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Wood and water: How trees modify wood development to cope with drought

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Societal Impact Statement

Drought plays a conspicuous role in forest mortality, and is expected to become more severe in future climate scenarios. Recent surges in drought-associated forest tree mortality have been documented worldwide. For example, recent droughts in California and Texas killed approximately 129 million and 300 million trees, respectively. Drought has also induced acute pine tree mortality across east-central China, and across extensive areas in southwest China. Understanding the biological processes that enable trees to modify wood development to mitigate the adverse effects of drought will be crucial for the development of successful strategies for future forest management and conservation.

Summary

Drought is a recurrent stress to forests, causing periodic forest mortality with enormous economic and environmental costs. Wood is the water-conducting tissue of tree stems, and trees modify wood development to create anatomical features and hydraulic properties that can mitigate drought stress. This modification of wood development can be seen in tree rings where not only the amount of wood but also the morphology of the water-conducting cells are modified in response to environmental conditions. In this review, we provide an overview of how trees conduct water, and how trees modify wood development to affect water conduction properties in response to drought. We discuss key needs for new research, and how new knowledge of wood formation can play a role in the conservation of forests under threat by climate change.

KEYWORDS
abiotic stress, climate change, drought, forests, genomics, molecular mechanisms, secondary xylem, wood

1 | INTRODUCTION

Water is key to forest growth and survival. Drought and heat-induced forest mortality have affected forests worldwide (Allen et al., 2010) and is expected to worsen through the 21st century (McDowell &

Allen, 2015). For example, severe drought was associated with the death of more than 129 million trees in California from 2010 to 2017, 300 million trees in Texas in 2011 (USGCRP, 2018), and 40 to 80% stand level mortality of *Cedrus atlantica*-dominated forests in Algeria (Bentouati, 2008). Droughts have induced tree mortality of

Pinus tabulaeformia across 0.5 million hectares in east-central China (Wang, Zhang, Kong, Lui, & Shen, 2007) and across extensive areas of *Pinus yunnanensis* in southwest China (Li, 2003). Drought is expected to affect global processes including carbon cycles as well as regional issues including hydrology and water availability (Adams et al., 2010). Covering about 30% of the global land area (FAO, 2018), forests can remove large amounts of carbon dioxide (CO_2) from the atmosphere (Bonan, 2008), totaling 3,300 teragrams of CO_2 annually from 1993 to 2003 (IPCC, 2007). Anthropogenic CO_2 emissions can be partially counteracted by forest carbon uptake, and 11% of U.S. CO_2 emissions were offset by net storage of atmospheric carbon by forests from 1990 to 2015 (USGCRP, 2018). Drought, however, is expected to decrease forest carbon sequestration through diminished gross primary production and increased tree mortality (Pan et al., 2011). These drought-induced effects on trees can also disrupt hydrologic cycles by decreasing the flux of water to the atmosphere through reduced transpiration (Reed, Ewers, & Pendall, 2014).

In contrast to more intensively cultivated agricultural crops, the majority of forests harvested for timber and other products are not irrigated, and survival and yields for forest industry are limited by water availability. In an ecological sense, water availability has myriad impacts on both industrial and natural forests. Namely, drought-induced tree mortality can directly and indirectly alter many ecosystem services provided by forests. These services include primary and secondary forest products, carbon storage, water yield and quality, recreational value, and wildlife habitat (USFS, 2016). Primary and secondary forest products in particular represent a significant part of the global economy, with production and trade valued at $227 billion in 2016 (FAO, 2018). Trees weakened by drought stress show increased mortality due to biotic factors, as dramatically illustrated by large-scale losses to bark beetles in North America (Bentz et al., 2010; Logan, Beverly, Arjan, & Jeffrey, 2017). Drought and associated-forest mortality are a primary driver of catastrophic wildfire that affected 9.8 million acres in the United States in 2017 alone (https://www.nifc.gov/fireInfo/nfn.htm).

Our current understanding of how trees respond and succumb to drought is incomplete. Physiologically, drought stress can cause direct mortality of trees through at least two, non-exclusive mechanisms (McDowell et al., 2008). The first is through "carbon starvation," where closing of stomata pores in leaves minimizes water loss to transpiration but also limits the entry of CO_2 necessary for photosynthesis into the leaf, leading to mortality over time. The second is through hydraulic failure, which is dictated in part by wood anatomy.

In this paper, we discuss the important role of wood formation in determining how trees respond to drought. Wood is the water-conducting tissue of tree stems, and trees modify wood formation in response to drought to produce wood with hydraulic properties that mitigates the likelihood of hydraulic failure. In the following sections, we present the complex mechanisms of water conduction and drought response in trees through integration of knowledge of wood development, wood anatomy and tree physiology.

