The Drought Response of Eastern US Oaks in the Context of Their Declining Abundance

KIMBERLY NOVICK, INSU JO, LOÏC D'ORANGEVILLE, MICHAEL BENSON, TSUN FUNG AU, MALLORY BARNES, SANDER DENHAM, SONGLIN FEI, KELLY HEILMAN, TAEHEE HWANG, TARA KEYSER, JUSTIN MAXWELL, CHELCY MINIAT, JASON MCLACHLAN, NEIL PEDERSON, LIXIN WANG, JEFFREY D. WOOD, AND RICHARD P. PHILLIPS

*The oak (*Quercus*) species of eastern North America are declining in abundance, threatening the many socioecological benefits they provide. We discuss the mechanisms responsible for their loss, many of which are rooted in the prevailing view that oaks are drought tolerant. We then synthesize previously published data to comprehensively review the drought response strategies of eastern US oaks, concluding that whether or not eastern oaks are drought tolerant depends firmly on the metric of success. Although the anisohydric strategy of oaks sometimes confers a gas exchange and growth advantage, it exposes oaks to damaging hydraulic failure, such that oaks are just as or more likely to perish during drought than neighboring species. Consequently, drought frequency is not a strong predictor of historic patterns of oak abundance, although long-term climate and fire frequency are strongly correlated with declines in oak dominance. The oaks' ability to survive drought may become increasingly difficult in a drier future.*

Keywords: Quercus, drought, hydraulic traits, gas exchange, growth mortality, mesophication, isohydric

Oaks (*Quercus*) are an ecologically dominant genus (Cavender-Bares 2019) that has influenced ecosystem function across eastern US forests for millennia. Relative to other woody genera, oaks rank high in species diversity, biomass, and carbon storage (Cavender-Bares 2016), and they are widely viewed as being tolerant of both fire and drought (Abrams 1992, Cavender-Bares 2019). These unique functional traits connect oaks to multiple services, including high-quality timber production (Luppold and Pugh 2016), water cycle regulation (Caldwell et al. 2016), and the provisioning of a keystone forest food resource (i.e., their acorns; Wolff 1996). Without question, oaks are a critical part of the eastern US deciduous forest biome (Dey 2014).

Unfortunately, the socioecological benefits of oaks are threatened by a widespread, ongoing loss in oak relative abundance. Land surveys show that present-day eastern US forests contain surprisingly few white oak (*Quercus alba*) trees when compared with their eighteenth century counterparts (Abrams 2003), and region-wide survey data reveal that oak abundance is continuing to decline relative to other species (Fei et al. 2011). Although it is still a matter of debate, the decline in relative abundance of eastern US oaks is likely caused by multiple drivers (McEwan et al. 2011), including management-driven shifts in wildfire regimes (Nowacki and Abrams 2008) that occurred together with a period of relatively wet hydroclimatic conditions (McEwan et al. 2011). Wildfire and moisture conditions are closely related (i.e., drier conditions promoting more wildfire; Lynch and Hessel 2010) and interactive (i.e., less wildfire favors the establishment of species that tend to improve local water balance; Nowacki and Abrams 2008). Therefore, it is generally believed that decreasing wildfire and drought frequency over the past 50–80 years have conspired to favor the establishment of species that are less fire and drought tolerant than oaks. At the same time, the episodic mortality of mature oaks, which is often linked to insects and pathogens (Kabrick et al. 2008) but incited by drought events (Haavik et al. 2015, Voelker et al. 2008), may also play a role in the oaks' declining abundance.

The long-standing view that oaks are relatively drought tolerant (Niinemets and Valladares 2006, Meinzer et al. 2013, Cavender-Barres 2019) can be traced to early studies highlighting morphological and leaf-level physiological adaptations that reduce the sensitivity of oak gas exchange and growth to soil moisture deficits (Bahari et al. 1985, Abrams 1990), including deep roots and stomatal insensitivity to

BioScience 72: 333–346.
https://doi.org/10.1093/biosci/biab135 Advance Access publication 25 January 2022

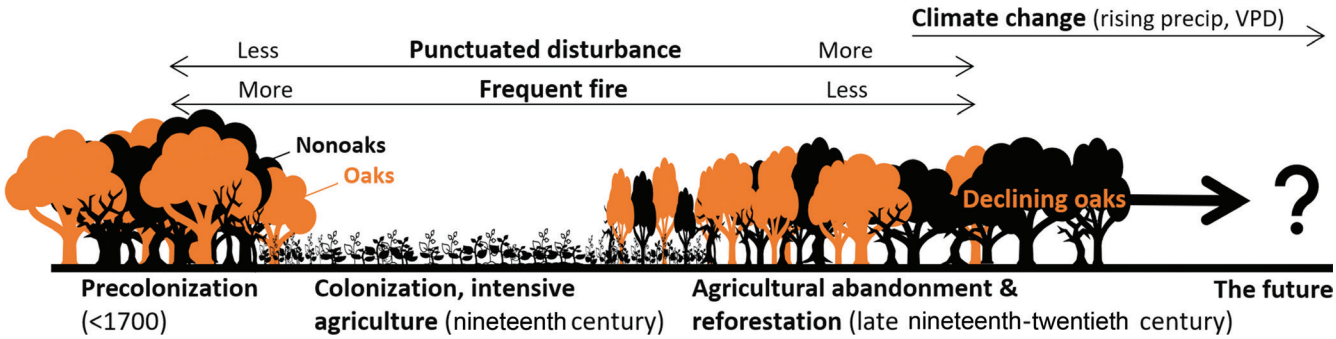

Figure 1. Management and climatic factors driving the disappearance of eastern oaks.

moisture stress. The paradigm is reinforced by the fact that oaks are known to dominate more xeric landscape positions (Abrams 2003). However, recent work has questioned the notion that oaks are indeed more tolerant of drought than their neighbors, in terms of both growth sensitivity (D'Orangeville et al. 2018) and hydraulic function (Benson et al. 2021). Moreover, hydrologic stress continues to be recognized as a key inciting factor driving elevated mortality of mature oak trees relative to other species (Voelker et al. 2008, Haavik et al. 2015, Wood et al. 2018, Druckenbrod et al. 2019).

Looking forward, the eastern US can expect a hydrologic regime characterized by more rainfall but also more frequent drought events (Cook et al. 2015) and an overall increase in atmospheric aridity linked to rising vapor pressure deficit (VPD; Ficklin and Novick 2017) and potential evapotranspiration (PET). On the one hand, a continuing trend of increased precipitation may favor mesophytic non-oak species. On the other, more frequent droughts may favor oaks (Clark et al. 2016) but only if these droughts do not promote widespread mortality and if the mechanisms by which oaks tolerate drought are effective in drier atmospheres.

The overall goal of this article is to attain a more holistic understanding of how eastern US oaks respond to soil and atmospheric drought and to apply this new knowledge to better understand their historic decline and future fate. Considering a diverse range of ecophysiological responses and traits, we ask, "In what ways are eastern US oaks more (or less) drought tolerant than co-occurring species, and how might oak drought-response mechanisms be driving long-term demographic shifts?" Our work is motivated by recent theoretical progress concerning how plant hydraulic functioning coordinates tree drought response along the entire soil–plant–atmosphere continuum (Anderegg 2015), determining trade-offs among carbon uptake, growth, and mortality (McDowell et al. 2008). The study is also driven by the wealth of information accumulating in networks such as the USDA Forest Inventory and Analysis (FIA) survey and tree-ring databanks, which afford novel opportunities to understand the extent to which conclusions drawn from site-level ecophysiological studies are ubiquitous across the landscape or influenced by spatial heterogeneity in pedoclimatic conditions.

Long-term trends in regional hydroclimate

Historically, drought has been a central part of the climatology of the eastern United States (defined in the present article as land between approximately 98 degrees west and the Atlantic Ocean). The infamous Dust Bowl drought, the 1950s drought, and the 1988–1989 drought were widespread across the region (Woodhouse and Overpeck 1998), and more recent droughts in 2012 and 2016 caused massive reductions in crop yields (Mallya et al. 2013) and wildfires (Williams et al. 2017). Notwithstanding these high-profile events, across much of the eastern US, water supply (e.g., precipitation, soil moisture) has increased over the last 100 years (figure 1; Hayhoe et al. 2018). In the Midwest and the Northeast, the last few decades were the wettest in the instrumental record (Mishra and Cherkauer 2010) and potentially the wettest period in the last several centuries (Pederson, et al. 2015, Maxwell and Harley 2017), although the trends have been more heterogeneous in the Southeast (Ficklin et al. 2015). If the data underlying deeper time studies on hydroclimate are correct, the last millennium could be the wettest period of the Holocene (Shuman and Marsicek 2016).

Although these data suggest a regional wetting in terms of water supply, long-term increases in VPD—and, therefore, atmospheric water demand—suggest a regional drying driven by rising temperatures (figure 1; Ficklin and Novick 2017). Elevated VPD is an important constraint on plant function, increasing transpiration that can decrease plant water potential (Novick et al. 2019) and thereby increase the risk of damaging hydraulic failure (McDowell et al. 2008). To mitigate this risk, plant stomates close when VPD rises (Grossiord et al. 2020, Woodruff et al. 2010), although the relationship between stomatal conductance and VPD is mediated by soil moisture and varies across species (Denham et al. 2021). Looking forward, the decoupling of precipitation and VPD is expected to continue, with relatively small and spatially heterogeneous increases in precipitation and soil moisture but nearly global increases in VPD (Ficklin and Novick 2017). Consequently, future droughts

and their impacts on many ecosystems may be increasingly driven by atmospheric drivers (Novick et al. 2016).

