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REVIEW

Genetic architecture of fruit size and shape variation in cucurbits: a comparative perspective

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Abstract

The Cucurbitaceae family hosts many economically important fruit vegetables (cucurbits) such as cucumber, melon, watermelon, pumpkin/squash, and various gourds. The cucurbits are probably best known for the diverse fruit sizes and shapes, but little is known about their genetic basis and molecular regulation. Here, we reviewed the literature on fruit size (FS), shape (FSI), and fruit weight (FW) QTL identified in cucumber, melon, and watermelon, from which 150 consensus QTL for these traits were inferred. Genome-wide survey of the three cucurbit genomes identified 253 homologs of eight classes of fruit or grain size/weight-related genes cloned in Arabidopsis, tomato, and rice that encode proteins containing the characteristic CNR (cell number regulator), CSR (cell size regulator), CYP78A (cytochrome P450), SUN, OVATE, TRM (TONNEAU1 Recruiting Motif), YABBY, and WOX domains. Alignment of the consensus QTL with candidate gene homologs revealed widespread structure and function conservation of fruit size/shape gene homologs in cucurbits, which was exemplified with the fruit size/shape candidate genes *CsSUN25-26-27a* and *CsTRM5* in cucumber, *CmOFP1a* in melon, and *ClSUN25-26-27a* in watermelon. In cucurbits, the *andromonoecy* (for 1-aminocyclopropane-1-carboxylate synthase) and the *carpel number* (for CLAVATA3) loci are known to have pleiotropic effects on fruit shape, which may complicate identification of fruit size/shape candidate genes in these regions. The present work illustrates the power of comparative analysis in understanding the genetic architecture of fruit size/shape variation, which may facilitate QTL mapping and cloning for fruit size-related traits in cucurbits. The limitations and perspectives of this approach are also discussed.

Introduction

'Cucurbits' is a broad term used to describe crops in the Cucurbitaceae family, which comprises ~ 1000 species in 15 tribes and ~ 95 genera that are predominantly distributed in the tropics and subtropics (Schaefer and Renner

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2011). Major cultivated cucurbit crops with global economic importance include cucumber (*Cucumis sativus* L.), melon (*Cucumis melo* L.), watermelon [*Citrullus lanatus* (Thunb.) Matsum. and Nakai], and squash/pumpkin (*Cucurbita* spp.). Other cucurbits that are more popular in many Asian countries include bitter gourd (*Momordica charantia* L.), bottle gourd [*Lagenaria siceraria* (Molina.) Standley], wax gourd [*Benincasa hispida* (Tunb.)], sponge/ridge gourd (*Luffa* ssp.), and snake gourd (*Trichosanthes* ssp.). Cucurbit fruits provide important sources of nutrition and improved dietary health, which can be consumed immature or mature, fresh or processed, as vegetables or desserts; and in the case of squashes and pumpkin, they also serve as mainstays of the diet (Robinson and Decker-Walters 1997). In many cultures, the shoots, leaves, male and female flowers, ovaries, fruit rinds, seeds, and seed oils of cucurbits are utilized for food or medicinal purposes. Cucumber extracts are used in products for skin care; dried gourd shells may be used as ornaments, storage containers, or as musical instruments. Cucurbits are often an indispensable component for display in modern recreational agriculture.

Visually, cucurbits are probably best known for their colorful and morphologically very diverse fruits, notably the fruit size and shape (Fig. 1). The fruits of wild cucurbits are usually small in size and round in shape, while the domesticated ones in general have much larger fruits and vary considerably in shape. Changes in fruit size and shape are not only the results of natural selection during domestication, but also artificial selection during improvement in adaptation to diverse environments, cultivation practices, consumer preferences, product storage/processing methods, etc. For example, wild cucumber (*C. s.* var. *hardwickii*) or melon usually bears small and round fruits (3–5 cm in diameter) with 25–35 g per fruit, while cultivated ones can weigh up to 5 kg or 35 kg, respectively. The shapes can vary from slightly flat, ellipsoid, obovoid, and round to long or extremely long (Bisht et al. 2004; Yang et al. 2012; Pitrat 2016; also Fig. 1). Some pumpkin (*Cucurbita maxima*) varieties (for example, Atlantic Giant) have been consistently the winner of the world's record for the largest fruit, which may weigh 600–1000 kg (Paris 2016a; https://www.bigpumpkins.com/). Bottle gourd and squash (*Cucurbita pepo*) are among the species with the highest diversity in fruit shape, which may be spherical, oblate, obovoid, drum-shaped, pear-shaped (pyriform), spindle-shaped (fusiform), long and cylindrical, elongated, curved, and crooked necked (Xu et al. 2014; Paris

Fig. 1 Morphological diversity of fruit size and shape in cucurbit crops. Representative fruits of cucumber, melon, watermelon, and squash are shown in **a** thru **d**, respectively. Squash fruits in **d** were taken from a vendor's sale stand at a Farmers' Market in Madison, Wisconsin. All images were taken by the authors

2016a; Dhillon et al. 2016). Not surprisingly, fruit size and shape are often a defining feature classifying different market groups or classes of cucurbits in commercial production. For example, major cucumber market classes with significant commercial production include the European greenhouse (European Long) and pickling (European short) cucumbers, the North China fresh market (Chinese Long), and Japanese Long cucumbers, North American slicing (moderately long) and pickling (short) cucumbers, and the Beit Alpha (mini) cucumber. Each market class of cucumbers has unique commercial standards in fruit length and diameter (Weng et al. 2015, 2019). Similar cultivated types or groups are also recognized in melon, watermelon, and pumpkin/squash based on typical size and shape characteristics (Levi et al. 2016; Monforte et al. 2014; Paris 2016a; Pitrat 2016). Therefore, fruit size/shape constitutes a horticulturally important fruit quality/yield trait from a crop breeding perspective.

The remarkable diversity of fruit size/shape in cucurbits provides excellent research systems to explore the underlying genetic basis and molecular mechanisms driving fruit development, which in turn will facilitate efficient manipulation of fruit size and shape in cucurbit breeding. Due to its quantitative nature, little was known about the genetic basis of fruit size/shape variation in cucurbits until the genomics era came of age. Draft genome for all important cucurbits is now publicly available including cucumber (Huang et al. 2009; Yang et al. 2012), melon (Garcia-Mas et al. 2012; Ruggieri et al. 2018), watermelon (Guo et al. 2013), bottle gourd (Xu et al. 2014; Wu et al. 2017), bitter gourd (Urasaki et al. 2017), as well as pumpkin and squash (*Cucurbita pepo*, *C. maxima,* and *C. moschata*) (Sun et al. 2017; Montero-Pau et al. 2018). These genomic resources combined with high-throughput genotyping are accelerating QTL mapping studies for fruit size/shape in cucurbit crops. In particular, significant progress has been made in cucumber, melon, and watermelon, which will be the focus of the present study. We first reviewed fruit size, shape, and fruit weight QTL in the three cucurbits, from which consensus QTL were inferred. We then conducted genome-wide survey among the three genomes to identify homologs of cloned genes underlying fruit or grain size/weight variation in Arabidopsis, tomato, and rice. Alignment of consensus QTL and candidate gene homologs revealed conservation in structure and function of those homologs across cucurbit genomes.

Dynamics of cucurbit fruit development

Systematic investigation of cucurbit fruit development was pioneered by Edmund W. Sinnott in pumpkin and squash. In a series of studies, Sinnott (1931, 1936, 1939, 1945, 1958) found that pumpkin fruit growth started with cell multiplication followed by cell expansion, and the varying size of different pumpkins could be attributed to the timing and duration of cell division and cell expansion. He observed a positive correlation between ovary shape and final fruit shape. Sinnott and co-workers also studied the genetic basis of fruit shape variation in summer squash (*C. pepo*) and found that the disk/round fruit shape was controlled by a single gene (Sinnott 1922, 1927, 1935; Sinnott and Durham 1922, 1929; Sinnott and Hammond 1930). These early observations are generally true for other cucurbits.

Most cucurbits such as cucumber, melon, watermelon, bitter gourd, and wax gourd exhibit relatively simple fruit shape variation (e.g., round, oblong/oval, or cylinder). Fruit length (FL) and fruit diameter (FD) are often used to describe fruit elongation and radial growth, respectively, during fruit development. Fruit shape could be conveniently defined using fruit shape index (FSI) which is the ratio of FL to FD. The typical cucurbit fruit growth and development dynamics from pre-anthesis ovary development to maturity could be exemplified in cucumber shown in Fig. 2. Among the 11 cucumber lines examined (Fig. 2a), WI7221 is a wild cucumber and the progenitor of cultivated cucumber (Yang et al. 2012, 2014). WI7104 (True Lemon, andromonoecious), WI7120 (PI 330628), WI7200 (PI 249561), WI7237, and WI7239 are landraces with varying fruit size and shape from different geographic regions (He et al. 2013; Wang et al. 2016a; Pan et al. 2017a). The inbred lines 9930, Gy14, WI7150, WI7204, and WI7632 are representatives of Chinese Long, US pickling, European greenhouse, Beit Alpha, and South China type market groups, respectively. The FL, FD, and corresponding FSI for the ovary/fruit beginning from 6 days before to 30 days after anthesis (DAA) are plotted in Fig. 2b–d, respectively. Despite the very diverse fruit size, shape, geographic origin, or taxonomic status, post-pollination fruit growth among all lines exhibits a typical sigmoidal pattern: Fruit development starts with a short fruit set phase, which is followed immediately by a rapid cell division phase until approximately 6 DAA, and then by an exponential expansion (6–15 DAA) phase. This growth pattern is consistent with results from the previous studies in cucumber (e.g., Marcelis and Hofmann-Eijer 1993; Fu et al. 2008, 2010; Ando and Grumet 2010; Yang et al. 2013; Colle et al. 2017), which also follows the general pattern observed in most fleshy fruits (Coombe 1976; Gillaspy et al. 1993; Okello et al. 2015).

The diverse size and shape of cucurbit fruits (e.g., Figs. 1 and 2a) are often characteristics of particular genotypes. The fruit of each genotype will grow to its defined size and shape, suggesting that genetic factors are playing the most important role for determination of final size and shape (Gillaspy et al. 1993; Tanksley 2004; Colle et al.