2 | WOOD STRUCTURE AND FUNCTION

Wood, also known as secondary xylem, is the product of the vascular cambium (Figure 1), a lateral meristem whose initials divide to produce daughter cells that differentiate into wood and secondary phloem (the inner bark) (Larson, 1994). Fusiform and ray initials produce an axial and radial set of tissues, respectively. The radial tissues consist of rays, whose cells play roles in storage, biochemistry, and lateral transport of water and nutrients in the stem. The axial tissues include tracheary elements, the cells directly responsible for water conduction.

Tracheary elements are among the most developmentally plastic plant cells, showing amazing diversity in morphology across plant lineages, different stages of plant growth, and different environmental conditions. In gymnosperm trees (e.g. pines) the axial tissues of wood are composed primarily of tracheids, a type of tracheary element that provides mechanical support (Figure 1c). Tracheids are long cells (up to 6 mm) (Sperry, Hacke, & Pittermann, 2006) that interconnect with each other through pits, which are cell wall perforations that allow water to flow between cells. In most angiosperm trees (e.g. broadleaved trees such as poplars), water conduction is achieved by the vessel element (Figure 1f), a type of tracheary element that can
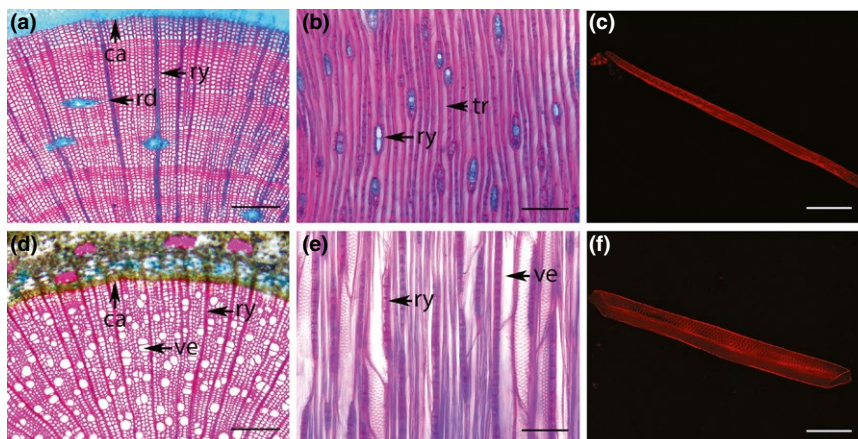

FIGURE 1 Transverse stem sections of a gymnosperm species, *Pinus radiata* (a) and an angiosperm hybrid, *Populus deltoides × Populus nigra* (d); scale bars are 200 μm. Tangential stem sections of *Pinus radiata* (b) and *P. deltoides × P. nigra* (e); scale bars are 100 μm. Single *Pinus radiata* tracheid (c) and *P. deltoides × P. nigra* vessel element (f); scale bars are 100 μm. Cambium (ca); Ressin duct (rd); Ray (ry); tracheid (tr)

join end-on-end with other vessel elements to produce longer conduits termed vessels (Sperry et al., 2006). During vessel element differentiation, the end walls are degraded resulting in low resistance of water flow between cells within the vessel. While vessel elements have a secondary cell wall similar to tracheids, the mechanical strength of angiosperm wood comes from the production of another cell type, the fiber.

Central to the function of both tracheids and vessel elements, pits are perforations through cell walls connecting tracheary elements to each other or other cell types. Pits are formed in specific locations of tracheary elements in which secondary cell wall deposition is prevented by recently uncovered molecular mechanisms (see below). A simple pit is formed by the localized, partial degradation of primary cell wall, leaving a fine mesh of material that allows passage of water but inhibits passage of air bubbles. Some gymnosperms, including conifer species, can form more specialized pits, containing a flap like structure (torus-margo) that can seal the pit against the surrounding cell wall to prevent the spread of air bubbles.

The development of this complex wood tissue system is modified in response to environmental conditions, including drought, to balance tradeoffs between the efficiency of water conduction and risk of failure during water stress. To understand the ramifications of these modifications, it is first necessary to consider how water is transported through the woody tissues of trees stems.

3 | HOW WATER IS TRANSPORTED IN TREES

Trees move water from roots to leaves, sometimes spanning hundreds of feet. Notably, the coast redwood (*Sequoia sempevirens*), the tallest tree species in the world, can reach heights of 100 m or more. The ascent of sap (water and solutes) in trees is ultimately the result of the molecular properties of water. Hydrogen bonds that form between water molecules give rise to the property of cohesion, while hydrogen bonds between water and tracheary element cell walls give rise to the property of adhesion. Together, cohesion and adhesion allow water to move upward inside tracheary elements against the force of gravity in a process known as the cohesion-tension mechanism of water transport (Dixon & Joly, 1895; Pickard, 1981). The force moving water from roots to shoots is largely generated by capillary action in the leaves, specifically in the walls of mesophyll cells (Figure 2). Water evaporates (transpires) when leaf stomata are open during the day (Figure 2), generating a force (tension, or negative pressure) that pulls water by cohesion through the xylem.