The mechanisms behind the disappearance of oaks from eastern US forests

Prior to European colonization, natural disturbance and Indigenous land use sustained midsuccessional oak–chestnut–hickory (*Quercus–Castenea–Carya*) forests over much of the region (Abrams 1992, Guyette et al. 2002). During and after colonization, the region experienced widespread and severe disturbances, including frequent burning, conversion of forestland to agriculture and pastureland, exploitive logging, and the loss of a keystone species (e.g., *Castanea dentata*) from a nonnative pathogen (Russell et al. 1993, Abrams 2003, McEwan et al. 2007). As the forests recovered during the late nineteenth and early twentieth centuries (figure 1), the complex mosaic of the precolonization landscape was initially replaced by homogeneous, even-aged second oak growth forests (Rhemtulla et al. 2007, Hanberry et al. 2012). Forest management became strongly oriented toward timber production and extraction, initially relying on even-aged regeneration methods (e.g., clearcutting) and, later, on low residual density two-aged methods. The consequence of implementing punctuated and intense disturbances into even-aged oak forests was an abrupt shift from stands dominated by mixed-oak species to stands dominated by other species (Swaim et al. 2018). Although small oak seedlings are initially abundant in canopy openings, they are often outcompeted by shade-tolerant individuals that compose the understory (Holzmueller et al. 2012). By the mid- to late twentieth century, exogenous disturbances considered integral to the oak regeneration processes (e.g., frequent fire, and episodic mortality from drought) became increasingly rare.

Through a process often called *mesophication* (Nowacki and Abrams 2008), the failure of oaks to regenerate under contemporary disturbance regimes is believed to be a self-reinforcing process. Damper and shadier conditions favor shade-tolerant species while deteriorating conditions for shade-intolerant, fire-adapted species such as oaks (e.g., Ford et al. 2011, Kreye et al. 2018). Although the feedback mechanisms that drive forest mesophication may have been initiated by management activities (e.g., decreased fire frequency and harvest), they are likely exacerbated by the decades-long shift to wetter climate conditions.

However, the disappearance of oaks is not merely a problem of recruitment. Biotic agents such as pests and pathogens are contributing to mortality of large canopy dominant eastern US oaks (Haavik et al. 2015). Oaks are relatively susceptible to attack by insects including but not limited to European gypsy moth (*Lymantria dispar* L.; Davidson et al. 1999) and red oak borer (*Enaphalodes rufulus*; Fan et al. 2008), and pathogens such as *Biscogniauxia* spp. (formerly *Hypoxylon*; Bassett and Fenn 1984), *Bretziella fagacearum* (oak wilt; Pedlar et al. 2020), and *Armillaria* spp. (McCarthy et al. 2001, Voelker et al. 2008), among others (Millers et al. 1989). Declining trees subjected to predisposing (e.g., site quality) or inciting (e.g., drought) factors face greater risk of catastrophic damage induced by insects and pathogens (Haavik et al. 2015). For example, in Missouri, there was a pulse of elevated white and black oak mortality in the year following the exceptional 2012 drought, with high incidence of stem cankers caused by *Biscogniauxia* spp. on trees that died (Wood et al. 2018). Other emerging threats to oak health include the root pathogen *Phytophthora*, which has been associated with *Q. alba* mortality (Balci et al. 2010) and implicated in unusual rapid white oak (*Q. alba*) mortality, whereby trees with full green crowns can die in a matter of weeks (Reed et al. 2019). It has been hypothesized that shifting climate patterns may exacerbate forest health risks through a combination of excessive soil wetness conducive to survival of soil-borne pathogens punctuated by more frequent or extreme droughts that can stress trees and make them more susceptible to infection (Hubbart et al. 2016).

In some places, additional mechanisms beyond hydroclimate and management may also be contributing to declining oak abundance. Nitrogen deposition, which continues to be substantially elevated over historic levels across the eastern United States (Van Houtven et al. 2019), may inhibit oak regeneration (Thomas et al. 2010, BassiriRad et al. 2015) and has been associated with an increase in dominance of species that associate with arbuscular mycorrhizal fungi (Jo et al. 2019, noting that oaks associate with ectomycorrhizal fungi). Additionally, in many places, recruitment failure is also facilitated by grazing pressure from herbivores such as white-tail deer (*Odocoileus virginianus*), which are increasing in abundance and preferentially favor oak seedlings (Steiner et al. 2008, McEwan et al. 2011).

A fresh look at the drought response strategy of eastern oaks

To better understand why eastern oaks are more (or less) tolerant of drought than their neighbors, we first conduct a meta-analysis of previously published information on tree drought-response variables and associated traits from across eastern North America. We then harness information contained in tree-ring networks and the FIA database to explore drought impacts on growth and mortality at landscape to regional scales. We end with an updated look at what FIA data reveal about the drivers of long-term changes in oak abundance, including patterns of drought and fire frequency, hydroclimate, and stand composition. A unifying feature of all these analyses is a focus on comparing the ecophysiological function of oaks with that of co-occurring non-oak competitors—minimizing biases linked to spatial heterogeneity in species distributions or hydroclimate conditions (e.g., greater overall abundance of oaks in more xeric landscapes). The geographic location of data informing each analysis is shown in figure 2.

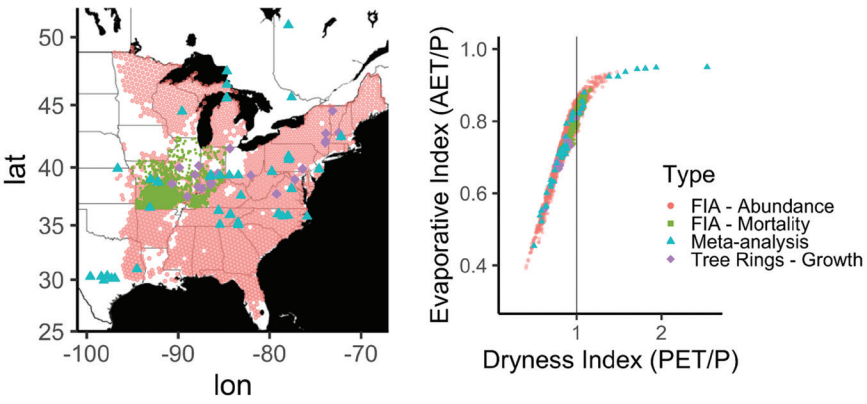

Figure 2. Left panel shows locations of data collected for use in the meta-analysis, tree-ring growth analysis, the FIA mortality analysis (limited to a four-state portion of the region that experienced severe drought conditions in 2012), and the FIA abundance analysis. The right panel shows climatic representativeness of these locations in the model of the Budyko curve. Most of the data were from locations at which the ratio of potential evapotranspiration to precipitation was less than 1.0, implying a predominant influence of energy versus water limitation over long time scales.

A meta-analysis of site-level observations of drought response variables and traits. The meta-analysis synthesizes previously reported observations of leaf- or canopy-scale gas exchange variables (including photosynthesis, stomatal conductance, and transpiration), radial stem growth, predawn and midday leaf water potential, xylem vulnerability to embolism, the hydraulic safety margin, and drought-driven mortality. The data were extracted from display items in published papers or obtained from data sets curated by the author team (see the supplemental material for more details). For gas exchange, growth, and water potential, data were included from all studies in which the occurrence of a substantial dry-down event was noted. These data were then evaluated as a relative reduction between the peak of the dry down and a preceding well watered period. Both field and greenhouse studies were considered, although the vast majority of studies occurred in the field. The Hedge's *D* effect size metric was used as the basis of our meta-analysis (supplemental section S1 for extensive documentation). Because ecologists adopt diverse and subjective definitions of drought (Slette et al. 2019), our meta-analysis incorporates data collected during droughts that vary in intensity from one study to the next. To the extent that physiological responses to drought are linear, the reliance on effect sizes minimizes the impacts of site-to-site differences in drought severity. However, for responses that are more nonlinear, differences in drought severity from one study to the next is an important source of uncertainty that should continue to motivate future work.

For assimilation, conductance, transpiration, and growth, the effect size was determined from the relative reduction in each during droughted versus nondrought periods. For leaf water potential and mortality, the effect size was determined from the observed value during or after the drought period, respectively. The xylem vulnerability effect size was determined from laboratory-derived measurements of the water potential associated with a 50% loss in stem hydraulic conductivity (the P_{50}). The bases for the hydraulic safety margin is the observed safety margin informed by the minimum leaf water potential during drought and the lab-derived P_{50}.

In addition, we considered two derived hydraulic traits, which do not lend themselves to effect size analyses. The first is the sensitivity of canopy conductance to VPD, which is often reported in sap flow studies in which canopy conductance is measured at a high temporal resolution (see supplemental section S1.4 for more details). The second is the degree of isohydry, which describes the change in midday leaf water potential as soil water decreases or VPD rises (Martínez-Vilalta et al. 2014, Novick et al. 2019). Midday leaf water potential is relatively stationary for isohydric plants whose stomates close quickly during drought, but decreases for anisohydric species that keep stomates open longer. As described in more detail in supplemental section S1.5, we considered multiple metrics for the degree of isohydry.

Gas exchange dynamics and the degree of isohydry. Compared with their co-occurring neighbors, the gas exchange of oaks (and especially photosynthesis and stomatal conductance) appears to be less affected by drought (figure 3; mean effect size of 0.54 and 0.47 for photosynthesis and stomatal conductance, respectively). That oaks sustain relatively high rates of gas exchange during drought is consistent with earlier work (Abrams 1990) and is often hypothesized to reflect greater oak rooting depth, which has been confirmed in some places using canopy-level isotope measurements (McElrone et al. 2004, Chimner and Resh 2014, Matheny et al. 2017, Lanning et al. 2020a).