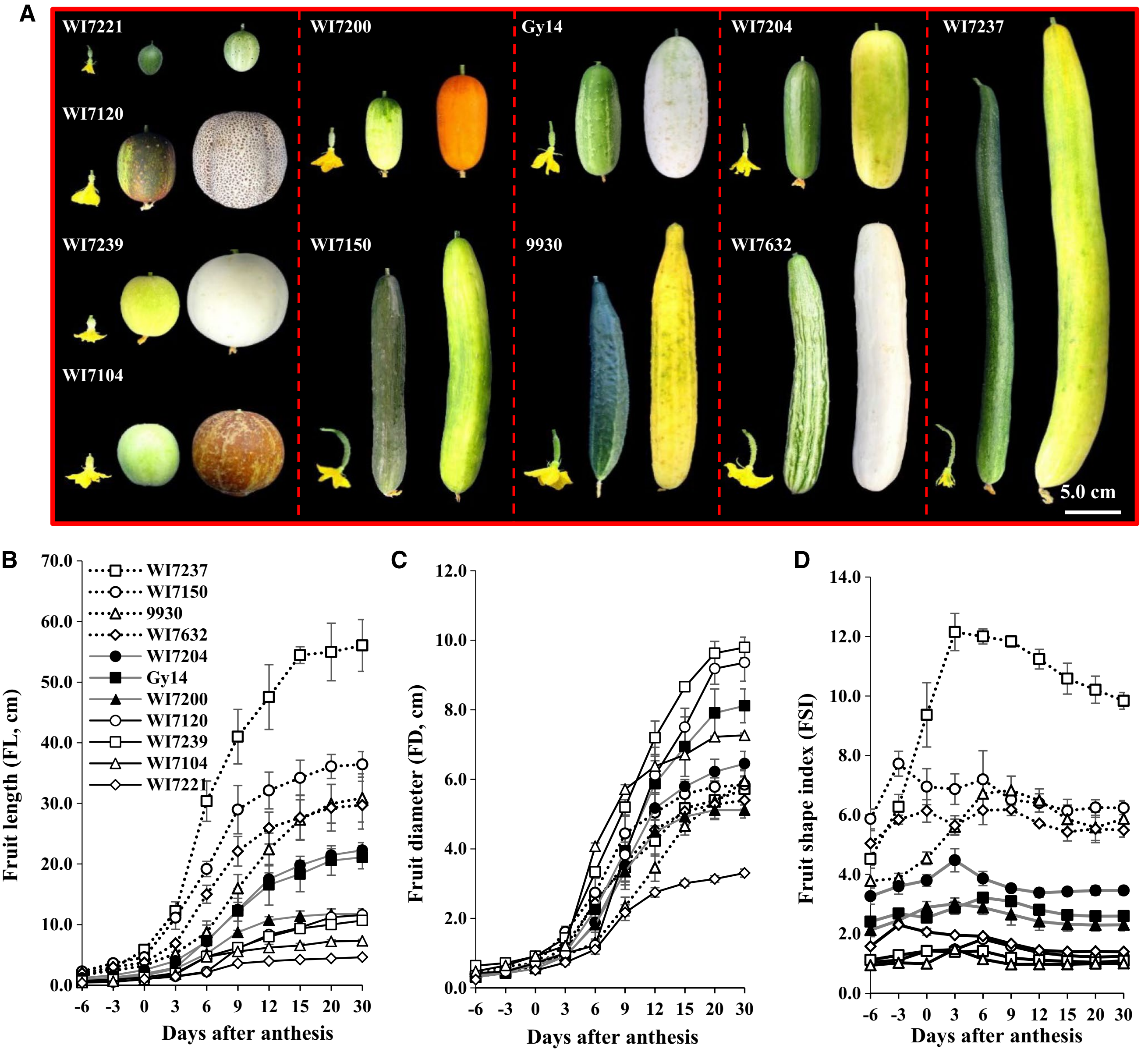


Fig. 2 Fruit development dynamics of cucumbers with diverse genetic backgrounds. **a** Ovary and fruit images of 11 cucumber lines, which were taken at 0, 12, and 30 days after pollination, respectively. **b** and **c** illustrate fruit elongation (FL) and radial growth (FD) dynamics of these lines from 6 days before anthesis to 30 days after pollination (fully mature), respectively. **d** shows fruit shape index (FSI) of these lines during fruit development

2017). The fruit growth dynamics among the 11 cucumber lines revealed some common features of cucurbit fruit development. For example, in each genotype, the FL was highly correlated with FSI throughout the fruit development (Pearson's correlation coefficient $r > 0.95$ between FL at any post-anthesis time point and FSI at 30 DAA), indicating that fruit elongation plays an important role in determination of final fruit shape. The FSI of the ovary and mature fruit among the 11 cucumber lines was also highly correlated ($r = 0.9876$ between FSI at 0 and 30 DAA) (Fig. 2d). The high correlation of ovary and final fruit shape has been observed in many studies in cucurbits (e.g., Sinnott 1936; Perin et al. 2002; Weng et al. 2015; Montero-Pau et al. 2017; Pan et al. 2017a), suggesting that cucurbit fruit shape is controlled mainly by critical factors acting pre-anthesis.

Among the 11 cucumber lines, the mature FL seemed highly correlated with the fruit elongation rate pre- and post-anthesis (Fig. 2b), but the correlation between radial growth rate and mature fruit FD was not as strong (Fig. 2c). For example, as compared with other genotypes, the radial growth of WI7239 and WI7120 was slower in early stage (before 6 DAA), but became much faster from 6–20 DAA; in WI7104 and WI7150, the trend seemed the opposite. On the other hand, WI7632 and 9930 had almost the same FL and FD, and WI7120, WI7221, and WI7104 all had FSI close to 1.0 (round fruit) throughout the fruit growth stages, but the timing and duration of fruit elongation or radial growth were clearly different (Fig. 2b–c). These observations were consistent with the poor correlation between FL and FD or between FD and FSI found in a number of early studies in cucumber (e.g., Bo et al. 2015; Wei et al. 2014, 2016; Weng et al. 2015; Pan et al. 2017a, b; Shimomura et al. 2017). Such genotype-specific fruit growth patterns may reflect the underlying genes that differentially regulate the timing, magnitude, duration, and plane of cell division, as well as isotropic and anisotropic cell enlargement during fruit growth (Colle et al. 2017; van der Knaap and Ostergaard 2018; Wu et al. 2018).

Fruit is a multidimensional organ, and its outgrowth occurs along three different axes: proximal–distal, medial–lateral, and abaxial–adaxial (Van der Knaap et al. 2014; Lazzaro et al. 2018). Fruit length and diameter largely describe fruit growth along the first two axes, but less for the abaxial–adaxial growth. In this sense, fruit weight (FW) seems a useful indictor complementary to FL and FD in description of the three-dimensional fruit growth. FW and fruit size/shape seem to be different traits, but they are inherently correlated. Indeed, in many QTL mapping studies, QTL for these traits are often co-localized (see below). Obviously, no single factor dictates the tremendous diversity in cucurbit fruit size/shape. Therefore, in this review, we will summarize QTL for FS, FSI, and FW for a more complete description of the genetic architecture of fruit growth.

Genetic architecture of fruit size, shape, and fruit weight variation in cucurbits

From the above discussion, clearly, a number of pre- and post-anthesis factors can influence the size and shape of cucurbit fruits. A large number of QTL for FL, FD, FSI, and FW have been identified in cucumber, melon, and watermelon, making it possible to conduct comparative analyses of the genetic architecture of fruit size and shape in cucurbits. One complicating factor is the inconsistent names of fruit size and shape QTL used in various studies. For convenience, here we proposed control vocabularies to depict QTL for fruit length, diameter, and fruit shape at different stages (Table 1), which was adapted from Diaz et al. (2011) in melon and Weng et al. (2015) in cucumber. In brief, oFL, oFD, oFSI, cFL, cFD, cFSI, FL, FD, FSI, oFW, cFW, and FW stand for the length, diameter, fruit shape index, and weight of ovary, fruit at commercial harvest (immature) and mature fruit, respectively. A QTL was named accordingly to indicate its location and relative order on the chromosome (Chr hereinafter) (Table 1). Often, the same QTL were identified in multiple environments or different genetic backgrounds. By examining their physical locations (LOD support intervals), it is possible to infer a consensus QTL for this trait. Here, a consensus fruit size (FS) QTL will be defined by synopsis of QTL information from fruit length and/or diameter. We assume that an FS QTL is underlying both fruit elongation (FL) and radial growth (FD). Thus, an FS consensus QTL was assigned even if only FL or FD QTL was reported in one or more studies. Similarly, a fruit shape (FSI) or fruit weight (FW) consensus QTL will be established based on individual FSI or FW QTL, respectively. The naming rules for consensus QTL were the same as individual QTL (see examples in Table 1).

QTL for FS, FSI, and FW in cucumber

Cucumber fruit size and weight have been a subject of research for a long time. Early studies indicated that FL in general has a relatively high narrow-sense heritability (e.g., Smith et al. 1978; Strefeler and Wehner 1986; Owens et al. 1985). Kennard and Havey (1995) were probably the first to conduct QTL analysis for fruit size and shape in cucumber, but pre-draft genome studies were sporadic (e.g., Dijkhuizen and Staub 2002; Fazio et al. 2003; Yuan et al. 2008). Using a recombinant inbred line (RIL) population developed from the cross between Chinese Long and Beit Alpha cucumbers, Yuan et al. (2008) identified 15, 6, and 5 QTL for cFL/cFD, cFSI, and cFW, respectively. Cucumber was the first among all horticultural crops with a publicly available draft genome (Huang et al. 2009; Yang et al. 2012). The draft genome sequences combined with high-throughput genotyping and phenotyping methods significantly expedited QTL mapping in cucumber (e.g., Wei et al. 2014; Zhu et al. 2016; Shimomura et al. 2017). With a RIL population derived from Chinese Long × European Long cucumbers, Miao et al. (2011) identified 14 QTL for cFL, cFD, FL, FD, FSI, and FW. QTL mapping with populations derived from crosses between cultivated and wild or semi-wild (*C. s.* var. *xishuangbannesis*, XIS) cucumbers identified a number of fruit size and weight QTL, some of which were suggested to be under selection during domestication (Cheng et al. 2010; Qi et al. 2013; Wang et al. 2014; Bo et al. 2015; Sheng et al. 2019). With Gy14 (US pickling type) × 9930 (Chinese Long) RILs, Weng et al. (2015) detected 22 QTL for fruit length and diameter at ovary, immature, and mature fruit stages. In QTL analysis for FS/FSI with segregating populations derived from a cross between WI7238 (long fruit) and WI7239 (round fruit), the round fruit shape in WI7239 was found to be controlled by two QTL, *FS1.2* and *FS2.1,* that encode the tomato homologs *SUN* (*CsSUN25-26-27a*) and *SlTRM5* (*CsTRM5*), respectively (Pan et al. 2017a; Wu

