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Review

Genetic and signalling pathways of dry fruit size: targets for genome editing-based crop improvement

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Summary

Fruit is seed-bearing structures specific to angiosperm that form from the gynoecium after flowering. Fruit size is an important fitness character for plant evolution and an agronomical trait for crop domestication/improvement. Despite the functional and economic importance of fruit size, the underlying genes and mechanisms are poorly understood, especially for dry fruit types. Improving our understanding of the genomic basis for fruit size opens the potential to apply gene-editing technology such as CRISPR/Cas to modulate fruit size in a range of species. This review examines the genes involved in the regulation of fruit size and identifies their genetic/signalling pathways, including the phytohormones, transcription and elongation factors, ubiquitin-proteasome and microRNA pathways, G-protein and receptor kinases signalling, arabinogalactan and RNA-binding proteins. Interestingly, different plant taxa have conserved functions for various fruit size regulators, suggesting that common genome edits across species may have similar outcomes. Many fruit size regulators identified to date are pleiotropic and affect other organs such as seeds, flowers and leaves, indicating a coordinated regulation. The relationships between fruit size and fruit number/seed number per fruit/seed size, as well as future research questions, are also discussed.

Introduction

The term 'fruit' normally refers to the fleshy seed-containing structure of a plant that is edible in the crude state, such as apple, banana, grape, lemon, orange, strawberry and tomato (Schlegel, 2003). It also includes the structures that are not commonly called 'fruit', such as pod, silique, kernel and grain. Fruit, therefore, account for a substantial part of the world's agricultural output for human and livestock diet (Giovannoni, 2004; Tanksley, 2004), and they are a major target for crop improvement. Genome editing offers the potential to accelerate fruit size breeding gains and facilitate the introduction of novel mutations that are unavailable in current germplasm (Scheben and Edwards, 2017; Scheben *et al.*, 2017).

Botanically, the fruit is a feature of angiosperms that develop a gynoecium derived from carpels after flowering. As such, fruit represents the reproductive organ for seed development and a structure that offers protection from insects and pests as well as a mechanism for seed dispersal (Bennett *et al.*, 2011; Giovannoni, 2004; Pesaresi *et al.*, 2014; Seymour *et al.*, 2013). Fruit types can be classified using several characteristics: dry or fleshy, dehiscent or indehiscent and apocarpous or syncarpous carpels (Karlova *et al.*, 2014; Pesaresi *et al.*, 2014). Capsules and siliques (as seen in *Arabidopsis* and relatives) are dry, dehiscent and syncarpous (Figure S1); achenes and nuts are dry, indehiscent and unicarpellate; berries are fleshy, indehiscent and syncarpous; and drupes (e.g. stone fruit) are fleshy and indehiscent with the single seed enclosed in a hard endocarp (Seymour *et al.*, 2013).

From a biological point of view, fruit size is a vital fitness character for plant evolution. From a human perspective, fruit size is an important agronomic trait for crop improvement, and is, therefore, a target for artificial selection (Pesaresi *et al.*, 2014; Seymour *et al.*, 2013; Tanksley, 2004). A classic example is the fruit of fleshy, tomato, which is nearly 1,000 times larger than its ancestor, and where size is modulated by the additive contribution of tens of quantitative trait loci (QTL), some of which have been cloned (Lin *et al.*, 2014; Tanksley, 2004). Also, studies in *Arabidopsis* have identified several critical regulators for fruit development (Giovannoni, 2004; Seymour *et al.*, 2008, 2013). As a model plant and member of the *Brassicaceae* family, *Arabidopsis* has contributed significantly to our understanding of fruit size regulation, with identification and functional characterization of many genes. From an ontogenetic standpoint, final fruit size is determined by successive processes of gynoecium formation, fertilization, fruit growth involving cell proliferation, differentiation and expansion, with partial overlaps in time (Tanksley, 2004; Wang *et al.*, 2016). Before fertilization, the first patterning event in *Arabidopsis* gynoecium is the construction of the apical-basal, mediolateral and abaxial–adaxial axes (Figure 1) that determine fruit length, width and thickness, respectively (Seymour *et al.*,

2013). Fruit size in *Arabidopsis* is mainly determined by fruit length that is governed by elongation of the apical-basal axis. The developmental switch that turns gynoecium into growing fruit is dependent on the fertilization of ovule, which otherwise senesces and dies (Seymour *et al.*, 2013). After the fertilization of fruit, it enters a stage where ovary growth and maturation are tightly cooperated with seed development.

Although dry fruit types (such as cereal and oilseed crops) account for the majority of plants, fruit size studies have focused primarily on fleshy-fruit species because of their importance in the human diet (Giovannoni, 2004). Despite the importance of fruit size to grain production, there are little-published reviews in dry fruit types.

Whilst tomato is an ideal system for studying fruit development, including size regulation (Karlova *et al.*, 2014; Pesaresi *et al.*, 2014; Seymour *et al.*, 2008, 2013), significant advances have been made in *Arabidopsis* since it was sequenced in 2000 (Kaul *et al.*, 2000). Information from *Arabidopsis* is often directly applicable to the polyploid crop relatives of the *Brassicaceae*, such as rapeseed, as well as other taxa including legumes, and lesser extent cereals. As genome editing technology and plant transformation protocols make knockout and knockin of most fruit size genes and regulatory elements in crops feasible (Scheben *et al.*, 2017), the challenge becomes selecting appropriate editing targets. Identifying and reviewing the broad range of genes and regulatory elements controlling fruit size, therefore, provides a foundation for crop improvement through genome editing. This review summarizes the genes and regulatory networks affecting fruit size and classifies the individual genetic/signalling pathways. We aim to provide new insights into the molecular mechanisms of fruit size regulation, which may help identify novel targets for genome editing and facilitate crop genetic improvement, especially for dry fruit types, including many important crops such as soya bean, peanut and rapeseed.

Fruit size regulators

Phytohormones

Plant hormones (also known as phytohormones) are a group of low-abundance chemical substances (signal molecules) produced within plants, which can act either locally or more remotely by long-distance transport through the vascular system (Lacombe and Achard, 2016). Phytohormones can regulate or influence almost all aspects of plant growth and development (including fruit size) in response to environmental and endogenous signals (https://en.wikipedia.org/wiki/Plant_hormone). At the cellular and molecular levels, phytohormones can affect gene expression and transcription, cell division and growth. According to their chemical structures and physiological effects, phytohormones are divided into ten classes: abscisic acid (ABA), auxins (AUX), brassinosteroids (BR), cytokinins (CTK), ethylene (ETH), gibberellins (GA), jasmonates (JA), salicylic acid (SA), strigolactones (SL) and others (Lin and Tan, 2011); their roles in regulating fruit size are summarized below (Figure 2; Table 1).

Auxins (AUX)

The action of auxins is demonstrated to be regulated in three layers: synthesis, transport and perception/signal transduction. In recent years, several genes involved in these processes have been shown to affect fruit growth and development.

The *YUCCA* flavin monooxygenase is a key enzyme in the simple two-step pathway that converts tryptophan to IAA (Zhao, 2012), the most abundant endogenous auxin in plants. Overexpression of a soya bean *YUCCA* gene, *GmYUCCA5,* in *Arabidopsis* resulted in higher plants with long and narrow leaves as well as few and short siliques (Wang *et al.*, 2017b).

Auxin is perceived by the receptor of F-box family proteins (such as *TIR1* and *AFB*), which recruit *AUX/IAA* proteins to the $SCF^{TIR1/AFB}$ complex for subsequent ubiquitination and proteasome-mediated degradation, leading to de-repression of *ARFs* that activate auxin-induced gene expression (Kong *et al.*, 2016). The *Arabidopsis PROTEASOME REGULATOR1* (*PTRE1*) is a homologue of the mammalian *proteasome inhibitor 31* (*PI31*), which is involved in auxin-mediated *AUX/IAA* degradation by repressing 26S proteasome activity. The loss-of-function *ptre1* mutant exhibited auxin-insensitive phenotypes: growth inhibition, including dwarf plants, small leaves and short siliques as well as arrested embryogenesis (Yang *et al.*, 2011). The *Arabidopsis MOB1A* is involved in the auxin-activated signalling pathway and auxin-controlled cell division, which is uniformly expressed in embryos and suspensor cells during embryogenesis. The loss-of-function

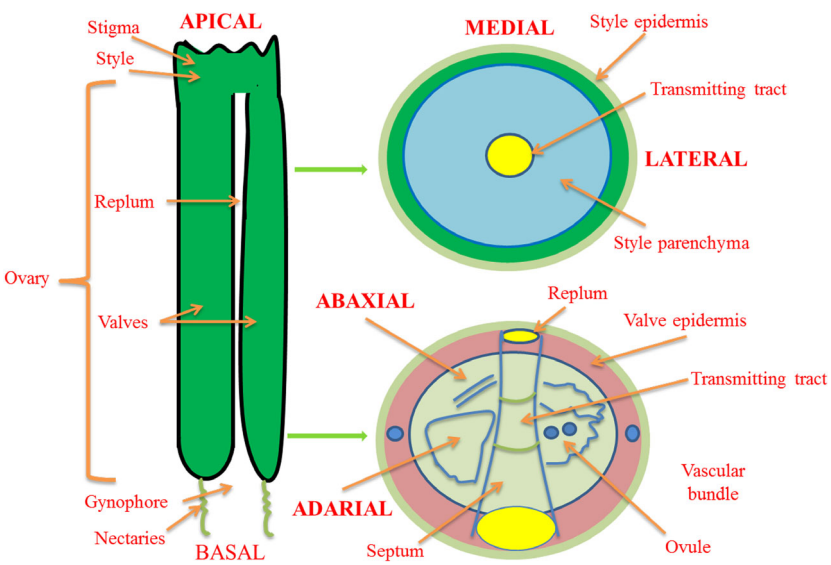

Figure 1 Model of a mature gynoecium in *Arabidopsis*. The entire silique is viewed from three axes: apical-basal, mediolateral and abaxial–adaxial. All main tissue types viewed from an assumed section from the three axes are indicated.

