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Beyond porosity: 3D leaf intercellular airspace traits that impact mesophyll conductance

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The leaf intercellular airspace (IAS) is generally considered to have a high conductance to CO_2 diffusion relative to the liquid phase. Yet, while previous studies accounted for leaf-level variation in porosity and mesophyll thickness, they omit inherently 3D IAS traits that potentially influence IAS conductance (g_{IAS}): tortuosity, lateral diffusivity, and IAS connectivity. We theoretically re-evaluated the standard equation for g_{IAS} by incorporating tortuosity, lateral diffusivity, and IAS connectivity. Then, we measured and spatially mapped these geometric IAS traits using X-ray microCT imaging and a novel computational approach within a broad range of species, from ferns to angiosperms, as well as within a family with diverse leaf architecture, the *Bromeliaceae*, including CAM and C3 species. photosynthesis. We found substantial variation in porosity, tortuosity, lateral diffusivity, and IAS connectivity across our dataset and especially in *Bromeliaceae* leaves, predicting significantly lower g_{IAS} in CAM versus C3 plants due to a coordinated decline in these traits. Moreover, we observed high spatial heterogeneity in these IAS geometric traits throughout the mesophyll, especially within CAM leaves. In conclusion, we argue that IAS traits beyond porosity influence g_{IAS} and that the impact of the IAS on mesophyll conductance should be carefully considered with respect to leaf anatomy, including stomatal distribution. Imaging tools such as X-ray microCT and novel 3D image processing techniques provide a platform for future investigation.