



Commentary

Linking stomatal sensitivity and whole-tree hydraulic architecture

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After moving from aquatic to terrestrial habitats, plants developed a suite of traits largely devoted to limiting the loss of a resource that they once had in excess: water. These traits include, among others, a cuticle and stomata, which allow plants to reduce and selectively reduce water loss, respectively. The unique importance of stomata lies in the need for the amount of water lost from leaves to not exceed the amount supplied, while simultaneously allowing a passageway for carbon dioxide to enter the leaves for photosynthesis. The supply of water in vascular plants is determined by the plant architecture (e.g., root-to-shoot-area ratios, rooting depths, etc.), the hydraulic architecture, radial hydraulic conductance as governed by aquaporin expression in the roots and leaves (Steudle and Peterson 1998, Cochard et al. 2007, Almeida-Rodriguez et al. 2011) and soil moisture availability. In woody plants, hydraulic architecture (Zimmermann 1978) is a term that describes the xylem network within the plant and varies with wood type, age and growth form (e.g., liana vs. shrub vs. tree).

Despite stomata being a particularly ancestral trait among land plants, the sensitivity of stomata to water deficits in the atmosphere is quite varied (Oren et al. 1999), and this variation is the focus of the paper in this issue by Litvak et al. (2012). Stomatal sensitivity (m) is described in this case as the magnitude of the response of stomatal conductance (g_s) to increasing vapor pressure deficit (D) relative to a reference conductance at $D = 1$ kPa (g_{s-ref}). Species with lower sensitivity have lower g_{s-ref} values due to factors such as smaller stomatal pores, lower stomatal densities and/or partial stomatal closure at $D = 1$ kPa. Thus, an equivalent response to an increase in D in terms of the proportion that stomata are open reduces g_s a smaller amount in these less sensitive species. Using urban Los Angeles, California as a common garden, this paper evaluated both leaf-level (m_L) and whole-tree

level (m_T) stomatal sensitivity in tree species by examining changes in transpiration (which was used instead of g_s to elegantly avoid the autocorrelation that results when D is used to calculate conductance) in response to natural variation in D . Aside from the possibility of seeing movie stars and surfing, the semi-arid climate in urban Los Angeles also provides an extremely large range of D (~0.25 to 4 + kPa), and yet, the trees studied did not suffer from significant soil water deficit because they were irrigated. These conditions are important to note because the sensitivity of stomata to D has been shown to change considerably when soil water deficits compound the stress a plant is experiencing (Ewers et al. 2001, Bovard et al. 2005).

The results of Litvak et al. (2012) showed a strong relationship between the sensitivity of transpiration to D at the whole-tree level (m_T) and the whole-tree reference transpiration (E_{T-ref} = transpiration at $D = 1$ kPa), which was expected given the physical relationship between E_{T-ref} and g_{s-ref} discussed above. This relationship has also been observed before, but either across a smaller range of D (Oren and Pataki 2001, Peters et al. 2010) or a smaller number of species (Bush et al. 2008). However, unlike the results achieved by Bush et al. (2008), who found that ring-porous trees had much greater stomatal sensitivity than diffuse-porous trees, Litvak et al. (2012) did not find a systematic difference in sensitivity with wood type. The resistance to embolism did correlate with both whole-tree and leaf-level sensitivity to D in angiosperms, but not in conifers (measured at whole-tree level, only). m_T correlated with vulnerability to embolism along parallel slopes with different intercepts, with the more embolism-resistant diffuse-porous trees grouped separately from the vulnerable non-diffuse-porous species. In contrast, m_L showed a consistent correlation with vulnerability to embolism across all angiosperms.

These results, principally the relationship between xylem vulnerability and stomatal sensitivity, raise a number of questions. Particularly, why is there not a relationship between sensitivity and embolism resistance in the conifers? The answer may be due to one of the limitations of the study design. Stomata are responding to the integrated changes of both the upstream hydraulic supply and the atmospheric demand for transpired water. It is becoming clear that in some species, the hydraulic conductance of the entire xylem network can change during daily cycles of water stress because of the loss of hydraulic function of one or more parts of the path. It is also increasingly evident that the distal portions of the path (roots and/or distal stems or leaves) are more likely to experience loss of function during the day and then be refilled at night than are the main portions of stems. Conifers, in particular tend to lose substantial amounts, and in some cases all, hydraulic conductance in their leaves on a daily basis and then regain function in the late afternoon and overnight (Johnson et al. 2009, 2011). The xylem of the stems is much more conservatively constructed and there tends to be considerable difference between the xylem pressures they experience daily and the pressure at which 50% of their hydraulic function is lost (P_{50}). Thus, by measuring the P_{50} of the stems and not the leaves, Litvak et al. (2012) did not measure the segment of the hydraulic continuum to which the stomata may be responding.

A second question that arises when considering Figure 7 in Litvak et al. (2012) is what is the cause of the observed difference between angiosperms with diffuse-porous vs. non-diffuse-porous wood? The parallel lines mean that at a given stomatal sensitivity, the non-diffuse-porous species, which were mostly ring-porous, are less resistant to embolism than the diffuse-porous species. The patterns in the two groups may have different explanations. For the ring-porous species, observed trends of diurnal hydraulic function may illuminate the situation. It is well documented that the ring-porous species *Quercus gambellii* Nutt. loses hydraulic conductivity in small diameter branches daily and regains it overnight (Tenada and Sperry 2008, Christman et al. 2012). While this pattern has not been observed in the species examined by Litvak et al. (2012), higher values of native embolism measured at mid-afternoon were observed in the ring-porous species than in the diffuse-porous species, and the highly vulnerable stems of the ring-porous species may need to be able to refill embolisms that regularly develop. This highly vulnerable segment of the network may act as a fuse that isolates the stomata from the water conducting system and results in stomatal closure.