The predawn leaf water potential, often interpreted as a proxy for the root-zone integrated soil water potential and therefore rooting depth, was higher for oaks more often than not (figure 3). This result is consistent with the expectation that oaks are more deeply rooted (Abrams 1990), although cross-site variability in predawn leaf water potential effect size from one site to the next was large, and the 95% confidence interval overlaps with zero. Although predawn leaf water potential may be higher for oaks, the leaf water potential at midday was lower for oaks compared with their neighbors in 14 of 17 studies (mean effect size –0.96). Therefore, whatever advantage is conferred to oaks by having deeper roots (e.g., sustaining gas exchange), the benefit does not prevent negative excursions in midday leaf water

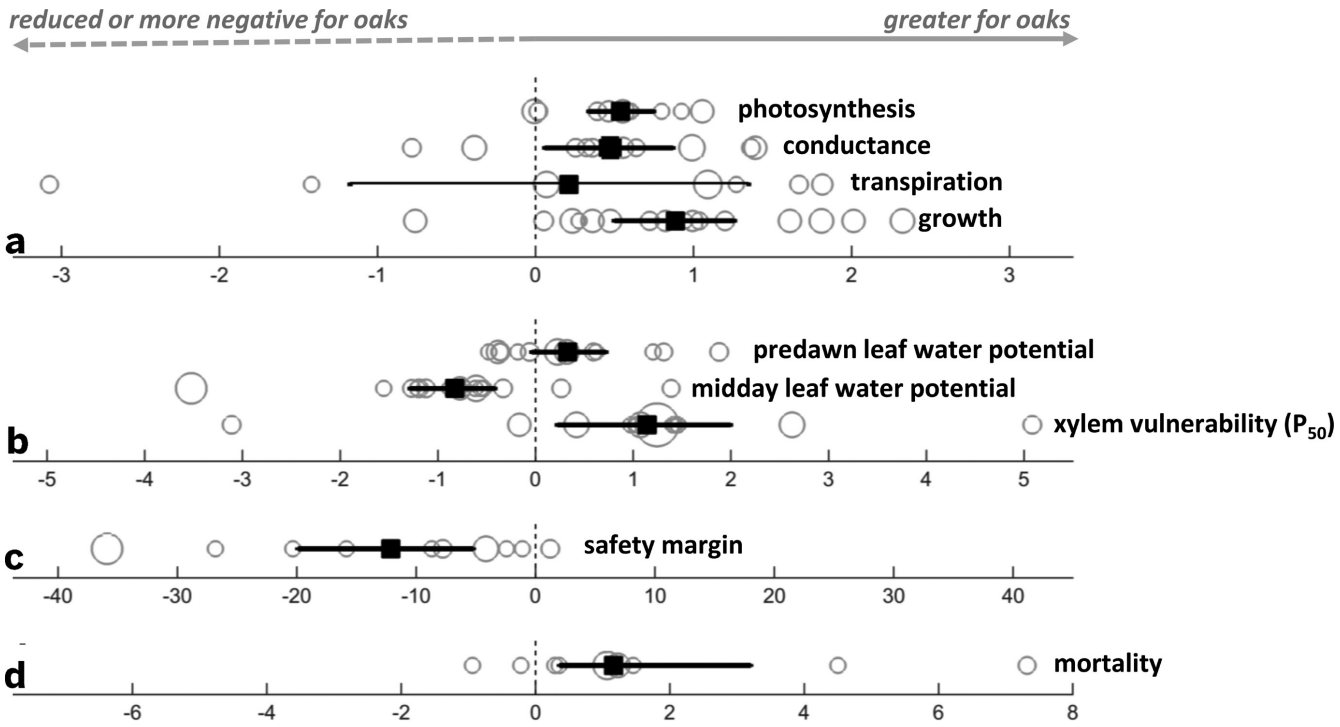

Figure 3. Effect size (Hedges' D) of response variable and trait differences between oak and non-oak species. The Hedge's D metric can be interpreted as indicating a small difference between samples when it is less than 0.2, intermediate difference when it is approximately 0.5, and a large difference when it is at least 0.8. Grey circles show the site-level effect size, with symbol size scaled according to the number of oak–other combinations within each site. Black squares show the mean site-level effect size, and horizontal black lines show the 95% confidence interval on the mean from a nonparametric bootstrap. Data falling to the right of the vertical dashed line indicate a greater value of the trait or response variable (during drought conditions) for oaks compared with non-oaks. Note that the x-axis range varies from one group of variables or traits to the next.

potential, which may increase the risk of hydraulic damage to the xylem.

The synthesis of canopy conductance sensitivity to VPD reveals that oak stomates are less sensitive to VPD when compared with other species (figure 4). In other words, oaks keep their stomata relatively more open not only as soil moisture declines but also as VPD increases. Consistent with these results, the meta-analysis also revealed that oaks tend to be more anisohydric than colocated species, at least when the degree of isohydry is evaluated as the sensitivity of leaf water potential to soil water potential or VPD (see supplemental figure S7). When assessed on the basis of sensitivity to predawn leaf water potential, the degree of isohydry is more similar between oak and non-oak species. The lack of coherence across the various definitions of isohydry may reflect the confounding influence of rooting depth (Martínez-Vilalta and Garcia-Forner. 2017), the disequilibrium between predawn leaf water potential and the integrated root-zone soil water potential (Donovan et al. 1999), and/or the difference in cuticular conductance across species (Lanning et al. 2020b), among other factors. In any event, the weight of the evidence presented in this study, as well as in prior work (see also Meinzer et al. 2013, Roman et al. 2015, Matheny et al. 2017, Kannenberg et al. 2019a), suggests that eastern oaks are more anisohydric than their neighbors.

Connecting leaf and canopy dynamics to whole-plant responses. Anisohydric species that tolerate low water potential during drought are widely believed to have xylem elements that are particularly resistant to embolism (McDowell et al. 2008, Choat et al. 2012, Sperry and Love 2015). Indeed, this assumption underlies the parameterization of multiple new plant hydraulics modules in terrestrial ecosystem models (Mirfenderesgi et al. 2016, Kennedy et al. 2019). However, consistent with other evidence (Maherali et al. 2006, Kannenberg et al. 2019a, Benson et al. 2021), our meta-analysis reveals that oak stem xylem are substantially more vulnerable to embolism when compared with their neighbors. Specifically, the stem water potential associated with 50% loss of hydraulic conductivity (P_{50}) is higher for oaks in 12 of 14 sites (figure 3; mean effect size 1.11).

Therefore, eastern oaks appear to possess a perplexing assemblage of hydraulic traits that sustain high rates of leaf

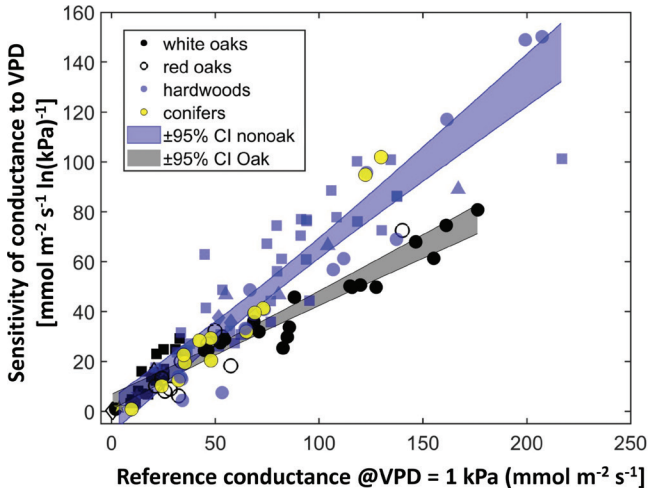

Figure 4. The stomatal sensitivity of canopy stomatal conductance to ln(VPD) as a function of the reference, well watered conductance rate when VPD = 1 kPa, using previously published information from sap flow studies. Although the sensitivity is well correlated with the reference rate within and across species and sites, oaks tend to have lower VPD sensitivity for a given reference conductance when compared with other species, noting that all data are from sites at which oaks co-occur with non-oak species. Different shapes indicate unique species. More details on the data informing this figure are available in supplemental section S1.4.

gas exchange but at the cost of dangerously low negative excursions in midday leaf water potential despite having xylem that are relatively vulnerable to embolism. As a result, the *hydraulic safety margin*, defined as the difference between minimum midday leaf water potential and P_{50} and widely recognized a key control on overall plant water relations during drought (Anderegg et al. 2018), is clearly smaller for oaks than for non-oak species (figure 3; average effect size –15.9) and is often negative (see the supplemental material). It is interesting to interpret this result in the context of recent work on western US oak species, which shows that P_{50} tends to be low in general but higher in wetter biomes where safety margins approach zero (Skelton et al. 2021).

The results concerning the hydraulic safety margins come with some important caveats. First, this analysis considers branch xylem vulnerability alone, and there is a need for more integrated studies of hydraulic traits and functioning across whole plants (McCulloh et al. 2019, Rodriguez-Dominguez and Brodribb 2020). Second, the majority of the data informing safety margin meta-analysis rely on minimum leaf water potential observations performed on leaves that were not bagged prior to excision. Differences in hydraulic conductance between stems and leaves can cause leaf water potential to be substantially lower than the water potential of nearby stems, which, in turn, would cause the hydraulic safety margin to be underestimated. The problem could be especially acute in species with low hydraulic leaf conductance. However, at least two previous studies included in our meta-analysis reported that the midday leaf water potentials of oaks tended to be relatively low even after bagging (Kannenberg et al. 2019a, Benson et al. 2021), suggesting that the narrow safety margins are not merely artifacts. Nonetheless, the decoupling of leaf and stem water potential is, generally speaking, a major source of uncertainty surrounding the estimation of hydraulic safety margins that could be confronted with more open and aggregated databases of plant water potential (Konings et al. 2021, Martinez-Vilalta et al. 2021, Kannenberg et al. 2021.

