

## FE SPOTLIGHT

## New insight into leaf drought tolerance

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Drought-induced forest dieback appears to have increased in frequency over the last decade (Van Mantgem *et al.* 2009; Allen *et al.* 2010; Peng *et al.* 2011). These diebacks have occurred across a wide diversity of forest types, suggesting that no forest biome is invulnerable to climate change (Choat *et al.* 2012). However, drought-influenced mortality rates differ substantially between species growing at the same site (Breshears *et al.* 2005) and populations within the species' distribution range (Benito-Garzón, Ruiz-Benito & Zavala 2013). These dieback episodes may therefore lead to major vegetation shifts, substantial decreases in carbon uptake by the ecosystem (Ciais *et al.* 2005), and interactions, with invading alien species, for example. We need to understand the mechanisms by which drought stress affects tree performance and causes tree dieback if we are to identify the forests most vulnerable to climate change and to predict important vegetation processes, such as changes in community composition caused by differential plant mortality among species.

Many studies have tried to identify the traits associated with improved plant survival during periods of drought. Three main strategies have been identified: water stress tolerance, avoidance and escape (see Fig. 1). Escape is when plants are temporarily absent during the drought period, due to mechanisms such as the shedding of leaves, as in ephemerophytes that complete their life cycle very rapidly and enter a dormant state during the long dry period in deserts. Avoidance includes a variety of mechanisms delaying or preventing the negative impact of stress. For drought stress, this involves minimization of water loss in plants experiencing drought, for instance, through strong stomatal closure to prevent decreases in water potential and subsequent runaway embolism. Tolerance involves xylem vascular system and/or leaf cells resisting dehydration (in plants able to sustain very negative water potentials) through the construction of xylem conduits resistant to cavitation and the maintenance of cell turgor. New technologies developed over the last 15 years have made it possible to assess xylem resistance to cavitation in many species (Delzon *et al.* 2010; Cochard *et al.* 2013) and populations within species (Lamy *et al.* 2014). However, the broad characterization of turgor loss point has proved more of a challenge.

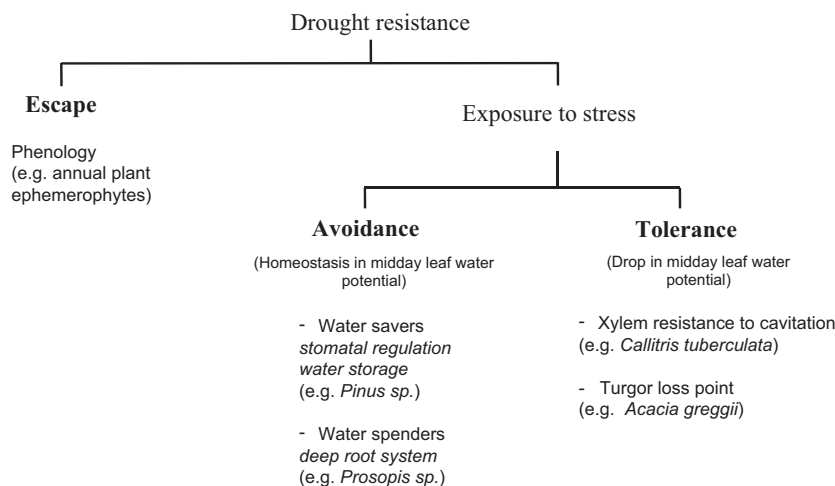
In this issue of *Functional Ecology*, Maréchaux *et al.* 2015; report an investigation of the leaf water potential at

turgor loss point ( $\pi_{tlp}$ ) for a broad range of tropical tree species (71 in total). They report significant differences in  $\pi_{tlp}$  values between species and show that  $\pi_{tlp}$  might be associated with ecological drought tolerance (species with high  $\pi_{tlp}$  are more frequently distributed in the tropical forest studied). Species growing in drier biomes have also been shown to have more negative values of  $\pi_{tlp}$  (Bartlett, Scoffoni & Sack 2012b). Maréchaux *et al.* 2015 also provide evidence for the absence of a link with leaf economic spectrum, particularly as concerns specific leaf area (SLA). Together with the lack of relationship between SLA and forest water availability, these results strongly suggest that the broad and untimely use of SLA to predict species drought tolerance and distribution is likely to yield misleading results. The inclusion of  $\pi_{tlp}$  in process-based vegetation models could therefore improve the accuracy of predictions of climate change impacts on forest ecosystems. Future studies are nevertheless required to confirm the correlation between leaf water potential at turgor loss point and species habitat suitability over a broader range of soil water availability.

