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Forum

Viewpoint

Tree drought physiology: critical research questions and strategies for mitigating climate change effects on forests

Summary

Droughts of increasing severity and frequency are a primary cause of forest mortality associated with climate change. Yet, fundamental knowledge gaps regarding the complex physiology of trees limit the development of more effective management strategies to mitigate drought effects on forests. Here, we highlight some of the basic research needed to better understand tree drought physiology and how new technologies and interdisciplinary approaches can be used to address them. Our discussion focuses on how trees change wood development to mitigate water stress, hormonal responses to drought, genetic variation underlying adaptive drought phenotypes, how trees 'remember' prior stress exposure, and how symbiotic soil microbes affect drought response. Next, we identify opportunities for using research findings to enhance or develop new strategies for managing drought effects on forests, ranging from matching genotypes to environments, to enhancing seedling resilience through nursery treatments, to landscape-scale monitoring and predictions. We conclude with a discussion of the need for co-producing research with land managers and extending research to forests in critical ecological regions beyond the temperate zone.

Introduction

Climate change is associated with periods of drought and heat that are increasing in frequency and severity, resulting in forest mortality and decreased tree growth (Breshears *et al.*, 2005; Brodribb *et al.*, 2020). Given the central role forests play in the carbon cycle, drought-related changes in tree growth and mortality have implications for carbon cycle–climate feedback on a global scale (Paschalis *et al.*, 2024). At local and regional levels, drought-related mortality affects forest community structure and function, with cascading effects on other trophic levels including the diversity of plants, animals, and microbes found within forest ecosystems. Drought-related forest mortality also has major impacts on society through increased wildfire, economic losses to traditional forest industries and tourism, and the myriad other ecological and societal benefits associated with forests (Cheng *et al.*, 2024). An example of the impacts of drought on forests in the Northern Hemisphere is given by forest mortality and associated wildfires in California (Fig. 1), with estimated annual economic losses averaging $117 M per year between 2017 and 2021 (Paci *et al.*, 2023).

Currently, we lack critical elements needed to understand how trees respond to and mitigate drought-related stress that are needed to meet forest management goals under drought scenarios. Tree drought physiology describes the biological processes underlying responses to drought from the cellular level to forest levels, including how trees ultimately die or survive (Choat *et al.*, 2018; Brodribb *et al.*, 2020; McDowell *et al.*, 2022a,b). As long-lived perennials, trees experience environmental changes at sub-hourly to millennial time scales. Tree physiological responses to drought mirror those timescales and range from rapid responses such as stomatal closure, to annual changes in wood development, to responses that can take decades to manifest in mortality (Cailleret *et al.*, 2017), and to the eventual mismatch in long-lived trees whose genotypes and adaptive traits no longer match contemporary conditions (Ledig & Kitzmiller, 1992). Legacy effects of a current year's drought on future years' growth (Anderegg *et al.*, 2015) is but one example of the many complexities involved in understanding drought physiology in trees without direct parallels in better studied model annual plants.

In a practical sense, managed forests are typically grown on heterogeneous landscapes with minimal cultivation or irrigation, limiting direct agronomic interventions. Strategies promoting drought resilience thus rely on landscape-scale interventions such as the selection of resilient species or genotypes, nursery practices that increase the survival of outplanted seedlings, and silvicultural practices. The most challenging of all is to understand and manage the diversity among the thousands of tree species of interest including angiosperm and gymnosperm species separated by 300 million years (Myr) of evolution, and the various strategies they exhibit to mitigate drought effects.

The complex biological responses of trees to drought are at best partially described, which limits innovation and the translation of research findings into effective strategies for forest conservation and management. Encouragingly, new technologies, an increasing base of knowledge, and opportunities for integrative research can enable significant advances. Here, we present ideas developed during a workshop 'Forest Tree Drought Physiology Research Innovation Group' held at the Arnold Arboretum, with the goals of identifying key research questions that, if addressed, might enable new transformative approaches for forest management under drought. The participants of the workshop were varied in approach and scope, and we thus are a broad but incomplete representation of the many research and management needs posed by drought. The topics selected for discussion here reflect the expertise of the authors and areas we believe are strategic for new discoveries that can be translated to forest management. While many of the

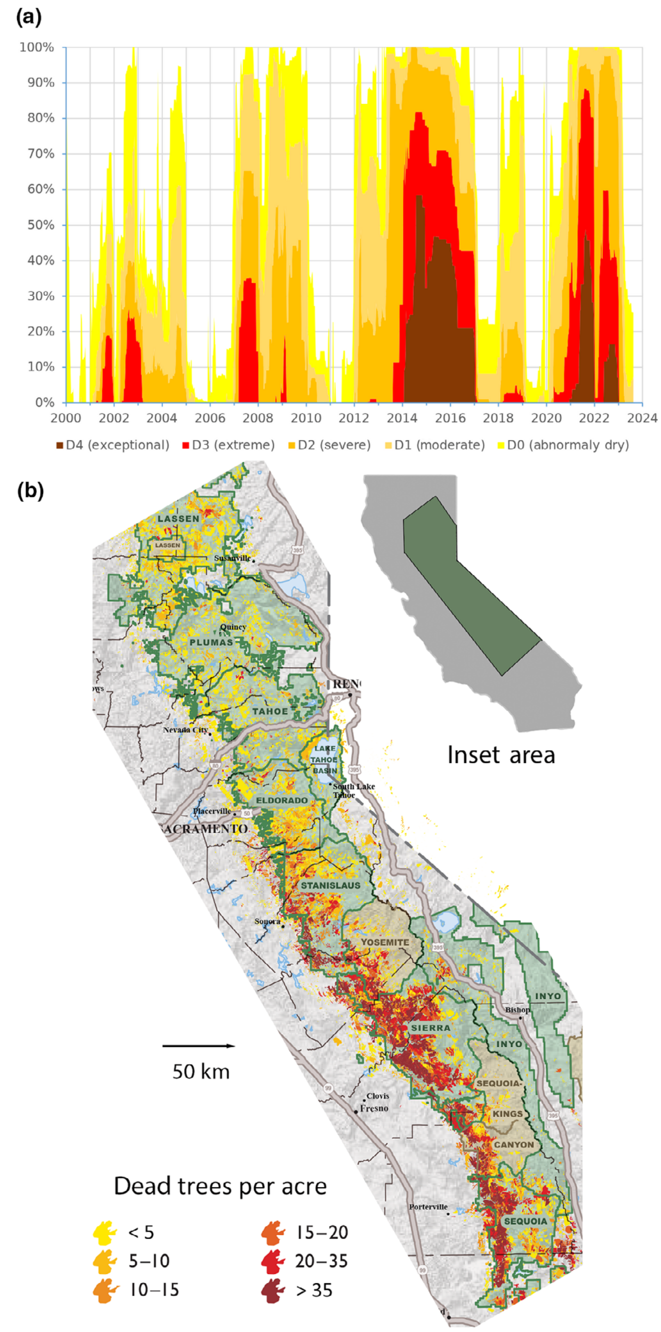

Fig. 1 Drought impacts on forest mortality in California. (a) California is characterized by a Mediterranean climate that experiences seasonal droughts. Drought severity is shown as percent area affected for 2000–2024, including exceptional drought from 2014 to 2017. (b) Tree mortality is shown for the Sierra Nevada of California from 2014 to 2017. (a) US Drought Monitor https://droughtmonitor.unl.edu/, (b) adapted from US Forest Service Forest Health Protection.

concepts and problems discussed are applicable to different forest types, our examples are drawn primarily from temperate forests, and do not adequately address the additional complexities of tropical and boreal forests. We also acknowledge that our discussion of molecular and genetic regulation of drought response skewed toward model angiosperm trees supported by genomic and gene function studies (notably *Populus* and *Eucalyptus*), despite the ecological and environmental importance of coniferous species.

In the first section of this paper, we highlight basic research knowledge gaps and opportunities to address them. In the second section, we then examine ways to translate research findings to enhance or even develop new strategies for forest management and conservation under climate change and drought. In the conclusion, we provide perspectives on practical research issues, as well as broader societal and ecological issues.

The concepts and approaches discussed in the paper are presented in Fig. 2.

From cells to forests: critical research questions for tree drought physiology

Below, we discuss missing information about the basic biology of drought response in trees that, if addressed, would enable new insights and approaches for forest management. This section is not intended to be a review of all tree drought physiology research, but rather to highlight examples of what are now tractable problems that can produce transformative insights.

How do trees adjust wood development and physiology to avoid hydraulic failure?

The anatomy and related physiology of tree stems play a major role in how trees respond to and potentially succumb to drought (Rodriguez-Zaccaro & Groover, 2019; Anfodillo & Olson, 2021; Olson *et al.*, 2023), including embolism resistance and regulation of osmotic potential. Tree stems are composed of secondary vascular tissues (wood and inner bark) produced by the cambium meristem. Wood evolves as a complex, heterogeneous tissue containing both dead and living cells (Olson, 2023), which collectively are responsible for water conduction, mechanical support, transport of signaling molecules, carbohydrate storage, and mineral nutrient transport (Carlquist, 2013).

The movement of water through nonliving tracheary elements in wood is explained by a cohesion-tension mechanism in which transpiration from leaves creates negative pressure that is transmitted down the water column to 'pull' water from roots through the stem to the canopy. Under drought, transpiration leads to increasingly low xylem pressures within tracheary elements potentially causing the formation and spread of air embolisms that disrupt the transport of water. The propagation of air embolisms can cause hydraulic failure and the irreversible desiccation of downstream tissues, which if widespread can lead to whole tree mortality (Choat *et al.*, 2018; Arend *et al.*, 2021; Lens *et al.*, 2022).

Wood development and subsequent anatomy undergo striking changes under drought, although direct functional relationships between anatomy and drought resistance are not always clear and have been debated in the literature (Olson *et al.*, 2023). In north-temperate conifers, embolism resistance is associated with narrow, thick-walled tracheids and small pit aperture diameters that hold across different species (Pittermann *et al.*, 2006; Delzon *et al.*, 2010). In woody angiosperms, narrower vessel diameter and increased pit membrane thickness have been implicated in