How do these ecophysiological responses and traits govern drought impacts on growth and mortality? The results from the meta-analysis are mixed. On one hand, in a majority of the studies, oak stem growth was less limited by drought than it was for their neighbors (figure 3; mean effect size 0.44). On the other hand, in 8 of the 10 site-level studies informing the mortality meta-analysis, the drought-driven mortality rate of oaks was substantially greater than the mortality rates of co-occurring species (figure 3; mean effect size 1.16). In the next sections, we will leverage rich information about tree growth and demographics available from long-term network observations to better understand landscape-level variables that ultimately determine these critical, and integrative, drought response variables.

Using tree-ring networks to better understand how drought affects growth over long time scales. Tree rings have long been used as a proxy for reconstructing historic hydroclimate conditions and are increasingly being leveraged for the ecological information they contain. For example, using chronologies from a wide network of eastern US sites, D'Orangeville and colleagues (2018) and Phillips and colleagues (2016) showed that oak species, despite being commonly classified as drought tolerant, demonstrated relatively high sensitivity of radial growth to drought when compared with other hardwoods. In contrast, other studies, and particularly those using tree rings to evaluate drought response from a limited number of sites with co-occurring oak and non-oak species, showed that oaks do appear to be less sensitive to drought (Elliott et al. 2015, Kannenberg et al. 2019b, Yi et al. 2019, Au et al. 2020). Many factors could potentially explain this discrepancy, including heterogeneity in soil conditions and meteorological drought severity. However, whether drought sensitivities are evaluated within a site or by aggregating responses across sites could be an important contributing factor, especially if oaks tend to predominate in more xeric portions of the landscape where soil water deficits are exacerbated during drought.

Therefore, we leveraged an eastern US tree-ring network, previously described in Maxwell and colleagues (2020), to specifically quantify the relative drought sensitivity of oak growth compared with a wide range of co-occurring species. The network includes tree-ring data from 34 sites that each had co-occurring oak and non-oak species, resulting

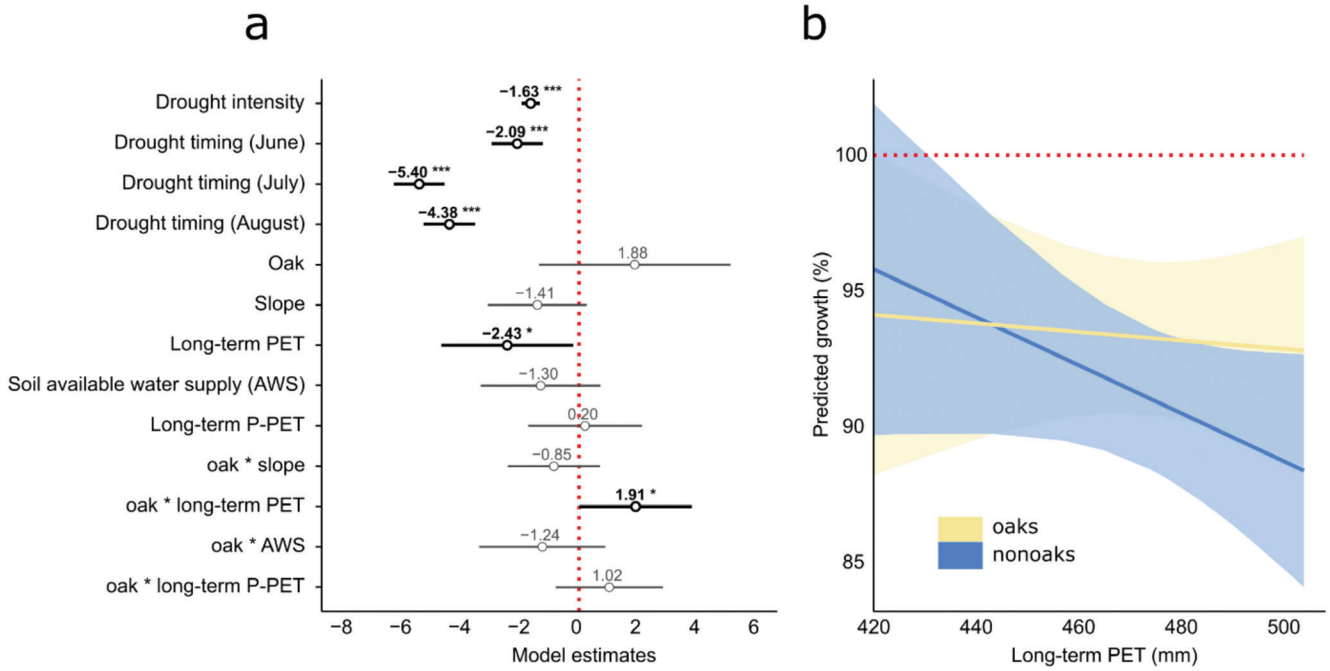

Figure 5. Average radial growth of oak versus non-oak trees in response to drought across 34 stands. (a) Fixed-effect estimates of the multispecies linear mixed model; the error bars represent the standard error. The bold values indicate significant effects. The effects for drought timing (June, July, and August) are relative to the baseline of May. (b) Modelled growth of oak versus non-oak trees across the observed long-term PET gradient, controlling for all other factors. The colored ribbons indicate the standard error. *$p < .05$. ***$p < .001$.

in 748 canopy-dominant trees across a 7-degree latitudinal gradient (see figure 2), synthesized into 76 site-level chronologies. The growth drought sensitivity was expressed as a dimensionless tree-growth index (after D'Orangeville et al. 2018) during 1901–2013 drought identified as years with a 6-month Standardized Precipitation–Evapotranspiration Index (SPEI; Beguería et al. 2014) below –1.5. Similar results were obtained using a 3-month SPEI. We selected drought anomalies from May to August, when drought sensitivity is highest across the entire study gradient (D'Orangeville et al. 2018).

The richness and spatial representativeness of this data set afforded us an opportunity to investigate the importance of pedoclimatic conditions on the growth drought sensitivities. Specifically, we investigated the influence of long-term PET (which is predominantly determined by VPD, Cook et al. 2014); the difference between precipitation and PET, a proxy for site water availability; local topographic slope; and soil available water supply, which describes the storage capacity of the top 1 meter of soil. The details on these data sources and the linear mixed model used to investigate how interactions among these factors determine drought growth sensitivity are given in supplemental section S2.

Across all species, tree growth was significantly reduced during severe drought conditions (figure 5a). Growth was also sensitive to drought timing, with drought conditions in July having the largest impact, consistent with prior work (D'Orangeville et al. 2018, Kannenberg et al. 2019b). Across species, atmospheric demand (PET) drives growth more than water availability (which is surrogated to the difference between precipitation and potential evapotranspiration, or P-PET), which did not have a significant influence on growth (figure 5a).

When comparing oaks with other colocated species, oaks tended to experience smaller reductions in growth during drought (see the oak fixed effect in figure 5a), although the effect was not significant at the $\alpha = .05$ threshold. In general, interactions between species groups (i.e., oaks versus non-oaks) and the majority of pedoclimatic drivers were negligible, with a notable exception of interactions with PET. Specifically, drought growth sensitivities of non-oak species are generally greater where the mean summer PET is higher. However, for oaks, the PET effect is in the opposite direction (note the oak × long-term PET interaction in figure 5b). This result suggests that relative to their neighbors, oak growth may be more resistant to drought in biomes in which PET is particularly high. One explanation for this result relates to the fact that oak gas exchange is relatively insensitive to soil moisture stress (figure 2; Denham et al. 2021), because of a combination of deeper roots or anisohydric water use strategies (Au et al. 2020). Therefore, if soil moisture declines more sharply during drought in areas where evaporative

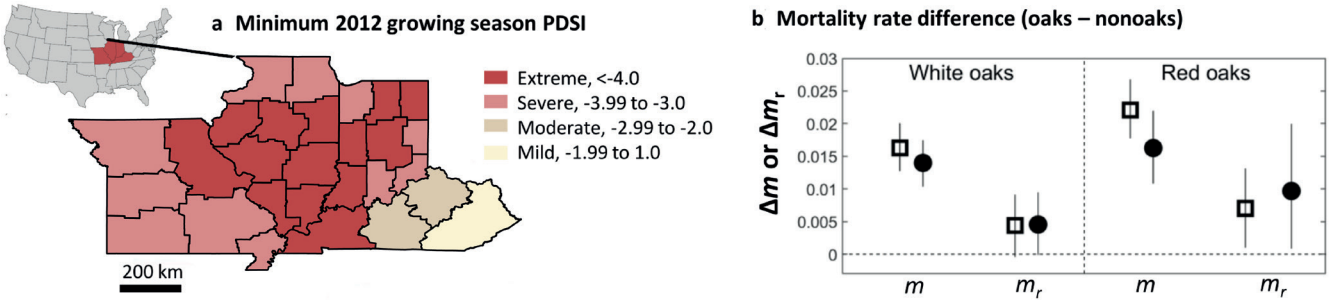

Figure 6. Panel (a) shows the study area for the FIA mortality analysis, noting that only plots located in areas experiencing extreme or severe drought were retained for the analysis. Panel (b) shows the mortality rate difference comparing oaks with non-oaks, aggregated across all plots in the study area (where positive values indicate greater mortality for oaks). The variable* m *is the apparent mortality rate derived from live stem counts;* m_r *is the mortality rate corrected by baseline, nondrought mortality rates. White oaks include* Quercus alba *and* Quercus stellata*; red oaks include* Quercus rubra*,* Quercus velutina*, and* Quercus conccinea*. The open symbols show the arithmetic mean, and the closed symbols show the weighted mean. The error bars represent 95% confidence intervals, which were generated from a nonparametric bootstrap. When averaging across species, we considered the arithmetic mean as well as means weighted by the number of oak trees occurring in each plot. The confidence intervals overlapped between weighted and nonweighted means, suggesting that the results are not strongly influenced by the number of oaks trees in each plot.

demand is generally high, interspecific differences in soil moisture sensitivity should be accentuated.

