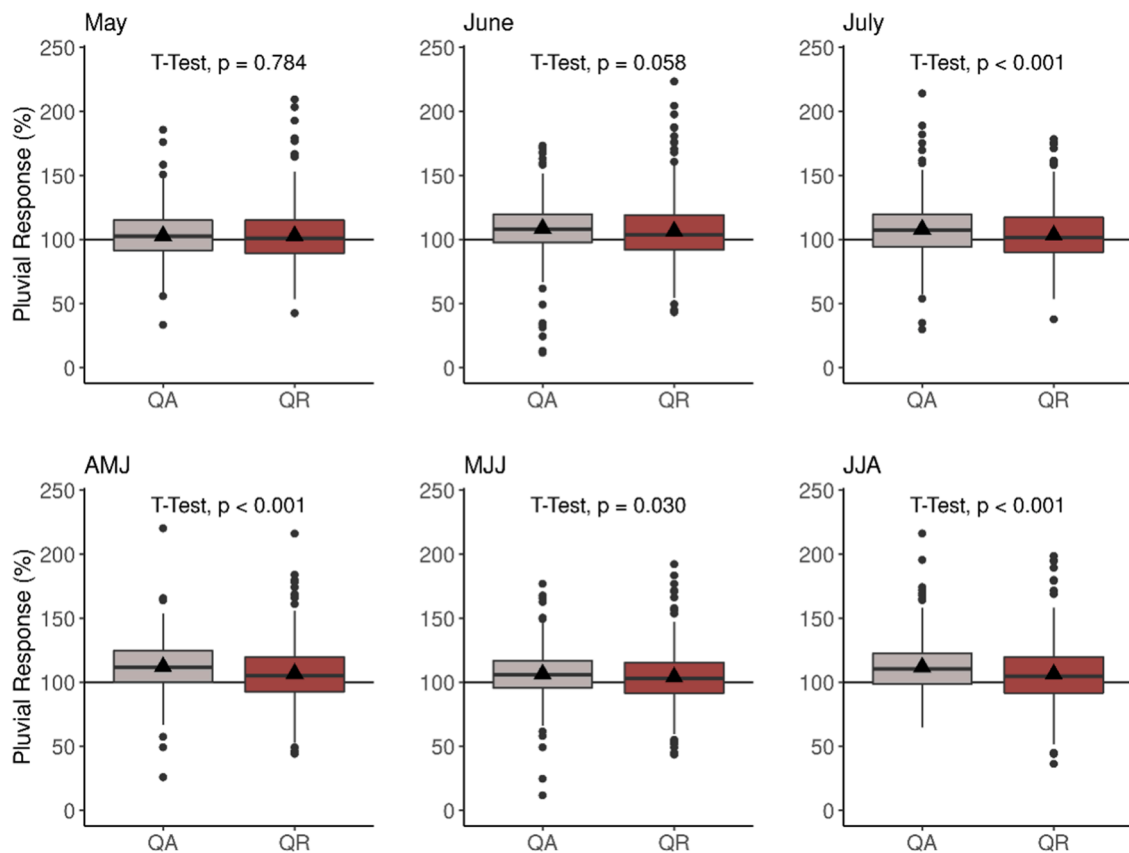Sap flux measurements were made using the compensation heat

Fig. 6. Pluvial response, as the percent of BAI during pluvial years compared to non-pluvial years, for monthly combinations of May, June, July, April-June, May-July, and June-August with paired *t*-test p-values. Boxplot shows interquartile range (IQR) of drought response, with whiskers indicating the fences no further than 1.5 times the IQR with points indicating outliers beyond the whiskers (https://cran.r-project.org/web/packages/ggplot2/ggplot2.pdf).

Table 2
ANOVA table of multivariate model results for interspecies pluvial response paired difference. The *Year* term is included in the model to account for the growth trend present in BAI chronologies.

Term	F-value	p-value
Adjusted $R^2 = 0.08$, $p < 0.001$		
Year	1.82	0.178
Site	3.36	< 0.001
Year:Site	2.27	< 0.001
SPEI	4.27	0.039

pulse method (Green et al., 2003), on two trees of both species at Morgan Monroe State Forest, in Monroe County, Indiana (Fig. 1). These measurements were filtered to include only data from day of year (DOY) $150 - 240$, photosynthetic active radiation (PAR) > 1000 w/m^2, and $D > 1$ kPa. We then used these measurements to estimate stomatal conductance using a simplified Penman-Monteith equation (see Denham et al., 2021 for details).

While his approach is used commonly to classify species along the isoydric/anisohydric spectrum, it does not account for the independent effects of vapor pressure deficit on stomatal conductance (Denham et al., 2021). Thus, to disentangle the effects of vapor pressure deficit (VPD) from soil water content (SWC), we separated the stomatal conductance (G$_c$) time series sets into five quintile bins, and within each bin, we created five parameter sets for each species by fitting a quasi-empirical function to normalized G$_c$ and VPD:

$$G_C = b - m \ln(VPD) \text{ (mmol } m - 2 \text{ } s - 1) \qquad (4)$$

Where b represents the conductance when VPD $= 1.0$ kpa and m is the sensitivity of stomatal conductance (G$_c$) to *VPD* (Oren et al., 1999).

This produces five parameterized bins of moisture availability, which we used to quantify the individual effects of both SMC and VPD on stomatal conductance (G$_c$), via changes in the intercept and slope of the G$_c$-VPD relationship (Denham et al., 2021).

3. Results

The relationship between radial growth and SPEI of both species was nonlinear for all 1- and 3-month comparisons (Fig. 2). Using the mean *Year* value within chronologies to control for growth trends (Figs. A.1, A.2), the sensitivity of BAI (mm^2) to SPEI was nearly identical between species (Fig. 2), particularly during the month of May. For all monthly comparisons, *Q. alba* and *Q. rubra* BAI values increased at highly similar rates as SPEI values increase from -3 to 0, and tended to plateau, or decrease, at high positive values, though the sensitivities diverge at the highest SPEI values. Both species experience a greater sensitivity to SPEI during the month of June compared to May and July. Including both year and SPEI terms in the model accounted for a high proportion of variance for all monthly comparisons (87–89%).

