



Commentary

Let's not forget the critical role of surface tension in xylem water relations

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Received March 25, 2011; accepted March 30, 2011; handling Editor Danielle Way

The widely supported cohesion–tension theory of water transport explains the importance of a continuous water column and the mechanism of long-distance ascent of sap in plants (Dixon 1914, Tyree 2003, Angeles et al. 2004). The evaporation of water from the surfaces of mesophyll cells causes the air–water interface to retreat into the cellulose matrix of the plant cell wall because the cohesion forces between water molecules are stronger than their attraction to air. As a result, the interface between the gas and liquid phases places the mass of water under negative pressure (tension). This pulling force is then transmitted to soil water via a continuous water column since the strong hydrogen bonding of the water molecules also allows water to stay liquid under tension (Oertli 1971). Related to these cohesive forces is surface tension, which characterizes how difficult it is to stretch the surface of a liquid.

Most laboratory and field studies dealing with xylem cavitation and embolism repair assume that surface tension is equal to that of pure water and constant within and between species. Although surface tension is a crucial parameter in xylem water movement, few studies have tested whether this parameter differs from that of pure water (Bolton and Koutsianitis 1980). In this issue, the study by Christensen-Dalsgaard et al. (2011) looked at the instantaneous surface tension of xylem sap extracted from branches of three tree species and its change over time. Using the pendant-drop method, they showed that in all three species studied, the instantaneous sap surface tension was indeed equal to that of pure water. However, in one species, *Populus tremuloides*, surface tension decreased by 15% after half an hour, which was related to the formation of surfactants caused by amphiphilic molecules present in the

xylem sap. Moreover, this lower surface tension was more pronounced in terminal branches, with a reduction of 25% compared with pure water.

These results have several implications for water movement in plants. The first is related to winter embolism because the radius above which an air bubble will expand rather than disappear upon thawing is proportional to the surface tension of the xylem sap. The breakdown of water columns in xylem conduits following a frost–thaw event is due to the expansion of air bubbles formed during sap freezing. If the difference in gas pressure in the bubble and the sap pressure is less than the capillary pressure originating from the surface tension, then the gas will dissolve. If upon thawing the sap is still under lower surface tension than that of pure water, then the bubbles will dissolve at less negative xylem pressure. The direct consequence of lower xylem sap surface tension will therefore be to limit the reduction in xylem conductivity of trees due to winter embolism. Second, it indicates that in some species this decrease in the surface tension of xylem sap will increase the vulnerability of xylem to embolism (Cochard et al. 2009). There is considerable evidence that rather than conduit diameter, it is the pore diameters in the intervessel pit membranes that determine a conduit's vulnerability to water stress-induced embolism. If cavitation occurs, or if a conduit is damaged (through herbivory for example), the air bubble does not expand to a neighboring conduit because of the surface tension effect at the pore of the pit membranes (Bailey 1916). The radius of curvature (r) needed to sustain a difference in pressure (P) at which a pit fails as a barrier and allows gas to enter the vascular system depends directly on the liquid's surface tension

(τ , which equals $7.3 \times 10^{-2} \text{ N m}^{-1}$ or $7.3 \times 10^{-8} \text{ MPa m}$ for pure water at 20 °C) by the following capillarity equation:

$$r = -2t/P \quad (1)$$

where the negative sign expresses a negative pressure (i.e., a tension). As P gets lower (more negative), so does r , and when r falls below the radius of the pit membrane pore an air bubble will be pulled into the adjacent conduit inducing cavitation (Zimmermann 1983, Crombie et al. 1985). The results of Christensen-Dalsgaard et al. (2011) indicate therefore that using pure water as the perfusing liquid in laboratory experiments could overestimate resistance to embolism by 15–25%. For *P. tremuloides*, this would have significant consequences in predicting plant resistance to water stress in field conditions since this species has been shown to be very vulnerable to embolism (Sperry and Sullivan 1992). On the other hand, it also means that if surface tension is reduced over time, a reduction by 25% in pit size would have to occur to maintain the same resistance to embolism. Such a decrease will lead to a decline in pit membrane conductivity by >95% since membrane resistivity scales with pore diameter to the third power (Vogel 1994, Sperry and Hacke 2004). Furthermore, assuming that end-wall and lumen resistivities are co-limiting conduit conductivity, then a reduction by 25% in surface tension would reduce the overall xylem conductivity by 50%.

In his classical book, Zimmermann (1983) stated that some of the issues pertaining to plant water movement are ultimately related to the improvement of tree growth through the understanding of whole-plant xylem function. The importance of surface tension in plant water relations reinforces this call. Christensen-Dalsgaard et al. (2011) 'finger-printed' the discrepancies that can exist between the surface tension of xylem sap and that of pure water, which provides the rationale to further study the effects of surface tension on tree physiology and plant growth. Future research on water transport must therefore investigate whether sap surface tension varies in living conditions with regard to biotic and abiotic stresses and its role across species, soils and climatic regimes. For instance, soluble organic compounds such as amino acids and low molecular weight organic acids secreted in response to stress (Dicke et al. 2009) and nutrient deficiency (Marschner 1995) can potentially act as surfactants, thereby reducing sap surface

tension and the air-seeding threshold. The results of Christensen-Dalsgaard et al. (2011) also raise the question of whether plants could limit the production of surfactants. Since the activity of these extraneous substances is chemically modified by temperature (Harkis and Alexander 1959), it is possible that future climate conditions may significantly affect some species' ecological distribution through seasonal variations in xylem surface tension.

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