Review

Genetic and Molecular Regulation Mechanisms in the Formation and Development of Vegetable Fruit Shape

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Abstract: Vegetable crops have a long history of cultivation worldwide and rich germplasm resources. With its continuous development and progress, molecular biology technology has been applied to various fields of vegetable crop research. Fruit is an important organ in vegetable crops, and fruit shape can affect the yield and commercialization of vegetables. In nature, fruits show differences in size and shape. Based on fruit shape diversity, the growth direction and coordination mechanism of fruits remain unclear. In this review, we discuss the latest research on fruit shape. In addition, we compare the current theories on the molecular mechanisms that regulate fruit growth, size, and shape in different vegetable families.

Keywords: fruit growth and development; fruit shape; hormonal and genetic interactions; cell division

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1. Introduction

The diversity of plant fruit morphology is related to the adaptation to environmental changes during evolution. In the case of vegetables, fruits can be divided into dry dehiscent and fleshy fruits [1]. Dry dehiscent fruits are mainly distributed in Cruciferae crops, whereas fleshy fruits are found in Solanaceae, Cucurbitaceae, and Asteraceae. Predictive reports about the evolution of angiosperms indicate that fleshy fruits begin with silique, and their genetic regulation network is highly conserved [1,2]. Similar to the different kinds of fruits, the edible parts are also diverse. In the case of Cruciferae, most people feed on edible leaves, whereas in Asteraceae, mainly roots or tubers are consumed. However, in certain vegetable crops, the fruit is not only used for consumption but also cultivated and used to spread seeds. Solanaceae and Cucurbitaceae fruits are large, delicious, and rich in nutritional value. Therefore, the edible part in these families is often the fruit part that can carry seeds. Fruits have evolved into different shapes to adapt to various forms of seed dispersal. In addition, human domestication has promoted the formation of fruit diversity, which has led to a variety of fruit shapes among the same species [3–5] (Figure 1). Humans select large fruits in fleshy fruit domestication. The fruit length (FL) of domesticated squash deviated from the original round shape, resulting in flat scallop and long crookneck shapes [6]. Through elongation and flattening, fruits change shape from having similar lengths and widths to dimensions greater or less than 1:1 [7]. Although fruit morphology presents a diversified distribution, the related mechanism research has not been fully explored. This review mainly summarizes the developmental process of fruit shape in vegetables. Understanding the diversity of vegetable fruit morphology and their molecular regulatory mechanism will provide a basis for molecular biology research on vegetable fruit shape.

Figure 1. Diverse variations in fruit morphology of the Solanaceae and Cucurbitaceae families. Row one: Solanaceae; Row two: Solanaceae; Row three: Cucurbitaceae. Bar = 5 cm.

2. Cell Development Process of Vegetable Fruit Formation

Cell development is closely related to fruit shape. In general, cell development mainly occurs due to changes in internal cell shape and fruit structure, which affect the development of fruit shape in a particular direction. The direction, period of cell division, and expansion can affect the fruit shape and ovary size, which are related to the rate of cell division [8,9].

In vegetable crops, such as tomatoes, numerous genes (*OVATE*, *SUN*, *FAS* (*FASCIATED*), and *LOCULE NUMBER* (*LC*)) affect the fruit shape and size. In cucurbits, the above gene family members exhibit different distributions on seven chromosomes such as melons and cucumbers [5,10]. In pumpkins (*Cucurbita pepo*), the increase in cell number can lead to a large fruit size [11]. Two cucumber varieties, Gy14 and CL9930, have different fruit shapes. During fruit growth, the division and expansion of fruit cells lead to different cell numbers and shapes in the transverse and longitudinal sections [12]. In addition to cell development, the cell cavity between cells plays a decisive role in fruit shape [13]. The changes in pumpkin fruit shape are caused by cell proliferation in the early stages and cell expansion in the later stages [14,15]. In addition, in cucumbers, melons, and other horticultural crops, the timing and duration of cell expansion and division may cause the fruit size difference [16–28].

Fruit development can be roughly divided into four stages [29]. The first stage involves the formation of floral organs and the production of mature flowers. This process lasts for about 14–21 days and determines the identity, number, and shape of floral organs. The second stage, which lasts for two weeks, is the intensive cell division period, and it starts at the beginning of anthesis and ends after fertilization. The third stage is the cell expansion period, during which cells expand more than 20-fold [30,31]; this starts from the end of the second stage and continues until the first week before the mature period begins. The fourth stage involves fruit maturity. At this stage, the size and shape of the fruit show no change, but the aroma, color, texture, and internal biochemical components transform rapidly [32,33]. The proliferation and expansion stages of cells are generally considered the

main stages that affect the growth of floral organs [34,35]. In floral organs, the duration and rate of cell proliferation determine the number of cells, whereas cell expansion determines the final size [36].

