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Scaling of stomatal size and density optimizes allocation of leaf epidermal space for gas exchange in angiosperms

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Stomata on plant leaves are key traits in the regulation of terrestrial fluxes of water and carbon. The basic morphology of stomata consists of a diffusion pore and two guard cells that regulate the exchange of CO_2 and water vapour between the leaf interior and the atmosphere. This morphology is common to nearly all land plants, yet stomatal size (defined as the area of the guard cell pair) and stomatal density (the number of stomata per unit area) range over three orders of magnitude across species. Evolution of stomatal sizes and densities is driven by selection pressure on the anatomical maximum stomatal conductance (gsmax), which determines the operational range of leaf gas exchange. Despite the importance of stomata traits for regulating leaf gas exchange, a quantitative understanding of the relation between adaptation of gsmax and the underlying co-evolution of stomatal sizes and densities is still lacking. Here we develop a theoretical framework for a scaling relationship between stomatal sizes and densities within the constraints set by the allocation of epidermal space and stomatal gas exchange. Our theory predicts an optimal scaling relationship that maximizes gsmax and minimizes epidermal space allocation to stomata. We test whether stomatal sizes and densities reflect this optimal scaling with a global compilation of stomatal trait data on 923 species reflecting most major clades. Our results show optimal scaling between stomatal sizes and densities across all species in the compiled data set. Our results also show optimal stomatal scaling across angiosperm species, but not across gymnosperm and fern species. We propose that the evolutionary flexibility of angiosperms to adjust stomatal sizes underlies their optimal allocation of leaf epidermal space to gas exchange.