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Meeting Report

Plant hydraulics as a central hub integrating plant and ecosystem function: meeting report for 'Emerging Frontiers in Plant Hydraulics' (Washington, DC, May 2015)

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ABSTRACT

Water plays a central role in plant biology and the efficiency of water transport throughout the plant affects both photosynthetic rate and growth, an influence that scales up deterministically to the productivity of terrestrial ecosystems. Moreover, hydraulic traits mediate the ways in which plants interact with their abiotic and biotic environment. At landscape to global scale, plant hydraulic traits are important in describing the function of ecological communities and ecosystems. Plant hydraulics is increasingly recognized as a central hub within a network by which plant biology is connected to palaeobiology, agronomy, climatology, forestry, community and ecosystem ecology and earth-system science. Such grand challenges as anticipating and mitigating the impacts of climate change, and improving the security and sustainability of our food supply rely on our fundamental knowledge of how water behaves in the cells, tissues, organs, bodies and diverse communities of plants. A workshop, 'Emerging Frontiers in Plant Hydraulics' supported by the National Science Foundation, was held in Washington DC, 2015 to promote open discussion of new ideas, controversies regarding measurements and analyses, and especially, the potential for expansion of up-scaled and down-scaled inter-disciplinary research, and the strengthening of connections between plant hydraulic research, allied fields and global modelling efforts.

Key-words: cavitation; drought; embolism; genomics; phloem; stomata; vascular pathogens; vascular transport; xylem.

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Water plays a central role in plant biology (Kramer & Boyer 1995) and the efficiency of water transport throughout the plant (i.e. 'plant hydraulics') affects both photosynthetic rate and growth, an influence that scales up deterministically to the productivity of terrestrial ecosystems (Jones 2014; Smith & Sperry 2014). Moreover, hydraulic traits mediate the ways in which plants interact with their abiotic (e.g. drought, temperature extremes) and biotic (e.g. pathogens, invasive species) environment (Anderegg & Callaway 2012; Choat *et al*. 2012; Jacobsen *et al*. 2012; Jactel *et al*. 2012; McDowell *et al*. 2013a; Urli *et al.* 2013). At landscape to global scale, plant hydraulic traits are important in describing the function of ecological communities and ecosystems (Choat *et al.* 2012; Gleason *et al.* 2015). Indeed, as a discipline, plant hydraulics is increasingly recognized as a central hub within a network by which plant biology is connected to palaeobiology, agronomy, climatology, forestry, community and ecosystem ecology and earth-system science. Such grand challenges as anticipating and mitigating the impacts of climate change, and improving the security and sustainability of our food supply rely on our fundamental knowledge of how water behaves in the cells, tissues, organs, bodies and diverse communities of plants (Table 1). A workshop entitled 'Emerging Frontiers in Plant Hydraulics' supported by the National Science Foundation, was held in Washington DC, 2015, over 2.5 days with 36 participants. The goal of the workshop was to promote open discussion of new ideas, controversies regarding measurements and analyses, and especially, the potential for expansion both of up-scaled and down-scaled inter-disciplinary research, and the strengthening of connections between plant hydraulic research, allied fields and global modelling efforts.

Previous workshops on hydraulics have facilitated or enabled breakthroughs or the dissemination of breakthroughs – for example the 2003 meeting at Harvard Forest (Holbrook & Zwieniecki 2005), the highly productive workshop, 'Structure and Function of Plant Hydraulic Systems' in Fullerton, CA in 2008 (Pratt *et al.* 2008), the Canadian Society of Plant Biologists Annual Meeting in Edmonton, Canada in 2012 (Hacke *et al.* 2012) and the International Workshop on Plant Hydraulic Techniques meeting in Ulm 2014 (Jansen *et al.* 2015). The need for such workshops underscores the bottleneck that continues to arise because of the lack of scientific exchange that would normally occur through a structure such as a national or international meeting attended by the many practitioners working in the field; for example, US researchers working in plant hydraulics are equally likely to attend the meetings of the American Society for Plant Biology, the Ecological Society of America, the Botanical Society of America, and the American Geophysical Union; analogous splitting of the research core occurs every year in the conferences in Europe and Australia. A Gordon Research Conference entitled 'Multi-Scale Plant Vascular Biology', meeting for the first time June 26 – July 1, 2016 (https://www.grc.org/programs.aspx?id=17277), should help to fill this gap.

