Meetings

New research on plant–water relations examines the molecular, structural, and physiological mechanisms of plant responses to their environment

Canadian Society of Plant Biologists Annual Meeting in Edmonton, AB, Canada, June 2012

Water availability impacts the health and productivity of both managed and natural ecosystems, and, in the light of global climate change, it is becoming increasingly important to better understand the physiological and molecular aspects of how plants respond to water stress. Water availability is often a limiting factor for the productivity of crops and the growth and survival of plantation trees. As evidenced in hybrid poplar plantations, fast growth of plants is often associated with high water demand, but this comes at the cost of increased sensitivity to drought (Silim *et al.*, 2009). Numerous recent reports have described forest productivity declines and tree mortality from drought (Allen *et al.*, 2010; Anderegg *et al.*, 2012). Increasingly erratic climate associated with global change also makes agricultural productivity less predictable (Reynolds *et al.*, 2009). At the recent annual meeting of the Canadian Society of Plant Biologists (CSPB), several speakers in the water relations sessions focused on these issues. They agreed that there is a critical need for synthesis of water relations research at the molecular, organ, organismal, community, and ecosystem scales. Research across these different scales is also essential to improve our understanding of plant responses to water deficit stress.

A diversity of approaches

Because of the importance of water in biological processes at scales from molecules to ecosystems (Kramer & Boyer, 1995), plant–water relations have long been an important area of research. Additionally, water is required by all plants, but the requirements vary across growth forms, taxonomic groups, habitat, and even by plant part. Thus, there is much to be learned from interspecific comparisons of functionally divergent species in addition to mechanistic studies of model organisms.

In recent years, considerable effort has been placed on understanding the molecular aspects of plant–water transport. Much has been learned about how plants regulate water transport quickly and effectively at the cellular level (Maurel *et al.*, 2008; Lee *et al.*, 2012). Future challenges will be to understand the significance of water transport regulation at the whole plant level (Fig. 1, 'Scale'), and to apply this knowledge across a wide range of plants and environments (Fig. 1, 'System'). While *Arabidopsis* or rice may offer model systems for studies of water relations in herbaceous plants, there are unique challenges to the study of water transport in large trees. For example, it is clear that among long-lived woody plants, size and age related changes affect function (Domec *et al.*, 2009; Lachenbruch *et al.*, 2011). Moreover, the environment of seedlings may be very different from adults leading to greater demands on functional plasticity (Poorter, 2007). The woody growth habit also diverges from the herbaceous one in having different transport, biomechanical, storage, reproductive, stress tolerance, and damage repair demands.

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At the sub-organismal level, research examined the integrated function and regulation of water channel proteins (aquaporins) (Christophe Maurel, CNRS-INRA, France, France; Joan Laur, Uwe Hacke, and Seong Hee Lee (all University of Alberta, Canada)). Other papers examined the structure and function of xylem both within and between plant organs and across different woody plant developmental stages (Barbara Lachenbruch, Oregon State University, USA; Anna Jacobsen and Brandon Pratt (both California State University, Bakersfield, USA); Lenka Plavcová, University of Alberta, Canada).

At the organismal level, considerable research effort focused on the importance of plant growth response and performance within managed forest systems. Poplars are cultivated in Canada as fiber sources and may be used for other applications in the future. Since hybrid poplars are generally regarded as drought sensitive, there is interest in identifying maker traits and candidate genes for drought tolerance breeding. This broad research topic was examined using multiple scales and approaches including anatomical, physiological, and molecular (Maria Equiza, Kelsey Ayton, and Lenka Plavcová (all University of Alberta, Canada); Muhammad Arshad, Simon Fraser University, Canada). Breeding poplars for increased drought tolerance will likely come at the cost of reduced growth and future studies will need to identify these