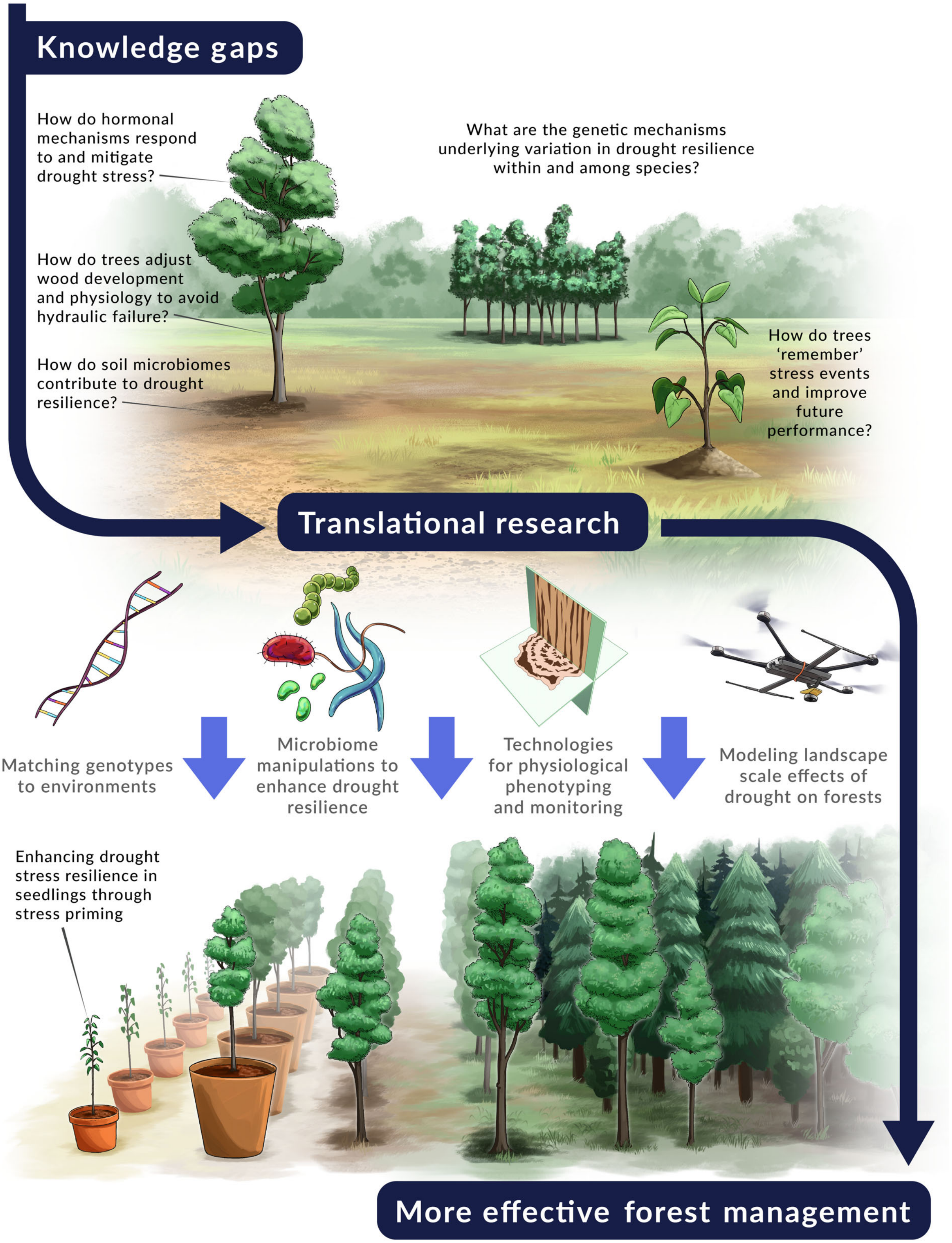

Fig. 2 Examples of knowledge gaps and how addressing them can enable translation to new approaches for forest management under drought. While not intended to be comprehensive, examples of key knowledge gaps of tree drought physiology are highlighted that, if rigorously addressed by research, have potential to translate into new applications for more effective forest management under drought scenarios.

embolism resistance, but the causative factors are unclear (Hacke *et al.*, 2017; Lemaire *et al.*, 2021; Levionnois *et al.*, 2021; Lens *et al.*, 2022; Isasa *et al.*, 2023). Fibers have thick secondary cell walls that act as mechanical support in wood and increase vessel resistance to implosion (Jacobsen *et al.*, 2005; Janssen *et al.*, 2020). Fibers can also act as reservoirs of water that can be used during water transport under drought stress (Jupa *et al.*, 2016; Knipfer *et al.*, 2017; Ziemińska *et al.*, 2020). These roles of fibers and variation in fiber development under drought are understudied. The degree of plasticity for key hydraulic traits such as pit membrane thickness that ultimately determine embolism resistance has been evaluated in Arabidopsis (Thonglim *et al.*, 2021). Similar studies are needed for trees to resolve the regulation and functional consequences of wood anatomy changes under drought. Furthermore, homologies and unique attributes among wood hydraulic traits in angiosperm vs gymnosperm tree species separated by over 300 Myr of evolution can now be explored using functional genomics.

The cellular and molecular processes driving drought response in woody tissue are a promising area for physiology research in forest trees and could provide insights useful for applications such as monitoring and predicting mortality, or breeding for drought resilience. Living cells within secondary xylem can concentrate solutes (sugars, organic acids, etc.) to lower water potential and reach equilibrium with the xylem (Ozturk *et al.*, 2021). Such osmoregulation occurs over hours or days and prevents water loss from living cells to the vessels. When present, xylem parenchyma appears to be involved in mitigating embolism, presumably because the parenchyma stores water and solutes, and can offer an osmotic means of regulating water potential (Pratt *et al.*, 2021). Some highly specialized parenchyma cells known as vessel-associated cells (VACs; also referred to as contact cells) are in direct contact with vessel elements via contact pits and are responsible for transport of water, sugars, amino acids, and possibly proteins, lipids, and surfactants into and out of vessel elements (Słupianek *et al.*, 2021, 2024). Molecular exchange between xylem parenchyma and vessels is highly regulated under drought, and VACs may facilitate embolism recovery (Brodersen & McElrone, 2013; Brodersen *et al.*, 2020). However, knowledge of the underlying molecular mechanisms and cellular processes is incomplete, including how ray parenchyma cells facilitate the exchange of water and solutes between xylem and phloem, and how movement of sugars from the phloem to the xylem is regulated to increase conduit resistance to embolism.

How do hormonal mechanisms respond to and mitigate drought stress?

Hormonal regulation is central to tree drought physiology, involving primary and interacting effects of multiple hormones (Table 1) that mediate acclimation of the hydraulic system to drought. The phytohormone abscisic acid (ABA) is arguably the best studied and plays a direct role in drought sensing, triggering known protective measures such as stomatal closure (Raghavendra *et al.*, 2010) and changes in wood development, including production of smaller diameter and more interconnected vessels (Yu *et al.*, 2021), but ABA sensitivity varies among tree species (Brodribb & McAdam, 2013) and how ABA affects wood growth and physiology is only recently being revealed at the molecular level. Basic questions include whether living cells in wood directly sense drought and respond through ABA production or whether wood primarily responds to signals from other drought-sensing tissues (notably roots). Grafting experiments in Arabidopsis between root stocks of ABA-deficient mutants and wild-type scions did not impair stomatal response to water stress, while reciprocal grafts were impaired, suggesting that ABA signals from stems are necessary and sufficient for stomatal response (Christmann *et al.*, 2007). In trees, comparative phytohormone profiling in the immature xylem from drought-stressed and control poplars showed a drastic increase in ABA levels, which was much greater than in leaves and roots (Yu *et al.*, 2021). Transcripts for the homologs to all ABA biosynthetic enzymes were detected in immature xylem (Yu *et al.*, 2021). In drought-stressed immature xylem, the transcript abundances of putative ABA exporter genes, as well as of the key genes for ABA biosynthesis, were increased (Yu *et al.*, 2021). These changes were accompanied by phenotypic shifts from thin- to thick-walled fiber cells, and from large to smaller and

Table 1 Phytohormones with documented roles in plant drought response.

Phytohormone	Roles in drought response and key references
Abscisic acid (ABA)	Stomatal regulation (Munemasa *et al.*, 2015; Kuromori *et al.*, 2018); suppression of lateral root formation in air (i.e. 'xerobranching'; Mehra *et al.*, 2022); putative role in xylem development (Arend & Fromm, 2007; Yu *et al.*, 2021); drought-induced leaf senescence (Zhao *et al.*, 2016)
Auxin (IAA and IBA)	Lateral root formation/root branching in response to water (i.e. 'hydropatterning'; Bao *et al.*, 2014); leaf senescence and abscission (Jin *et al.*, 2015; Ma *et al.*, 2021); putative role in vessel diameter and patterning (Hacke *et al.*, 2017; Johnson *et al.*, 2018); crosstalk with ABA (Sharma *et al.*, 2023)
Brassinosteroids (BR)	Root development and architecture (Wei & Li, 2016); stomatal development (with ABA; Serna, 2014); crosstalk with numerous other hormones (Choudhary *et al.*, 2012)
Cytokinins (CK)	Crosstalk with SL (Li *et al.*, 2019); with IAA re : root : shoot ratio (Kurepa & Smalle, 2022); and with ABA (Li *et al.*, 2016)
Ethylene (ET)	Root development and leaf senescence (Baharudin & Osman, 2023); crosstalk with ABA in stomatal regulation (Kazan, 2015) and with JA in root growth (Song *et al.*, 2014); reactive oxygen species (ROS) defense (Depaepe *et al.*, 2021)
Gibberellins (GA)	Root growth and crosstalk with JA (Koo *et al.*, 2020)
Jasmonates (JA, JA-Ile)	Stomatal closing, root physiology and cross talk with ABA (Kazan, 2015); root growth and crosstalk with ET and GB (Song *et al.*, 2014)
Salicylic acid (SA)	Osmotic stress and ROS response (Koo *et al.*, 2020); crosstalk with ABA and JA (Muñoz-Espinoza *et al.*, 2015); crosstalk with BR (Choudhary *et al.*, 2012)
Strigolactones (SL)	Indirectly implicated via roles in shoot branching inhibition (e.g. for reduced transpirational demand; Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2008) and root architecture (Koltai, 2011)

more frequent vessels. Similar anatomical changes in the xylem were found in many drought studies (Polle *et al*., 2019) and can be induced locally by the application of ABA to the stem of poplars (Arend & Fromm, 2007). However, direct experimental validation demonstrating ABA production in wood is missing.

Abscisic acid signaling initiates changes in development to produce anatomy more suited to water stress (Yu *et al*., 2021), but how ABA connects with the other hormones affecting wood development remains poorly defined. The control of cell division in the cambium and subsequent cell differentiation can involve auxin, cytokinin, brassinosteroids, jasmonates, and gibberellin (Table 1). In developing xylem of drought-stressed poplars, some of these hormones show significant changes in response to drought (Table 1). Vessel expansion and patterning depend on cambial auxin concentrations and transport processes (Schrader *et al*., 2003; Junghans *et al*., 2004; Johnson *et al*., 2018), and there is accumulating evidence for the interaction of ABA and auxin signaling in plants (Ortiz-García *et al*., 2023). Cytokinin concentrations modulate the sensitivity of the cambium to auxin and thereby affect radial growth (Immanen *et al*., 2016). Auxins also contribute to drought response by altering root development to maximize water acquisition, adjusting the root : shoot ratio in response to water demand and availability (Bao *et al*., 2014), and regulating leaf shedding (Jin *et al*., 2015). How ABA affects other hormonal signaling pathways to affect wood development and physiological changes is a promising area for the development of new drought-resistant genotypes or applications such as stress priming (discussed below) and could provide new diagnostic tools for evaluating drought stress in forests.

How do soil microbiomes contribute to drought resilience?

Understanding how microbes impact tree drought physiology could facilitate the development of climate- or site-specific inocula that could improve tree performance as climates change. Soil microbiota can improve leaf water potential and photosynthetic rates in drought-stressed seedlings (Kannenberg & Phillips, 2017). Their benefits can be locally adapted, as microbes from dry, hot, or cold sites can improve tree seedling survival when faced with the same stressors (Allsup *et al*., 2023). Leaf endophytes, too, can improve conifer seedling survival and photosynthesis under drought (Aghai *et al*., 2019). Microbial effects on plant drought response can depend on the time scale on which the drought is imposed (Ulrich *et al*., 2019), and on the variety of microbial interactions that a plant can engage in (e.g. arbuscular mycorrhizal vs ectomycorrhizal host plants) (Allsup *et al*., 2023). Ectomycorrhizal symbiosis alters tree response, both locally and systemically, to abiotic cues such as water limitation (de Freitas Pereira *et al*., 2023), a process which is mediated by ABA and other key drought-responsive hormones detailed above.

Hormones can all be impacted by or modulate microbial interactions (Kim *et al*., 2012; Foo *et al*., 2019), but it remains difficult to predict which microbial strains or consortia have particular effects. Adding complexity, microbial communities themselves respond strongly to drought stress (Baldrian *et al*., 2023), potentially changing their impacts on drought-stressed plants by shifting the density or behavior of mutualistic or pathogenic organisms. This balance between helpful and harmful microbes in the microbiome may be controlled, in part, by plant genetics. Drought-tolerant genotypes of *Populus trichocarpa* support more beneficial microbes than drought-susceptible genotypes (Kristy *et al*., 2022). Molecular interactions between tree roots and beneficial microbes can impact plant drought response. Ectomycorrhizal networks facilitate the exchange of nonstructural carbohydrates and impact drought tolerance-related traits in *Pinus ponderosa* (Sapes *et al*., 2021). Ectomycorrhizal fungi can increase tree production of ABA and salicylic acid, potentially priming the plant to better endure drought stress (Kebert *et al*., 2023), while fungi can enhance tree drought tolerance by improving plant antioxidant function and enhancing mitogen-activated protein kinase (MAPK) signaling cascades linked to drought tolerance (Wang *et al*., 2023). However, the drivers of microbial communities, adaptive traits of microbes, and interactions with tree genotypes within the context of drought resilience are not well understood presently.

