# Watermelon: Advances in Genetics of Fruit Qualitative Traits

Sudip Kumar Dutta, Padma Nimmakayala, and Umesh K. Reddy

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## Abstract

Watermelon (*Citrullus lanatus*) belongs to the family Cucurbitaceae. The crop is grown commercially in regions with extended warm, frost-free months. Watermelon is cultivated for its colorful, tender, juicy, and sweet fruit. They are generally consumed fresh and make an excellent and delicious dessert, particularly during the summer months. Because of its smaller genome and large number of gene mutations, watermelon is a suitable crop species for genetic research. Watermelon's genome has 424 million base pairs. DNA sequencing found significant conservation, which is relevant for comparative genomics within Cucurbitaceae and other species.

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S. K. Dutta (✉)
Gus R. Douglass Institute, Department of Biology, West Virginia State University, Institute, WV, USA

ICAR RC NEH Region, Sikkim centre, Gangtok, Sikkim, India

P. Nimmakayala · U. K. Reddy
Gus R. Douglass Institute, Department of Biology, West Virginia State University, Institute, WV, USA
e-mail: padma@wvstateu.edu; ureddy@wvstateu.edu

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There exists a huge genetic variability in the fruit quality characteristics of watermelon with respect to seed traits, fruit shape, fruit size, skin color, skin pattern, flesh color and sugar/acid composition, fruit bitterness, and many more. This chapter serves as a guide to show the prospects and advances made in the genetics of fruit qualitative traits in watermelon breeding programs depending on profitability and consumer preferences.

**Keywords**

Watermelon · Fruit · Genomics · Quality · Flesh color · Rind pattern

## 1 Introduction

Watermelon (*Citrullus lanatus* [Thunb.] Matsum. and Nakai var. *lanatus*; $2n = 2x = 22$) belonging to the family Cucurbitaceae is primarily cultivated for its fresh and nutritious fruit. *Citrullus lanatus* var. *citroide*s, *C. naudinianus, C. mucosospermus*, *C. rehmii*, *C. ecirrhosus*, and *C. colocynthis* are the species of the genus *Citrullus* (Chomicki and Renner 2015). Most *Citrullus* species have their origins and genetic diversity in continental Africa (Dane and Lang 2004). One theory claims that it came from a species of *Citrullus lanatus* that is a common wild plant in central Africa, while another believes that it was domesticated from the perennial *Citrullus colocynthis* that is a common plant in ancient sites. Watermelons have been grown in Africa for over 4000 years. Watermelons were commonly planted in the Nile valley region prior to 2000 BCE, according to seeds and plant pieces found in Egyptian tombs. They were transported from Africa to India in the year 800 CE and to China in the year 900 CE, after which they expanded to other continents in the year 1500s. Annual watermelon plants have lobed leaves, long, angular vines that trail, branching tendrils, and solitary male and female flowers. Watermelon of various shapes like round, oval, or elongated can weigh anywhere between 1.5 kg and 15 kg. The rind varies in color from light to dark green and has different striped patterns. Despite the fact that the flesh may be white, green, yellow, orange, or red, customers favor inner qualities like sweetness and texture and colors like deep red, pink, or dazzling yellow. Fruit types and cultivars differ widely in size and form, and the outside skin is smooth, sutured, or netted, with a white, green, or yellow tone. Normal colors for the flesh (mesocarp) are green or orange; however, pink and white are also found. Fig. 1 is a panel displaying the variety in morphology of watermelon fruits. A small genetic background of sweet watermelon has resulted from modern breeding practices that have mostly focused on fruit quality characteristics including sugar content, flesh color, and rind pattern (Levi et al. 2017). It is uncertain how phenotypic alterations brought about by human and natural choices affected the watermelon genome. For the creation and marketing of new products, sweet watermelon fruit characteristics are essential. The pharmaceutical industry, the processing industry, and the fresh market will all profit from the novel and value-added genotypes. Pickles, jam, fruit puree, popsicles, and watermelon juice are a few examples of items with added value that are made from recently created cultivars with superior qualities. The new cultivars ought to have a range of bioactive

