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1 Getting variable xylem hydraulic resistance under control – interplay of structure and function.

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18 Running head: XYLEM HYDRAULIC RESISTANCE UNDER CONTROL

19

1 Over three decades ago, it was first observed that the hydraulic resistance of perfused  
2 stem segments of *Acer* twigs was significantly decreased when deionized water was accidentally  
3 replaced by tap water that contained a low concentration of metal ions (Zimmermann 1978).  
4 Initially, the effect of ions on xylem hydraulic resistance was seen as a methodological problem  
5 of limited biological importance rather than an evolved xylem trait (Sperry et al. 1988). The  
6 recognition that this phenomenon might substantially contribute to the regulation of water flow  
7 through plants came much later (van Ieperen et al. 2000; Zwieniecki et al. 2001). These reports  
8 challenged the classical paradigm of vessels being purely passive in water transport (Gartner  
9 1995; Zimmermann 1983; Zimmermann and Milburn 1982). Recently, a new view has emerged:  
10 that these tubes can control/regulate sap flow in response to changing plant physiological status  
11 (Nardini et al. 2011; Zwieniecki et al. 2001). These follow-up studies were aimed at  
12 understanding the biophysical basis for the ion-mediated variable resistance of xylem and  
13 demonstrating the potential for a variable conductance in regulating water distribution in large  
14 dendritic structures that can help optimizing plant resource utilization or mitigate the effects of  
15 environmental perturbations (van Ieperen 2007).

16 The initial biophysical focus had a positive effect on refining our understanding of the  
17 central role that bordered pits play in plant water transport. It was proposed that porosity of the  
18 bordered pit membranes can be actuated by swelling/de-swelling activity of pectin based  
19 hydrogels that permeates the fibrous membrane structure (Zwieniecki et al. 2001). The role of  
20 hydrogel in the variable xylem resistance phenom was indicated by combination of response to  
21 ion concetration, resposne to pH and resposne to non-polar solution (ethanol) all resulting in  
22 drop of bordered pit field resistnce. .However, the initial hypothesis that de-swelling opens micro  
23 channels in the bordered pit membrane (Zwieniecki et al. 2001; van Ieperen 2007) had to be

1 modified to reflect the recent results from direct observations of conformational changes of  
2 bordered pit structure using an atomic force microscope (AFM) (Lee et al. 2012). Lee and co-  
3 authors showed that while the general idea of hydrogels being responsible for the hydraulic  
4 properties of bordered pits did not change, the decrease of the membrane thickness is behind the  
5 decrease of the hydraulic resistance rather than change in membrane porosity. AFM analysis  
6 delivered a clear image of the change from an amorphous featureless surface of the membrane in  
7 DI water to a rigid sharp fibrous surface in 50 mMol KCl solution (Figure 1). No submicron  
8 pores were observed in the membrane suggesting that water flow occurs via a hydrated hydrogel  
9 matrix rather than through the pores between cellulose fibers (Figure 1). We feel that these  
10 recent findings clarified the basic understanding of the variable xylem resistance and allow for a  
11 re-focus from questions such as ‘how does it happen?’ to the analysis of the physiological role of  
12 the variable hydraulic resistance of xylem in plants (Holbrook et al. 2002; Trifilo et al. 2011; van  
13 Ieperen 2007; Zwieniecki et al. 2004).

14         There is no doubt that an ever growing dendritic structure of the tree requires an efficient  
15 water distribution system. It was shown that xylem distribution system is often optimized  
16 following Murray’s law that aims at minimization of xylem resistance for a given investment in  
17 transport tissue (McCulloh et al. 2004; Sperry et al. 2008) or fractal geometry that allow for  
18 vascular design where resistance is independent from path length (West et al. 1999). Once in  
19 place, this transport path remains active throughout the season without the possibility for  
20 structural changes. However, tree micro-environment is not constant. It undergoes continuous  
21 variations at multiple temporal scales from minutes (sun flecks, wind gusts) and hours (direction  
22 of sunlight) to days (drought, temperature) and weeks (competition, growth). Thus, an inflexible  
23 transport system acting in the variable environment may be temporarily inefficient causing a

