Letter

On research priorities to advance understanding of the safety–efficiency tradeoff in xylem

A response to Bittencourt et al.'s (2016) comment 'On xylem hydraulic efficiencies, wood space-use and the safety–efficiency tradeoff'

We appreciate Bittencourt et al.'s (2016) constructive contributions following our paper, Gleason et al. (2016), on the proposed tradeoff between hydraulic safety and efficiency. To continue this dialog we would like to comment on which of the research directions proposed by Bittencourt et al. seem most promising to us.

We agree that various xylem tissue fractions could potentially modify the safety–efficiency relationship. In principle, any tissue fraction could trade off with any other tissue fraction. However, as a matter of observation, parenchyma fraction is negatively correlated with fiber fraction, whereas parenchyma and fiber fractions are not strongly correlated with vessel lumen fraction (Ziemińska et al., 2015; Morris et al., 2016). As such, vessel lumen fraction, vessel diameter, and vessel frequency are largely uncoupled from nonvessel tissue fractions across self-supporting angiosperm species (Zanne et al., 2010), and are therefore unlikely to trade off with mechanical safety and hydraulic efficiency (or safety). Furthermore, vessel lumen fraction itself does not vary markedly across angiosperms, ranging from c. 5% to 20% (mean ≈ 15%) (Zanne et al., 2010; Morris et al., 2016), although larger fractions are not uncommon in ring-porous and climbing species. Contrasts between climbing (e.g. lianas) and freestanding growth forms are more likely to show differences in allocation to vessel vs nonvessel space, and the climbing habit therefore may offer a more appropriate system for evaluating this idea (Gartner, 1991).

Gymnosperm xylem differs from angiosperm xylem in that it generally lacks axial parenchyma, and conduits are both conductive and load-bearing. Greater *mechanical* safety may be negatively correlated with both hydraulic safety and efficiency across gymnosperm species (Mayr & Cochard, 2003; Mayr et al., 2003). Considering angiosperms, it is likely that nonvessel tissue fractions influence the safety–efficiency tradeoff indirectly (e.g. via their contribution to xylem capacitance, or whole-plant growth), rather than being forced by limited xylem space.

Bittencourt et al. suggest that expressing conductivity as a ratio with mass, rather than cross-sectional area, might better characterize the energetic costs associated with xylem. We agree with this

suggestion and did consider the influence of specific gravity on the safety–efficiency tradeoff in our paper (Table 2 and Figs 3d, 4d in Gleason et al., 2016). Here, we formulate these results by expressing the y axis explicitly as xylem-specific conductivity/specific gravity (Fig. 1), as suggested by Bittencourt et al. Specific gravity, safety and efficiency values were generally obtained from the same published reports. Similar to the results we report in Gleason et al. (2016), including specific gravity in the analyses increases the tradeoff r^2 in both angiosperms (0.11–0.14) and gymnosperms (0.10–0.15) when safety is defined as P_{50}. A similar increase in r^2 is achieved when defining safety as P_{88} and there is no change when defining safety as P_{12}. Although including xylem density does increase the amount of variation explained by the models, they still fall far short of explaining why many species exhibit both low safety and low efficiency.

Despite the analysis provided in Fig. 1, we feel that the clearest approach to analyzing these inter-correlated variables will be to consider all known sources of variation (e.g. structural equation models) rather than expressing them as a ratio with conductivity (e.g. conductivity/parenchyma fraction). Such ratios build an assumption of proportionality between the two elements of the ratio, which are not necessarily what we should expect.

