Invited reply

Response to comment on Coomes *et al.* ‘Scaling of xylem vessels and veins within the leaves of oak species’

We are pleased that Price and Enquist (P&E) have come to appreciate the important contribution that leaves make to whole-plant hydraulic resistance. We wish to point out, however, that our paper did not ‘purport to test’ the theory of West, Brown & Enquist (‘WBE’; West *et al.* 1999), as they claim. Instead, we examined novel scaling patterns for leaf venation that were neglected by WBE. We respond to their four points, and explain why we advocate a different approach from WBE.

(i) P&E argue that WBE was never intended to be applied to leaves. We agree. We stated explicitly that WBE neglected leaves, and that they considered only stem xylem. Furthermore, our paper gave several reasons, now repeated by P&E, why WBE should not be applicable to leaves, because leaf vascular systems are fundamentally different from those of stems. In our paper, we did consider whether models of whole-plant vascular scaling, such as WBE, could be justified in neglecting leaves: that might be the case if leaf xylem conduits tapered identically to those of stem, or if leaves were invariant hydraulically. However, leaf and stem xylem taper differently, and leaves vary hydraulically across species, and within canopies (Sack & Holbrook 2006), necessitating the inclusion of leaves in realistic models of whole-plant vasculature. P&E further stated that WBE would be justified in neglecting leaves if leaf xylem conduit size is uncorrelated with plant size, and that they were unaware of such a correlation. However, for species sets in which leaf and plant size are correlated, this scaling may be expected (e.g. Dunbar-Co *et al.* 2009). None of the reasons for neglecting leaves are convincing, and we question the relevance of models of whole-plant vascular architecture that do not include them.

(ii) P&E claim that they produced a model of plant vascular architecture that includes leaf vasculature. P&E (2007) presented scaling relationships for leaf simple dimensions—area, mass, length and petiole outer diameter—for 21 species, but they did not actually present data or make any prediction for leaf or plant vascular anatomy or hydraulics. P&E (2007) also speculated on further implications of their scaling relationships, but one major testable prediction, that photosynthetic rate per leaf mass should generally decline with increasing leaf size in dicotyledonous

species, has not been supported by empirical studies of diverse species (e.g. Ackerly & Reich 1999). Thus P&E (2007) was peripheral to our topic, and we were unable to discuss it given the limited space available.

(iii) P&E claimed that we misinterpreted the xylem vessel tapering predictions of WBE. In discussing stem xylem vessel tapering, we simply repeated exactly the prediction made by WBE for the optimal value of the tapering parameter $\hat{a}$: ‘for $\hat{a} > 1/6$, Z_i [the total hydraulic resistance of a tapering tube running from the trunk to the petiole in a tree] is a constant independent of the total tube length and is the same for all plants, regardless of size ... To avoid excess tapering, $\hat{a}$ should be the minimum possible value consistent with constant Z_i , namely $1/6$ ’. P&E alert readers to the first part of this passage, but neglect the second part. In any case, we found a stronger tapering of conduits in leaves than predicted, or observed for stems (e.g. Coomes *et al.* 2007). However, contrary to what P&E claim, recent work indicates this tapering of conduits in leaves would not principally function to mitigate increasing leaf hydraulic resistance (R_{leaf}) with increasing xylem path length. R_{leaf} typically decreases with increasing vein length per leaf area, because of a greater number of parallel flow pathways, greater permeable surface area, and/or shorter extra-vascular pathways (Sack & Frole 2006; Brodribb *et al.* 2007).

(iv) P&E claim that WBE should not be applied to leaves but then use WBE to make a prediction for leaves. P&E derived a value of $\hat{a}$ of 0.41, without providing their calculations, on the basis that ‘most leaves have approximately three to five branching generations’. We question the reasoning, and also these data; actual dicotyledonous leaves commonly have up to six to seven branching orders (LAWG 1999). We welcome an appropriate application of models based on correct information.

We are excited by the promise of new models of plant vascular function that include leaves. To that end, we welcome new, theoretical models based on knowledge of real processes. When knowledge does not exist for accurate allometric modelling, we advocate for classical, ground-up studies: fitting allometries to data, testing specific hypotheses for observed relationships, and linking relationships when adequate insight is available. Using these approaches, ongoing scaling studies can yield reliable and long-lasting understanding of the important function of leaves and whole plants.

D. A. Coomes^{1,*} and L. Sack²

¹Forest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK

²Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA

*dac18@cam.ac.uk

Ackerly, D. D. & Reich, P. B. 1999 Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *Am. J. Bot.* **86**, 1272–1281. (doi:10.2307/2656775)

Brodribb, T. J., Feild, T. S. & Jordan, G. J. 2007 Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiol.* **144**, 1890–1898. (doi:10.1104/pp.107.101352)

The accompanying comment can be viewed on page 380 or at <http://dx.doi.org/doi:10.1098/rsbl.2009.0013>.

- Coomes, D. A., Jenkins, K. L. & Cole, L. E. S. 2007 Scaling of tree vascular transport systems along gradients of nutrient supply and altitude. *Biol. Lett.* **3**, 86–89. (doi:10.1098/rsbl.2006.0551)
- Dunbar-Co, S., Sporck, M. J. & Sack, L. 2009 Leaf trait diversification and design in seven rare taxa of the Hawaiian *Plantago* radiation. *Int. J. Plant Sci.* **170**, 61–75. (doi:10.1086/593111)
- LAWG 1999 *Manual of leaf architecture: morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms*. Washington, DC: Smithsonian Institution. See <http://www.peabody.yale.edu/collections/pb/MLA>.
- Price, C. A. & Enquist, B. J. 2007 Scaling mass and morphology in leaves: an extension of the WBE model. *Ecology* **88**, 1132–1141. (doi:10.1890/06-1158)
- Sack, L. & Frole, K. 2006 Leaf structural diversity is related to hydraulic capacity in tropical rain forest trees. *Ecology* **87**, 483–491. (doi:10.1890/05-0710)
- Sack, L. & Holbrook, N. M. 2006 Leaf hydraulics. *Annu. Rev. Plant Biol.* **57**, 361–381. (doi:10.1146/annurev.arplant.56.032604.144141)
- West, G. B., Brown, J. H. & Enquist, B. J. 1999 A general model for the structure and allometry of plant vascular systems. *Nature* **400**, 664–667. (doi:10.1038/23251)