Spatiotemporal patterns of drought-driven tree mortality. Information contained in the FIA data set has been used to investigate drought-driven mortality of oaks in the southeastern US (Klos et al. 2009, Klockow et al. 2018), with mixed results regarding the mortality risk of oaks versus non-oaks. However, these network-level analyses aggregate mortality information across coarse spatial scales, making it difficult to disentangle species-specific physiological responses from factors that determine the distribution of species across pedoclimatic gradients. Therefore, we conducted a novel analysis to understand what FIA data can tell us about mortality rates of oaks versus non-oak species growing in the same place. The analysis is a case study of four states (figure 6a) that experienced severe or extreme drought conditions during the 2012 Midwestern drought event (Mallya et al. 2013). The analysis was limited to species accounting for more than 10,000 observations in the FIA subset for these states, and excluded plots that experienced substantial timber removals or contained species experiencing widespread insect-driven mortality (i.e., ash, *Fraxinus* spp.). Ultimately, mortality rates were assessed for 23 species, including 5 oak species, that together account for approximately 75% of all FIA observations in the study area during the study period (supplemental table S2). Mortality dynamics were assessed at the plot level, and only for plots in which oak and non-oak groups co-occur.

We considered two approaches for estimating mortality. The first (m) was informed by live stem counts and sampling interval time using the approach of Sheil and colleagues (1995). However, this approach is sensitive to biases associated with recruitment, which can increase the total number of live stems, and ongoing mortality from causes other than drought. Therefore, plot-level mortality rates were also corrected for baseline (non-drought) mortality rates observed during two successive survey periods prior to 2012 (m_r; see supplemental section S3 for more details).

When considering the uncorrected mortality estimates, the apparent drought-driven mortality rate was approximately 2% higher for oaks versus non-oaks (figure 6b) and confidence intervals did not overlap zero. However, when considering the corrected mortality metric (i.e., m_r), the difference in drought-driven mortality between oaks and non-oaks is reduced to less than 1% (figure 7b; approximately 0.45% for white oak group species and approximately 0.97% for red oak groups species). This result is consistent with prior work (Fan et al. 2008, Kabrick et al. 2008, Druckenbrod et al. 2019) showing that red oak group species were more prone to mortality following drought when compared with both non-oaks and white oak species.

The difference between m and m_r implies that oaks have a higher apparent baseline mortality rate than neighboring species. Oaks are vulnerable to a diverse suite of insects and pathogens that are known to be a proximate cause of mortality (Kabrick et al. 2008, Haavik et al. 2015). Drought legacies, which may be more pronounced for oaks (Pedersen 1998, Voelker et al. 2008, Kannenberg et al. 2019c) and can persist for many years (Berdanier and Clark 2016), may also play an important role in predisposing oaks to mortality over long periods of time. Finally, it is important to recognize that this baseline rate—calculated from the change in live stems—incorporates not only actual mortality but also recruitment

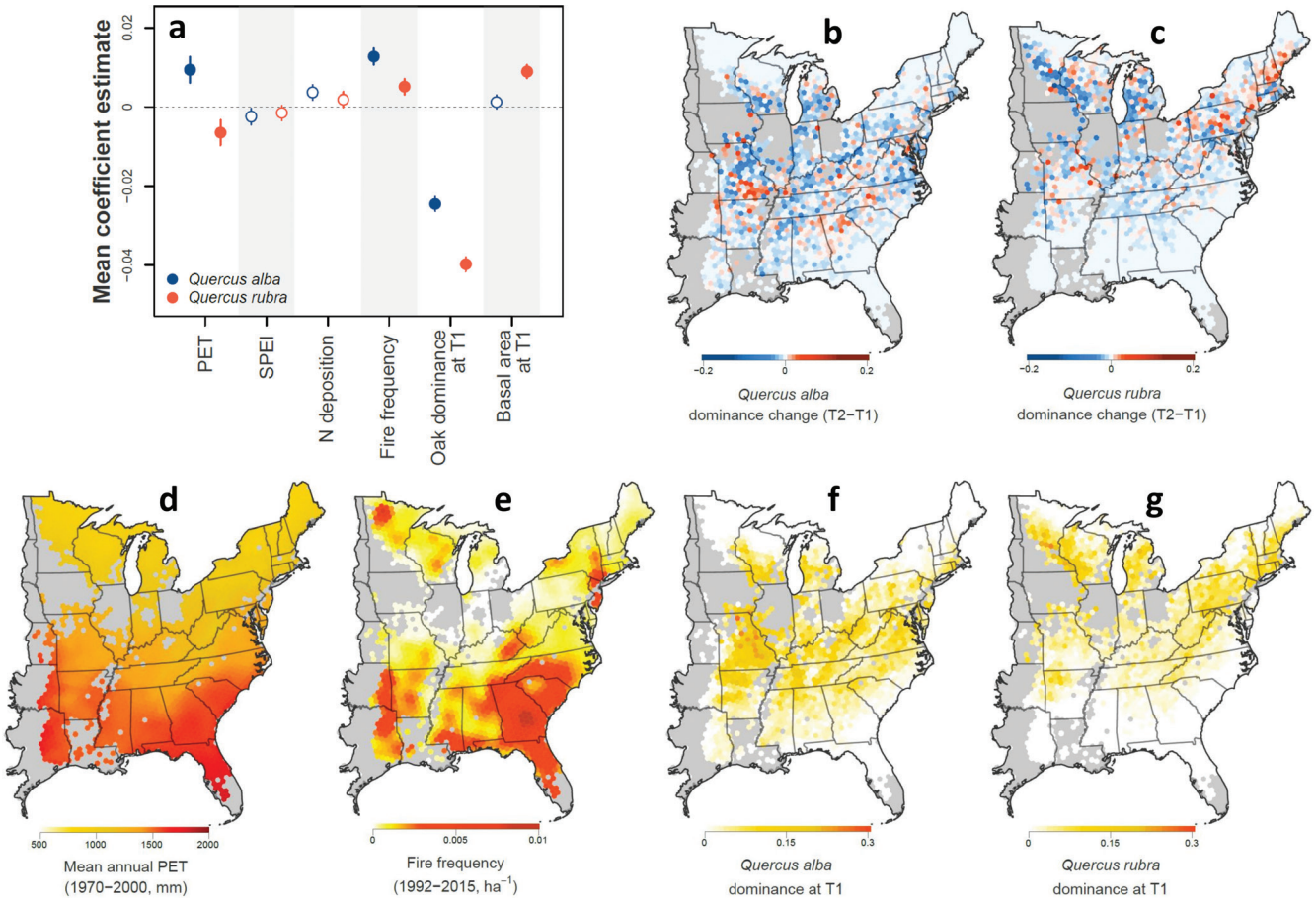

Figure 7. Panel (a) shows relative effects of multiple biophysical and climatic drivers on the change in dominance of* Quercus alba *and* Quercus rubra*, including mean PET (averaged over the years 1970–2000), SPEI (averaged over the years 1980–2015), nitrogen deposition (averaged over the years 2000–2015), fire frequency (averaged over the years 1992–2015), and oak dominance and basal area (from t_1, circa 1985). The coefficients were assessed using a generalized mixed-effects model. Significant coefficients (i.e., $p < .05$) are indicated with solid circles. Panels (b) and (c) show the pattern of oak dominance change, and panels (e)–(h) show the spatial pattern of key model drivers.

of new trees, which is known to be strongly limited for oaks (see Section 2).

By normalizing for differences in baseline mortality, the corrected metric m_r presents a more accurate assessment of drought-driven mortality. When m_r is the basis for analysis, the difference in drought-driven mortality between oaks and non-oaks was reduced. Nonetheless, white oaks were just as susceptible, and red oaks more susceptible, to drought-driven mortality than most other species. Overall, our analysis of mortality using FIA data indicates that oaks are not more drought tolerant than their neighbors when the metric of success is survival.

Linking oak demographic shifts to multiple long-term drivers. Ultimately, the historic and future fate of eastern oaks reflect the combined influence of dynamic shifts in growth and mortality. Therefore, as a final step, we used FIA data to assess the extent to which historic trends in oak dominance are correlated with long-term shifts in key management and hydroclimatic drivers, as well as long-term trends in other factors such as nitrogen deposition. The approach largely follows the methodology of Jo and colleagues (2019). Briefly, the analysis focused exclusively on *Q. alba* and *Quercus rubra*, which are the two most important species in the white and red oak families (Iverson et al. 2008). Dominance was determined at the plot level by dividing the basal area of *Q. alba* (or *Q. rubra*) by the basal area of all trees in a given plot, separately for an initial inventory period (t_1, performed between 1980 and 1995) and again during the last FIA inventory phase (t_2, mean inventory year 2015). The data were aggregated to pixels at a scale that matches the mean area of eastern US counties (see supplemental section S4 for more details). Next, oak dominance change was related to multiple drivers describing spatial variability in climate and disturbance regime, including mean annual potential ET (in millimeters per year) from 1970 to 2000, mean annual nitrogen deposition during the period 2000–2015,

and fire frequency during the period from 1992 to 2015. The frequency of drought occurrence (from SPEI) was also included as a variable describing the occurrence of hydroclimatic anomalies during the FIA data period (e.g., t_1 to t_2). Initial oak dominance and stand basal area (during t_1) were also included as predictor variables. More details on data sources are available in the supplemental material.