Current questions in microbiome research for forest tree drought physiology reflect a shift from correlative observations to descriptions of causative biological mechanisms and processes. Ongoing advances in nucleic acid, protein, and metabolite analysis are being used to explore mechanisms of and physiological responses to microbial associations by employing ‘multi-omic’ approaches to reveal the specific organisms and biochemicals involved in tree-microbe interactions (de Freitas Pereira *et al*., 2023; Nosenko *et al*., 2023). Although often employed in isolation, combining sequencing with fine-scale biochemical analyses will be an important step toward developing a predictive framework of how microbes impact tree drought response, and expand our understanding beyond seedlings to encompass adult trees in field contexts. Identifying the mechanisms involved will also require growth chamber experiments whose design can be guided by correlative multi-omic datasets, allowing for the isolation of specific microbes and compounds responsible for shifts in tree drought response. Questions that can be addressed with such methods include whether trees actively select or recruit microbes suited for drought conditions, the role tree genotypic variation might play in microbiome assemblage, the degree to which variation in microbial traits contributes to drought-relevant phenotypes (Allsup *et al*., 2023), and what genes and mechanisms are associated with drought resistance and resilience during the interaction of trees and microbes under drought. Importantly, studies describing the population-level variation in functional traits of soil microbes associated with drought could provide the foundations for effective microbiome treatments, which would also be informative for assisted migration applications.

What are the genetic mechanisms underlying variation in drought resilience within and among species?

Identifying and harnessing natural genetic variation for tree drought response underpins forest conservation under climate change. Variation among and within species for drought response is observed, but the ability to relate resilience to specific genes remains

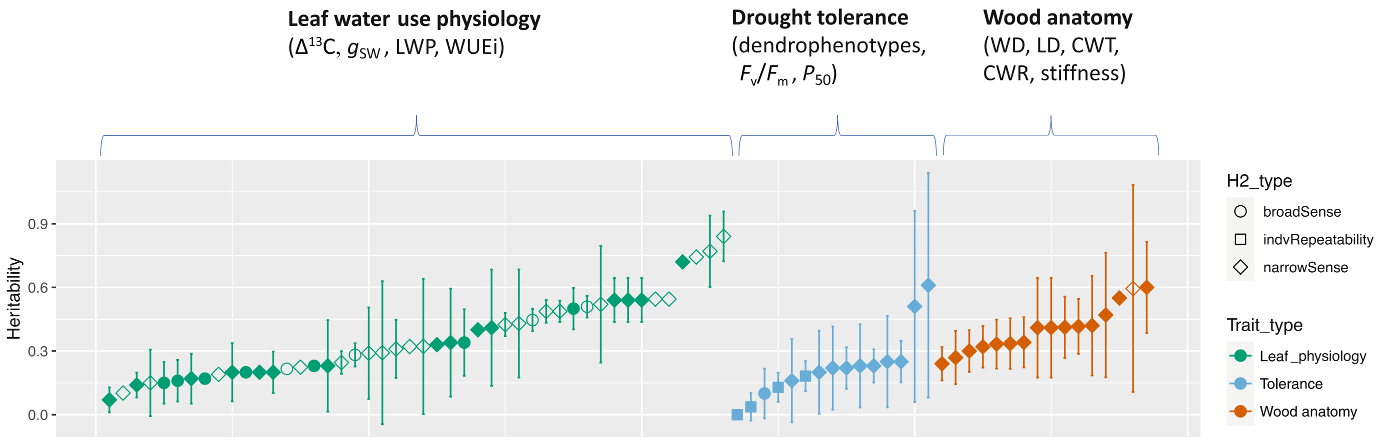

Fig. 3 Within-species genetic variation for forest tree drought response. Values shown are heritabilities (i.e. the proportion of phenotypic variance attributed to genetic effects) estimated from common garden or provenance trial experiments, displayed in order of increasing magnitude along the *x*-axis for different classes of drought-related traits. Symbol shapes denote the type of heritability estimate (narrow-sense, broad-sense, or individual repeatability). Filled symbols are for coniferous trees, while open symbols are estimates from angiosperm trees. Values represent a nonexhaustive sampling of 26 studies reporting natural genetic variation in drought response traits across 14 tree species. Estimates are means ± 95% CI, when reported. CWR, cell wall reinforcement; CWT, cell wall thickness; dendrophenotypes, tree-ring derived growth traits in response to drought; F_v/F_m, maximum efficiency of Photosystem II; g_{sw}, stomatal conductance; LD, lumen diameter; LWP, leaf water potential; P_{50}, pressure at 50% loss of xylem hydraulic conductance; stiffness, wood stiffness measured by acoustic velocity; WD, wood density; WUEi, instantaneous water use efficiency; Δ^{13}C, carbon isotope discrimination. Further details are available in Supporting Information Table S1.

challenging for both technical and biological reasons. The inherent capacity to tolerate drought reflects complex, polygenic mechanisms that are highly responsive to the environment and present challenges for traditional genetic analysis where experimental variation reduces the power to detect quantitative genetic effects. A major technical challenge is to establish phenotyping methods that both measure complex physiological phenotypes and can scale to the large numbers of genotypes required for genomic studies. Typical experimental approaches for tree genomic studies require hundreds or thousands of trees and include field trials and common garden studies that permit phenotyping under quasi-natural conditions (Jaramillo-Correa *et al.*, 2015; de Villemereuil *et al.*, 2016), and glasshouse-based studies that permit manipulation of environmental conditions and application of experimental treatments. Advances in sequencing technologies have largely removed the technical challenge of extending genomic approaches to tree species and allow experimental designs with large sample sizes, but the technical hurdle to identify and accurately measure relevant physiological traits in large numbers of trees remains. To date, phenotyping in genome-wide association studies (GWAS) has been largely limited to water use efficiency since the isotopic ratio of carbon ^{13}C : ^{12}C can be used as a proxy for a time-integrated measure of water use efficiency due to plant carbon isotope discrimination (CID) (Farquhar *et al.*, 1989). CID can be estimated using mass spectrometry on either leaf or woody tissue and is feasible for large sample sizes (González-Martínez *et al.*, 2008; Cumbie *et al.*, 2011). While water use efficiency displays extensive plasticity in response to soil water availability, there is also evidence for natural genetic variation, with GWAS of CID in a variety of conifer and broad-leaved tree species returning a wide range of heritabilities, from 0.07 to 0.84 (mean = 0.36; Fig. 3). However, these measures reflect an amalgam of component traits contributing to water use efficiency. Only recently, there is some progress in describing metabolic mechanisms underlying ^{13}C signatures (Wieloch *et al.*, 2024). More problematic is that, to date, only a fraction of observed phenotypic variation for any drought-related traits can be explained based on genetic predictions.

These genetic predictions could be useful for understanding water relations in trees, but relatively few studies have addressed these linkages to more direct physiological and anatomical traits associated with mortality because of additional phenotyping challenges (Brodribb *et al.*, 2020). For example, xylem vulnerability to embolism can be estimated from dose–response curves that determine the pressure at which xylem is embolized (P_x), which corresponds closely to lethal water potential (ψ lethal) in trees (Liang *et al.*, 2021). High-precision methods for estimating xylem vulnerability curves involve the use of optical techniques or high-speed centrifugation (e.g. 'Cavitrons'), but are time-intensive to collect and not easily adapted for population-level or genomic studies (Plomion *et al.*, 2016). As previously discussed, wood anatomical traits are correlated with hydraulic failure, but are time consuming to assay through traditional histology. Genetic studies in poplar identified significant heritabilities, quantitative trait loci, and candidate genes for vessel traits associated with drought resilience in a large pedigree carrying induced chromosomal lesions (Rodriguez-Zaccaro *et al.*, 2021, 2024). Such studies could be expanded and made much more informative if higher throughput methods for phenotyping were available.

An important question for trees is how genotypes respond to variation in drought stress across many years of growth, including the basis for plasticity in drought responses. The response to past drought stress can be derived from tree rings ('dendrophenotypes') sampled from trees growing in established provenance trials

(Housset *et al.*, 2018). Such time-series data can be used to estimate the climatic sensitivity of different genotypes and provenances and to derive measures of resistance, resilience, and recovery in response to drought (Depardieu *et al.*, 2020). Drought response in dendrophenotypes measured from tree rings showed low to moderate, but often significant heritabilities (Fig. 3), suggesting the presence of plasticity, but also some promise for genetic mapping of responses to naturally occurring drought episodes in the field. Applying this approach in white spruce (*Picea glauca*) using GWAS on dendrophenotypes spanning a natural drought event revealed strong associations identifying a suite of candidate genes and mechanisms (Depardieu *et al.*, 2021).

How do trees 'remember' stress events and improve future performance?

Given that trees have long lifespans, they must adjust their physiological responses at different time scales to increase resilience to repeated stress and drought. Epigenetics is emerging as a key mechanism by which forest trees respond to environmental stresses including drought (Bräutigam *et al.*, 2013; Amaral *et al.*, 2020). The epigenome, which is a proxy for stress memory in plants, is increasingly seen as a key point of regulation of drought-responsive genes and associated mechanisms (Lämke & Bäurle, 2017; Balao *et al.*, 2018; Sadhukhan *et al.*, 2022; Gallusci *et al.*, 2023). Histone modifications and DNA methylation are epigenetic marks known to be dynamic in response to environmental changes in plants (Gallusci *et al.*, 2023). These marks are modified in individual trees in response to stress and, in some cases, can be transmitted across generations (Zolfaghari *et al.*, 2022). For instance, induced drought stress for 12 yr in *Quercus ilex* was correlated with an increase in hypermethylated loci and a decrease in fully methylated loci (Rico *et al.*, 2014). Do Nascimento *et al.* (2022) pre-exposed genetically identical trees raised from somatic embryos of *Pinus radiata* to either a control or heat stress and found that prestressed trees later had improved drought response that was correlated with DNA methylation. A direct relationship between epigenetic modifications and drought response was observed in transgenic poplars, where suppressing DNA methylation using RNAi resulted in increased drought tolerance (Sow *et al.*, 2021). A recent study on poplar (*Populus tomentosa*) demonstrated a connection between DNA methylation, structural changes, and gene expression in response to drought (Zhou *et al.*, 2023). This study also showed cross-generational epigenetic changes, which is challenging to address in organisms as long-lived as forest trees. A mechanism for Histone H3 lysine-4 methylation activation of drought-responsive genes has also been identified recently in poplar (Zhang *et al.*, 2024).

Progress in describing the functional relationships between epigenetics and drought physiology is being made and the above-mentioned studies demonstrate general correlations among chromatin marks and drought response, but the specific molecular mechanisms and target genes connecting drought perception, epigenetic changes, and downstream physiological and developmental changes remain uncertain. Further extending knowledge of evolutionarily conserved epigenetic mechanisms from model herbaceous species to trees is an obvious area of opportunity to advance this field. How to effectively manipulate epigenetic variation within the framework of operational forestry genetics, nursery, or management context is largely unaddressed, but could open exciting opportunities for drought preconditioning (e.g. see stress priming below).

Translating research to applications for mitigating climate effects on forests

The current pace of climate change is causing increasing frequency and severity of drought within the lifetimes of individual trees, and the rate of natural dispersal is far slower than the rate of warming (Aitken *et al.*, 2008). Thus, a question increasingly discussed among tree biologists working at the intersections of physiology, genetics, conservation, and forest health is, how to facilitate adaptation of forests to future climate (Isabel *et al.*, 2019)?