3. Genetic and Molecular Regulation Mechanisms of Vegetable Fruit Shape

In the past ten years, in order to classify the fruit shape of a tomato accurately and effectively, Brewer et al. have developed a software program called Tomato Analyzer [37]. They analyzed eight species of tomatoes as follows: round, obovoid, long, heart, oxheart, rectangular, flat, and ellipsoid [38]. Cucumber, melon, watermelon, and other cucurbit crops have a relatively single fruit shape change, such as cylindrical, oval, or round [39]. The fruit morphogenesis and development are influenced by the combination of internal and external factors, which ultimately dictate the fruit shape. The internal factors include regulatory genes and protein interactions. On this basis, we classify and summarize different fruit shapes and study the specific regulation mechanism of fruit shape formation.

3.1. Carpel Number (CN)

The CN is one of the most important fruit traits among vegetables, it can affect the fruit shape and size. In nature, fruits generally have two or more carpels. These differences are related to domestication and mutation. In addition, further research shows that common regulatory factors can play a role in the CN of fruits. In *Arabidopsis*, *CLAVATA* (*CLV*) and *WUSCHEL* (*WUS*) can generate negative feedback in regulating the size of the meristem and the number of floral organs [40,41]. Mutations in the *CLV* family genes lead to an increased number of undifferentiated cells in the central region, causing the expansion of the meristem [42]. Large floral meristems result in increased CN and fruit width [43–45]. Moreover, the function of the *CLV*-*WUS* pathway is conserved in higher plants [46] and regulates the number of fruit carpels in cucurbitaceous, solanaceous, and cruciferous plants [47–50]. In cucumbers, two transcription factors (TFs), namely, *FRUITFULL*-like *MADS-box* gene (*CsFUL1^A*), and *CsARF14*, can regulate the *CsWUS*-*CsCLV3* pathway and work together to participate in the regulation mechanism of the cucumber CN [47]. In tomatoes, the loss-of-function mutation *SlCLV3* leads to a large fruit with an increased number of locules [48,49], and the up-regulation *WOX1* TF family members of *SlWUS* can increase the CN and affect fruit shape [51,52]. In tomatoes, *LC* is encoded by *WUS*, whereas *FAS* is encoded by *CLV3*; *lc* and *fas* can lead to a high locule number [53]. In addition, the transcriptional regulation of small and long non-coding RNAs can regulate fruit shape. MicroRNA 156 (*MIR156*) overexpression alters the locule number of the tomato fruit [54]. In rapeseed, the interruption of *CLV1* results in a trilocular phenotype [50] (Table 1). In addition, the *YABBY* family is also a plant-specific TF, and several of its members can increase the number of locules and flat fruit shape in tomatoes [38,55].

3.2. FL

In vegetable crops, the FL is an important phenotypic trait. Numerous factors affect the FL (Table 1). With FL as a quantitative trait, people have discovered several related loci by Quantitative trait locus (QTLs) mapping, whereas numerous candidate genes related to FL have been discovered (*FS3.2*, *FS3.3*, *fl3.2*, *mfl3.2*, *fl7.1*, *fl4.1*, and *fs10.1*) [56–59]. In addition to the loci, researchers identified a series of genes and regulatory pathways that are involved in vegetable FL. In cucumbers, *short fruit* (*sf1*) and *CsFUL1* can change the FL [60,61]. Wang et al. identified the *sf3* mutant in cucumbers and observed a homolog of the *KTN1* (*CsKTN1*) candidate gene, which encodes a katanin p60 subunit, is associated with the regulation of FL [62].