We find that oak species have experienced a clear loss in relative abundance across much of the region (figure 7), consistent with prior work (Fei et al. 2008). Specifically, oak dominance decreased in 61% of pixels for *Q. alba*, and 56% of pixels for *Q. rubra* (figure 7b, 7c). Small but noticeable areas of oak dominance increase were evident in the Southeast and the south-central United States (for *Q. alba*) and in the Northeast (for *Q. rubra*). For both species, the change in oak dominance is positively related to fire frequency (i.e., oaks gaining where fires are more frequent), and negatively related to initial oak dominance (i.e., oaks losing ground in stands in which oak density is relatively high). Nitrogen deposition was not a strong predictor of oak dominance change for either species. For *Q. rubra*, but not *Q. alba*, gains in dominance were significantly related to stand basal area in t_1. Trends in growing season drought (e.g., SPEI) over the last 35 years did not explain changes in oak dominance for either species. However, the long-term PET was a significant predictor of oak dominance change, although it affected the two species differently. The relative abundance of *Q. alba* tended to increase in areas in which PET is high, whereas *Q. rubra a*bundance decreased in areas of high PET. Finally, collinearity among the driver variables is generally low (see supplemental section S4).

In summary, this analysis provides support for the hypothesis that fire frequency plays an important role in driving the oak dominance dynamics across the landscape, and this is especially true for *Q. alba*. Beyond the influence of fire, we also find that both oak species tend to be losing basal area dominance more quickly in stands in which they are especially dominant. Shifting frequency of drought, defined as the cumulative SPEI from 1970 to 2000, was not a significant predictor of oak dominance change for either species. However, the local hydroclimate, characterized on the basis of long-term PET, was closely related to the observed shifts in oak dominance, but differentially for each species. *Q. alba* tended to gain dominance, and *Q. rubra* tended to lose dominance, where PET and VPD are relatively high.

What have we learned about oak drought tolerance?

Taken together, our results suggest that whether eastern US oaks are more drought tolerant than their neighbors firmly depends on the metric of success. Confirming earlier work, the gas exchange of oaks (red and white alike) emerged as less sensitive to drought (figure 3a), whether defined as an absence of precipitation or specifically as an increase in VPD (figure 4). Consequently, the midday leaf water potential of oaks becomes more negative during drought when compared with the water potential of co-occurring species (figure 3, supplemental section S1.5), confirming prior work suggesting that oaks adopt an anisohydric water use strategy (Meinzer et al. 2013, Matheny et al. 2015, Roman et al. 2015).

But does the anisohydric water use strategy of oaks translate to an advantage in stem growth during drought? The meta-analysis of site-level results suggest it does (figure 3; mean effect size approximately 1.0). However, analysis of the information-rich tree-ring network data highlights a need for a more cautious interpretation. Although oak growth tended to be less sensitive to drought than other species, the effect was not significant (figure 5). When considering interactions with hydroclimate (i.e., PET), a clearer picture emerges. Oak growth tends to be particularly insensitive to drought, compared with neighboring species, where PET is especially high (figure 5), whereas the growth of non-oak species is more sensitive to drought under higher PET. Therefore, the oaks' water use strategy appears to confer the most advantage, at least in terms of growth, in more xeric portions of its range.

Although sustaining growth is critical, avoiding extensive hydraulic damage is also a key metric of drought tolerance. In this regard, one of the strongest results to emerge from the meta-analysis is the clear tendency for oaks to have xylem that are more vulnerable to embolism than colocated species (figure 3). As a result, oak hydraulic safety margins are quite low, and oftentimes near zero or negative (figure 3, and see the supplemental material). Although this result has been previously reported by Benson and colleagues (2021) and Kannenberg and colleagues (2019a), it remains a surprising one, because most plant hydraulic frameworks operate under the assumption that more anisohydric plants have xylem that are relatively resistant to hydraulic failure. It also highlights the need for additional work to understand the extent to which rising VPD may further suppress midday leaf water potential of oaks and therefore their already low hydraulic safety margins.

Finally, what have we learned about oak survivorship during drought? First, it's important to recognize that oaks are generally more likely to die than other species, even in years preceding a major drought event. This pattern may reflect interactions between climate triggers (which can have persistent legacies; Voelker et al. 2008, Berdanier and Clark 2016, Kannenberg et al. 2019c) and proximate damage caused by a diverse set of pests and diseases (Wood et al. 2018). This result may also represent a methodological bias; the fractional loss of live stems is affected not only by actual stem loss, but also recruitment of new stems into the canopy, which is known to be low for oaks. Regardless, any effort to characterize drought-driven mortality of oaks compared with other species should correct for baseline rates. For the 2012 drought case study, even after correcting for baseline mortality, oaks are just as or more likely to die than most of their colocated neighbors (figure 6). The case study results are consistent with the meta-analysis of figure 3, as well as other efforts to synthesize prior site-level work on the topic (Druckenbrod et al. 2019).

How does our new understanding of oak drought tolerance inform our perspective on the historic and future fate of oaks?

The analysis of changes in oak dominance (i.e., figure 7) suggests that recent changes in drought occurrence, defined as long-term shifts in SPEI over the past few decades, are not a strong driver of oak dominance shifts. Although this result is consistent with the other results suggesting that oaks are not particularly drought tolerant with respect to either growth or mortality, this result should be viewed with some caution. In particular, although the past 30–40 years have been characterized by occasional high-severity drought events (e.g., the 2012 drought), conditions have been generally since the reestablishment of many eastern US forest stands in the 1930s (Clark et al. 2016). Although FIA surveys are, at this time, too short to permit a clearer perspective on long-term (e.g., century-scale) interactions between hydroclimate and stand development, future work may be able to harness additional information contained in public land surveys, tree core records, and other paleoecological data (e.g., Goring et al. 2016).

On the other hand, long-term PET appears to be an important determinant of oak demographics, although it affects *Q. rubra* and *Q. alba* differently. *Q. alba* dominance shifts are positively related to PET (i.e., white oak gaining ground in more arid parts of the region), whereas *Q. rubra* dominance shifts are negatively related to PET. VPD is an important determinant of PET. Therefore, one interpretation is that, in places in which PET and VPD are high (and in which *Q. alba* is abundant), the relative insensitivity of oak gas exchange to drought or elevated VPD has thus far conferred a carbon advantage for growth that outweighs the mortality risk. Looking forward toward a future characterized by higher VPD and PET (Ficklin and Novick 2017), it is tempting to infer that *Q. alba*, at least, will be advantaged over their neighbors. However, this prediction must account for the possibility that oaks operate with narrow hydraulic safety margins (figure 3) that may contribute to mortality risk or, at least, create conditions that leave the trees' hydraulic system more susceptible to pests or pathogens, especially when atmospheric water demand is elevated. However, future work is recommended to understand how differences between stem and leaf water potential affect the determination of stem hydraulic safety margins.

Beyond the influence of drought and hydroclimate, our results also reinforce the view that fire and other disturbances play an important role in shaping the historic demographics of eastern US oaks—and especially *Q. alba*—across the region. Finally, the biggest factor determining the overall rate of loss of both *Q. alba* and especially *Q. rubra* is the initial dominance of these species at the start of the study period. That oaks are more often losing ground where they are most abundant could be merely artifactual or reflect stand development processes such as self-thinning. However, it may also be the case that oaks more readily established on cleared and burned lands following extensive logging and the extirpation of chestnut (Castanea dentata) in the early twentieth century (Kabrick et al. 2008, Elliott and Swank 2008), generating a relative overabundance of oaks that now predisposes these trees to greater losses in basal area.

Conclusions

The meta-analysis confirms the perspective, informed by decades of prior work, that oaks sustain relatively high levels of gas exchange during drought and builds on that paradigm by demonstrating the hydraulic consequences of this water use strategy. Specifically, oaks adopt an anisohydric water use strategy, despite having xylem that are especially vulnerable to damage driven by the low water potentials that evolve while stomates are kept open. At the site level, the risk is often worth the reward in terms of productivity: The meta-analysis reveals that the growth of oaks is relatively less limited by drought. When expanding the scale of inference to the entire region, it becomes clear that oak growth is least sensitive to drought in the more xeric parts of the range, characterized by high PET and an overall higher abundance of *Q. alba*. Both the site-level meta-analysis and FIA analysis suggests that oaks (and especially red oaks) are often more likely to perish following a drought than other colocated species, which is difficult to reconcile with the perspective that oaks are a drought tolerant group of species. Therefore, it is not surprising that shifting drought frequency itself does not emerge as strong determinant of long-term shifts in oak dominance. But climate—and in particular PET—is an important predictor of oak demographics, with *Q. alba* gaining, and *Q. rubra* losing, in areas in which PET is relatively high. Efforts to forecast and manage future populations of oaks would benefit from additional experimental and monitoring work to identify thresholds of PET and VPD beyond which risks to hydraulic function and survival become severe enough to outweigh the benefits for carbon uptake and growth. This work should also proceed with the perspective that fire frequency is indeed an important constraint on both the historic and future fate of oaks.

Acknowledgments

This work was funded by the US Department of Agriculture Agriculture and Food Research Initiative (grants no. 2017-67013-26191 and no. 2012-67019-19484), the US National Science Foundation Division of Environmental Biology (grant no. 1552747), and the Indiana University Environmental Resilience Institute.

Supplemental material

Supplemental data are available at *BIOSCI* online.

References cited

Abrams MD. 1990. Adaptations and responses to drought in Quercus species of North America. Tree Physiology 7: 227–238.

Abrams MD. 1992. Fire and the development of oak forests. BioScience 42: 346–353.

Abrams MD. 2003. Where has all the white oak gone? BioScience 53: 927–939.

Anderegg WR. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation New Phytologist 205: 1008–1014.

Anderegg WR, et al. 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. Nature 561: 538–541.

Au TF, et al. 2020, Demographic shifts in eastern US forests increase the impact of late-season drought on forest growth. Ecography 43: 1475–1486.