4 | THE INTERPLAY OF WOOD DEVELOPMENT, WOOD ANATOMY, AND PHYSIOLOGY

As previously mentioned, drought-induced tree mortality can be caused by two non-mutually exclusive physiological mechanisms: carbon starvation and hydraulic failure (McDowell et al., 2008). Hydraulic failure involves the loss of vascular function when air bubbles (emboli) form and spread throughout the xylem, producing breaks in the otherwise continuous water column (Figure 3). Air-filled xylem is unable to transport water, leading to desiccation and death (Barigah et al., 2013). Air bubbles in the xylem are the result of cavitation (the phase change of water from liquid to gas) under large negative pressures inside the xylem during water stress (as low as −11 MPa in some species) (Jacobsen, Pratt, Ewers, & Davis, 2007). Xylem sap is kept in a metastable liquid state due to the lack of nucleation sites, which initiates the phase change into gas (Tyree & Sperry, 1989). Drought-induced cavitation likely occurs when an air bubble enters the system through a pit from an adjacent air-filled space and serves as a nucleation site for cavitation (Cochard, Cruiziat, & Tyree, 1992; Crombie, Hipkins, & Milburn, 1985; Sperry & Tyree, 1990). Specifically, air-seeding occurs when the difference in pressure between both sides of the pit becomes sufficiently large (Figure 3), with larger pit pores at greater risk. The differences between angiosperm and conifer pit anatomy result in slightly different air-seeding mechanisms, but ultimately air-seeding in both taxa is driven by the difference in pressure between both sides of the pit.

Variation in the morphology and arrangement of tracheary elements can have large impacts on water transport and risk of cavitation under water stress. The Hagen-Poiseuille equation predicts that hydraulic conductivity of vessels increases with the 4th power of diameter, meaning that small changes in diameter have large effects on conductivity. For example, it would take 16 vessels of 10 μm diameter to equal the flow rate of a single 20 μm diameter vessel. However, increased diameter also elevates the risk of cavitation and air embolism, and thus there is a tradeoff between hydraulic conductivity and drought-induced cavitation (Hacke, Spicer, Schreiber, & Plavcová, 2017; Tyree & Zimmermann, 2002; Wheeler, Sperry, Hacke, & Hoang, 2005). Wider vessels might be more vulnerable to cavitation through an increased chance of a rare large pore in a pit membrane that enables air-seeding (Christman et al., 2012). The interplay of wood anatomy and drought response is best studied in angiosperm trees, where the risk of hydraulic failure is highly correlated with the diameter, number, and spacing of vessels (McDowell et al., 2008; Tyree & Sperry, 1989; Venturas, Sperry, & Hacke, 2017). Vessel trait properties thus represent a balance of optimizing water flow rates with the risk of hydraulic failure, and can be dramatically altered during development to in response to water stress and other ongoing environmental changes (Venturas et al., 2017).

