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Popular Article

## Genetic Control of Different Fruit Shapes in Tomato

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Tomato (*Lycopersicon esculentum*) remains one of major horticultural food crops across the globe since its worldwide introduction. The area of origin is Central America and it gradually spread to Europe only after the Spanish Conquest of the Aztec Empire during the colonial times. The genome size of tomato is around 950Mb (megabases), which comprises a total around of 35,000 genes which were analyzed in the euchromatin regions.

Fruit shape plays a crucial role in the yield and marketability of vegetable crops, highlighting the significance of this organ within the plant. Fruit shapes have diversified over time to suit different methods of seed dispersal. Furthermore, human cultivation practices have further encouraged the development of diverse fruit shapes within the same species (Paran et al. 2007; Pickersgill 2007). While fruit-bearing crop species exhibit taxonomic diversity, they commonly share a notable characteristic: the significant enlargement of fruit compared to their wild progenitors. For instance, the putative wild ancestor of the cultivated tomato, *Lycopersicon esculentum* cv Cerasiforme, produces fruit weighing only a few grams and comprising two locules. Alongside increases in fruit size, the domestication of fruit-bearing species has frequently led to significant shape variation. While wild and semi-wild forms of tomatoes typically produce fruit that is nearly always round, cultivated tomatoes exhibit a diverse array of shapes, including round, oblate, pear-shaped, torpedo-shaped, and bell pepper-shaped varieties. In contrast, modern tomato varieties can yield fruit with numerous locules weighing up to 1 kg, representing a nearly 1000-fold increase in weight. The development of fruit shape is intricately linked to cell development. Typically, cell development primarily occurs as

1388



a result of alterations in internal cell shape and fruit structure, influencing the trajectory of fruit shape development. Factors such as the orientation and timing of cell division and expansion can significantly impact both fruit shape and ovary size, which are intricately tied to the rate of cell division. Nearly 30 QTLs, including OVATE, SUN, FAS (FASCIATED), and LOCULE NUMBER (LC), play pivotal roles in determining fruit shape and size in tomato. In this article we have discussed the genetic control behind different fruit shape and sizes in tomato.

### Stages of fruit development

Critical stages of fruit size and shape regulation can be divided into four phases;

1. In the first phase, floral meristem is produced. This developmental process typically spans approximately 14–21 days and is critical in establishing the identity, quantity, and configuration of floral organs.
2. During the second stage, which spans approximately two weeks, there is a rapid and concentrated phase of cell division. This phase commences at the onset of anthesis and concludes following fertilization.
3. The third stage is characterized by a period of cell expansion, during which cells undergo a significant enlargement of more than 20-fold. This phase begins immediately after the second stage and persists until approximately one week before the onset of maturity.
4. In the fourth stage, fruit maturity is reached. During this phase, the size and shape of the fruit remain stable, but there are rapid transformations in aroma, colour, texture, and internal biochemical components (Tran et al. 2017).

### Genes for fruit shape and size regulation

The majority of the shape variation in fruit is attributed to mutations in four key genes: SUN, OVATE, LC, and FAS9. SUN and OVATE play roles in fruit elongation, while LC and FAS regulate the number of locules within the fruit, thereby influencing both its shape and size. Conversely, mutations at two loci, FW2.2 and FW3.2, are primarily responsible for the substantial increase in fruit size.

*SUN*

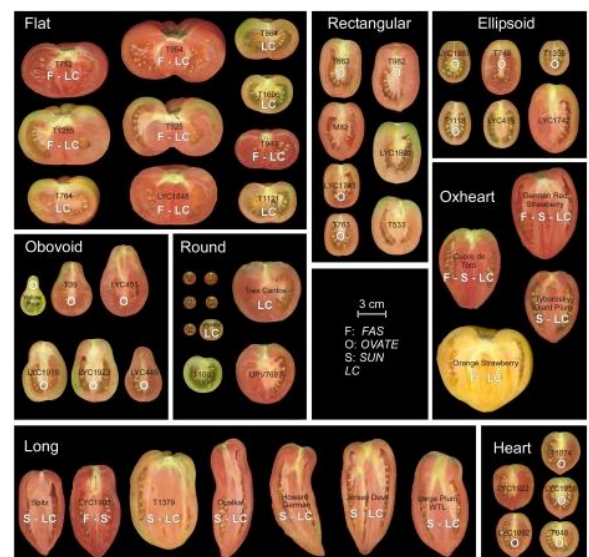


Fig 1: Each fruit is distinguished by its variety name, and information regarding mutations in the SUN, OVATE, LC, and FAS genes, abbreviated as S, O, LC, and F, respectively, can be found at <http://solgenomics.net/> (Rodríguez et al. 2011).