Translating advances in tree drought physiology into effective applications for land managers is part of the answer, but there are significant challenges to address. Long generation times and inefficient phenotyping of drought traits of relevance to forest management make the development of new drought-resistant genotypes a slow and costly enterprise. Rotation ages measured in decades translate into long periods with limited options for changes in management strategies or interventions. However, there are significant opportunities for research advances in drought physiology that enable more effective strategies for forest management. Below, we discuss examples of enhanced or new applications for forest management under drought that would take advantage of new research findings, including those discussed in the previous section. We first consider how land managers can anticipate and monitor drought impacts to guide silvicultural practices, and then outline areas for management interventions including nursery practices for reforestation, microbiome manipulations, and selection of genotypes for future climates. These examples are not intended to be exhaustive of all existing or potential applications, but rather to present some promising avenues toward effective mitigation of practical problems faced by land managers on large scales.

Predicting and monitoring landscape-scale effects of drought on forests

Forest managers need the ability to assess current and predict future conditions when making decisions about reforestation and silvicultural treatments. The development of predictive process-based models of tree mortality is a very active area of research, drawing heavily on new insights from tree physiology (McDowell *et al.*, 2022a,b). For instance, physiological studies have shown that hydraulic failure is involved in many drought-related mortality events (Adams *et al.*, 2017), but is not universal (Körner, 2019). Many modelling groups have incorporated a representation of the hydraulic pathway and the processes leading up to embolism, to enable use of thresholds of xylem embolism as a predictor for tree mortality (McDowell *et al.*, 2013; Xu *et al.*, 2016, 2023; Mencuccini *et al.*, 2019). This suite of hydraulic processes can be usefully characterized by a small number of plant traits, particularly the P_{50} or xylem water potential for 50% loss of hydraulic conductivity (MPa) (Brodribb, 2017; Venturas *et al.*, 2017). This threshold appears to vary systematically among species and provenances depending on their climate of origin (e.g. Larter *et al.*, 2017; Li *et al.*, 2018). Knowledge of variation in hydraulic thresholds among genotypes is advancing our capacity to predict species-level differences in drought vulnerability (De Kauwe *et al.*, 2022), with the ultimate goal of matching species or populations to future climates. However, challenges remain including how to accurately capture whole soil–plant hydraulic vulnerability, particularly in mature large trees, and/or where along the soil–plant–atmosphere continuum the most relevant thresholds are, and which respective physiological processes prevent or delay reaching these thresholds.

Additionally, interacting physiological characteristics are also needed to predict risk of mortality (Trugman *et al.*, 2021). Studies of the relationship between stomatal behavior and hydraulic thresholds suggest that in many woody species, stomatal closure is coordinated with the onset of xylem embolism (Li *et al.*, 2018), and models link these two sets of processes (e.g. Sperry *et al.*, 2017). Predictions of the time to mortality are also sensitive to the representation of processes occurring after the point of stomatal closure, particularly the rate of water loss via cuticles and incomplete sealing of stomatal pores $g_{\min}$ (Duursma *et al.*, 2019). This conductance appears to be variable with environmental conditions, and in particular increases significantly at high temperatures (Cochard, 2021). This increase in conductance exacerbates hydraulic failure under heatwaves and be a mechanism by which hot droughts drive mortality (Hammond *et al.*, 2022).

A deeper, preferably quantitative, physiological description of drought legacies is thus a priority if we are to predict the long-term impacts of drought stress. Drought stress can also cause long-term legacy effects on tree health and forest functioning (Anderegg *et al.*, 2015) relevant to long-term management strategies. Mechanistic and predictive models of recovery from drought stress and the effects of repeated droughts are growing research areas. Recovery from drought requires rebuilding of canopy foliage, root biomass, carbohydrate stores, and xylem conduits (Gauthey *et al.*, 2022). The recovery rate of wood growth can last decades and trees that do not recover wood growth are more likely to die than those that fully recover (Cailleret *et al.*, 2017). The recovery rate of carbohydrate stores after drought is short in angiosperms but long in gymnosperms (Piper & Paula, 2020) and depletion of stored carbohydrates reduce osmoregulation capacity (Sapes *et al.*, 2021). Ultimately, there is little evidence that trees in nature die directly of carbon starvation during drought by reaching zero carbohydrate concentrations, but the interaction of carbohydrate stores and plant water relations are fundamentally intertwined and can affect long-term growth and recovery (McDowell *et al.*, 2022a,b).

While predictive models can potentially assist in targeting management interventions, broad-scale monitoring of drought stress impacts is critical to evaluate such models. However, quantifying these impacts at scales relevant for land management remains a significant challenge (Hartmann *et al.*, 2018). Ground-based forest inventory methods can be too infrequent and too sparse to assess and attribute impacts of drought. Satellite remote sensing offers high temporal and spatial coverage, but detecting mortality remains difficult due to high spatial heterogeneity in mortality rates and the problem of how to interpret the remote sensing signal (Yan *et al.*, 2024). Greenness can often recover rapidly following a drought stress event, but this may reflect the recovery of understory or weeds rather than overstorey trees. Nonetheless, several promising approaches are in development. Airborne LiDAR can be used to map biomass at high spatial resolution and identify tree mortality at scales of individual trees (Stovall *et al.*, 2019). High-resolution satellite optical imagery, capable of distinguishing individual tree crowns, is also becoming available, and machine learning approaches trained on airborne LiDAR show promise for large-scale tree detection (Dixon *et al.*, 2013). These methods have the potential to deliver regular monitoring of tree mortality, although ground-based inventory data will continue to remain essential for ground-truthing such approaches.

Technologies for physiological phenotyping and monitoring

Measuring physiological traits that describe drought response and resilience remains a key challenge for both high-throughput/high-precision phenotyping required for genomic studies, and for evaluation of landscape-scale studies (e.g. common gardens) and informing management strategies. High-resolution imaging data (e.g. spectral, hyperspectral, Chl fluorescence, and infrared) has the potential for widespread use for precision phenotyping of drought response in trees, as recently demonstrated for crops (Al-Tamimi *et al.*, 2022). Recent work by Castillo-Argaez *et al.* (2024) and Sapes *et al.* (2024) show that both drought stress and disease can be monitored with remote sensing technology for more rapid assessment of large forest tracts, and the ability to detect stress before visual symptoms appear. For field studies, image-based phenotyping of plant stress has the capacity for high-throughput measurements suitable to common gardens, provenance trials using ground vehicles or unmanned aerial vehicles (D'Odorico *et al.*, 2020). Glasshouse-based studies that can incorporate precisely applied experimental treatments are supported by automated high-throughput phenotyping platforms capable of precision phenotyping of plant stress responses that are non-destructive and that permit repeated measurements of the temporal dynamics of drought response with high temporal resolution (Bian *et al.*, 2022). An example is the Advanced Plant Phenotyping Laboratory (APPL; Department of Energy, Oak Ridge National Lab) designed for capturing detailed image-based tree phenotypes utilizing multiple sensors to estimate features of plant water balance, stress response and stomatal regulation on hundreds of samples over short time intervals within an automated glasshouse (Fig. 4). This facility now enables functional 'omic' studies integrating genome, gene expression, proteomic and metabolic data to ultimately provide mechanistic understanding and predictions of tree drought phenotypes.

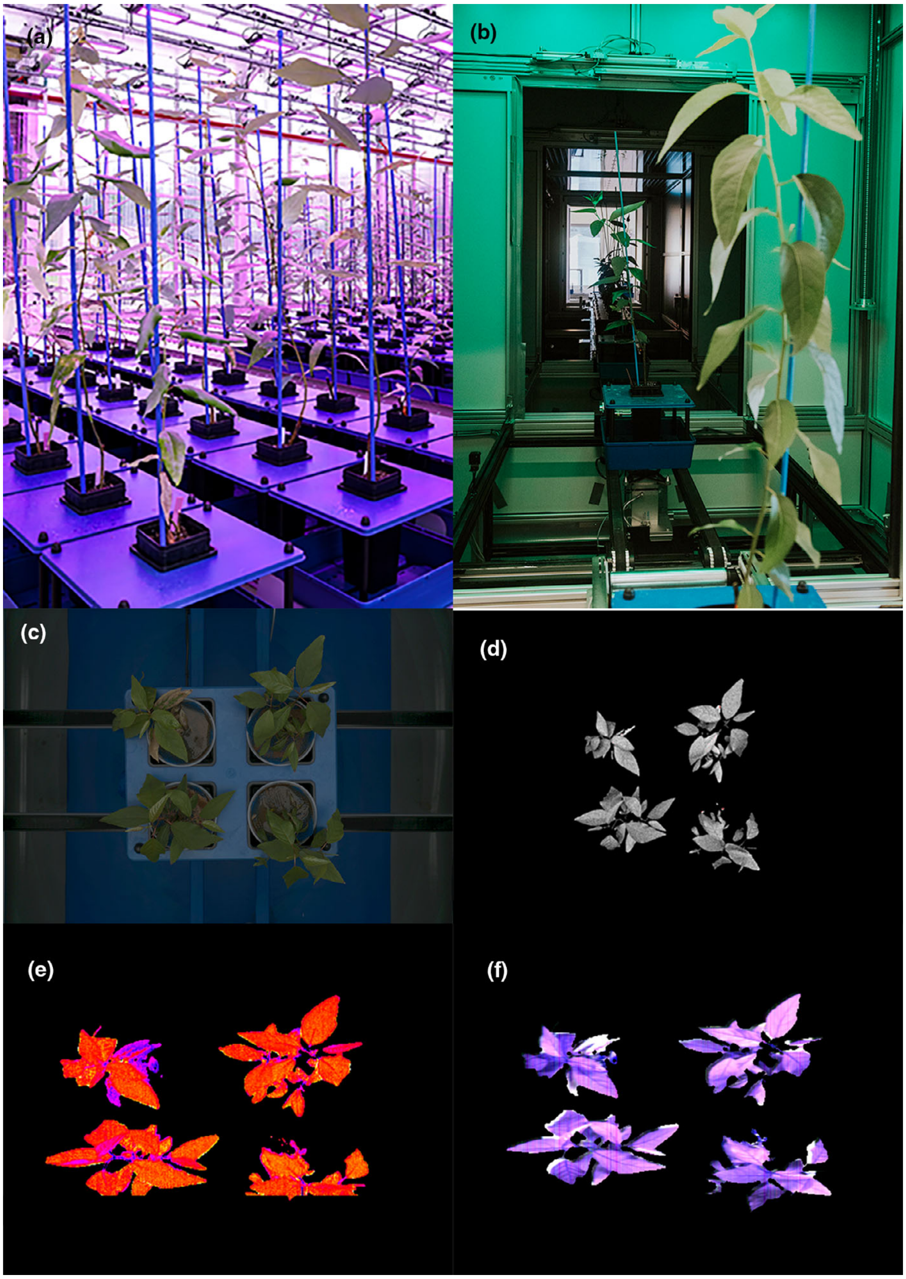

Fig. 4 Automated precision phenotyping platform for poplar growth and physiological studies. The Advanced Plant Phenotyping Laboratory (APPL) at Oak Ridge National Laboratory was established to conduct high-throughput plant physiological, morphological, and spectral characterization using multimodal phenotyping stations. Photographs show (a) *Populus trichocarpa* genotypes from a genome-wide association study being grown under precise water and nutrient regimes, and (b) individual plants sequentially entering a series of phenotyping cabinets. Other photographs show trays of four plants for greater capacity as imaged by four different modalities, including (c) red, green blue (RGB) for plant size and morphology, (d) chlorphyll fluorescence for estimations of photosynthetic efficiency, (e) visible to near-infrared (VNIR) hyperspectral signatures in the 400–900 nm range, such as Normalized Difference Vegetation Index (NDVI), and (f) short wave infrared (SWIR) for spectral signatures in the 900–1700 nm range for the detection of water content or chemical composition. Images (c–f): courtesy of Larry York, Jun Lee, and David Weston.