1 drop in photosynthetic activity and possibly more permanent losses to transport functionality  
2 (embolism). The notion that xylem resistance is variable and can be controlled by both plant  
3 physiological activity and potentially by environmental conditions could make the xylem  
4 distribution system more robust and efficient. In this issue of *Tree Physiology*, Nardini and  
5 colleagues unequivocally show that the degree of variability of xylem hydraulic properties in  
6 response to ion concentration in xylem sap is correlated with plant habitat even among closely  
7 related species (Nardini et al. 2012). They reported that trees growing in shady and humid areas,  
8 with generally low evaporative demand and limited temporal/spatial variability in transpiration  
9 rates experienced by different parts of the tree crown, showed smaller variation in resistance to  
10 changes to ion concentration. This was in contrast to a greater ion-mediated hydraulic response  
11 in the trees growing in open areas with high sun exposure, high evaporative demand and  
12 potential for high variation in transpiration rates among different parts of the crown. The  
13 differences in responsiveness to changes in ion concentration seemed to be further supported by  
14 the fact that species growing in open environments have generally lower ion concentrations in  
15 xylem sap and that they operate in the range of concentrations where hydrogels are more  
16 responsive. This study suggests that the ionic response of xylem resistance is an evolved trait  
17 and can provide competitive or survival advantage related to water transport. Nardini and  
18 colleagues elegantly showed that the original hypothesis that ‘ion-dependent mechanism for  
19 altering the hydraulic resistance of the xylem could allow plants to compensate for increases in  
20 resistance due to cavitation’ (Zwieniecki et al. 2001) may indeed be supported by their data  
21 collected from *Acer* trees.

22         The crucial role that the structure of bordered pit membranes may play in the transport of  
23 water by providing protection from embolisms spreading (Plavcova et al. 2011; Sperry et al.

1 2006; Trifilo et al. 2008) should be extended to include their role in control of water fluxes. This  
2 warrants more thorough studies of the evolution of bordered pit membranes, their chemistry and  
3 most importantly their detailed anatomy in relation to ion response. Analysis of pectin  
4 distribution in fossilized plants suggests that evolution of bordered pit membranes responsiveness  
5 to ion concentration might be present in multiple lines with angiosperms being most responsive  
6 due to high concentration of pectin like material (Boyce et al. 2004). In addition, the fact that  
7 changes of membrane thickness are the basis for the hydraulic response can help to understand  
8 differences between species response, with *Laurus nobilis* showing one of the highest recorded  
9 responses (Zwieniecki et al. 2001) and having one of the highest recorded thicknesses of the  
10 membrane (Jansen et al. 2009). As thicker membranes also provide better protection from  
11 embolism spread, there is a striking link between membrane functions: protection and flow  
12 control. Yet despite the research progress and growing interest, we still know very little on the  
13 true role of the ionic effect at the whole plant level with many unsolved questions regarding its  
14 role in nutrient management, resource distribution and transport optimization.

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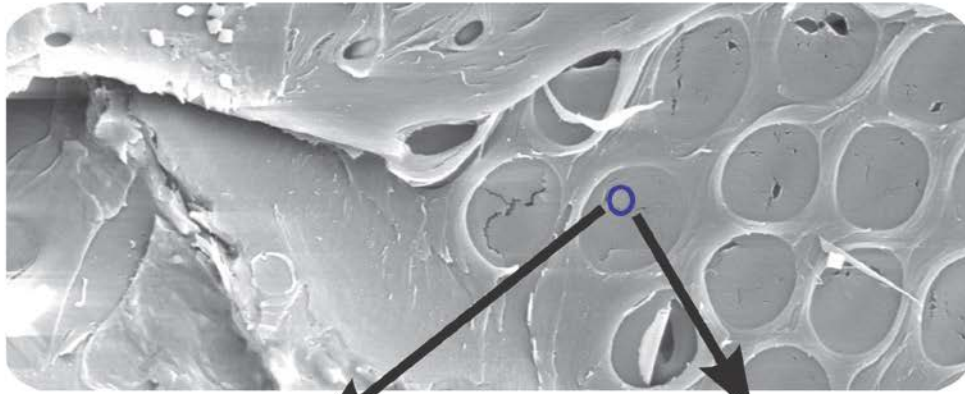
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- 17