Bahari ZA, Pallardy SG, Parker WC. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak–hickory forests in central Missouri. Forest Science 31: 557–569.

Balci Y, Long RP, Mansfield M, Balser D, MacDonald WL. 2010. Involvement of Phytophthora species in white oak Quercus alba decline in southern Ohio. Forest Pathology 40: 430–442.

Bassett EN, Fenn P. 1984. Latent colonization and pathogenicity of Hypoxylon atropunctatum on oaks. Plant Disease 68: 317–319.

BassiriRad H, Lussenhop JF, Sehtiya HL, Borden KK 2015. Nitrogen deposition potentially contributes to oak regeneration failure in the Midwestern temperate forests of the USA. Oecologia 177: 53–63.

Benson MB, Miniat CF, Oishi AC, Denham SO, Missik JE, Phillips RP, Wood JD, Novick KA. 2021. The xylem of anisohydric *Quercus alba* L. is more vulnerable to embolism than isohydric co-dominants. Plant Cell and Environment, in press. DOI: 10.22541/au.163451218.80057296/v1.

Beguería S, Vicente-Serrano SM, Reig F, Latorre B. 2014. Standardized precipitation evapotranspiration index SPEI revisited: Parameter fitting, evapotranspiration models, tools, data sets and drought monitoring. International Journal of Climatology 34: 3001–3023.

Berdanier AB, Clark JS. 2016. Divergent reproductive allocation trade-offs with canopy exposure across tree species in temperate forests. Ecosphere 76: e01313.

Caldwell PV, Miniat CF, Elliott KJ, Swank WT, Brantley ST, Laseter SH. 2016. Declining water yield from forested mountain watersheds in response to climate change and forest mesophication. Global Change Biology 229: 2997–3012.

Cavender-Bares J. 2016. Diversity, distribution and ecosystem services of the North American oaks. International Oaks 27: 37–48.

Cavender-Bares J. 2019. Diversification, adaptation, and community assembly of the American oaks Quercus, a model clade for integrating ecology and evolution. New Phytologist 221: 669–692.

Chimner RA, Resh SC. 2014. Are riparian bur oak phreatophytic? A stable water isotope study in Homestead National Monument, Nebraska. Natural Areas Journal 34: 56–64.

Choat B, et al. 2012. Global convergence in the vulnerability of forests to drought. Nature 491: 752–755.

Clark JS, et al. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22: 2329–2352.

Cook BI, Smerdon JE, Seager R, Coats S. 2014. Global warming and 21st century drying. Climate Dynamics 43: 2607–2627.

Cook BI, Ault TR, Smerdon JE. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1: e1400082.

D'Orangeville L, et al. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Global Change Biology 24: 2339–2351.

Davidson CB, Gottschalk KW, Johnson JE. 1999. Tree mortality following defoliation by the European gypsy moth *Lymantria dispar* L in the United States: A review. Forest Science 45: 74–84.

Denham SO, Oishi AC, Miniat CF, Wood JD, Yi K, Benson MC, Novick KA. 2021. Eastern US deciduous tree species respond dissimilarly to declining soil moisture but similarly to rising evaporative demand. Tree Physiology 41: 944–959.

Dey DC. 2014. Sustaining oak forests in eastern North America: Regeneration and recruitment, the pillars of sustainability. Forest Science 60: 926–942.

Donovan LA, Grise DJ, West JB, Pappert RA, Alder NN, Richards JH. 1999. Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. Oecologia 120: 209–217.

Druckenbrod DL, Martin-Benito D, Orwig DA, Pederson N, Poulter B, Renwick KM, Shugart HH. 2019. Redefining temperate forest responses to climate and disturbance in the eastern United States: New insights at the mesoscale. Global Ecology and Biogeography 285: 557–575.

Elliott KJ, Miniat CF, Pederson N, Laseter SH. 2015. Forest tree growth response to hydroclimate variability in the southern Appalachians. Global Change Biology 21: 4627–4641.

Elliott KJ, Swank WT. 2008. Long-term changes in forest composition and diversity following early logging 1919–1923 and the decline of American chestnut Castanea dentata. Plant Ecology 197: 155–172.

Fan Z, Kabrick JM, Spetich MA, Shifley SR, Jensen RG. 2008. Oak mortality associated with crown dieback and oak borer attack in the Ozark Highlands. Forest Ecology and Management 255: 2297–2305.

Fei S, Kong N, Steiner KC, Moser WK, Steiner EB. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. Forest Ecology and Management 262: 1370–1377.

Ficklin DL, Maxwell JT, Letsinger SL, Gholizadeh H. 2015. A climatic deconstruction of recent drought trends in the United States. Environmental Research Letters 10: 044009.

Ficklin DL, Novick KA. 2017. Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere. Journal of Geophysical Research: Atmospheres 122: 2061–2079.

Ford CR, Hubbard RM, Vose JM. 2011. Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. Ecohydrology 4: 183–195.

Goring SJ, et al. 2016. Novel and lost forests in the upper Midwestern United States, from new estimates of settlement-era composition, stem density, and biomass. PLOS ONE 11: pe0151935.

Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RT, Sperry JS, McDowell NG. 2020. Plant responses to rising vapor pressure deficit. New Phytologist 226: 1550–1566.

Guyette RP, Muzika RM, Dey DC. 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5: 472–486.

Haavik LJ, Billings SA, Guldin JM, Stephen FM. 2015. Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. Forest Ecology and Management 354: 190–205.

Hanberry BB, Palik BJ, He HS. 2012. Comparison of historical and current forest surveys for detection of homogenization and mesophication of Minnesota forests. Landscape Ecology 27: 1495–1512.

Hayhoe K, Wuebbles DJ, Easterling DR, Fahey DW, Doherty S, Kossin J, Sweet W, Vose R, Wehner M. 2018. Our changing climate. Pages 72–144 in Reidmiller DR, Avery CW, Easterling DR, Kunkel KE, Lewis KLM, Maycock TK, Stewart BC, eds. Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, vol. 2. US Global Change Research Program.

Holzmueller EJ, Gibson DJ, Suchecki PF. 2012. Accelerated succession following an intense wind storm in an oak-dominated forest. Forest Ecology and Management 279: 141–146.

Hubbart JA, Guyette R, Muzika RM. 2016. More than drought: Precipitation variance, excessive wetness, pathogens and the future of the western edge of the eastern deciduous forest. Science of the Total Environment 566: 463–467.

Iverson LR, Prasad AM, Matthews SN, Peters M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management 254: 390–406.

Jo I, Fei S, Oswalt CM, Domke GM, Phillips RP. 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. Science Advances 54: eaav6358.

Kabrick JM, Dey DC, Jensen RG, Wallendorf M. 2008. The role of environmental factors in oak decline and mortality in the Ozark Highlands. Forest Ecology and Management 255: 1409–1417.

Kannenberg SA, Novick KA, Phillips RP. 2019a. Anisohydric behavior linked to persistent hydraulic damage and delayed drought recovery across seven North American tree species New Phytologist 222: 1862–1872.

Kannenberg SA, Maxwell JT, Pederson N, D'Orangeville L, Ficklin DL, Phillips RP. 2019b. Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US. Ecology Letters 22: 119–127.

Kannenberg SA, Novick KA, Alexander MR, Maxwell JT, Moore DJ, Phillips RP, Anderegg WR. 2019c. Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. Global Change Biology 25: 2978–2992.

Kannenberg S, Guo J, Novick K, Anderegg WRL, Feng X, Kennedy D, Konings A, Martínez-Vilalta J, Matheny A 2021. Opportunities, challenges, and pitfalls in characterizing plant water-use strategies. Functional Ecology. https://dx.doi.org/10.1111/1365-2435.13945.

Kennedy D, Swenson S, Oleson KW, Lawrence DM, Fisher R, Lola da Costa AC, Gentine P. 2019. Implementing plant hydraulics in the community land model, version 5. Journal of Advances in Modeling Earth Systems 11: 485–513.

Klos RJ, Wang GG, Bauerle WL, Rieck JR. 2009. Drought impact on forest growth and mortality in the southeast USA: An analysis using Forest Health and Monitoring data. Ecological Applications 193: 699–708.

Konings AG, et al. 2021. Detecting forest response to droughts with global observations of vegetation water content. Global Change Biology. https://doi.org/10.1111/gcb.15872.

Kreye JK, Varner JM, Hamby GW, Kane JM. 2018. Mesophytic litter dampens flammability in fire-excluded pyrophytic oak–hickory woodlands. Ecosphere 9: e02078.

Lanning M, Wang L, Benson M, Zhang Q, Novick KA. 2020a. Canopy isotopic investigation reveals different water uptake dynamics of maples and oaks. Phytochemistry 17: 112389.

Lanning M, Wang L, Novick KA. 2020b. The importance of cuticular permeance in assessing plant water–use strategies. Tree Physiology 40: 425–432.

Lynch C, Hessl A. 2010. Climatic controls on historical wildfires in West Virginia 1939–2008. Physical Geography 31: 254–269.

Luppold W, Pugh S. 2016. Diversity of the eastern hardwood resource and how this diversity influences timber use. Forest Products Journal 66: 58–65.

Mallya G, Zhao L, Song XC, Niyogi D, Govindaraju RS. 2013. 2012 Midwest drought in the United States. Journal of Hydrologic Engineering 18: 737–745.

Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB. 2006. Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. Plant, Cell, and Environment 39: 571–583.

Martínez-Vilalta J, Santiago LS, Poyatos R, Badiella L, de Cáceres M, Aranda I, Delzon S, Vilagrosa A, Mencuccini M 2021. Towards a statistically robust determination of minimum water potential and hydraulic risk in plants. New Phytologist 232: 404–417.

Martínez-Vilalta J, Poyatos R, Aguadé D, Retana J, Mencuccini M. 2014. A new look at water transport regulation in plants New Phytologist 204: 105–115.

