Bringing Anatomy Back into the Equation

There is more than metaphorical appeal to the thought that humanity feeds off the sweat of vascular plants. This statement has factual grounds in the sense that plant water loss by transpiration is an inevitable companion to the photosynthetic process that nourishes the human population. A fascinating corollary of this linkage between water and carbon is that leaf productivity in well-watered plants is constrained by the efficiency with which the plant vascular system can deliver water to the sites of photosynthetic gas exchange in leaves. Plant history shows us that species with a high capacity for transporting water have prevailed over less efficient predecessors (Raven, 1977), and this trajectory is particularly evident in studies of the evolution of angiosperm leaf vascular systems (Boyce et al., 2009).

The realization that leaf water transport efficiency constitutes a fundamental governor on plant productivity (Brodribb et al., 2007) emphasizes an important new challenge in plant biology: to quantify the role of leaf anatomy in setting the limits of water transport. Different studies have pointed to the branching density of water-delivering minor veins as the primary determinant of water transport efficiency in leaves (Sack and Holbrook, 2006), an understandable connection given that these nonliving tubes of the xylem provide an efficient shortcut through the very resistive leaf mesophyll tissue. However, the slow hydraulic pathway through living tissue between the veins and stomata has also attracted attention as an additional source of variation in water transport properties among leaves of different species. Anatomical structures such as leaf sclereids (Fig. 1) and bundle sheath extension cells have been suggested as adaptations to increase water movement outside the xylem (Wylie, 1943; Foster, 1947), while others have proposed that aquaporin expression can dynamically regulate the flow pathway from veins to stomata (Prado et al., 2013). Most recently, the results from two independent modeling studies indicate that water can be transported within the leaf in vapor phase as well as liquid phase (Rockwell et al., 2014; Buckley, 2015), adding a new dimension to the interaction of leaf tissue organization and water transport efficiency.

This exciting atmosphere of conceptual evolution in the science of leaf water transport has created the need for models that can be used to evaluate the relative importance of various leaf structural influences on water transport efficiency. An article in this edition of *Plant Physiology* (Buckley et al., 2015) addresses this issue by parameterizing a new three-dimensional model of water flow in leaves, with data from a small group of common dicot species, to examine how core features of leaf anatomy affect the theoretical water transport capacity of leaves of different species. This study clearly illustrates the importance of minor vein density as the principal limiter of leaf water transport capacity, but it also highlights the influence of cell wall thickness, tissue density, and mesophyll arrangement on the steepness of the pressure gradient from veins to stomata. By formulating a theoretical framework that incorporates meaningful leaf structural variables, the model provides a new opportunity to examine the adaptive significance, in terms of water transport, of recurrent patterns of leaf organization that occur in vascular plants.

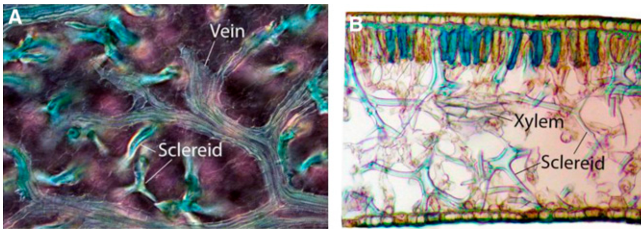

Figure 1. Foliar sclereids, seen as blue-staining cells in paradermal (A) and transverse (B) sections of *Alloxylon* spp. (Proteaceae) leaves, connect the minor veins with other tissues in the leaf. Thick-walled sclereids are observed in many species, and they often appear to be involved in conducting water outside the xylem through the leaf mesophyll.

Timothy J. Brodribb*
Department of Biological Science,
University of Tasmania, Hobart,
Tasmania 7001, Australia

*Address correspondence to timothyb@utas.edu.au.
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