Table 1 Nomenclature of fruit size/shape QTL used in the present research

Traits	QTL name	QTL examples	Description of examples
Individual QTL			
Ovary length	oFL	*oFL1.1*	First oFL QTL on Chr1
Ovary diameter	oFD	*oFD3.3*	Third oFD QTL on Chr3
Ovary shape index	oFSI	*oFSI5.2*	Second QTL of oFSI on Chr5
Ovary weight	oFW	*oFW5.1*	First oFW QTL on Chr5
Immature fruit length	cFL	*cFL4.1*	First cFL QTL on Chr4
Immature fruit diameter	cFD	*cFD6.1*	First cFD QTL on Chr6
Immature fruit shape index	cFSI	*cFSI7.1*	First cFSI QTL on Chr7
Immature fruit weight	cFW	*cFW6.1*	First cFW QTL on Chr6
Mature fruit length	FL	*FL2.2*	Second FL QTL on Chr2
Mature fruit diameter	FD	*FD3.1*	First FD QTL on Chr3
Mature fruit shape index	FSI	*FSI1.2*	Second FSI QTL on Chr2
Mature fruit weight	FW	*FW9.2*	Second FW QTL on Chr9
Consensus QTL			
Cucumber fruit size	CsFS	*CsFS1.2*	Second consensus FS QTL on cucumber Chr1
Cucumber fruit weight	CsFW	*CsFW3.1*	First consensus FW QTL on melon Chr3
Cucumber fruit shape index	CsFSI	*CsFSI5.2*	Second consensus FSI QTL on cucumber Chr5
Melon fruit size	CmFS	*CmFS2.1*	First consensus FS QTL on melon Chr2
Melon fruit weight	CmFW	*CmFW8.1*	First consensus FW QTL on melon Chr8
Melon fruit shape index	CmFSI	*CmFSI11.3*	Third consensus FSI QTL on melon Chr11
Watermelon fruit size	ClFS	*ClFS3.3*	Third consensus FS QTL on watermelon Chr3
Watermelon fruit weight	ClFW	*ClFW2.4*	Fourth consensus FW QTL on watermelon Chr2
Watermelon fruit shape index	ClFSI	*ClFSI3.3*	Third consensus FSI QTL on watermelon Chr3

et al. 2018). In another study using populations derived from WI7200 (elongated fruit) × WI7167 (round fruit, semi-wild XIS), Pan et al. (2017b) identified eight consensus FS/FSI QTL, each of which contributed to both longitudinal and radial growth during fruit development. Among them, *FS5.2* exhibited the largest effect on the determination of round fruit shape that is characteristic of the WI7167 cucumber.

In some cucumber genetic backgrounds, fruit size, especially fruit elongation, is controlled by simply inherited genes or few major-effect QTL. For example, with an $F_{2:3}$ population derived from CC3 (North China type) × NC76 (landrace), Wei et al. (2014, 2016) identified 8 QTL for cFL, FL, and FW with the major-effect cFL/FL QTL on Chr3 explaining ~ 45% of observed phenotypic variance (PVE, or R^2). Wang et al. (2017) fine mapped a spontaneous mutation *short fruit-1* (*sf-1*) in a 174 kb region on Chr6. The EMS mutant *short fruit-2* (*sf-2*) encodes a RING-type E3 ligase (Xin et al. 2019). In natural cucumber populations, the *FRUITFULL-like* MADS-box gene (*CsFUL1*) plays an important role in fruit elongation in Chinese Long cucumbers (Zhao et al. 2019). Fruit size could also be influenced by genes regulating general organ size variation. For example, the cucumber *littleleaf* (*ll*) gene for a WD40-domain containing protein exhibits pleiotropic effects on fruit size (Yang et al. 2018).

From the literature, 135, 30, and 20 fruit size (FS), shape (FSI), and fruit weight (FW) QTL have been reported in cucumber, respectively. The details of all 185 QTL including their chromosomal locations, PVE, and flanking markers are presented in supplemental Table S1. Consensus FS, FSI, and FW QTL were inferred based on physical locations of individual QTL as defined by 1.5 or 2.0 LOD intervals from different studies. Previous studies have established 14 consensus FS QTL (*FS1.1*, *FS1.2*, *FS2.1*, *FS2.2*, *FS3.1, FS3.2, FS3.3, FS4.1, FS5.1, FS5.2, FS6.1, FS6.2*, *FS6.2*, and *FS7.1*) in cucumber (Weng et al. 2015; Pan et al. 2017b). Synthesis of information of the 135 FL and/or FD QTL (Table S1) identified five new ones (*FS1.3, FS4.2, FS4.3, FS5.3*, and *FS7.2*). Information of all 19 consensus FS QTL including component QTL from each study is presented in supplementary Table S2 and graphically presented in supplemental Fig. S1. Note that the numbering of FS consensus QTL on each chromosome was not in sequential order from top to bottom. Rather, the order followed the dates when these QTL were identified (the earliest is the first) (Weng et al. 2015; Pan et al. 2017b). Among the 19 consensus FS QTL, 13 could be detected in at least four populations; only two (*CsFS2.2*, and *CsFS4.3*) were identified in one population/study (Table S2; Fig. S1). Among them, 9 (*CsFS1.1*, *CsFS1.2*, *CsFS2.1*, *CsFS4.1*, *CsFS4.2*, *CsFS5.1*, *CsFS6.2*, *CsFS6.3*, and *CsFS7.1*) were detected in ovary, immature, and mature fruit stages. For three FS QTL (*CsFS2.2*, *CsFS3.3*, and *CsFS4.3*), only FL or FD QTL were detected in respective studies (loci with asterisks in Table S2 and Fig. S1). However, since many factors affect the power of fruit size QTL detection (Weng et al. 2015), it is possible that most QTL may play roles throughout the fruit development stages to control both fruit elongation and radial growth.

Eleven FSI and 12 FW consensus QTL were also inferred in cucumber. For convenience, the FSI and FW consensus QTL were numbered following the co-localized consensus FS QTL. The approximate physical locations of all 42 FS/FSI/FW consensus QTL were plotted against the Gy14 V2.0 draft genome, which is graphically presented in both Fig. 3 and Fig. S1. Relatively few studies included FSI and FW in QTL analysis. Therefore, some 'consensus' FSI or FW QTL were based on only a single study. In addition, the physical intervals of many consensus QTL on the chromosomes are large (Fig. 3). As such, the locations of those consensus QTL should be considered tentative. For example, considering that *FS1.2* and *CsFSI1.2* were co-localized and thus probably the same locus, it is reasonable to speculate that *CsFW1.2* and *CsFW1.4* may belong to the same locus too, but additional evidence is needed to confirm this. Nevertheless, most FSI and/or FW consensus QTL are co-localized with FS consensus QTL, which is consistent with the significant correlations of FSI or FW with fruit size in almost all QTL mapping studies. This may also suggest their possible common genetic basis. In particular, the *FW6.2* consensus QTL has been consistently detected in multiple studies (e.g., Miao et al. 2011; Bo et al. 2015; Pan et al. 2017b; Sheng et al. 2019). *FS6.3* was also detected in at least eight populations (Table S2). These data may suggest that the *FS6.3/FW6.2* QTL plays a very important role in regulating fruit size and weight variation in cucumber.

QTL for FS, FSI, and FW in melon

The quantitative nature of melon fruit size and shape was observed in some early studies (e.g., Lippert and Hall 1982; Kalb and Davis 1984). Perin et al. (2002) conducted QTL analysis for ovary and mature fruit size/shape in two melon