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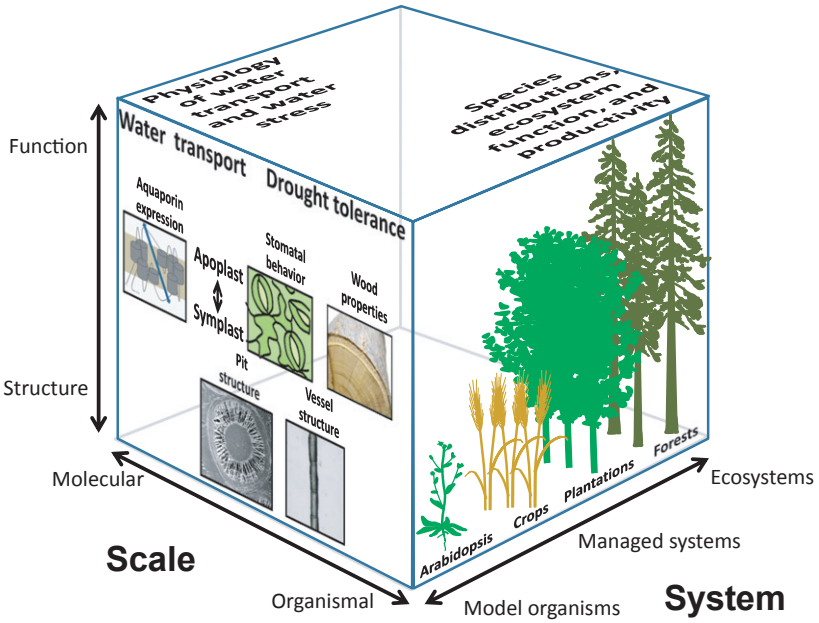

Fig. 1 Future progress in understanding plant responses to water stress requires research across multiple scales (molecular to organismal), in different fields of specialty (structure and function), and across different systems including the use of model organisms, managed systems, and whole ecosystems. Each of these areas as well as the connections between them, where discussed in several oral papers and plenaries presented in the Water Relations sessions at the 2012 meeting of the Canadian Society of Plant Biologists (CSPB). Illustrations of these diverse approaches are shown, including examination of water flow through membranes facilitated by aquaporins ('Scale' face; aquaporin illustration courtesy of Joan Laur). How these water channels are regulated has been studied in *Arabidopsis,* poplar, and other model organisms ('System' face). On its way from roots to leaves, water flows through living cells and xylem. Transport in the xylem is affected by pit and vessel structure ('Scale' face; torus-margo pit image courtesy of Lenka Plavcová; vessel cast image courtesy of Anna Jacobsen). A mechanistic understanding of water transport at molecular to organismal scales can help to predict stomatal behavior and water use in managed systems and ecosystems ('System' face).

costs in order to maximize success of selective breeding/bioengineering programs.

Similar efforts are underway in food crops. Wheat provides approximately one-fifth of the total calorific input of the World's population (Reynolds *et al.*, 2009). While global demand for cereals like wheat is projected to increase rapidly, production is challenged by the consequences of climate change and other factors. Matthew Reynolds (CIMMYT, Mexico) explained how physiological traits are used in breeding programs designed to generate drought-adapted wheat lines. He also emphasized that high throughput phenotyping methods are needed, and how airborne remote sensing can be applied in selection. Two other talks were on stress responses of cereals (Maciej Grzesiak, PAS, Poland; Uwe Hacke, University of Alberta, Canada).

Making broad connections

The question of how plants cope with water shortage applies to crops and trees alike, and water stress impacts range from the cellular to ecosystem levels. Because of the broad range of fields, areas of specialty, study organisms, and regions that are encompassed within this research topic, it has become increasingly clear that the scientific progress will ultimately depend on cross-disciplinary research. Connections across scale and specialty (e.g. anatomy, physiology, molecular and developmental biology) are difficult to realize, but when successful, they undoubtedly can provide novel insights. We feel that the water relations sessions at the CSPB meeting could provide a starting point for such efforts. The three talks presented during the Plenary Session on Water Relations (by Christophe Maurel, CNRS-INRA, France; Matthew Reynolds, CIMMYT, Mexico; Barbara Lachenbruch, Oregon State University, USA) provided a model exemplar, with topics ranging from aquaporin-mediated water flow in *Arabidopsis* to water transport in the stems of giant conifers. In the former case, it was shown how auxin-dependent regulation of aquaporins determines a novel role for these proteins in secondary root emergence, thereby providing an original example of hydraulic control of growth in plants (Péret *et al.*, 2012). In the latter case, the multi-scale effects of anatomy in forest trees were shown to affect plant–water relations as well as wood quality.

Although these topics are typically studied separately (because of the inherent complexity of each system), the fact remains that water moves through living tissue as well as xylem conduits. Because of this, neither component can be neglected, and either system may become limiting, depending on species and environmental conditions. The hydraulic properties of leaves, for instance, are determined by both vascular (xylem) and extravascular pathways. While the former pathway is subject to cavitation under drought conditions, as shown in rice (U. Hacke; Stiller *et al.*, 2005), the latter pathway is controlled by light-dependent aquaporin phosphorylation in the veins of *Arabidopsis* leaves (Christophe Maurel, CNRS-INRA, France). Thus, basic research on both aquaporins

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and xylem properties points to traits that are related to efficient water transport and drought tolerance. Such knowledge may ultimately be used in breeding programs.

