

## Sl-ALMT9 regulates malate accumulation and aluminum tolerance in tomato

With the support by the National Natural Science Foundation of China, the research team led by Prof. Ye ZhiBiao (叶志彪) from the Key Laboratory of Horticultural Plant Biology, Ministry of Education, Huazhong Agricultural University, characterized that Sl-ALMT9 contributes to tomato malate accumulation both in fruit and root and enhances aluminum tolerance of tomato, which was published in *Plant Cell* (2017, 29 (9): 2249–2268).

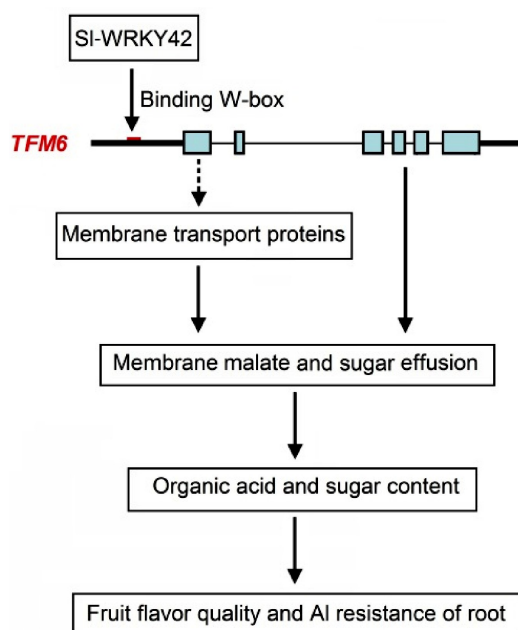
Malate, a widely occurring organic acid in plants, is a crucial compound that contributes to fruit flavor and palatability. Variation in acid content has a much greater impact on flavor than does the limited variation in sugar content that exists among tomato cultivars. Additionally, plants counteract  $\text{Al}^{3+}$  toxicity in the surrounding soil by pumping malate out of root cells. Al-activated malate transporters (ALMT) are plant-specific anion channel proteins that transport malate in and/or out of the tonoplast or plasma membrane. Previous studies of ALMTs have focused on their protective role based on their ability to transport malate out of cells, where it chelates surplus  $\text{Al}^{3+}$ .

The regulation of malate metabolism is poorly understood in crops such as tomato (*Solanum lycopersicum*). They aimed to unravel the genetic basis of tomato malate variation: Which genes regulating the accumulation of malate were selected during the domestication and improvement of tomato and how do these genes operate?

They integrated the mGWAS approach with analyses of gene expression patterns, genetic variations, and transfer DNA (CRISPR/Cas9)—derived mutants to functionally characterize a malate content-related QTL. They identified *TFM6* (tomato fruit malate 6), which corresponds to *ALMT9* in the model plant *Arabidopsis*, as the major contributor to variation in fruit malate accumulation among tomato genotypes. A 3-bp indel in the promoter region of Sl-ALMT9 was linked to high fruit malate content. Further analysis indicated that this indel disrupts a W-box binding site in the Sl-ALMT9 promoter, which prevents binding of the WRKY transcription repressor Sl-WRKY42, thereby alleviating the repression of Sl-ALMT9 expression and promoting high fruit malate accumulation. Evolutionary

analysis revealed that this highly expressed version of Sl-ALMT9 was selected during tomato domestication. Furthermore, they found that tonoplast-localized Sl-ALMT9 increases in abundance following exposure to Al, thereby elevating malate transport out of the cell and enhancing Al resistance.

In addition to identifying an ALMT in tomato, their discoveries explain how this gene improves the flavor of tomatoes and protects tomato plants from Al toxicity. Future research will aim to discover other ALMTs or tonoplast—localized proteins that work with Sl-ALMT9 to affect malate transport in tomato. Now that it is known that a particular version of Sl-ALMT9 has favorable properties, strategies can be designed to improve flavor and resistance qualities in other tomato varieties.



**Figure** *TFM6* contributes to tomato fruit malate content and  $\text{Al}^{3+}$  resistance in roots.