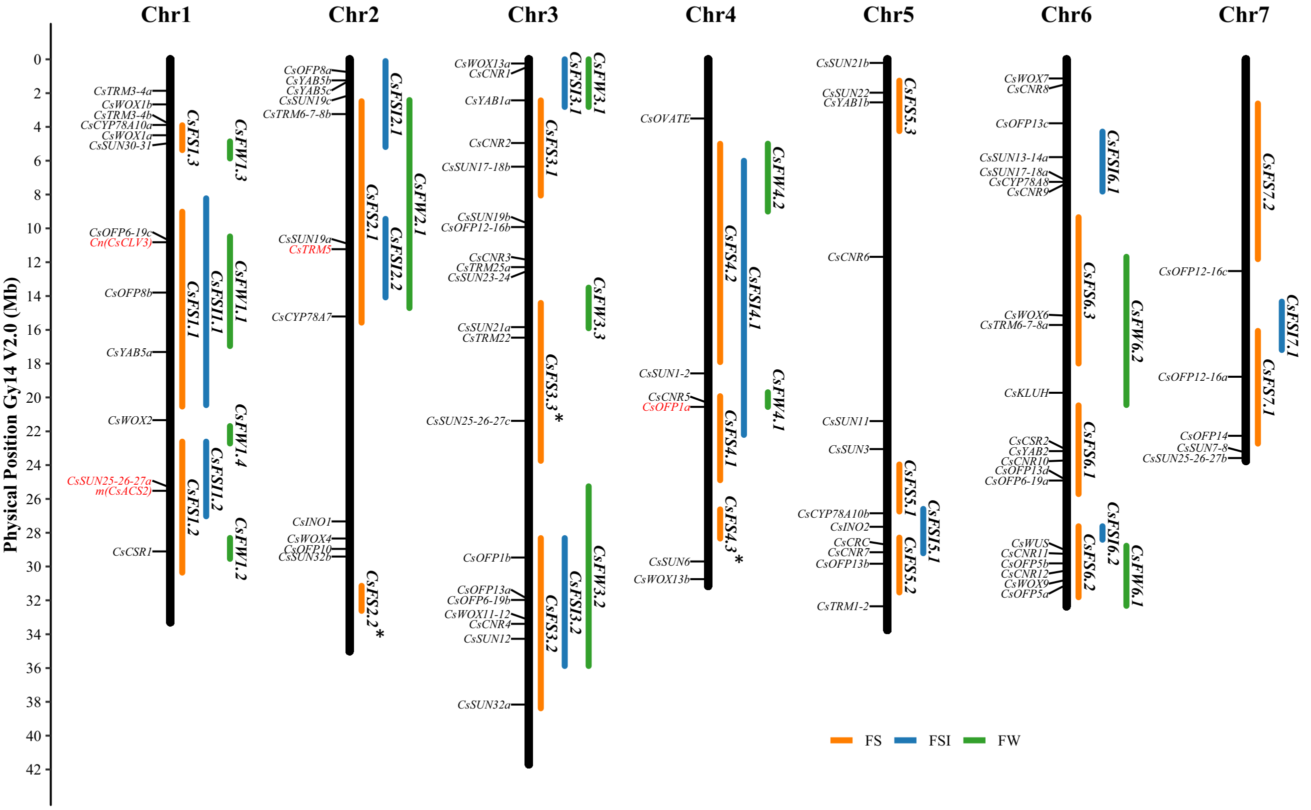
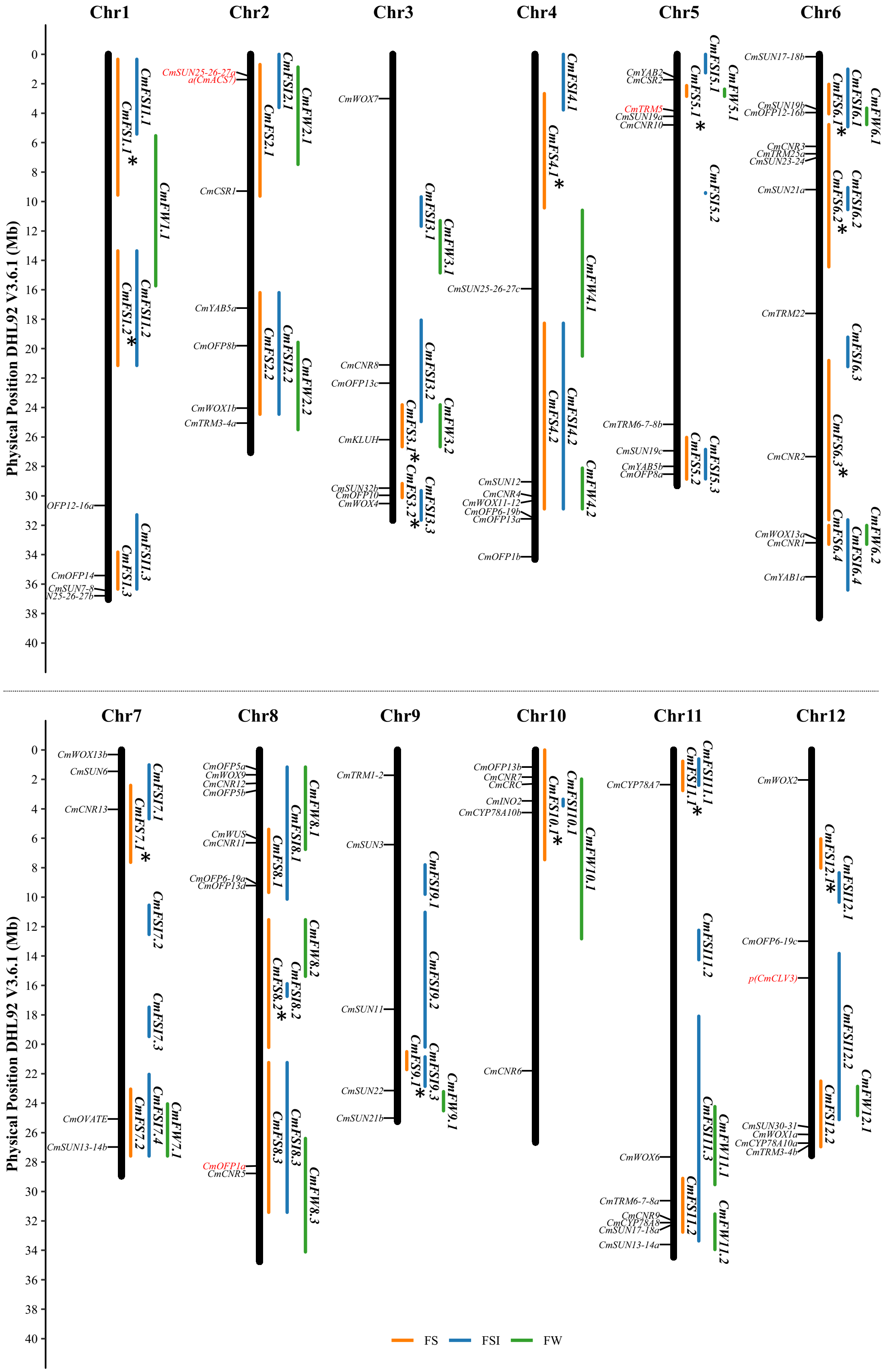


Fig. 3 Distribution of 42 fruit size (FS, orange), shape (FSI, blue), and weight (FW, green) consensus QTL on 7 cucumber chromosomes. The vertical bar alongside each QTL delimits approximate physical range that is based on LOD support intervals of component QTL identified from different studies. FS/FSI/FW gene homologs are aligned to the left of each chromosome. Candidate genes (*CsSUN25-26-27a* for *CsFS1.2*, and *CsTRM5* for *CsFS2.1*) or genes with pleiotropic effects (*m/CsACS2*, and *Cn/CsCLV3*) for fruit size and shape are highlighted in red. FS QTL with asterisks indicate only FL or FD QTL have been detected (color figure online)


Chr1
Chr2
Chr3
Chr4
Chr5
Chr6
Physical Position DHL92 V3.6.1 (Mb)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
CmFSI1.1
CmFS1.1*
CmFW1.1
CmFS1.2*
CmFSI1.2
OFP12-16a
CmFSI1.3
CmFS1.3
CmOFP14
CmSUN7-8
N25-26-27b
CmSUN25-26-27a
a(CmACS7)
CmFSI2.1
CmFW2.1
CmFS2.1
CmCSR1
CmYAB5a
CmOFP8b
CmFSI2.2
CmFS2.2
CmFW2.2
CmWOX1b
CmTRM3-4a
CmWOX7
CmFSI3.1
CmFW3.1
CmCNR8
CmOFP13c
CmFSI3.2
CmFW3.2
CmKLUH
CmFS3.1*
CmSUN32b
CmOFP10
CmWOX4
CmFS3.2*
CmFSI3.3
CmFSI4.1
CmFS4.1*
CmFW4.1
CmSUN25-26-27c
CmFS4.2
CmFSI4.2
CmFW4.2
CmSUN12
CmCNR4
CmWOX11-12
CmOFP6-19b
CmOFP13a
CmOFP1b
CmFSI5.1
CmFW5.1
CmYAB2
CmCSR2
CmFS5.1*
CmTRM5
CmSUN19a
CmCNR10
CmFSI5.2
CmTRM6-7-8b
CmSUN19c
CmYAB5b
CmOFP8a
CmFS5.2
CmFSI5.3
CmSUN17-18b
CmSUN19b
CmOFP12-16b
CmFS6.1*
CmFSI6.1
CmFW6.1
CmCNR3
CmTRM25a
CmSUN23-24
CmSUN21a
CmFS6.2*
CmFSI6.2
CmTRM22
CmFSI6.3
CmCNR2
CmFS6.3*
CmWOX13a
CmCNR1
CmFS6.4
CmFSI6.4
CmFW6.2
CmYAB1a
Chr7
Chr8
Chr9
Chr10
Chr11
Chr12
CmWOX13b
CmSUN6
CmFSI7.1
CmCNR13
CmFS7.1*
CmFSI7.2
CmFSI7.3
CmOVATE
CmFS7.2
CmFSI7.4
CmFW7.1
CmSUN13-14b
CmOFP5a
CmWOX9
CmCNR12
CmOFP5b
CmFW8.1
CmFSI8.1
CmWUS
CmCNR11
CmFS8.1
CmOFP6-19a
CmOFP13d
CmFW8.2
CmFS8.2*
CmFSI8.2
CmFS8.3
CmFSI8.3
CmFW8.3
CmOFP1a
CmCNR5
CmTRM1-2
CmSUN3
CmFSI9.1
CmFSI9.2
CmSUN11
CmFS9.1*
CmFSI9.3
CmFW9.1
CmSUN22
CmSUN21b
CmOFP13b
CmCNR7
CmCRC
CmINO2
CmCYP78A10b
CmFSI10.1
CmFS10.1*
CmFW10.1
CmCNR6
CmCYP78A7
CmFSI11.1
CmFS11.1*
CmFSI11.2
CmFSI11.3
CmFW11.1
CmWOX6
CmTRM6-7-8a
CmCNR9
CmCYP78A8
CmSUN17-18a
CmSUN13-14a
CmFS11.2
CmFW11.2
CmWOX2
CmFS12.1*
CmFSI12.1
CmOFP6-19c
p(CmCLV3)
CmFSI12.2
CmFS12.2
CmFW12.1
CmSUN30-31
CmWOX1a
CmCYP78A10a
CmTRM3-4b
FS
FSI
FW

◂**Fig. 4** Distribution of 78 fruit size (FS, orange), shape (FSI, blue), and weight (FW, green) consensus QTL on 12 melon chromosomes. The vertical bar alongside each QTL delimits approximate physical range that is based on LOD support intervals of component QTL identified from different studies. FS/FSI/FW gene homologs are aligned to the left of each chromosome. Candidate gene (*CmOFP1a* for *CmFS8.3*) or genes with pleiotropic effects (*a/CmACS7*, and *p/CmCLV3*) for fruit size and shape are highlighted in red. FS QTL with asterisks indicate only FL or FD QTL have been detected (color figure online)

RIL populations (Ved161 and Ved414). In the Ved161 population, they identified 19 QTL for oFL/oFD/oFSI, and 15 for FL/FD/FSI, many of which were co-segregating indicating early control of fruit shape. In the Ved414 population, 8 FL/FD/FSI QTL were detected, but only one shared between the two populations. Perin et al. (2002) also found co-localization of the fruit shape QTL *fs2.1*, and *fs11.1* with the simply inherited genes *a* (*andromonoecious*) and *p* (*pentamerous*), respectively. Monforte et al. (2004) conducted QTL mapping for multiple fruit related traits including FSI and FW; four of the 8 fruit shape QTL identified in Perin et al. (2002) were also detected in this study. A number of these major-effect fruit shape and weight QTL were validated or fine mapped in subsequent studies using NILs (near isogenic lines) or ILs (introgression lines (ILs) (e.g., Eduardo et al. 2005, 2007; Moreno et al. 2008; Fernandez-Silva et al. 2009, 2010; Diaz et al. 2014). Zalapa et al. (2007) and Paris et al. (2008) identified FS, FSI, and FW QTL using a RIL population derived from exotic × elite US Western Shipping melon lines. Harel-Beja et al. (2010) conducted QTL analysis on FL, FD, and FW in a RIL population from the cross between PI 414,723 (subspp. *agrestis*) and 'Dulce' (subspp. *melo*). These studies revealed the diverse genetic bases of fruit size/weight variation in different genetic backgrounds. Díaz et al. (2011) and Monforte et al. (2014) reviewed the literature on QTL mapping in melon and inferred 9 meta-QTL (5 for FS and 4 for FW), which could be detected in multiple melon mapping populations.