In tomatoes, *SUN*, *Ovate family protein* (*OFP*), and *Tonneau1-recruiting motif* (*TRM*) regulatory factors can affect the FL individually or together. In 2002, Liu et al. identified a pear-shaped fruit regulatory gene *OVATE* in tomato [63]. *OFPs* with a conserved *OVATE* domain play an important role in regulating fruit size. *OFPs* are plant-specific TFs. Two members of the family, namely, *OVATE* and *SIOFP20*, have been extensively studied in

vegetables. The *OVATE* gene can cause the pear-shaped fruit, and *SLOFP20* can affect the development of floral organs and pollen tubes by modulating brassinosteroid (BL) and gibberellin (GA) signaling in tomatoes [64]. In *Arabidopsis*, the overexpression of *AtOFP1* results in a reduced length of floral organ phenotype, which is similar to *OVATE* and *SLOFP20* overexpression tomato plants [63,65]. In the *ovate* mutant, the cell division pattern of the fruit proximal part changes, the numbers of cells in the proximal and distal directions increase, whereas the number of cells in the middle direction decrease [66]. Additionally, the locus *suppressors of OVATE 1* (*SOV1*) can enhance the *OVATE* mutation [67]. In addition, the overexpression of *Arabidopsis* OFP homologous genes (*AtOFP13*, *AtOFP15*, *AtOFP16*, and *AtOFP18*) results in a reduced length of siliques [68–70], these genes are also involved in the regulation of fruit shape, indicating that this family may also control the organ shape in other plants [71]. At present, the molecular mechanism of *OVATE* is unclear, but it has been shown to interact with microtubule-related proteins, such as TRM [72]. *OVATE* and *SLOFP20* interact with the TRM M8 motif through the OFP domain, and the co-expressions of *OVATE* or *SLOFP20* with *SITRM3/4* causes the re-localization of OFPs and TRMs from microtubules to the cytoplasm, suggesting that the OFP–TRM protein complex plays a role in cell division and organ growth through a dynamic balance between cytoplasmic and microtubular localizations [73,74]. In other vegetables, the down-regulation of the *CaOvate* gene leads to the oblong fruit shape of peppers [75], which indicates that the OFP family is relatively conserved in relation to fruit size [65].

SUN encodes a protein of the IQ 67 domain (IQD) family, which has a conserved IQD and is involved in the binding of Calmodulin (CaM) [38,76]. *SUN* is reported to control the FL and shape in tomatoes, melons, and cucumbers [5,76–79]. The IQD is a conserved region of 67 amino acids and contains up to three regularly spaced IQ motifs that promote CaM binding in the presence of Ca^{2+} [80–82]. In tomatoes, the shape change mediated by *SUN* is consistent with the cell division stage after 7–10 days of pollination [83], which increases cell elongation and division along the proximo-distal axis [84] and can be used to determine the fruit morphology by regulating the microtubule dynamics. Lazzaro et al. [65] proposed a model to describe the regulation of the tomato fruit shape by *SUN*, OFP, and TRM interaction, in association with microtubule development. Rho proteins of plants (ROPs) are plant-specific Rho GTPases [85], and one of their functions is to organize microtubules and act on the cytoskeleton to determine a cell's final shape [65]. Several IQD proteins can guide the formation of ROP domains to regulate the cytoskeletal architecture in the plasma membrane [65]. In the interaction network, the up-regulation of TRMs and *SUNs* or down-regulation of OFPs can lengthen the tomato fruit [65]. Studies further show that OFPs, TRMs, and *SUN/IQD* can affect the activity of microtubules and fruit shape. In addition, in different species, *SUN* family proteins play a role in regulating FL. In cucurbitaceous crops, *CsGy1G026840.1* and *Csa1G575000*, *CmSUN-14*, and *Clao11257* belong to the *SUN* family and can regulate the FL [5,39,65,78,86]. Further research revealed that *Clao11257* acts on the ovary (pre-anthesis) to affect the FL during the development period [87].

The MADS-box family TFs are closely related to plant development and play an important role in flower and fruit development [88]. As an important TF member of the MADS-box family, *FUL* affects FL in different plants. In tomatoes, *MBP7/FUL2* can regulate fruit shape through cell division and expansion. When the *FUL* genes encoding MADS-box are knocked out in different species, the fruits cannot elongate after fertilization, and the valve is significantly reduced [89,90]. In cucumbers, *CsFUL1^A* as a negative regulator can inhibit auxin transport and cell division to affect the FL [61]. *CsFUL1^A* is a MADS-box family TF that can bind to the CARG-box to regulate cell division and expansion, and it can inhibit the expression of auxin transporters PIN-FORMED1 (PIN1) and PIN7, resulting in the decreased auxin accumulation and regulation of FL [61].

