No Stakes for High Strength Corn

In September 2019, hurricane Dorian swept across to the southeast coast of the United States, and strong winds and downpours led to major crop losses in corn (*Zea mays*) and soybean (*Glycine max*). There is little plants can do in the face of a hurricane, yet it does raise the issue of how crops will stay standing with increasingly variable climates, including storms and high winds, and continual increases in grain yields leading to heavier loads to bear. The need for crops, such as corn, to have strong stalks has never been more apparent. In this issue, Jiao et al. (2019) generate corn plants with super-strong stems, able to withstand higher forces in mechanical tests. There is a tight correlation between stem strength values and lodging, otherwise known as flattening or breakage of a standing crop, usually by wind or rain in the field (Robertson et al., 2014).

The plant stem can be considered the backbone of the plant, supporting the weight of the body and keeping it upright. Anyone with back pain will know that stems must therefore be vulnerable to damage or loss of integrity. The plant's skeleton is the cell wall, which not only provides incredible strength but is also highly dynamic and plays important roles in plant development. Woody tissues in stems contain cells with secondary cell walls that are thick, rich in cellulose and often contain lignin. Cells with secondary walls include vascular tissues and fibers that enable movement of water and nutrients and provide additional strength. Cellulose is the scaffold of plant cell walls, and changes in cellulose in secondary walls influence the mechanical strength of stems, as has been observed in *irregular xylem* and *fragile fiber* phenotypes in Arabidopsis (*Arabidopsis thaliana*), *brittle culm* in rice (*Oryza sativa*), and *brittle stalk* phenotypes in corn. Investigation of these mutants has revealed key regulators involved in cellulose biosynthesis and secondary wall formation.

In this issue, Jiao et al. (2019) identify *brittle stalk4* (*bk4*) mutants in corn that show a dwarf phenotype and reduced mechanical strength in stems. Reduced thickness of secondary cell walls is observed in *bk4* stems, with dramatic differences in staining of bundle sheath fiber cells surrounding vascular tissue as well as deformed cell shapes (Fig. 1). Along with changes in wall composition, these phenotypes point to defects in cell wall biosynthesis/deposition leading to loss of wall integrity. Using a neat PCR-based amplification and cloning approach, a *Mutator* insertion was identified in *Chitinase-like protein1* (*ZmCtl1*). Studies of *ctl1* mutants in Arabidopsis and rice show similar brittle stem

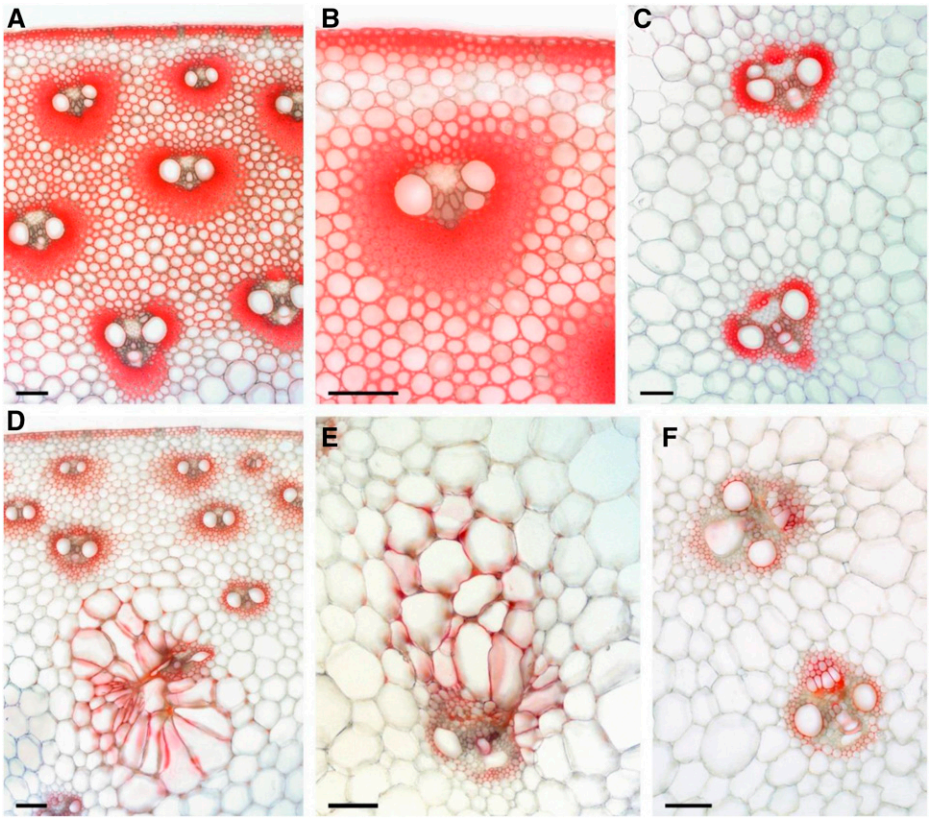

Figure 1. Cross sections through corn stems of the wild type (WT; top) and *brittle stalk4* (*bk4*/*Zmctl1*; bottom) stained with phloroglucinol for lignin. In the wild type, lignin staining of thickened secondary walls is clearly visible in the epidermis, collenchyma, and bundle sheath fiber cells surrounding vascular bundles. A significant reduction in lignin staining and wall thickness is evident in *bk4* mutants, often leading to deformed vascular bundles and collapsed metaxylem vessels. (*Taken from figure 4, Jiao et al. [2019].*)

phenotypes, suggesting that the role of CTL1 is conserved (Sánchez-Rodríguez et al., 2012; Wu et al., 2012). A member of the glycosyl hydrolase 19 family of enzymes that are proposed to trim carbohydrates, CTL1 itself is unlikely to bind or cleave chitinase, as it lacks key catalytic residues (Wu et al., 2012). So how does loss of CTL1 have such a dramatic effect on the cell wall? Decreased cellulose levels are consistently observed in *ctl1* mutants along with increases in sugars such as Ara, Xyl, and Gal (Sánchez-Rodríguez et al., 2012; Wu et al., 2012; Jiao et al., 2019). Arabidopsis CTL1 can bind glucans, leading to a proposed role for CTL1 as a scaffold protein that influences the cellulose-hemicellulose network (Sánchez-Rodríguez et al., 2012). To explore the relationship with cellulose, *bk4/Zmctl1* was crossed to mutants in cellulose synthase genes (*ZmCesA10* or *ZmCesA11*) involved in secondary cell wall formation in corn. Double mutants showed more severe brittle stem phenotypes and reduced height, supporting an association between CTL1 and cellulose (Jiao et al., 2019). When CTL1 was overexpressed in corn, it led to more cellulose and stronger stems; as yet, the performance of these plants in the field, with or without wild weather, has not been tested. The biochemical function of CTL1 remains unclear. Determining if CTL1 has hydrolase activity, and if so which carbohydrates it can cleave, would greatly advance our understanding of this fascinating protein. Combined with knowledge of how CTL1 influences the interaction of polysaccharides in secondary walls, we can work toward crops that will keep standing strong.

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