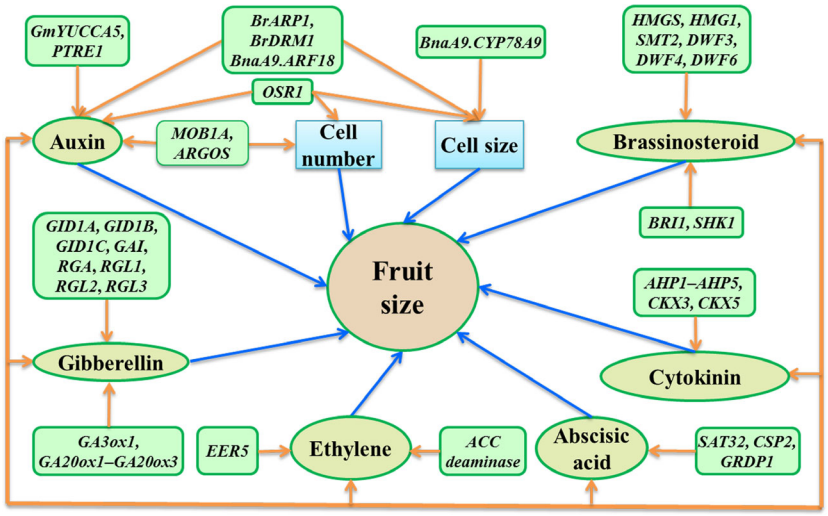

Figure 2 Fruit size is regulated by phytohormones pathways. The six main types of phytohormones and the underlying genes are indicated in oval and rounded rectangle boxes, respectively. In addition, several genes are involved in the regulation of cell number and size, which are shown in the rectangle box.

mob1a mutant displayed defects in organogenesis and growth, including reduced ovule number, shorter siliques and roots as well as smaller flowers (Cui *et al.*, 2016).

The *Arabidopsis AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE* (*ARGOS*) is a positive regulator of lateral organ size, which is highly induced by auxin and can transduce signals downstream of *AXR1* to regulate cell proliferation through *ANT* (Hu et al., 2003). Transgenic plants expressing sense or antisense cDNA of *ARGOS* display multiple phenotypic changes, including flowering time, plant height, leaf and flower size, as well as silique length and seed number per silique, which is resulted from the changes in cell number in these organs. The *Arabidopsis ORGAN SIZE RELATED 1* (*OSR1*) is an endoplasmic reticulum-localized hormone-responsive gene, which acts redundantly with *ARGOS* and *ARL* to regulate organ growth. The overexpression of *OSR1* in *Arabidopsis* delayed flowering time and increased the final size of many organs, including longer roots, larger leaves and flowers as well as longer siliques, which was resulted from increased cell number and size (Feng *et al.*, 2011).

Recently, a major QTL for both silique length and seed weight has been cloned on the A9 chromosome of *Brassica napus*, which is resulted from a 55-amino acid deletion in an orthologue of the *Arabidopsis auxin response factor 18* (designated as *BnaA9.ARF18*). The *BnaA9.ARF18* acts as a negative regulator of fruit and seed size by restricting cell elongation in the silique wall through its inhibitory activity on downstream auxin-responsive genes (Liu *et al.*, 2015). Overexpression of two auxin-repressed protein genes *BrARP1* and *BrDRM1* in *Brassica rapa* reduced vegetative and reproductive growth, including the number and length of siliques, possibly from inhibition of either cell elongation or expansion (Lee *et al.*, 2013).

Gibberellins (GA)

Despite the identification of more than 130 types of gibberellin, only *GA1, GA3, GA4* and *GA7* are bioactive (Daviere and Achard, 2013). In recent years, several genes in the gibberellin metabolism and signalling pathway have been shown to play an essential role in regulating fruit growth/size in *Arabidopsis*.

GA 20-oxidase (*GA20ox*) and GA 3-oxidase (*GA3ox*) are responsible for the last steps of the gibberellin biosynthetic and catabolic pathway, which catalyse consecutive reactions that convert GA intermediates to bioactive forms. The *Arabidopsis* contains four *GA3ox* genes (*GA3ox1–GA3ox4*): at the silique development stage, *GA3ox1* is expressed mainly in the replum, funiculus and receptacle of silique, whilst the other three are expressed only in developing seeds (Hu *et al.*, 2008). The mutants of *GA3ox1* and its combination with *GA3ox2–GA3ox4* showed GA-deficient phenotypes, including semi-dwarfism, smaller rosettes, shorter siliques, reduced male fertility and fewer seeds per silique. The *Arabidopsis* contains five *GA20ox* genes (*GA20ox1–GA20ox5*), knockout of *GA20ox1–GA20ox3* also showed GA-deficient phenotypes, including delayed flowering, dwarfism, reduced male fertility, shorter siliques and few seeds per silique (Plackett *et al.*, 2012; Rieu *et al.*, 2008).

Gibberellin bind to its receptor, *GIBBERELLIN-INSENSITIVE DWARF1* (*GID1*), which in turn interacts with the *DELLA* proteins. The *Arabidopsis* has three homologues of gibberellin receptors (*GID1A, GID1B* and *GID1C*) that are expressed in most tissues throughout the development but varied in expression level. A reverse genetic study showed that the combinatorial mutants of *GID1A*, *GID1B* and *GID1C* showed GA-insensitive phenotypes, including semi-dwarfism, short roots and siliques, reduced male fertility and fewer seeds per silique in *Arabidopsis* (Griffiths *et al.*, 2006; Livne and Weiss, 2014). *Arabidopsis* also has five *DELLA* genes (*GAI*, *RGA*, *RGL1—RGL3*), and the knockout of five *DELLA* proteins resulted in reduced fertility, seed number per silique, and silique length (Fuentes *et al.*, 2012). Further studies are required to identify the effectors or downstream components of gibberellin in fruit size control.

Cytokinins (CTK)

The cytokinin signal transduction pathway includes a His-Asp phospho-relay that is similar to bacterial two-component signalling systems, in which cytokinin binds to the *CHASE* domain of *HKs* (histidine kinases) receptors, and then *AHPs* (authentic histidine phosphotransferases) act as intermediates to transfer a phosphate from *HKs* to the downstream response regulators (Kieber and Schaller, 2018). The *Arabidopsis* has five *AHP* genes (*AHP1–AHP5*) that are redundant, positive regulators of cytokinin signalling, which can affect multiple developmental processes. The T-DNA insertion *ahp* quintuple mutant is less sensitive to cytokinin and has various abnormalities in growth and development, including reduced fertility and seed set, enlarged seeds, as

