Comment

Comment on Coomes *et al.* 'Scaling of xylem vessels and veins within the leaves of oak species'

Coomes *et al.* (2008) purport to test the predictions of the plant scaling model of West *et al.* (1999) by examining the scaling of xylem dimensions in 10 species of oaks (*Quercus* spp.). While we commend their efforts to gather much needed data on the scaling of xylem dimensions in leaves, their representation of the West, Brown and Enquist (WBE) model is based on incorrect assumptions, and their application of the WBE model to leaves requires significant correction.

First and foremost, the original model derivation of West *et al.* (1999) was never intended to be applied to leaves. Leaves within the model, and more specifically, the dimensions of xylem bundles within the petiole are assumed to be statistically invariant with changes in plant size. This does not mean that variability in the xylem dimensions across petioles of different species, or even within leaves of the same plant, does not exist, but rather that this variability does not change systematically as a function of size across plant species. For example, as a justification for their study, Coomes *et al.* (2008) state that 'For convenience (the WBE model has) considered petioles as the end of the transport system. However, the leaf accounts for 30% of the plant resistance... Thus, closer examination of scaling within leaves is important for predictions at the plant level.' This is a misleading statement with regard to the predictions of the WBE model. WBE predictions do not depend on the magnitude of the hydraulic resistance within leaves nor variability in xylem traits *per se*, but only require that vascular, physiological and hydraulic traits do not systematically scale with plant size. We are unaware of data showing a systematic change in petiole xylem dimensions or hydraulic properties across species that differ in adult size. Indeed, in support of this key WBE model assumption, Coomes and colleagues state that 'The leaf xylem properties were not correlated with... the average size of the adult tree.'

Second, Coomes *et al.* (2008) claim that the 'General models of plant vascular architecture... have neglected to consider the leaf...' This is not correct. The scaling of leaf vascular dimensions have already been specifically addressed by Price & Enquist (2007). This was done because several assumptions of the original model are clearly violated in leaves. In particular, leaves are not volume filling; are not typically hierarchical trees, rather they are reticulate, forming loops; leaves are composed of typically only a few branching generations; and leaf xylem is known to be 'leaky'. These and other issues were addressed in an extension of the WBE model (Price & Enquist 2007) that the authors did not cite in

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which we state, '...that no single 'universal' exponent(s) will describe scaling relationships across all leaves'. Because leaves lose liquid volume to transpiration, particularly in the higher order veins, a strict universal tapering rule is not expected to apply.

Third, Coomes *et al.* (2008) misinterpret the xylem vessel tapering predictions of the WBE model. They state that it '...predicts that the length dependence of hydraulic resistance is practically removed from branching stem systems when $d_h \propto D^{1/6}$...' The WBE model predicts that the hydraulic resistance is independent of path length if the scaling exponent is *greater than* or approximately equal to 1/6. This is a subtle but critically important distinction, as the WBE model predicts that xylem tapering will be optimal if the scaling exponent for the relationship between d_h and D is greater than 1/6. Indeed, the scaling exponents reported by Coomes and colleagues are greater than 1/6, indicating that the hydraulic resistance is independent of path length as predicted by the WBE model.

Fourth, Coomes *et al.* (2008) appropriately cite West *et al.* (1999) for the derivation of the tapering exponent; however, they fail to report that it also included box 2 of West *et al.*, as a caution about applying the tapering exponent to networks with few branching generations. Specifically, when N is small, as is the case in leaves (most leaves have approximately three to five branching generations), '...the correction can be large'. In fact, taking $N=3$ and $n=2$, common values for leaves yields $\alpha=0.41$, consistent with the lower end of the range of values reported by Coomes and colleagues. We report this value, not to validate the use of the tapering rule in leaves, but simply to illustrate that small networks, as found in leaves, were predicted to have significant tapering departures. However, the aforementioned violations of the models and other assumptions make this application unfounded.

Clearly, leaves will be important for understanding the nature of plant hydraulics and physiological scaling within plants. The empirical findings of Coomes *et al.* (2008) are important in furthering our understanding of the xylem dimensions in leaves. However, testing a model beyond its intended scope is essentially a straw man. A complete understanding of plant hydrodynamics will probably require both theoretical models that incorporate more biological variability and empirical data and testing within the appropriate scale of inference.

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