3.3. Fruit Weight (FW)

The size of the fruit is closely related to FW. In the breeding process of vegetables, people have discovered several loci that regulate FW (Table 1). FW is a quantitative trait and is controlled by numerous loci [3]. FW2.2 is the first cloned FW QTL in vegetables [91]. In Solanaceae vegetables, several genes that regulate FW have been cloned. These genes, including the *lc* and *fas* loci, are, respectively, homologous with *WUS* and *YABBY2*, can regulate the CN to increase FW [48,53,92,93]. FW3.2, *fw11.2*, *fw1.1*, *fw3.3*, and *Cell Size Regulator* (CSR) loci, which are related to FW, have been cloned in tomatoes [94–96]. In peppers, *fw2.1*, *fw4.1*, and *fw4.2* have been associated with FW [97]. In Cucurbitaceae, several loci have been related to FW. In cucumbers, three QTLs (*fw2.1*, *fw4.1*, and *fw6.1*) have been described [10]. In melons, two genomic regions, namely, FWQM8 and FWQM11, contain the loci that regulate FW [5]. A CYP78A subfamily gene *KLUH* can initially control the organ size in *Arabidopsis*. In vegetables, several members of the CYP78A subfamily have been reported to regulate FW; these members include *SIKLUH* (tomato), *GmCYP78A10* and *GmCYP78A72* (soybean), *BnaA9.CYP78A9* (rapeseed), and *CaKLUH* (pepper) [94,98–102]. In addition, a recent study shows that the overexpression of TF gene *SHINE1* (*SISHN1*) can decrease the tomato FW [102].

4. Hormonal Regulation of Fruit Shapes

Hormones can respond to environmental and endogenous signals throughout almost the entire life of a plant. Plant hormones directly or indirectly affect the division and expansion of fruit cells in the early stages of fruit development, to regulate fruit growth, and ultimately determine the size and shape of fruits [103–105]. There are many plant hormones in nature, including auxin, cytokinin (CK), GA, ethylene, and The abscisic acid (ABA). Several of them have been reported to affect fruit shape.

Auxin plays an important role in the development of fleshy fruits [106–108]. Liu et al. [107] measured the endogenous hormone content of fruits in different cucumber inbred lines. They found that in various developmental stages, the IAA content of the fruit is positively correlated with the fruit size and cell growth [109]. In *Solanum*, the LA1589 near-isogenic lines, which have elongated pear-shaped ovaries and fruits, were treated with auxin (2,4-D) before anthesis, resulting in an increased cell number and size of the ovary/fruit proximal end [110]. The auxin synthesis gene *CsYUC10b* is associated with fruit curvature, and its overexpression can induce the formation of straight fruits [109]. In addition, *SIIAA17*, an auxin transcriptional repressor of Auxin/indoleacetic acid (Aux/IAA), can lead to large fruits in tomatoes [103]. *SIARF9* and *BnaA9.ARF18* belongs to the Auxin response factors (ARFs) family, and they can regulate fruit size in tomatoes and *Brassica rapa*, respectively [103,110].

In addition to auxin, other hormones can work with certain regulatory factors to regulate fruit shape [111]. CKs mainly regulate cell division in plants and there is a positive correlation between them, which is consistent with the fruit cell division activity [112–114]. The CK biosynthetic gene *CYP735A* can change the cell volume and biomass accumulation to affect the fruit size [115]. In cucumbers, trans-Zeatin riboside (tZR) decreases in the initial stage of fruit development and is mainly involved in the cell division process at the early stage of ovary development. The content of zeatin (ZT) increases in the early stage of fruit development after flowering, which can promote the horizontal expansion of cells in the early stage [107]. GA may regulate flowering and stimulate fruit and seed development [114]. Exogenous application of GA can induce cell enlargement and lead to parthenocarpy [116,117]. In cucumbers, GA can promote cell expansion during fruit development [118] and antagonize IAA in the mid-to-early stage (9–12 days after anthesis); it may inhibit fruit elongation by hindering cell division [105]. During the development of the tomato fruit, the GA accumulation is consistent with the direction of cell division and expansion in the early stage [119]. Ethylene is mostly related to fruit ripening in tomatoes [120], but recent reports have shown that it can regulate the length of the cucumber fruit. Ethylene content also affects plant development [119]. 1-aminocyclopropane-1-

carboxylate synthase 2 (ACS2) can catalyze the biosynthesis of ethylene [119]; the ethylene-decreased cucumber mutant *acs2* shortens the FL. However, in *sf1* mutants, excessive ethylene content can also lead to the same phenotype [60]. Therefore, an excessive or inadequate amount of ethylene can affect the FL. The ACS homologous gene *CmACS7* is related to the round fruits of melons [5,121]. These results showed that the dose-dependent function of ethylene in Cucurbitaceae is relatively conserved. In a separate study on tomatoes, several Aux/IAA-like genes (*DR1*, *DR3*, *DR4*, and *DR8*) related to IAA transcript accumulation were differentially regulated by ethylene [122]. ABA is a plant growth inhibitory hormone [123], Nitsch et al. [124] pointed out that in tomatoes, the ABA-deficient mutant *not/flc* has a small fruit and cell shape [123,125]. The above research shows the possible antagonistic or synergistic effects between plant hormones, which together regulate fruit development and ultimately affect fruit shape.