5 | THE DEVELOPMENTAL STAGES OF TRACHEARY ELEMENT DIFFERENTIATION

Ultimately, the morphology and water-conducting properties of a tracheary element can be traced back to its initial differentiation, which can be broadly described by sequential morphological events leading to a functioning cell (Figure 4). The first event is specification of a cell produced by a fusiform initial to differentiate as a tracheary element, as opposed to some other cell type. Next is the radial
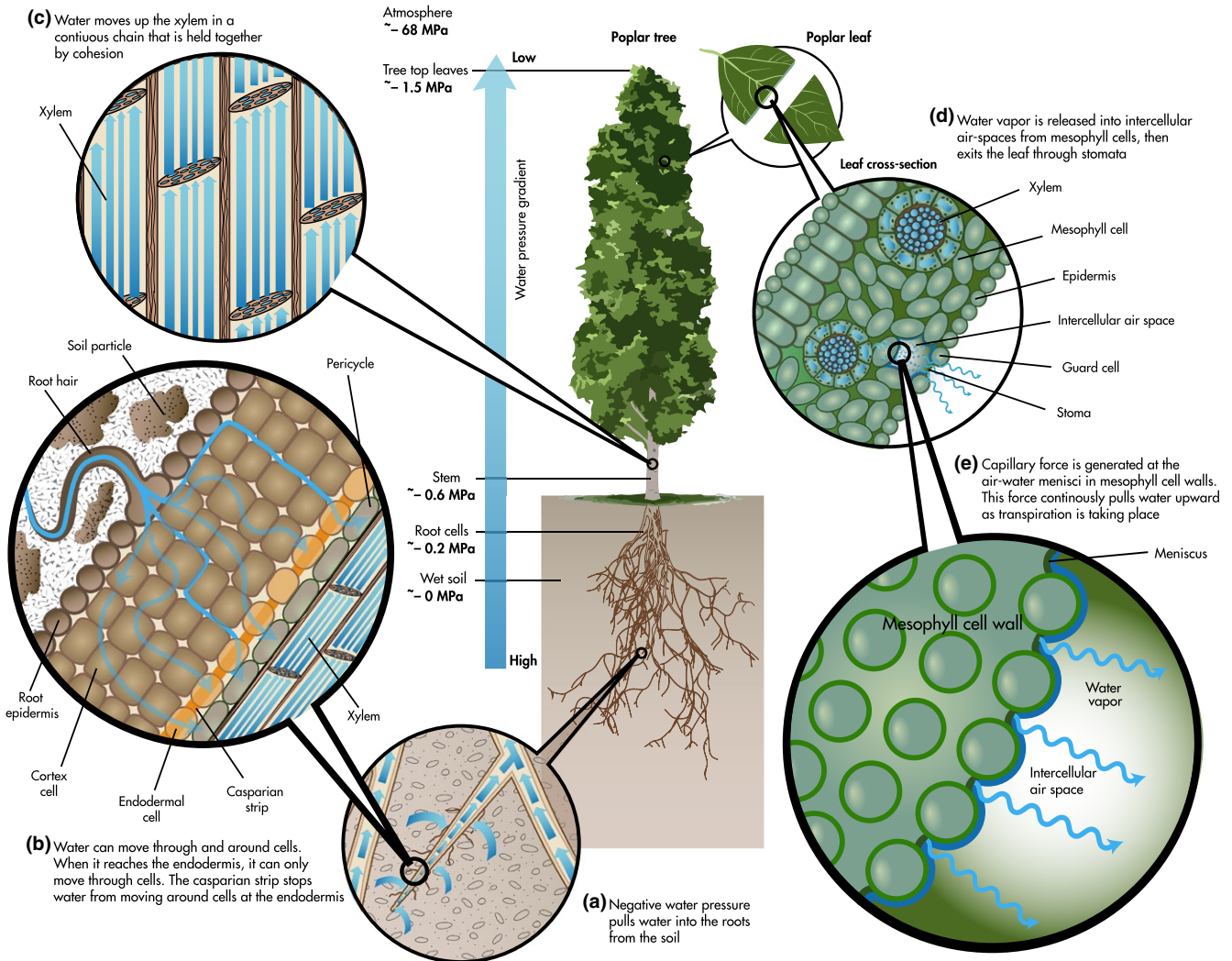
FIGURE 2 The path of water through a tree, and the cohesion-tension mechanism of water transport. (a) Water moves into the roots when root cell water potential is lower than soil water potential; (b) water moves through (symplastic movement) and around (apoplastic movement) the cells in the root cortex. The pathway of water around cells is blocked by the casparian strip at the endodermis, forcing water to take the symplastic pathway through the endodermal cells and enabling regulated entry of minerals and solutes into the vascular system (Karahara, Ikeda, Kondo, & Uetake, 2004); (c) water moves into the xylem, where water pressure becomes progressively negative with increasing height; (d, e) water escapes the tree as vapor through stomata in the leaves. Water vapor pressure in the atmosphere is almost always extremely negative compared to leaf vapor pressure, driving evaporation from the leaf mesophyll cell walls

expansion of the nascent tracheary element. This radial expansion is most dramatic in vessel elements, which can expand up to a 100-fold over the cambial initial. The next most conspicuous stage of development involves the production of a thick, lignified cell wall. Secondary cell wall synthesis is excluded from localized areas that will ultimately become pits interconnecting adjoining cells. As differentiation progresses, hydrolytic enzymes are sequestered in the vacuole of the cell. The dramatic end to this complex developmental process is programmed cell death, which is effected by the rapid rupture of the vacuole, resulting in mixing of the hydrolytic contents of the vacuole with the cytoplasm (Groover & Jones, 1999). The final product of differentiation is a hollow cell corpse defined by secondary cell wall.

Some aspects of tracheary element differentiation are relatively well described. The biosynthesis of the secondary cell wall has been