For the diffuse-porous species, the larger continuum of responses observed may reflect the link between stomatal sensitivity and whole-tree hydraulic conductance within this wood type. The potential connection between these two parameters

is the strong positive relationship between m_T and the whole-tree transpiration rate (at $D = 1$ kPa). Considerable previous work in hydraulic architecture has found a linear relationship between transpiration or g_s and whole-tree hydraulic conductance (Meinzer and Grantz 1990, Sperry and Pockman 1993, Meinzer et al. 1995, Saliendra et al. 1995, Hubbard et al. 2001). Species with more negative P_{50} s tend to have higher wood density and thicker fibers (Hacke et al. 2001, Jacobsen et al. 2005, Pratt et al. 2007), which could limit the wood volume available to wide diameter vessels that would allow for high hydraulic conductance. A final question then is, why is the hypothesized link between m_T and whole-tree hydraulic conductance not consistent across wood types? One potential answer is due to differences in the leaf-specific hydraulic conductance between the wood types. While Litvak et al. (2012) do consider the effects of leaf area-to-sapwood area ratios on their results and conclude that they do not expect systematic differences between the wood types, this ratio would not reflect the true ability to supply water to leaves as accurately as leaf-specific conductance would. An alternate hypothesis is that the diffuse-porous species do not possess the same kind of hydraulic fuse that is exhibited in the distal branches of ring-porous species and the leaves of conifers, and this masks the link between hydraulic conductance and m_T in the latter two groups.

The complexity of predicting stomatal responses to changes in D across species and wood types should not be surprising. It is becoming increasingly clear that there are a variety of approaches that plants employ to cope with both diurnal and seasonal drought. In fact, considerable variation in the relationship between stomatal sensitivity and stomatal conductance exists even among individuals of the same species (Oren et al. 1999, Pataki and Oren 2003, Ewers et al. 2008). In a study examining the response of g_s to changes in D along a height gradient in Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco.), it was found that g_s of detached branches with their bases in water peaked at progressively greater values of D as sampling height increased (Woodruff et al. 2010). This relationship suggests that foliage that has developed under conditions of greater water stress is associated with stomatal closure at more negative water potentials. From a mechanistic perspective, this analysis focused on how the turgor of stomatal subsidiary cells was influenced by osmotic adjustment associated with greater tree height, and it reflects a different type of stomatal sensitivity to D than that described in studies which have focused upon the magnitude of the decrease in g_s with increasing D . Despite these differences in study design and research question, plotting the data from Woodruff et al. (2010) as m_L vs. the maximum stomatal conductance (g_{s-max}) provides a strongly significant relationship ($P < 0.0000001$) with a slope of 0.60 (Figure 1), consistent with the theoretical analysis that '... as long as stomata are regulating leaf potential

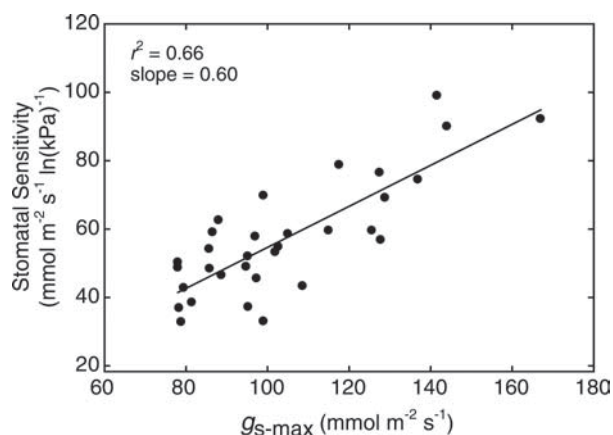


Figure 1. The sensitivity of leaf-level stomatal conductance (g_s) to increasing vapor pressure deficit at the leaf surface ($-d g_s / d \ln D$) as a function of maximum stomatal conductance ($g_{s\text{-max}}$). Gas-exchange measurements were conducted on detached and hydrated branches collected from near the tops of Douglas-fir trees of a range of height classes. Actual $g_{s\text{-max}}$ was used as opposed to a reference g_s at $D = 1$ kPa because of lower than maximal g_s values at $D \leq 1$ kPa. The suppression of g_s at low D was likely due to the mechanical pressure on guard cells exerted by subsidiary cells with high turgor in these rehydrated branches with their cut bases submerged in water, as discussed in Woodruff et al. (2010).

near a constant value, a slope near 0.60 is expected... (Oren et al. 1999).

Despite the complexity of the relationship between stomatal sensitivity, water loss and vulnerability to embolism, the goal of teasing apart the subtleties is a necessary one. As Litvak et al. (2012) mention, determining transpiration patterns based on vulnerability to embolism would be much easier than the lengthy and potentially expensive processes involved in sap flux or eddy flux measurements. Water loss from trees is a large component of the water cycle in natural systems, and an important cost (in terms of irrigation) and benefit (in terms of temperature mitigation) in urban environments. However, until we have a better understanding of hydraulic architecture on the whole-plant scale and know how that architecture changes with wood type, including how and where these potential hydraulic fuses function, we will continue to lack critical knowledge of how plants manage their hydraulic status and prevent excessive water loss.

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Conflict of interest

None declared.

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