QTL mapping was accelerated with the availability of the melon draft genome. In a number of QTL mapping studies, many fruit size, shape, and weight QTL identified early were validated, and novel ones were discovered. For example, using an F_2 population from snake melon (*flexuosus*) × cantaloupe (*cantalupensis*), Ramamurthy and Walters (2015) identified two QTL for oFD/oFSI, and 11 QTL for FL, FSI, and FW including two novel QTL for FSI. Perpina et al. (2016) developed IL libraries for several quantitative traits including FW, FL, FD, and FSI, which allowed evaluation of the effects of target QTL in different genetic backgrounds, and G by E interactions. Diaz et al. (2017) identified 13 QTL for FL, FD, FSI, and FW using segregating populations derived from the cross between the Indian wild melon and the Spanish cultivar 'Piel de Sapo', which helped identification of QTL under selection during domestication in melon. With GBS of a RIL population, Pereira et al. (2018) identified 17 QTL for FL, FD, FSI, FW, and FP (fruit perimeter). The high-density genetic map allowed to delimit the co-localized major-effect QTL *FW5.1, FD5.1, and FP5.1* into a 496-kb region with 48 predicted genes, among which the *FANTASTIC FOUR 2* (*MELO3C014402*) gene was proposed to be a possible candidate for this QTL (Pereira et al. 2018). All above-mentioned studies used biparental segregating populations in QTL mapping. Two studies took advantage of the rich fruit size and shape variation in natural melon populations and conducted genome-wide association analysis (GWAS) of these traits, which resulted in detection of novel QTL (Tomason et al. 2013; Gur et al. 2017). Detailed information of 105 FS (FL/FD), 103 FSI, and 57 FW QTL from 19 studies is summarized in supplementary Table S3 and graphically presented in supplemental Fig. S2. Based on the confidence interval of each QTL, 26, 33, and 19 consensus FS, FSI, and FW QTL could be inferred, respectively (Fig. 4; supplemental Table S4).

There are significantly more consensus QTL in melon than in cucumber (78 vs. 42), which seems consistent with the higher genetic diversity in melon in fruit size and shape (and probably also more studies conducted). The consensus QTL for FS, FSI, and FW were distributed across all 12 chromosomes with Chr10 harboring only one each while Chr6 and Chr8 the most (10 and 9, respectively) (Fig. 4). Among the 78 consensus QTL, almost half (12 for FS, 16 for FSI, and 10 for FW) were detected only in one study/population. Fourteen of the 16 FSI consensus QTL were detected through association analysis among 117 accessions (Gur et al. 2017) implying higher power of GWAS in detection of novel loci/alleles in natural populations. However, additional work is needed to validate these QTL. On the other hand, 9, 10, and 5 out of the 26 FS, 33 FSI, and 19 FW consensus QTL, respectively, were detected in at least three studies/populations (Table S4). In particular, the 9 FS consensus QTL *CmFS2.1, CmFS2.2, CmFS4.2, CmFS7.2, CmFS8.1, CmFS8.3, CmFS10.1, CmFS11.2*, and *CmFS12.2* are co-localized with nine corresponding FSI consensus QTL (Fig. 4). In addition, there were five consensus FW QTL (*CmFW2.1, CmFW2.2, CmFW8.1, CmFW8.3,* and *CmFW11.2*) that were co-localized with relevant FS and FSI QTL. These observations were consistent with the significant correlations between FS (FL and/or FD) and FSI or FW found in those studies. They also suggest that these QTL are highly stable across different genetic backgrounds and environments, and they may share possible common genetic basis.

QTL for FS, FSI, and FW in watermelon

Fruit shape variation in watermelon is relatively simple, which could be classified roughly into round, oval, blocky, or elongated (Wehner et al. 2001). McKay (1936) and Weetman (1937) found that the shapes of ovaries and mature fruits in watermelon were highly correlated. They also found that the difference between elongate/oblong and spherical fruits was determined by a single gene with incomplete dominance, which was later designated as the *O* locus. Thus, genotypes *OO*, *Oo,* and *oo* have elongated, blocky, and round fruits, respectively (Weetman 1937; Poole and Grimball 1945; Tanaka et al. 1995). Nevertheless, a number of subsequent studies have shown the quantitative nature of fruit size/shape in watermelon (e.g., Gusmini and Wehner 2005, 2007; Kumar and Wehner 2013).

Relatively few QTL mapping studies have been conducted in watermelon for fruit size and shape. Sandlin et al. (2012) conducted comparative QTL analysis for FS, FSI, and FW in three segregating populations (RIL or F_2) involving elite (*Citrullus lanatus*) × elite, elite × wild egusi (*C. mucosospermus*), and elite × wild *C. amarus* crosses. Stable QTL for FL, FD, FW, and FSI across genetic backgrounds and environments were identified which were mainly clustered at two linkage groups: LG9 (Chr2) and LG11 (Chr3). Ren et al. (2014) developed a high-density genetic map for watermelon, and the fruit size/shape and weight QTL from Sandlin et al. (2012) were anchored to this map as well as the watermelon (97,103) draft genome (Guo et al. 2013). More FS QTL were identified in several subsequent QTL mapping studies using biparental segregating populations in watermelon (e.g., Kim et al. 2015; Lu et al. 2009, 2016; Liu et al. 2014, 2016; Chang et al. 2016; Dou et al. 2018). In addition, Reddy et al. (2015) conducted GWAS with 96 watermelon accessions and identified four QTL associated with FL and FD, but none of them shared with those mapped by Sandlin et al. (2012). From the limited number of studies, 33, 17, and 7 QTL for FS, FSI, and FW have been identified in watermelon, respectively (Supplemental Table S5, and Fig. S3). From them, 15, 9, and 6 'consensus' FS, FSI, and FW QTL were established, which were distributed on all watermelon chromosomes except Chr11 (Supplemental Table S6; Fig. 5). Of the 15 consensus FS QTL, only four (*ClFS2.3*, *ClFS3.3*, *ClFS4.1*, and *ClFS8.1*) could be detected in more than one population/experiment. The 6 'consensus' FW QTL were detected from only one study (Sandlin et al. 2012), in which *ClFW2.3* was detected in two populations (Tables S5). Therefore, all 'consensus QTL' detected in a single population/experiment should be deemed preliminary.

The consensus fruit shape QTL *ClFSI3.1* and the co-localized fruit size QTL *ClFS3.3* were detected in all studies with segregating populations derived from two parental lines with different fruit shapes (round vs elongated) (Tables S5 and S6; Fig. 5). Sandlin et al. (2012) postulated that the major-effect FSI QTL, *fsi11.1* (LOD = 30.8; $R^2 = 56.6\%$) (i.e., *ClFSI3.1*), may be a candidate of the *O* locus for fruit shape proposed long time ago (Weetman 1937; Poole and Grimball 1945; Tanaka et al. 1995). In a round × elongated F_2 population, Kim et al (2015) identified a major-effect FSI QTL, *fsi3.1* (PVE = 79.7%), that is at the same location as *fs11.1* (Sandlin et al. 2012). Kim et al. (2015) suggested that the homolog of tomato FW gene *SUN* (*Cla011257*) may be the candidate gene for the *O* locus; and three SNPs in the coding region of this gene are probably responsible for the round vs elongated fruit shape between the two parents. Later, Dou et al. (2018) provided further evidence that *Cla011257* is the candidate gene for the *fsi11.1/fsi3.1/O* locus. However, instead of SNPs, Dou et al. (2018) found that the elongated fruit in one parent is due to a 159-bp deletion in *Cla011257*. In addition, among 105 watermelon lines examined, this deletion was present in all lines with elongated fruits (Dou et al. 2018). From our recent studies, it seems additional allele variants at this locus may also contribute to the fruit shape variation (Gao et al. unpublished data; Legendre and McGregor, unpublished data).

QTL for FS, FSI, and FW in other cucurbits

Fruit shape/size and weight variation in some cucurbit crops such as squash/pumpkin (*Cucurbita spp*) and bottle gourd (*Lagenaria siceraria*) is more fascinating (e.g., Xu et al. 2014; Paris 2016a; Dhillon et al. 2016; Fig. 1d), but very few studies have been conducted to investigate the genetic basis of fruit size/shape variation in these economically important crops. It has been known for a long time that in summer squash (*C. pepo*), the disk shape of scallop fruit is dominant over the sphere or pear fruit shape, which seems to be due to a single gene, *Di* (for *disk fruit* shape) (Sinnott 1922; Sinnott and Durham 1922; Whitaker 1932; Paris and Brown 2005). In winter squash (*C. moschata*), the *butternut fruit* shape (*Bn*) from 'New Hampshire Butternut' is dominant to *bn* for crookneck fruit shape (Mutschier and Pearson 1987). In *Cucurbita pepo*, Esteras et al. (2012) and Montero-Pau et al. (2017) conducted QTL analysis for fruit size and shape at both immature and mature fruit stages with segregating populations from an intersubspecific cross between Zucchini (ssp. *pepo*) and Scallop (ssp. *ovifera*) squashes. Two QTL for each of the FL, FD, and FSI at both immature and mature fruit stages were consistently detected, which were located on LG3 (major-effect) (Chr14) and LG12 (moderate effect) (Chr8). Montero-Pau et al. (2017) postulated that an *OFP* gene might be a candidate for the major-effect QTL on LG3. In another study, using an F_2 population developed from two *C. moschata* lines with contrasting fruit diameter, chamber width, and pulp thickness (no difference in fruit length), Zhong et al. (2017) found that