3.1. Drought response

The mean reduction in radial growth of *Q. alba* was greater than that of *Q. rubra* during years with droughts for all 1- and 3-month comparisons, although not significantly greater during May-July or June-August droughts (Fig. 3). Across all drought years, mean radial growth was reduced by an average of 11.76 percent in *Q. alba* chronologies, compared to an average reduction of 9.96 percent in *Q. rubra* chronologies (paired *t*-test, $p < 0.001$). Though *Q. alba* experienced a greater reduction in growth as a percent of non-drought growth, the magnitude of growth was reduced more in *Q. rubra* (Fig. A.3), particularly in later
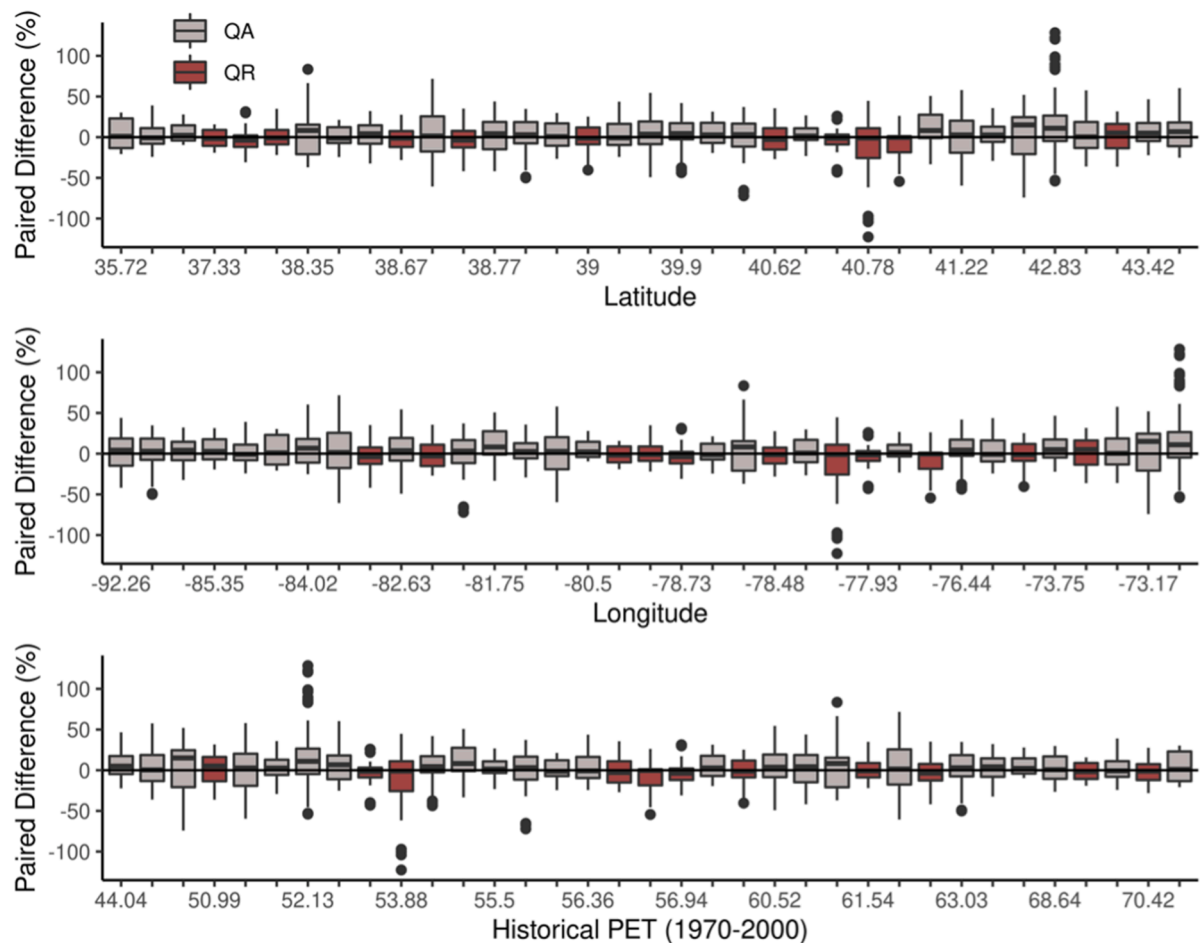
Fig. 7. Paired difference in pluvial response during all drought years by site according to increasing site latitude. Positive numbers indicate a greater pluvial response in *Q. alba* for a given year while negative numbers represent a greater response in *Q. rubra*. Boxplots are colored according to greater mean pluvial response in *Q. alba* (gray) or *Q. rubra* (red). Boxplot shows interquartile range (IQR) of drought response, with whiskers indicating the fences no further than 1.5 times the IQR with points indicating outliers beyond the whiskers (https://cran.r-project.org/web/packages/ggplot2/ggplot2.pdf).

season 3-month droughts (*t*-test, *p* = 0.0088). The interquartile range of the percent reduction of radial growth during all drought years was slightly greater in *Q. rubra* (25.74%) than in *Q. alba* (24.31%), while the variance was significantly greater in *Q. rubra* (*F* = 0.86, *p* < 0.001).

The interspecific differences in drought response had a weak or nonexistent functional relationship to drought severity and drought timing (Fig. A.3). In other words, during years with droughts occurring in all monthly combinations, the difference between *Q. rubra* and *Q. alba* drought responses did not meaningfully change as drought severity increased, and drought response difference during all drought years was not strongly correlated with SPEI (Pearson's product-moment, *p* = 0.18).

A multivariate model constructed using the paired species difference during all drought years indicated moderate site-level influences and weak climatological influences on the drought response differences (Table 1, adjusted *R²=0.1*). Here, the interaction between site and year was strongly related to the response difference, indicating that growth trend differences between species vary by site.

The site-level variables of latitude, longitude, and historical PET were not included in the final model due to their weak explanatory power of drought response differences. However, the site-variable itself was strongly associated with interspecies differences in drought response. The response of *Q. alba* was, on average, slightly greater than *Q. rubra* at lower latitude sites and sites with higher historical PET values (Fig. 4, top and bottom rows, respectively). Greater drought responses in *Q. rubra* are moderately clustered at sites with mid-high latitude, mid longitude, and lower historical PET values.

Sap flux measurements at Morgan Monroe State Forest revealed that both species experienced reductions in G_c similar to reductions in growth, due to both soil and atmospheric drying, though reductions differed slightly between species (Fig. 5). Reductions in stomatal conductance due to SWC limitations were greater in *Q. alba* (9.15%) than in *Q. rubra* (2.77%). Overall, both species experienced much greater reductions in G_c due to VPD limitations. The between-species differences in G_c reductions were much smaller (42.27% for *Q. alba* and 43.63% for *Q. rubra* respectively).