Matching genotypes to environments

Given the highly polygenic nature of tree drought responses and the long breeding cycle for most tree species, selecting genotypes and breeding for drought tolerance is a challenging prospect. Genomic selection (GS), in which a genomic relatedness matrix and trait measurements on potential parents is used to predict offspring trait values, has proven a valuable strategy that can shorten the breeding cycle (Resende *et al.*, 2012). For example, in white spruce (*P. glauca*), GS was used to predict components of drought response impacting radial growth following natural drought episodes in a large breeding trial (Laverdière *et al.*, 2022). A persistent challenge for GS is that prediction accuracies are often reduced under novel environments (Resende *et al.*, 2012), although recent developments incorporating multi-site phenotyping and G × E into models are promising in this regard (Crossa *et al.*, 2022). An important consideration of using GS for breeding stress-tolerant genotypes arises from potential genetic correlations with other traits due to pleiotropy, which constrains breeding targets due to tradeoffs with other desirable traits, such as growth and productivity (Sebastian-Azcona *et al.*, 2018). Additionally, the genetic architecture of drought tolerance and growth is likely to be species-specific (Csilléry *et al.*, 2020; Compton *et al.*, 2023).

While genomics holds promise for accelerating breeding for drought response, this approach may not be possible or efficient for many species due to constraints of generation time and/or availability of resources in noncommercial species. Alternatively, if existing drought-tolerant genotypes or populations can be identified from natural stands on the landscape and prioritized for underplanting or reforestation in regions where they are preadapted to future climate, it is possible to mitigate losses due to maladaptation (Williams & Dumroese, 2013). Such a strategy forms the basis for assisted migration – the intentional translocation of individuals to facilitate adaptation. Depending on the specific context, assisted migration can refer to movement within the current range (also known as assisted gene flow) or movement beyond the current range (assisted range expansion) (Aitken & Whitlock, 2013). Implementing assisted migration is a topic of much debate and still faces several uncertainties, but it is increasingly being discussed as an important management option for climate change adaptation (Palik *et al.*, 2022). Provenance trials and seedling common gardens are providing some answers to the question of how survival and growth are impacted by climate transfer distance (i.e. the difference in climate between source and planting site) (Risk *et al.*, 2021; Park & Rodgers, 2023), with maximal fitness often attained in sites most similar to a genotype's source climate (Wang *et al.*, 2010; but see Browne *et al.*, 2019). Field trials of assisted migration in three North American conifer species showed tree populations moved northward or upward in elevation had good productivity (Sáenz-Romero *et al.*, 2021), providing initial support for the rationale that pairing source genotypes or populations with landscape location(s) that minimize transfer distance under future climate can provide useful targets for assisted migration. Indeed, the mismatch between local genetics and need for assisted migration may already be present for some species and not just a future consideration. In a study on two species of North American oaks, climate warming over the last century is evident as adaptation lags, whereby selection at northern sites favors trait values expressed by southern ecotypes (Etterson *et al.*, 2020).

Confidence in assisted migration as a strategy to combat future maladaptation to drought requires more empirical tests, particularly ones that address the impact of episodic or extreme events of temperature or drought stress that can critically determine long-term success (Park & Rodgers, 2023). An example of the latter comes from a long-term provenance trial in lodgepole pine (*Pinus contorta*) that spanned a severe drought episode (Montwé *et al.*, 2016; Isaac-Renton *et al.*, 2018). Lodgepole pine provenances in the northern part of the range showed persistent growth reductions indicating physiological maladaptation to drought, with reduced stomatal responsiveness and thinner-walled tracheids less resistant to xylem embolism. In comparison, provenances from the southern range edge had thick-walled, drought-resistant tracheids, and recovered growth more quickly following drought (Montwé *et al.*, 2016; Isaac-Renton *et al.*, 2018). Given the maladaptation of northern provenances under a drier climate, assisted migration of southern genotypes northward could help increase resilience to future drought, although this must be weighed against the potential susceptibility of southern genotypes to risk from freezing damage (Montwé *et al.*, 2016, 2018). These and other studies serve as a reminder that assisted migration must be approached cautiously and after consideration of genetic and physiological tradeoffs between tolerance to different types of stressors and components of climate adaptation (e.g. cold and drought stress) (Schreiber *et al.*, 2013; Sebastian-Azcona *et al.*, 2018; Sang *et al.*, 2021). It should also be kept in mind that a major limitation of the assisted migration approach is the focus almost exclusively on climate, while ignoring biotic interactions (Bucharova, 2017). More studies are needed to ascertain whether translocating genotypes to minimize climate offset has net fitness benefits when taking both beneficial (e.g. soil microbiome) and negative (e.g. exposure to new insect pest or pathogens) biotic interactions into account.

Enhancing drought stress resilience in seedlings through stress priming

The seedling stage is especially vulnerable to heat and drought conditions because seedlings have a limited root system and reserves. Improving nursery practices to enhance seedling resilience is an obvious target for increasing reforestation success. While nursery managers have long used practices to 'drought harden' tree seedlings before planting through controlled water stress exposure, a recent meta-analysis (Puértolas *et al.*, 2024) found little evidence for significant increase in outplanting survival and growth across all studies examined. However, within the many species and approaches examined, there were successes, and research in crop species suggests these practices can be significantly improved. Stress priming methods involve controlled exposure of seed or seedlings to stress or chemical surrogates followed by recovery, which enables more robust and effective responses to future exposure to stress in the field for crops (Liu *et al.*, 2022; Saha *et al.*, 2022). The mechanisms responsible for stress priming and subsequent stress 'memory' and enhanced resilience are complex, and involve the interplay of physiology, gene expression, epigenetics, and other factors (Hilker & Schmülling, 2019).

The nursery setting represents the rare opportunity in forestry to apply treatments enhancing stress resilience to large numbers of seeds or seedlings. Initial research to establish effective stress priming treatments could be performed in controlled nursery conditions and overlayed with the production of genomic, imaging, and other data types to describe physiological responses and underlying mechanisms in a critical forest management setting. Such data can be used to rigorously evaluate treatment effects and correlated with seedling performance after outplanting in operational reforestation settings. While actual drought and heat stress can be directly applied as priming agents, beneficial priming has also been achieved using the application of chemical surrogates, including hormones, reactive oxygen species, and different synthetic compounds that promote priming, often with protection against multiple types of stress (Savvides *et al.*, 2016). In one example, treatment of containerized oaks with paclobutrozol (an inhibitor of gibberellin biosynthesis) resulted in higher recovery rates after drought treatment (Percival & AlBalushi, 2007). Other priming agents, such as glycine betaine, affect stress resilience through the manipulation of antioxidant and osmotic compounds (Giri, 2011). Seed pretreatments before sowing include osmopriming, which involves hydrating seed in a low osmotic solution followed by dehydrating before sowing (Lutts *et al.*, 2016).

Microbiome manipulations to enhance drought resilience

Similar to stress priming, microbiome treatments can be applied *en masse* to nursery seedlings before outplanting. In a practical sense, it has been known for many decades that soil microbes are essential for forest tree growth and health (Baldrian *et al*., 2023), but the practical challenges of cultivating the growth of beneficial microbes in nursery settings are significant (Hagh-Doust *et al*., 2022). Some challenges include sourcing and cultivating appropriate microbes and successfully encouraging their growth in nursery soils and conditions. While some microbes, such as mycorrhizal fungi, are known to be beneficial or even essential for tree growth, there is now increasing evidence for the idea that, like the trees themselves, these microbes are adapted to specific environmental conditions and can impart drought and heat resilience to trees (Allsup *et al*., 2023). With sequencing technologies, it is now possible to perform landscape genetic surveys of forest mycorrhizal fungi and other microbes, pairing these with common garden studies to obtain functional information about what microbes and genotypes of microbes impart resilience to drought and stress.

In a practical sense, after the fundamental work of identifying sources of beneficial microbial communities has matured, the next challenge will be to develop methods to source inocula for nursery applications and to encourage the growth of those microbes in nursery soils. In agriculture, various formulations with arbuscular mycorrhizal fungal and beneficial bacteria are commercially available. However, when and under which environmental conditions these inocula afford beneficial effects on yield is not fully understood and is currently an expanding field of active research (Lutz *et al*., 2023). In forestry, this area is understudied. Environmental DNA sequencing of soils can be used to guide and evaluate nursery methods for encouraging the growth of such beneficial microbial communities within operational nursery settings, and at the same time identify the presence of potential soil pathogens.

Implementing translational physiology to co-produce research questions

Translational ecology describes a creative approach to applied research (Enquist *et al*., 2017). In this practice, scientists collaborate with various partners who are invested in the forest to co-create research questions and agendas. Within the United States, the Northern Institute of Applied Climate Science and the regional Climate Adaptation Science Centers are examples of organizations that coordinate interactions among research, land management, and tribal organizations. A corollary approach of 'Translational Physiology' could similarly be informed by collaborations between physiologists and landowners, foresters, silviculturists, indigenous land managers, or fire management teams to optimize management practices. Specific research questions would be co-produced by the collaborative team to move forward with both basic and applied research.

Importantly, forests cover a third of the Earth's land, forest types are ecologically highly diverse, and the utilization and societal values associated with forests vary dramatically. The effects of drought disproportionately harm regions, countries, and individuals that are economically vulnerable, inflicting damage that is exacerbated by social inequality (Salvador *et al*., 2023). To be the most effective, tree drought research and the associated research community should thus recognize and reflect these realities. Focusing research on regions that stand to lose the most as forests succumb to drought stress, and on applications and technologies that can improve outcomes in those regions, would be a productive way forward. In general, ethnic minorities are currently underrepresented in ecology and evolution-related fields in the United States (O'Brien *et al*., 2020). Increased inclusion and support of new researchers from underrepresented regions and communities affected by drought and forest mortality is thus one obvious step.

Conclusions

There remain many other fundamental questions not discussed here that should be addressed to not only provide new insights into the basic biology of tree drought physiology, but also to develop effective new applications to increase forest resilience to drought and heat stress. Such questions include the following. How do trees perceive water and heat stress? What are the signaling mechanisms that link stress perception and complex physiological responses? How does drought stress predispose trees to subsequent insect or pathogen susceptibility? While past research has provided insights, for the most part these and other critical questions remain largely unanswered.

Despite the importance of this field to addressing climate change effects on forests, the size of the research community and available research funding arguably do not match the scope of research and management needs, or the magnitude of environmental, societal, and economic impacts. Thus, effective collaboration within the research community, cross-disciplinary research, and advocacy are all critical activities. Even more challenging is the translation of research findings to new effective applications, including the ones discussed here. This will require increased interaction among researchers and nursery practitioners, silviculturists, and land managers. For translation of research to application, infrastructure for forest management must be supported, including nurseries, tree breeding, and propagation facilities and associated staff. In recognition of how forests impact climate, ecosystems, and societies across the planet, the field of forest tree physiology must engage and encourage participation from the diverse geographic regions, societies, and people affected by drought and forest mortality to help prioritize research and link them to effective forest management.

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Competing interests

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References

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD *et al.* 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution* 1: 1285–1291.

Aghai MM, Khan Z, Joseph MR, Stoda AM, Sher AW, Ettl GJ, Doty SL. 2019. The effect of microbial endophyte consortia on *Pseudotsuga menziesii* and *Thuja plicata* survival, growth, and physiology across edaphic gradients. *Frontiers in Microbiology* 10: 1353.

Aitken SN, Whitlock MC. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44: 367–388.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95–111.

Allsup CM, George I, Lankau RA. 2023. Shifting microbial communities can enhance tree tolerance to changing climates. *Science* 380: 835–840.

Al-Tamimi N, Langan P, Bernád V, Walsh J, Mangina E, Negrão S. 2022. Capturing crop adaptation to abiotic stress using image-based technologies. *Open Biology* 12: 210353.