In this study, Maréchaux *et al.* 2015; used a recently developed method based on the use of an osmometer to predict  $\pi_{tlp}$  (Bartlett *et al.* 2012a). This method is based on the accurate prediction of  $\pi_{tlp}$  by leaf osmotic water potential at full hydration, as experimentally determined for 30 species by Bartlett *et al.* (2012a). This is consistent with interspecific differences in  $\pi_{tlp}$  being driven principally by osmotic rather than elastic adjustments (Lenz, Wright & Westoby 2006; Bartlett, Scoffoni & Sack 2012b). This technique is much faster than the commonly used pressure–volume curve approach, opening up new possibilities for studying leaf drought tolerance within (phenotypic plasticity and genetic differentiation) and between (at the community and biome levels) species. It is particularly useful for studies in tropical forests, in which most of the plant species present have long vessels, making it more difficult to measure xylem resistance to cavitation, and making it all the more necessary to identify traits useful for the assessment of drought tolerance.

Many studies have shown that leaf water potential at turgor loss point ( $\pi_{tlp}$ ) plays a key role in maintaining gas exchanges and growth rate under moderate water stress (Brodribb *et al.* 2003; Mitchell *et al.* 2008), but the direct relationship between  $\pi_{tlp}$  and drought-induced tree mortality has never been investigated. As in the xylem hydraulics community, which has used the xylem

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**Fig. 1.** The three strategies allowing a plant to survive drought. Escape is defined as a temporal absence during the drought period, due to the shedding of leaves, as in ephemerophytes. Avoidance is the minimization of water loss in plants experiencing drought or an increase in water uptake, through better stomatal control or a greater investment in the below-ground biomass, respectively. The midday leaf water potential is therefore maintained relatively constant despite fluctuations in soil water content. Tolerance involves mechanisms allowing plants to survive dehydration by constructing xylem conduits more resistant to cavitation and implosion and/or by having a more negative turgor loss point, corresponding to the water potential at which leaf cells lose turgor (leaf wilting). *Callitris tuberculata* is the species with the highest level of cavitation resistance ever measured ( $-18.8$  MPa, Larter *et al.* 2015), whereas *Acacia greggii* is the species with the most negative turgor loss point ( $-4.25$  MPa, Bartlett, Scoffoni & Sack 2012b). Those species can withstand low water potentials.

pressure inducing a 50% loss of hydraulic conductance ( $P_{50}$  in MPa) for many years without knowing the physiological and ecological significance of this trait, urgent investigations of the link between  $\pi_{tlp}$  and tree survival under conditions of severe drought are required. One appropriate strategy would be to carry out the drought-recovery experiments recently proposed for the characterization of cavitation thresholds linked to the lethal water potential (minimum survivable water potential) in both angiosperms (Urli *et al.* 2013) and conifers (Brodribb & Cochard 2009). Is the  $\pi_{tlp}$  reported by Maréchaux and colleagues equivalent to the threshold of xylem cavitation ( $P_{88}$ ) leading to death in angiosperms (Delzon & Cochard 2014)? A meta-analysis of the correlation between  $\pi_{tlp}$  and xylem resistance to cavitation would be highly informative, as very little is currently known about links to hydraulic failure in leaves and stems (Blackman, Brodribb & Jordan 2010). However, as  $\pi_{tlp}$  seems to be more strongly correlated with the water potential at stomatal closure, its absolute values should be much higher than the minimum survivable water potential. In conclusion,  $\pi_{tlp}$  is a key trait that can be used to characterize the ability to maintain leaf function under moderate drought, although further studies are required to determine the extent to which it is useful as a fitness trait under conditions of severe drought.

Finally, regarding the current debate about whether hydraulic failure or carbon starvation is the key process underlying tree mortality during severe or acute drought, a recent study by O'Brien *et al.* (2014) showed that non-structural carbohydrate (NSC) reserves attenuate the effect of drought, likely by maintaining a higher osmolality.

Experimental evidence is required to confirm this maintenance of osmoregulation and could be potentially be acquired by comparing the change in  $\pi_{tlp}$  in response to drought between trees with depleted and enriched reserves.  $\pi_{tlp}$  has indeed been reported to display plasticity in response to increases in drought stress: solute accumulation shifts  $\pi_{tlp}$  to more negative values (Bartlett *et al.* 2014). The use of this trait should help to resolve the debate, by improving our understanding of the role of NSC as a source of organic solutes.

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