Editorial

Hydraulics in the 21st century

Introduction

The science of plant hydraulics has long sought to understand the fundamental mechanisms of how water moves through plant vascular systems (Dixon & Joly, 1895). Over the last 50 years, advances in our understanding of embolism formation (Tyree & Sperry, 1989), hydraulic segmentation (Zimmermann, 1978), and refilling (Sperry *et al.*, 1987) were generated both through novel measurements (Scholander *et al.*, 1965; Sperry *et al.*, 1988; Alder *et al.* 1997) and model development (Tyree & Sperry, 1989; Sperry *et al.*, 1998). This knowledge provided a foundation of mechanistic understanding that has impacted fields of study from crop physiology to the global hydrologic cycle (Fig. 1; Sperry *et al.*, 2003; Tang *et al.*, 2015; Peters-Lidard *et al.*, 2019). Scientific advances in our understanding of plant hydraulics and its implications for plant function have arguably accelerated over the last two decades. New empirical (Holbrook *et al.*, 2001; Choat *et al.*, 2015) and modeling (Christoffersen *et al.*, 2016; Sperry *et al.*, 2016; Venturas *et al.*, 2018; Kennedy *et al.*, 2019; Mencuccini *et al.*, 2019) approaches have been applied to tackle some of our largest challenges, and different perspectives have been integrated to better understand the entire vascular system (e.g. carbon metabolism and xylem hydraulics; Hölttä *et al.*, 2009; Secchi *et al.*, 2011).

Here we highlight some of the most exciting recent advances in our understanding of plant hydraulics, and address some of the new frontiers that have emerged. These advances and frontiers all have implications far beyond the study of how water moves through plants, as highlighted graphically in Fig. 1. We conclude with speculation on where plant hydraulics science will progress in the 21st century.

Advance: understanding the evolution and ecology of hydraulics

An exciting aspect of plant hydraulics has been the discovery that adaptation in the form and function of the water transport system constitutes a fundamental axis in terrestrial plant evolution. This situation arises because of three unavoidable consequences of undertaking photosynthesis and growth on the land. First is the inevitable connection between transpiration and photosynthesis caused by the parallel fluxes of water and CO_2 through stomata; second is the relatively narrow functional hydration window required for photosynthetic, stomatal and xylem operation; third is the cost associated with vascular construction and maintenance. Assuming that selection drives towards maximizing net photosynthetic profit (Givnish, 1987) then it is expected that plants should invest just enough hydraulic capacity to maintain stomata open for maximum photosynthesis under favorable soil and atmospheric conditions (Dewar *et al.*, 2018). This argument has found strong support in the literature in the form of clear correlations between the efficiency of xylem water supply and both the photosynthetic capacity (Hubbard *et al.*, 2001; Brodribb *et al.*, 2005; Maherali *et al.*, 2008) and productivity (Poorter *et al.*, 2010) of plant species. Coordination is evidenced by covariation of hydraulic and stomatal anatomy to achieve a balance between water supply and photosynthesis (Sack *et al.*, 2005; Brodribb & Jordan, 2011; Fiorin *et al.*, 2016; Schneider *et al.*, 2017). Key patterns have emerged linking water transport properties such as leaf vein density with stomatal density through cell size (Carins Murphy *et al.*, 2012), enabling plasticity but also determining adaptive trajectories into different light climates (Brodribb *et al.*, 2013). Recent work shows how these different structural, hydraulic and water relations traits adapt across different scales from the individual up to the level of plant family (Rosas *et al.*, 2019). The stability of some hydraulic traits within species and even larger phylogenetic groupings has allowed a degree of historical reconstruction of hydraulics within major clades, revealing connections between adaptive improvement in hydraulic efficiency of leaves and the rise of the angiosperms to global dominance (Feild & Brodribb, 2013).

Modelers have realized the potential of plant hydraulics as a means of better representing the behavior of vegetation in regulating global fluxes of carbon and water vapor. The incorporation of hydraulic frameworks into land surface models allow variables such as rooting depth, plant allometry and capacitance to produce a more meaningful representation of plant functional types in large scale modeling (Xu *et al.*, 2016). In addition, the application of hydraulic optimization models formulated on principles of minimizing costs associated with hydraulic dysfunction during water deficit, provide much needed improvements to predictions of vegetation response to rainfall (Sperry *et al.*, 2016; Wolf *et al.*, 2016; Venturas *et al.*, 2018). Ecologists have also embraced the plant hydraulic system as a new tool to connect ecological patterns with functional properties of plants (Choat *et al.*, 2007; Markesteijn *et al.*, 2011). This has allowed the traditional 'functional trait' network to be expanded from basic economics (e.g. leaf mass per area) to include hydraulics traits that have a more direct mechanistic association with plant function and climate (Choat *et al.*, 2007; Larter *et al.*, 2017). This approach is enabling researchers to address more complex ecological questions about community assembly (Xu *et al.*, 2016) and species distributions (Blackman *et al.*, 2012).

