

Meetings

New developments in understanding plant water transport under drought stress

Fourth Xylem International Meeting, Padua, Italy, 25–27 September 2019

The Fourth Xylem International Meeting (XIM4) brought together over 100 plant scientists to discuss a wide range of topics related to embolism resistance and efficiency of long-distance water transport through plants, and their implications for cultivated and natural systems. The diversity of methods, plant species, and physiological processes discussed in the context of water stress at the meeting highlighted a need to integrate spatial and temporal data about plant functioning, specifically in regard to climate-change-related challenges.

A more holistic view of the plant water transport

Structural traits, such as pit characteristics and conduit diameter, have been traditionally associated with xylem safety and efficiency. Furthering our understanding of these relationships, it was shown that the hydration of pit membranes, their chemical composition, and three-dimensional structure play a key role in the resistance to air-seeding and embolism spread (J. Werner, Ulm University, Germany; Zhang *et al.*, 2020). Resolving conduit network characteristics, such as conduit grouping and intra-organ anatomical trait correlations like those between pit membrane porosity and conduit diameter, was also shown to be important in upscaling xylem anatomy to drought-induced embolism resistance (Mrad *et al.*, 2018). Though conduit diameter remains the easiest anatomical trait to measure, the lack of more comprehensive knowledge on the inter and intraspecific scaling of conduit size and pit traits prevents a more robust understanding of the link between conduit diameter and drought-induced (F. Lens, Leiden University, the Netherlands) or freeze-induced embolism resistance (A. Lintunen, University of Helsinki, Finland).

The development of noninvasive techniques (e.g. optical vulnerability and synchrotron-based X-ray microtomography) has enabled the study of hydraulics in soft organs, creating a breakthrough in plant vascular research, as demonstrated by the many studies presenting the application of such methods at XIM4. By using noninvasive methods, for instance, a high number of investigations highlighted intraspecific variation in xylem resistance in the stems (C. Lemaire, Université Clermont Auvergne, France; L. Lamarque, University of Bordeaux, France) and leaves (A. Cardoso, Purdue University, West Lafayette, IN, USA; Hochberg *et al.*,

2017) of woody species, both in time (seasonally) and in space (on different locations of the plant). Large intraspecific variation in xylem resistance has also been shown to result in heterogeneous mortality across the canopy in a tree species exposed to drought, with considerable impacts on plant photosynthesis even after rehydration (Cardoso *et al.*, 2020a). On the contrary, little intraspecific plasticity of functional and anatomical xylem traits was reported for different species across wide aridity gradients when samples were taken at a fixed distance from the apex (E. Robert, CREAM, Barcelona, Spain). Such contrasting results indicate the need to consider known axial trends of anatomical traits when selecting the site on a branch/stem axis for physiological experiments to avoid potential bias in the interpretation of results (Lechthaler *et al.*, 2019). The use of more rigorous sampling protocols and the new, noninvasive methods will likely lead to further insights into the phenotypic plasticity of xylem's anatomical and functional traits that plants may develop as a response to future climate changes.

A number of XIM4 contributions emphasized that, in order to build a holistic picture of the hydraulic processes controlling plant responses to drought, hydraulics at the extremities of the water transport system (i.e. soil–roots and leaves–atmosphere) must be further investigated. The presence of biochemical barriers at both root–soil and leaf–atmosphere interfaces (suberized cell walls of exo and endodermis in roots and extracellular biopolymers of the leaf cuticle, respectively) likely play a key role in water transport efficiency and safety, as they reduce the free diffusion of water and nutrients (Schreiber, 2010). Moreover, declines in soil hydraulic conductivity and root hydraulic conductance during moderate drought have been shown to be linked to the disconnection between roots and the rhizosphere (Rodríguez-Domínguez & Brodribb, 2020), with consequent limitations to leaf transpiration (A. Carmignati, University of Bayreuth, Germany). At the other extremity of the hydraulic path, increasing vapor pressure deficit in the atmosphere is long known to be tightly associated with leaf water losses through stomata (McAdam & Brodribb, 2015) and the leaf cuticle (L.-M. Billon, Université Clermont Auvergne, France). A better integration of the hydraulics at the extremities in the modeling of plant–water relations will increase our ability to understand plant behavior in the context of water stress.

