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Variations in the *CRABS CLAW* modulate fruit elongation in cucumber

Chunhua Wang[1,2,3*]

[1] *College of Horticulture, Hunan Agricultural University, Changsha 410128, China*
[2] *Key Laboratory for Evaluation and Utilization of Gene Resources of Horticultural Crops (Vegetables, Tea, etc.), Ministry of Agriculture and Rural Affairs of China, Changsha 410128, China*
[3] *Engineering Research Center for Horticultural Crop Germplasm Creation and New Variety Breeding, Ministry of Education, Changsha 410128, China*
* Corresponding author, E-mail: chwang@hunau.edu.cn

YABBY family proteins control almost every aspect of reproductive development in plants, and thus are proposed as important selection targets during crop breeding with improved yield and high quality. CRABS CLAW (CRC) (a member of YABBY family protein) orthologues play a crucial role in carpel development, floral meristem determinacy, gynoecium formation and leaf midrib formation across angiosperms[1]. A recent study reported CRC also controls the sex transition from female to male in melon[2].

Fruit length is an important parameter in cucumber (*Cucumis sativus*) breeding. The fleshy cucumber fruit initiates from the female floral meristem, and display extreme diversity in its length and shape[3]. Despite the identification of several regulators and multiple quantitative trait loci (QTLs) underlying fruit length, the natural variation and molecular mechanisms underlying differences in fruit length are poorly understood. In a previous study, Zhang et al. team discovered one MADS-box transcription factor (CsFUL1) that plays a negative role in fruit elongation in Asian long cucumber[4]. Interestingly, the team recently discovered and characterized a nonsynonymous polymorphism (G to A) in *CRABS CLAW* (*CsCRC*) as underlying the major-effect fruit size/shape QTL *FS5.2* in cucumber[5]. The authors found that the short fruit allele CsCRC^{A} is a rare allele that has only been found in round-fruited semi-wild Xishuangbanna cucumbers, while both wild cucumbers and cultivated cucumbers were CsCRC^{G} by analyzing the allelic diversity in 165 cucumber germplasms. They developed a near-isogenic line (NIL) *fs5.2*_NIL and found 34%–39% reduction in fruit length. Overexpression of CsCRC^{G} rescued the short-fruit phenotype in the *fs5.2*_NIL caused by CsCRC^{A}. In addition, a CsCRC^{G} knockdown line had shorter fruit length by reducing the cell size, while the CsCRC^{G} overexpression line displayed longer fruits. More importantly, in natural cucumber lines, CsCRC^{G} expression was positively correlated with fruit length. The authors did not stop here but investigated the CsCRC regulated gene pathways and the putative downstream targets. They identified the CsCRC^{G} downstream target gene, an auxin-responsive protein gene CsARP1, by RNA-seq analyses in the R1461 (wild-type) and CsCRC^{G} knockdown line. Through multiple biochemical analyses they found that CsCRC^{G}, but not

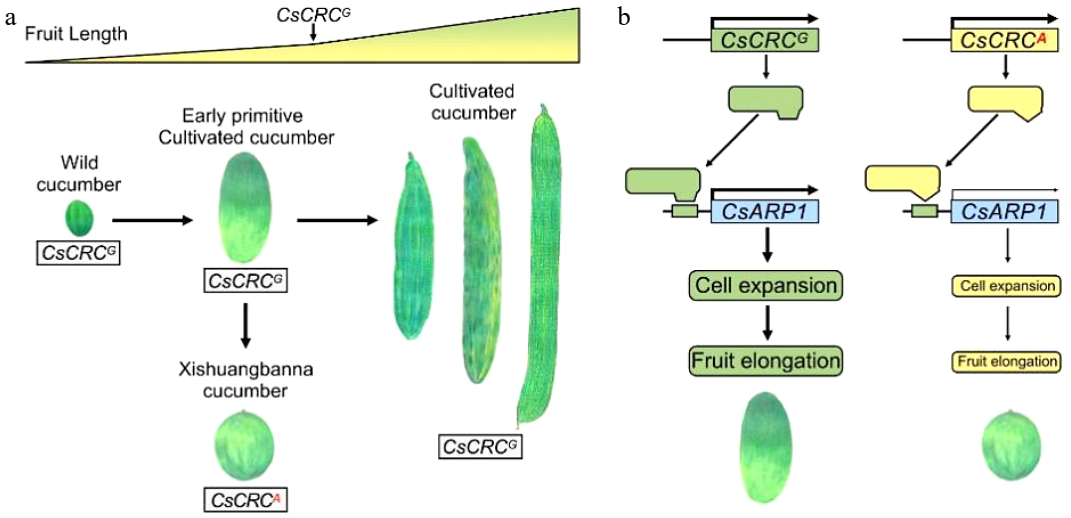

Fig. 1 The model depicting roles of CsCRC alleles associated with fruit length variation in cucumber. (a) Schematic diagram of the origin of the CsCRC^{A} allele in cucumber. The Xishuangbanna cucumber was domesticated from a primitive cultivated cucumber that carried an SNP change in CsCRC, resulting in shorter fruit. In cultivated cucumber, *CsCRC*^{G} expression shows a positive correlation with fruit length. (b) A proposed model for CsCRC fine-tuning fruit elongation in cucumber. CsCRC^{G} positively regulates cell expansion and fruit elongation through direct binding to the promoter of *CsARP1* and enhancing CsARP1 activity. CsCRC^{A} protein is unable to activate *CsARP1* expression, resulting in reduced cell expansion and decreased fruit elongation.

CsCRC^{A}, activates the expression of *CsARP1* by a direct protein-DNA interaction. To gain insight into the function of *CsARP1* in cucumber fruit development, the authors generated two mutant *Csarp1* lines by CRISPR-Cas9 system. Similar to the results in CsCRC-knockdown line, they observed the reduction in fruit length and cell size in the *Csarp1-1* mutant. Finally, cell wall-related genes, such as xyloglucan endotransglucosylase (XET) and expansins (EXPs) that were reported to mediate plant growth by reorganization of the cell wall and facilitating non-enzymatic cell wall loosening, are identified by using a transcriptome analysis of the *Csarp1-1* mutant plants compared with the control plants. Therefore, their work demonstrates that CsCRC^{G} positively regulates fruit elongation through transcriptional activation of *CsARP1* and thus enhances cell expansion in cucumber (Fig. 1).

This study elucidated the functional divergence of YABBY family transcription factor CRC in different crop species. According to Che et al.[5], in the future, their discoveries could be used to manipulate fruit length by either modulating the expression levels of *CsCRC^{G}* or utilizing different *CsCRC* alleles (*CsCRC^{G}* or *CsCRC^{A}*) in cucumber breeding practices.

Linked article: This is a Research Highlight discussing the research by Che et al.[5]. To view this article, visit https://doi.org/10.1093/plcell/koac335.

Conflict of interest

The author declares that there is no conflict of interest.

Dates

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