particularly well studied, in part because of its economic value as a major constituent of woody biomass utilized by forest industries. For example, genes encoding biosynthetic enzymes and cell wall-related transcription factors have been characterized (Carpita, 2011; Turner & Somerville, 1997), and transcriptional networks regulating cell wall synthesis have been modeled (Taylor-Teeples et al., 2015). In contrast, our understanding of the traits influencing water conduction and drought response is at best fragmentary and in some cases completely lacking. Below we focus on three key unresolved research questions: (a) How do trees sense and transmit signals to change wood development in response to water stress? (b) How is pit formation altered to mitigate cavitation vulnerability in response to water stress? and (c) How is the diameter of differentiating tracheary elements modified in response to drought stress? Examples
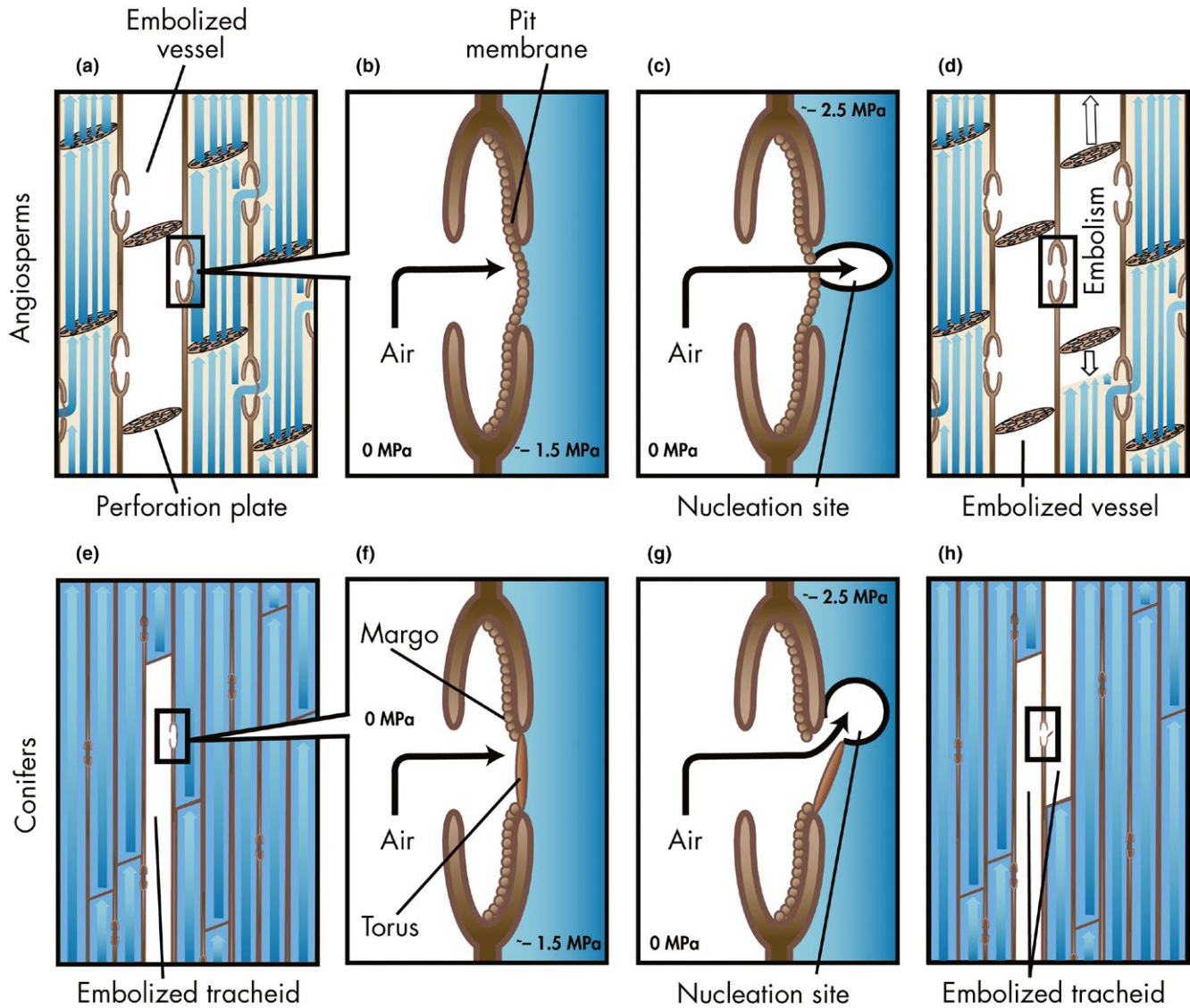
FIGURE 3 Drought-induced cavitation through the air-seeding mechanism in angiosperms and conifers. Inter-vessel (a) and inter-tracheary pits (e) allow lateral movement of water between cells. The pit membrane stops air from an embolized vessel from entering an adjacent water-filled vessel (b). Similarly, the torus of a conifer pit stops air from spreading into an adjacent functioning tracheid (f). As water stress increases, pressure inside the functioning vessel further decreases (becomes more negative) while the embolized vessel remains at atmospheric pressure. The difference in pressure between both sides of the pit membrane becomes large enough to force an air bubble through a pore. (c) A large difference in pressure can also tear or deform the conifer torus, allowing air bubbles through (g). An air bubble serves as a nucleation point for cavitation, producing an embolism, or air-pocket (d, h). Greater connectivity between vessel elements allows for the rapid spread of the embolism (d). Emboli in tracheids will not spread as readily due to the low connectivity between each cell (h)

are presented from angiosperm wood development, for which we have the most complete studies.

6 | HOW DO TREES SENSE AND TRANSMIT SIGNALS TO CHANGE WOOD DEVELOPMENT IN RESPONSE TO WATER STRESS?

