



## **Apparent over-investment in leaf venation relaxes leaf morphological constraints on photosynthesis in arid habitats**

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The close relationship between leaf water status and stomatal conductance implies that the hydraulic architecture of leaves poses an important constraint on transpiration, specifically in arid environments with high evaporative demands. However, it remains uncertain how morphological, hydraulic and photosynthetic traits are coordinated to achieve optimal leaf functioning in arid environments. Critical is that leaf veins supply the mesophyll with water that evaporates when stomata are open to allow CO<sub>2</sub> uptake for photosynthesis. Theoretical analyses suggest that water is optimally distributed in the mesophyll when the lateral distance between veins ( $dx$ ) is equal to the distance from these veins to the epidermis ( $dy$ ), expressed as  $dx:dy \approx 1$ . Although this theory is supported by observations on many derived angiosperms, we hypothesize that plants in arid environments may reduce  $dx:dy$  below unity owing to climate-specific functional adaptations of increased leaf thickness and increased vein density. To test our hypothesis we assembled leaf hydraulic, morphological and photosynthetic traits of 68 species from the *Eucalyptus* and *Corymbia* genera (termed eucalypts) along an aridity gradient in southwestern Australia. We inferred the potential gas exchange advantage of reducing  $dx$  beyond  $dy$  using a model that links leaf morphology and hydraulics to photosynthesis. Our observations reveal that eucalypts in arid environments have thick amphistomatous leaves with high vein densities, resulting in  $dx:dy$  ratios that range from 1.6 to 0.15 along the aridity gradient. Our model suggests that as leaves become thicker, the effect of reducing  $dx$  beyond  $dy$  is to offset the reduction in leaf gas exchange that would result from maintaining  $dx:dy$  at unity. This apparent over-investment in leaf venation may be explained from the selective pressure of aridity, under which traits associated with long leaf lifespan, high hydraulic and thermal capacitances, and high potential rates of leaf water transport confer a competitive advantage. Our results highlight the need to consider the specific leaf hydraulic architecture of aridity-adapted plants when studying ecohydrological processes in arid ecosystems.