Table 1 List of fruit size regulators in plants

Pathways	Gene name	Species	Accession number	Biological function	Reference(s)
Gibberellin (GA)	*GA3ox1*	Arabidopsis	*AT1G15550*	GA biosynthetic process	Hu *et al.* (2003)
	GA3ox4	Arabidopsis	*AT1G80330*	GA biosynthetic process	Hu *et al.* (2003)
	GID1A	Arabidopsis	*AT3G05120*	Cellular response to hypoxia	Griffiths *et al.* (2006)
	GID1B	Arabidopsis	*AT3G63010*	Catabolic process	Griffiths *et al.* (2006)
	GID1C	Arabidopsis	*AT5G27320*	Catabolic process	Griffiths *et al.* (2006)
	GA20ox2	Arabidopsis	*AT5G51810*	Oxidation–reduction process	Plackett *et al.* (2012)
	GAI	Arabidopsis	*AT1G14920*	Gibberellic acid homeostasis	Peng *et al.* (1997)
	RGA	Arabidopsis	*AT2G01570*	Multicellular organism development	Silverstone *et al.* (2016)
	RGL1	Arabidopsis	*AT1G66350*	DELLA proteins response to GA	Wen and Chang, (2002)
	RGL2	Arabidopsis	*AT3G03450*	Defence response	Lee *et al.* (2006)
	RGL3	Arabidopsis	*AT5G17490*	Multicellular organism development	Fuentes *et al.* (2012)
Auxin (IAA)	*PTRE1*	Arabidopsis	*AT3G53970*	Regulates auxin signalling	Yang *et al.* (2011)
	MOB1A	Arabidopsis	*AT5G45550*	Promotes auxin signalling	Cui *et al.* (2016)
	GmYUCCA5	Arabidopsis, soybean	*AT5G43890*	Auxin biosynthetic process	Wang *et al.* (2017c)
	BnaA9. ARF18	Rapeseed	*BnaA09g55580D*	Auxin response factor	Liu *et al.* (2008a)
	BrARP1	*Brassica rapa*	*AT1G43170*	Auxin-repressed protein 1	Lee *et al.* (2016)
	BrDRM1	*Brassica rapa*	*Bra032894*	Dormancy-associated protein 1	Lee *et al.* (2016)
	OSR1	Arabidopsis	*AT2G41230*	Organ growth and overall organ size	Feng *et al.,* (2011)
	ARGOS	Arabidopsis	*AT3G59900*	Response to auxin	Hu *et al.* (2003)
Cytokinin (CK)	*AHP5*	Arabidopsis	*AT1G03430*	Signal transduction	Hutchison *et al.* (2006)
	AHP4	Arabidopsis	*AT3G16360*	Signal transduction	Hutchison *et al.* (2006)
	AHP1	Arabidopsis	*AT3G21510*	Signal transduction	Hutchison *et al.* (2006)
	AHP2	Arabidopsis	*AT3G29350*	Signal transduction	Hutchison *et al.* (2006)
	AHP3	Arabidopsis	*AT5G39340*	Signal transduction	Hutchison *et al.* (2006)
	CKX3	Arabidopsis	*AT5G56970*	Cytokinin catabolic process	Bartrina *et al.*, 2011
	CKX5	Arabidopsis	*AT1G75450*	Cytokinin catabolic process	Bartrina *et al.*, 2011
Brassinosteroid (BR)	*BRI1*	Arabidopsis	*AT4G39400*	Brassinosteroid receptor	Noguchi *et al.* (1999)
	DWF4	Arabidopsis	*AT3G50660*	Brassinosteroid biosynthesis	Si *et al.* (1998)
	SMT2	Arabidopsis	*AT1G20330*	Brassinosteroid biosynthesis	Hwang *et al.* (2007)
	CYP72C1	Arabidopsis	*AT1G17060*	Brassinosteroid metabolic process	Takahashi *et al.* (2005)
	BjHMGS1	*Brassica juncea*	*AT4G11820*	Sterols biosynthetic process	Liao *et al.* (2014)
Abscisic acid (ABA)	*CSP2*	Arabidopsis	*AT4G38680*	Regulation of cellular respiration	Nakaminami *et al.* (2006), Sasaki *et al.* (2013)
	GRDP1	Arabidopsis	*AT2G22660*	Response to osmotic stress	Rodríguez-Hernández *et al.* (2017)
	SAT32	Arabidopsis	*AT1G27760*	Salt and ABA-responsive	Park *et al.* (2009)
Ethylene (ETH)	*EER5*	Arabidopsis	*AT2G19560*	Ethylene-signalling	www.arabidopsis.org
	–	Arabidopsis	*AT1G48420*	1-aminocyclopropane-1-carboxylic acid oxidase	Walton *et al.* (2012)
Phytohormone	*CYP78A9*	Arabidopsis/ Rapeseed	*AT3G61880*	Fruit and seed development	Ito and Meyerowitz (2000); Shi *et al.* (2019)
Transcription factors	*BoMF2*	*Brassica oleracea*	*Bol029968*	Transcriptional regulatory factor	Kang *et al.* (2014)
	MSH1	Arabidopsis	*AT3G24320*	Mitochondrial genome maintenance	www.arabidopsis.org
	CSP4	Arabidopsis	*AT2G21060*	Regulation of transcription	Nakaminami *et al.* (2006); Yang and Karlson (2011)
YABBY family	*CRC*	Arabidopsis	*AT1G69180*	Regulation of transcription	Prunet *et al.* (2008)
Zinc finger family	*SUP*	Arabidopsis, cucumber	*AT3G23130*	Transcription factor	Zhao *et al.* (2012)
	DOF4.2	Arabidopsis	*AT4G21030*	Regulation of transcription	Zuo *et al.* (2013)
	DOF4.4	Arabidopsis	*AT4G21050*	Regulation of transcription	Zuo *et al.* (2013)
	NTT	Arabidopsis	*AT3G57670*	Zinc finger transcription factor	Chung *et al.* (2013)
Tri-helix family	*ASIL1*	Arabidopsis	*AT1G54060*	Regulation of transcription	Gao *et al.* (2016)
AP2-ERF family	*SlERF36*	Tomato, Arabidopsis	*AT1G50640*	Regulation of transcription	Upadhyay *et al.* (2014)
	ANT	Arabidopsis	*AT4G37750*	Control of cell proliferation	Mizukami and Fischer (2000)

Table 1. Continued

Pathways	Gene name	Species	Accession number	Biological function	Reference(s)
MADS-box family	*GbAGL2*	Arabidopsis, cotton	*AT5G15800*	Plant ovule development	Liu *et al.* (2015)
	SHP1/2	Arabidopsis	*AT3G58780*	Regulation of growth	Liljegren *et al.* (2004); Pinyopich *et al.* (2003)
	FUL	Arabidopsis	*AT5G60910*	Fruit development	Liljegren *et al.* (2000)
	STK	Arabidopsis	*AT4G09960*	Ovule development	Zhang *et al.* (2016)
Homeobox	*RPL*	Arabidopsis	*AT5G02030*	Homeodomain transcription factor	Roeder *et al.* (2003)
	WOX14	Arabidopsis	*AT1G20700*	Vasculature development	Deveaux *et al.* (2008)
bHLH family	*AMS*	Arabidopsis	*AT2G16910*	Regulation of transcription	Sorensen *et al.* (2003)
	IND	Arabidopsis	*AT4G00120*	Regulation of transcription	Liljegren *et al.* (2000)
	ALC	Arabidopsis	*AT5G67110*	Fruit development anddehiscence	Liljegren *et al.* (2000)
B3 family	*REM22*	Arabidopsis	*AT3G17010*	Transcriptional factor B3 family protein	www.arabidopsis.org
Elongation factor	*TaTEF-7A*	Wheat, Arabidopsis	*CJ655632.1/ AT5G46030*	Transcript elongation factor	Zheng *et al.* (2014)
	SPT4-1	Arabidopsis	*AT5G08565*	Chromatin organization	Dürr *et al.,* (2014)
	SPT4-2	Arabidopsis	*AT5G63670*	Chromatin organization	Dürr *et al.,* (2014)
MicroRNA	*MaEF1A*	Arabidopsis, Banana	*AT1G18070*	Translation elongation	Liu *et al.* (2008a)
	miR172	Arabidopsis/Peanut	*AT2G28056*	Gene silencing by miRNA	José Ripoll *et al.* (2015)
	miR397b	Arabidopsis/Peanut	*AT4G13555*	Gene silencing by miRNA	Wang *et al.* (2014)
	Md-miRNA156	Arabidopsis/Apple	*AT5G55835*	Flower and fruit development	Sun *et al.* (2013)
Ubiquitin-proteasome pathway	*UBP15*	Arabidopsis/Rice	*AT1G17110*	Ubiquitin-specific proteases	Liu *et al.* (2016)
	UBP26	Arabidopsis	*AT3G49600*	Ubiquitin-specific proteases	Luo *et al.* (2008)
	SWA1	Arabidopsis	*AT2G47990*	Embryo sac development	Shi *et al.* (2005)
	RHF1A	Arabidopsis	*AT4G14220*	Regulation of cell cycle	Liu *et al.* (2008b)
	RHF2A	Arabidopsis	*AT5G22000*	Regulation of cell cycle	Liu *et al.* (2008b)
	MMS21	Arabidopsis	*AT3G15150*	Regulation of meristem development	Liu *et al.* (2014a)
	UBC22	Arabidopsis	*AT5G05080*	Protein polyubiquitination	Wang *et al.* (2016)
	DA1	Arabidopsis	*AT1G19270*	Ubiquitin receptor	Li *et al.* (2018)
	SAP	Arabidopsis	*AT5G35770*	E3 ubiquitin ligase complex	Wang *et al.* (2017c)
G-protein signalling	*XLG1*	Arabidopsis	*AT2G23460*	G-protein γ-subunit	Wang *et al.* (2017b)
	AGB1	Arabidopsis	*AT4G34460*	G-protein β-subunit	Lease *et al.* (2001)
Arabinogalactan protein	*AGP19*	Arabidopsis	*AT1G68725*	Arabinogalactan protein	Yang *et al.* (2007)
	AGP6	Arabidopsis	*AT5G14380*	Arabinogalactan glycoproteins	Levitin *et al.* (2008)
	AGP11	Arabidopsis	*AT3G01700*	Arabinogalactan glycoproteins	Levitin *et al.* (2008)
	HPGT1	Arabidopsis	*AT5G53340*	Hydroxyproline O-galactosyltransferase	Ogawa-Ohnishi and Matsubayashi (2015)
	HPGT2	Arabidopsis	*AT4G32120*	Hydroxyproline O-galactosyltransferase	Ogawa-Ohnishi and Matsubayashi (2015)
	HPGT3	Arabidopsis	*AT2G25300*	Hydroxyproline O-galactosyltransferase	Ogawa-Ohnishi and Matsubayashi (2015)
	FLA3	Arabidopsis	*AT2G24450*	Anchored component of membrane	Li *et al.* (2015)
	FLA4	Arabidopsis	*AT3G46550*	Mucilage biosynthetic process	Shi *et al.* (2019)
RNA-binding protein	*LSM1A*	Arabidopsis	*AT1G19120*	RNA metabolic process	Perea-Resa *et al.* (2012)
	LSM8	Arabidopsis	*AT1G65700*	RNA metabolic process	Perea-Resa *et al.* (2012)
	LSM1B	Arabidopsis	*AT3G14080*	RNA metabolic process	Perea-Resa *et al.* (2012)
Receptor kinase signalling	*SNF4*	Arabidopsis	*AT1G09020*	Carbohydrate metabolic process	www.arabidopsis.org
	ER	Arabidopsis	*AT2G26330*	Regulation of cell adhesion	Zanten *et al.* (2010)
	RPK2	Arabidopsis	*AT3G02130*	Meristem maintenance	Mizuno *et al.* (2007)
	BAM3	Arabidopsis	*AT4G20270*	Regulation of meristem growth	DeYoung *et al.* (2006)
	CLV1	Rapeseed/ Arabidopsis	*AT1G75820*	Shoot and floral meristem size	Xiao *et al.* (2018)
	CLV3	Rapeseed/ Arabidopsis	*AT2G27250*	Shoot apical meristem size	Yang *et al.* (2018)
Other proteins	*HSP70*	Arabidopsis	*AT3G12580*	Protein folding	Leng *et al.* (2016)
	CINV1	Arabidopsis	*AT1G35580*	Sucrose catabolic process	Qi *et al.* (2007)
	CcCCOAOMT1	Jute, Arabidopsis	*AT4G34050*	Lignin biosynthetic process	Zhang *et al.* (2014)

