Ecological relevance of minimum seasonal water potentials
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The minimum seasonal water potential a plant experiences, $\psi_{\text{min}}$, provides an important measure of plant water status, as it reflects the maximum water deficit that leaves and xylem must tolerate to maintain physiological activity. $\psi_{\text{min}}$ also acts as a selective force on xylem structure which, in turn, generates correlations between $\psi_{\text{min}}$ and numerous hydraulic traits. This review focuses on the ecological relevance of $\psi_{\text{min}}$ as a reflection of overall plant hydraulic strategy. The focus is on plant functional strategies with respect to soil drought, but we conclude with preliminary findings on the role of atmospheric drought.

To remain physiologically active, plants must be able to supply water from the soil to the leaves to balance transpirational losses or, alternatively, withstand extreme tensions generated in the xylem due to water loss. The greatest xylem tension experienced by a species during the course of the year is defined as its minimum seasonal water potential, $\psi_{\text{min}}$. $\psi_{\text{min}}$ is a plant property that emerges from the balance between soil water availability, the rate of leaf water loss, and the capacity of the plant transport system to supply water to the leaves. However, $\psi_{\text{min}}$ also acts as a selective force on xylem structure which, in turn, generates functional associations with a number of hydraulic traits. Our goal in this review is to focus on the ecological relevance of $\psi_{\text{min}}$ as a reflection of overall hydraulic strategy and the implications for species distribution. We address the ecological relevance of $\psi_{\text{min}}$ primarily in the context of soil drought, which has been the focus of considerable research. We then conclude with some recent studies on the relationship between hydraulic strategies and atmospheric drought (i.e. high vapor pressure difference).

Factors influencing minimum water potential
Plant water status, as indicated by either leaf or xylem water potentials, reflects a balance between water supply, largely determined by soil water availability, and atmospheric evaporative demand (Fig. 1). $\psi_{\text{min}}$ is an informative measure of plant water status because it represents the maximum xylem tension that a species must tolerate to remain physiologically active. It is necessarily lower (more negative) than pre-dawn water potentials, so factors influencing soil water supply set an upper bound on $\psi_{\text{min}}$. Soil type and texture play a large role in determining soil water availability and thus contribute to variation in $\psi_{\text{min}}$ as was found in a study of species growing on coarser-textured sandy soils compared to finer-textured loam soils (Sperry and Hacke 2002). In addition, the quantity and seasonality of rainfall contribute to differences in water availability within the soil profile. Arid environments with pronounced dry seasons will experience surface drying and a gradient of increasing water availability with depth (Davis and Mooney 1986). In contrast, environments with small, irregular rainfall events may be characterized by pulses of

Abbreviations – LA, leaf area; SA, sapwood area; VPD, vapor pressure difference.
high water availability in shallow soils (Sala and Lauenroth 1982). Variation in water availability with soil depth can shape rooting strategies (Schwinning and Ehleringer 2001), which in turn influence patterns of whole plant water use and minimum water potentials (e.g. Davis and Mooney 1986, Goulden 1996, Oren and Pataki 2001).

In addition to soil water availability, rates of water loss together with properties of plant hydraulic architecture mediate how negative xylem water potentials become diurnally and, by extension, seasonally. Aspects of climate, in particular the vapor pressure difference (VPD) between the air and the leaf, create the driving gradient for water loss. The rate of transpirational water loss is then determined by the interaction of VPD and stomatal conductance. Thus, stomatal regulation and the interaction with whole plant conductance play a critical role in preventing water potentials from dropping excessively (Sperry et al. 2002). Functional traits that increase whole plant conductance, such as large or numerous vessels and low leaf area/sapwood area (LA/SA) ratios (inverse Huber value), can buffer leaf water potentials in the face of transpirational losses. \( \psi_{\text{min}} \) reflects the interactions among aspects of plant hydraulic architecture as well as the abiotic factors determining soil water supply and evaporative demand (Fig. 2).

**Decoupling from soil water availability**

Historically, much research has focused on strategies of drought avoidance and tolerance in relation to soil water availability. However, because \( \psi_{\text{min}} \) is partially determined by plant hydraulic architecture, differences among species in \( \psi_{\text{min}} \) do not necessarily mirror patterns of soil water availability. Species that differ in their hydraulic capacitance, or transient use of stored water, may differ in their diurnal water potential differentials (the difference between pre-dawn and minimum midday values), thus decoupling soil water availability and diurnal minimum water potentials. Work by Goldstein, Meinzer, Stratton and others (Goldstein et al. 1998, Stratton et al. 2000, Meinzer 2003) has demonstrated the importance of stored water in contributing to total water lost in daily transpiration—in a study of five diverse tree species in a seasonal tropical forest, Goldstein et al. (1998) found that 9–15% of total transpirational water loss came from stored reserves, and that the proportion scaled with tree height. They proposed that, due to increased hydraulic resistance with height, the increased reliance on stored water allowed trees to offset the development of large diurnal differentials in water potential without any reduction in stomatal conductance and carbon gain. Species with greater storage capacity sustained maximum transpiration rates and kept stomata open for longer, supporting the idea that stored water helps reduce hydraulic constraints on gas exchange.