The 2015 'Emerging Frontiers in Plant Hydraulics' workshop highlighted numerous areas for increased collaboration and inter-disciplinary and trans-disciplinary research. Firstly, the workshop clearly demonstrated that water transport within plants, as a key feature influencing the soil–plant–atmosphere continuum, is by its very nature an interdisciplinary topic, given that aspects of the pathway involve fundamental processes at the interfaces of physics, biochemistry, meteorology and physiology (Stroock *et al.* 2014). Water moves through the xylem under tension, and through a number of living tissues in the roots and leaves. All of these tissues exhibit features of anatomy (e.g. pits in xylem conduit walls) and/or molecular regulation (e.g. water channel proteins in the cell membranes) that allow the plant to respond to key environmental and physiological challenges (Chaumont & Tyerman 2014; Maurel *et al.* 2015). Physically, water transport relies on heat and mass transport through porous media in solid, liquid and vapour phases. The transport of water in the xylem is integrated with that of sugars in the phloem, and has subsequent feedbacks across carbon metabolism, allocation and storage (McDowell *et al.* 2011; Dietze *et al.* 2014). Plant water transport relies on physical and biochemical processes, and thus breakthroughs in physics and molecular biology both inform and extend our core understanding and capacity for making accurate measurements and contribute new methods of measurement and analysis (Prado & Maurel 2013; Stroock *et al.* 2014). The NSF Hydraulics 2015 workshop gathered researchers with primary foci on diverse aspects of the hydraulic system and its interfaces with other fields of science, including phloem function, ecological genomics, xylem pathology, plant physiology, ecology, hydrology and nanodesign. The invitees were selected based on centrality of water transport in their research programmes

Table 1. Centrality of the role of hydraulics in plant biology, ecology, evolution, palaeobiology and climate change

Topic	Recent publications
1. Woody plant responses to climate	Limousin *et al.* 2013; Sevanto *et al.* 2014; Anderegg 2015; De Kauwe *et al.* 2015; Dickman *et al.* 2015; Domec *et al.* 2015; Hartmann *et al.* 2015; Manzoni *et al.* 2015; Sperry & Love 2015; Ward *et al.* 2015
2. Species distributions and ecosystem function	Choat *et al.* 2012; Gleason *et al.* 2015; Nguyen *et al.* 2015; Pausas *et al.* 2015; Skelton *et al.* 2015
3. Prediction of photosynthetic productivity under contrasting environments	Osborne & Sack 2012; Mackay *et al.* 2015
4. Maximum tree and ecosystem height	Givnish *et al.* 2014; Klein *et al.* 2015
5. Reconstruction of paleo-climate, paleo-ecology and the evolution of plant lineages	Boyce & Leslie 2012; de Boer *et al.* 2012; Pittermann *et al.* 2012; Sack *et al.* 2012; Voelker *et al.* 2012; Feild & Brodribb 2013; Merkhofer *et al.* 2015
6. Plant pathogens, microbiomes and plant responses to infection	Gaylord *et al.* 2013; Pouzoulet *et al.* 2014; Romero *et al.* 2014; Reblin & Logan 2015
7. Increasing agricultural productivity (biomass yield and tolerance to salinity, flooding, freezing, heat, as well as drought)	Caldeira *et al.* 2014; Barrios-Masias *et al.* 2015; Borland *et al.* 2015; Miniussi *et al.* 2015; Moshelion *et al.* 2015
8. Biomimetic applications	Wheeler & Stroock 2008

Table 2. Current major controversies in plant hydraulics, where a controversy is defined as a problem that engendered debate among two or more scientific points of view and that remains unresolved, potentially because of a lack of a decisive theoretical framework or adequate information for a final decision