Table 1. Genes involved in the fruit size regulation of vegetables.

Type	Pathways	Gene Name	Species	Function in Size	Reference
CN	CLV-WUS pathway	<i>CsWUS</i> , <i>CsCLV3</i>	Cucumber	<i>CsFUL1^A</i> and <i>CsARF14</i> can regulate the <i>CsWUS</i> - <i>CsCLV3</i> pathway and work together to participate in the regulation mechanism of cucumber CN.	[47]
		<i>SICLV</i> , <i>CLV3</i> , and <i>WUS</i>	Tomato	Loss-of-function mutation <i>SICLV3</i> leads to a large fruit with an increased number of locules. A mutation of <i>CLV3</i> in tomatoes can increase the fruit size. <i>LC</i> , which is encoded by <i>WUS</i> , and <i>FAS</i> , which is encoded by <i>CLV3</i> , can lead to an increased locule number.	[48–50,53]
		<i>CLV1</i>	Rapeseed	The interruption of <i>CLV1</i> results in a trilocular phenotype.	[50]
		<i>SIWUS</i>	Tomato	Up-regulation of <i>SIWUS</i> can increase the CN and affect fruit shape.	[52]
		<i>MIR156</i>	Tomato	<i>MIR156</i> overexpression alters the tomato fruit locule number.	[54]
FL	MicroRNA	<i>CmSUN2</i> (<i>CmSUN-14</i>)	Melon	<i>CmSUN-14</i> belongs to the SUN family and can regulate the FL.	[5,79]
	OFP-TRM-SUN pathway	<i>OVATE</i> , <i>SIOFP20</i> , <i>SUN</i>	Tomato	<i>OVATE</i> is a pear-shaped fruit regulatory gene. OFPs with a conserved <i>OVATE</i> domain play an important role in regulating fruit size. <i>OVATE</i> and <i>SIOFP20</i> interact with the TRM and work together to regulate cell division and organ growth. <i>SUN</i> encodes a protein of the IQD family, which has a conserved IQD and is involved in the binding of CaM, which controls the FL and fruit shape.	[38,66,73,76]
	Cell development	<i>CsSUN25-26-27a</i> (<i>CsGy1G026840.1</i> , <i>Csa1G575000</i>)	Cucumber	<i>CsGy1G026840.1</i> and <i>Csa1G575000</i> belong to the SUN family and can regulate the FL.	[39,78]
	Hormones and cell development		Cucumber	In cucumbers, ACS2 can catalyze the biosynthesis of ethylene, ethylene decreases mutant <i>acs2</i> , resulting in a shortened FL; however, in <i>sf1</i> , the excessive ethylene content of the mutant can also lead to a short fruit.	[60]
	TF and Hormonal regulation	<i>CsFUL1</i>	Cucumber	<i>CsFUL1</i> can inhibit the expression of auxin transporters PIN1 and PIN7, resulting in the decreased accumulation of auxin, which affects the cucumber fruit length.	[61]
FW	TF	<i>CaOvate</i>	Pepper	Down-regulation of the <i>CaOvate</i> gene leads to an oblong fruit shape of pepper.	[75]
	QTLs	<i>CISUN25-26-27a</i> (<i>Cla011257</i>)	Watermelon	<i>Cla011257</i> acts on the ovary (pre-anthesis) to affect the fruit length during the development period.	[86,87]
		<i>FWQM8</i> and <i>FWQM11</i>	Melon	<i>FWQM8</i> and <i>FWQM11</i> are genomic regions related to FW in melons.	[5]
		<i>fw2.1</i> , <i>fw4.1</i> , and <i>fw6.1</i>	Cucumber	In cucumbers, three QTLs (<i>fw2.1</i> , <i>fw4.1</i> , and <i>fw6.1</i>) are associated with FW.	[10]

Table 1. Cont.