Trees sense water stress and transmit signals to coordinate physiological responses (e.g. closing stomata) and changes in growth, including wood development. Multiple non-exclusive mechanisms have been suggested for sensing of water stress, but a primary

mechanism appears to be the sensing of stress at the individual cell level by plasma membrane-localized receptors (Osakabe, Yamaguchi-Shinozaki, Shinozaki, & Tran, 2013). An example is sensing of osmotic changes resulting from water stress by transmembrane histidine kinase K^+ transporters (HKT1-like proteins) that have been shown to activate intracellular water stress signaling mechanisms in both poplar (Bertheau et al., 2015; Chefdor et al., 2005; Héricourt et al., 2016) and eucalyptus (Liu, Fairbairn, Reid, & Schachtman, 2001). Interestingly, K^+ levels peak in the cell expansion zone of the cambium, and cambial K^+ levels correlate with seasonal changes in vessel element diameter in poplar (Ache, Fromm, & Hedrich, 2010; Arend et al., 2005; Fromm, 2010; Langer et al., 2002; Wind, Arend, & Fromm,
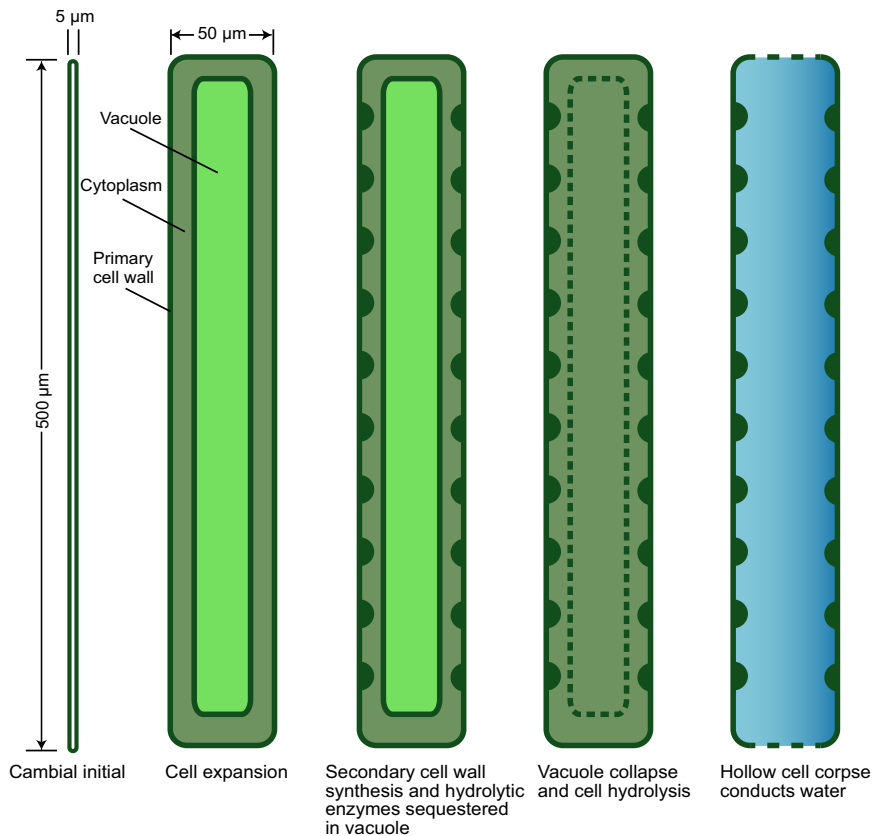
Tracheary Element Differentiation

FIGURE 4 Sequential events defining the differentiation of tracheary elements (left to right). Cambial initials divide one or more times to produce a daughter that acquires the cell fate of a vessel element. The cell undergoes radial expansion driven by turgor pressure to a diameter reflective of growth conditions and water stress. Secondary cell wall is deposited between the plasma membrane and primary cell wall. At the same time, hydrolytic enzymes are produced and sequestered within vacuoles. Programmed cell death results in the rapid collapse of vacuoles, mixing hydrolytic enzymes in the vacuoles with the cytoplasm, resulting in hydrolysis of the cell contents. End walls and primary cell walls are variously hydrolyzed depending on the species, developmental stage and other factors. The final product is a hollow cell corpse

2004), potentially linking HKT1-like intracellular signaling to tissue-level changes in wood development. As potassium is a primary osmoticum in plant cells (Wang, Zheng, Shen, & Guo, 2013), these observations are also consistent with potassium potentially playing a causative role as an osmoticum affecting turgor and ultimately diameter growth of differentiating vessels in response to water stress (see below).