Topic	Current controversies and challenges	Recent publications (2013-)
1. Embolism of xylem and refilling	• Does xylem refilling under tension exist? If it exists, is it common or rare in given species or across species? If it exists, does it provide an advantage in tolerance or productivity? • Is there a publication bias for xylem refilling? • Are r-shaped stem or root hydraulic vulnerability curves real? • Can matching of lab and field data resolve controversies? Can vulnerability curves be matched with native percent loss of conductivity in the field? Do these datasets already exist? • Is it possible to develop a protocol to completely avoid artefacts across labs? • Are visualization methods (e.g. Fig. 1) more reliable than indirect hydraulic methods? What potential artefacts exist in modern visualization tools? e.g. can microCT distinguish air versus tyloses versus gels versus droplets; how can we best truth the visualization tools? • If we calibrate hydraulic methods against visualization, do we have to do it for every species or will a few dramatically different representative species suffice? How to know? • What resolution is needed among visualization and measurement tools that provide contrasting clues regarding embolism? e.g. microCT does not reveal the embolism suggested by certain methods, e.g. the cavitron. • Does embolism act as a signal or promote signalling for stomatal closure? • What are the energy costs of water transport and or embolism refilling? • What exactly is the role of hydraulic failure, and avoidance thereof, in drought-induced mortality?	Brodersen & McElrone 2013; Cochard *et al.* 2013; Zwieniecki *et al.* 2013, Choat B. *et al.*, 2016, Hacke *et al.* 2015b; Pratt *et al.* 2015; Tombesi *et al.* 2015, Torres-Ruiz *et al.* 2015
2. Important hydraulics traits	• What traits most strongly influence plant performance? What kills plants during drought? When is a plant dead? • What are the important plant traits (hydraulic vulnerability, capacitance of water storage, dormancy, lethal water potentials, compartmentalization, resprouting) that cause or predict plant mortality? • Which traits are best to characterize communities and ecosystems? • Which traits should be measured in model plant systems and for crop phenotyping? • How can we model the integrated function of individual and multiple traits? • Do different traits matter for different organs and life stages? • How important are tradeoffs?	Lachenbruch & McCulloh 2014; Reich 2014; Sevanto *et al.* 2014; Anderegg *et al.* 2015; Marechaux *et al.* 2015; Moshelion *et al.* 2015; Sperry & Love 2015
3. What are the roles of non-structural carbon compounds?	• What role do NSCs play, if any, in plant hydraulics, including embolism refilling? How important are NSCs for osmotic adjustment and drought resistance? Do NSCs influence drought-survival thresholds? • Does metabolic water from NSC hydrolysis play a role in localized water relations/refilling?	Dickman *et al.* 2015; Germino 2015; Hartmann 2015; Plavcová *et al.* 2016; Quentin *et al.* 2015; Woodruff *et al.* 2015
4. Are there clear categories of hydraulic responses and drought tolerance?	• Different ways to classify plant hydraulic strategies: water spender versus water saver, isohydric versus anisohydric, dehydration sensitive versus dehydration tolerant, and desiccation sensitive versus desiccation tolerant.	McDowell *et al.* 2013a; Martinez-Vilalta *et al.* 2014; Attia *et al.* 2015; Mencuccini *et al.* 2015; Pivovaroff *et al.* 2015; Skelton *et al.* 2015

NSC, non-structural carbon.

and included women and underrepresented minorities, as well as individuals from both research institutions and primarily undergraduate serving institutions.

Much emphasis was placed on designating and debating the key controversies and challenges in the field (Table 2), many of which revolve around methods. Work in plant hydraulics encompasses fundamental and newly developed approaches in bio-imaging, plant anatomy, computational models and lab measurements (Fig. 1), and includes both *in situ* and destructive approaches. Debate over methods has grown to include controversies concerning the conditions under which xylem embolism occurs, the methods to quantify the impact of water stress on xylem conductivity, and the mechanisms by which plants respond to and recover from drought (Cochard *et al.* 2013; McDowell *et al.* 2013b; Wheeler *et al.* 2013; Rockwell *et al.* 2014; Wang *et al.* 2014; Hacke *et al.* 2015b; Jansen *et al.* 2015; Torres-Ruiz *et al.* 2015). Other controversies in the field are related to the application of hydraulics in understanding a range of other processes, such as expansive growth and storage, especially of carbon, within plant hydraulic tissues and their role in drought mortality and recovery (Dietze *et al.* 2014; Hartmann 2015; Quentin *et al.* 2015). These issues are not merely technical in nature; they have the potential to transform our current understanding of the stability of water under tension in the xylem, the conditions under which embolism can be reversed, and thus the water-use, productivity and survival of plants both in well-watered soil and during progressive drought.