3.2. Pluvial response

Mean increases in radial growth of *Q. alba* were greater than those of *Q. rubra* during pluvial years in all monthly combinations, though not significantly greater during May pluvial years (Fig. 6). Increases in the magnitude of BAI were also significantly greater in *Q. alba* (Fig. A.5). Across all pluvial years, mean radial growth increased by an average of 8.42 percent in *Q. alba* chronologies, compared to an average increase of 5.14 percent in *Q. rubra* chronologies (paired *t*-test, *p* < 0.001). This difference (3.2 percent) was larger than the drought response difference between species (1.8 percent) and is likely due to between-species differences in the nonlinearity of BAI in response to SPEI (Fig. 2). The interquartile range of the percent increase of radial growth during all pluvial years was slightly greater in *Q. rubra* (26.67%) than in *Q. alba* (24.26%), while the variance was significantly greater in *Q. rubra* (*F* = 0.78, *p* < 0.001).

The between-species paired difference in pluvial condition response had stronger, but still generally weak, relationships to both pluvial intensity and pluvial timing than drought responses (Fig. A.6). During years when pluvial conditions occurred during the months June, April-June, and June-August, the difference in pluvial response tended to increase with pluvial intensity, indicating a greater increase in *Q. alba* chronologies. Across all months, the Pearson's product-moment correlation between the interspecies difference in pluvial response and SPEI was 0.04 ($p = 0.05$).

Similar to drought responses, a multivariate model constructed using the paired species differences during all pluvial years indicated moderate site-level and climatological influences on pluvial response differences (Table 2, $R^2 = 0.08$). The interaction between site and year was strongly related to the pluvial response difference, indicating again that growth trend differences between species vary by site.

Like drought responses, the site-level variables of latitude, longitude, and historical PET were not included in the final model due to their weak explanatory power of pluvial response differences. Pluvial responses of *Q. alba* were greater than *Q. rubra* at higher latitude sites, particularly sites above 40° (Fig. 7).

4. Discussion

Overall, we found that both the radial growth, and stomatal conductance, of *Q. alba* appears to experience greater reductions in response to drought, but greater increases in response to pluvial conditions. The variability of growth responses to drought and pluvial conditions were also consistently and significantly greater in *Q. rubra*. We also found that the increase in growth of both species due to pluvial conditions were less than the decreases due to drought.

In response to both 1- and 3-month drought occurrences both species exhibited highly similar patterns in the reductions of radial growth. This is consistent with their similar physiological, ecological and biogeographical characteristics (Abrams 1990; Abrams 1996; LeBlanc and Terrell 2011; Cavender-Bares 2016; Meinzer et al., 2013). For example, oaks are deep-rooting species with ring-porous xylem anatomy and narrower late-wood vessels that may reflect resistance to cavitation during drought (Abrams 1990). The similar distributions of *Q. alba* and *Q. rubra* are the result of broad *Quercus* geographic range expansion following the last glacial period, combined with fire regime change and land-clearing practices, and the similarities in drought response may also be linked to ecophysiological similarities such as stomatal regulation of leaf water potential (Meinzer et al., 2013; Kannenberg et al., 2019). Thus, the high degree of drought response similarity between these two species is unsurprising.

While oaks in general are considered to be anisohydric and drought tolerant species, the reductions in radial growth and stomatal conductance of *Q. alba* in response to drought was moderately, but consistently and significantly greater than *Q. rubra* during short term drought conditions. This may represent a more isohydric response to drought in *Q. alba*, or in other words, a more anisohydric response to drought in *Q. rubra*, though considerable variation in hydraulic behaviors has been reported within both species (Bryant et al., 2021). This may correspond to greater variation in *Quercus* radial growth observed along geographic gradients than taxonomic classification (Martin-Benito and Pederson, 2015). The difference in drought responses was slightly decreased during longer term droughts, though *Q. alba* still exhibited consistently greater reductions in growth than *Q. rubra*. The finding that soil moisture limitation produced greater reductions of stomatal conductance in *Q. alba* lends additional support to a physiological difference between the two species.

The finding that *Q. alba* experiences a greater increase in growth during pluvial conditions compared to *Q. rubra* is a previously unknown difference between these two species. Interestingly, *Q. alba* exhibited greater increases in both total growth and growth as a percentage of non-pluvial years. The difference between the species pluvial response

was also greater than the difference in drought responses. Taken together, these trends suggest that growth of these species does not respond linearly to moisture availability, which lends limited support to recent findings that increases in growth due to pluvial conditions may not compensate for decreases due to drought in angiosperm species in eastern North American forests (Jiang et al., 2019). This has added importance in light of potential changes to regional precipitation regimes that may result in more extreme pluvial conditions in addition to increases in drought duration or severity (IPCC et al., 2021), which could contribute to ongoing demographic shifts in eastern North American forests (Novick et al., 2022) and may coincide with drought and/or pluvial sensitivity, in addition to overall mortality risk following drought events. Thus, *Q. rubra* may be at a greater risk of drought-induced mortality, and, simultaneously, may be less able to capitalize on increases in water availability compared to *Q. alba*.

Neither drought severity nor drought timing were related to the difference in drought response between species. This suggests that *Q. alba* employs more drought-sensitive responses across a broad range of drought conditions, and that this difference persists temporally throughout the growing season, which is in line with existing evidence that *Q. alba* exhibits slightly stronger growth-climate relationships (Tardif and Conciatori, 2006; LeBlanc and Terrell, 2011).

The difference in both drought and pluvial responses was significant at the site level, though relationships with spatial and climatological factors were weak to moderate. The greater reduction in growth of *Q. alba* during droughts was most notable at the highest latitude sites, while differences converged toward zero at sites with higher historical June PET. This is in line with reportedly stronger growth-climate correlations in *Q. alba* at higher latitudes (Tardif and Conciatori, 2006), and also with the abundance of literature highlighting the importance of site water balance to *Quercus* radial growth (Friesner and Friesner, 1941; Miller, 1950; Fritts, 1962; Estes, 1970; Guyette et al., 1982; Jacobi and Tainter, 1988; Robertson, 1992; Foster and LeBlanc, 1993; Rubino and McCarthy, 2000; LeBlanc and Terrell, 2001; Tardif et al., 2006, 2011). Site-level influence may also be due to forest stand dynamics and finer-scale variables such as soil types, topography, and aspect of sampling locations.