Plant hydraulics is still a relatively new science, and its application to understand a diversity of ecological and global scale processes remains constrained by basic knowledge about the function of the hydraulic system as a whole. The foundational

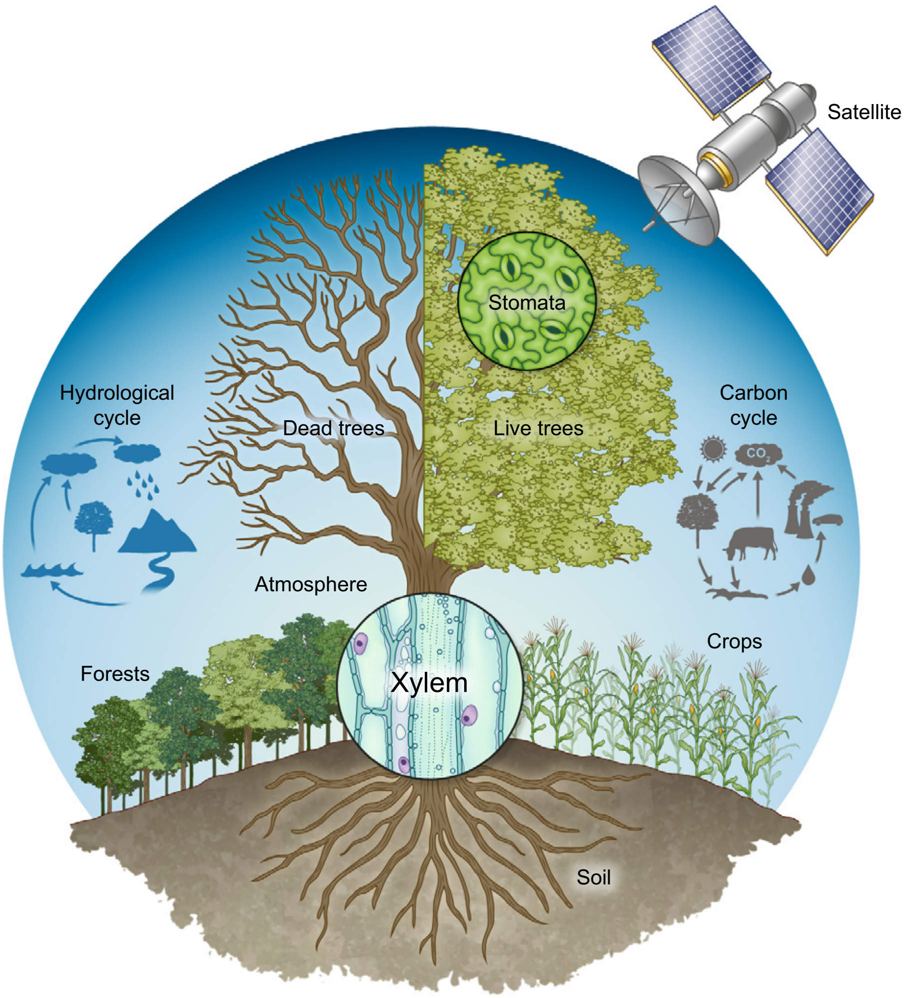

Fig. 1 Plant hydraulics has influenced a broad suite of scientific fields. Plant hydraulics originates from the study of water transport through the xylem, but is now extended to consider soil–root, leaf, and whole-plant transport processes, and is even now being applied at global scales via satellite remote sensing. Fields influenced by plant hydraulics include plant ecology and vegetation dynamics, crop and wild-land function and structure, and the global carbon and water cycles.

knowledge about plant hydraulics was built from studies of hydraulic processes in stems, but these are the simplest and least important resistors in the whole plant vascular system. Now there is an urgent need to expand our understanding of the major resistors in plants; the roots, leaves and flowers. New tools and methods are providing insights into the performance of these complex organs, but progress remains slow, with roots and flowers particularly underrepresented in the literature. Only armed with a detailed knowledge of whole plant hydraulic function will we be able to confidently interpret and predict the responses of whole plants to atmospheric and soil conditions.