Several presenters discussed the impact of root or stem hydraulics on whole plant function, highlighting the need for water transport within plants to be understood at the organismal scale (Fig. 1, 'Scale'). Water molecules move through roots, stems, and leaves and we ultimately need to integrate these findings into whole plant models that would incorporate aquaporin-mediated transport through living tissues and realistic models of xylem transport (e.g. Pratt *et al.*, 2010). Ultimately, these approaches can be extended to the entire soil–plant–atmosphere continuum (Sperry *et al.*, 1998).

All these efforts would benefit from a better understanding of functional plant anatomy and whole-plant physiology (Fig. 1, structure–function axis). In the new era of whole genome sequencing, well-trained plant anatomists and eco-physiologists are still (or perhaps more than ever) expected to provide crucial contributions to this field (Tyree, 2003). We also need well-trained people and effective methods for high throughput phenotyping to keep up with advances in genomics technology.

Open questions

Of the many questions that remain unanswered, there are some that stand out as being both important for advancement of the current state of knowledge and that also have potential to be readily answered through future research and inter-disciplinary collaborations. Many of these topics were important themes of the 2012 CSPB meeting.

Scaling from molecules to whole plant function

We clearly need to better understand how aquaporins are regulated (Christophe Maurel, CNRS-INRA, France; Joan Laur and Song Hee Lee (both University of Alberta, Canada)) and how their function relates to whole-plant–water relations (Fig. 1, 'Scale'). The use of a wider range of plant species in aquaporin research is likely to enrich our understanding of the role of cell membranes in plant–water relations. While data from three model species were presented (*Arabidopsis*, rice, and poplar), key insights will likely be gained by studying species representing a wider range of growth forms and water use strategies. Such work may reveal similarities in fundamental aspects of aquaporin regulation at molecular and cellular levels. However, due to differences between small herbaceous plants and large trees, we expect that some of the physiological findings from *Arabidopsis* may not directly apply to larger woody plants.

Examination of plant structure and function across multiple scales

Developing a more comprehensive understanding of xylem anatomy and development will likely be required to understand how whole plants function (Barbara Lachenbruch, Oregon State University, USA; Anna Jacobsen, California State University, Bakersfield, USA). Plant anatomy remains a critical area of research, and knowledge of plant structure is important in understanding plant function (Fig. 1, structure–function axis). This has implications at the cellular level, where anatomical analysis is a crucial step in localization of gene expression as well as the scale of organisms. Additionally, anatomical measures used in combination with functional measures may help us to resolve current debates within the field of xylem hydraulics (Choat *et al.*, 2010; Jacobsen & Pratt, 2012; Sperry *et al.*, 2012). Increased knowledge of vessel length in different species and plant organs may be particularly important to studies of plant hydraulics.

Developmental variation and phenotypic plasticity

Plant structure and function are not static and change over the course of plant development (see earlier) or in response to environmental changes (Lachenbruch *et al.*, 2011). New research suggests that poplars exhibit large phenotypic changes and that their xylem is highly plastic (Lenka Plavcová, University of Alberta, Canada). More work is necessary to assess limits of plasticity and how phenotypic responses are mediated at the molecular level (Plavcová *et al.*, 2012). Such knowledge could also be important in breeding programs, assuming that genotypes with great potential for acclimation will better be able to cope with environmental stress and climate change than genotypes that lack acclimation potential.

The use of physiological traits in plant breeding

Research aimed at identifying candidate genes for drought tolerance breeding is promising, but much work remains to test the hypotheses (including those not directly related to plant hydraulics) that are being generated by such studies. In trees, it will also be crucial to see if wood properties can be modified (e.g. reduced lignin content) without compromising hydraulic conductivity, vascular integrity, and tree growth (Coleman *et al.*, 2008; Voelker *et al.*, 2011).

A call for interdisciplinary collaboration

Water relations has been, and will continue to be, a field of intense interest. Many researchers from broadly divergent specific disciplines appear to have converged on similar research questions, including the response of plants to water stress. Progress on this important research question requires the synthesis of information gathered from multiple scales, species, and specialties. As we look to the future of this field and the CSPB, the greatest scientific advancement will likely stem from increased collaboration of researchers working across these scales.

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