The hormone ABA has been implicated as a primary signal of water stress in plants including trees, coordinating responses including stomatal closure, reduced growth, and changes in wood development. Like other plants, ABA levels are elevated in poplar under water stress (Chen et al., 2002; Jia et al., 2017). Treatment with ABA results in poplar stems with smaller diameter and more frequent vessel elements (Popko, Hänsch, Mendel, Polle, & Teichmann, 2010), similar to developmental changes seen in response to water stress. ABA elicits changes in large number of genes associated with stress response (Fujita, Fujita, Shinozaki, & Yamaguchi-Shinozaki, 2011), resulting in the observed complex changes in physiology and development. Interestingly, epigenetic factors have been shown in poplar to play roles in changing gene expression or maintaining a "memory" of previous water stress (Raj et al., 2011).

6.1 | Perspectives

Currently a large base of knowledge about water stress at the molecular, genetic and cell biology levels in model crop plants is largely untranslated to trees. While physiology studies are numerous in trees, much of that knowledge remains unconnected to mechanisms. A major challenge is thus to comprehensively describe for at least one tree species the mechanistic basis of water stress sensing, signal transduction, and how signals are translated in physiological and developmental responses.

7 | HOW IS PIT FORMATION ALTERED TO MITIGATE CAVITATION VULNERABILITY IN RESPONSE TO WATER STRESS?

Recent research has detailed molecular mechanisms regulating where and how pits form in the secondary cell walls of Arabidopsis vessels. Deposition of cellulose microfibrils in secondary cell walls is directed by a plasma membrane-localized cellulose synthase complexes that track microtubules. Protein complexes containing MICROTUBULE DEPLETION DOMAIN1 (MIDD1) and RHO-RELATED PROTEIN FROM PLANTS11 (ROP11) actively promote the disassembly of cortical microtubules and thus exclude cellulose synthase complexes and secondary cell wall formation in regions destined to become pits (Oda & Fukuda, 2013; Oda, Iida, Kondo, & Fukuda, 2010; Sasaki, Fukuda, & Oda, 2017). Interestingly, mutation or changes in expression of these and MIDD1/ROP11 interacting proteins can dramatically change the spacing and size of pits (Nagashima et al., 2018). Mathematical modeling shows that pit

formation has features consistent with a classical Turing reaction-diffusion mechanism (Nagashima et al., 2018).

7.1 | Perspectives

While these molecular details are exciting, it is currently unknown how this mechanism is modified to produce variation in the spacing or size of pits in nature, or how variation is ultimately linked to physiological properties of water transport or hydraulic failure during water stress. One critical area for new research is to examine how components of the MIDD1/ROP11 complex are modified during water stress to change pit patterning and size. Another need is to determine the range of natural variation in genes encoding components of the MIDD1/ROP11 mechanism, and to what degree they predict variation in pit properties in nature. Both of these questions are now highly tractable, including determining natural variation using existing genome wide association populations in poplar.

8 | HOW IS THE DIAMETER OF DIFFERENTIATING TRACHEARY ELEMENTS MODIFIED IN RESPONSE TO DROUGHT STRESS?

The diameter of tracheary elements (most dramatically in vessel elements) is correlated with both water conduction and cavitation vulnerability. The change in wood development in response to water stress can be striking, for example in poplar the diameter, number and clustering of vessel elements produced all change in response to water stress (Fichot et al., 2009). Unfortunately the regulation of tracheary element diameter and frequency are among the most poorly understood aspects of tracheary element differentiation. Understanding the molecular regulation of vessel element diameter is thus a crucial area for new research to understand how physiological changes during drought translate into compensating features of wood anatomy.

Cell expansion in plant cells is driven by turgor, and turgor-driven swelling is the only known mechanism that could potentially drive tracheary element expansion. Water crosses the plasma membrane and enters a cell when the concentration of solutes inside the cell is greater than that outside of the cell, causing the cell to swell. How much and in what dimensions the cell expands is determined not only by solute concentrations but also by the resistance of the cell wall. Turgor is an active process that occurs while the plasma membrane is intact, and thus the final diameter of a tracheary element is realized while the cell is still living, prior to programmed cell death. Also, because the secondary cell wall is rigid, expansion and the final diameter of the cell must be realized before secondary cell wall synthesis is complete.

A number of possible mechanisms might control the final diameter of the developing tracheary element, but ultimately the diameter is a function of the turgor pressure in the differentiating cell and the rigidity of the cell wall. The primary walls of cells within the cambial zone are relatively thin and pliable, and it can be deduced that the primary cell wall must be dramatically extended during tracheary element expansion. For example, to expand from a 5 to 50 μm diameter, the cell must extend 10-fold in circumference and add 10-fold more cell wall material to maintain a constant cell wall thickness. One outstanding question is whether the secondary cell wall plays a role in restricting cell expansion. One observation arguing against that possibility is presented by Arabidopsis *irregular xylem* (*irx*) mutants, which have weakened secondary walls but do not have enlarged vessel elements (Turner & Somerville, 1997). Similarly, downregulation of homologous genes in poplar results in mechanically weakened secondary cell walls, but only a ~5% increase in vessel element diameter (Li et al., 2011). It would thus appear that the primary wall or even pressure from surrounding cells, and not the secondary cell wall, may be the determinants of resistance against turgor during vessel element differentiation.