In a study of six Hawaiian dry forest species, Stratton et al. (2000) found a strong negative correlation between diurnal differentials in water potential and saturated water content, an estimate of relative stem water storage capacity. Similarly, in a study of co-occurring species in a seasonally dry tropical forest in Panama, species with greater sapwood capacitance experienced less negative midday branch water potentials, although all experienced similar pre-dawn water potentials (Meinzer 2003). These studies illustrate how variation in water storage capacity may decouple pre-dawn water potentials from midday water potentials, both diurnally and seasonally. Therefore, \( \psi_{\text{min}} \) rather than measures of soil water availability, may serve as a better indicator of hydraulic parameters.

**Selective effects: cost of resistance and xylem structure**

As summarized above, \( \psi_{\text{min}} \) is in part dependent on overall hydraulic architecture. However, \( \psi_{\text{min}} \) also imposes a selective pressure on xylem structure, particularly cavitation resistance. For example, in a study of six closely related species pairs, evolutionary divergences in \( \psi_{\text{min}} \) were repeatedly associated with divergences in stem resistance to embolism (R. Bhaskar, unpublished). This apparent adaptive link between \( \psi_{\text{min}} \) and xylem resistance to cavitation can be explained in physiological terms. The cost of xylem
that cannot tolerate $\psi_{\text{min}}$ is clear—extreme minimum water potentials result in complete conduit cavitation and/or shoot death (Tyree and Sperry 1988, Davis et al. 2002). But what is the cost of increased resistance? A general trade-off between hydraulic efficiency and safety has been proposed on the grounds that low resistance to water flow through the xylem involves changes in stem anatomy that presumably come at the cost of resistance to embolism (Zimmermann 1983, Tyree et al. 1994). To date, the evidence has been inconclusive. When conduit diameter, which largely determines conduit conductivity, was plotted against stem resistance to embolism, as reflected by the tension at which 50% conductivity is lost (PLC$_{50}$), the trend across diverse taxa was in the right direction, but weak. Species with conduits of larger diameter also had lower stem resistance to embolism (Tyree et al. 1994). A test of evolutionary correlations between hydraulic traits showed a weak negative relationship between sapwood specific conductivity and resistance to embolism within the conifers, but when these findings were pooled with a broader survey of woody plants no correlations were found (Maherali et al. 2004).

Recent work has focused on the role of conduit pit structure; inter-conduit pit membranes, in particular, are the largest pits in conduit walls and the potential site of air-seeding (Sperry et al. 1996, Hacke and Sperry 2001). Based on their model of pit size and cavitation resistance, Sperry and Hacke (2004) identified a negative relationship between maximum pore diameter and safety from air-seeding, because larger pores are more susceptible at lower tensions. Minimizing pore size to decrease vulnerability to cavitation may, however, come at the cost of transport efficiency. An examination of the relative contribution of end wall resistivity to total flow suggests that 50% of xylem flow is dictated by flow through inter-conduit pits (Sperry et al. 2005). Together, these results provide a foundation for the trade-off between safety and efficiency. However, rather than pore size alone, the trade-off appears to involve the total pit area of a conduit, which roughly scales with conduit size, and influences both the transport efficiency and the probability that a single large pit will fail (Wheeler et al. 2005).

In addition to trade-offs involving hydraulic efficiency, more resistant xylem may also incur costs related to either mechanical support or stem construction or both. Aspects of stem structure clearly play an important role in hydraulic conductance. Because factors increasing sapwood transport efficiency, such as
increased vessel diameter, may come at the cost of weaker wood, Wagner et al. (1998) proposed a trade-off between mechanical strength and transport efficiency. Recognizing that selective pressures for wood density may vary strongly between growth forms and habitats, they chose two co-occurring congeneric species pairs and found that increased vessel diameter and transport efficiency were associated with lower wood density within each pair (Wagner et al. 1998). Another potential trade-off with resistance is higher construction cost associated with increasing wood density. In a survey of 16 different families and 48 different species, Hacke et al. (2001) examined the extent to which variation in wood density and wood structure is linked to support against implosion by negative pressure in the xylem. The more drought tolerant the plant, the more negative the pressures can become in the xylem without cavitation, resulting in greater internal load on the xylem walls. Therefore, wood density should scale with cavitation resistance (Hacke et al. 2001). Moreover, increased wood density is frequently associated with lower growth rate, which may explain the trade-off seen in a study of 17 Florida oak species between stem resistance to embolism and growth rate (Reich et al. 2003).