Amaral J, Ribeyre Z, Vigneaud J, Sow MD, Fichot R, Messier C, Pinto G, Nolet P, Maury S. 2020. Advances and promises of epigenetics for forest trees. *Forests* 11: 976.

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP *et al.* 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349: 528–532.

Anfodillo T, Olson ME. 2021. Tree mortality: testing the link between drought, embolism vulnerability, and xylem conduit diameter remains a priority. *Frontiers in Forests and Global Change* 4: 704670.

Arend M, Fromm J. 2007. Seasonal change in the drought response of wood cell development in poplar. *Tree Physiology* 27: 985–992.

Arend M, Link RM, Patthey R, Hoch G, Schuldt B, Kahmen A. 2021. Rapid hydraulic collapse as cause of drought-induced mortality in conifers. *Proceedings of the National Academy of Sciences, USA* **118**: e2025251118.

Baharudin NF, Osman NI. 2023. Plant development, stress responses, and secondary metabolism under ethylene regulation. *Plant Stress* **7**: 100146.

Balao F, Paun O, Alonso C. 2018. Uncovering the contribution of epigenetics to plant phenotypic variation in Mediterranean ecosystems. *Plant Biology* **20**: 38–49.

Baldrian P, López-Mondéjar R, Kohout P. 2023. Forest microbiome and global change. *Nature Reviews Microbiology* **21**: 487–501.

Bao Y, Aggarwal P, Robbins NE II, Sturrock CJ, Thompson MC, Tan HQ, Tham C, Duan L, Rodriguez PL, Vernoux T *et al.* 2014. Plant roots use a patterning mechanism to position lateral root branches toward available water. *Proceedings of the National Academy of Sciences, USA* **111**: 9319–9324.

Bian L, Zhang H, Ge Y, Čepl J, Stejskal J, El-Kassaby YA. 2022. Closing the gap between phenotyping and genotyping: review of advanced, image-based phenotyping technologies in forestry. *Annals of Forest Science* **79**: 1–21.

Bräutigam K, Vining KJ, Lafon-Placette C, Fossdal CG, Mirouze M, Marcos JG, Fluch S, Fraga MF, Guevara MÁ, Abarca D *et al.* 2013. Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecology and Evolution* **3**: 399–415.

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J *et al.* 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences, USA* **102**: 15144–15148.

Brodersen C, McElrone A. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Frontiers in Plant Science* **4**: 108.

Brodersen C, McElrone A, Choat B, Matthews M, Shackel K. 2020. The dynamics of embolism repair in xylem: *in vivo* visualizations using high-resolution computed tomography. *Plant Physiology* **154**: 1088–1095.

Brodribb T. 2017. Progressing from 'functional' to mechanistic traits. *New Phytologist* **215**: 9–11.

Brodribb T, McAdam S. 2013. Abscisic acid mediates a divergence in the drought response of two conifers. *Plant Physiology* **162**: 1370–1377.

Brodribb TJ, Powers J, Cochard H, Choat B. 2020. Hanging by a thread? Forests and drought. *Science* **368**: 261–266.

Browne L, Wright JW, Fitz-Gibbon S, Gugger PF, Sork VL. 2019. Adaptational lag to temperature in valley oak (*Quercus Lobata*) can be mitigated by genome-informed assisted gene flow. *Proceedings of the National Academy of Sciences, USA* **116**: 25179–25185.

Bucharova A. 2017. Assisted migration within species range ignores biotic interactions and lacks evidence. *Restoration Ecology* **25**: 14–18.

Cailleret M, Jansen S, Robert EMR, Desoto L, Aakala T, Antos JA, Beikircher B, Bigler C, Bugmann H, Caccianiga M *et al.* 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* **23**: 1675–1690.

Carlquist S. 2013. *Comparative wood anatomy.* Berlin, Heidelberg, Germany: Springer.

Castillo-Argaez R, Sapes G, Mallen N, Lippert A, John GP, Zare A, Hammond WM. 2024. Spectral ecophysiology: hyperspectral pressure–volume curves to estimate leaf turgor loss. *New Phytologist* **242**: 935–946.

Cheng Y, Oehmcke S, Brandt M, Rosenthal L, Das A, Vrieling A, Saatchi S, Wagner F, Mugabowindekwe M, Verbruggen W *et al.* 2024. Scattered tree death contributes to substantial forest loss in California. *Nature Communications* **15**: 641.

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn B. 2018. Triggers of tree mortality under drought. *Nature* **558**: 531–539.

Choudhary SP, Yu J, Yamaguchi-Shinozaki K, Shinozaki K, Tran LP. 2012. Benefits of brassinosteroid crosstalk. *Trends in Plant Science* **17**: 594–605.

Christmann A, Weiler EW, Steudle E, Grill E. 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *The Plant Journal* **52**: 167–174.

Cochard H. 2021. A new mechanism for tree mortality due to drought and heatwaves. *Peer Community Journal* **1**: e36.

Compton S, Stackpole C, Dixit A, Sekhwal MK, Kolb T, De la Torre AR. 2023. Differences in heat tolerance, water use efficiency and growth among Douglas-fir families and varieties evidenced by GWAS and common garden studies. *AoB Plants* **15**: lad008.

Crossa J, Montesinos-López OA, Pérez-Rodríguez P, Costa-Neto G, Fritsche-Neto R, Ortiz R, Martini JWR, Lillemo M, Montesinos-López A, Jarquin D *et al.* 2022. Genome and environment based prediction models and methods of complex traits incorporating genotype × environment interaction. *Methods in Molecular Biology* **2467**: 245–283.

Csilléry K, Buchmann N, Fady B. 2020. Adaptation to drought is coupled with slow growth, but independent from phenology in marginal silver fir (*Abies alba* Mill.) populations. *Evolutionary Applications* **13**: 2357–2376.

Cumbie WP, Eckert A, Wegrzyn J, Whetten R, Neale D, Goldfarb B. 2011. Association genetics of carbon isotope discrimination, height and foliar nitrogen in a natural population of *Pinus taeda* L. *Heredity* **107**: 105–114.

D'Odorico P, Besik A, Wong CYS, Isabel N, Ensminger I. 2020. High-throughput drone-based remote sensing reliably tracks phenology in thousands of conifer seedlings. *New Phytologist* **226**: 1667–1681.

De Kauwe M, Sabot M, Medlyn B, Pitman A, Meir P, Cernusak L, Gallagher R, Ukkola A, Rifai S, Choat B. 2022. Towards species-level forecasts of drought-induced tree mortality risk. *New Phytologist* **235**: 94–110.

Delzon S, Douthe C, Sala A, Cochard H. 2010. Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell & Environment* **33**: 2101–2111.

Depaepe T, Hendrix S, Janse van Rensburg HC, Van den Ende W, Cuypers A, Van Der Straeten D. 2021. At the crossroads of survival and death: the reactive oxygen species–ethylene–sugar triad and the unfolded protein response. *Trends in Plant Science* **26**: 338–351.

Depardieu C, Gérardi S, Nadeau S, Parent GJ, Mackay J, Lenz P, Lamothe M, Girardin MP, Bousquet J, Isabel N. 2021. Connecting tree-ring phenotypes, genetic associations and transcriptomics to decipher the genomic architecture of drought adaptation in a widespread conifer. *Molecular Ecology* **30**: 3898–3917.

Depardieu C, Girardin MP, Nadeau S, Lenz P, Bousquet J, Isabel N. 2020. Adaptive genetic variation to drought in a widely distributed conifer suggests a potential for increasing forest resilience in a drying climate. *New Phytologist* **227**: 427–439.

Dixon DJ, Zhu Y, Brown CF, Jin Y. 2013. Satellite detection of canopy-scale tree mortality and survival from California wildfires with spatio-temporal deep learning. *Remote Sensing of Environment* **298**: 113842.

Do Nascimento AMM, Montalbán IA, Llamazares De Miguel D, Goicoa T, Ugarte MD, Moncaleán P. 2022. High temperature and water deficit cause epigenetic changes in somatic plants of *Pinus radiata* D. Don. *Plant Cell, Tissue and Organ Culture (PCTOC)* **151**: 107–121.

Duursma RA, Blackman CJ, Lopéz R, Martin-StPaul NK, Cochard H, Medlyn BE. 2019. On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls. *New Phytologist* **221**: 693–705.

Enquist CA, Jackson ST, Garfin GM, Davis FW, Gerber LR, Littell JA, Tank JL, Terando AJ, Wall TU, Halpern B *et al.* 2017. Foundations of translational ecology. *Frontiers in Ecology and the Environment* **15**: 541–550.

Etterson JR, Cornett MW, White MA, Kavajecz LC. 2020. Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species. *Ecological Applications* **30**: e02092.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**: 503–537.

Foo E, Plett JM, Lopez-Raez JA, Reid D. 2019. Editorial: the role of plant hormones in plant–microbe symbioses. *Frontiers in Plant Science* **10**: 1391.

de Freitas Pereira M, Cohen D, Auer L, Aubry N, Bogeat-Triboulot M-B, Bure C, Engle NL, Jolivet Y, Kohler A, Novák O *et al.* 2023. Ectomycorrhizal symbiosis prepares its host locally and systemically for abiotic cue signaling. *The Plant Journal* **116**: 1784–1803.

Gallusci P, Agius DR, Moschou PN, Dobránszki J, Kaiserli E, Martinelli F. 2023. Deep inside the epigenetic memories of stressed plants. *Trends in Plant Science* **28**: 142–153.

Gauthey A, Peters JMR, Lòpez R, Carins-Murphy MR, Rodriguez-Dominguez CM, Tissue DT, Medlyn BE, Brodribb TJ, Choat B. 2022. Mechanisms of xylem hydraulic recovery after drought in *Eucalyptus saligna. Plant, Cell & Environment* **45**: 1216–1228.

Giri J. 2011. Glycinebetaine and abiotic stress tolerance in plants. *Plant Signaling & Behavior* **6**: 1746–1751.

Gomez-Roldan V, Fermas S, Brewer PB, Puech-Pagès V, Dun EA, Pillot J, Letisse F, Matusova R, Danoun S, Portais J *et al.* 2008. Strigolactone inhibition of shoot branching. *Nature* **455**: 189–194.

González-Martínez SC, Huber D, Ersoz E, Davis JM, Neale DB. 2008. Association genetics in *Pinus taeda* L. II. Carbon isotope discrimination. *Heredity* **101**: 19–26.

Hacke UG, Spicer R, Schreiber SG, Plavcová L. 2017. An ecophysiological and developmental perspective on variation in vessel diameter. *Plant, Cell & Environment* **40**: 831–845.

Hagh-Doust N, Färkkilä SMA, Hosseyni Moghaddam MS, Tedersoo L. 2022. Symbiotic fungi as biotechnological tools: methodological challenges and relative benefits in agriculture and forestry. *Fungal Biology Reviews* **42**: 34–55.

Hammond W, Williams A, Abatzoglou J, Adams H, Klein T, López R, Sáenz-Romero C, Hartmann H, Breshears D, Allen C. 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications* **13**: 1761.

Hartmann H, Moura CF, Anderegg WRL, Ruehr NK, Salmon Y, Allen CD, Arndt SK, Breshears DD, Davi H, Galbraith D *et al.* 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist* **218**: 15–28.

Hilker M, Schmülling T. 2019. Stress priming, memory, and signalling in plants. *Plant, Cell & Environment* **42**: 753–761.

Housset JM, Nadeau S, Isabel N, Depardieu C, Duchesne I, Lenz P, Girardin MP. 2018. Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. *New Phytologist* **218**: 630–645.

Immanen J, Nieminen K, Smolander O-P, Kojima M, Alonso Serra J, Koskinen P, Zhang J, Elo A, Mähönen AP, Street N *et al.* 2016. Cytokinin and auxin display distinct but interconnected distribution and signaling profiles to stimulate cambial activity. *Current Biology* **26**: 1990–1997.

Isaac-Renton M, Montwé D, Hamann A, Spiecker H, Cherubini P, Treydte K. 2018. Northern forest tree populations are physiologically maladapted to drought. *Nature Communications* **9**: 5254.