**Fig. 1** A panel showing watermelon fruit morphological diversity

substances that are both nutritive and therapeutic in nature (Mashilo et al. 2022). A viable and alternate method for hastening the creation and release of watermelon varieties with sufficient agronomic and quality traits to meet the crop's value chains is nonconventional breeding using gene-editing technology. For instance, changing watermelon genes associated with agronomic traits using clustered regularly interspaced short palindromic repeats (CRISPR/Cas9) allowed the development of novel cultivars (Wang et al. 2021). The development of superior cultivars with higher nutritional contents, market-preferred traits, and a longer shelf life will be aided by the information on the genetic control of fruit qualities in watermelons that will be possible by gene-editing and related technologies. The goal of this chapter is to illustrate the prospects and developments made in the genetic study of fruit quality characteristics in watermelon as a guide for quality breeding based on economic and end-user qualities, taking into account the aforementioned context.

## 2 Organic Acids and Sugar

Sugars and organic acids have a substantial influence on organoleptic fruit quality and are key components in fruit flavor development. Contrary to staple food crops, where production is the ultimate breeding goal, watermelon places greater emphasis on flavor and aroma, both of which are influenced by the metabolite composition of the fruit. During development, watermelon fruits go through a variety of biochemical changes, including as adjustments to sugar metabolism, an increase in organic acid and color, fruit softening, flavor, and volatile aromatic compounds (Zhu et al. 2017). In one study, researchers examined the coexpression patterns of gene networks linked to sugar and organic acid metabolism using transcriptome profiles. They found three gene networks or modules comprising 2443 genes that were substantially associated with organic acids and carbohydrates. Seven more genes involved in the metabolism of organic acids and carbohydrates were found. *SWEET*, *EDR6*, and *STP* were recognized as sugar transporters (*Cla97C01G000640*, *Cla97C05G087120*, and *Cla97C01G018840*, r 2 = 0.83 with glucose content), while *Cla97C03G064990* (*Cla97C03G064990*, r 2 = 0.92 with sucrose concentration) was identified as a sucrose synthase. *Cla97C07G128420*, *Cla97C03G068240*, and *Cla97C01G008870* were identified as malate and citrate transporters, respectively, since they displayed strong associations with malic acid (r 2 = 0.75) and citric acid (r 2 = 0.85) (ALMT7, CS, and ICDH) (Umer et al. 2020a). The two enzymes that regulate sugar metabolism in watermelon most crucially are sucrose synthase and sucrose phosphate synthase (Guo et al. 2015). The expression of gene clusters involved in sugar biosynthesis, including a-galactosidase, invertase, and urease diphosphate (*UDP*)-galactose/glucose pyrophosphorylase (*UDP-Gal/Glc PPase*), rises as the watermelon fruit ripens. The *Cla013902* gene reportedly affects how sugar is metabolized in watermelons (Guo et al. 2015). There are nine a-galactosidase genes in the watermelon genome. The nine genes are reportedly involved in the hydrolysis of stachyose and raffinose, according to studies (Guo et al. 2013). Additionally, the buildup of sugar in watermelon is influenced by five genes for insoluble acid invertase (*IAI*) (Guo et al. 2015). The watermelon fruit's extracellular sucrose degeneration, which permits fructose and glucose transfer and intercellular sugar accumulation, is linked to the IAI gene *Cla020872* (Guo et al. 2015). Recent research has identified *ClAGA2*, an alkaline a-galactosidase gene expressed in the vascular bundle, as a critical regulator of the hydrolysis of stachyose and raffinose in watermelon. *ClAGA2* controls fruit raffinose hydrolysis and reduces the amount of sugar in fully grown watermelon fruits (Ren et al. 2021). Tonoplast sugar transporter (*ClTST2*) and sugar transporter 3 (*ClSWEET3*) genes control sugar storage and transfer in watermelon fruit cell vacuoles (Ren et al. 2021). Several important genes involved in sugar production and translocation that are up- or downregulated throughout developmental processes have been found by several researches. Differentially expressed genes such NAD-dependent malate dehydrogenase (*NAD-cyt MDH*), aluminum-activated malate transporter (*ALMT*), and citrate synthase (*CS*) affect the accumulation of organic acids in watermelon (Gao et al. 2018). The reversible conversion of malate to oxaloacetate is catalyzed by the NAD-dependent malate dehydrogenase (*NAD-cyt MDH*) gene (*OAA*) (Yao et al. 2011), whereas citrate synthase (*CS*) gene controls citric acid production. Malate dehydrogenase genes and aluminum-triggered malate transporters control the regulation and breakdown of malates (Umer et al. 2020a). It is believed that the genes for citrate synthase (*Cla97C03G068240*) and isocitrate dehydrogenase (*Cla97C01G008870*) are involved in the generation and breakdown, respectively, of citric acid (Umer et al. 2020b). Malic and citric acid accumulation are linked to higher expression of the genes for malate dehydrogenases (*Cla008235* and *Cla011268*) and citrate synthases (*Cla013500*) (Gao et al. 2018). From the sweet and sweet-and-sour genotypes, *Cla97C01G000640* (*SWEET*), *Cla97C05G087120* (*EDR6*), and *Cla97C01G018840* were shown to control glucose biosynthesis, whereas *Cla97C03G064990* controls sucrose production in watermelon (Umer et al. 2020b). *ClVST1*, a gene for a vacuolar sugar transporter, was shown to be highly expressed during the ripening of watermelon fruit and was connected to the accumulation of sucrose (Ren et al. 2021).