1 Figures

2 Figure 1. Current model describing the role of hydrogels in variable resistance of bordered pit  
3 membrane in response to changes in ion concentration. (A) Scanning electron microscope image  
4 of bordered pit field between adjacent vessels in *Nicotiana tabacum*. (B) Atomic force  
5 microscope (AFM) images depicting bordered pit field membrane surface that was initially  
6 submerged in deionized water (DI) and later switched to 50 mMol KCl solution (same exact  
7 region). Dramatic change from cloudy, featureless surface in DI water to sharp edges and visible  
8 fibrous structures can be observed (Lee et al. 2012). In addition, membrane was found to  
9 collapse in thickness upon switch from DI water to solution as the AFM cantilever had to be  
10 lowered several tens of nanometers to a new position to acquire new image. Shades of gray  
11 surface elevation (bar). (C) Schematics of the membrane cross section depicting current  
12 understanding of the hydrogel role in variable resistance of the xylem in response to ion  
13 concentration. Cellulose microfibrils are imbedded in pectin hydrogel and water flows through  
14 the hydrogel matrix. Upon change from DI water or low ion concentration to solution with  
15 higher ion concentration, hydrogel matrix collapses decreasing the membrane thickness vertical  
16 distance between fibers and overall resistance of the path through the membrane (as resistance is  
17 inversely related to distance).

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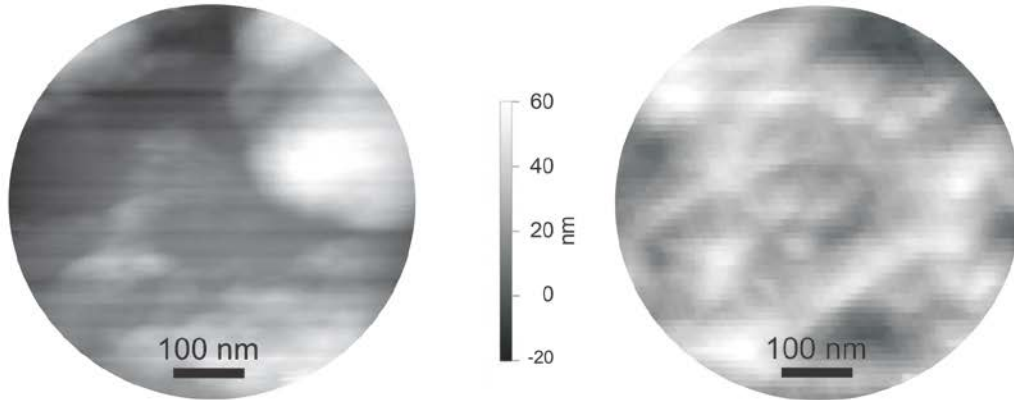
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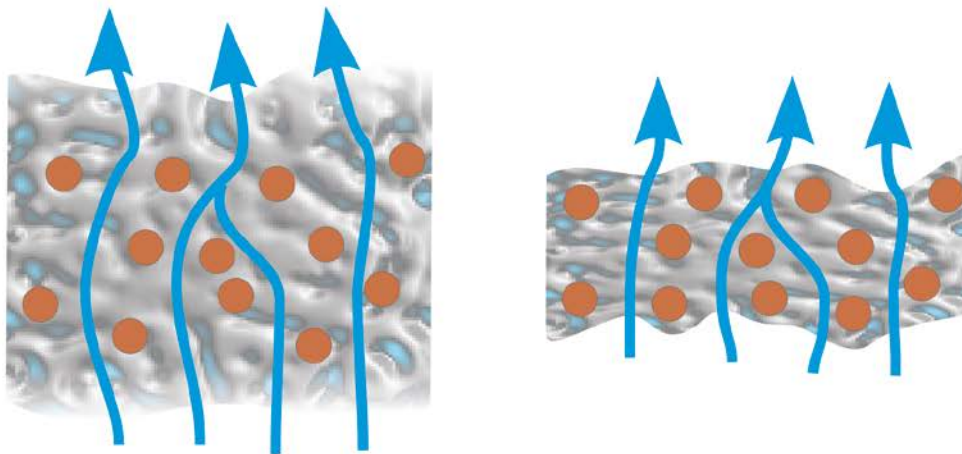
DI water

50 mMol KCl

B



C



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