

SHOU4 proteins control cellulose levels in *Arabidopsis* through regulating exocytosis of cellulose synthase A.

Joanna K. Polko¹, William Barnes², Cătălin Voiniciuc⁴, Stephanie Doctor¹, Blaire Steinwand¹, Joseph L. Hill³, Ming Tien³, Markus Pauly⁴, Charles Anderson², Joseph J. Kieber^{1*}

¹ Department of Biology, University of North Carolina, Chapel Hill, NC, 27599, USA.

² Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802, USA.

³ Department of Biochemistry and Molecular Biology, Pennsylvania State University, University Park, Pennsylvania 16802, USA.

⁴ Institute for Bio- and Geosciences (IBG-2: Plant Sciences), Forschungszentrum Jülich, Jülich, Germany; Institute for Botany and Molecular Genetics, BioEconomy Science Center, RWTH Aachen University, Aachen, Germany.

⁵ Department of Plant and Microbial Biology, University of California, 111 Koshland Hall, Berkeley, CA, 94720, USA

* Corresponding author

Plant cell walls provide mechanical support, define cell size and generate a physical barrier against pathogen attack. The primary load-bearing elements of cell walls are paracrystalline cellulose microfibrils, which are a product of the catalytic activity of plasma membrane-localized cellulose synthase (CESA) complexes. Despite the rigidity of microfibrils, plant cell walls are highly dynamic in nature due to mechanisms that sense and monitor cell wall integrity (CWI). A number of receptor-like kinases (RLKs) have been proposed as candidates for such CWI sensors. Previously, we identified two leucine-rich-repeat RLKs, FEI1 and FEI2, that regulate cell wall biosynthesis in multiple tissues. The *fei1 fei2* double mutant exhibits radial root swelling as a result of decreased cellulose synthesis. To identify new components of the FEI signaling pathway we conducted a suppressor screen of the *fei1 fei2* swollen root phenotype. One of the candidate suppressor genes, *SHOU4*, encodes an uncharacterized plasma membrane protein. Our genetic analyses, combined with biochemistry and cell biology studies show that *SHOU4* and its paralog, *SHOU4L*, are crucial regulators of cellulose biosynthesis. They control the abundance of the CESA proteins at the plasma membrane through mediating CESA trafficking and also contribute to microfibril crystallization. These results give novel insight into the mechanism of plant cell wall integrity sensing and maintenance.