The short arm of chromosome 7 contains the SUN gene, where a 24.7 kb insertion is associated with elongated fruit shape. Research has shown that this segment was duplicated from chromosome 10 by a Copia-like retrotransposon called Rider, which is present at both loci. This rearrangement placed SUN under the control of a defensin (DEFL1) promoter, leading to its heightened expression in the fruit. As a result of this mutation, there is an increase in the number of cells in the longitudinal area of the fruit and a decrease in the transversal area, ultimately leading to elongated fruit shape without a significant impact on fruit weight.

### ***OVATE***

The OVATE gene codes for a member of the Ovate Family Proteins (OFP), which are considered a crucial class of regulatory genes involved in plant development. A single nucleotide polymorphism (SNP) located in the second exon of the OVATE gene leads to a premature stop codon, resulting in fruit that can exhibit various shapes such as pear-shaped, round, elongated, or ellipsoid, depending on the genetic background. Furthermore, OVATE interacts with the *sov1* and *sov2* loci located on chromosomes 10 and 11, respectively. The *sov1* locus influences the degree of pear shape, while the *sov2* locus affects fruit elongation.

### ***FAS and LC***

FAS and LC, situated on chromosomes 2 and 11, respectively, play crucial roles in regulating the number of locules in the fruit, thereby influencing both its shape and size. The *fas* mutation arises from a 294-kb inversion that disrupts the expression of *SICLV3*, impacting meristem organization and boundary formation within the floral meristem, consequently altering the number of locules in the fruit. On the other hand, *SIWUS* is the gene responsible for the *lc* mutant, which governs inflorescence and floral meristem formation, ultimately affecting the final size of the fruit. Two single nucleotide polymorphisms (SNPs) located 1080 bp downstream of *SIWUS* are thought to disrupt the regulatory region of this gene, leading to increased expression and influencing the phenotype. *ENO*, a recently identified transcription factor of the AP2/ERF superfamily, may potentially be involved in the *SIWUS-SICLV3* network by regulating *SIWUS* expression. A natural 85-bp deletion in the promoter of *ENO* results in decreased expression and an increased locule number. Evidence suggests that this mutation occurred before tomato domestication and is now fixed in cultivated tomato varieties.

### ***FW2.2***

*fw2.2* accounts for up to 30% of the variation in fruit size between modern cultivated tomatoes and their wild counterparts. This gene enhances fruit weight by promoting the expansion of the placenta and columella within the fruit. *FW2.2*, identified as a cell number regulator (CNR), is situated



on the lower portion of chromosome 2. It is hypothesized that a mutation in the promoter region of FW2.2 increases fruit size by modulating the rate of cell division.

### **FW3.2**

FW3.2, located on chromosome 3, belongs to the Cytochrome P450 gene family, previously identified as SIKLUH. Members of this family are recognized for their role in regulating organ and plant size. The increase in fruit weight attributed to W3.2 results from expansion of the pericarp and septum. SIKLUH likely influences these changes by modulating the duration of cell division, thereby increasing the overall number of cells. Initially, it was believed that a single nucleotide polymorphism (SNP) in the promoter region of the SIKLUH gene was responsible for fw3.2. However, recent findings revealed that a tandem duplication of approximately 50 kilobase pairs (Kbp) at this locus resulted in the presence of two copies of SIKLUH, thereby impacting fruit size through heightened gene expression. SIKLUH expression is notably high in developing seeds, suggesting that a compound produced by the seeds may play a role in the observed increase in fruit mass. Additionally, other significant quantitative trait loci (QTLs) related to fruit size and shape include fs8.1, which regulates fruit elongation, and fw11.3, explaining 8 to 13% of the variation in fruit weight between domesticated and wild tomato accessions.

### **Conclusions**

Advancing research on the function of fruit morphology proteins holds the promise of providing essential insights into plant developmental processes. Particularly, understanding processes that regulate cell proliferation and enlargement patterns, as well as their rate and duration, is of paramount importance as they directly impact the growth of all plant organs and eventual yield. Overall, the discoveries made using tomato fruit morphology as a model are poised to support both fundamental and applied research that is applicable to a wide range of other plant systems.

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