**Subfunctionalization of cellulose synthases in seed coat epidermal cells mediates secondary radial wall synthesis and mucilage attachment.**

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**Abstract**

Arabidopsis (Arabidopsis thaliana) epidermal seed coat cells follow a complex developmental program where, following fertilization, cells of the ovule outer integument differentiate into a unique cell type. Two hallmarks of these cells are the production of a doughnut-shaped apoplastic pocket filled with pectinaceous mucilage and the columella, a thick secondary cell wall. Cellulose is thought to be a key component of both these secondary cell wall processes. Here, we investigated the role of cellulose synthase (CESA) subunits CESA2, CESA5, and CESA9 in the seed coat epidermis. We characterized the roles of these CESA proteins in the seed coat by analyzing cell wall composition and morphology in cesa mutant lines. Mutations in any one of these three genes resulted in lower cellulose content, a loss of cell shape uniformity, and reduced radial wall integrity. In addition, we found that attachment of the mucilage halo to the parent seed following extrusion is maintained by cellulose-based connections requiring CESA5. Hence, we show that cellulose fulfills an adhesion role between the extracellular mucilage matrix and the parent cell in seed coat epidermal cells. We propose that mucilage remains attached to the seed coat through interactions between components in the seed mucilage and cellulose. Our data suggest that CESA2 and CESA9 serve in radial wall reinforcement, as does CESA5, but CESA5 also functions in mucilage biosynthesis. These data suggest unique roles for different CESA subunits in one cell type and illustrate a complex role for cellulose biosynthesis in plant developmental biology.