## 3 Amino Acid Compositions

The amino acid citrulline is the most abundant in ripe watermelon fruit (Joshi et al. 2019). Citrulline is a nonessential amino acid which is generated throughout the urea cycle as a metabolic intermediate (Bahri et al. 2013). This amino acid serves as a precursor to arginine, another essential amino acid contained in watermelon fruit (Joshi et al. 2019). Watermelon has many genes that are involved in citrulline metabolism. Citrulline biosynthesis in watermelon is associated with ornithine carbamoyltransferase (*OTC; ClCG05G018820*), N-acetylornithine aminotransferase (*N-AOA*; *ClCG09G003180*), N-acetylornithine-glutamate acetyltransferase (*N-AOGA*), *CPS*-1 (*ClCG11G013120*) and *CPS-2* (*ClCG09G021680*), N-acetylornithine deacetylase (*AOD-1*), N-acetylornithine deacetylase (*AOD-3*), and nitric-oxide synthase gene (*ClCG01G004960*) (Joshi et al. 2019). Citrulline catabolism is also connected to ASS, 1,2,3-argininosuccinate synthase; *ASL*, *1,2-argininosuccinate lyase*; *ARG*, *arginase*; *ODC*, *ornithine decarboxylase*; and *ADC*, *arginine decarboxylase* (Joshi et al. 2019). Citrulline biosynthesis is mediated by the genes *argininosuccinate lyase*, *N-acetylglutamate kinase*, and *ornithine decarboxylase*, whereas arginine biosynthesis and accumulation is mediated by the genes *ornithine carbamoyltransferase* (Fall et al. 2019).

## 4 Fruit Bitterness

Watermelons in the wild create bitter cucurbitacin molecules, a kind of highly oxygenated tetracyclic triterpene that repels pests. Cucurbitacin B (CuB), cucurbitacin C (CuC), cucurbitacin E (CuE), and cucurbitacin E-2-O-glucoside are all found in *Citrullus* fruits, leaves, roots, and stems (CuE-Glu) (Kim et al. 2018). The principal bitter ingredient in *Citrullus* fruit is CuE, commonly known as elaterinide (Matsuo et al. 1999). Despite the fact that these protective chemicals evolved in plants millions of years ago, humans have bred them to make them more appealing to our taste buds. In domesticated varieties of watermelon, a single point mutation in a transcription factor results in a faulty protein and diminished bitter compounds (Everts 2016). The genetic basis of two watermelon fruit traits were studied in a backcross generation arising from the hybridization of an interspecific F, hybrid of *Citrullus lanatus* and *C. colocynthis* with the domesticated parent *Citrullus* *lanatus*. Bitterness of the fruit, which distinguishes wild *C. colocynthis*, was revealed to be governed by a single dominant gene (*Bi*) that was linked to the isozyme marker *Pgm-1* at a distance of 11.3 cm (Navot et al. 1990). In one study, it was shown that *Cla011508* (located on chromosome 1) regulates the bitterness of watermelon fruit, and the crucial mutation locus in this gene provided molecular insights for marker-assisted breeding of target characteristic (Gong et al. 2022). The dominant *Bi* gene regulates cucurbitacin production, which is responsible for bitterness in *Citrullus* fruits, whereas the recessive su (bitterness suppressor) gene regulates the presence or absence of bitterness in watermelon fruit. The *Bi* gene has been identified as an oxidosqualene cyclase (*OSC; Cla007080*) gene on watermelon chromosome 6 (Chambliss et al. 1968; Robinson et al. 1976; Navot et al. 1990; Lu et al. 2016). Furthermore, one watermelon fruit bitterness gene on chromosome 1 was found; the significant locus with the highest LOD score (58.361) was designated *qbt-c1-1*, and it explained 82.927% of phenotypic variation with a negative additive effect of −0.465 (Li et al. 2018). Watermelon breeders looking to improve their carotenoid profiles should hunt for progenies with genes that condition the carotenoid synthesis pathway.