Table 1. Continued

Pathways	Gene name	Species	Accession number	Biological function	Reference(s)
	GhWBC1	Cotton	*AY255521.1*	ATP-binding cassette transporter	Zhu *et al.* (2003)
	LNG1	Arabidopsis	*AT5G15580*	Unidimensional cell growth	Lee *et al.* (2013)
	LNG2	Arabidopsis	*AT3G02170*	Unidimensional cell growth	Lee *et al.* (2013)
	AXY3/XYL1	Arabidopsis	*AT1G68560*	Glycoside hydrolase family 3	Günl and Pauly (2011)
	CALS7	Arabidopsis	*AT1G06490*	Callose synthase 7	Xie *et al.* (2011)
	BGAL10	Arabidopsis	*AT5G63810*	Glycoside hydrolase family 35	Sampedro *et al.* (2012)
	FATA2	Arabidopsis	*AT4G13050*	Fatty acid biosynthetic process	Wang *et al.* (2016)
	HEMN1	Arabidopsis	*AT5G63290*	Oxidation–reduction process	Pratibha *et al.* (2017)
	GGT1	Arabidopsis	*AT4G39640*	Glutathione catabolic process	Giaretta *et al.* (2017)
	GGT2	Arabidopsis	*AT4G39650*	Glutathione transmembrane transport	Giaretta *et al.* (2017)
	BcRISP1	Cabbage, Arabidopsis	*AT5G13440*	Oxidation–reduction process	Liu *et al.* (2014a)
	BnaC9.SMG7b	Rapeseed	*BnaC09g38310D*	Meiotic cell cycle	Li *et al.* (2008)
	LPAT2	Arabidopsis	*AT3G57650*	CDP-diacylglycerol biosynthetic process	Kim *et al.* (2005)

well as shortened siliques and roots (Hutchison *et al.*, 2006). The degradation of cytokinin is catalysed by cytokinin oxidase/dehydrogenase (*CKXs*), which is coded by seven homologous genes (*CKX1*–*CKX7*) in *Arabidopsis*. Of these, the *ckx3* and *ckx5* mutants had more and larger flowers, more and longer siliques, more ovules per ovary, leading to higher seed yield (Bartrina *et al.*, 2011).

Abscisic acid (ABA)

Abscisic acid is well known to regulate seed germination, root and shoot development and abiotic stress responses (Humplik *et al.*, 2017; Lin and Tan, 2011), whereas its role on fruit development is unclear. The *Arabidopsis GRDP1* encodes the glycine-rich domain protein involved in the abscisic acid-activated signalling pathway. The *Arabidopsis grdp1* mutant lines exhibited many developmental defects, including shortened siliques and aborted ovules as well as reduced seed number and weight (Rodríguez-Hernández *et al.*, 2017). The *Arabidopsis CSP2* encodes a glycine-rich protein that responds to cold stress through the ABA pathway, which is highly expressed in shoot apical meristems and siliques (Nakaminami *et al.*, 2009). The overexpression of *CSP2* in *Arabidopsis* resulted in later flowering, shorter siliques, and fewer seeds per silique (Sasaki *et al.*, 2013). The *Arabidopsis Salt-tolerance 32* (*SAT32*) encodes a protein similar to the human interferon-related development regulator, which is involved in salt resistance through the ABA signalling pathway. The T-DNA knockout mutant of *SAT32* in *Arabidopsis* showed slightly longer roots but shorter siliques and fewer seeds per silique (Park *et al.*, 2009).

Ethylene (ETH)

1-aminocyclopropane-1-carboxylic acid (ACC) is the direct precursor of ethylene biosynthesis, whilst ACC-deaminase can decrease the level of ACC. The ACC-deaminase transgenic canola line had reduced levels of ethylene in the siliques and seeds, as well as smaller siliques and seeds, and fewer seeds per silique (Walton *et al.*, 2012). Interestingly, the contents of endogenous GA1, GA4 and IAA also declined in the siliques and seeds of transgenic lines, suggesting that ethylene can interact with other phytohormones to regulate fruit and seed development (Walton *et al.*, 2012). The *Arabidopsis ENHANCED ETHYLENE RESPONSE 5* (*EER5*) encodes a PAM domain protein involved in ethylene-activated signalling pathway (www.arabidopsis.org). The *eer5* mutant showed hypersensitivity to ethylene with various developmental defects, such as shorter siliques, curly leaves, shorter primary roots and less lateral roots (Christians *et al.*, 2008).

Brassinosteroids (BR)

Several genes involved in brassinosteroid synthesis and signal transduction affect fruit growth/size. The *Arabidopsis HMGS/FKP1* encodes hydroxymethylglutaryl-CoA synthase, which is involved in the mevalonate pathway of sterols biosynthetic process (Ishiguro *et al.*, 2010). *The Arabidopsis HMGS/FKP1* is expressed strongly in floral buds, moderately in roots and weakly in leaves, and its T-DNA insertion mutant was male-sterile with short silique with few seeds, due to defect in pollen coat formation. Whereas, the overexpression of *Brassica juncea BjHMGS1* in tobacco increased both vegetative growth (such as root, stem and leaf) and seed yield (pod size and seed number per pod), which was caused by the higher sterols content through regulating the expression of isoprenoid biosynthesis genes (Liao *et al.*, 2014). The *Arabidopsis HMG1* encodes a 3-hydroxy-3-methylglutaryl coenzyme A reductase, another enzyme of the mevalonate pathway involved in sterols biosynthetic process. The T-DNA insertion *hmg1* mutant showed dwarfism, early senescence and male sterility with short siliques and few seeds, which was caused by suppression in cell elongation due to reduced sterol level (Suzuki *et al.*, 2004). The *Arabidopsis SMT2* encodes a sterol-C24-methyltransferase involved in sterol biosynthesis, and its T-DNA knockout mutant displayed reduced fertility, few seeds and shorter siliques (Hwang *et al.*, 2007). The *Arabidopsis DWF6/DET2* is similar to mammalian steroid-5-alpha-reductase that is involved in the brassinolide biosynthetic pathway, and its mutant also showed dwarfism, reduced male fertility, short siliques (Fujioka and Yokota, 2003). The *Arabidopsis DWF3/CPD* and *DWF4* encode cytochrome P450 monooxygenase *CYP90A1* and *CYP90B1,* respectively, which are the rate-limiting enzymes in the

brassinosteroid biosynthetic pathway. Overexpression of *Populus euphratica DWF4* or *CPD* in *Arabidopsis* increased plant height and silique length but decreased silique number (Si *et al.*, 2016).

The *Arabidopsis BRI1/BIN1/DWF2* encodes a plasma membrane-localized leucine-rich repeat receptor kinase, which is involved in brassinosteroid signal transduction. Its mutant showed multiple defects in growth and development, including dwarfism, reduced male fertility, few seeds and short siliques (Clouse *et al.*, 1996). The *Arabidopsis SHK1* encodes cytochrome P450 monooxygenase *CYP72C1* similar to *BAS1/CYP734A1* that regulates BR inactivation. The *shk1*-D mutant showed dwarfism, short siliques and smaller seeds along the longitudinal axis, which is caused by reduced cell elongation (Takahashi *et al.*, 2005).

Recently, a major QTL for silique length and seed weight has been cloned on the A9 chromosome of *Brassica napus*, which is resulted from a CACTA-like transposable element inserted in the upstream region of an orthologue (designated as *BnaA9.CYP78A9*) of *Arabidopsis CYP78A9* that acts as an enhancer to increase its expression (Shi *et al.*, 2019). In fact, *CYP78A9* has been long known to play an important role in reproductive development (Sotelo-Silveira *et al.*, 2013), as its overexpression caused large flowers, siliques, and seeds but reduced fertility and seed number per silique in *Arabidopsis* (Ito and Meyerowitz, 2000). Further studies should be conducted to make clear the reactions catalysed by *CYP78A9* so as to uncover its relationship with the known hormone pathways.

Transcription factors

Transcription factors (TFs) are usually classified into different families based on their DNA-binding domains, which play a key role in plant development by temporally and spatially regulating the transcription of the corresponding target genes (Jin *et al.*, 2017). A previous expression profiling study showed that most of the transcript factors were involved in the development of siliques in *Arabidopsis* (De Folter *et al.*, 2004); their roles in regulating fruit size are summarized below (Figure 3; Table 1).

The *Brassica oleracea BoMF2* encodes a nuclear-localized AT-hook DNA-binding protein homologous to *Arabidopsis AHL16* (Kang *et al.*, 2014), which is required for tapetum proliferation during anther development. The overexpression of *BoMF2* led to reduced pollen viability, shorter siliques and fewer seeds per silique (Kang *et al.*, 2014). The *Arabidopsis MSH1* is a plant organelle DNA-binding and thylakoid protein that can influence genome stability and growth pattern (Xu *et al.*, 2011). Inhibition of this gene by RNA interference causes multiple defects in the growth and development of several species, including slower growth, dwarfism, shorter siliques and reduced male fertility in *Arabidopsis* (Xu *et al.*, 2012). The *Arabidopsis* cold shock domain proteins (CSPs) are highly conservative DNA-binding transcript factors, which are involved in the transition to flowering and silique development (Nakaminami *et al.*, 2009). Of which, the overexpression of *CSP4* in *Arabidopsis* reduces fruit length and induces embryo lethality (Yang and Karlson, 2011).

B3 family

The *Arabidopsis Reproductive Meristem* (*REM*) genes encode B3 family transcription factors (Swaminathan *et al.*, 2008), which are preferentially expressed in flower and ovule/seed development (Mantegazza *et al.*, 2014). Of these, the *rem22* mutant exhibited reduced fertility and slow growth, including dwarf plants and short siliques (https://www.arabidopsis.org/).

