

Commentary

Progressing from 'functional' to mechanistic traits

This issue of *New Phytologist* contains a very exciting paper by Larter *et al.* (2017, pp. 97–112) showing how millions of years of progressive aridification in Australia led to dramatic evolution in water transport capabilities in this country's most successful extant conifer clade. The genus examined is *Callitris*, a remarkably resilient clade of Cupressaceae that ranges from the rainforested slopes of New Caledonia, across much of the parched Australian continent. Indeed the current world title for the most water-stress tolerant xylem comes from a small tree species of *Callitris* that inhabits desert margins in southern Australia (Larter *et al.*, 2015). In their latest work on the *Callitris* clade, Larter *et al.* (2017) find that a single functional trait (xylem resistance to cavitation) is very strongly correlated with species distributions in terms of aridity across the extensive climatic range of the group. Together with similar studies from different scales (Blackman *et al.*, 2012; Pittermann *et al.*, 2012; Brodribb *et al.*, 2014) this work paves the way for using mechanistic traits to explain broad patterns of evolution and ecology in plants. By 'mechanistic traits', I mean traits whose function can be clearly physiologically defined, as opposed to the more abstract 'functional' traits, such as leaf mass per area (LMA), that have been used to great effect in explaining plant economics over the last 15 years (Wright *et al.*, 2004).

'Can xylem vulnerability become a super trait with the capacity to globally predict species distribution and drought sensitivity?'

Xylem vulnerability is a quantitative measure of the sensitivity of xylem tissue to cavitation during water stress, a process that blocks the water transport function of the plant vascular system. The spread of cavitation during intensifying water stress ultimately leads to tree death as leaves become progressively disconnected from soil water (Sperry & Pockman, 1993). Links between species susceptibility to hydraulic failure, mortality and distribution have long been hypothesized (Brodribb & Hill, 1999), but Larter *et al.* (2017) are the first to comprehensively connect these axes in a way that explains the influence of climate change on plant evolution. This paper, along with recent work by ecologists and modellers (Mitchell

et al., 2016; Wolf *et al.*, 2016; Xu *et al.*, 2016), all add to a growing momentum supporting a critical role of xylem hydraulics, particularly cavitation, in explaining global patterns in plant ecology. However, despite the enormous potential of xylem vulnerability as a metric of stress tolerance, the broad application of xylem cavitation as an ecological tool has been hampered by technical limitations (particularly in terms of the labour-intensive methodologies required) which have, until recently, prevented 'ecologically significant' numbers of individuals and species from being reliably sampled. Fortunately new methods are evolving which promise to make the complex task of quantifying xylem vulnerability accessible to researchers outside the small community of plant hydraulic specialists. The most recent of these new methods is an optical technique that allows cavitation to be visualized and quantified using unsophisticated imaging technology such as cameras or flatbed scanners (Brodribb *et al.*, 2016). Such tools will soon make it possible to assess the xylem vulnerability of whole plant communities, adding a mechanistic perspective that will provide powerful new insights into the process of plant community assembly.

Can xylem vulnerability become a super trait with the capacity to globally predict species distribution and drought sensitivity? The short answer is that xylem vulnerability can reliably inform us when a plant is likely to die from drought (Brodribb & Cochard, 2009; Urli *et al.*, 2013), but more information is required to precisely explain the outcome of competition for water resources between disparate taxa. For example, despite the excellent correlations shown by Larter *et al.* (2017), the relationship between rainfall distribution and resistance to cavitation (P_{50}) becomes much less predictive when different conifer families are compared (Brodribb *et al.*, 2014). The reason for this is that xylem cavitation determines a lethal threshold of dehydration, yet the rate at which plants approach this deadly threshold is determined by other traits such as evaporation rate, rooting depth and plant capacitance, all of which appear to vary considerably between plant species.