## 5 Fruit Shape and Size

Fruit form and size are important horticultural sector traits that exhibit a large range of phenotypic variation, emphasizing their importance in breeding programs. The shape of watermelon fruits was assumed to be controlled by an incompletely dominant gene, resulting in elongate (OO), oval (Oo), and spherical (oo) fruits (Guner and Wehner 2004). It was also shown that a single gene regulates both spherical (Os) and oval (O+) watermelon fruits, exhibiting partial dominance when a spherical fruit inbred line crosses with an oval fruit inbred line (Tanaka et al. 1995). The similar pattern of inheritance was seen in F2 populations of ‘Peerless’, ‘Baby Delight’, ‘Northern Sweet’, and ‘Dove’ (Poole and Grimball 1945). For the dominant elongate fruit, allele *ObE* was proposed; for the recessive oblong fruit, allele *Ob*; and for the round fruit, allele *ObR* (not the same as the o gene for round) (Lou and Wehner 2016). Segregation analysis in F2 and BC1 populations derived from a cross between two inbred lines ‘Duan125’ (elongate fruit) and ‘Zhengzhouzigua’ (spherical fruit) revealed that watermelon fruit shape is controlled by a single locus and that elongate fruit (OO) is only partially dominant to spherical fruit (oo), with the heterozygote (Oo) being oval fruit and a 159 bp deletion (Dou et al. 2018). The *SUN* gene, a member of the IQ domain (*IQD*) family, has long been recognized to influence tomato fruit elongation early in fruit development, following pollination and fertilization (Van Der Knaap and Tanksley 2001). Several QTLs linked with FD (and fruit weight) and FL (fruit length) have been found in diverse genetic backgrounds; however, the genes underlying these QTLs remain unknown.

## 6 Flesh Color

There are many different fruit flesh colors in watermelons (Fig. 1); fruit flesh color is a key feature that influences nutritional value, customer choice, and breeder selection. The composition of chlorophyll and carotenoids in the flesh determines its color. Watermelon flesh colors have been classified as scarlet red, red, pink, orange, canary yellow, pale yellow, and white based on carotenoid levels. Watermelons with red flesh (including flaming red and pink) are high in lycopene (Sun et al. 2018). Prolycopene and carotene concentrations are considerably higher in watermelons with orange flesh (Branham et al. 2017). Watermelons with yellow flesh (canary yellow and light yellow) contain a high concentration of neoxanthin, followed by neochrome and violaxanthin (Fang et al. 2020). Watermelons with white flesh have very little violaxanthin and lutein in them (Lv et al. 2015). The idea of genetic variability in the color of watermelon fruit flesh is supported by the existence of separate mechanisms regulating carotenoid metabolism. Understanding the process of carotenoid inheritance enables for the development of cultivars with improved phytochemical component compositions. The genetics of skin color are extremely complex, with numerous genes and quantitative trait loci (QTLs) influencing carotenoid production. Genes involved in the carotenoid biosynthesis and metabolism pathway's genome-wide comparative expression study showed complex gene expression and regulatory networks that led to the accumulation of different carotenoids in watermelon fruit (Fang et al. 2020; Mashilo et al. 2022). Based on genotyping data, two Kompetitive Allele-Specific PCR (KASP) markers were created for the candidate gene *Cla97C10G185970*, which was annotated as plastid lipid-associated protein and showed a strong connection between pale green and non-pale green meat fruits (Pei et al. 2021). During fruit ripening, the carotenoid profiles of four watermelon cultivars – red-fleshed 'CN66', pink-fleshed 'CN62', yellow-fleshed 'ZXG381', and white-fleshed 'ZXG507' – were examined. It was revealed that the amounts of violaxanthin and lutein in yellow fruit were positively correlated with *CHYB* and *ZEP* transcription levels (Lv et al. 2015). *ClPAPs, Cla006670, Cla010946*, *Cla008831, Cla014416, Cla021506, Cla003468*, and *Cla003198* are plastid lipid-associated genes that are thought to be involved in the development of plastoglobules and globular and crystalloid chromoplasts (Fang et al. 2020).

