

## IN BRIEF

## Sweet and Juicy: Identification and Origins of the *Dry* Alleles in Sorghum<sup>[OPEN]</sup>

Sorghum (*Sorghum bicolor*) is the fifth most important cereal crop globally and is considered to be the “camel among crops” due to its ability to flourish in low-nutrient soils and to withstand prolonged drought. Cultivated varieties are phenotypically and morphological diverse. Consequently, sorghum is grown as both a food source (grain sorghum) and as an emerging bioenergy crop (sweet sorghum) due to its juicy stems rich in soluble sugars (Mathur et al., 2017).

Sorghum stem juiciness is controlled by a single locus, *Dry*, and stalks are either dry and pithy (frequently found in grain sorghum) or juicy and sweet, where pithy is dominant to juicy. In a new study, Zhang et al. (2018) identify the *Dry* gene as encoding a plant-specific NAC transcription factor (TF) and present compelling evidence implicating *Dry* as a major regulator of secondary cell wall (SCW) biosynthesis.

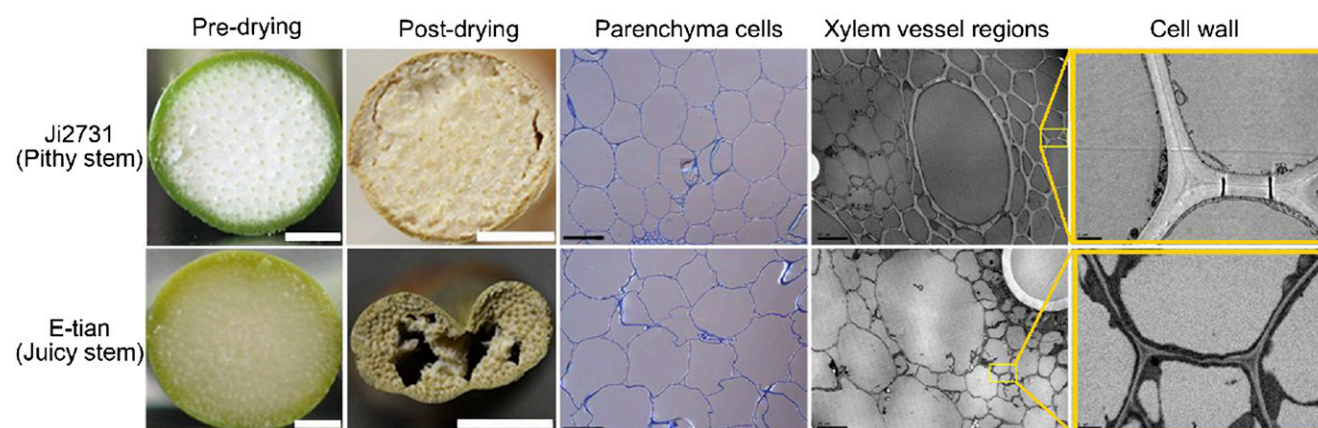
Using a combination of classical map-based cloning and genome-wide asso-

ciation studies, the authors identified a narrow region on Chromosome 6 containing four candidate genes. Detailed sequence comparisons and expression analysis of dry/pithy versus juicy lines revealed that the *Dry* locus encodes a NAC TF. Notably, juicy stem sorghum lines contain various loss-of-function mutations in the *Dry* exonic regions. Complementation analysis in an elite sweet sorghum line resulted in the pithy stem phenotype and a significantly reduced stem water content, confirming the identity of the *Dry* locus.

The authors also observed striking morphological and compositional differences in the cell walls of stems from sorghum lines containing the functional *Dry* allele (pithy) with those from lines carrying the null *dry* allele (juicy). The latter exhibited reduced cell wall thickness and widespread cell shape irregularities and collapse, likely resulting from altered cellulose/hemicellulose content (see figure). Indeed, orthologs of the *Dry* NAC TF in several other plant species have been shown to control SCW formation via a

downstream regulatory network composed primarily of MYB TFs (Nakano et al., 2015). To confirm the involvement of *DRY* as a master regulator of SCW biosynthesis in sorghum, the authors examined the transcript levels of these TF orthologs together with known cellulose/hemicellulose biosynthetic genes in four sorghum lines via RNA-seq analysis. Most genes showed high correlation (positive or negative) with the *Dry/dry* alleles, supporting the conservation of this SCW NAC/MYB regulatory network in sorghum. Functional conservation may also extend to other major cereals including maize (*Zea mays*) and rice (*Oryza sativa*), since they also contain *Dry* orthologs, pointing to a common ancestor.

The ancestry of sweet sorghum is not well defined, with evidence suggesting that it is of polyphyletic origin and, therefore, not easily separated from grain sorghum lines phylogenetically. Using a population genetics approach, the authors sequenced 241 sorghum accessions with a broad geographical distribution,



Sweet sorghum stems have a distinctive appearance and cellular morphology. Sections of mature stems from the pithy stem grain sorghum line, Ji2731, and the juicy stem sweet sorghum line, E-tian, with the latter exhibiting irregular cell morphology and thinner cell walls. Bars = 0.5 cm (whole stem sections), 50  $\mu$ m (parenchyma cells), 10  $\mu$ m (xylem vessel regions), and 1  $\mu$ m (cell wall). (Adapted from Zhang et al. [2018], Figures 1 and 6.)

including wild and cultivated lines, and identified several *Dry* gene haplotypes, indicative of a high degree of polymorphism. However, the complete lack of juicy haplotypes in wild sorghum strongly supports its occurrence as a result of relatively recent and intensive breeding selection, primarily for syrup production.

Although the locus for sorghum stem juiciness was discovered over 100 years ago, the gene responsible for this agriculturally and commercially important trait had not been identified previously. These findings are of major significance

since they pave the way for developing multipurpose sorghum (and potentially other cereal) varieties with juicy stems for biofuel production and other applications concomitant with high grain yield. In addition to characterizing the *Dry* gene, this study provides tantalizing historical insights into the domestication of sorghum.

**Emily Breeze**

**School of Life Sciences,  
emily.breeze@warwick.ac.uk  
ORCID ID: 0000-0001-5383-5448**

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