It remains a possibility that xylem safety, expressed as the xylem water potential at which a fraction of maximal conductance is lost, may not be an accurate approximation for all species in all situations. Although we agree *in principle* that safety (e.g. P_{50}) may not correlate with mortality similarly across species, there is good evidence to suggest that it does for many angiosperm and gymnosperm species (Pratt et al., 2008; Brodribb & Cochard, 2009; Brodribb et al., 2010). This suggests that there may be an intrinsic property of xylem to resist desiccation (angiosperm $\Psi_{leaf} > P_{88}$; gymnosperm $\Psi_{leaf} > P_{50}$), beyond which the probability of mortality increases precipitously. Measurements of hydraulic safety, as well as conductivity during drought, should serve as more appropriate predictors of mortality than other measurements of water status (e.g. turgor loss point in leaves or stomatal response) because percentage loss of conductance is a meaningful representation of xylem desiccation. However, it is also clear that there are mechanisms that delay the time to reach a desiccation–mortality threshold. As suggested by Bittencourt et al. and Brodersen (2016), these would include deciduousness, deep rooting, reduced stomatal 'leakiness', reduced cuticular conductance, CAM and C_4 metabolism, and capacitance. However, considering tradeoffs with either safety or efficiency, in isolation of one another (e.g. safety–capacitance), does not inform our efforts to understand the proposed link between safety and efficiency. For example, if greater capacitance reduces the requirement for safety, natural selection should still be free to improve efficiency, which would provide benefit via greater
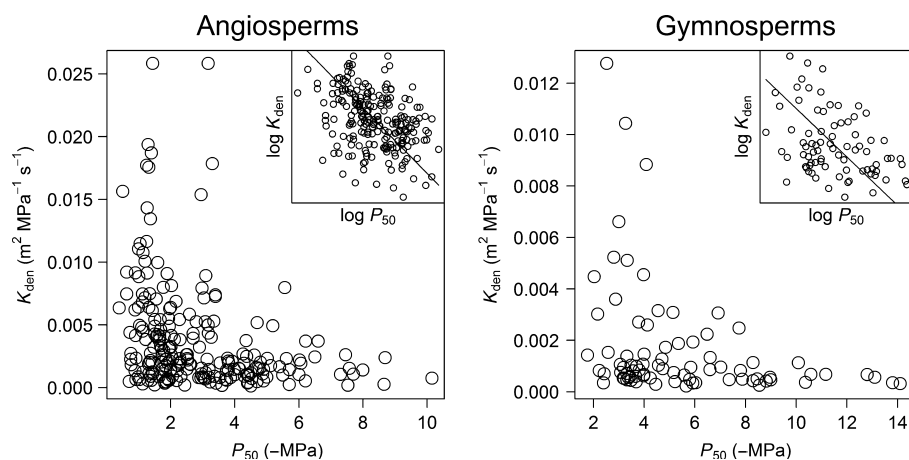
Fig. 1 Hydraulic efficiency (K_{den})–hydraulic safety (P_{50}) plots for all angiosperm and gymnosperm species. Efficiency is expressed per unit specific gravity (K_{den}), i.e. xylem-conductivity/specific gravity. Inset plots have been drawn to show log-transformed relationships. Fitted angiosperm model: $r^2 = 0.137$, $P < 0.001$, $n = 222$. Fitted gymnosperm model: $r^2 = 0.154$, $P < 0.001$, $n = 80$.

stomatal conductance or lower stem construction and maintenance costs.

In addition to acquiring traits that delay the onset of critical levels of xylem desiccation, individual species within communities may have different strategies for tolerating embolism, and these could modify the safety–mortality relationship, e.g. *Coleogyne ramosissima* in Jacobsen *et al.* (2008), which routinely tolerates > 50% loss of stem conductivity. Species that exhibit re-sprouting after permanent damage to the xylem may have lower whole-plant mortality rates at a given level of xylem safety (Pratt *et al.*, 2007). The presence of nonperforate tracheary elements (e.g. vasicentric and true tracheids) may represent a small, but particularly robust contribution to water transport, and confer greater survival at a given level of safety (Carlquist, 1984; Pratt *et al.*, 2015). Recovery strategies, based on formation of new xylem or repair of embolized xylem (Nardini *et al.*, 2011; Mayr *et al.*, 2014; Earles *et al.*, 2016), may allow species to tolerate greater levels of conductivity loss.

The proximate causes for why safety and efficiency should tradeoff with one another are a separate issue from the ecological contexts in which it occurs. For example, a species may be present in a habitat that requires less hydraulic efficiency (or safety) but this does not inform us about which xylem or vessel traits should give rise to a tradeoff in the first place. Determining the proximate causes of safety and efficiency are important, e.g. Wheeler *et al.* (2005), Loepfe *et al.* (2007), Schenk *et al.* (2015). In particular, understanding why pit-level tradeoffs exist but are not manifested at the branch level is an important gap in the current state of our field. Mechanistic information that would allow up-scaling safety and efficiency from the pit- to plant-level, if aligned with the proper genetic understanding, could be used to improve plant performance in dry habitats (e.g. crop and forestry species). We suggest this area of research could potentially provide a large social benefit.

Progress on the issues discussed here and in Bittencourt *et al.* would benefit by considering the 'currency' in which conductivity loss should be evaluated. Declining xylem water potential and subsequent loss of conductivity during drought will eventually result in mortality if precipitation is not received to alleviate stress. If we think mortality should be our focus, then we can understand its effect on metapopulations from a demographic approach (Martínez-Vilalta *et al.*, 2010). When precipitation is received

before plant death, damaged xylem must be replaced (Brodribb *et al.*, 2010) or refilled (Nardini *et al.*, 2011; Earles *et al.*, 2016), but see Cochard & Delzon (2013). If xylem refilling represents an important cost, then the refilling mechanism itself must first be understood before costs can be estimated. However, if damaged xylem cannot be refilled (Cochard & Delzon, 2013; Choat *et al.*, 2015), we might expect photosynthesis to be reduced until new xylem can be added. This loss of photosynthetic income is likely to be important, and therefore, we need to know its cost, as well as the cost of xylem replacement. Choosing the most appropriate among these currencies will be important for assessing the tradeoffs involved in plant water transport.

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