Basic helix-loop-helix family

The *ABORTED MICROSPORES* (*AMS*) gene belongs to the MYC subfamily of basic helix-loop-helix (*bHLH*) superfamily, which is essential for microspore development. The *ams* mutant produced by T-DNA insertion showed a sporophytic recessive male-sterile phenotype as well as undeveloped silique (Sorensen *et al.*, 2003). Also belonging to the *bHLH* superfamily, both *IND* and *ALC* genes are well known to involve in the regulation of fruit development and dehiscence (Ballester and Ferrándiz, 2017). Mutations in both *IND* and *ALC* can partly restore fruit elongation in *flu* mutant (Liljegren *et al.*, 2004).

AP2-ERF family

The *APETALA2-ETHYLENE RESPONSE FACTOR* (*AP2-ERF*) is the major family of transcription factors with 140–280 members in several plants (Nakano *et al.*, 2006). The *Arabidopsis AINTEGUMENTA* (*ANT*) is a member of the *AP2* subfamily, which is well known to control the size of organs (including root, leaf, flower, fruit and seed) by regulating cell proliferation in plants (Mizukami and Fischer, 2000). *SlERF36* is an EAR motif-containing *ERF* gene from tomato, and its overexpression reduced vegetative growth, including the size of rosettes, flowers and siliques (Upadhyay *et al.*, 2014).

Homeobox family

The *Arabidopsis WOX14* belongs to the *WUSCHEL-related homeobox* (*WOX*) subfamily, and its knockout mutant plants are partially male-sterile, with aborted and shorter siliques (Deveaux *et al.*, 2008). The *Arabidopsis REPLUMLESS* (*RPL*) gene (also encodes a homeodomain protein) is required for the replum development, and its loss-of-function mutant showed shorter siliques (Roeder *et al.*, 2003).

MADS-box family

Several members of the MADS-box family are involved in the development and dehiscence of fruits in *Arabidopsis*. *SHATTERPROOF1* (*SHP1*) and *SHP2* are two closely related and functionally redundant genes, which control the differentiation of dehiscence zone and promote the lignification of adjacent cells (Liljegren *et al.*, 2000), by up-regulating *IND* and *ALC* (Ballester and Ferrándiz, 2017). As a negative regulator of *SHP* genes, the *Arabidopsis FRUITFULL* (*FUL*) is required for valve differentiation and expansion after fertilization, and its loss-of-function mutation results in fruit that fail to elongate (Ferrandiz *et al.*, 2000; Zhang *et al.*, 2016). The *Gossypium barbadense AGL2* was an *AGAMOUS* (*AG*)-like gene, which was highly expressed in reproductive tissues (including ovules and carpels) but lowly in vegetative tissues. The overexpression of *GbAGL2* in *Arabidopsis* resulted in longer siliques with more seeds per silique (Liu *et al.*, 2009; Zhang *et al.*, 2016). *SEEDSTICK* (*STK*) encodes a MADS-box transcription factor that is expressed in the carpels and ovules. *STK* is required for funiculus development by regulating cell expansion and division, and its loss-of-function mutant showed shorter siliques with rounder and smaller seeds (Pinyopich *et al.*, 2003).

Tri-helix family

The *Arabidopsis ASIL1* gene is a member of the tri-helix DNA-binding protein family, which is localized in the nucleus and

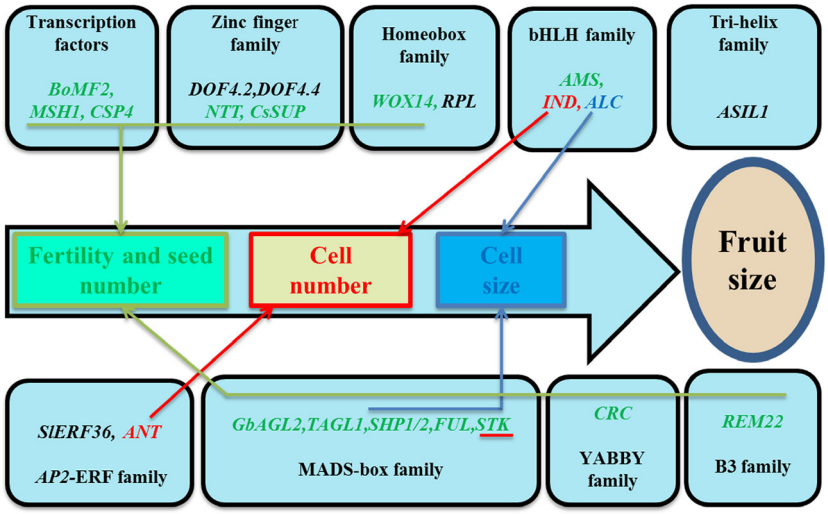

Figure 3 Fruit size is regulated by transcription factor pathways. These transcript factors are mainly from several families, such as tri-helix, YABBY, AP2-ERF, MADS-box, bHLH, zinc finger, homeobox and B3. These regulators control fruit size by affecting fertility and seed number, cell number and cell size, which is distinguished by green, red and blue colours, respectively.

belongs to the subfamily of 6b-interacting protein 1-like 1. *ASIL1* is involved in the repression of early and seed mature genes via competitive binding to the GT-box-like element (Gao *et al.*, 2009). The *asil1* mutant in *Arabidopsis* had shorter siliques, smaller seeds and reduced seed weights per plant compared with the wild type.

YABBY family

The *Arabidopsis CRABS CLAW* (*CRC*), a member of the *YABBY* gene family (Bowman, 2000), is mainly expressed in nectary and carpel (Bowman and Smyth, 1999; Siegfried *et al.*, 1999). In the loss-of-function mutants of *CRC*, carpels are smaller and unfused at their top (the so-called crab's claw phenotype); siliques are also shorter (Alvarez and Smyth, 1999; Prunet *et al.*, 2008).

Zinc fingers family

The *SUPERMAN* (*SUP*) gene encodes a C2H2-type zinc finger protein, which has a conserved function for the stamen and fruit development in plants. The *Arabidopsis sup* mutant showed low fertility, few seeds per silique and short silique (Zhao *et al.*, 2014). Plant-specific *DOF*-type (DNA-binding with one finger) transcription factors control various biological processes, of which the *Arabidopsis dof4.2* mutant showed increased silique length and seed yield (Zou *et al.*, 2013). The *Arabidopsis NO TRANSMITTING TRACT* (*NTT*) gene encodes a C2H2/C2HC zinc finger transcription factor that is specifically expressed in the transmitting tract and responsible for replum development (Chung *et al.*, 2013). *NTT* loss function in *Arabidopsis* leads to reduced male fertility, seed set and silique length (Marsch-Martínez *et al.*, 2014).

Elongation factors

Eukaryotic elongation factors can be divided into transcript and translation elongation factors according to their respective roles in biological processes. Recently, several genes belonging to the elongation factors have been shown to play a role in fruit size regulation (Figure 4; Table 1).

The transcript elongation factors (*TEFs*) can facilitate efficient mRNA synthesis and perform diverse functions during transcription (including the modification of histone and RNA polymerase II activity), which can regulate growth and development by participating in various processes (Van Lijsebettens and Grasser, 2014). Overexpression of the wheat *TaTEF-7A* gene in *Arabidopsis* has multiple effects on asexual and reproductive traits, including increased silique number and length as well as grain length (Zheng *et al.*, 2014). The heterodimeric *SPT4/SPT5* complex is a *TEF* that interacts with RNA polymerase II to regulate mRNA synthesis in the chromatin context. Each subunit is encoded by two genes in *Arabidipsis*, and the RNAi-mediated down-regulation of *SPT4-1/2* showed reduced cell elongation and vegetative and reproductive defects, including short roots and stems, small leaves, flowers and siliques with fewer seeds (Dürr *et al.*, 2014).

Plant translation *elongation factor 1 alpha* (*EF1A*) is not only involved in protein synthesis but also a core part of plant protein trafficking, signal transduction, immune responses and apoptosis. Overexpression of banana *MaEF1A* in *Arabidopsis* greatly increased plant height, root length, as well as rhachis and silique length by promoting cell expansion and elongation (Liu *et al.*, 2016).

MicroRNA

The *microRNAs* (*miRNAs*), which are about 21 nucleotides (nt) in length, are key components within the gene regulatory networks of eukaryotes (Bao *et al.*, 2014). In recent years, several *miRNAs* have been shown to involve in fruit size regulation across several plant species (Figure 4; Table 1). The overexpression of orange *Pt-miR156a* in *Arabidopsis* leaded to late flowering, short siliques and small leaves (Wang *et al.*, 2017a). Similarly, the overexpression of apple *Md-miRNA156* in *Arabidopsis* resulted in late flowering, dwarfism, more leaves, short siliques with partially aborted seeds, by down-regulating its target *SPL* genes (Sun *et al.*, 2013). As the downstream of *FUL* and *ARF6/8*, the *miR172* plays a key role in regulating fruit development, as it is required for valve growth by restricting *AP2* and *TOE3* activity (José Ripoll *et al.*, 2015). The reduced lignin deposition and increased silique number/length and seed size/yield was observed in transgenic *Arabidopsis* overexpressing *miR397b*, which regulated a laccase gene *LAC4* that can polymerize monolignols into lignin (Wang *et al.*, 2014). In peanut, a small RNA profiling and degradome analysis revealed several active modules during early pod development, including *AP2* (*miR172*) and *GRF* (*miR396*), *NAC*

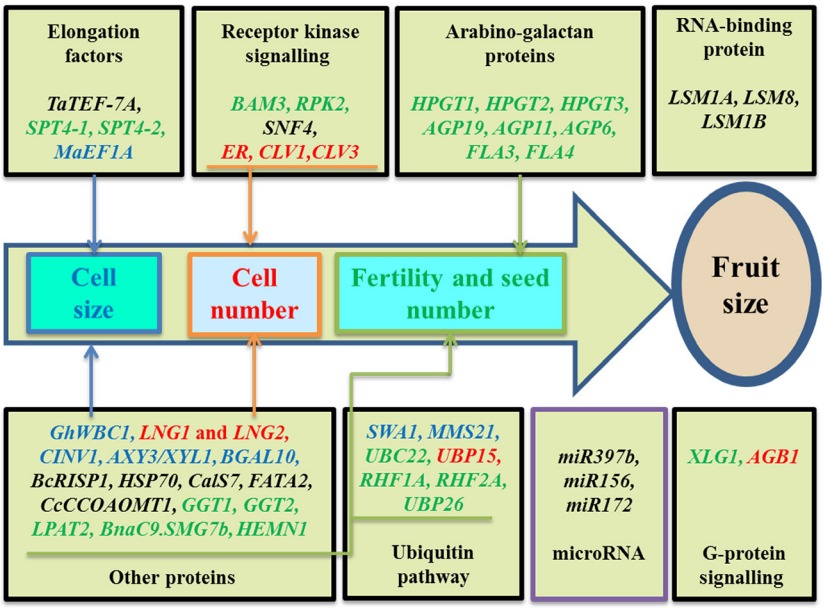

Figure 4 Fruit size is regulated by several other signalling pathways. These pathways include the ubiquitin-proteasome, elongation factors, microRNA, G-protein signalling, arabinogalactan proteins, RNA-binding proteins, receptor kinase signalling and other proteins. These regulators control fruit size also by affecting fertility and seed number, cell number and cell size, which is distinguished by green, red and blue colours, respectively.

