Meetings

Plant hydraulics: new discoveries in the pipeline

Structure and Function of Plant Hydraulic Systems. A workshop at the Fullerton Arboretum, Fullerton, California, USA, March 2008

Increasing numbers of plant scientists are recognizing the importance of hydraulic design in determining plant function. Hydraulic design – which can be broadly defined as the functional properties of the plant vascular system – is a determinant not only of plant water balance but also of photosynthetic rates and ecological niche differentiation. Classic approaches (Tyree & Zimmermann, 2002) and newer concepts (Holbrook & Zwieniecki, 2005) are being applied to questions central to the evolution and ecology of plant species, ranging from organ to organism to ecosystem. A recent workshop held in southern California reflected diverse research programs but also highlighted a convergence of interest on key questions and promising approaches. Several breakout sessions focused on defining pressing questions of plant hydraulics and on addressing the critical need for standardization of practices for research on these topics.

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Xylem transport: resistance, redundancy and repair

The xylem of plants has three basic functions: transport of water and minerals; mechanical support; and storage (Fig. 1). The transport function of xylem has been an area of much interest for at least 25 yr and continues to attract attention.

Much of the research presented at the conference focused on cavitation resistance or avoidance, and how both properties are affected by xylem integration. Redundancy of transport conduits and of vascular bundles can confer safety, but increased numbers of xylem conduits may involve increased construction cost and may increase the probability of mortality, depending on the connectivity among conduits and the risk of runaway embolism or of damage (Ewers *et al.*, 2007; Sack *et al.*, 2008). A modular hydraulic system with limited connectivity among xylem conduits and/or vascular bundles is thought to enable plants to minimize the spread of emboli between vessels. The degree of hydraulic modularity vs integration will probably affect hydraulic efficiency, resistance to hydraulic failure, embolism repair, resistance to xylem pathogens, wound repair, root-to-shoot signaling, and hydraulic redistribution within root systems. A low degree of hydraulic integration (also referred to as sectoriality) appears to be an important design feature among arid land plants, especially in desert shrubs (Schenk, 1999). An unanswered question is whether the phloem can add another layer of redundancy and act as a pathway of water transport when the xylem is completely embolized as a result of drought or freeze–thaw stress. Hydraulic redundancy and connectivity emerged as common themes in the presentations of Susana Espino (California State University (CSU), Fullerton, USA), Frank Ewers (California State Polytechnic University, Pomona, USA), Peter Kitin (Oregon State University, USA), Lawren Sack (University of California, Los Angeles (UCLA)) and Jochen Schenk (CSU, Fullerton, USA).

Refilling of embolized conduits while the xylem is under considerable negative pressure has been shown in the stems and leaves of a few species (Bucci *et al.*, 2003; Hacke & Sperry, 2003; Salleo *et al.*, 2004). The process appears to involve living cells and to require energy. This mechanism may play an important role in the diurnal and seasonal dynamics of gas exchange and growth, and in drought responses. Yet, little is known about how widespread this process is, highlighting the need for more data from stems, leaves and roots of a wider variety of plant species. We also need to know whether refilling becomes more difficult in conduits that have previously suffered cavitation and that have a greater vulnerability to subsequent cavitation (Stiller & Sperry, 2002). Notably, refilling under tension may require phloem activity. If water that refills conduits comes from the phloem (Hölttä *et al.*, 2006), then we need to determine the pathways by which this 'Münch water' moves (cambium? rays?) and to clarify how this process is regulated alongside other phloem processes, including phloem loading and unloading and the movement of cations.

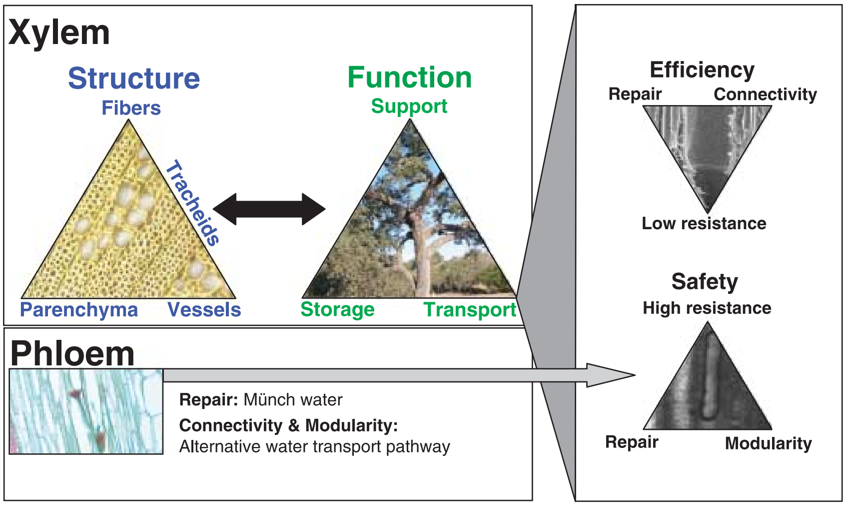

Fig. 1 Diagram of relationships between xylem structure and function with an emphasis on xylem transport safety and efficiency. Fibers and tracheids have a central role in structural support and may be important in resistance to cavitation (Jacobsen *et al*., 2005), parenchyma in storage and embolism repair (Salleo *et al*., 2004), and vessel and tracheids in efficient water transport and in providing redundancy to the transport system (Tyree & Zimmermann, 2002; Ewers *et al*., 2007). Münch water flowing between phloem and xylem has been hypothesized to play a role in embolism repair (Salleo *et al*., 2004; Hölttä *et al*., 2006), and may play a role in preventing embolisms, especially in species with abundant phloem parenchyma. Phloem may also act as a temporary pathway of water transport at the start of the growing season in completely embolized stems.

