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Calcium Compartmentation in Arabidopsis Mesophyll Cells, A Mechanism to Regulate Apoplastic Calcium, Photosynthetic Rates and Growth, Involves Low-affinity, High-capacity $\text{Ca}^{2+}/\text{H}^{+}$ Antiporters

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The way calcium (Ca) is stored in plants impacts upon plant, human and animal nutrition. An X-ray microanalysis study of over 40 angiosperm species has highlighted conserved accumulation patterns for Ca across different plant families; Ca is often stored in specific leaf cell-types. For instance, in grass monocots Ca accumulation occurs within vacuoles of epidermal cells whereas in the majority of eudicots Ca is predominantly stored within mesophyll cell vacuoles. To correlate gene expression with Ca accumulation profiles we micropipetted RNA from epidermal and mesophyll cells of the eudicot *Arabidopsis thaliana*. Cell specific RNA libraries were analysed by microarray and qPCR revealing a number of candidate membrane transporters with greater relative expression in the Ca-rich mesophyll. Knockout mutagenesis of one candidate *AtCAX1*, a tonoplast-localized $\text{Ca}^{2+}/\text{H}^{+}$ -antiporter, resulted in no mutant phenotype. When the expression of *AtCAX3*, a complementing family member was also abolished, this resulted in a reduction in total leaf [Ca] and perturbation of the Ca distribution pattern. The double knockout plant had a 3-fold higher apoplastic [Ca] which correlated with reduced stomatal conductance, photosynthetic rate and consequently growth. Apoplastic [Ca], stomatal conductance and growth rate could be recovered to wild-type levels by reducing [Ca] in the growth medium. We implicate CAX1 and its homologues as major regulators of Ca distribution and apoplastic [Ca] in leaves within and between plant orders. Such information will be helpful for the manipulation of Ca within specific cell types of leafy vegetables as a tool for improving human and animal nutrition.