## 7 Rind Pattern

The most common rind (or skin) colors in watermelon are solid green (dark, medium, and light), striped (narrow, medium, and large dark green stripes on a light green background), and grey. Gray is also written grey, although the names of watermelons have been standardized to the grey spelling. The expression of genes responsible for rind color and pattern does not appear to be uniform across different genetic backgrounds. Furthermore, the inheritance of gray or medium green rind colors has not been recorded, despite the fact that they have been two of the most prevalent rind colors in watermelon breeding during the previous century. ClCG08G017810 (ClCGMenG), a protein encoding a 2-phytyl-1,4-beta-naphthoquinone methyltransferase, is linked to the production of dark green rind vs light green rind in watermelon (Li et al. 2018). For the '0901', '10909', '109905', and '90509' rind trait-segregating F2 populations, genotyping analyses were done using subsets of 188, 273, 287, and 113 probes, respectively. For the '0901', '10909', '109905', and '90509' populations, 26, 34, 30, and 15 linkage groups containing 175, 254, 269, and 79 probes were created, respectively. The genetic order of the probes is mainly collinear with the physical order on the reference genome, with a few exceptions on chromosomes 1, 3, and 11. S, D, and Dgo, together with chr4 150/chr4 249 on chromosome 4 and chr6 25767 on chromosome 6, were identified nearby (Park et al. 2016). As a consequence of genetic investigations, a team of researchers found three unique genes in watermelon. In comparison to Angeleno Black Seeded, the type line for the hue of watermelon red flesh, scarlet red flesh (*Scr*) gave more vivid red color in Dixielee and Red-N-Sweet. They suggest calling the original red skin color coral red in order to distinguish it from scarlet red. As a single dominant gene, *Scr* is inherited. A single dominant gene called *Yellow Belly* (*Yb*) was identified as the cause of Black Diamond's ground spot's transition from creamy white to dark yellow. A single recessive gene called intermittent stripes (*ins*), with the dominant allele, was found to be responsible for the difference between continuous and intermittent stripes on the rind of Navajo Sweet (Gusmini and Wehner 2006).

## 8 Flesh Firmness

The firmness of the flesh determines the texture and quality of watermelon fruit. Multigenes control flesh firmness as a qualitative attribute. For watermelon genetic breeding, it is crucial to identify the regulatory elements that most significantly affect the firmness of the fruit's flesh. According to localization interval transcriptome analysis, *Cla012507* (MADS-box transcription factor) may be involved in the control of fruit ripening and affect the hardness of watermelon fruit. *Cla016033* (*DUF579* family member), which may impact the cell wall component contents to alter the flesh firmness in watermelon fruit, was distinct in W1-1 and PI186490 (Sun et al. 2020). The hardness of watermelon flesh is controlled by phytohormone levels, particularly ABA (Wang et al. 2017). *Cla009779* (*NCED*), *Cla005404* (*NCED*), *Cla020673* (*CYP707A*), *Cla006655* (*UGT*), and *Cla020180* (*SnRK2*) are implicated in ABA biosynthesis in watermelon (Wang et al. 2017). *Cla009779*, *Cla005404*, and *Cla005457* were the most effective at increasing ABA accumulation. On chromosome 6 of the watermelon genome here is a significant QTL (*Qffi6.1*) for flesh firmness from *C. amarus* (Gao et al. 2016). The putative candidate gene for *Qffi6.1* is *Cla018816*, a xyloglucan endotransglucosylase/hydrolase (*XTH*) gene that is variably expressed across firm- and soft-bodied near-isogenic lines (Anees et al. 2021). Another *XTH* gene

(*Cla006648*), cellulose synthase (*Cla012351*), galactosyltransferase (*Cla006648*), pectinesterase gene (*Cla004251*), ethylene response element transcription factor 1 (*Cla004120*), and ethylene response element transcription factor 2a (*Cla007092*) all played important roles in watermelon flesh firmness, according to transcriptome analysis (Anees et al. 2021).