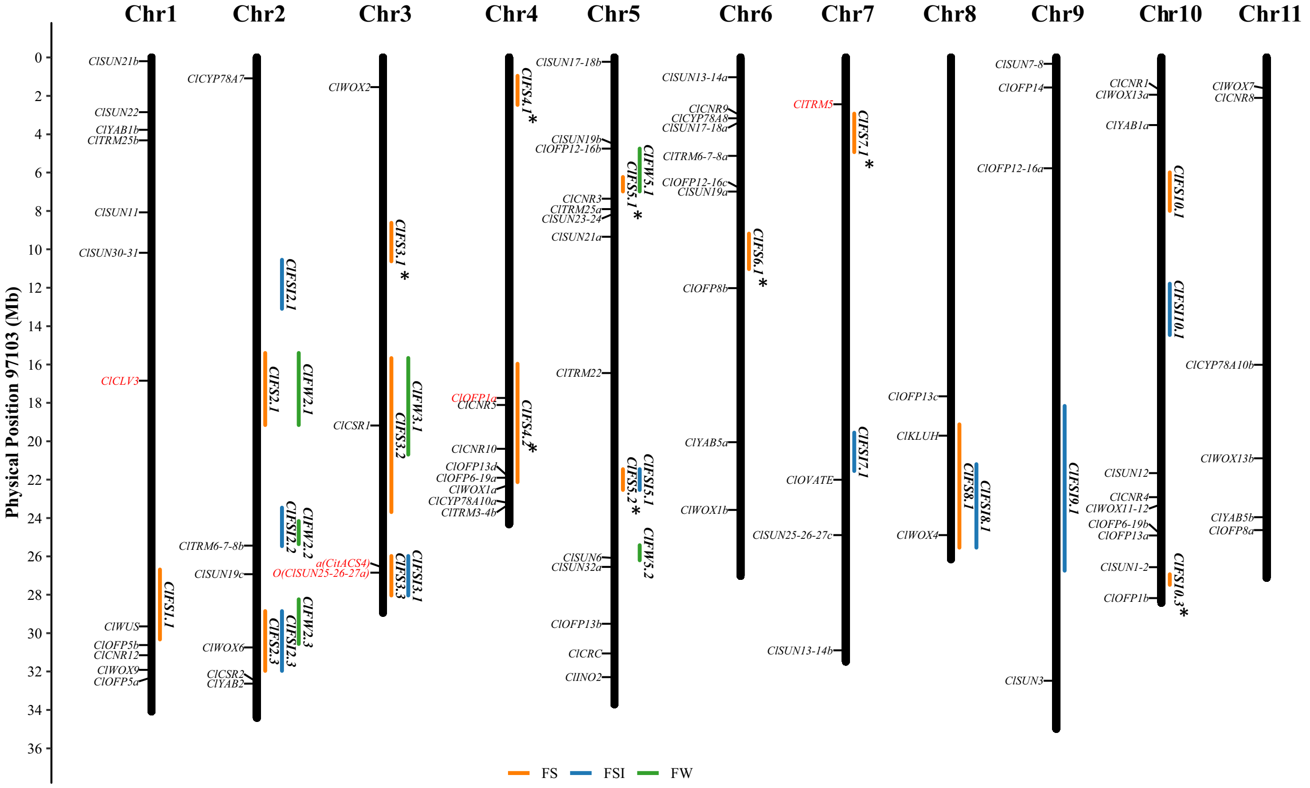


Fig. 5 Distribution of 30 fruit size (FS, orange), shape (FSI, blue), and weight (FW, green) consensus QTL on 10 of 11 watermelon chromosomes. The vertical bar alongside each QTL delimits approximate physical range that is based on LOD support intervals of component QTL identified from different studies. FS/FSI/FW gene homologs are aligned to the left of each chromosome. Candidate gene (*ClSUN25-26-27a* for *O*/*ClFS3.3*) or genes with pleiotropic effects (*a/CitACS4*, and possibly *ClCLV3*) for fruit size and shape are highlighted in red. FS QTL with asterisks indicate only FL or FD QTL have been detected (color figure online)

the QTL for the three traits were co-localized on two linkage groups (LG8 and LG13).

QTL identification of fruit size and shape in minor cucurbits is sporadic. Kole et al. (2012) and Wang and Xiang (2013) conducted QTL mapping for FL, FD, FSI in bitter gourd. In wax gourd, Liu et al. (2018) identified nine QTL associated with FL, FD FW, and FT (flesh thickness) with four QTL having major effects and co-localized. No further studies were carried out yet to validate these QTL. In addition, generalization of these QTL is difficult due to lack of sequence information for associated markers. Therefore, inference of consensus QTL is not possible from these studies.

Fruit shape variation in cucurbits due to pleiotropic effects at the *andromonoecious* and *carpel number* loci

In cucurbits, fruit size/shape is affected by sex expression of the plants. Major cucurbit crops bear different combinations of flower types: monoecious (both male and female flowers), andromonoecious (male and hermaphrodite flowers), trimonoecious (male, female, and hermaphrodite flowers), androecious (male flowers only), and gynoecious (only female flowers). The genes for 1-aminocyclopropane-1-carboxylate synthase (ACS) catalyzing the rate-limiting step in ethylene biosynthesis play the most important role in sex determination in cucurbits. For example, andromonoecy in cucumber, melon, watermelon, and zucchini squash all results from mutations in the orthologous *CsACS2* (the *m* locus), *CmACS7* (*a* locus), *CitACS4* (*ClACS7*), and *CpACS27A*, respectively (Boualem et al. 2008, 2009, 2015, 2016; Li et al. 2009; Ji et al. 2015, 2016; Martínez et al. 2014; Zhang et al. 2017). The association of hermaphroditic flowers with round fruit shape has been observed for long in major cucurbits (e.g., Rosa 1928; Poole and Grimball 1945; Kubicki 1962; Wall 1967), although a novel allele of the *m* gene (*m-1*) in cucumber encoding for a truncated protein of CsACS2 exhibits elongated fruit shape (Tan et al. 2015). Consistent with this, QTL mapping in biparental or natural populations has identified fruit shape QTL that are co-segregating with the *andromonoecy* locus in cucumber (Li et al. 2009), melon (e.g., Perin et al. 2002; Abdelmohsin and Pitrat, 2008; Diaz et al. 2014; Galpaz et al. 2018), watermelon (Prothro et al. 2013), and zucchini squash (Martínez et al. 2014). Loss-of-function mutations in the melon *a* gene (*CmACS7*) reduce ethylene production in pistillate flowers, which results in hermaphroditic flowers and andromonoecious plants; other traits affected by the mutations include reduction in fruit set, fruit weight, and number of total and viable seeds, as well as an alteration of fruit shape (Martos-Fuentes et al. 2018; Galpaz et al. 2018). Similarly, in watermelon, Aguado et al. (2018) found that the *a* locus (*CitACS4*, *Cla011230*) not only controls sex determination, but also affects floral organ maturation, fruit and seed set, the ovary and fruit shape, and growth rate. Therefore, in mapping populations involving andromonoecious parental lines, fruit shape variation may be due to pleiotropic effects of the *andromonoecy* locus.

Fruit size and shape variation in cucurbits may also be influenced by carpel number (CN) of the fruit. In tomato, a large portion of fruit size variation is due to *locule number* (*lc*) and *fasciated* (*fas*), which have synergistic effects on locule number and thus fruit size (Barrero and Tanksley 2004). The *fas* mutation is due to partial loss of the *CLAVATA3* (*SlCLV3*) gene expression, whereas a regulatory change in *WUSCHEL* (*WUS*) is the likely cause of *lc* (Muños et al. 2011; Rodriguez et al. 2011; Xu et al. 2015). The enlarged meristem caused by mutations in the two genes results in fruit with more locules associated with large and flat fruits. The association of carpel number variation with fruit size has been examined in several cucurbit crops. In melon, the carpel number (five vs three) is controlled by the *pentamerous* (*p*) locus. Fruits with five carpels are rounder than those with three carpels (Perin et al. 2002; Monforte et al. 2004; Eduardo et al. 2007; Paris et al. 2008). In populations segregating for carpel numbers, fruit size and fruit shape FSI QTL are often co-localized with the *p* locus due probably to its pleiotropic effect (e.g., Baudracco-Arnas and Pitrat 1996; Perin et al. 2002; Monforte et al. 2004; Fernandez-Silva et al. 2010). In cucumber, most varieties have fruit with three carpels, while fruit of some landraces and the semi-wild XIS cucumbers have five. Li et al. (2016) showed that carpel number variation in cucumber was controlled by a single locus *Cn*, and *CLAVTATA3* is a candidate gene for the *Cn* locus in cucumber (*CsCLV3*), and possibly the *p* locus in melon (*CmCLV3*). In addition, increased fruit weight in some cucumber lines may be due to pleiotropic effects of the increased CN (Li et al. 2016). Thus, the *andromonoecy* and *carpel number* loci should not be considered the true fruit size/shape genes. However, true fruit size/shape QTL have indeed been identified near the two loci in studies using populations that are not segregating for either trait. For example, in cucumber, the consensus QTL *CsFS1.1/CsFSI1.1/CsFW1.1* and *CsFS1.2/CsFSI1.2/CsFW1.2* (or *CsFW1.4*) are co-localized with the *Cn* (*CsCLV3*) and *m* loci, respectively (Fig. 3). *CsSUN25-26-27a* has been shown to be the candidate gene of *CsFS1.2*, which is only ~ 200 kb away from the *m* locus (Pan et al. 2017a; Fig. 3). In melon, Diaz et al. (2014) identified a fruit shape QTL *fsqs12.1* (*CmFSI12.2* in Fig. 4) which spanned the *p* locus; however, carpel number did not segregate in the population used. In squash (*C. pepo*), Esteras et al. (2012) did not detected any fruit size/shape QTL in the region where a QTL for carpel number was located. Therefore, in a QTL mapping study for fruit size and shape, if andromonoecious sex expression or carpel number is segregating in the population, pleiotropic effect on fruit size/shape should be considered in data interpretation. Since both genes (*ACS* and *CLV3*) are highly conserved among cucurbit crops, it should be relatively straightforward to examine the homologs of these genes in the vicinity of the fruit size/shape QTL identified. The locations of the two genes in cucumber (*m/CsACS2, Cn/CsCLV3*), melon (*a/CmACS7*, *p/CmCLV3*), and watermelon (*a/CitACS4, ClCLV3*) are presented in Figs. 3, 4 and 5, respectively. Interestingly, in all three crops, the *andromonoecy* locus is very closely linked with *SUN25-26-27a*, which is the candidate gene for *CsFS1.2* in cucumber (Pan et al. 2017a), and the *O* locus in watermelon (Sandlin et al. 2012; Kim et al. 2015; Dou et al. 2018).

Association of cucurbit fruit size/shape QTL with fruit size/shape gene homologs

Several genes underlying fruit size, shape, and weight variation have been cloned in tomato. The first cloned fruit weight (FW) QTL, *fw2.2*, in tomato encodes a member of the cell number regulator (CNR) protein family (Frary et al. 2000; Guo et al. 2010). *FW3.2* encodes an ortholog of *KLUH*, a member of the cytochrome P450 subfamily CYP78A (Chakrabarti et al. 2013). Tomato *LOCULE NUMBER*

(*LC*) influences fruit shape and size, which is an ortholog of Arabidopsis *WUSCHEL* (*WUS*), the founding member of the *WOX* gene family (Muños et al. 2011). The tomato fruit shape gene *SUN* encodes a protein of the IQD family with the conserved IQ67 domain involving calmodulin binding (Rodríguez et al. 2011; Wu et al. 2011). In rice, the GSE5/GW5 protein encoded by the *qSW5/GW5* locus for grain size also contains an IQ domain (Duan et al. 2017; Liu et al. 2017). Liu et al. (2002) identified *OVATE*, a novel class of regulatory genes underlying the tomato pear-shaped fruit. OVATE FAMILY PROTEINS (OFPs) with the conserved OVATE domain (for example, tomato *SlOFP20*) have been shown to play important roles in regulation of fruit size (Wu et al. 2018). In Arabidopsis, Lee et al. (2006) identified two homologous proteins, LONGIFOLIA1 (LNG1) and LONGIFOLIA2 (LNG2), regulating leaf morphology. Both LNG1 and LNG2 are TONNEAU1 Recruiting Motif (TRM) proteins. In rice, a major QTL (*GL7/GW7/SLG7*) for grain length encodes a TRM member (Wang et al. 2015a, b; Zhou et al. 2015). The tomato gene *SlTRM5* was recently shown to participate in regulation of fruit size (Lazzaro et al. 2018; Wu et al. 2018). The tomato *fw11.3* locus encodes a cell size regulator (CSR) with unknown functions (Mu et al. 2017). The seven groups of genes are ubiquitous in the plant genomes, which are often present as gene families. Their functions on fruit size/shape, or fruit weight control also seem highly conserved across diverse plant species (reviewed by van der Knaap et al. 2014; Liang et al. 2017; van der Knaap and Ostergaard 2018). As mentioned early, the candidate genes for the cucumber fruit size QTL *FS1.2* and *FS2.1* (Fig. 3) are *SUN* and *TRM* homologs, respectively (Pan et al. 2017a; Wu et al. 2018). The watermelon fruit shape locus *O* is also a *SUN* homolog (Sandlin et al. 2012; Kim et al. 2015; Dou et al. 2018). The melon *CmOFP1a* is a candidate for the fruit size QTL *CmFS8.3/CmFSI8.3* (Wu et al. 2018).

