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Angiosperms evolved a higher mesophyll surface area per volume to maximize exchange surface under a low CO_2 world

Guillaume Théroux-Rancourt (1), J. Mason Earles (2), Matthew E. Gilbert (1), Maciej A. Zwieniecki (1), C. Kevin Boyce (3), Andrew McElrone (4,5), and Craig Brodersen (2)

(1) Department of Plant Sciences, University of California, Davis, CA 95616, USA (gtrancourt@ucdavis.edu), (2) School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA, (3) Department of Geological Sciences, Stanford University, Stanford, CA 94305, USA, (4) USDA-Agricultural Research Service, Davis, CA 95616, USA, (5) Deparment of Viticulture and Enology, University of California, Davis, CA 95616, USA

Variation in leaf mesophyll structure strongly affects CO_2 diffusion and photosynthetic rates. One key trait is the surface of mesophyll cells exposed to intercellular airspace (S_m) which increases mesophyll conductance. Consequently, S_m is a key control of CO_2 diffusion among species and genotypes. Using S_m values from the literature ($>$ 200 species with 500 data points) and from our high-resolution X-ray computed tomography (μCT) dataset (currently 117 species), S_m shows little variation from pteridophytes to early angiosperms, while eudicots show the greatest structural diversity. However, S_m increases with total thickness of the mesophyll. By considering the exposed surface of the mesophyll to the intercellular air space (IAS) on a leaf or mesophyll volume (A_{mes}/V_{mes}) rather than leaf area basis (S_m), we demonstrate that angiosperms, and most specifically commelinids and non-basal eudicots, have constructed leaves with more surface per volume, while gymnosperms keep a constant A_{mes}/V_{mes} ratio. Thus, this strong phylogenetic signal suggests that angiosperms have developed IAS properties favoring leaves with higher surface to volume ratio, trait that allowed for the potential of high productivity even as atmospheric CO_2 declined over the Cenozoic.