We also found a slightly, but significantly, greater variation in the drought response of *Q. rubra* than *Q. alba*. This may be due to differences in the variation of *Q. rubra* ecophysiology (Kubiske and Abrams, 1992; Cavender-Bares and Bazzaz, 2000). Seedlings of *Q. rubra* from mesic sites have been found to exhibit greater variation in gas exchange during drought compared to those from xeric sites, indicating ecotype-specific responses to drought (Kubiske and Abrams, 1992). Cavender-Bares and Bazzaz (2000) reported greater predawn leaf potentials in *Q. rubra* juveniles during a drought compared to mature trees, indicating age-specific vulnerability to drought. This effect may partially explain the greater variation observed in *Q. rubra* drought response here due to the greater variation in size of sampled trees compared to *Q. alba* (A6). These findings are particularly important in the context of mortality rates, as oaks in the red oak group experience higher mortality rates than the white oak group, which also correspond to size and growth rates (Shifley et al., 2006; Wood et al., 2018; Druckenbrod et al., 2019). The greater reduction in total BAI observed in *Q. rubra* likely reflects its greater overall growth rate as a species and indicates important physiological differences that should be considered in ecophysiological models. These subtle differences highlight the need to diversify tree-ring data repositories, such as the ITRDB, which have been shown to contain species bias particularly with respect to *Q. alba* (Zhao et al., 2019).

5. Conclusions

Our results indicate that across their geographic ranges, *Q. alba* exhibits a moderately stronger response to drought and pluvial conditions than *Q. rubra*. This has important implications for species-specific models of forest ecosystem functioning. We also found that the

increase in growth of both species due to pluvial conditions were less than the decreases due to drought, which highlights the need to link physiological and ecological processes to better understand responses at the ecosystem scale (Yi and Jackson, 2021). We believe this study highlights the need for additional investigations into intra and inter-specific responses to drought and pluvial responses, particularly those that assess the ecophysiological mechanisms underpinning drought and pluvial responses.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A

Table A1
Site data and chronology statistics.

Site	Site ID	Lat	Lon	Series (QA)	Series (QR)	Years (QA)	Years (QR)	SIC (QA)	SIC (QR)
Catlin Woods	CT_CW	41.67	73.17	30	30	1812–1981	1890–1981	0.51	0.64
Pioneer Mothers	IN_PM	38.54	−86.45	30	45	1817–2011	1861–2012	0.55	0.55
Wilbur Wright	IN_WW	39.97	−85.35	30	30	1875–1997	1826–1997	0.63	0.60
Rifle River State Park	MI_RR	44.42	−84.02	32	32	1879–1997	1881–1998	0.65	0.62
Ashland Forest	MO_AF	38.77	−99.26	32	31	1869–1998	1873–1997	0.74	0.70
Reifsneider State Forest	MO_RS	38.78	−91.11	32	30	1866–1998	1859–1997	0.76	072
Pigsah State Park	NC_PS	42.83	−72.41	25	13	1780–2014	1789–2014	0.59	0.54
Goose Egg State Forest	NC_PS	43.07	−73.28	31	109	1681–2013	1804–2014	0.59	0.62
Prospect Man Lake George	NY_LG	43.42	−73.75	32	28	1659–2001	1816–2001	0.66	0.61
Saratoga Spa	NY_SS	43.25	−73.67	28	29	1930–1981	1930–1981	0.35	0.35
Barneby	OH_B	39.60	−82.63	30	30	1814–1982	1845–1982	0.65	0.62
Cuyahoga Valley	OH_CV	41.22	−81.52	29	30	1810–1981	1887–1981	0.54	0.62
Cuyahoga Valley 2	OH_CV2	41.22	−81.53	30	30	1872–1981	1868–1981	0.56	0.66
Site	Site ID	Lat	Lon	Series (QA)	Series (QR)	Years (QA)	Years (QR)	SIC (QA)	SIC (QR)
Johnson State Nature Preserve	OH_JW	40.88	−81.75	36	19	1708–2012	1790–2016	0.62	0.56
Mohican State Forest	OH_MS	40.58	−82.30	28	26	1831–1982	1832–1982	0.61	0.48
Mohican State Forest 2	OH_MS2	40.62	−82.32	30	30	1860–1982	1880–1982	0.62	0.60
Shawnee State Forest	OH_SS	38.75	−83.32	32	30	1883–1982	1890–1982	0.62	0.64
Shawnee State Forest 2	OH_SS2	38.75	−83.32	28	30	1903–1981	1919–1982	0.54	0.58
Otter-Creek Red Lion	PA_OC	39.90	−76.44	28	29	1755–2003	1827–2002	0.61	0.46
Rockview	PA_RV	40.85	−77.78	32	32	1930–1982	1930–1982	0.50	0.55
Stone Valley Forest	PA_SV	40.68	−77.93	30	30	1930–1982	1930–1982	0.61	0.71
Stone Valley Forest 2	PA_SV2	40.67	−77.93	30	32	1930–1981	1930–1981	0.49	0.61
The Barrens	PA_TB	40.78	−77.95	28	28	1930–1982	1930–1982	0.45	0.64
Cumberlands 1	TN_C1	35.72	−84.88	30	30	1651–1982	1930–1982	0.55	0.56
Cumberlands 2	TN_C2	35.72	−84.90	30	32	1930–1982	1930–1982	0.63	0.50
Craig Creek	VA_CC	37.33	−80.35	30	30	1930–1982	1930–1982	0.44	0.45
Clover Hollow	VA_CH	37.32	−80.50	30	30	1930–1982	1930–1982	0.52	0.50
Shenandoah Big Bend	VA_SB	38.35	−78.52	30	30	1930–1982	1930–1982	0.45	0.49
Shenandoah Dryrun	VA_SD	38.40	−78.53	30	29	1930–1982	1930–1982	0.45	0.64
Shenandoah Madison	VA_SM	38.25	−78.75	30	30	1930–1982	1930–1982	0.44	0.49
Shenandoah Moorman	VA_SMO	38.18	−78.73	30	30	1930–1982	1920–1982	0.39	0.52
USGS 1	VA_UM1	38.97	−78.32	28	30	1850–1982	1930–1983	0.75	0.64
USGS 2	VA_UM2	38.67	−78.48	30	32	1908–1982	1920–1982	0.70	0.72
USGS Piedmont	VA_UP	39.01	−76.00	32	32	1900–1981	1920–1982	0.61	0.65
USGS Piedmont 2	VA_UP2	39.32	−76.20	32	34	1930–1982	1930–1982	0.57	0.55

