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research highlights

TOMATO DEVELOPMENT

MADS-box engineering

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Wild-type tomato plants bear unbranched inflorescences with jointed pedicels. Branched inflorescences produce more flowers and, presumably, more fruits. However, excessively branched variants exhibit sterility and are avoided by breeders. Compared to jointed pedicels, jointless pedicels enhance fruit retention and facilitate machine harvesting. A desirable tomato inflorescence is thus weakly branched with jointless pedicels. Although a range of inflorescence variants exist in tomato germplasm, our understanding of the genetic programme controlling inflorescence architecture has remained limited, hindering effective breeding. By exploring branched tomato variants, Sebastian Soyk, from the Cold Spring Harbor Laboratory, and colleagues uncovered two artificially selected MADS-box genes that control meristem maturation and inflorescence development.

The researchers studied four rare accessions from their core collection that have weakly branched inflorescences and jointless pedicels. Genetic analysis revealed two unlinked recessive mutations underlying the inflorescence phenotype, designated as *jointless2* (*j2*) and *enhancer-of-jointless2* (*ej2*) mutations. Following analyses, including

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genetic mapping by sequencing, gene expression analysis and allele engineering with CRISPR–Cas9, the researchers localized and validated two MADS-box genes on chromosome 12 and chromosome 3 as the causal genes. The *j2* mutation was found to be a transposable-element insertion or an early stop codon, while the *ej2* mutation was an insertion in an intron causing missplicing. Loss-of-function of *J2* results in jointless unbranched inflorescences, while functional disruption of *EJ2* results in unbranched inflorescences with exceptionally large sepals.

The *j2* mutation is known to have been selected for during the last century, while the newly found *ej2* mutation appears to be a domestication allele that experienced a continuous frequency increase from wild tomato through landraces to modern cultivars. Moreover, the frequency of *ej2* increases with fruit size, suggesting that breeders may have selected this mutation, which confers larger sepals, for improved fruit support and/or aesthetic value.

The *j2* and *ej2* mutations display a negative epistatic interaction, which causes extreme inflorescence branching and sterility. However, many elite lines carrying both *j2* and *ej2* mutations do not exhibit undesirable branching, probably due to suppressors selected by breeders.

By screening other similar MADS-box genes, the researchers found a further gene that also modulates meristem maturation and inflorescence architecture with an expression pattern similar to *J2* and *EJ2*. Different combinations among the natural and gene-edited alleles of these three MADS-box genes created a dose-dependent continuum of inflorescence complexity and yield, allowing breeding of higher-yielding lines.

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