The participants affirmed that the structural and physiological diversity of plants necessitates a diversity of approaches and techniques, but that all methods must continually be examined for bias and artefact. One suggestion was for studies to be more transparent and comprehensive in reporting the details of their experimental methods, something that should be achievable in the age of on-line supplemental materials. A second proposal was to develop protocol resources for given measurements that would facilitate reporting of approaches and methodologies (Sack *et al.* 2010). Several felt that such resources could reduce the rejection of papers or grant proposals on the basis of methodology, as reviewers might recognize that given the explicit details, future researchers could account for imperfect methods in interpreting the results and conducting future meta-analyses.

The workshop equally focused on new research frontiers (Table 3), including next steps and potential solutions to address methodological challenges listed in Table 2. Additionally, workshop sessions identified areas for productive collaboration between plant hydraulics and other fields (e.g. disease ecology, ecological genomics, ecohydrology and climate change). Here the relevant questions are not only where the productive interfaces among fields lie, but also the issue of scaling hydraulic measurements, typically made on only small portions of a plant, to processes relevant for the whole plant, coordinated plant-soil systems and complex watersheds in their natural ecological or agricultural context, and in using plant hydraulics to inform models of ecosystem and Earth system processes (Mackay *et al.* 2015; Sperry & Love 2015). Detailed discussions focused on the value of understanding the molecular and genetic mechanisms driving plant hydraulics and how to utilize genomic tools such as transcriptomics, genome wide association studies and candidate gene analysis to further our understanding of plant function (Chory *et al.* 2000). Of particular

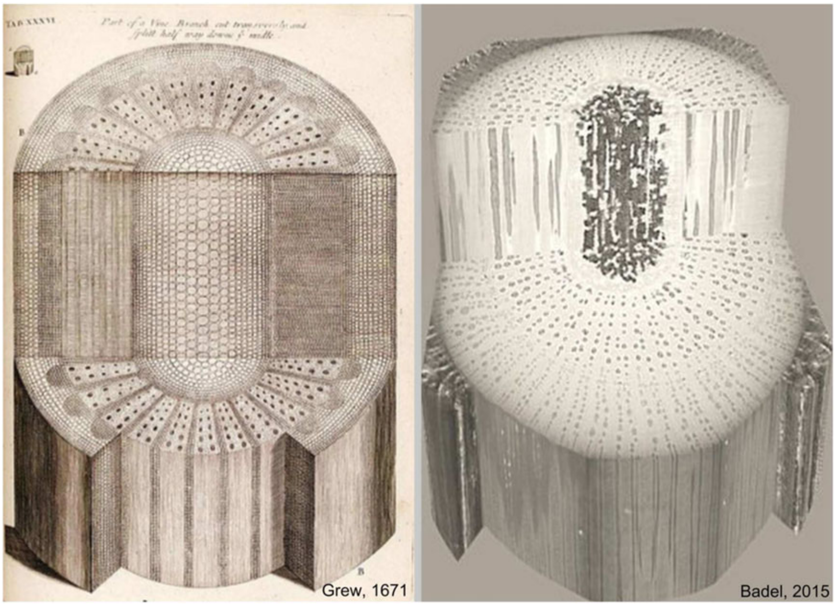

Figure 1. New technologies are revolutionizing the field of plant hydraulics, including non-invasive imaging (e.g. nuclear magnetic resonance imaging and X-ray micro-tomography); while both panels show the cross-sectional anatomy of the stem of *Vitis*, featuring the xylem, the left panel shows a painstaking illustration based on light microscopy (Grew 1671), while the right panel shows a micro-tomographic image taken in 2015, *in vivo*, and faithfully documents the three-dimensional organization of the xylem network, but also reveals the functional status of the plant, where darker, air-filled vessels can be clearly distinguished from their water-filled, functional counterparts (Badel, pers. comm). These images highlight an important turning point in our understanding plant water transport and are an example of the emerging tools available for validating methodologies and longstanding hypotheses. Picture credit: Eric Badel.