(*miR164*), *PPRP* (*miR167/miR1088*), *SPL* (*miR156/157*), respectively (Gao *et al.*, 2017).

Ubiquitin-proteasome pathway

Ubiquitin-specific protease (*UBP*) is a highly conserved protein family in eukaryotes, which plays an important role in protein de-ubiquitination (Liu *et al.*, 2008b). Of these, the *Arabidopsis ubp15* mutants have defect in cell proliferation and display late flowering and short root, stem, leaf, flower and fruit, as well as reduced fertility, whilst its overexpression shows opposite phenotypes (Liu *et al.*, 2008b). The *Arabidopsis UBP26* is essential for heterochromatin silencing by catalysing the de-ubiquitination of histone *H2B*, and its T-DNA insertion mutant showed short siliques, reduced fertility and few seeds (Luo *et al.*, 2008).

The *Arabidopsis* ubiquitin-conjugating enzyme 22 (*UBC22*) is the only member of the *Arabidopsis E2* subfamily, which can catalyse ubiquitin dimer formation in vitro in a Lys11-dependent manner. The knockout mutants of *UBC22* in *Arabidopsis* had reduced silique length and seed number per silique, which was caused by ovule sterility due to severe defects in embryo sac that often contained no gamete nuclei (Wang *et al.*, 2016).

The *Arabidopsis SWA1* encodes a transducin family nucleolar protein that is involved in the E3 ubiquitin ligase complex, which is required for the normal progression of mitotic division cycles by regulating cell metabolism. The *SWA1* mutation causes ovule abortion, and short silique in *Arabidopsis* (Shi *et al.*, 2005). The RING-H2 group F1a *(RHF1a)* and *RHF2a* encode two RING-finger E3 ubiquitin ligases, of which *RHF1a* can directly interact with a cyclin-dependent kinase inhibitor *ICK4/KRP6*, leading to proteasome-mediated degradation. The *rhf1a rhf2a* double mutant showed reduced fertility and short siliques, which was caused by the defect in the gametophytes formation due to arrested mitotic cell cycle (Liu *et al.*, 2008a). The *Arabidopsis MMS21* encodes a SUMO E3 ligase, which is highly conserved in eukaryotes and essential for DNA repair and chromosome stability (Liu *et al.*, 2014a). The mutation *of MMS21* in *Arabidopsis* caused dwarfism and semi-sterility with short siliques and few seeds per silique, due to defect in gametogenesis (Liu *et al.*, 2014a). The *Arabidopsis STERILE APETALA* (*SAP*) encodes an F-box protein that is involved in SCF (Skp1/Cullin/F-box) E3 ubiquitin ligase complex, which can promote meristemoid cells proliferation to control organ size by interacting with and targeting *PPD* proteins for degradation (Wang *et al.*, 2016). The *sap* mutant displayed small leaves, flowers and siliques, due to decreased cell number in these organs.

The *Arabidopsis DA1* encodes an ubiquitin-activated peptidase that acts as a putative ubiquitin receptor and functions cooperatively with the E3 ubiquitin ligases *DA2* and *EOD1/BB* to negatively regulate organ size by restricting cell proliferation. The mutation of *DA1* in *Arabidopsis* showed thicker stems, larger leaves and flowers, wider siliques and higher seed weight and yield due to increased cell numbers in these organs (Li *et al.*, 2008).

G-protein signalling

The heterotrimeric GTP-binding proteins (G proteins) are highly conservative signalling components in eukaryotes, which consist of three subunits—Gα, Gβ and Gγ. In *Arabidopsis thaliana*, there is one canonical Gα (*GPA1*), one Gβ (*AGB1*) and three Gγ genes (*AGGs*). In addition to *GPA1*, there are three Gα-like genes (named *XLGs*) in *Arabidopsis*, which can interact with E3 ligases *PUB4* and *PUB2* and act in cytokinin signalling (Wang *et al.*, 2017c). The *xlg1/2/3* triple knockout mutant showed reduced male fertility and short siliques in *Arabidopsis* (https://www.arabidopsis.org/). The *Arabidopsis AGB1* gene is involved in the regulation of organ shape, and its mutation increased the width but decreased the length of leaf, flower and silique, by promoting cell proliferation (Lease *et al.*, 2001).

Receptor kinase signalling

The fruit size is largely determined by the classical *CLAVATA–WUSCHEL* (*CLV-WUS*) pathway, firstly identified in *Arabidopsis* and appeared to be conserved in other higher plants (Somssich

et al., 2016), which can control locule number by regulating the size of shoot apical meristem (SAM). This pathway included three *CLAVATA* genes in *Arabidopsis*, of which *CLV1* encodes a leucine-rich repeat receptor-like kinase (*LRR-RLK*), *CLV2* encodes an LRR receptor-like protein (*RLP*) that lacks a kinase domain, and *CLV3* encodes a stem cell-specific protein that can be further processed into a 12–amino acid peptide ligand for the *CLV1* receptor (Kitagawa and Jackson, 2019). The loss-of-function *clv* mutants in *Arabidopsis* showed similar phenotypic changes, including larger inflorescence meristem, leading to fasciated stems and multilocular siliques. The *BAM1* (derived from *barely any meristem 1*), *BAM2,* and *BAM3* encode *CLV1*-related receptor-like kinases, which are required for ovule specification and male gametophyte development (DeYoung *et al.*, 2006). The double and triple mutants of *BAM1/2/3* genes displayed many defects in organ development, including reduced fertility and smaller leaf, flower and silique (DeYoung *et al.*, 2006). Recently, the *BjLn1* and *BjMc1* gene (responsible for multilocular siliques) were successfully cloned, which was caused by the natural mutations in the *CLV1* orthologues, respectively, on the A and B genome of *Brassica juncea* (Xiao *et al.*, 2018; Xu *et al.*, 2017). In recent years, the *CLV-WUS* pathway has become an attractive target of genome editing for crop improvement (Rodriguez-Leal *et al.*, 2017), which has produced a series of exciting achievements. The genome editing of *CLV3* orthologues can produce multilocular siliques in several dry fruit crops, including *Brassica rapa* and *B. napus* (Fan *et al.*, 2014; Yang *et al.*, 2018). In addition, the genome editing of *CLV1/2/3* also produced multiple locular fruits with increased size in fleshy fruit crops, such as tomato and groundcherry (Lemmon *et al.*, 2018; Li *et al.*, 2018; Rodrı´guez-Leal *et al.*, 2017; Xu *et al.*, 2015; Zsögön *et al.*, 2018).

In addition to the known *CLV-WUS* pathway, several genes encoding receptor kinase are also shown to involve in the fruit size regulation. As a plant-specific subunit of the *SNF1*-related protein kinase 1 complex, the *Arabidopsis KINβγ* is required for the pollen germination on the stigma surface (Gao *et al.*, 2016), and its mutant had short stature and silique (https://www.arabidopsis.org/). *ERECTA* (*ER*) encodes receptor protein kinases containing a cytoplasmic protein kinase catalytic domain, an extracellular leucine-rich repeat, and a transmembrane region, which is required for the specification of organs originating from shoot apical meristem. The *er* mutant showed reduced plant height, increased inflorescence thickness and shorter but wider silique (Torii *et al.*, 1996). The *RECEPTOR-LIKE PROTEIN KINASE2* (*RPK2*) encodes a leucine-rich repeat receptor-like kinase, which functions as a regulator of meristem maintenance. The *rpk2* mutants caused male sterility with more and short siliques failed to produce seeds due to defects in anther dehiscence and pollen maturation (Mizuno *et al.*, 2007).

Arabinogalactan proteins

Arabinogalactan proteins (*AGPs*) are plant-specific extracellular glycoproteins, which are involved in various processes in growth and development, including cell division, expansion and differentiation (Pereira *et al.*, 2015). Arabinogalactan proteins are classified into several types: classical *AGPs*, lysine-rich *AGPs*, *AGP* peptides, fasciclin-like *AGPs* and chimeric *AGPs*.

