



Linking stomata geometries and densities to leaf gas exchange – new opportunities and old pitfalls

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Historical trends in stomatal sizes and numbers are believed to be directly related to trends in atmospheric CO₂ concentrations, where lower atmospheric CO₂ concentrations selected for larger leaf conductance to achieve adequate CO₂ assimilation rates. In addition to affecting maximum stomatal conductance, stomatal size is considered to affect transition time between full opening and full closure with smaller stomata responding faster. Stomatal sizes and numbers are often deduced by direct microscopy of leaf surfaces (fresh or fossil), or from nail polish imprints obtained from leaf epidermis. The maximum stomatal conductance is then calculated for fully open stomata of assumed aperture shape based on gas diffusion from within the leaf across a leaf boundary layer. Direct microscopic observations of leaves in specialised gas exchange chambers or snap-frozen leaves right after removal from a gas exchange chamber enabled correlation of actual stomatal apertures with directly measured bulk stomatal conductance. We combined systematic analyses of stomatal conductance and response times with laser scanning microscopy of epidermis imprints using fast setting dental imprint that preserve highly resolved stomatal apertures after removal from a gas exchange chamber. The simplicity of data collection relative to previous approaches enables data collection across a range of species with different stomatal sizes and numbers. The dataset was used to evaluate the adequacy of different physically-based stomatal conductance formulas based on geometrical attributes relative to measured conductance for a range of external CO₂ concentrations. We also investigated the link between stomata size and response time to environmental perturbation. Results point to uncertainties in inferred geometrical attributes and suggest highly patchy stomatal opening that complicates links between stomata aperture and density for estimation of actual stomatal conductance. Additionally, we identified exceedingly large uncertainty in inferred stomatal conductance values from standard gas exchange chambers (errors >100% of the nominal value) for conditions with high conductance and low gradients (e.g., high external relative humidity). Results help establish realistic bounds on conductance estimates from stomatal geometrical attributes and point to limitations of widely-used gas exchange methods for certain conditions.