Table 3. Emerging frontiers in plant hydraulic transport

Topic	Specific opportunities and frontiers	Recent publications (2013-)
1. New visualization and sensor methods	• New imaging methods, including synchrotron-based micro computed tomography • Can best practices and visualization techniques (e.g. microCT) eliminate long-standing controversies regarding apparently conflicting results? • How do we reduce the error in whole tree transpiration and conductance estimates based on sapflow? • Need to recognize wide opportunities, especially for bio-inspired engineering of novel sensors which do not currently exist, e.g. for imaging flow rates *in vivo*, or sensing turgor in cells, such as mechano-osmotic sensor from *E. coli*	Brodersen *et al.* 2013; Cochard *et al.* 2013; Coates *et al.* 2015; Cochard *et al.* 2015
2. Application of hydraulics in whole plant models, climate models, DGVMs	• What is a realistic representation of hydraulics in models of plant growth, and in ecosystem function and earth models, especially for predicting effects of climate change? • How do hydraulics determine rates of photosynthetic productivity? • Links to development (structure and function), across multiple organs, across organisms and scaled up (temporal and developmentally), • Apply hydraulic principles/issues to conservation/restoration and ecohydrology • What are the feedbacks and interactions between available carbohydrates and hydraulics? • How do hydraulics influence stomatal behaviour? • How to account for large variation in anatomy and function within given organs and individuals? (e.g. large variation in vessel diameter even within poplar) • How can hydraulics and xylem-phloem interactions contribute to simulated global fluxes, productivity and survival? • How do hydraulic traits vary under different growth environments? • What are the important climate traits to characterize hydraulic response?	Duan *et al.* 2014; De Kauwe *et al.* 2015; Givnish *et al.* 2014; Holtta *et al.* 2015; Mackay *et al.* 2015; Skelton *et al.* 2015; Sperry & Love 2015
3. Methodology, best practices needed, standard spreadsheets	• Need to partner labs to resolve methods issues. • Need for best practices, methods repository, improved terminology, standardized units and a plant hydraulics handbook • How can NSCs be measured in a standard way? Can they be measured accurately? • Stem vulnerability: presenting PLC in absolute versus relative terms; cavitron versus standard centrifuge; initial sample preparation, such as cutting under tension ('Wheeler effect') and flushing before measuring v-curves; accounting for variability among stems and seasonal effects; measurement details, such as time of adjustment, repeated cutting, eliminating wounding effects. Can hydraulic phenomena be investigated in cut or excised plant parts to represent those in intact plants? • What potential artefacts exist in modern visualization tools? e.g. can microCT distinguish air versus tyloses versus gels versus droplets? • Methods comparisons are needed. Challenges—high biodiversity, time consuming measures, general acceptance of methods	http://prometheuswiki.publish.csiro.au/Cochard *et al.* 2013; Perez-Harguindeguy *et al.* 2013; Hacke *et al.* 2015b; Torres-Ruiz *et al.* 2015
4. Genomic basis for hydraulics traits and their impact on plant performance	• The genomic basis for xylem structure and function within and across species for improving drought tolerance, and crop improvement.	Cobb *et al.* 2013; Sengupta & Majumder 2014

(*Continues*)

Table 3. (Continued)