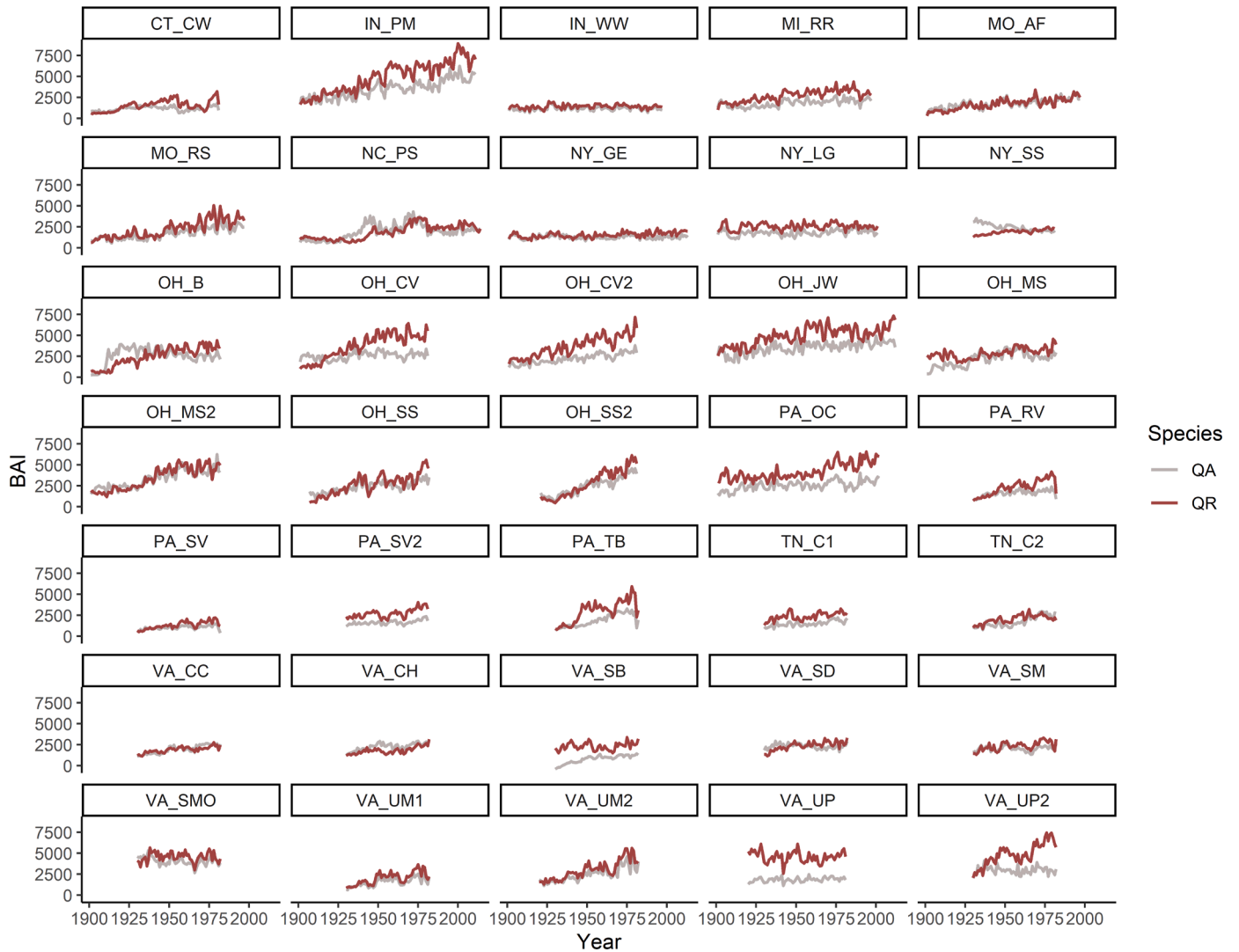**Fig. A1.** Basal area increment (mm^2) time series for *Q. alba* and *Q. rubra* at all 35 tree-ring sites.
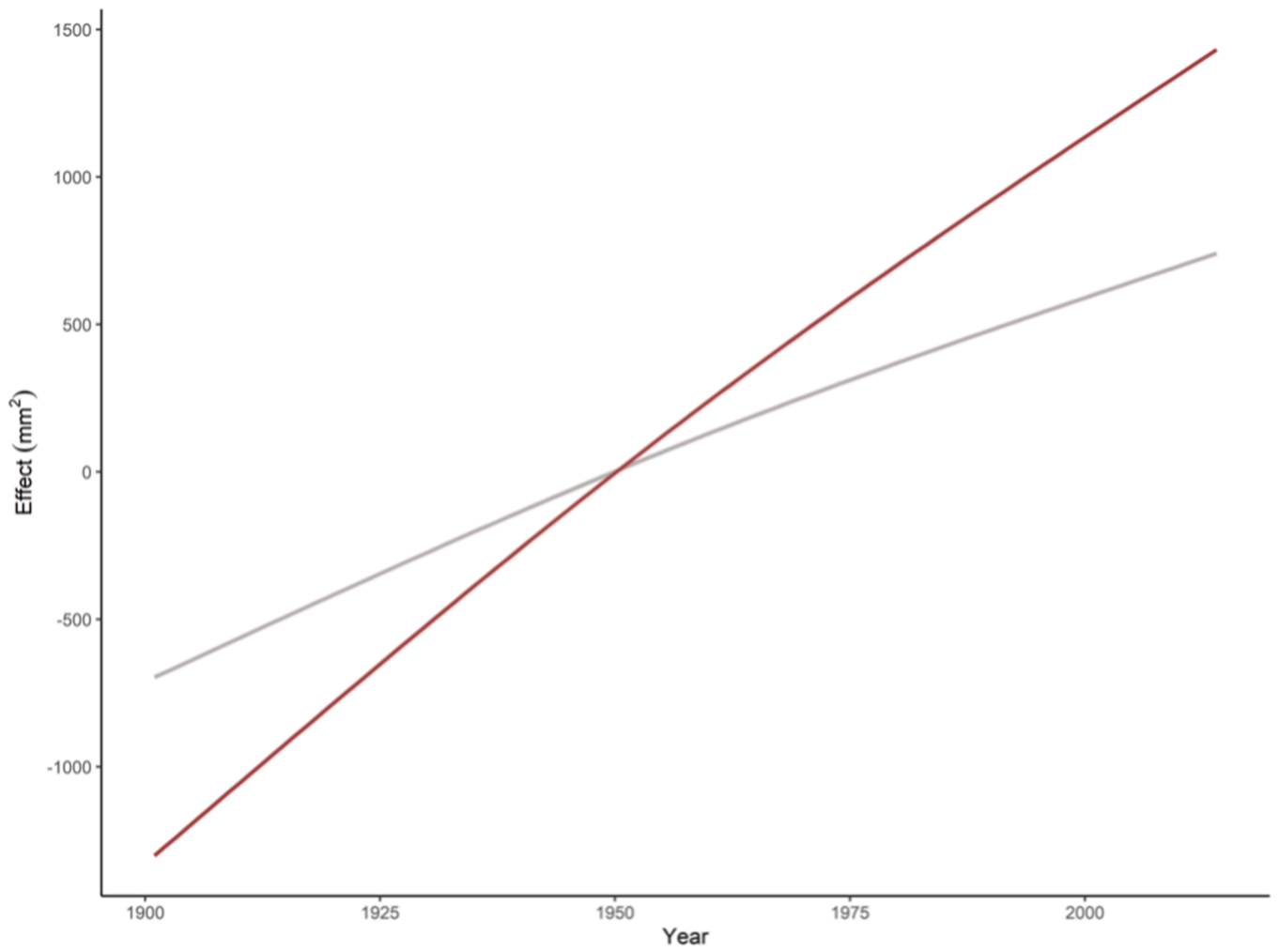
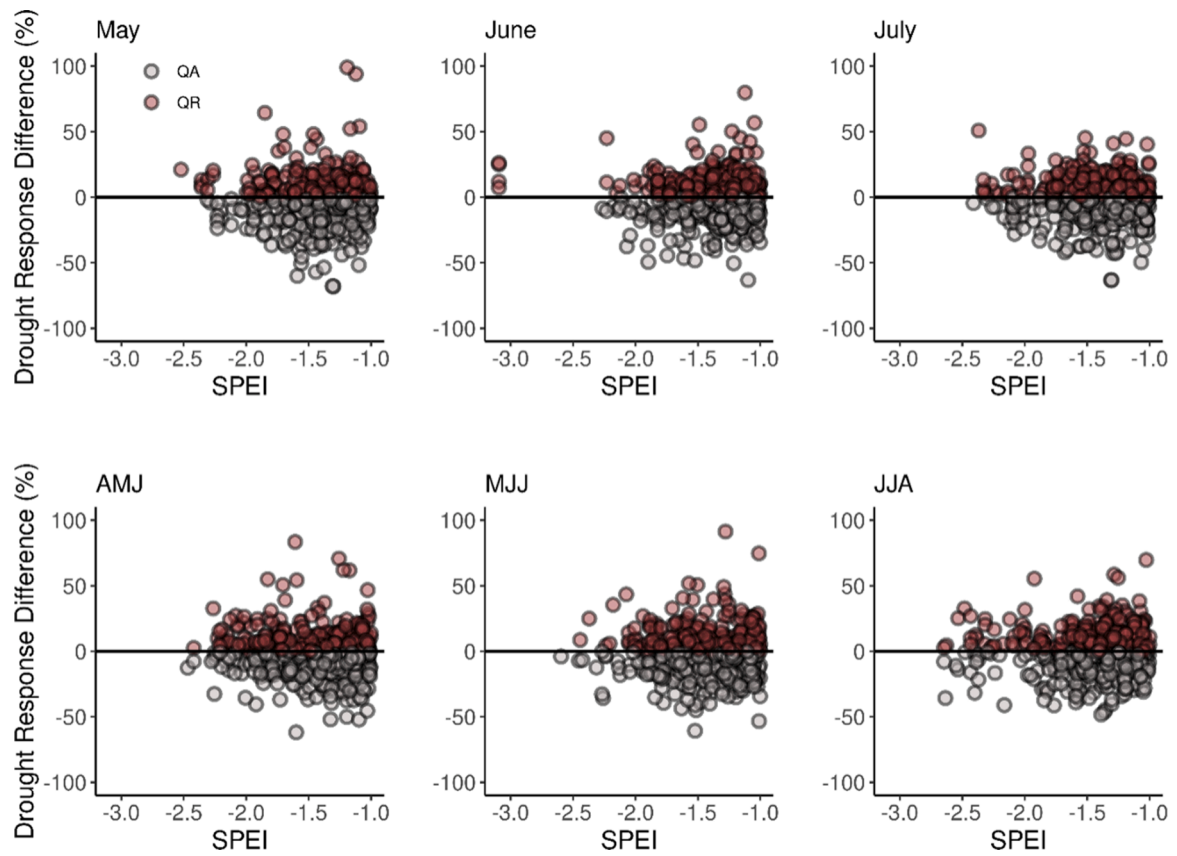**Fig. A2.** Species-specific mean growth trend.