Among these other traits, stomatal control of evaporation has traditionally been the most difficult to unravel, due to the complexity of stomatal physiology. However, recent years have seen a number of advances in our understanding of stomatal behaviour during drought, and these promise to make the process of stomatal closure during water stress a more tractable trait for use in ecological analysis. One such advance develops from the well-known observation that the water potential at stomatal closure can be reasonably estimated from the turgor-loss point of the leaf (Raschke, 1975). Recent work shows how this previously time-consuming measurement can be very quickly estimated from rapid psychrometric measurement of leaf discs (Bartlett *et al.*, 2012), opening up the prospect of evaluating evolutionary variation in stomatal control across plant communities. In addition to such technical advances are conceptual insights linking plant hydraulics,

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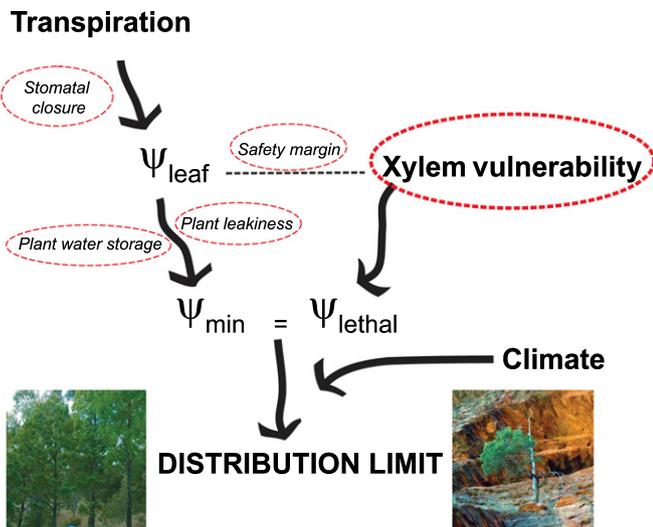


Fig. 1 Links between functional traits, climate and plant distribution. The framework is broken down to key processes responsible for correlations between plant distribution and hydraulic physiology. These 'mechanistic traits' (circled) together determine the time between the cessation of rainfall and the death of an individual by hydraulic failure (when minimum water potential – Ψ_{min} is equal to the lethal threshold – Ψ_{lethal}). Climate parameters such as rainfall and evaporation then determine where species can inhabit without suffering hydraulic failure. A very tough species, the Australian conifer, *Callitris*, is shown growing in the middle (left), and at the edge of its distributional range (right).

leaf hormone production and stomatal dynamics. This integrated approach lends itself to mechanistic modelling and is likely to provide a quantitative explanation for diversity in stomatal sensitivity to dehydration (Deans *et al.*, 2017), progressing from the dichotomous view of stomatal behaviour as either isohydric or anisohydric (Martínez-Vilalta & Garcia-Fornier, 2016). Combining stomatal control information with xylem vulnerability to embolism provides critical information about so-called 'safety margins' in plant species (Fig. 1), describing the proximity of stomatal closure and hydraulic failure. This important trait appears to range enormously among species, and is likely to be highly adaptive in water-limited environments.

One key part of the equation linking rainfall deficit to death by hydraulic failure that remains poorly defined is the magnitude of the residual leak of water from leaves after stomata have closed. During water stress, leaf transpiration becomes massively reduced as stomata close, greatly delaying the onset of cavitation. However, when exposed to prolonged drought, plants continue to slowly dry after stomatal closure, and the rate of this residual transpiration is a critical determinant of how long trees can avoid the long-term damage caused by cavitation (Fig. 1). The amount of leakage can vary greatly among species (Schreiber & Riederer, 1996) and future work will be critical in determining how much of this vapour leak is due to incomplete stomatal closure, and how much is due to cuticular water loss.

Modellers and ecologists now recognize the importance of using algorithms based on realistic physiological control in order to explain global vegetation patterns (Mitchell *et al.*, 2016). These new models must ultimately connect research at the

microscopic and molecular-scale (e.g. guard cells and xylem conduits), to macroscopic fluxes and storage of water. Critical in this process are studies such as Larter *et al.* (2017) that identify mechanistic traits operating at broad phylogenetic and ecological timescales. Such studies inform us about the key drivers and processes that determine plant distribution, based upon evidence from plant adaptation in natural systems, but must be carefully interpreted to consider the possible impact of other key limiters of distribution, such as cold and disturbance (e.g. by fire and biotic agents). Based on a number of similar large-scale studies (Brodrribb *et al.*, 2014; Anderegg *et al.*, 2015) we can now confidently use xylem vulnerability in combination with climate data to predict the distribution, or drought damage in particular species or clades. The future challenge will be to understand how this trait interacts with other processes, such as stomatal behaviour and carbon costs of construction and respiration (McDowell *et al.*, 2013), such that general models of plant ecohydrology can be used to predict the impact of rainfall on plant community assembly.

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