

## Aridity induces super-optimal investment in leaf venation by *Eucalyptus* and *Corymbia*

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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 carbon uptake, 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.

Zwieniecki and Boyce (2014) proposed a generic framework on the hydraulic architecture of leaves based on the argument that water is optimally distributed when the lateral distance between neighboring water transport veins  $(d_x)$  is approximately equal to the distance from these veins to the epidermis  $(d_y)$ , expressed as  $d_x:d_y \approx 1$ . Many derived angiosperms realize this optimal hydraulic architecture by closely coordinating leaf vein density with leaf thickness and the lateral position of veins inside the leaf. Zwieniecki and Boyce (2014) further suggested that over-investment in veins  $(d_x:d_y < 1)$  provides no functional benefit owing to the minor additional increases in leaf gas exchange that may be achieved by reducing  $d_x$  beyond  $d_y$ .

Although this framework is valid for derived angiosperms adapted to temperate and moist (sub)tropical environments, we hypothesize that super-investment in leaf venation (resulting in dx:dy<<1) may provide a specific gas exchange advantage in arid environments that select for thick and amphistomatous leaf morphologies. The relatively long  $d_y$  inherent to these leaf morphologies imposes hydraulic constraints on productivity that may (partially) be offset by reducing  $d_x$  beyond  $d_y$ . To test our hypothesis we assembled the leaf hydraulic, morphological and photosynthetic traits of 65 species (401 individuals) within the widely distributed and closely related genera *Eucalyptus* and *Corymbia* along a 2000-km-long aridity gradient in Western Australia (see Schulze et al., 2006). We inferred the potential functional benefit of reducing  $d_x$  beyond  $d_y$  using a semi-empirical model that links leaf morphology and hydraulics to photosynthesis.

Our results reveal that *Eucalyptus* and *Corymbia* evolved extremely high vein densities in addition to thick amphistomatous leaf morphologies along the natural aridity gradient resulting in  $d_x:d_y$  ratios ranging between 0.8 and 0.08. We propose that as the thickness of amphistomatous leaves increases, the effect of reducing  $d_x$  beyond  $d_y$  is to offset the reduction in photosynthesis that would result from the theoretical optimal architecture of  $d_x:d_y \approx 1$ . Our model quantified the resulting relative gain in photosynthesis at 10% to 15%, which could provide a crucial gas exchange advantage. We conclude that aridity confounds selection for leaf traits associated with a long leaf lifespan and thermal capacitance as well as those supporting higher rates of leaf water transport and photosynthesis.

## References

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