Fig. A3. Paired differences in drought responses for monthly combinations of May, June, July, April-June, May-July, and June-August. Paired difference was calculated by subtracting the percent of BAI during drought years to non-drought years in *Q. rubra* from the percent of BAI during drought years of *Q. alba*, such that positive values represent a greater reduction in *Q. rubra*, and negative values represent a greater reduction in *Q. alba*. .
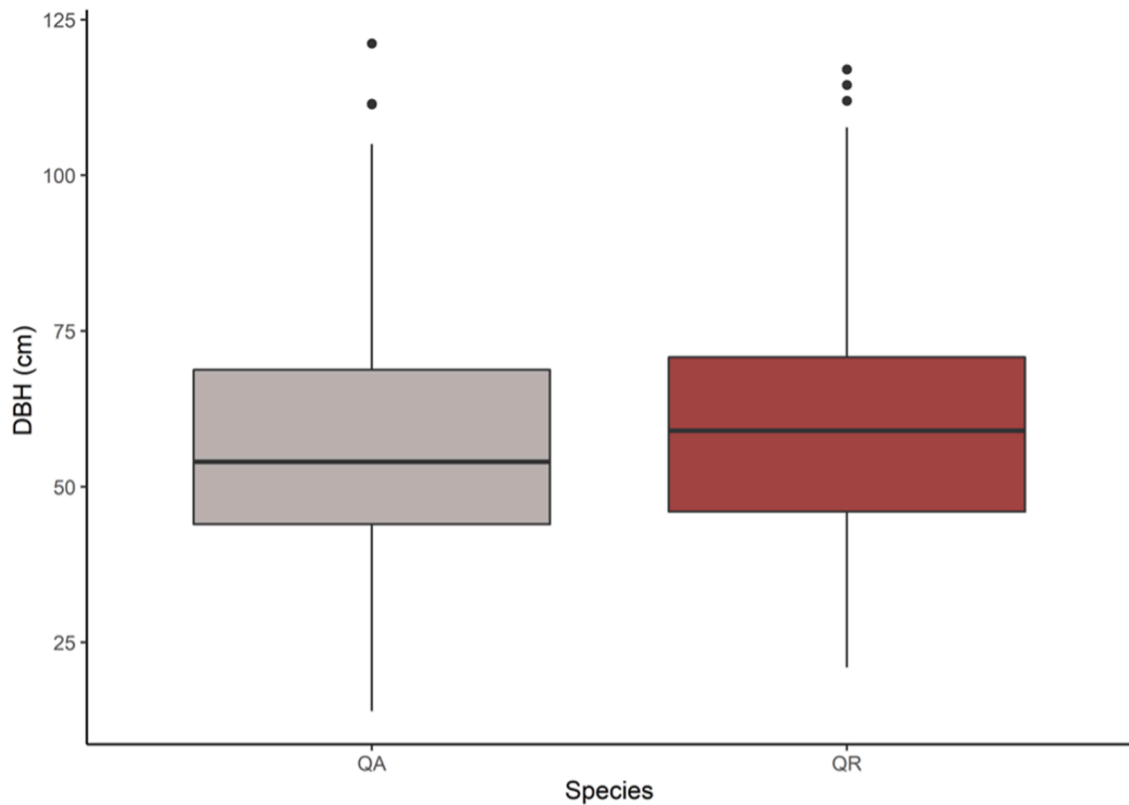