The *Arabidopsis AGP6* and *AGP11* encode classical *AGPs*, both of which are specifically expressed in stamens, pollen grains and tubes and required for male reproductive function. Loss of function in *AGP6* and *AGP11* caused reduced pollen tube growth, leading to lower male fertility, fewer seeds per silique and shorter silique (Levitin *et al.*, 2008).The *Arabidopsis AGP19* encodes a lysine-rich *AGP*, which was highly expressed elongating siliques and floral buds, moderately expressed in young seedlings and lowly expressed in roots and leaves (Yang *et al.*, 2007). The T-DNA knockout mutant of *AGP19* displayed multiple defects, including slow growth and reduced fertility, fewer and shorter siliques and fewer seeds per silique. The *Arabidopsis FLA3* encodes a fasciclin-like *AGP*, which is involved in embryogenesis and microspore development. Both the *Arabidopsis FLA3* RNAi and overexpression transgenic plants showed reduced fertility, fewer seeds and shorter siliques (Li *et al.*, 2010). Similarly, the *Arabidopsis FLA4* encodes a fasciclin-like *AGP* required for normal cell expansion, and its mutant showed short silique with fewer seeds per silique (Shi *et al.*, 2003). The *Arabidopsis HPGT1*, *HPGT2* and *HPGT3* encode hydroxyproline O-galactosyltransferases that are required for *AGP*s biosynthesis (Ogawa-Ohnishi and Matsubayashi, 2015). The loss-of-function *hpgt1, hpgt2, hpgt3* mutant exhibited reduced growth in vegetative organs, including small leaves, short stems and siliques.

RNA-binding proteins

RNA-binding proteins can bind to RNA molecules and play an important role in the post-transcriptional regulation of RNAs (Hentze *et al.*, 2018), which are known to involve in plant growth, development and stress response (Lee and Kang, 2016). The SM-like proteins (*LSMs*) are a large family of RNA-binding proteins that involve in multiple aspects of RNA metabolism. The *Arabidopsis* contains 11 genes that encode the eight highly conserved SM-like proteins in yeast and animals (Perea-Resa *et al.*, 2012). Of which, the *LSM1A, LSM1B* and *LSM8* mutant plants showed severe development defects, including smaller leaves and shorter siliques with fewer seeds, which was caused by altering development-related gene expression through the regulation of mRNA splicing and decay (Perea-Resa *et al.*, 2012).

Other proteins

The heat shock proteins (*HSPs*) functions as molecular chaperones to maintain cellular homeostasis and facilitate plants to adapt to environmental stimuli. Of the *Arabidopsis HSP70* family, the knockout/down mutants of *hsp70-1/4* and *hsp70-2/4/5* displayed multiple phenotypic changes, including accelerated development, smaller leaves, thinner stems and shorter siliques (Leng *et al.*, 2016). The *Arabidopsis CINV1* encodes alkaline/neutral invertase that breaks sucrose down into fructose and glucose, which is highly expressed in leaf vasculature, shoot stipules, root tip and vascular cylinder, playing multiple roles in plant development. The EMS mutant of *CINV1* in *Arabidopsis* showed earlier floral transition, smaller rosette leaves and siliques (Qi *et al.*, 2007). The Caffeoyl-CoA 3-O-methyltransferase is a key enzyme in the lignin biosynthetic pathway, which is encoded by *CCoAOMT* genes found in many plant species. The overexpression of jute *CCoAOMT1* gene in *Arabidopsis* led to taller plants and longer siliques, as well as higher lignin content (Zhang *et al.*, 2014). The *WBC1* encodes an ATP-binding cassette transporter of the white/brown complex subfamily. Overexpression of the cotton *GhWBC1* gene in *Arabidopsis* led to 13% transformants producing short siliques with shrivelled embryos and few seeds (Zhu *et al.*, 2003). The *Arabidopsis LONGIFOLIA1*

(LNG1) and *LNG2* encode novel proteins that can regulate longitudinal cell elongation, which is expressed in various tissues (Lee *et al.*, 2006). The overexpression and loss-of-function of *LNG1/LNG2* in *Arabidopsis* could, respectively, increase and decrease the length of many organs, including leaves, flowers, siliques and seeds. The *Arabidopsis AXY3/XYL1* encodes a bifunctional alpha-l-arabinofuranosidase/beta-d-xylosidase that belongs to glycoside hydrolases family 3, which can affect the structure and accessibility of the hemicellulose xyloglucan in cell walls. The mutations in axy3 led to reduced silique length and seed number per silique, likely due to the altered xyloglucan metabolism and cell wall structure (Günl and Pauly, 2011). The *Arabidopsis BGAL10* encodes a member of glycoside hydrolase family 35, whose expression pattern and functions are similar to *XYL1*. The *bgal10* mutant displayed unusual xyloglucan subunits and growth defects, especially shorter sepals and siliques (Sampedro *et al.*, 2012). The *Arabidopsis CALS7* encodes a phloem-specific callose synthase 7 required for callose deposition, which is specifically expressed in the phloem of vascular tissues (Xie *et al.*, 2011). The T-DNA insertion cals7 mutants showed growth and reproduction defects, including short root, stem and silique as well as reduced male fertility and seed number per silique (Xie *et al.*, 2011) The *Arabidopsis FATA2* gene encodes Acyl-ACP thioesterase involved in fatty acid biosynthetic process, which was expressed d in roots, seedlings, leaves, stems, flowers, with especially high abundance in siliques. The *fata2* T-DNA insertion mutants produced longer siliques with more but smaller seeds as well as increased oil content (Wang *et al.*, 2013). *Lysophosphatidyl acyltransferase (LPAT)* is a key enzyme for adjusting the metabolic conversion of lysophosphatidic acid into exclusive phosphatidic acids in numerous tissues (Kim *et al.*, 2005). The *Arabidopsis LPAT2* is ubiquitously expressed in diverse tissues and is required for female but not male gametophyte development. The homozygous *lpat2* mutant was lethal, and its heterozygous mutant showed shorter siliques with aborted ovules (Kim *et al.*, 2005). The *Arabidopsis HEMN1* encodes coproporphyrinogen III oxidase involved in the tetrapyrrole biosynthesis pathway, which is mainly expressed in anthers, ovules and endosperm of developing seeds. The T-DNA insertion *hemen1* mutant showed defects in gametophyte development, leading to reduced fertility, seed number per silique and silique length (Pratibha *et al.*, 2017). The *Arabidopsis GGT1* and *GGT2* encode apoplastic gamma-glutamyl transferases responsible for glutathione degradation, of which *GGT1* is expressed in the vascular system and inside leaves, whilst *GGT2* is expressed in trichomes, seeds, and roots. The knockdown of *GGT1/GGT2* by RNAi showed reduced vegetative growth rate (such as smaller leaves and roots) and lower seed yield due to fewer siliques with lower length (Giaretta *et al.*, 2017). The *Brassica cabbage RISP1* gene is highly homologous to the *Arabidopsis AT5G13440*, which encodes ubiquinol-cytochrome C reductase iron-sulphur subunit involved in mitochondrial electron transport. The overexpression of *BcRISP1* in *Arabidopsis* showed reduced seed set and short siliques, which is caused by the reduced pollen formation and impaired pollen tube elongation due to the interruption of the mitochondrial electron transport chain by affecting the expression of mitochondrial breathing chain-related genes (Liu *et al.*, 2014b). A major QTL *qSS.C9* for seeds per silique has been cloned on the C9 chromosome of *Brassica napus* (Li *et al.*, 2015), which encodes a predicted small protein with 119 amino acids homologous to the *Arabidopsis SMG7* gene that is involved in meiotic cell cycle. The *BnaC9.SMG7b* was mainly expressed in the vascular tissue of various organs, including cotyledons, rosette leaves, roots, young pedicels and pistils, but not in stamens, petals, stems and mature siliques. Natural loss or artificial knockdown of *BnaC9.SMG7b* resulted in decreased seed number per silique, silique length and seed yield but increased seed weight, which was caused by the reduced ovule fertility due to the developmental defects in the formation of functional female gametophytes.

Conclusions and future prospects

In recent years, many genes that regulate fruit size have been identified, mostly from *Arabidopsis* and tomato (Table S1), the two model plants for fruit development studies. Although several reviews have discussed genetic and epigenetic regulation of fruit size in the fleshy fruit type tomato (Pesaresi *et al.*, 2014; Seymour *et al.*, 2013; Tanksley, 2004), current knowledge of fruit size control in the dry fruit type *Arabidopsis* and related crops is limited. Such information is essential if a comprehensive genome editing approach is to be applied. Some initial targets for fruit size have been targeted using editing approaches, with some success (Lemmon *et al.*, 2018; Li *et al.*, 2018; Rodríguez-Leal *et al.*, 2017; Zsögön *et al.*, 2018), suggesting that, with a more comprehensive understanding of the genetic and signalling pathways underlying this trait, major gains could be achieved. In addition to improving fruit size in elite germplasm, genome editing can be used for improvement of orphan crops (Lemmon *et al.*, 2018) or *de novo* domestication of crop wild relatives (Zsögön *et al.*, 2018), which often harbour agronomically valuable disease resistance traits (Dangl *et al.*, 2013).