Martínez-Vilalta J, Garcia-Forner N. 2017. Water potential regulation, stomatal behaviour and hydraulic transport under drought: Deconstructing the iso/anisohydric concept. Plant, Cell, and Environment 40: 962–976.

Matheny AM, Bohrer G, Garrity SR, Morin TH, Howard CJ, Vogel CS. 2015. Observations of stem water storage in trees of opposing hydraulic strategies. Ecosphere 6: 1–13.

Matheny AM, Fiorella RP, Bohrer G, Poulsen CJ, Morin TH, Wunderlich A, Vogel CS, Curtis PS. 2017. Contrasting strategies of hydraulic control in two codominant temperate tree species. Ecohydrology 10: pe1815.

Maxwell JT, Harley GL. 2017. Increased tree-ring network density reveals more precise estimations of sub-regional hydroclimate variability and climate dynamics in the Midwest, USA. Climate Dynamics 49: 1479–1493.

Maxwell JT, Harley GL, Matheus TJ, Strange BM, Van Aken K, Au TF, Bregy JC. 2020. Sampling density and date along with species selection influence spatial representation of tree-ring reconstructions. Climate of the Past 16: 1901–1916.

McCarthy BC, Small CJ, Rubino DL. 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. Forest Ecology and Management 140: 193–213.

McCulloh KA, Domec JC, Johnson DM, Smith DD, Meinzer FC. 2019. A dynamic yet vulnerable pipeline: Integration and coordination of hydraulic traits across whole plants. Plant, Cell, and Environment 42: 2789–2807.

McDowell N, et al. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytologist 178: 719–739.

McElrone AJ, Pockman WT, Martínez-Vilalta J, Jackson RB. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. New Phytologist 163: 507–517.

McEwan RW, Hutchinson TF, Long RP, Ford DR, McCarthy BC. 2007. Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern North America. Journal of Vegetation Science 18: 655–664.

McEwan RW, Dyer JM, Pederson N. 2011. Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34: 244–256.

Meinzer FC, Woodruff DR, Eissenstat DM, Lin HS, Adams TS, McCulloh KA. 2013. Above-and belowground controls on water use by trees of different wood types in an eastern US deciduous forest. Tree Physiology 33: 345–356.

Mirfenderesgi G, Bohrer G, Matheny AM, Fatichi S, de Moraes Frasson RP, Schäfer KV 2016. Tree level hydrodynamic approach for resolving aboveground water storage and stomatal conductance and modeling the effects of tree hydraulic strategy. Journal of Geophysical Research: Biogeosciences 121: 1792–1813.

Mishra V and Cherkauer KA. 2010. Retrospective droughts in the crop growing season: Implications to corn and soybean yield in the midwestern United States. Agricultural and Forest Meteorology 150: 1030–1045.

Niinemets Ü, Valladares F 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76: 521–547.

Novick KA, Konings AG, Gentine P. 2019. Beyond soil water potential: An expanded view on isohydricity including land–atmosphere interactions and phenology. Plant, Cell and Environment 42: 1802–1815.

Novick KA, et al. 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes Nature Climate Change 6: 1023–1027.

Nowacki GJ, Abrams MD. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58: 123–138.

Pederson N, et al. 2015. Climate remains an important driver of post-European vegetation change in the eastern United States. Global Change Biology 21: 2105–2110.

Pedlar JH, McKenney DW, Hope E, Reed S, Sweeney J 2020. Assessing the climate suitability and potential economic impacts of Oak wilt in Canada. Scientific Reports 10: 1–12.

Phillips RP, Ibáñez I, D'Orangeville L, Hanson PJ, Ryan MG, McDowell NG. 2016. A belowground perspective on the drought sensitivity of forests: Towards improved understanding and simulation. Forest Ecology and Management 380: 309–320.

Reed SE, English JT, Muzika RM. 2019. Phytophthora species detected in two Ozark forests with unusual patterns of white oak mortality. Plant Disease 103: 102–109.

Rhemtulla JM, Mladenoff DJ, Clayton MK. 2007. Regional land-cover conversion in the US upper Midwest: Magnitude of change and limited recovery 1850–1935–1993. Landscape Ecology 22: 57–75.

Rodriguez-Dominguez CM, Brodribb TJ. 2020. Declining root water transport drives stomatal closure in olive under moderate water stress. New Phytologist 225: 126–134.

Roman DT, Novick KA, Brzostek ER, Dragoni D, Rahman F, Phillips RP. 2015. The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought. Oecologia 179: 641–654.

Russell EW, Davis RB, Anderson RS, Rhodes TE, Anderson DS. 1993. Recent centuries of vegetational change in the glaciated north-eastern United States. Journal of Ecology 91: 647–664.

Sheil D, Burslem DF, Alder D. 1995. The interpretation and misinterpretation of mortality rate measures. Journal of Ecology 83: 331–333.

Shuman BN, Marsicek J. 2016. The structure of Holocene climate change in mid-latitude North America. Quaternary Science Reviews 141: 38–51.

Slette IJ, Post AK, Awad M, Even T, Punzalan A, Williams S, Smith MD, Knapp AK 2019. How ecologists define drought, and why we should do better. Global Change Biology 25: 3193–3200.

Skelton RP, Anderegg LD, Diaz J, Kling MM, Papper P, Lamarque LJ, Delzon S, Dawson TE, Ackerly DD. 2021. Evolutionary relationships between drought-related traits and climate shape large hydraulic safety margins in western North American oaks. Proceedings of the National Academy of Sciences 118: e2008987118.

Sperry JS, Love DM. 2015. What plant hydraulics can tell us about responses to climate-change droughts. New Phytologist 207: 14–27.

Steiner KC, Finley JC, Gould PJ, Fei S, McDill M. 2008. Oak regeneration guidelines for the central Appalachians. Northern Journal of Applied Forestry 25: 5–16.

Swaim JT, Dey DC, Saunders MR, Weigel DR, Thornton CD, Kabrick JM, Jenkins MA. 2018. Overstory species response to clearcut harvest across environmental gradients in hardwood forests. Forest Ecology and Management 428: 66–80.

Thomas RQ, Canham CD, Weathers KC, Goodale CL 2010. Increased tree carbon storage in response to nitrogen deposition in the US. Nature Geoscience 3: 13–17.

Voelker SL, Muzika RM, Guyette RP. 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. Forest Science 54: 8–20.

Williams AP, Cook BI, Smerdon JE, Bishop DA, Seager R, Mankin JS. 2017. The 2016 southeastern US drought: An extreme departure from centennial wetting and cooling. Journal of Geophysical Research: Atmospheres 122: 888–10,905.

Wolff JO. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy 77: 850–856.

Wood JD, Knapp BO, Muzika RM, Stambaugh MC, Gu L. 2018. The importance of drought–pathogen interactions in driving oak mortality events in the Ozark Border Region. Environmental Research Letters 13: 015004.

Woodhouse CA, Overpeck JT. 1998. 2000 years of drought variability in the central United States. Bulletin of the American Meteorological Society 79: 2693–2714.

Woodruff DR, Meinzer FC, McCulloh KA. 2010. Height-related trends in stomatal sensitivity to leaf-to-air vapour pressure deficit in a tall conifer. Journal of Experimental Botany 61: 203–210.

Yi K, Maxwell JT, Wenzel MK, Roman DT, Sauer PE, Phillips RP, Novick KA. 2019. Linking variation in intrinsic water-use efficiency to isohydricity: A comparison at multiple spatiotemporal scales New Phytologist 221: 195–208.

Kimberly Novick (knovick@indiana.edu) is an associate professor and Fischer Faculty Fellow, Michael Benson and Sander Denham are PhD students, and Mallory Barnes is an assistant professor in the O'Neill School of Public and Environmental Affairs at Indiana University, in Bloomington, Indiana, in the United States. Insu Jo is a forest ecologist at Manaaki Whenua, Landcare Research, in Lincoln, New Zealand. Loic D'Orangeville is an associate professor in the Faculty of Forestry and Environmental Management, at the University of New Brunswick, in Fredericton, New Brunswick, Canada. Tsun Fung Au is a PhD student in the Department of Geography at Indiana University, in Bloomington, Indiana, in the United States. Songlin Fei is a professor and Dean's Chair of Remote Sensing in the Department of Forestry and Natural Resources at Purdue University, in West Lafayette, Indiana, in the United States. Kelly Heilman was a PhD student in the Department of Biological Sciences at Notre Dame University, in Notre Dame, Indiana, and is now a postdoctoral research associate in the Laboratory of Tree Ring Research at the University of Arizona, in Tucson, Arizona, in the United States. Taehee Hwang and Justin Maxwell are both associate professors in the Department of Geography at Indiana University in Bloomington, Indiana, in the United States. Tara Keyser is a research forester with the US Department of Agriculture (USDA) Forest Service Bent Creek Experimental Forest, Southern Research Station, in Asheville, North Carolina, in the United States. Chelcy Miniat was project director of the USDA Forest Service Coweeta Hydrologic Laboratory, Southern Research Station, in Otto, North Carolina, and is now program manager with the USDA Forest Service Rocky Mountain Research Station, in Albuquerque, New Mexico, in the United States. Jason McLachlan is an associate professor in the Department of Biological Sciences at Notre Dame University, in Notre Dame, Indiana, in the United States. Neil Pederson is a senior biologist with the Harvard Forest in Petersham, Massachusetts, in the United States. Lixin Wang is an associate professor in the Department of Earth Sciences at Indiana University–Purdue University Indianapolis, in Indianapolis, Indiana, in the United States. Jeffrey Wood is an assistant professor in the School of Natural Resources at the University of Missouri in Columbia, Missouri, in the United States. Rich Phillips is a professor in the Department of Biology at Indiana University in Bloomington, Indiana, in the United States.