Fig. A4. Distribution of DBH of sampled trees for each species.
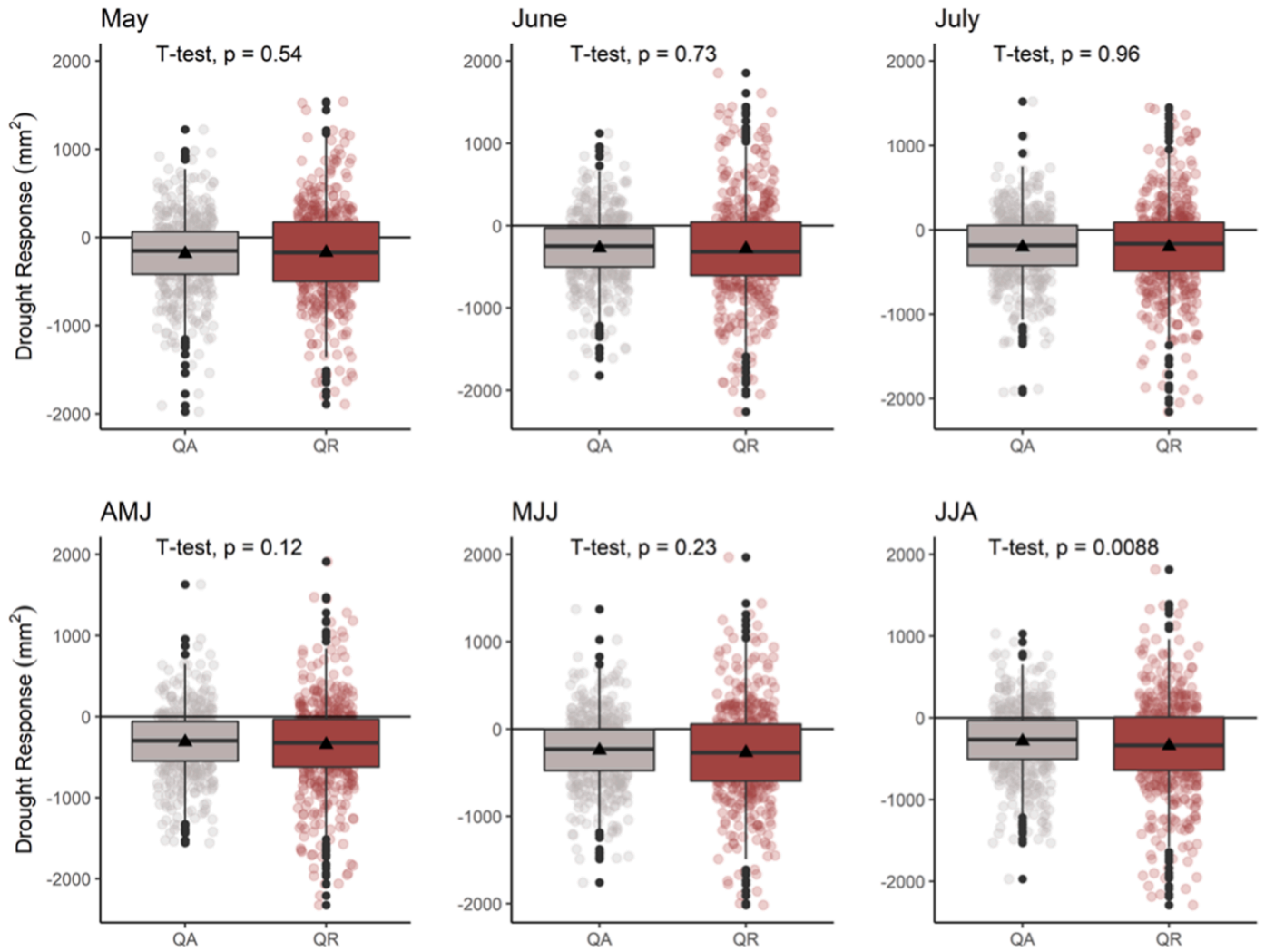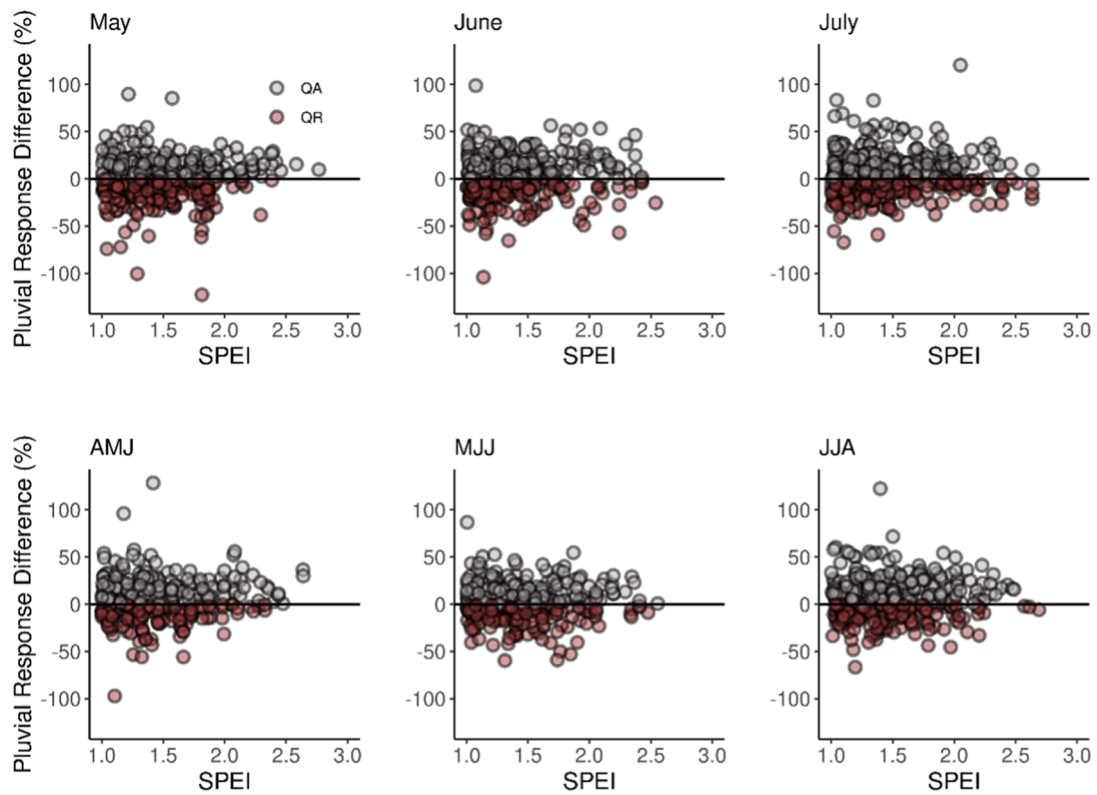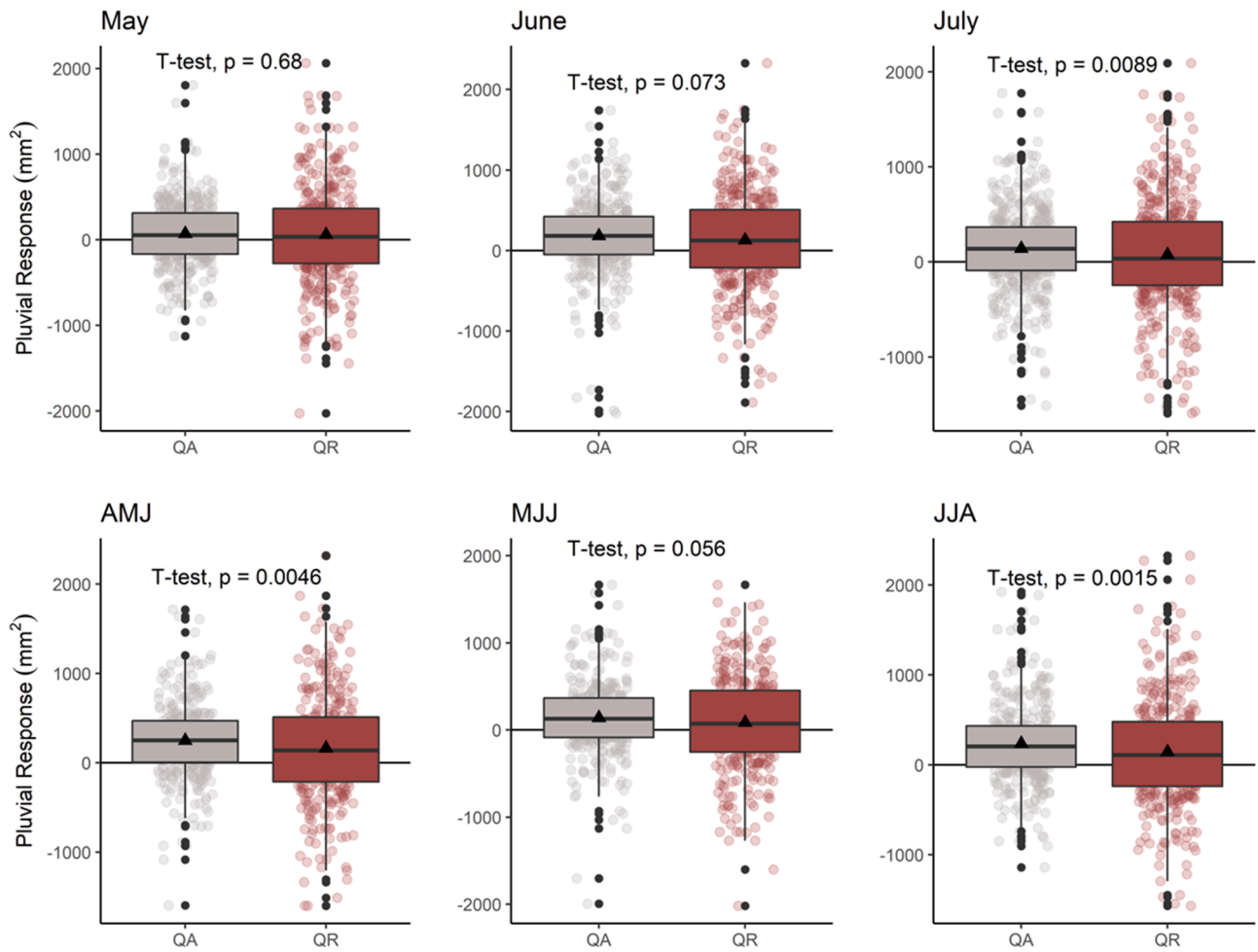
Fig. A5. Drought response, as the magnitude of BAI during drought years compared to non-drought years, for monthly combinations of May, June, July, April-June, May-July, and June-August with paired *t*-test p-values.

Fig. A6. Paired differences in pluvial responses for monthly combinations of May, June, July, April-June, May-July, and June-August. Paired difference was calculated by subtracting the percent of BAI during pluvial years to non-pluvial years in *Q. rubra* from the percent of BAI during pluvial years of *Q. alba*, such that positive values represent a greater increase in *Q. alba*, and negative values represent a greater increase in *Q. rubra*.

Fig. A7. Pluvial response, as the BAI during pluvial years compared to non-pluvial years, for monthly combinations of May, June, July, April-June, May-July, and June-August with paired *t*-test p-values.

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