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Because cavitation is such a threat to sustained hydraulic transport, the question arose at the conference as to why plants would be filled with gas. Plants commonly have a large volume of gas spaces within their tissues, not only in intercellular spaces but also in fiber cells of vessel-bearing species (Utsumi *et al.*, 1998). Having gas-filled fibers adjacent to vessels under tension would seem to create a great risk of hydraulic failure. It may be that air-seeding in some species is a design feature of xylem that staves off vessel collapse, thus preventing permanent conduit failure and possibly enabling embolism repair. Abundant air in xylem would also help to provide adequate oxygen supply to parenchyma cells (Sorz & Heitz, 2006), which may in turn be active in embolism repair.

Xylem biomechanics

There are intense mechanical stresses on the xylem walls during transport of water under negative pressure. A number of mechanical traits have been correlated with cavitation resistance (e.g. vessel wall thickness to span ratio, fiber traits, xylem density, and modulus of elasticity and rupture of xylem), suggesting that transport stresses have been an important factor shaping xylem structure (Jacobsen *et al.*, 2005). Cynthia Jones (University of Connecticut, USA) presented work on several xylem structural traits and how they vary among plant groups and across transcontinental aridity transects. The specific functional relationships between xylem anatomy and transport stresses continue to be an active area of research. An important outstanding question is whether reversible bending of vessel walls plays an important role in air seeding. Several studies have shown that tracheids may collapse in gymnosperms (Cochard *et al.*, 2004), and there is anatomical evidence that vessels may also collapse (Schweingruber *et al.*, 2006). Thus, questions concerning transport-related biomechanics promise to be a fruitful avenue of future research.

Beyond stems: hydraulics of leaves, roots, flowers and fruits

Species can show dramatic differences in the properties of the terminal components of the hydraulic pathways – roots and leaves – with considerable impacts on plant function. The hydraulic function of roots and leaves were the subject of presentations by Jung-Eun Lee (UC Berkeley, USA), Gretchen North (Occidental College, CA, USA), Brandon Pratt (CSU, Bakersfield, USA) and Lawren Sack (UCLA, USA). Leaves and roots show diurnal rhythms as well as dynamic responses to light, temperature and water availability, and these responses require clarification. Unanswered questions related to both leaf and root hydraulics scale from the cell to the ecosystem, with a continued need to determine contributions to overall plant hydraulic resistance. Like leaves, roots present three pathways for water flow (i.e. transmembrane, apoplastic and symplastic), and research is needed to understand how these pathways help determine overall plant hydraulic resistance. Furthermore, information is needed on the relative hydraulic contributions of young vs old and shallow vs deep roots, as well as the hydraulic redistribution between roots in dry and wet soil.

The hydraulic properties of flowers and fruit are also of strong interest, with a particular goal of understanding how hydraulic pathways change during development and seasonally, as shown in presentations by Brendan Choat (UC Davis, USA) and Louis Santiago (UC Riverside, USA).

Ecology and phylogeny

The last 20 yr have seen tremendous advances in understanding hydraulic adaptations to the environment. Examples of this progress were clearly illustrated in three presentations: Anna Jacobsen (CSU, Bakersfield, USA) detailed how three California shrub communities are divergent in their hydraulic traits; Brandon Pratt (CSU, Bakersfield, USA) discussed links between hydraulics and life history type in seedlings; and Yasuhiro Utsumi (Kyushu University, Japan) showed that the hydraulic properties of adult shoots can differ strongly from those of resprout shoots, with implications for how plants respond to disturbance.

Adaptations in hydraulic design may differ considerably across plant lineages. For instance, the long-studied trade-off between xylem cavitation resistance and xylem transport efficiency varies in strength among lineages. Anna Jacobsen (CSU, Bakersfield, USA), Cynthia Jones (University of Connecticut, USA) and Lawren Sack (UCLA, USA) presented work on the divergences and convergences in hydraulic and anatomical traits in specific lineages. Comparative analyses continue to drive much hydraulics research, as shown in presentations on comparisons of urban trees (Heather McCarthy, UC Irvine, USA), conifers of different families (Jarmila Pittermann, UC Berkeley, USA), plants differing in wood density (Calvin Threat (CSU, Fullerton, USA) and C. Jones) and species of contrasting life history (Brandon Pratt, CSU, Bakerfield, USA). Incorporating phylogenetic analyses will help to highlight the evolutionary underpinnings of the observed trends.

A critical need for common protocols and standardized methods

Science moves most rapidly when the majority of researchers use similar methods and can easily and rapidly repeat and build upon each others' discoveries. However, in hydraulics research, there appears to be much diversity in the methods and specific protocols used for given types of measurements. There is an especially pressing need for a common toolbox of methods for hydraulic measurements to increase comparability of data sets, and a need for dissemination of standardized protocols, especially as researchers increasingly wish to compile large data sets for a systems-level approach to hydraulics across communities and climate types. The meeting participants resolved to develop a web repository of hydraulics protocols and will contact researchers around the world in creating this resource. With the increasing numbers of questions and approaches that bear on hydraulic design, common protocols and increased collaborations will lead to a stream of new discoveries from the pipeline.

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