Contrasting leaf thickness and saturated water content explain wide-ranging air/water fractions, nutrient contents, and water-use efficiency among arid succulents

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## Abstract

Eight species in the Namib Desert, South Africa were assessed for their leaf area (A), thickness (z), saturated (Q) and dry mass, relative volume of air ( $F_a$ ), water and dry mass, intrinsic water-use efficiency (based on  $\delta^{-13}$ C), and N, P and cation (Na+K) contents. As water-storage capacity is a function of  $Q_v$  and z, this means Q/A (=  $Q_v^*z$ ) is an ideal index of succulence compared with specific-leaf-area and other indices that highlight mass rather than volume. Specific gravity ( $\rho_1$ ) has a different relationship with the  $F_a$  of sclero-mesophylls: rising  $\rho_1$  infers decreasing air content is replaced by water rather than dry matter. The trend among succulent species, including Argentinian/Spanish added to our study, was Q/A exceeding 1 mg water/mm<sup>2</sup> whose overall slope was ten times that for co-occurring sclerophyll-mesophyll species, and shows the futility of seeking a universal relationship among plants regarding their water-storing properties. (Na+K), N and P concentrations varied on a dry-matter, but not water-volume, basis.  $W_1$  relationships were essentially functions of variations in z and increased metabolic efficiency. We conclude that z and  $Q_v$  are keys to the special physiological properties of succulent leaves. Adding succulents would force many current monotonic relationships to dichotomize.

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