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IN BRIEF

A growing reputation for *FRUITFULL* genes

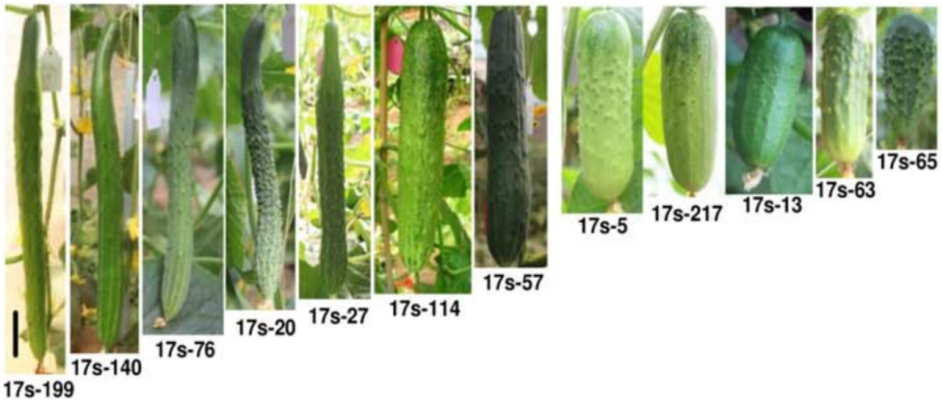
The sub-functionalization and neo-functionalization of duplicated MADS-domain containing transcription factor coding genes has driven angiosperm evolution. These transcription factors control almost every facet of reproductive development in plants and are key breeding targets for crop yield improvement. Modulating their activities can have a dramatic effect on plant development, a strategy that has been used to improve yield in several crops (Schilling et al. 2018). Fruit length is an important parameter in cucumber (*Cucumis sativus L.*) breeding; however, few candidate genes underlying this trait have been identified while none have been validated. Now, Zhao et al. (2019) have revealed how the activities of the MADS-domain transcription factor FRUITFULL (FUL) have been modulated in cucumber to regulate fruit length.

The authors identified a particular allele of *CsFUL1* (*FUL1^A*) that underlies longer fruits through a genome-wide association study of 150 cucumber lines with various fruit lengths at maturity (Figure). When the *CsFUL1^A* sequence was aligned with the other *FUL1* variants of these cucumber lines, a single non-synonymous substitution was identified in a protein–protein interaction domain of CsFUL1^A (Theiβen et al. 2016). Ectopic expression of *CsFUL1^A* (CsFUL1^A-OX) reduced fruit length, whereas ectopic expression of a *CsFUL1* variant that lacked the non-synonymous substitution (named *FUL1^C*) had little effect. Closer inspection revealed that pericarp cells of CsFUL1^A-OX fruits were smaller than those of controls, indicating that cell division and expansion were perturbed in these transgenic plants. In agreement with these results, plants whose *CsFUL1^A* expression levels were decreased *via* an RNA-interference (RNAi) approach bore longer fruits that were composed of larger cells; however, no effect was observed when *CsFUL1^C* levels were decreased. The absence of a phenotypic difference in plants with perturbed *CsFUL1^C* activity indicates that this gene variant is functionally distinct from *CsFUL1^A* and is possibly inactive. Interestingly, *CsFUL1* expression was ~50% lower in plants harbouring the *CsFUL1^A* allele than in those harboring *CsFUL1^C*. This suggests that the lower gene expression levels of *CsFUL1^A* serve to balance the modulated activity of the corresponding protein.

To determine the molecular mechanism underlying CsFUL1^A activity, the authors compared the transcriptomes of CsFUL1^A-OX plants with corresponding controls. They identified the cucumber homolog of the Arabidopsis *SUPERMAN* (*SUP*) gene, which controls cell proliferation (Prunet et al., 2017), as being expressed at less than 1% of control levels in CsFUL1^A-OX plants. Furthermore, they identified genes related to auxin transport and signalling and genes involved in cell cycle control as having reduced expression. *CsSUP* and two genes encoding polar auxin transporters were shown to be direct targets of CsFUL1^A through a combination of *in vitro* and *in vivo* methods. The authors also demonstrated that a loss of *CsSUP* activity through RNAi mimicked CsFUL1^A-OX plants, with both bearing shorter fruits composed of smaller pericarp cells compared to controls. Furthermore, a set of 10 genes with functions related to cell division and expansion were differentially expressed in both transgenic backgrounds.

To determine if the modulated protein–protein interactions were responsible for the phenotypic differences of *CsFUL1^A* plants, CsFUL1^A was tested for interactions with other CsMADS-domain containing proteins, and cucumber orthologs of known interactors from other species, in heterologous yeast and *Nicotiana benthamiana* systems. CsAGL20 was found to interact with CsFUL1^A but not CsFUL1^C. Notably, while a combination of CsFUL1^A and CsAGL20 repressed the expression of a reporter for an identified direct target of CsFUL1^A (CsPIN7pro:GUS) in *N. benthamiana* leaves, co-expression of CsFUL1^C and CsAGL20 did not. In addition, the combination of CsFUL1^A and CsAGL20 repressed the expression of a CsFUL1pro:GUS reporter to a greater degree than did incubation with either single component or with CsFUL1^C. This latter observation provides a potential mechanism for the lower expression of *CsFUL1^A* variants relative to *CsFUL1^C* variants. Together these results suggest that the mutation in the K-domain of CsFUL1^A modulates protein–protein interactions, which rewires the gene regulatory network underlying fruit growth.

This work demonstrates the power of comparative and functional genomics in identifying and characterizing novel gene variants that influence agronomically important traits. The potential to modulate fruit length in other important crops through *CsFUL1^A* expression, as has been done with other variants of MADS-domain coding genes (Schilling et al. 2018), is an exciting prospect.



Fruits from a selection of cucumber plant lines used for a genome-wide association study for fruit length *[Adapted from Zhao et al. (2018), Figure 2A].*

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