The plant-specific YABBY transcription factors play many important roles in fruit development (Bowman and Smyth 1999). In tomato, the *fas* locus was first thought to encode SlYABBY2b, a homolog of Arabidopsis YAABY2 (Lippman and Tanksley 2001; Cong et al. 2008; Huang et al. 2013), which was later proved not true; instead, *SlCLV3* was shown to underlie the *fas* locus (Xu et al. 2015). Nevertheless, some clues hint possible involvement of the YABBY family member CRABS CLAW (CRC) in fruit size/shape control. In Arabidopsis, the *crc-1* mutants cause the gynoecium to develop into a wider but shorter structure, suggesting that CRC suppresses radial growth of the developing gynoecium but promotes its longitudinal growth (Alvarez and Smyth 1999; Bowman and Smyth 1999). In melon, transgenic plant overexpressing the *CmCRC* gene results in elongated fruit (Switzenberg et al. 2015).

We conducted genome-wide search for homologs of the eight classes of genes in the cucumber, melon, and watermelon draft genomes (https://cucurbitgenomics.org/). The details of these genes including characteristic domain(s) of each protein family (SUN, OVATE, CYP78A, TRM, CNR, CSR, YABBY, and WOX) are presented in Table 2. Since the *andromonoecy* and *carpel number* loci have pleiotropic effect on fruit size and shape in cucurbits, they are also included in Table 2. Homolog identification of proteins using the typical OVATE, CNR, or YABBY domain was

Table 2 Classification of cloned fruit size/shape and weight genes with characteristic domains and number of homologs in cucumber, melon, and watermelon genomes

Genes	Protein families	Domain/motif (Pfam identifier)	Cucumber[a]	Melon[a]	Watermelon[a]	Total
SUN (tomato), GSE5/GW5 (rice)	SUN	IQ67 (PF00612), DUF4005 (PF13178)	22	21	22	65
OVATE (tomato)	OFP (Ovate Family Protein)	OVATE (PF0844)	19	18	17	54
FW2.2 (tomato)	CNR (Cell Number Regulator)	PLAC8 (PF04749)	12	13	8	33
FW3.2 (tomato)	P450/CYP78A subfamily	CYP78A (PF00067)	5	5	5	15
GL7 (rice), SlTRM5 (tomato)	TRM (TONNEAU1 Recruiting Motif)	DUF4378 (PF14309), VAR-LMGL (PF14383)	8	8	7	23
FW11.3(tomato)	CSR (Cell Size Regulator)	FAF-like (PF1125)	2	2	2	6
CRABS CLAW (AtCRC) (Arabidopsis)	YABBY	YABBY (PF04690)	9	7	8	24
WUSCHEL(tomato)	WOX	Homeobox (PF00046)	11	11	11	33
CLAVATA3(tomato, cucumber, melon)	CLV3	Not applicable	1	1	1	3
ACS2 (Cucumber, melon, watermelon)	ACS	Aminotran_1_2 (PF00155)	1	1	1	3
			90	87	82	259

[a]Based on cucumber Gy14 V2.0, melon DHL92 V3.6.1, and watermelon 97103 V1.0 draft genomes

relatively straightforward. For SUN, only those containing both the IQ67 and DUF4005 domains were counted. Since CYP78A is a subfamily of P450, all CYP78A-containing homologs were further verified by BLASTP using six CYP78A members of Arabidopsis (Table S7) as queries against target genomes. To extract the TRM homologs, protein sequences of Arabidopsis TRM2 (LNG2) (Lee et al. 2006), rice GL7 (Wang et al. 2015a), and the cucumber CsFS2.1/CsTRM5 (Wu et al. 2018) were first checked for conserved domains; only those containing both DUF4378 and VARLMGL domains were kept. For WOX, the homologs were first identified with the homeobox domain (PF00046) and then, the family members were verified with the WUS-box motif following van der Graaff et al. (2009). In the case of CSR, only those with the FAF-like domain (Mu et al. 2017) were retained. To understand the congruent relationship of these cucurbit homologs with those of Arabidopsis (Table S7) and tomato (Table S8), phylogenetic trees of SUN, OFP, YABBY, CYP78A, TRM, CNR, and WOX were constructed (see below). The protein sequences of tomato SlSUN, SlOFP, and SlYABBY gene families were obtained from Huang et al. (2013); SlCNR, SlWOX, and SlCYP78A were retrieved from Monforte et al. (2014). SlTRM was from Wu et al. (2018). Arabidopsis protein sequences of AtIQD (Abel et al. 2005), AtOFP (Hackbusch et al. 2005; Wang et al. 2016a, b, c), AtTRM (Drevensek et al. 2012), AtYABBY (Bowman and Smyth 1999), AtCYP78A (Monforte et al. 2014), AtWOX (van der Graaff et al. 2009), and AtCNR were retrieved from TAIR (https://www.arabidopsis.org). Naming of cucurbit homologs followed the original Arabidopsis names if they were clustered in the same clade. For example, the Arabidopsis genome contains six YABBY members: AtCRC (CRABS CLAW), AtFIL (FILAMENTOUS FLOWER), AtINO (INNER NO OUTER), AtYAB2, AtYAB3, and AtYAB5 (Bowman and Smyth 1999; Lee et al. 2006). Thus, CsCRC, CmCRC, and ClCRC are all homologs of AtCRC. For CNR, no naming conventions are available in either Arabidopsis or tomato, so the CNR homologs in cucumber were named sequentially in the order of their appearances on chromosomes starting from top of Chr1 until bottom of Chr7. In melon and watermelon, CNR homologs were assigned the same number as cucumber if they were grouped in the same clade in clustering analysis, and with top hit during BLASTp alignment against the cucumber genome, and were located in a syntenic block to cucumber. In total, 90, 87, and 82 homologs for the 10 fruit size/shape/weight-related genes were identified in cucumber, melon, and watermelon, respectively (Table 2). Detailed information of these homologs in the three genomes is presented in supplemental Tables S9-S11, respectively. There were one ACS2 and one CLV3 member in each genome. For the rest, SUN and OFP families have the most members (17–22 per genome) and CSR has the least (2 each). Nevertheless, the number of homologs in each gene family in the three genomes was very similar, suggesting that they are highly conserved across the cucurbit genomes. All homologs were anchored to the three draft genomes, and non-random distribution in each genome was clear (Figs. 3, 4, 5). Many consensus FS, FSI, and FW QTL were co-localized with those homologs. In a few cases, the FS QTL were located in a region with only one or two members of candidate gene homologs (e.g., *CsFS4.2/CsFSI4.1* in Fig. 3 or *CmFS6.3/CmFSI6.2* in Fig. 4). This may help decide if a homolog is a potential candidate gene for the QTL. There were also many QTL regions with no homologs or homologs were mapped in regions with no QTL, which was particularly true in watermelon with relatively few fruit size/shape and weight QTL mapped (Fig. 5). Additional fruit size and shape QTL could be mapped in those regions in the future. Alternatively, it is possible that novel genes are underlying those QTL. However, in many regions, fruit size/shape gene homologs from different families or multiple members from the same family were clustered in a QTL region, which may complicate identification of candidate genes for those QTL through the candidate gene approach (see examples below).

Synteny, structure/function conservation of FS/FSI/FW gene homologs in cucurbits

Genetic mapping and cloning of genes could be facilitated by comparative analysis across different crops with the promises of conserved functions of target genes in syntenic regions. The syntenic relationships among different cucurbit genomes have been well established (e.g., Li et al. 2011; Garcia-Mas et al. 2012; Guo et al. 2013; Yang et al. 2014). Using annotated genes in the cucumber (Gy14 V2.0) and melon (DHL92 V3.6.1) draft genomes, we examined the syntenic relationships of consensus QTL mapped in the two genomes. As an example, the syntenic blocks harboring consensus FS/FSI QTL in cucumber and melon were aligned and are illustrated in Supplemental Fig. S4. For all 19 cucumber FS QTL, their melon syntenic blocks harbor at least 25 FS or FSI QTL implying possible common genetic basis for at least some QTL pairs located in those cucumber and melon syntenic regions.

A gene family often includes multiple members with potentially diverse functions. On the other hand, members from different plant species with a similar structure may serve similar functions. As such, we conducted clustering analysis using protein sequences of 257 homologs of seven fruit size/shape genes (SUN, OFP, TRM, CYP78A, CNR, YABBY, and WOX) identified in the three cucurbit genomes (Table 2; Tables S9-11). The CSR, ACS, and CLV3 homologs were not included due to limited members in each family. The phylogenetic trees are presented in supplemental