Advance: understanding and simulation of hydraulic failure and mortality

Hydraulics play a critical role in the survival and mortality of plants experiencing drought, be it through direct failure to avoid desiccation (Brodribb & Cochard, 2009; Blackman *et al.*, 2016), and/or through stomatal reductions in photosynthesis that promote carbon starvation and vulnerability to pests (Martínez-Vilalta *et al.*, 2002). Building on the hydraulic framework for mortality prediction (McDowell *et al.*, 2008) it has emerged that plants which spend long durations (e.g. months) with low residual xylem hydraulic conductivity tend to die (McDowell *et al.*, 2013; Anderegg *et al.*, 2015; Sperry & Love, 2015; Adams *et al.*, 2017). The critical loss of conductance (commonly referred to as percentage loss of conductance, PLC) leading to hydraulic failure has been reported to be variable among species, sites and experiments. This is not unexpected, as the relevant parameter to be considered is not PLC *per se*, but the actual hydraulic conductance and its sufficiency to maintain cells hydrated above a critical water content, under a given evaporative demand and residual leaf conductance to water vapor. Models can now simulate hydraulic failure with relatively high accuracy throughout the entire plant vasculature (McDowell *et al.*, 2013; Sperry *et al.*, 2016), with rigorous hydraulics now entering into ecosystem and global scale models of Earth system processes (Christoffersen *et al.*, 2016; Kennedy *et al.*, 2019). The identification of thresholds of critical residual hydraulic conductance under different scenarios of evaporative demand suggests models can directly predict mortality from hydraulic failure when they properly represent plant hydraulics. Likewise, these trait-enabled hydraulics models can simulate hydraulic safety margins (e.g. the difference between observed minimum water potentials and the water potential of embolism), which is a primary correlate of drought-induced mortality (Anderegg *et al.*, 2016).

The challenges facing our understanding of the role of hydraulics in drought-induced mortality remain numerous. First, mortality is likely a product of a cascade of influences and mechanisms (e.g. Manion, 1981; Waring, 1987) and is unlikely to be a case of hydraulic failure in twigs in isolation, thus the assumption that hydraulics is all we must know to predict mortality seems premature and overly simplistic. Research considering the myriad of processes that can promote mortality is the most likely to yield mechanistic insight from which simplified modeling schemes can be developed. Second, understanding the degree of hydraulic failure belowground has emerged as a critical frontier, as model analysis suggests hydraulic failure in the roots and/or root–soil interface may dominate during drought (McDowell *et al.*, 2013; D. M. Johnson *et al.*, 2018; Mackay *et al.*, 2019). This is a large challenge due to the difficult nature of quantifying plant hydraulics belowground. Third, we need to better understand hydraulic fluxes and degree of associated embolism during periods when root water uptake and transpiration are curtailed and cuticular conductance and capacitance dominate the output and input fluxes of water to the foliage (Blackman *et al.*, 2016; Duursma *et al.*, 2019; Körner, 2019). It is these small fluxes that may define the critical point of hydraulic failure during drought (Cochard, 2019), and thus more detailed focus is merited. Finally, determining the role of carbohydrate supply and utilization in embolism avoidance and repair/regrowth of xylem (Vandegehuchte *et al.*, 2015; Tomasella *et al.*, 2017) is essential if we are to understand and simulate coupled carbon-hydraulic function (McDowell *et al.*, 2013; Fisher *et al.*, 2018).

Advance: recovery from xylem embolism

Experimental evidence suggests that plants can survive drought when xylem embolism remains below critical thresholds (Nardini *et al.*, 2013). Still, the loss in water transport capacity caused by gas-filled conduits reduces gas exchange and photosynthesis even after drought relief (Kannenberg *et al.*, 2019), possibly implying long-term legacies on plant health and productivity. A still open question is whether plants can recover from nonlethal levels of xylem embolism following rehydration, by regaining full pre-drought hydraulic functionality. While growth of new xylem provides a mid- to long-term solution for woody plants (Brodribb *et al.*, 2010), it is debated if plants can refill embolized conduits with water, or if these gas-filled conduits are functionally lost forever despite the significant carbon costs incurred by plants in their construction (Klein *et al.*, 2018). Some woody and herbaceous plants are known to seasonally repair frost-induced embolism via generation of positive and over-atmospheric pressure in their xylem system, either at root or stem level (Yin *et al.*, 2018).

Do plants repair embolized conduits by generating positive xylem pressure after drought relief? Early reports based on hydraulic measurements of embolism dynamics under drought and recovery suggested that some plants can refill embolized conduits even under negative water potential (Salleo *et al.*, 1996), and it was proposed that an osmotic mechanism based on the dynamics of wood and bark nonstructural carbohydrates might provide the forces necessary to overcome water potential gradients (Schmitz *et al.*, 2012). This view has been challenged by reports suggesting that destructive hydraulic techniques overestimate xylem embolism and generate artefactual fluctuations in recorded PLC levels (Jansen *et al.*, 2015). Other studies with micro-computed tomography (micro-CT) observations of embolism build-up during drought roughly correlate with hydraulic measurements of PLC (Nardini *et al.*, 2017; Nolf *et al.*, 2017; Losso *et al.*, 2019), but hydraulic evidence of refilling is currently considered with suspicion. The occurrence of refilling has been detected with *in vivo* imaging techniques in some cases (Kaufmann *et al.*, 2009; Brodersen *et al.*, 2018) but not in others (Choat *et al.*, 2015). However, it has been argued that very local damage by X-rays in the imaging region of a stem (< 5 mm) during repeated micro-CT scans can damage parenchyma cells in some species (Petruzzellis *et al.*, 2018), possibly hindering the vital processes that are putatively required to refill the entire stem (Lovisolo *et al.*, 2008; Laur & Hacke, 2014; Secchi *et al.*, 2017). Further work will be required to confirm the majority view from CT work, that refilling in plants is not possible under tension.