Isabel N, Holliday JA, Aitken SN. 2019. Forest genomics: advancing climate adaptation, forest health, productivity, and conservation. *Evolutionary Applications* **13**: 3–10.

Isasa E, Link RM, Jansen S, Tezeh FR, Kaack L, Sarmento Cabral J, Schuldt B. 2023. Addressing controversies in the xylem embolism resistance–vessel diameter relationship. *New Phytologist* **238**: 283–296.

Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD. 2005. Do xylem fibers affect vessel cavitation resistance? *Plant Physiology* **139**: 546–556.

Janssen TA, Hőltta T, Fleischer K, Naudts K. 2020. Wood allocation trade-offs between fiber wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees. *Plant, Cell & Environment* **43**: 965–980.

Jaramillo-Correa JP, Prunier J, Vázquez-Lobo A, Keller S, Moreno-Letelier A. 2015. Molecular signatures of adaptation and selection in forest trees. *Advances in Botanical Research* **74**: 265–306.

Jin X, Zimmermann J, Polle A, Fischer U. 2015. Auxin is a long-range signal that acts independently of ethylene signaling on leaf abscission in *Populus*. *Frontiers in Plant Science* **6**: 634.

Johnson D, Eckart P, Alsamadisi N, Noble H, Martin C, Spicer R. 2018. Polar auxin transport is implicated in vessel differentiation and spatial patterning during secondary growth in *Populus*. *American Journal of Botany* **105**: 186–196.

Junghans U, Langenfeld-Heyser R, Polle A, Teichmann T. 2004. Effect of auxin transport inhibitors and ethylene on the wood anatomy of poplar. *Plant Biology* **6**: 22–29.

Jupa R, Plavcová L, Gloser V, Jansen S. 2016. Linking xylem water storage with anatomical parameters in five temperate tree species. *Tree Physiology* **36**: 756–769.

Kannenberg SA, Phillips RP. 2017. Soil microbial communities buffer physiological responses to drought stress in three hardwood species. *Oecologia* **183**: 631–641.

Kazan K. 2015. Diverse roles of jasmonates and ethylene in abiotic stress tolerance. *Trends in Plant Science* **20**: 219–229.

Kebert M, Kostić S, Stojnić S, Čapelja E, Markić AG, Zorić M, Kesić L, Flors V. 2023. A fine-tuning of the plant hormones, polyamines and osmolytes by ectomycorrhizal fungi enhances drought tolerance in pedunculate oak. *International Journal of Molecular Sciences* **24**: 7510.

Kim Y-C, Glick BR, Bashan Y, Ryu C-M. 2012. Enhancement of plant drought tolerance by microbes. In: Aroca R, ed. *Plant responses to drought stress: from morphological to molecular features*. Berlin, Heidelberg, Germany: Springer, 383–413.

Knipfer T, Cuneo I, Earles M, Reyes C, Brodersen C, McElrone A. 2017. Storage compartments for capillary water rarely refill in an intact woody plant. *Plant Physiology* **175**: 1649–1660.

Koltai H. 2011. Strigolactones are regulators of root development. *New Phytologist* **190**: 545–549.

Koo YM, Heo AY, Choi HW. 2020. Salicylic acid as a safe plant protector and growth regulator. *Plant Pathology Journal* **36**: 1–10.

Körner C. 2019. No need for pipes when the well is dry – a comment on hydraulic failure in trees. *Tree Physiology* **39**: 695–700.

Kristy B, Carrell AA, Johnston E, Cumming JR, Klingeman DM, Gwinn K, Syring KC, Skalla C, Emrich S, Cregger MA. 2022. Chronic drought differentially alters the belowground microbiome of drought-tolerant and drought-susceptible genotypes of *Populus trichocarpa*. *Phytobiomes Journal* **6**: 317–330.

Kurepa J, Smalle JA. 2022. Auxin/cytokinin antagonistic control of the shoot/root growth ratio and its relevance for adaptation to drought and nutrient deficiency stresses. *International Journal of Molecular Sciences* **23**: 1933.

Kuromori T, Seo M, Shinozaki K. 2018. ABA transport and plant water stress responses. *Trends in Plant Science* **23**: 513–522.

Lämke J, Bäurle I. 2017. Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. *Genome Biology* **18**: 124.

Larter M, Pfautsch S, Domec J, Trueba S, Nagalingum N, Delzon S. 2017. Aridity drove the evolution of extreme embolism resistance and the radiation of conifer genus *Callitris*. *New Phytologist* **215**: 97–112.

Laverdière J-P, Lenz P, Nadeau S, Depardieu C, Isabel N, Perron M, Beaulieu J, Bousquet J. 2022. Breeding for adaptation to climate change: genomic selection for drought response in a white spruce multi-site polycross test. *Evolutionary Applications* **15**: 383–402.

Ledig FT, Kitzmiller JH. 1992. Genetic strategies for reforestation in the face of global climate change. *Forest Ecology and Management* **50**: 153–169.

Lemaire C, Quilichini Y, Brunel-Michac N, Santini J, Berti L, Cartailler J, Conchon P, Badel É, Herbette S. 2021. Plasticity of the xylem vulnerability to embolism in *Populus tremula x alba* relies on pit quantity properties rather than on pit structure. *Tree Physiology* **41**: 1384–1399.

Lens F, Gleason SM, Bortolami G, Brodersen C, Delzon S, Jansen S. 2022. Functional xylem characteristics associated with drought-induced embolism in angiosperms. *New Phytologist* **236**: 2019–2036.

Levionnois S, Jansen S, Wandji RT, Beauchêne J, Ziegler C, Coste S, Stahl C, Delzon S, Authier L, Heuret P. 2021. Linking drought-induced xylem embolism resistance to wood anatomical traits in Neotropical trees. *New Phytologist* **229**: 1453–1466.

Li W, Herrera-Estrella L, Tran LP. 2016. The Yin–Yang of cytokinin homeostasis and drought acclimation/adaptation. *Trends in Plant Science* **21**: 548–550.

Li W, Herrera-Estrella L, Tran LP. 2019. Do cytokinins and strigolactones crosstalk during drought adaptation? *Trends in Plant Science* **24**: 669–672.

Li X, Blackman C, Choat B, Duursma R, Rymer P, Medlyn B, Tissue D. 2018. Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant, Cell & Environment* **41**: 646–660.

Liang X, Ye Q, Liu H, Brodribb TJ. 2021. Wood density predicts mortality threshold for diverse trees. *New Phytologist* **229**: 3053–3057.

Liu H, Able A, Able J. 2022. Priming crops for the future: rewiring stress memory. *Trends in Plant Science* **27**: 699–716.

Lutts S, Benincasa P, Wojtyla L, Kubala S, Pace R, Lechowska K, Quinet M, Garnczarska M. 2016. Seed priming: new comprehensive approaches for an old empirical technique. In: Balestrazzi A, ed. *New challenges in seed biology – basic and translational research driving seed technology*. London, UK: InTech. doi: 10.5772/64420.

Lutz S, Bodenhausen N, Hess J, Valzano-Held A, Waelchli J, Deslandes-Hérold G, Schlaeppi K, van der Heijden MGA. 2023. Soil microbiome indicators can predict crop growth response to large-scale inoculation with arbuscular mycorrhizal fungi. *Nature Microbiology* **8**: 2277–2289.

Ma C, Jiang C, Gao J. 2021. Regulatory mechanisms underlying activation of organ abscission. *Annual Plant Reviews Online* **4**: 27–56.

McDowell NG, Ball M, Bond-Lamberty B, Kirwan ML, Krauss KW, Megonigal JP, Mencuccini M, Ward ND, Weintraub MN, Bailey V. 2022a. Processes and mechanisms of coastal woody-plant mortality. *Global Change Biology* **28**: 5881–5900.

McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N *et al.* 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytologist* **200**: 304–321.

McDowell NG, Sapes G, Pivovaroff A, Adams HD, Allen CD, Anderegg WRL, Arend M, Breshears DD, Brodribb T, Choat B *et al.* 2022b. Mechanisms of woody-plant mortality under rising drought, CO_2 and vapour pressure deficit. *Nature Reviews Earth & Environment* **3**: 294–308.

Mehra P, Pandey BK, Melebari D, Banda J, Leftley N, Couvreur V, Rowe J, Anfang M, De Gernier H, Morris E *et al.* 2022. Hydraulic flux–responsive hormone redistribution determines root branching. *Science* **378**: 762–768.

Mencuccini M, Manzoni S, Christoffersen B. 2019. Modelling water fluxes in plants: from tissues to biosphere. *New Phytologist* **222**: 1207–1222.

Montwé D, Isaac-Renton M, Hamann A, Spiecker H. 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. *Global Change Biology* **22**: 806–815.

Montwé D, Isaac-Renton M, Hamann A, Spiecker H. 2018. Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature Communications* **9**: 1574.

Munemasa S, Hauser F, Park J, Waadt R, Brandt B, Schroeder JI. 2015. Mechanisms of abscisic acid-mediated control of stomatal aperture. *Current Opinion in Plant Biology* **28**: 154–162.

Muñoz-Espinoza VA, López-Climent MF, Casaretto JA, Gómez-Cadenas A. 2015. Water stress responses of tomato mutants impaired in hormone biosynthesis reveal abscisic acid, jasmonic acid and salicylic acid interactions. *Frontiers in Plant Science* **6**: 997.

Nosenko T, Zimmer I, Ghirardo A, Köllner TG, Weber B, Polle A, Rosenkranz M, Schnitzler J-P. 2023. Predicting functions of putative fungal sesquiterpene synthase genes based on multiomics data analysis. *Fungal Genetics and Biology* **165**: 103779.

O'Brien LT, Bart HL, Garcia DM. 2020. Why are there so few ethnic minorities in ecology and evolutionary biology? Challenges to inclusion and the role of sense of belonging. *Social Psychology of Education* **23**: 449–477.

Olson ME. 2023. Imperforate tracheary element classification for studies of xylem structure-function relations. *IAWA Journal* **44**: 439–464.

Olson ME, Pace MR, Anfodillo T. 2023. The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide. *IAWA Journal* **43**: 335–354.

Ortiz-García P, Ortega-Villaizán AG, Onejeme FC, Müller M, Pollmann S. 2023. Do opposites attract? Auxin-abscisic acid crosstalk: new perspectives. *International Journal of Molecular Sciences* **24**: 3090.

Ozturk M, Turkyilmaz Unal B, García-Caparrós P, Khursheed A, Gul A, Hasanuzzaman M. 2021. Osmoregulation and its actions during the drought stress in plants. *Physiologia Plantarum* **172**: 1321–1335.

Paci J, Newman M, Gage T. 2023. *The economic, fiscal, and environmental costs of wildfires in California.* Palo Alto, CA, USA: Gordon and Betty Moore Foundation. [WWW document] URL https://www.moore.org/docs/default-source/default-document-library/the-economic-fiscal-and-environmental-costs-of-wildfires-in-ca.pdf?sfvrsn=1b1b620c_0 [accessed 1 June 2024].

Palik BJ, Clark PW, D'Amato AW, Swanston C, Nagel L. 2022. Operationalizing forest-assisted migration in the context of climate change adaptation: examples from the Eastern USA. *Ecosphere* **13**: e4260.

Park A, Rodgers J. 2023. Provenance trials in the service of forestry assisted migration: a review of North American field trials and experiments. *Forest Ecology and Management* **537**: 120854.

Paschalis A, De Kauwe MG, Sabot M, Fatichi S. 2024. When do plant hydraulics matter in terrestrial biosphere modelling? *Global Change Biology* **30**: e17022.

Percival G, AlBalushi A. 2007. Paclobutrazol-induced drought tolerance in containerized English and evergreen oak. *Arboriculture and Urban Forestry* **33**: 397–409.

Piper F, Paula S. 2020. The role of nonstructural carbohydrates storage in forest resilience under climate change. *Current Forestry Reports* **6**: 1–13.