In this review, we summarized those genes that have been identified as regulating fruit size, with emphasis on their genetic and molecular mechanisms. In addition, we revealed the complex genetic regulatory networks for the first time (Figure 5), based on an examination of the current knowledge on fruit size control in *Arabidopsis* and other dry fruits. These include phytohormone (e.g. AUX, GA, CTK, ABA, ETH and BR), transcription factors (e.g. tri-helix, YABBY, AP2-ERF, MADS-box, bHLH, zinc finger, homeobox and B3), transcription/translation elongation factors, ubiquitin-proteasome and microRNA pathways, G-protein and receptor kinase signalling, AGPs, RNA-binding proteins (Figure S2) and indicate the complexity of fruit size regulation in plants. Interestingly, many of these genes have a conserved function in regulating fruit development in both dry and fleshy fruit types, suggesting broad applicability of common genome edits. For instance, *CYP78A9* and *CLV-WUS* pathway genes can regulate both silique size in *Arabidopsis*/rapeseed (Fan *et al.*, 2014; Shi *et al.*, 2019; Xiao *et al.*, 2018; Xu *et al.*, 2017; Yang *et al.*, 2018) and fruit size in cherry/tomato (Lemmon *et al.*, 2018; Li *et al.*, 2018; Qi *et al.*, 2007; Rodriguez-Leal *et al.*, 2017; Xu *et al.*, 2015). Besides, many of these genes have similar functions in regulating fruit size in *Arabidopsis* and other crops. For example, *ARF18*, *ARP1*, *BoMF2*, *DRM1*, *CYP78A9*, *CLV1*, *CLV3* and *SMG7* can regulate silique length in *Arabidopsis* and rapeseed (Kang *et al.*, 2014; Lee *et al.*, 2013; Li *et al.*, 2015; Liu *et al.*, 2015; Shi *et al.*, 2019; Xiao *et al.*, 2018; Yang *et al.*, 2018). More importantly, many of the fruit size regulatory genes have expression activity and additional effects on other organs, such as roots, stems, leaves, flowers and seeds, indicating a cooperative/synergistic regulation. These results strongly suggest the conserved function of these genes in

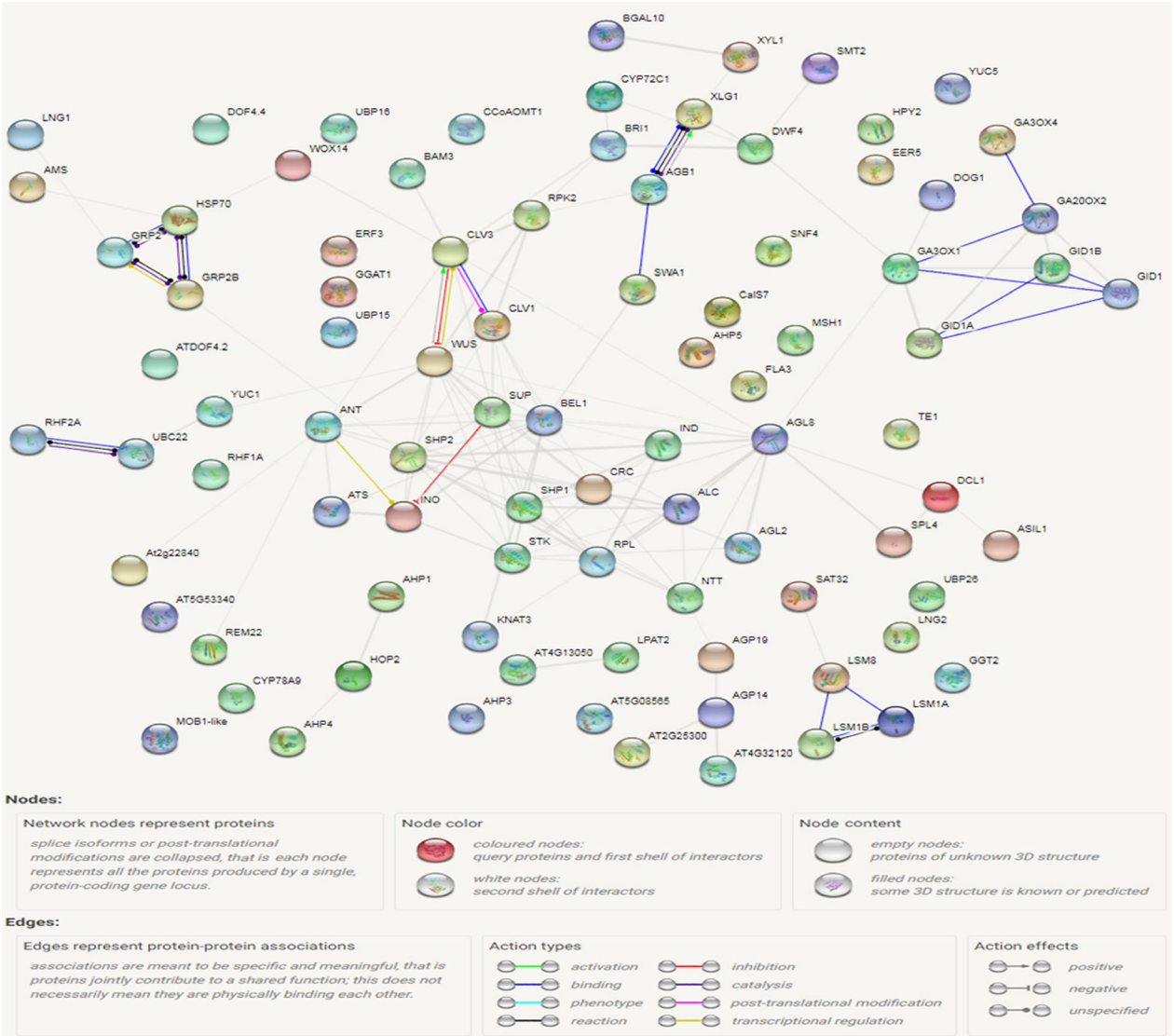

Figure 5 Genetic regulatory network constructed for fruit size genes. The figure shows different action types and effects, which are represented by different colours of lines and arrows between different genes/proteins. For example, the blue colour lines/arrows show binding; green colours represent activation whilst red colours show inhibition, black colours represent reaction between different genes, and so on. The different types of arrows show the positive, negative and unspecified effects of genes.

regulating the size of different organs among plant species, and so can be targeted for molecular improvement of size for fruit and other plant organs through genome editing approaches such as CRISPR/Cas.

The most complicated issue in terms of regulatory networks is the relationship between fruit size and other seed yield components, including fruit number, seed number per fruit and seed size (Figure 6). Analyses of mutants with phenotypic changes in both fruit size and fruit number show an inverse relationship between the two characters/traits. This indicates a trade-off between them, which can be explained by the competition among sink organs and which is entirely consistent with many decades of agronomic research in crop plants. However, there are also some exceptions, such as *miR397b*, *GGT1*, *GGT2* and *TaTEF-7A* can affect silique size and silique number per plant, in the same direction, which provides a unique opportunity to simultaneously improve both traits. Another important question involves the relationships between fruit size and seed number per fruit and seed size. Analyses of mutants with phenotypic changes in fruit size and seed number per fruit showed that changes in fertilization rate and seed number per fruit are usually associated with changes in fruit length, but the reverse is not true. For example, *AHP1-5*, *BRI1*, *FATA2*, *GbAGL2*, *GhWBC1*, *GID1A*, *GRDP1*, *HEMN1*, *SWA1* and *WOX14* are genes that control fruit size and seed number per fruit, always in the same direction. Therefore, the fertilization rate and seed number per fruit are likely upstream of fruit size. As expected, mutants with reduced fertility and seed number per fruit are usually accompanied by reductions in fruit growth/size, which indicates feedback or cross-talk between seed development and fruit growth. However, the relationship between fruit size and seed size is rather confused: in many cases (e.g. *ANT*, *ARF18*, *ASIL1*, *CYP78A9*, *DA1*, *UBP15*), they are regulated in the same direction; whereas in other cases (e.g. *FATA2*, *AHP1-5*, *STURDY*), they are affected in the opposite

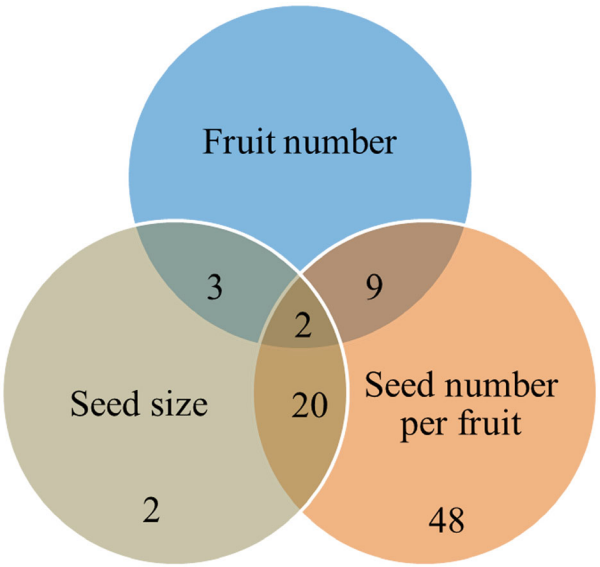

Figure 6 Demonstration of the pleiotropic effects of fruit size genes and their relationship with seed yield components. Obviously, the fruit size genes are mostly overlapped with the seed number per fruit, followed by seed size and fruit number.

direction. Therefore, attention should be paid to the relationships between fruit size and fruit number and between seed number per fruit and seed size (i.e. the three components of seed yield) when selecting targets for editing.

Identification of these regulatory pathways is still in the early stages: the identified fruit size genes are limited, and only a little is known about the relationships between different genes within the same pathway and between pathways (such as phytohormone → signalling transduction/ubiquitin-proteasome degradation → transcription factors → response genes). The major goal for the future is to fully demonstrate the molecular mechanisms underlying fruit size regulation and construct its genetic networks. The application of modern biotechnologies, such as genome-wide association, genome editing, omics and bioinformatics, will accelerate the identification and confirmation of the fruit size regulators in plants and provide the basis for the accelerated improvement of these crops.

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Conflict of interest

The authors declared that they have no conflict of interest.

Author Contributions

J.Q. Shi, H.Z. Wang, G.H. Liu and X.F. Wang jointly developed the conceptual structure of manuscript. Q. Hussain, J.Q. Shi and J.P Zhang collected the fruit size genes from the published literatures and analysed and integrated the relevant information. J.Q. Shi and Q. Hussain wrote the manuscript, including all the figures and tables. D. Edwards, G.J. King, A. Scheben and G.J. Yan provided a critical feedback and revised the manuscript.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 List of fruit size genes from different plant species.
Figure S1 Fruit of rapeseed (*Brassica napus*) and *Arabidopsis thaliana* (five on the right).
Figure S2 A comprehensive genetic and molecular framework for fruit size regulation in plants.