**Ecological relevance of minimum water potentials: species distribution and hydraulic strategies**

The evolutionary pressure to balance \( \psi_{\text{min}} \) and xylem resistance to embolism can result in an association between \( \psi_{\text{min}} \) and species distribution with respect to water availability. One of the first field studies to demonstrate a connection between minimum water potentials, xylem resistance and species distribution was done by Pockman and Sperry (2000). Their study focused on the hydraulic traits of 15 Sonoran desert species distributed across a range of soil moisture but within a small geographic area. Consistent with many other studies, they found a strong correlation between stem resistance to embolism and the minimum water potentials experienced in the field. In addition, by comparing species vulnerability curves they were able to demonstrate that riparian species would not have been able to survive the extreme water potentials found in the upland environments. Thus, within a small geographic scale, stem resistance to embolism strongly limited species distribution. Similarly, a study of *Ceanothus* species that were sequentially replaced along an elevational and precipitation gradient found that xylem resistance corresponded with site parameters as well as \( \psi_{\text{min}} \) (Davis et al. 1999). Pooling their field data with available values from the literature, which included temperate and tropical habitats from three continents, Pockman and Sperry (2000) found a significant correlation between resistance to embolism and minimum water potentials. Xylem resistance to embolism may therefore largely determine the limits of species distribution and, through evolutionary feedback, result in a general correspondence with \( \psi_{\text{min}} \).

The balance between \( \psi_{\text{min}} \) and xylem resistance is a critical component of overall plant hydraulic strategy; as a result, numerous hydraulic traits are functionally associated with \( \psi_{\text{min}} \). Theoretical models have predicted that tolerance of extreme tension in the xylem is an important factor limiting rates of plant water loss. Sperry et al. (1998) defined critical water potential, \( \psi_{\text{crit}} \), as the lowest water potential still allowing water uptake. Their model proposed that plants should operate as close as possible to this hydraulic limit, without risking complete cavitation of the conducting pathway, to maximize stomatal conductance—and carbon gain—while minimizing root biomass and cavitation resistance (Sperry et al. 1998). Results from their greenhouse drought experiments as well as field studies support their prediction that hydraulic considerations, specifically prevention of water potentials dropping to the point of cavitation, will impose a limit on gas exchange (Kolb and Sperry 1999).

A study of functional strategies within a California chaparral community identified a suite of correlated hydraulic traits co-varying with degree of drought experienced (Ackerly 2004). Correlations among hydraulic traits, including larger vessel diameters, lower wood density, and higher LA/SA, were associated with less negative minimum water potentials. These results are consistent with the patterns identified by other recent studies of functional convergence in hydraulic traits; in neotropical savanna species, higher wood density was associated with more negative \( \psi_{\text{min}} \), lower leaf specific and stem specific conductivity, and whole plant hydraulic conductivity, and lower saturated water content (e.g. Meinzer 2003, Bucci et al. 2004, Macinnis-Ng et al. 2004). In a compilation of 27 species from diverse environments, Meinzer (2003) found that high wood density was associated with greater fluctuations in leaf water potential, probably due to different transport efficiency and ability to resupply leaves with water through the day. Minimum water potentials were correlated with transport efficiency per sapwood area in a survey of several species from four different habitats in Australia (Macinnis-Ng et al. 2004). From all of these studies, we can conclude that variation in \( \psi_{\text{min}} \) is a strong predictor of corresponding variation in a suite of characteristics related to hydraulic transport and resistance.
With repeated studies finding evidence of a suite of traits correlated with $\psi_{\text{min}}$, it is interesting to consider the extent to which these traits are related to suites of leaf photosynthetic and economic (e.g. leaf lifespan) traits. Leaf lifespan and associated traits have been previously identified as an important ecological strategy axis, representing trade-offs among instantaneous carbon gain and long-term nutrient use efficiency (Westoby et al. 2002). Interestingly, in chaparral species, the hydraulic axis was largely distinct from the suite of economic traits related to leaf lifespan, specific leaf area, gas exchange and nitrogen use efficiency (Ackerly 2004). This suggests that minimum water potentials may represent an independent axis of functional diversity, but studies in other environments are needed to evaluate how broadly these results apply.

One system in which leaf lifespan (or at least evergreen deciduous leaf habit) does appear to be associated with hydraulic strategies is within the seasonally dry rainforest in Australia. In a study of two evergreen and two deciduous tree species coexisting in northeastern Australia, Choat et al. (2005) found that drought deciduous trees have less negative seasonal water potentials, associated with higher vessel diameters, lower wood density, and in some cases more vulnerable stems. In addition, higher sapwood specific conductivity together with higher Huber values resulted in higher leaf potentials compared to the evergreen species (Choat et al. 2005). The authors themselves caution that, on the whole, the results are inconsistent in seasonally dry forests worldwide (e.g. Brodribb et al. 2002) and the relationship between hydraulic architecture and leaf phenology is unresolved.