Extended frontiers of xylem hydraulics to better understand plant responses to climate change

Hydraulic failure due to xylem embolism is recognized as a major trigger of tree mortality under drought (Choat *et al.*, 2018). Plant species display different mechanisms to avoid air-seeding and subsequent hydraulic failure. Declines in stomatal conductance were shown to preserve leaf and stem xylem from embolism in a herbaceous grass (D. Corso, University of Tasmania, Australia) and in woody angiosperms (Creek *et al.*, 2019), as well as in a pair of

lycophyte species (S. McAdam, Purdue University, West Lafayette, IN, USA), suggesting an evolutionary trait coordination across land plants (Cardoso *et al.*, 2020b). Indeed, a trait-based model showed that the time of plant desiccation was longer with wider differences between the water potential at 50% loss in stem hydraulic conductance and stomatal closure (Blackman *et al.*, 2019). Nevertheless, water loss through the cuticle (g_{\min}) was shown to continue well beyond the point of stomatal closure, potentially leading to further increases in xylem tension during prolonged droughts (Duursma *et al.*, 2018). Owing to the importance of leaf water loss to the whole-plant water status, lowering g_{\min} was proposed as an important mechanism preventing the development of excessively low water potentials during drought (L-M. Billon). Additionally, reversible collapse of minor veins in leaves has also been suggested to effectively buffer embolism in major veins in red oak leaves (N. Holbrook, Harvard University, Cambridge, MA, USA; Zhang *et al.*, 2016).

It has long been debated whether plants can refill embolized conduits with water, or if embolized conduits are permanently lost. Through the direct observation of embolism via noninvasive methods, refilling under tension has been shown to be an artefact. However, xylem refilling upon rewatering remains uncertain. Lack of refilling upon rewatering in intact plants was found in leaves of a herbaceous grass (Johnson *et al.*, 2018) and stems of two woody species (L. Lamarque, University of Bordeaux, France; R. Rehschuh, Karlsruhe Institute of Technology, Germany), and it has been suggested to occur in silver birch (Y. Salmon, University of Helsinki, Finland). This suggests that xylem refilling upon rewatering may be possible in some species and plant organs but not in others.

The formation of new xylem every year plays a key role in plant responses to environmental cues, as a central process in stress acclimation (E. Ziaco, University of Nevada, Reno, USA; G. Battipaglia, University of Campania, Caserta, Italy) and recovery (J. Gričar, Slovenian Forestry Institute, Ljubljana, Slovenia). Growing areas of research on cambial activity and retrospective dendro-anatomy (i.e. the study of time series of wood anatomical traits) are expanding the time resolution of our analyses of xylem physiology, extending our understanding of how intra and interannual environmental variability affects the xylem hydraulic functioning.

Alongside hydraulic failure, carbon (C) starvation is an important factor contributing to plant damage during drought, and a combination of these processes has been proposed to result in a cascade of events that ultimately lead to plant mortality (N. G. McDowell, Pacific Northwest National Laboratory, Richland, WA, USA). The association between hydraulic failure and C starvation may be due to the role of carbohydrate supply for preventing and repairing xylem embolism, as well as the role of carbohydrates in regrowth following drought relief and osmotic regulation (McDowell *et al.*, 2019). The interplay of C and water dynamics is a novel frontier for plant physiologists, and novel techniques such as Raman spectroscopy (enabling the measurement of sucrose at the cellular level; J. Gersony, Harvard University, Cambridge, MA, USA) could help us better understand phenomena like drought-induced tree mortality.

Future directions of plant hydraulics

The plant hydraulic community is aware of climate change threats – see the manifesto signed by all conference participants in Cochard *et al.* (2019). Our ability to predict, and therefore mitigate, the negative effects of climate change in plants from both cultivated and natural systems relies on a deep and comprehensive knowledge of the plant hydraulic system as a whole. A better understanding of plant water relations is also critical for predicting the contribution of forest ecosystems to the global C and water cycles by implementing the information of plant hydraulics into climate models. To achieve this, several gaps in our understanding of basic plant functioning still need to be filled. Whereas most experimental plant hydraulic studies have been performed using potted plants under controlled environments, it is clear from XIM4 that our current understanding would benefit from experiments on plants in their natural environment. Such experiments would allow us to access the whole soil–plant–atmosphere continuum and the interaction between the different components of this continuum during drought. Robust studies in the field are also important in improving our ability to scale-up plant processes from the individual to the ecosystem level.

Significant recent progress has been made in developing new technologies to assess drought damage, understanding the traits associated with drought resistance and building a more holistic picture of plant resistance to drought. However, a number of important questions surrounding plant hydraulics have been highlighted at XIM4, such as the role of carbohydrate metabolism in drought physiology, the existence and importance of post-drought refilling, the intraspecific variation in plant hydraulic traits, and the interaction of different components of the soil–plant–atmosphere continuum. New tools and methodologies presented at XIM4 provide us with the opportunity to address some of these critical knowledge gaps to improve our understanding of plant biology with implications for industry and broader society in the face of global climate change.

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