Fig. S5 (A to G). Several cloned fruit/grain size/weight genes in Arabidopsis (*LNG1, LNG2, AtFIL, AtINO*, and *AtCRC*), tomato (*SUN, OVATE, SlTRM5, SlOFP20,* and *SlKLUH*), and rice (*GSE5/GW5*, and *GL7*) were set as references. As expected, in each gene family, homologs from the same family member (with the same number in their names) were grouped in the same clade (Fig. S5). Those genes in the same clade were also located in syntenic regions of the three genomes. These observations support the high degree of conservation in both structure and function of these homolog genes in cucurbits, which could be further evidenced from cloned genes in cucurbits. For example, *CsSUN25-26-27a* and *ClSUN25-26-27a* (*Cla011257*) are the candidate genes of cucumber fruit size QTL *CsFS1.2* (Pan et al. 2017a) and watermelon fruit shape gene *O* (*ClFS3.3/ClFSI3.1*) (Dou et al. 2018), respectively. The three members, CsSUN25-26-27a, CmSUN25-26-27a, and ClSUN25-26-27a, were in the same clad as the rice GSE5/GW5 protein (but not SUN and OVATE of tomato) (Fig. S5A), suggesting that the structure and function of *SUN* genes in this region are highly conserved in the three crops. The syntenic relationship of the region harboring the *SUN25-26-27a* and *andromonoecy* (*a* or *m*) loci of the three cucurbit genomes is graphically presented in Fig. 6a. In melon, *CmSUN25-26-27a* is co-localized with the consensus QTL *CmFS2.1* (also *CmFSI2.1* and *CmFW2.1*) (Fig. 4). Therefore, it is reasonable to speculate that *CmSUN25-26-27a* might be a good candidate for this QTL in the absence of the pleiotropic effect by the *a* locus (for example, Perin et al. 2002). In melon, *CmFS8.3* encodes CmOFP1a (CmOFP13 in Wu et al. 2018). Its homologs *CsOFP1a* in cucumber and *ClOFP1a* in watermelon were co-localized with *CsFS4.1* (also *CsFSI4.1/CsFW4.1*) and *ClFS4.2*, respectively (Figs. 3 and 5). CmOFP1a, CsOFP1a, and ClOFP1a were clustered in the same clade as tomato SlOFP20 (Fig. S5B). Thus, *CsOFP1a* and *ClOFP1a* might be considered top candidates for the two QTL in cucumber and watermelon, respectively (Fig. 6b). Finally, *CsTRM5*, a homolog of tomato *SlTRM5,* has been shown to be the candidate gene for cucumber *CsFS2.1* (Wu et al. 2018). Its melon homolog CmTRM5 and watermelon homolog ClTRM5 were clustered in the same clade as tomato SlTRM5 (Fig. S5C). It may be of value to test their candidacy for the *CmFS5.1* (also *CmFSI5.1*, and *CmFW5.1*) and *ClFS7.1* QTL in melon and watermelon, respectively (Fig. 4).

This synteny-based inference could be expanded to more distantly related cucurbit species. For example, Montero-Pau et al. (2017) identified a major-effect fruit size and shape QTL in LG3 (designated as *CpFS3.1* here) with 20–40% PVE. Whole genome alignment indicated that LG3 is syntenic to pumpkin (*C. moschata*) Chr14, and the QTL region is syntenic to the regions where *ClFS10.3*, *CmFS4.2*, and *CsFS3.2* have been mapped in watermelon, melon, and cucumber, respectively (Fig. 6c). *CsFS3.2* and *CmFS4.2* also have very large effects on fruit size (Tables S1, S3). In cucumber and melon, the consensus FW and FSI QTL were also co-localized with the FS QTL, respectively (Figs. 3, 4), suggesting that the FS/FSI/FW QTL at this locus among these crops might share a common genetic basis. However,

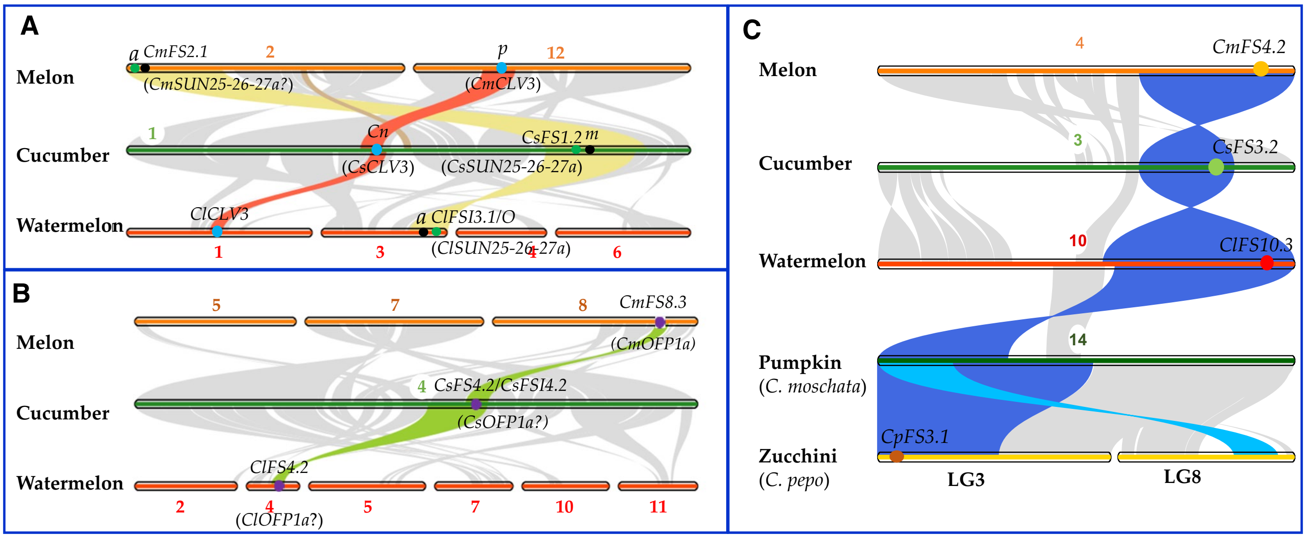


Fig. 6 Structure and function conservation of fruit size/shape-related QTL across cucurbit genomes. **a** The fruit size/shape-related genes (*m, Cn,* and *CsFS1.2/CsSUN25-26-27a*) in cucumber are located in syntenic regions of the melon and watermelon genomes. **b** The cucumber *CsFS4.2* and watermelon *ClFS4.2* are located in syntenic regions (same colors) as melon fruit size/shape QTL *CmFS8.3* for which *CmOFP1a* is a candidate gene. **c** A major-effect fruit size/shape QTL in a syntenic region in four cucurbit crops including *CpFS3.1* of zucchini squash (*C. pepo*), *CsFS3.2* in cucumber, *CmFS4.2* in melon, and *ClFS10.3* in watermelon. The Python version of MCscan (Tang et al. 2008) is used for scanning multiple genomes to align syntenic blocks (color figure online)

there are multiple fruit size/weight gene homologs from four families (OFP1b, OFP13a, OFP6-19b, WOX11-12, SUN12, and CNR4) that were located in this region (Figs. 3, 4, 5). It may be difficult to use homology-based prediction of fruit size/shape candidate genes in these QTL loci.

Perspectives

Here, we reviewed QTL for fruit size/shape, and fruit weight in major cucurbits and identified consensus QTL in the cucumber, melon, and watermelon genomes, which may explain the majority of fruit size/shape and weight variation in the three crops. However, many of these 'consensus QTL' were detected in a single study or genetic background and have not been independently validated, which is especially true in watermelon in which relatively few QTL mapping studies have been conducted. The physical intervals for most QTL are still very large. Therefore, the chromosome locations and syntenic relationships among different cucurbits for these QTL need to be validated and refined in future QTL mapping studies. On the other hand, many stable consensus QTL are located in syntenic blocks harboring known fruit size/shape gene homologs that are phylogenetically very close (Fig. S5) indicating that some similar genetic mechanisms may present in cucurbits in fruit size/shape control. Meanwhile, there are also many unique consensus QTL which are mapped in non-syntenic regions, or where fruit size/shape gene homologs are absent (Figs. 3, 4, 5). Additional QTL may be identified in these regions in future QTL mapping studies. It is also possible that these QTL may be controlled by novel genes or other cloned genes not belonging to the eight classes (Table 2). In fact, many genes controlling plant organ size (e.g., seed or grain size) including the cucumber *littleleaf* gene affect fruit size (Yang et al. 2018; reviewed by Li et al. 2018; 2019). Therefore, while the synteny and structure/function conservation of candidate genes may facilitate QTL mapping, painstaking map-based cloning for fruit size/shape QTL in cucurbits may still be necessary in most cases.

From the literature review, the imbalance of work among major and minor cucurbits is obvious. Limited work on QTL mapping for fruit size/shape has been done in pumpkin/squash, and practically none in all minor cucurbit crops (gourds). With the draft genomes of many of these gourds are underway, it is reasonable to expect more in the near future. In this review, we proposed a list of control vocabulary to describe fruit size variation for QTL mapping (Table 1), which should be readily applicable in most cucurbits with relatively simple shape variation (e.g., round, oblong/oval, or cylinder). In bottle gourd or squash with more complicated and diverse fruit shapes, more sophisticated parameters using mathematical models or image processing software may be helpful in accurate phenotyping of fruit shape variation (for example, Brewer et al. 2006; Shimomura et al. 2017).

The genetic diversity of fruit size and shape among cucurbits is amazing and fascinating. The fruit weight varies from 0.03 kg in wild cucumber and melon to more than 1000 kg in the giant pumpkin, which occurs in 3–6 months. The pumpkin/squash were first cultivated in the Americas at least 10,000 years ago, whereas watermelons, cucumber/melon were cultivated in Africa and Asia, respectively, 3000–4000 years ago (Paris 2016b; Pitrat 2016). Interestingly, in Cucurbita, Paris and co-workers observed that accessions bearing nearly round fruits (FSI close to 1.0) are primarily grown for eating their mature fruit flesh or seeds, whereas the long- and flat-fruited ones are primarily grown for consumption of the young fruits (Paris 1989, 2000, 2008, 2016a; Merrick 1995). Cucumber is consumed primarily for immature fruit, and the majority of cucumber set elongated fruits. The roles of cucurbit fruit size/shape genes during domestication or crop evolution to shape they are today are unknown, which would be an interesting topic in future studies.

The molecular mechanisms of fruit size in cucurbits are largely unknown. So far only four candidate genes on fruit size regulation have been identified. We do not know how they work or interact to regulate cucurbit fruit growth. A few studies examined the transcriptomes during fruit development in cucumber (e.g., Ando et al. 2012; Jiang et al. 2015; Colle et al. 2017; Wang et al. 2017), and pumpkin (Xanthopoulou et al. 2017). These studies in general find microtubule and cell cycle-related genes that are dramatically activated in fruit elongation, and many transcription factor genes are also involved. But how fruit size genes interact with these transcription factors to modulate spatial and temporal expression of genes for cell division and cell expansion, thus fine tune cucurbit fruit elongation and radial growth during fruit growth and development, is a challenging task ahead. In tomato, Wu et al. (2018) found that both OVATE and SlOFP20 interact with TRM, and upon the interactions, OFPs and TRMs are re-localized to different subcellular compartments. They suggested that a dynamic balance between cytoplasmic- and microtubular-localized OFP-TRM protein complexes regulates cell division and organ growth. Lazzaro et al. (2018) proposed a model to describe the control of organ shape in tomato in the context of interactions among SUN, OFP, and TRM, as well as the associations with microtubules. Considering the conservation in functions of some fruit size/shape genes across diverse plants, it will be interesting to test this hypothesis in cucurbit plants.

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Author Contribution statement YP and YQW conducted literature review and wrote the manuscript. YHW performed comparative bioinformatics analysis of the data. CM, SL, MG and FL helped review of melon and watermelon data. All authors reviewed and approved the final submission.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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