**Atmospheric drought**

Low soil water availability (dry soil) and high evaporative demand (dry air) are often treated together as aspects of ‘drought stress’. However, their effects on plant function may differ: one is a measure of how much water is available in the source, while the other reflects the ‘sink strength’ of the atmosphere. In contrast to low soil water availability, the influence of high evaporative demand or atmospheric drought on hydraulic traits is less well understood, in part due to the difficulty in isolating that factor (Zweifel et al. 2005).

Changes in atmospheric evaporative demand have been hypothesized to result in a homeostatic response, with trees maintaining a similar gradient of water potential with height by adjusting either hydraulic traits or regulating stomatal conductance (Whitehead 1998). Results from empirical studies suggest that LA/SA is one trait that varies as a function of evaporative demand. Mencuccini and Grace (1995), in their study of Scots pines (Pinus sylvestris L.), found a shift towards LA/SA in pines in drier sites. A decrease in LA/SA leads to higher leaf specific conductance, or more leaf water supply, assuming that no changes occur in sapwood transport efficiency, and would thus mitigate the increase in transpiration rate caused by high VPD (Mencuccini and Grace 1995).

Maherali and Delucia (2000, 2001) more formally proposed that increased allocation to sapwood in response to higher evaporative demand is part of a hydraulic strategy aimed at preventing excessive drops in minimum xylem water potentials. Their work assessed the hydraulic architecture of ponderosa pines (Pinus ponderosa) growing in both warm, dry desert environments and cool, moist montane environments. Despite large differences in annual precipitation, there were no significant differences in either soil water availability, reflected by pre-dawn water potential, or mid-day water potentials between the two sites, presumably due to adjustments in rooting depth. Xylem vulnerability to drought-induced embolism was also not significantly different between the populations. Therefore, the two populations differed only in atmospheric drought. Higher temperatures and VPD in the desert environment resulted in greater evaporative demand, and not surprisingly transpiration rates were significantly higher in desert populations. However, plants in the desert sites exhibited a shift towards higher leaf specific conductance, as a result of both changes in allocation (lower LA/SA in the desert) and changes in the actual sapwood specific hydraulic conductance. This allows desert trees to maintain higher rates of transpiration with less drop in minimum water potentials, and thus reduced risk of cavitation.

A similar pattern was found with an evergreen angiosperm, **Metrosideros polymorpha**, distributed throughout the Hawaiian islands (W. Cornwell, R. Bhaskar, L. Sack, S. Cordell, in review). A study comparing populations on the wet side of the island of Hawaii, averaging 5400 mm/year rainfall, with those on the dry side, averaging approximately 650 mm/year, found significant intraspecific variation in hydraulic traits. While pre-dawn water potentials were slightly more negative on the dry sites than on wet sites ($-0.22$ vs $-0.08$), values were close to zero and midday water potentials were not significantly different. Therefore, as in the study on the pines, the contrast between the two sites was largely due to differences in atmospheric demand and not drought stress experienced. Stem vulnerability to cavitation was not significantly different between the two sites, which is not unexpected, because that trait correlates most strongly with minimum water potential.
which in this case did not differ. However, leaf specific conductance did vary, and was five–to seven-fold greater in dry sites than in the wet sites. Again, this was due to increases in components that contribute to leaf specific conductance—both a higher sapwood specific conductance and lower allocation to leaf area relative to sapwood area in the dry sites.

While few empirical studies have been able to isolate atmospheric drought, the similarities in the studies discussed above suggest a general pattern of higher leaf water supply in sites at high VPD. A comparative study of species in Mediterranean and non-Mediterranean climates is underway to test whether interspecific differences across atmospheric gradients are similar (R. Bhaskar, unpublished). In response to high atmospheric demand, increased water supply may be a general strategy to prevent extreme drops in $\psi_{\text{min}}$ while at the same time allowing for continued gas exchange.

**Conclusions**

$\psi_{\text{min}}$ is an important measure of plant water status, as it reflects the maximum water deficit that leaves and xylem must tolerate to maintain physiologic activity. Because extreme tension in the xylem can compromise hydraulic integrity, $\psi_{\text{min}}$ also exerts selective pressure on xylem anatomy, particularly those traits that influence stem resistance to embolism. The general correspondence between $\psi_{\text{min}}$ and resistance to embolism is a central component of species hydraulic strategy; accordingly, we find, across species, a suite of hydraulic traits that are functionally associated with $\psi_{\text{min}}$. $\psi_{\text{min}}$ therefore provides insights into plant functional strategies with respect to soil drought, and may be an important aspect of response to atmospheric drought as well.

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