Type	Pathways	Gene Name	Species	Function in Size	Reference
Larger fruit	The CYP78A subfamily	<i>FW 2.2, lc, fas, FW3.2, fw11.2, fw1.1, fw3.3, and CSR</i>	Tomato	<i>FW2.2</i> is the first cloned FW QTL in vegetables. <i>lc</i> and <i>fas</i> are, respectively, homologous with <i>WUS</i> and <i>YABBY2</i> , and can regulate the CN to increase FW. <i>FW3.2, fw11.2, fw1.1, fw3.3, and CSR</i> loci have been cloned in tomatoes to increase FW.	[48,55,91–96]
		<i>GmCYP78A10 and GmCYP78A72</i>	Soybean	<i>GmCYP78A10</i> and <i>GmCYP78A72</i> genes in soybeans are related to FW.	[88,94,99]
		<i>fw2.1, fw4.1 and fw4.2</i>	Pepper	In peppers, <i>fw2.1, fw4.1, and fw4.2</i> are related to FW.	[97]
		<i>CaKLUH</i>	Pepper	<i>CaKLUH</i> gene in pepper is related to FW.	[100]
	The CYP78A subfamily	<i>BnaA9.CYP78A9</i>	Rapeseed	<i>BnaA9.CYP78A9</i> gene in rapeseed is related to FW.	[101]
		<i>SIKLUH</i>	Tomato	<i>SIKLUH</i> indirectly participates in the lipid metabolism of tomato fruits to regulate FW.	[102]
	TF	<i>SISHN1</i>	Tomato	TF gene <i>SISHN1</i> overexpression can decrease the tomato FW.	[102]
		<i>SIIAA17</i>	Tomato	<i>SIIAA17</i> , an auxin transcriptional repressor of Aux/IAA, can lead to large fruits in tomatoes.	[103]
	Hormonal regulation	<i>SIARF9</i>	Tomato	<i>SIARF9</i> and <i>BnaA9.ARF18</i> , which belongs to the ARFs family, can regulate fruit size in tomatoes and <i>Brassica rapa</i> , respectively.	[110]
		<i>BnaA9.ARF18</i>	Brassica rapa		
Round fruit	Hormonal regulation	<i>CmACS7</i>	Melon	The ACS homologous gene <i>CmACS7</i> is related to the round fruits of melons.	[5,121]
	Hormonal regulation	<i>not/flc</i>	Tomato	The ABA-deficient mutant <i>not/flc</i> results in a small fruit and cell shape in tomatoes.	[124]

5. Conclusions and Perspectives

Global climate change and urbanization affect crop cultivation. Numerous challenges, including the reduced planting land, the presence of pest hazards, and pesticide residues, are associated with vegetable crops. Therefore, the application of molecular biology techniques is a powerful solution to these challenges. The fruit shape of vegetable crops is one of the most important agronomic traits. The research on the development pathways and regulation mechanisms of fruit shape can not only increase vegetable market value but also contribute to the economic development of the whole vegetable industry. The shape of fleshy fruit vegetables, such as tomatoes and cucumbers, directly determines the market ranks and culinary use [126]. Thus, based on the fruit shape regulatory network, people can produce new varieties of vegetables that meet the needs of different consumers. In cruciferous and other dried fruit vegetables, the fruit shape is mainly related to crop yield. The research on fruit shape can not only increase crop yields but also bring great economic value.

In this review, we summarized the domestication process and analyzed the genetic and molecular regulation mechanisms in vegetable crops (Figure 2). Given the different fruit types in various species, the fruit shape of the same gene can be diverse. In addition, we observe that fruit shape is regulated by a single factor and common influencing factors. During fruit development, hormonal changes can affect the TF functions, which lead to cell morphological variations that affect the final fruit shape. At present, a limited number of genes have been reported to regulate fruit shape. Researchers should aim to discover more key genes in the future. In addition, comprehensive studies combining multiple levels, genomics, and perspectives (plant hormones, cytology, and candidate genes) should be performed. From the initial domestication to modern molecular breeding, the fruit shape of vegetable crops has been influenced by human selection. In recent years, molecular biological methods, such as whole-genome research and resequencing technology, have provided great help for fruit shape research. At present, people mainly focus on the discovery of important trait genes. In the future, breeders may combine omics research and

practical technology to cultivate plants with ideal fruit shapes through design breeding and use the gene-editing technology CRISPR/Cas9 for future applications.

Figure 2. Fruit shape is regulated by several other signaling pathways. These regulation pathways include hormonal regulations, OFP-TRM-SUN pathway, regulatory genes, cell division, QTLs, and TF, which affect the fruit length. The TF, CLV-WUS signaling pathway, MicroRNA, the CYP78A subfamily, and QTLs affect the CN and the FW. These pathways are shown around in red.

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