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From aquaporin to ecosystem: Plants in the water cycle☆

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ABSTRACT

Vascular plants are major intermediaries in the global water cycle, and are highly adapted to both facilitate and resist water fluxes, such as during root uptake, translocation in the xylem, and transpiration by leaves. Here, we summarize the contributions to a Special Issue on water in the *Journal of Plant Physiology*, which cluster around the theme of control and facilitation of water movement in plants. We conclude with an editorial view of the need for plant physiologists to consider larger cultural issues surrounding water use, especially in terms of the increasing agricultural demand for water to produce animal feed, with its associated trophic nutritive losses and environmental damage.

Life as we know it would not be possible without water. It is by far the most abundant molecule in living cells, and the medium in which all biochemical activity takes place. In the case of terrestrial plants, water is additionally required for the generation of cell turgor, turgor-driven growth, nastic movements, anatomical and morphological patterns, solute flow, and the stabilization of temperature (Damm et al., 2018). Plants are an intrinsic, and massive, part of the global water cycle, with transpirational water flux exceeding evaporation on land by as much as ten to one. As part of this cycle, they possess numerous pathways through which the movement of water can be conducted, and, conversely, many means by which it can be restricted.

In this Special Issue of the *Journal of Plant Physiology*, we present a group of reviews and original papers that span a wide range of research areas, but cluster, with one exception, around a common theme: facilitation of, and control over, water movement in plants. Such facilitation and control occur at many scales, from that of aquaporin proteins, reviewed here in terms of their function under hypoxic conditions by Tan et al. (2018), to that perceived via remote sensing, as discussed by Damm et al. (2018), who emphasize the importance of combining observation with mechanistic models of vegetation-driven water movements. Between these micro- and macro- levels of observation, we present three ground-breaking studies on the transfer of water from soil to atmosphere via plants, at organ and organism levels of structure and function (Meunier et al., 2018; Sundgren et al., 2018; Plavcová et al., 2018).

Plants can also maintain internal water and ion homeostases by exerting resistances *against* water flow, for example via the production and deposition of hydrophobic materials. Crucial among these are the waxes within and surrounding leaf cuticles, as discussed by Zeisler-Diehl et al. (2018), and the suberin lamellae that restrict apoplastic water flow in roots, a subject reviewed by Kreszies et al. (2018). Under flooded conditions, roots can restrict water uptake through anatomical changes, such as reductions in stele diameter, as shown by Sundgren et al. (2018) in wheat seedlings.

The Special Issue is rounded out by a review by Challabathula et al. (2018) on resurrection plants, a phylogenetically diverse group that can survive desiccation and a loss of 90% of cellular water. This is achieved, in part, by deactivating photosynthesis or even degrading the photosynthetic apparatus for later re-building. In this case, such extremophiles cope with a vanishingly small water flux by assuming a dormant state, not unlike the strategy found in some animal extremophiles, such as members of the Tardigrada (Boothby et al., 2017).

While the pure science of plant-water relations is a fascinating realm of inquiry, much study in this area is focused, as it should be, on the discovery of practical solutions to water-limited plant growth and productivity, particularly in agricultural settings. In 2015, The World Economic Forum listed water scarcity as the largest global risk in terms of potential impact, and it is estimated that nearly two-thirds of the world's human population ($\sim$ 4 billion people) live with severe water scarcity for at least one month of every year (Mekonnen and Hoekstra, 2016). This trend is aggravated by starkly dropping groundwater tables in many regions of the world, such as the North China Plain (Wang et al., 2008; Rodell et al., 2018), and changing climate patterns that, depending on locale, have already brought about both more intense drought and more intense flooding (Trenberth et al., 2003; Huntington, 2006).

Among our many roles as plant biologists, we are called upon to apply our knowledge of the inner workings of plant life to help improve crop productivity under drought and other stresses, while also preserving environmental integrity. Progress is clearly being made in the development of genotypes resistant to water stress or equipped with improved water-use efficiencies (Fang and Xiong, 2015; Todaka et al.,

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2015). However, it is necessary to also take a broader societal perspective and consider that, while more than two-thirds of freshwater withdrawals, and 90% of overall water consumption for all human uses globally, are for crop irrigation (West et al., 2014; Pore and Nemecek, 2018), the majority of crop production today, especially when calculated on a protein basis (Cassidy et al., 2013; West et al., 2014), does not go directly to feeding humans without trophic losses; rather, it is inefficiently made available by supporting animal agriculture and meat production. This entails, even in cases of relatively low-impact animal products, significant environmental costs not just in terms of water consumption, but also in terms of greenhouse gas emissions, eutrophication, terrestrial acidification, and land use (Pore and Nemecek, 2018). Crop plants differ greatly in water consumption per kg biomass produced, with root crops such as potato being especially economical (< 300 L/kg), while rice and soybean are especially water-demanding (~2,000–2,500 L/kg); all, however, are eclipsed, by one to two orders of magnitude, by many forms of livestock production, especially that of beef and lamb. Water used for beef production, nearly all in the service of rearing of crops for cattle feed, varies from 11,000 L/kg in Japan to 37,800 in Mexico (Hoekstra and Chapagain, 2007). Thus, while the development of water-use-efficient and drought-resistant plant genotypes and methods of cultivation will remain a critical focus for plant physiologists in the coming years, we must not fail to acknowledge that significant protection against the threat of more widespread water scarcity globally would be achieved by a reduction of the heavy reliance on animal products for human sustenance. Without such adjustment, progress from our combined efforts toward the improvement of water-use efficiencies of crops will continue to be eroded by cultural practice.

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Dev T. Britto, Herbert J. Kronzucker*

School of Agriculture and Food, Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, Parkville, Victoria 3010, Australia

E-mail address: herbert.kronzucker@unimelb.edu.au

* Corresponding author.