Topic	Specific opportunities and frontiers	Recent publications (2013-)
	• Applications of reverse genetics; genome editing; forward genetics, QTL and GWAS to determine the network of genes controlling hydraulic traits • Genotyping-phenotyping projects require rapid proxies for hydraulic conductivity and vulnerability and water status.	
5. Leaf and root hydraulics	• Clarifying the hydraulic pathways through organs that include xylem and living tissue pathways, and vapour versus liquid phase transport • Determining the functional roles of anatomical variation and response of individual tissues to water status • Clarifying the roles and dynamics of aquaporins in various tissues • Root hydraulics. How important are deep versus shallow roots? • Leaf hydraulic vulnerability: do the different methods measure the same pathways?	Prado & Maurel 2013; Scoffoni *et al.* 2014; Bouche *et al.* 2015; Buckley *et al.* 2015; Maurel *et al.* 2015
6. Drought tolerance	• What traits determine the response of photosynthesis, whole plant carbon balance and survival during droughts? • Impact of resource availability on the structure and function of water transport tissues • What are the tipping points for failure of the hydraulic system?	Sevanto 2014; Woodruff 2014; Pivovaroff *et al.* 2015
7. Mechanism of water transport in xylem given diverse and complex anatomy; integration of xylem with living parenchyma and phloem	• How do surfactants act to stabilize nanobubbles? Does a plant actually need to remove embolism on a fast time scale to survive? • CO_2 and ion permeation of aquaporins • The hydraulic architecture of the xylem and phloem and their developmental and functional interdependence and co-evolution • Interactions between xylem and phloem under different environmental conditions and in different organs (e.g. fruit, flowers and roots) • How does wood anatomy determine vulnerability to embolism? How does wood parenchyma act to promote or protect from embolism? • Integration of water transport system through all organs in the plant • Parenchyma: temporal dynamics of carbon storage (minutes to years) • Developmental determinants of hydraulic networks • ABA influence on stomata and/or on aquaporins in vascular parenchyma • Hydraulic capacitance, role of parenchyma and phloem in plant defence and resilience to disturbance • Are the mechanisms of embolism initiation (i.e. first conduits to embolize) and embolism spread the same? Do conduits embolize in isolation (i.e. no adjacent air filled vessels)? Can parenchyma cells act as a source of air seeds? • Xylem-phloem interactions in relation to behaviour of cambium/meristems	Chaumont & Tyerman 2014; Hacke *et al.* 2015a; Jansen & Schenk 2015; Rolland *et al.* 2015; Zwieniecki & Secchi 2015; Morris *et al.* 2016; Savage *et al.* 2016
8. Plant interactions with other organisms; water relations	• Applications of plant hydraulics for entomologists, pathologists, microbial biologists given that plant water relations influences susceptibility to herbivores and pathogens • Effects of plant hydraulics on the microbiome – plant host relationship	Gaylord *et al.* 2013; Pouzoulet *et al.* 2014
9. Evolution and comparative methods; diversity within individuals and across species and communities	• Clarifying the role of hydraulics in community ecology, including trait-based ecology and resource-use spectra	Charrier *et al.* 2014; Liu *et al.* 2015; Nguyen *et al.* 2015

(*Continues*)

Table 3. (Continued)

Topic	Specific opportunities and frontiers	Recent publications (2013-)
	• Embrace diversity of the ways that plants have evolved to survive in different environments, integrating physiology with models. • Clarifying the range of responses of species within communities • The interactive role of hydraulics with tolerance of other stresses, such as freezing and wildfires and other disturbances • The variation of hydraulics across life forms and diverse lineages and diverse ecosystems • Evolution of plant hydraulic systems.	
10. How can we leverage our knowledge of hydraulics to train others within the field and outside the field, especially to address climate change and to communicate what we do?	• Need for improved communication between scientists. • How can we teach non-traditional audiences about the importance of plant hydraulics (other fields, students, public)? • Collaborations with modellers • Teaching and outreach (videos with tools), high school videos, workshops for teachers, public outreach, modules for practical education.	Schon *et al.* 2015http://www.learnnc.org/?homehttps://www.youtube.com/watch?v=BickMFHAZR0https://www.youtube.com/user/crashcoursehttps://www.youtube.com/user/scishow

ABA, abscisic acid; DGVMs, dynamic global vegetation models; *E.coli*, *Escherichia coli*; GWAS, Genome wide association studies; microCT, X-ray Micro-tomography; NSC, non-structural carbon; PLC, percentage loss of conductivity; QTL, quantitative trait locus.

interest was identifying empirical methodologies such as gene expression analyses or gene knockouts that might expand our understanding of hydraulic mechanisms. Participants also discussed the need to expand the use of isotopic labelling techniques to understand better the rate and direction of water movement among plant tissues.

The outcomes of this workshop were organizational and community building in nature, and were immediately productive in setting out future papers, projects and grant proposals. The group resolved to co-author a paper in 2016 establishing important questions in the field and a framework or roadmap for future research in the field, as has been done for some applications of plant hydraulics research (McDowell *et al.* 2015) and more broadly for other specific fields or topics in plant biology (e.g. Yang *et al.* 2015). A review is needed of the points of consensus and controversy on the frontiers of the field, and the applications of this research in agriculture, biological conservation, resource management and ecosystem response to climate change. Further, the group began planning for the development of a research collaboration network, and, equally important, training workshops in ecological physiology (e.g. PHYS-Fest http://www.k-state.edu/ecophyslab/phys_fest.html). It is critical that students can be inspired by the importance and centrality of plant hydraulics, despite the rigorous methodology and open controversies. The Gordon Research Conferences will be locations for further development of these plans.

The workshop made clear the need for continuous emerging discussion and agreement on grand challenges, to promote full understanding of plant water transport and its implications – from genes through proteins to whole plant to ecosystems to biomimetic applications.

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