An open-minded analysis of available evidence suggests that post-drought embolism refilling under substantial residual tension is probably not common in plants, and at least problematic from a thermodynamic point of view (Vesala *et al.*, 2003). Rather, the actual question is whether active and fast hydraulic recovery is possible when plant water potential rises close to zero, via biological processes generating local positive xylem pressures using residual stores of non-structural carbohydrates (Savi *et al.*, 2016; Liu *et al.*, 2019). Answering this question without triggering new controversies will probably require at least two new methodological advances. The first one is the possibility to observe *in vivo* and in real-time the functional status of xylem conduits during drought and recovery, without damaging living wood and bark cells. While micro-CT might not be up to this task (Petruzzellis *et al.*, 2018), the optical method applied to leaf vasculature (Brodribb *et al.*, 2016) is a very promising and nondestructive approach, but until now it has only been seldom used to observe eventual xylem refilling (K. M. Johnson *et al.*, 2018). The second methodological advancement is related to the accurate measurement of water potential in the proximity and within the eventually refilling conduits. Previous studies aimed at detecting xylem refilling have measured water potential using bagged leaves to equilibrate leaf and stem water potential, or via psychrometric sensors attached to stems/leaves. In both cases, it is possible that measured water potential does not reflect the local conditions around the conduits, due to poor resolution or substantial water potential disequilibria within the plant during the rehydration phase. This might lead to incorrect conclusions on the occurrence of embolism repair under tension, or on the lack of refilling even when bulk water potential rises close to zero. Clearly, there is a need for more accurate measures of the water potential of living cells and water-filled conduits surrounding embolized conduits, as well as the osmotic potential of the sap in the eventually refilling conduit. This would allow us to conclude that: thermodynamic conditions make possible passive embolism reversal and biologically active processes allow refilling to overcome residual water potential gradients. While current technology does not allow such a level of spatial resolution in water potential measurements, it is possible that nanotechnology will provide means to overcome these major technical limitations (Kwak *et al.*, 2017).

The future of plant hydraulics science

Plant hydraulic regulation of water uptake provides the backbone of the plant carbon cycle and ecology because of its direct control over, and tight coordination with, canopy photosynthesis. Advances in measurements and modeling over the last few decades have enabled far-reaching influence of hydraulic discoveries, including impacting how we view and simulate the global water and carbon cycles and manage crop systems (Fig. 1). Perhaps most importantly in this era of a warming atmosphere and more variable droughts, is the critical role our understanding of plant hydraulics is having on our ability to predict and mitigate chronically-increasing stressors (e.g. temperature, vapor pressure deficit) on plant function and survival.

There are many challenges still in front of us. We do not know the critical thresholds of embolism that results in complete hydraulic failure of the vasculature, nor the role of carbohydrate metabolism in mitigation of, and repair of, embolized conduits. Hydraulic parameters are expected to aid in our understanding of trait-tradeoffs, yet thus far a mechanistic linkage between many of the spectrum of hydraulic traits is missing (Christoffersen *et al.*, 2016; Gleason *et al.*, 2016). Likewise, we do not understand the interactions of rising atmospheric [CO_2], rising vapor pressure deficit, and plant hydraulics. In the simplest terms, what will dominate the hydraulic responses: elevated CO_2, which aids water-use efficiency, or elevated vapor pressure deficit, which increases the risk of embolism? Without this knowledge it is difficult to predict future photosynthesis, growth and survival.

The 21st century offers a very exciting time for advancement of plant hydraulics understanding, approaches, and applications. Future directions range in scale from understanding the molecular regulation and feedbacks with maximum conductance and embolism avoidance, to improved understanding of water potential regulation at landscape to global scales (Momen *et al.*, 2017). Inherently, developments in understanding will be associated with continued methodological improvements at micro- to macro-scales, and with applications of refined hydraulic models to allow strong, process-based inferences. Perhaps the most important directions that plant hydraulics science can go is in applications to the prediction and management of both wild and crop systems under rising temperature and vapor pressure deficit and drought frequency, which threatens food production and the global carbon cycle alike.

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