## 9 Rind Thickness and Toughness

Watermelon fruit rind breaking not only facilitates disease invasion and reduces yield, but it also degrades the fruit's exterior aesthetic value. One of the simplest methods for gauging consumer acceptance during commercial purchases is the rind of a watermelon. After crossing 97103 and PI296341, a biparental F2 population was produced. Using RAPD and SSR markers, QTL analysis showed that there were a total of two rind thickness QTLs and three fruit weight QTLs (Fan et al. 2000). Additionally, a watermelon backcross (BC) generation was developed for measuring rind hardness, and a QTL location controlling rind hardness was found on chromosome 4 (Hashizume et al. 2003). Watermelon rind hardness is correlated with the ethylene *clerf4* transcription factor genes, according to the genotyping of 349-F2 individuals from 32 germplasm. The genotyping indicated a significant ascending allelic pattern of aa (hard) bb (soft) and substantial QTL region on chromosome 10 (Liao et al. 2020). Another recent study combined the hard-fleshed and soft-fleshed watermelon lines ‘PI186490’ and ‘W1–1’, and preliminary mapping in 175-F2 individuals identified the key genes on chromosomes 2 and 8 controlling central flesh hardness using BSAseq and CAPS marker-based QTL analysis (Sun et al. 2020). Using a combinatory genomic map and bulk segregant analysis, it was possible to link variations in rind hardness to the ethylene-responsive transcription factor 4 (*ClERF4*) (*BSA*). The *ClERF4* gene on chromosome 10 also has an 11-bp InDel and a neighboring SNP, which confers cracking resistance in F2 populations with different rind hardness (Liao et al. 2020). A transcriptome study demonstrated the molecular pathways involved in the enhancement of fruit attributes including greater rind toughness by watermelon and bottle gourd grafting (Garcia-Lozano et al. 2019).

## 10 Ethylene and Ripening in Watermelon

A microarray and quantitative real-time PCR-based investigation was conducted to better understand the sequence of events linked to fruit growth and ripening in watermelon (*Citrullus lanatus* [Thunb.] Matsum. and Nakai var. lanatus). This study found several of the ESTs with potential roles in the growth and ripening of watermelon fruits, particularly those involving the vascular system and ethylene (Wechter et al. 2008). The researchers noted differential expression of homologs of genes involved in ethylene biosynthesis (*ACC* oxidase) and signal transduction (ethylene receptor *Cm-ETR1*, ethylene insensitive [*EIN3/EIL*]-like transcription factor, ethylene-responsive binding protein [*EREBP*], and ethylene response factor [*ERF*]) in the same study. Fruit rind plays a major role in reducing moisture loss and disease, as well as cracking resistance, ease of transport, and storage stability quality of watermelon; an ethylene-responsive transcription factor 4 (*ClERF4*) linked with variation in rind hardness was discovered using a combinatory genetic map and bulk segregant analysis (BSA) (Liao et al. 2020). The ethylene biosynthesis and signaling pathway genes, such as ACC oxidase, ethylene receptor, and ethylene-responsive factor, showed highly ripening-associated expression patterns in the watermelon, a non-climacteric fruit, according to a comparative transcriptome profiling analysis of the cultivated watermelon 97103 and wild watermelon PI296341-FR. This suggests that ethylene may play a role in the development and ripening of the fruit (Guo et al. 2015). *XTH* gene (Cla006648), cellulose synthase (*Cla012351*), galactosyltransferase (*Cla006648*), pectinesterase gene (*Cla004251*), ethylene response element transcription factor 1 (*Cla004120*), and ethylene response element transcription factor 2a (*Cla007092*) all played important roles in watermelon flesh firmness, according to transcriptome analysis (Anees et al. 2021).

## 11 Conclusion

Watermelon fruit qualitative characters like seed color, seed size, fruit shape, skin color, rind pattern, flesh color and sugar/acid composition, fruit bitterness, and many more exhibit significant genetic diversity. With the advancement of genomics and availability of watermelon genome sequences, it has become possible to identify genes critical to valuable fruit quality traits. As the knowledge of the molecular mechanisms behind these characteristics improves, more effective and focused selection will enhance the efficiency of breeding of this important crop.

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