The best conceptual models for vessel element primary cell wall expansion are given by the classical auxin-mediated extensibility of primary cell walls by a pH and expansion-dependent mechanism. Auxin is well known to affect cell wall extensibility in an expansin-dependent manner by lowering apoplastic pH in the "acid growth" hypothesis (Barbez, Dunser, Gaidora, Lendl, & Busch, 2017). Auxin has long been implicated in vessel element differentiation, with auxin transport suggested as both a mechanism for interconnecting files of vessel elements as well as influencing the morphology of differentiating vessel elements (Barbez et al., 2017; Hacke et al., 2017; Spicer, Tisdale-Orr, & Talavera, 2013). In the zinnia in vitro system, auxin is required to induce vessel element differentiation, and increasingly acidic pH in vessel increases vessel element diameter (Roberts & Haigler, 1994). Intriguingly, treatment of poplar stems with an inhibitor of polar auxin transport results in the development of wood with smaller and more clustered vessels, similar to what is seen in response to water stress (Johnson et al., 2018).

Regulation of solute concentration and turgor during tracheary element expansion has several features that make this a primary candidate regulatory mechanism controlling final diameter. Perhaps the best studied example of turgor regulation is given by guard cells which control the aperture of stomata in leaves. Guard cells increase turgor pressure by the regulated influx of solutes, namely K^+ and sugars, which leads to the influx of water that causes the cell to swell (Kim, Böhmer, Hu, Nishimura, & Schroeder, 2010). Poplar trees treated with ABA have wood with decreased K^+ levels (Wind et al., 2004). Experimental depletion of K^+ results in poplar wood with changes in the distribution and size of vessels elements (Fromm, 2010; Wind et al., 2004), similar to what is seen in response to drought. Potassium and sugar levels are also both correlated with changes in tracheary element diameter occurring during seasonal changes in poplar (Ache et al., 2010). Mechanistically, a poplar K^+ channel was identified that could play a causative role in regulating K^+ levels and turgor in differentiating vessels (Arend et al., 2005; Langer et al., 2002). Importantly, both ABA and changes in K^+ and sugar levels provide potential mechanisms interconnecting tree

physiology during water stress with the development of tracheary elements.

8.1 | Perspectives

There are a number of challenges in providing a comprehensive understanding of the regulation of vessel element diameter. In vitro systems for the study of vessel element differentiation (e.g. the Zinnia system) lack the tissue-level context of normal vessel element differentiation, and may be of limited utility. New approaches enabling the experimental manipulation, cell biology and imaging of differentiating vessel elements within living stems are thus needed. Computed tomography (CT) and other imaging approaches capable of visualizing cells deep within tissue could be used in conjunction with genetically encoded sensors or molecular probes against putative osmolytes, for example, to better understand the dynamics of expansion and the basis for the driving force of osmotic pressure. Potential surprises could include a relatively rapid expansion of vessels, and cooperation from neighboring ray cells in providing osmoticum.

9 | CONCLUSIONS

The scale of societal, economic and ecological impacts of forest mortality and yield losses caused by heat and drought stress require coordinated responses at levels ranging from local and national governments, to intergovernmental bodies, to individual land managers. Complex decision making regarding forest management needs to be supported by the best possible science. Unfortunately, we currently have major knowledge gaps regarding the biology underlying water and abiotic stress responses in trees.

Importantly, new integrative approaches that cross traditional disciplines are needed to link how trees perceive water stress, transmit stress signals, and coordinate changes in development and physiology. Even now basic questions about the interaction of wood development and physiology remain, including how changes in wood development impact growth and survival over longer time periods. The explosion of information about water and abiotic stress responses in crops and model plants has largely not been extended to trees. Indeed, perennial plants likely have unique attributes not found in herbaceous annuals that require direct research efforts. Even within tree species, it remains debatable to what extent findings in model trees like poplar will translate to other species. Most dramatically, gymnosperms and angiosperm trees have distinct wood types and other differences that likely require independent research efforts.

Understanding the biological factors underlying the responses of individual trees, tree species and forests to drought stress will enable new approaches for predicting and mitigating the future effects of drought. For wood biology, understanding the mechanisms underlying tracheary element morphology is now technically tractable using molecular, cell biology and genomic tools.

But these mechanisms must then be interpreted in terms of physiology and ultimately whole tree responses to the environment. These efforts will require increased cooperation from researchers in previously disparate fields including tree physiology, anatomy, genomics and cell biology. Perhaps the most challenging will be to translate these basic findings into real solutions for predicting and mitigating drought, for example through direct selection of trees for breeding and restoration based on molecular markers rather than traditional tree breeding.

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