Pittermann J, Sperry JS, Wheeler JK, Hacke UG, Sikkema EH. 2006. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant, Cell & Environment* **29**: 1618–1628.

Plomion C, Bartholomé J, Bouffier L, Brendel O, Cochard H, de Miguel M, Delzon S, Gion J-M, Gonzalez-Martinez SC, Guehl J-M *et al.* 2016. Understanding the genetic bases of adaptation to soil water deficit in trees through the examination of water use efficiency and cavitation resistance: maritime pine as a case study. *Journal of Plant Hydraulics* **3**: e008.

Polle A, Chen S, Eckert C, Harfouche A. 2019. Engineering drought resistance in forest trees. *Frontiers in Plant Science* **9**: 1875.

Pratt RB, Tobin MF, Jacobsen AL, Traugh CA, De Guzman ME, Hayes CC, Toschi HS, MacKinnon ED, Percolla MI, Clem ME *et al.* 2021. Starch storage capacity of sapwood is related to dehydration avoidance during drought. *American Journal of Botany* **108**: 91–101.

Puértolas J, Villar-Salvador P, Andivia E, Ahuja I, Cocozza C, Cvjetković B, Devetaković J, Diez JJ, Fløistad I, Ganatsas P *et al.* 2024. Die-hard seedlings. A global meta-analysis on the factors determining the effectiveness of drought hardening on growth and survival of forest plantations. *Forest Ecology and Management* **572**: 122300.

Raghavendra AS, Gonugunta VK, Christmann A, Grill E. 2010. ABA perception and signalling. *Trends in Plant Science* **15**: 395–401.

Resende MDV, Resende MFR Jr, Sansaloni CP, Petroli CD, Missiaggia AA, Aguiar AM, Abad JM, Takahashi EK, Rosado AM, Faria DA *et al.* 2012. Genomic selection for growth and wood quality in *Eucalyptus*: capturing the missing heritability and accelerating breeding for complex traits in forest trees. *New Phytologist* **194**: 116–128.

Rico L, Ogaya R, Barbeta A, Peñuelas J. 2014. Changes in DNA methylation fingerprint of *Quercus ilex* trees in response to experimental field drought simulating projected climate change. *Plant Biology* **16**: 419–427.

Risk C, McKenney DW, Pedlar J, Pengxin L. 2021. A compilation of North American tree provenance trials and relevant historical climate data for seven species. *Scientific Data* **8**: 29.

Rodriguez-Zaccaro FD, Groover A. 2019. Wood and water: how trees modify wood development to cope with drought. *Plants, People, Planet* **1**: 346–355.

Rodriguez-Zaccaro FD, Henry I, Groover A. 2021. Genetic regulation of vessel morphology in *Populus*. *Frontiers in Plant Science* **12**: 705596.

Rodriguez-Zaccaro FD, Lieberman M, Groover A. 2024. A systems genetic analysis identifies putative mechanisms and candidate genes regulating vessel traits in poplar wood. *Frontiers in Plant Science* **15**: 1375506.

Sadhukhan A, Prasad SS, Mitra J, Siddiqui N, Sahoo L, Kobayashi Y, Koyama H. 2022. How do plants remember drought? *Planta* **256**: 7.

Sáenz-Romero C, O'Neill G, Aitken SN. 2021. Assisted migration field tests in Canada and Mexico: lessons, limitations, and challenges. *Forests, Trees and Livelihoods* **12**: 9.

Saha D, Choyal P, Mishra UN, Dey P, Bose B, Prathibha MD, Gupta NK, Mehta BK, Kumar P, Pandey S *et al.* 2022. Drought stress responses and inducing tolerance by seed priming approach in plants. *Plant Stress* **4**: 100066.

Salvador C, Nieto R, Vicente-Serrano S, Garcia-Herrera R, Gimeno L, Vicedo-Cabrera AM. 2023. Public health implications of drought in a climate change context: a critical review. *Annual Review of Public Health* **44**: 213–232.

Sang Z, Hamann A, Aitken SN. 2021. Assisted migration poleward rather than upward in elevation minimizes frost risks in plantations. *Climate Risk Management* **34**: 100380.

Sapes G, Demaree P, Lekberg Y, Sala A. 2021. Plant carbohydrate depletion impairs water relations and spreads via ectomycorrhizal networks. *New Phytologist* **229**: 3172–3183.

Sapes G, Schroeder L, Scott A, Clark I, Juzwik J, Montgomery RA, Guzmán QJA, Cavender-Bares J. 2024. Mechanistic links between physiology and spectral reflectance enable previsual detection of oak wilt and drought stress. *Proceedings of the National Academy of Sciences, USA* **121**: e2316164121.

Savvides A, Ali S, Tester M, Fotopoulos V. 2016. Chemical priming of plants against multiple abiotic stresses: mission possible? *Trends in Plant Science* **21**: 329–340.

Schrader J, Baba K, May ST, Palme K, Bennett M, Bhalerao RP, Sandberg G. 2003. Polar auxin transport in the wood-forming tissues of hybrid aspen is under simultaneous control of developmental and environmental signals. *Proceedings of the National Academy of Sciences, USA* **100**: 10096–10101.

Schreiber SG, Ding C, Hamann A, Hacke UG, Thomas BR, Brouard JS. 2013. Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. *Journal of Applied Ecology* **50**: 939–949.

Sebastian-Azcona J, Hamann A, Hacke UG, Rweyongeza D. 2018. Survival, growth and cold hardiness tradeoffs in white spruce populations: implications for assisted migration. *Forest Ecology and Management* **433**: 544–552.

Serna L. 2014. The role of brassinosteroids and abscisic acid in stomatal development. *Plant Science* **225**: 95–101.

Sharma A, Gupta A, Ramakrishnan M, Ha CV, Zheng B, Bhardwaj M, Tran LP. 2023. Roles of abscisic acid and auxin in plants during drought: a molecular point of view. *Plant Physiology and Biochemistry* **204**: 108129.

Słupianek A, Dolzblasz A, Sokołowska K. 2021. Xylem parenchyma-role and relevance in wood functioning in trees. *Plants* **10**: 1247.

Słupianek A, Myśkow E, Kasprowicz-Maluśki A, Dolzblasz A, Żytkowiak R, Turzańska M, Sokołowska K. 2024. Seasonal dynamics of cell-to-cell transport in angiosperm wood. *Journal of Experimental Botany* **75**: 1331–1346.

Song S, Qi T, Wasternack C, Xie D. 2014. Jasmonate signaling and crosstalk with gibberellin and ethylene. *Current Opinion in Plant Biology* **21**: 112–119.

Sow MD, Le Gac A-L, Fichot R, Lanciano S, Delaunay A, Le Jan I, Lesage-Descauses M-C, Citerne S, Caius J, Brunaud V *et al.* 2021. RNAi suppression of DNA methylation affects the drought stress response and genome integrity in transgenic poplar. *New Phytologist* **232**: 80–97.

Sperry J, Venturas M, Anderegg WRL, Mencuccini M, Mackay DS, Wang Y, Love DM. 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. *Plant, Cell & Environment* **40**: 816–830.

Stovall AEL, Shugart H, Yang X. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* **10**: 4385.

Thonglim A, Delzon S, Larter M, Karami O, Rahimi A, Offringa R, Keurentjes J, Balazadeh S, Smets E, Lens F. 2021. Intervessel pit membrane thickness best explains variation in embolism resistance amongst stems of *Arabidopsis thaliana* accessions. *Annals of Botany* **128**: 171–182.

Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. 2021. Why is tree drought mortality so hard to predict? *Trends in Ecology & Evolution* **36**: 520–532.

Ulrich DEM, Sevanto S, Ryan M, Albright MBN, Johansen RB, Dunbar JM. 2019. Plant–microbe interactions before drought influence plant physiological responses to subsequent severe drought. *Scientific Reports* **9**: 249.

Umehara M, Hanada A, Yoshida S, Akiyama K, Arite T, Takeda-Kamiya N, Magome H, Kamiya Y, Shirasu K, Yoneyama K *et al.* 2008. Inhibition of shoot branching by new terpenoid plant hormones. *Nature* **455**: 195–200.

Venturas MD, Sperry JS, Hacke UG. 2017. Plant xylem hydraulics: what we understand, current research, and future challenges. *Journal of Integrative Plant Biology* **59**: 356–389.

de Villemereuil P, Gaggiotti OE, Mouterde M, Till-Bottraud I. 2016. Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity* **116**: 249–254.

Wang T, O'Neill GA, Aitken SN. 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications* **20**: 153–163.

Wang S, Ren Y, Han L, Nie Y, Zhang S, Xie X, Hu W, Chen H, Tang M. 2023. Insights on the impact of Arbuscular Mycorrhizal symbiosis on *Eucalyptus grandis* tolerance to drought stress. *Microbiology Spectrum* **11**: e04381-22.

Wei Z, Li J. 2016. Brassinosteroids regulate root growth, development, and symbiosis. *Molecular Plant* **9**: 86–100.

Wieloch T, Holloway-Phillips M, Yu J, Niittylä T. 2024. New insights into the mechanisms of plant isotope fractionation from combined analysis of intramolecular ^{13}C and deuterium abundances in *Pinus nigra* tree-ring glucose. *bioRxiv*. doi: 10.1101/2024.02.21.581384.

Williams MI, Dumroese RK. 2013. Preparing for climate change: forestry and assisted migration. *Journal of Forestry* **111**: 287–297.

Xu C, Christoffersen B, Robbins Z, Knox R, Fisher RA, Chitra-Tarak R, Slot M, Solander K, Kueppers L, Koven C *et al.* 2023. Quantification of hydraulic trait control on plant hydrodynamics and risk of hydraulic failure within a demographic structured vegetation model in a tropical forest (FATES–HYDRO v.1.0). *Geoscientific Model Development* **16**: 6267–6283.

Xu X, Medvigy D, Powers J, Becknell J, Guan K. 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80–95.

Yan Y, Piao S, Hammond WM, Chen A, Hong S, Xu H, Munson SM, Myneni RB, Allen CD. 2024. Climate-induced tree-mortality pulses are obscured by broad-scale and long-term greening. *Nature Ecology & Evolution* **8**: 912–923.

Yu D, Janz D, Zienkiewicz K, Herrfurth C, Feussner I, Chen S, Polle A. 2021. Wood formation under severe drought invokes adjustment of the hormonal and transcriptional landscape in poplar. *International Journal of Molecular Sciences* **22**: 9899.

Zhang B, Wang Z, Dai X, Gao J, Zhao J, Ma R, Chen Y, Sun Y, Ma H, Li S *et al.* 2024. A COMPASS histone H3K4 trimethyltransferase pentamer transactivates drought tolerance and growth/biomass production in *Populus trichocarpa*. *New Phytologist* **241**: 1950–1972.

Zhao Y, Chan Z, Gao J, Xing L, Cao M, Yu C, Hu Y, You J, Shi H, Zhu Y *et al.* 2016. ABA receptor PYL9 promotes drought resistance and leaf senescence. *Proceedings of the National Academy of Sciences, USA* **113**: 1949–1954.

Zhou J, Xiao L, Huang R, Song F, Li L, Li P, Fang Y, Lu W, Lv C, Quan M *et al.* 2023. Local diversity of drought resistance and resilience in *Populus tomentosa* correlates with the variation of DNA methylation. *Plant, Cell & Environment* **46**: 479–497.

Ziemińska K, Rosa E, Gleason SM, Holbrook NM. 2020. Wood day capacitance is related to water content, wood density, and anatomy across 30 temperate tree species. *Plant, Cell & Environment* **43**: 3048–3067.

Zolfaghari R, Dalvand F, Fayyaz P, Solla A. 2022. Maternal drought stress on Persian oak (*Quercus brantii* Lindl.) affects susceptibility to single and combined drought and biotic stress in offspring. *Environmental and Experimental Botany* **194**: 104716.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 References and data used to produce Fig. 3.

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